TAXONOMY AND ADAPTIVE RADIATION OF THE PNIGMA BROME-GRASSES OF EUROPE

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DECLARATION

I hereby declare that this thesis was composed by myself and the contained matter herein to be my own work, except where otherwise indicated.

Carmen Fraile Martín

Edinburgh 1994

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"Pay more attention to the noise made
by grass growing than walls falling down"

CARDINAL MARTY

Abbreviations

§: section

sect.: section

subf.: subfamily

subg.: subgenus

subsp.: subspecies

var.: variety

ρ: density of a gas, Kgm m^{-3}

u: wind speed, ms^{-1}

A: area normal to the wind, m^2

se: standard error

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Abstract

Perennial species of *Bromus* (Gramineae) embracing section *Pnigma* in Europe were investigated. Four groups were compared as a working hypothesis: *B. ramosus* group, *B. erectus* group, *B. riparius* group and *B. inermis* group.

The objective of this research was twofold: first, to make a formal taxonomic assessment of all the putative taxa and second, to contribute to the understanding of the evolutionary trends occurring among them. In the most recent taxonomic account of this group in *Flora Europaea* (Smith 1980), 9 species and 8 subspecies were recognised. The final view of the relationship among different taxa can be summarised as 24 taxa, 5 species and 19 subspecies. New taxa (*B. parilicus*, *B. caprinus*, *B. condensatus* subsp. *microtrichus*, *B. riparius* subsp. *macedonicus*, *B. erectus* subsp. *aurouzensis*, the latter being a novel subspecies in *Pnigma* brome-grasses) or combinations (*B. ramosus* subsp. *sipyleus*, *B. cappadocicus* subsp. *crassipes*, *B. condensatus* subsp. *moellendorffianus*, *B. pannonicus* subsp. *vernalis*, *B. erectus* subsp. *montenegrinus*, *B. erectus* subsp. *longiflorus*, *B. erectus* subsp. *laxus*) were reported.

Several techniques were brought to bear on the problems including: micro and macromorphology, anatomy, cytology, taximetric analysis, as well as the formal herbarium study. Significant results were obtained. The chromosome counts here reported agreed with other researcher's work. The intuitive view of taxonomy of the taxa studied clashed to some extent with the results obtained from the taximetric analysis, probably because of the limited amount of information manipulated by the computer. Nevertheless, greater confidence was felt in the "intuitive" classification than in those generated taximetrically.

Research on sheath morphology was also carried out. Different kinds of sheath (used as states of a pivotal taxonomic character) were shown to have different functional characteristics. Thus they may be pivotal characters in explaining the evolutionary divergence of different species groups.

Western Eurasia is indicated as the centre of differentiation of *Bromus* sect. *Pnigma*. From there five migratory-evolutionary lines occurred, differing chronologically: two older, during the Miocene-early Pliocene and three more recent in the Pleistocene. The outcomes were evaluated in attempts to clarify the taxonomy, history and evolutionary currents within *Bromus*. The principal delimitation of four groups was confirmed, with an explanation of the adaptive radiation patterns presented.

Chapter 1 Introduction

Bromus L. (Gramineae) is the largest genus of the small pooid tribe Bromeae with approximately 130 species (Smith 1970). It comprises annual and perennial grasses with a very wide geographical distribution. Several groups have been defined, with limits and taxonomic status varying depending on authors interpretations. My own view of the relationships among them is discussed in chapter 2. Section *Pnigma*, being the object of this study, comprises approximately 60 or more perennial species (Smith 1970), found throughout Eurasia, North, Central and South America, and a few in Africa.

The first, accurate revision of this section was carried out by my supervisor Dr. P.M. Smith in 1980 for *Flora Europaea.* Nevertheless, he confessed: "I did my best, considering the short amount of time available, although there still exist very obscure taxa where relationships are not clear and must be sorted out" (Smith, pers. comm.). Using his work as an initial reference, I began with the task of producing an up to date and concise revision of all taxa in § *Pnigma* in Europe. It has proved to be a demanding endeavour. As a working hypothesis, four groups were defined, *B. ramosus*, *B. erectus*, *B. riparius* and *B. inermis*, partly on the basis of the character of the sheath pattern decay. The main obstacle to the clarification of the relationship among the putative taxa was the intrinsically variable nature of their elements. The first three groups were soon recognised as critical, i.e., they show an intricate network of connection among the taxa, frustrating the easy establishment of clear cut boundaries. The study of a large number of herbarium specimens on loan from numerous botanical gardens in Europe (chapter 9, sect. 9.2) and my own visits to five main herbaria, Berlin (B), Vienna (W, WU), Paris (P) and Florence (FI), enabled me to present a formal taxonomic account for the four groups (chapter 9). Different researching fields were also approached to amalgamate diverse sources of information with the aim to compare and corroborate my working hypothesis. Cytological and reproductive studies were carried out (chapter 5). Anatomical investigation of fresh leaves and herbarium material brought into light significant results (chapter 4). Taximetric analyses were also made (chapter 10). As a result of my provisional decision to recognise four groups associated with the sheath morphology, the fascinating task of unmasking the possible function that the sheaths could possibly discharge once dead, protecting in some way the emergent stems, encouraged me to devise a sheath investigation, including the design of artificial models (chapter 6). A detailed study of the form and function attributed to the sheaths clarified the understanding of the colonisation of very diverse niches by each group, and their respective evolutionary patterns. A formal discussion of the pattern of adaptive radiation occurring in the section was presented in chapter 11, as well as the corroboration of the four groups.

At no time during the initial discussions with my supervisor, concerning the nature of this study to be carried out, did I consider that I would be involved in such laborious, problematic study, though I recognise that it came to be very intriguing to expose the on-going evolutionary process occurring in this group of brome-grasses.

Although more work can still be done, particularly in the experimental field, it is my hope that this contribution has brought some clarity to the complex patterns of biodiversity and evolution in the group § *Pnigma* of *Bromus*.

Chapter 2 Taxonomic History of Bromus

2.1 Introduction

The name *Bromus* was derived from the Greek word βρωμα, meaning food. From this word came the name Βρόμος, meaning oat, a grass with high economic value to the ancient Greeks. The origin of the name *Bromus* was revealed by Linnaeus in his *Philosophia botanica* (1751, pp. 188). Here he indicated that Theophrastus used the word Βρόμος which was later used by Dioscorides. Plinius is cited as the first to use it in the Latin form of *Bromus*. Theophrastus, in his *Historia Plantarum*, designated a grass "*Avena (Aegilops) verò α bromos veluti silvestria quaedain α immitia sunt*" (This Latin protologue is included in the English translation of *The Historia Plantarum*, Amsterdam, pp. 953, 1644) and, on pp. 958 of this work, there is an illustration of a grass called *Bromus sterilis altera festuca*; Theophrastus used the words *avena, bromos* and *festuca* to describe some grasses close to oats (Sales 1991). This statement agrees with Lamarck's work (1810) where he cited "the *bromus* of Theophrastus and Plinius belong to the oat, and not to this genus" (English translation, *Encyclopédie Methódique Botanique Supplement*, pp. 701, 1810).

The first application of *Bromus* in a botanical context has been a subject of some controversy. When Linnaeus described *Bromus* in the *Genera Plantarum* (5th edition, 1754) he cited "Mont. 32" as one of the references for the name. Linnaeus also mentioned Dillenius in the protologue, and in earlier editions (2nd edition, 1742) included the citation "Festuca Scheuch. 5: 2.10.11.12". The interpretation of "Monti 32" differs among authors. Thus Shear (1900) stated that Monti was the first to apply the name *Bromus* in his *Catalogi Stirpium Agri Bononiensis Prodromus*...1719. Hitchcock (1920) referred the citation 32 to a figure under the same number which represents a spikelet of *Bromus* in a plate of Monti's work. Sales (1991) stated that the citation "32" is a mistake; the correct reference is to "35". The quotation *Festuca*

Scheuch. 5: 2.10.11.12 in the second edition of *Genera Plantarum* (1742), corresponds to the plate 5 with several figures. All of them show spikelets of *Bromus* with the exception of number 2. Later, in his *Bibliotheca Botanica* (1751) Linnaeus cited both Scheuchzer's works, 1708 and 1719. In the later there is found again a mention to the small plate 5 but the figure referred in this case is number 19, which may represent a spikelet of *Bromus*. It thus appears that Linnaeus was the first modern author to apply the name as currently used.

The corresponding adaptation of the Latin word *Bromus* into English is brome-grass. Stillingfleet (1811) suggested this "folk-name"; he stated: "It happens very luckily, that our common people know scarce any of the grasses by name, so that something may be done to remove this confusion..." This is rather a patronising, paternalistic view but perhaps not unhelpful. Concerned about this situation, he published a list of names with the intention to have sufficient influence to determine that everybody would adopt them, as a result of their easy and familiar pronunciation: "*Thus I have called the aira, hair-grass, the bromus, brome-grass...*"

One important question to be understood is the original concept of *Bromus* in Linnaeus' mind, which species he knew best, most indicative and would be considered as the standard species of his genus *Bromus*. Several interpretations have been given; these are various: *B. secalinus* (Shear 1900; Stapf 1928; Smith 1970), *B. arvensis* (Wagnon 1952) or *B. sterilis* (Hitchcock & Green 1929; Phillips 1951). Despite the differences all agree that Linnaeus enlarged the boundaries on his concept of *Bromus* in *Species Plantarum* (1753), including the subsequent species: *B. secalinus, B. squarrosus, B. purgans, B. ciliatus, B. sterilis, B. arvensis, B. tectorum, B. hordeaceus, B. giganteus, B. pinnatus* and *B. aristatus*. The last three have been transferred to different genera later, viz. *Festuca gigantea* (L.) Vill., *Brachypodium pinnatum* (L.) Beauv. and *Agropyrum aristatum* (L.) Gaertner respectively.

Bromus has from time to time been dismembered into subgenera and sections, occasionally some of these have been given a generic rank. Table 2.1 shows the historical evolution of the concept of the genus *Bromus* in different treatments, from 1737 with the publication of the first edition of *Genera Plantarum* to 1991, the most recent study of *Bromus* in Great Britain by Stace. Very few authors (Smith 1970; Stebbins 1981; Sales 1991) have explained the reasons for the corresponding subdivisions attributed to *Bromus s.l.* In most cases they have been ignored, an attitude which generates extraordinary confusion among readers who compare diverse works. Differences in morphological characters seem to represent the basis for the different approaches of most authors, although there are some evidences of mycological (Freeman 1902; Ward 1902, 1903; Salmon 1904), population biology (Kahler et al. 1981; Soreng et al. 1990), cytogenetical (Stebbins et al. 1944; Cugnac & Camus 1944; Armstrong 1990) and serological (Fairbrothers & Johnson 1961; Smith 1965, 1969a, 1969b) comparisons to support diverse interpretations of the status of groups and the relationships between them.

During the 18th century, species were understood as stable entities characterised by their constancy and differing from other species in morphological features. After the publication of the *Origin of Species* by Darwin (1859), the concept gradually shifted into an evolutionary context, where species represented essential units of evolution, displaying intra - as well as interspecific variation among them. Bearing this important conceptual change in mind, many authors, especially disciples of the German school (e.g., Ascherson & Graebner 1901; Hegi 1906; Hayek 1933) adopted further degrees of subdivisions, such as form, subform, variety and subvariety. Referring to the work by Ascherson and Graebner (1896-1901), *Synopsis der Mitteleuropäischen Flora*, I fully agree with Stapf (1896) criticising the system of classification adopted by the former authors:

Table 2.1. Recapitulation of the main features in the historical evolution of the genus *Bromus* from 1737 to 1991 according to diverse authors. Capitals indicate a generic rank, italics indicate a subgeneric rank, otherwise a sectional rank is indicated in underlinings.

Linnaeus	1737	BROMUS									
Panzer	1813	BROMUS					ZERNA				
Dumortier	1823	Bromium				Bromopsis	Pnigma	Genea			
Grenier & Godron	1856	SERRAFALCUS					Festucaria	Eubromus			
Hackel	1887	*Zeobromus*	*Libertia*				*Festucoides*	*Stenobromus*	*Ceratochloa*		
Ascherson & Graebner	1901	Serrafalcus	Michelaria				Festucaria	Eubromus	Ceratochloa		
Tournay	1961	Bromus					Bromopsis	Genea	Ceratochloa	Nevskiella	TRISETOBROMUS
Hitchcock	1950	Bromium				Bromopsis		Eubromus	Ceratochloa		Neobromus
Nevskii & Sochava	1963	BROMUS		BOISSIERA	LITTLEDALEA		*Zerna*	*Stenobromus*	CERATOCHLOA	*Nevskiella*	*Zeobromus*
Smith	1970	Bromus					Pnigma	Genea	Ceratochloa	Nevskiella	Neobromus
Stebbins	1981	*Bromus*		*Boissiera*			*Festucaria*	*Stenobromus*	*Ceratochloa*	*Nevskiella*	*Neobromus*
Tsvelev	1983	BROMUS		BOISSIERA	LITTLEDALEA		BROMOPSIS	ANISANTHA	CERATOCHLOA	NEVSKIELLA	
Stace	1991	BROMUS					BROMOPSIS	ANISANTHA	CERATOCHLOA		

"It involves, however, a risk of encumbering the text, and obscuring the more general and truly important features of the arrangement....the clearness of the classification and of the text generally has decidedly suffered". This method of grouping constitutes an analytical approach. Many taxa were named, probably many more than existed. Thus, each species quoted by any author had a large penumbra of relatively minor variants; this is a phase of taxonomic fashion known as polytypy. It was, perhaps, an understandable, though extremely primitive reaction to the acceptance of intraspecific diversity. In the most recent European treatment of *Bromus s.l.* (Smith 1980), the system of classification has acquired a more integrative approach, i.e., the specific rank returns to a clearer concept of species, though recognising that much intraspecific variation needs no name.

Bearing this in mind I present in this thesis an independent account of all the taxa discussing their taxonomic rank. My view will seek to reconcile perennial brome-grass diversity with the pattern of distribution in Europe.

2.2 Taxonomic History of Section Pnigma

Section *Pnigma*, the subject of this investigation, has been diversely treated by different authors. Its boundaries, as well as those of *Bromus s.l.*, have been enlarged as a result of deeper studies - see table 2.2.

Frequently *Zerna* species have been placed in a section or subgenus of *Bromus*. Panzer (1813) divided *Bromus* into two genera: *Bromus* and *Zerna*. The latter covered annual, perennial and several disparate species which have been transferred to different genera. Dumortier in 1823 proposed four sections incorporated in the genus *Bromus*: *Genea*, *Bromopsis*, *Pnigma* and *Bromium*. The latter is nowadays in *Bromus*, following Art. 22.1 of the *International Code of Botanical Nomenclature* (1988) which states:

Table 2.2. Some of the broadest classifications revealing the taxonomic history of § *Pnigma* by different authors. Only those species with a pattern of distribution in Europe are included.

Author		Taxonomic rank	Taxa recognised
Panzer	1813	Genus ***Zerna***	*Zerna erecta, Z. asper*
Dumortier	1823	Section ***Pnigma***	*Bromus erectus, B. inermis*
		Section ***Bromopsis***	*Bromus giganteus, B. asper*
Grenier & Godron	1856	Section ***Festucaria***	*Bromus erectus, B. inermis, B. asper*
Fourrier	1869	Genus ***Bromopsis***	*Bromopsis erecta, B. asper*
Hackel	1887	Subgenus ***Festucoides***	*Bromus erectus, B. inermis*
Ascherson & Graebner	1901	Section ***Festucaria***	*Bromus erectus* with many subspecies and varieties, *B. inermis*, *B. ramosus*
Nevskii & Sochava	1963	Subgenus ***Zerna***	*Bromus inermis, B. tomentellus, B. cappadocicus, B. riparius, B. benekenii, B. sibiricus*
Smith	1980	Section ***Pnigma***	*Bromus erectus, B. inermis, B. ramosus, B. tomentellus, B. cappadocicus, etc.*
Tsvelev	1983	Genus ***Bromopsis***	*Bromopsis erecta, B. inermis, B. ramosa, B. tomentella, B. riparia*
Stace	1991	Genus ***Bromopsis***	*Bromopsis erecta, B. inermis, B. ramosa, B. benekenii*

"The name of any subdivision of a genus that includes the type of the adopted, legitimate name of the genus to which it is assignated is to repeat that generic name unaltered..." His section *Pnigma* was described as follows: "*Axis basi circumsutus, seta dorsalis*". It is important to understand what Dumortier meant by "*axis*" for a comprehension of his work. I agree with the interpretation given by Tournay (1961) and Sales (1991): "*Dorsal surface of the glumes separated from the pedicel of the spikelet by an annular strangulation*". Despite being a very short, imprecise description, this indicates the valid and legitimate name for nomenclatural and conceptual purposes adopted here for the section *Pnigma*.

Initially sect. *Pnigma*, purged of any incongruous element, included two perennial species, *B. erectus* and *B. inermis* (Dumortier 1823). In the most recent account of the European flora 9 species and 8 subspecies were recognised (Smith 1980). Originally only perennial European taxa were defined. Nowadays it embraces perennial brome-grasses with a pattern of distribution in Eurasia, Africa and Madagascar, North and South America. The most recent and comprehensive definition of the section was given by Smith (1970), who revived it 147 years after Dumortier, although with great development especially in the number of species concerned: "Perennial grasses, forming sods or tufts; spikelets narrow, more or less lanceolate, terete; lower glume 1-(3)-nerved, upper glume 3-(5)-nerved; lemmas rounded or slightly keeled on the back, sometimes unevenly hairy; awns single, usually shorter than the lemma, rarely weak or absent".

Table 2.3 shows the correct names for the group of perennial brome-grasses according to different rank attributions.

Table 2.3. Correct generic, subgeneric or sectional name and the lectotype for each particular group in the perennial grasses of *Bromus*.

Taxonomic rank	Name	Author and date of publication	Lectotype	Author's citation
Genus	***Bromopsis***	(Dum.) Fourrier 1869	***Bromopsis aspera*** (Huds.) Fourrier	Tsvelev 1983
Subgenus	***Festucoides***	(Coss. & Dur.) Hackel 1887	***B. erectus*** Huds.	P. M. Smith 1970
Section	***Pnigma***	Dumortier 1823	***B. inermis*** Leyss.	Soderstrom & Beaman 1968

Some recent authors, Holub (1973), Tsvelev (1983) & Stace (1991) have treated these perennial species as a distinct genus *Bromopsis* Fourrier. Initially they were placed in *Zerna* (Panzer 1813), resulting in a very heterogeneous taxon, covering species of clearly different genera. For this reason *Zerna* Panzer is illegitimate. According to these authors, a practical replacement of *Zerna* would be *Bromopsis* Fourrier 1869. The name was used by Dumortier (1823) to designate a section, *Bromus* L. § *Bromopsis*; two species were included: *B. giganteus* L. (= *Festuca gigantea* in present classifications) and *B. asper* Murr. (referred to as *B. ramosus* Huds. nowadays). The name *Bromopsis* as a section violates the Art. 22.1 of the *International Code of Nomenclature* (1988); therefore the name is illegitimate. Fourrier (1869) adopted the name for a generic rank, which converts it to a valid name for the plants under consideration, if they are regarded as genetically distinct. Only two species were proposed by this author, *Bromopsis asper* and *B. erecta*.

The attribution of a suitable rank to taxa at or about the generic and infrageneric levels can represent a difficult task. In the case of the perennial brome-grasses the existence of so many names and different treatments (table 2.2) confirms the fact that this is a problematic group. My own view on its taxonomic status, generic or otherwise, will be found in the formal taxonomic account (chapter 9, sect. 9.1.2).

Chapter 3 Conspectus

The list below is in order of genera of all the synonyms that I can detect in the group which I have studied. The correct taxonomic names are referred to by the bracketed number (1a, 6 b, etc..11) which refer to the number taxa in my own revision (chapter 9, sect. 9.3).

***Bromopsis* (Dumor.) Fourr.**

Bromopsis benekenii (Lge.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[1b]**

B. cappadocica (Boiss. & Balansa) Holub, *Folia Geobot. Phytotax.* 8 (2): 167 (1973). **[9a]**

B. condensata (Hackel) Holub, *Folia Geobot. Phytotax.* 8 (2): 167 (1973). **[2a]**

B. erecta (Huds.) Four., *Ann. Soc. Linn. Lyon,* 17: 187 (1869). **[5a]**

B. erecta (Huds.) Four. subsp. *longiflora* (Willd. ex Spreng.) Dostal, *Folia Mus. Rerum. Nat. Bohemiae Occid., Bot.* 2: 16 (1984). **[5d]**

B. inermis (Leyss.) Holub, *Folia Geobot. Phytotax.* 8 (2): 158 (1973). **[11]**

B. lacmonica (Hausskn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[9c]**

B. moellendorffiana (Aschers. & Graebn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[2c]**

B. moesiaca (Velen.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[7]**

B. monoclada (Domin) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[3c]**

B. pannonica (Kummer & Sendtn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[3a]**

B. pannonica (Kummer & Sendtn.) Holub subsp. *monoclada* (Domin) Holub, *Folia Geobot. Phytotax.* 18 (2): 205 (1983). **[3c]**

B. pindica (Hausskn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[6a]**

B. ramosa (Huds.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973). **[1a]**

B. ramosa (Huds.) Holub subsp. *benekenii* (Lge.) Tsvelev, *Fl. Part. Europ. S.S.S.R.* 1: 175 (1974). **[1b]**

B. riparia (Rehm.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973). **[6a]**

B. riparia (Rehm.) Holub subsp. *barcensis* (Simonk.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973). **[6b]**

B. riparia (Rehm.) Holub subsp. *fibrosa* (Hackel) Tsvelev, *Fedorov Fl. Evr. Casti S.S.S.R.* 1: 176 (1974). **[6a]**

B. tomentella (Boiss.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973). **[10]**

B. tomentella (Boiss.) Holub subsp. *cappadocica* (Boiss. & Balansa) Tsvelev, *Zlaki S.S.S.R.*: 217 (1976). **[9a]**

Bromus L.

Bromus agrestis All., *Fl. Ped.* 2. 249 (1875). **[5a]**

B. angustifolius Schrk., *Baier Fl.* 366 (1789). **[5a]**

B. angustifolius Hornemann, *Hort. Hafn. Suppl.* 13 (1819), non Marschall. (5c)

B. arvensis Poll., *Pl. Palat.* 1. 113 (1776). **[5a]**

B. asper Murr., *Prodr. Stirp. Gotting.* 42 (1770). **[1a]**

B. asper Murr. var. *angustifolius* Nees ex Royle, *Bot. Him.* 3: 417 (1839). **[1a]**

B. asper Murr. var. *benekenii* Syme, *Sowerby Engl. Bot.* 11: 157 (1872). **[1b]**

B. barcensis Simonk., *Enum. Pl. Transs.* 584 (1886). **[6b]**

B. benekenii (Lge.) Trimen, *J. Bot.* 10: 333 (1872). **[1b]**

B. cappadocicus Boiss. & Balansa, *Bull. Soc. Bot. France*, 4: 306 (1857). **[9a]**

B. cappadocicus Boiss. & Balansa subsp. *lacmonicus* (Hausskn.) P.M. Smith, *Bot. J. Linn. Soc.* 76: 360 (1978). **[9c]**

B. cappadocicus Boiss. & Balansa var. *velutinus* Bornm., *Bot. Jahrb. Engler* 61, 140: 172 (1928). **[9b]**

B. caprearum Hackel, *Öesterr. Bot. Z.* 29: 209 (1879). **[4]**

B. condensatus Hackel, *Öesterr. Bot. Z.* 29: 209 (1879). **[2a]**

B. condensatus Hackel var. *microtrichus* (Borbás) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932). **[2b]**

B. condensatus Hackel var. *microtrichus* Borbás subvar. *australis* (Griseb.) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932). **[2b]**

B. condensatus Hackel var. *microtrichus* Borbás subvar. *cilifer* (Beck) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932). **[2b]**

B. condensatus Hackel var. *pomöensis* (Teyb.) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932). **[2a]**

B. crassipes Halácsy, *Öesterr. Bot. Z.* 56: 282 (1906). **[9b]**

B. erectus Huds., *Fl. Angl.* ed. 1. 39 (1762). **[5a]**

B. erectus Huds. subsp. *australis* (Griseb.) Hackel var. *condensatus* Hackel, in Bornm. *Mitth. Thüring. Bot. Vereins,* 29: 64 (1912). **[2a]**

B. erectus Huds. subsp. *australis* (Griseb.) Hackel var. *pomöensis* Teyb., *Öesterr. Bot. Z.* 70: 246 (1921). **[2a]**

B. erectus Huds. subsp. *barcensis* (Simonk.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 579 (1901). **[6b]**

B. erectus Huds. var. *caprinus* (Kerner ex Hackel) Fiori, *Fl. Anal. Ital.* 1: 98 (1896). **[4]**

B. erectus Huds. var. *condensatus* (Hackel) Fiori, *Fl. Anal. Ital.* 1: 98 (1896). **[2a]**

B. erectus Huds. subsp. *condensatus* (Hackel) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 585 (1901). **[2a]**

B. erectus Huds. subsp. *eu-erectus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901). **[5a]**

B. erectus Huds. subsp. *fibrosus* (Hackel) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 578 (1901). **[6a]**

B. erectus Huds. subsp. *fibrosus* (Hackel) Aschers. & Graebn. var. *lacmonicus* (Hausskn.) Stoy. & Stefanov, *Fl. Bulg.*, 3rd edition, 160 (1948). **[9c]**

B. erectus var. *glabriflorus* Borbás, *Öesterr. Bot. Z.* 32: 135 (1882). **[5a]**

B. erectus Huds. var. *hackelii* Borbás, *Földmvi. érdek.* 11 (1882). *Öesterr. Bot. Z.* 32: 135 (1882). **[5a]**

B. erectus Huds. var. *insubrica* Stebler, *Futterpfl. 2.2 Aufl. 29* (1895) *vgl. Schw. Gräs. - Samml.*, 237. **[2a]**

B. erectus Huds. var. *istrianus* Belli, known only from herbarium label. No publication found. **[2b]**

B. erectus Huds. var. *laxus* (Hornem.) Döll, *Fl. Bad.* 1: 144 (1857). **[5c]**

B. erectus Huds. var. *longiflorus* Parl., *Fl. Ital.* 1: 413 (1848). **[5d]**

B. erectus Huds. var. *microtrichus* Borbás, *Hirc. Fl. okoli bakarske*, 138 (1884). *Öesterr. Bot. Z.* 35: 124 (1885). **[2b]**

B. erectus Huds. subsp. *moellendorffianus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 582 (1901). **[2c]**

B. erectus Huds. var. *moesiacus* (Velen.) Stoy. & Stefanov, *Fl. Bulg.*, 3rd edition, 160 (1948). **[7]**

B. erectus Huds. var. *pannonicifolius* Prod., *Bul. St. Sect. Biol. Acad. R.P.R.* 9 (4): 292 (1957). **[3a]**

B. erectus Huds. var. *pannonicus* Aschers. & Kanitz, *Cat. Corm. et Anthoph. Serbiae, Bosniae*, 12 (1877). **[3a]**

B. erectus Huds. var. *pycnotrichus* Borbás, *Math. Term. Közlem,* 15, 9: 334 (1878). **[3a]**

B. erectus Huds. var. *stabianus* Guadagno, *Bull. Orto Bot. Regia Univ. Napoli,* 3: 85 (1913). **[4]**

B. erectus Huds. subsp. *stenophyllus* (Link) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 583 (1901). **[5c]**

B. erectus Huds. var. *stenophyllus* (Link) Fiori, *Nuov. Fl. Anal. Ital.* 1: 146 (1923). **[5c]**

B. erectus Huds. var. *transsilvanicus* Steud. subvar. *montenegrinus* (Sagorski) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 207 (1932). **[5e]**

B. erectus Huds. var. *vernalis* Pancic, *Verh. Zool.-Bot. Ges. Wien*, 6: 592 (1856). **[3b]**

B. eu-erectus var. *fasciculatus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901). **[5a]**

B. eu-erectus subsp. *longiflorus* (Willd.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 588 (1901). **[5d]**

B. eu-erectus subvar. *planifolius* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901). **[5a]**

B. eu-erectus var. *villosus* (Mart. & Kock) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901). **[5a]**

B. fibrosus Hackel, *Öesterr. Bot. Z.* 29: 209 (1879), based on *B. transsilvanicus* Schur, *Öesterr. Bot. Z.* 10: 227 (1860). **[6a]**

B. fibrosus Hackel var. *barcensis* (Simonk.) Jav., *Magyar Fl.* 1, 1: 108 (1924). **[6b]**

B. fibrosus Hackel subsp. *barcensis* (Simonk.) Hayek, *Prodr. Fl. Pen. Balc.* 3: 205 (1933). **[6b]**

B. fibrosus Hackel var. *contractus* Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53 (1899). **[6a]**

B. fibrosus Hackel subsp. *eu-fibrosus* Hayek, *Prodr. Fl. Pen. Balcan.* 3: 205 (1933). **[6a]**

B. fibrosus Hackel subsp. *macedonicus* Degen & Dörfler, *Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr.* 64: 741 (1897). **[6c]**

B. glaucus Lapeyr., *Hist. Arbr. Pyr.* 633 (1813). **[5a]**

B. inermis Leyss., *Fl. Halensis,* 16 (1761). **[11]**

B. inermis Leyss. var. *aristatus* Schur, *Enum. Pl. Transsilv.* 805 (1866). **[11]**

B. lacmonicus Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53 (1899). **[9c]**

B. laxus Hornemann, *Hort. Hafn.* 2: 954 (1815). **[5c]**

B. litoreus Reich., *Nachtr.* 259 (1802). **[11]**

B. longiflorus Willd., *Enum. Pl. Suppl.* 6 (1813), nom. nud., ex Spreng., *Pl. Pugill.* 2: 23 (1815). **[5d]**

B. macedonicus auct. Kozuh., Petr. & Ehrend., *Bot. Jahrb. Syst.* 102 (1-4): 382 (1981). **[6c]**

B. moellendorffianus (Aschers. & Graebn.) Hayek, *Prodr. Fl. Penins. Balcan.* 3: 208 (1933). **[2c]**

B. moesiacus Velen., *Fl. Bulg.* 616 (1891). **[7]**

B. monocladus Domin, *Mem. Soc. Sci. Boheme* 14, 14: 1-2 (1932). **[3c]**

B. nemorosus Vill., *Pl. Dauph.* 2: 117 (1787). **[1a]**

B. odoratus Gouan, *Hort. Monsp.* 11 (1768). **[5a]**

B. orbelicus Petr., Kozuh. & Ehrend., in press (1993). **[6c]**

B. pannonicus Kummer & Sendtn., *Flora*, 32: 757 (1849). **[3a]**

B. pannonicus Kummer & Sendtn. var. *hercegovinus* (Beck) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932). **[3a]**

B. pannonicus Kummer & Sendtn. var. *hirtiflorus* (Maly) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932). **[3a]**

B. pannonicus Kummer & Sendtn. var. *monoclados* (Domin) Soó, *Acta Bot. Acad. Sci. Hung.* 17: 115-125 (1971). **[3c]**

B. pannonicus Kummer & Sendtn. subsp. *monoclados* (Domin) P.M. Smith, *Bot. J. Linn. Soc.* 76: 360 (1978).**[3c]**

B. pannonicus Kummer & Sendtn. var. *reptans* Borbás, Faldmiv. Erdek. 11 (1882). **[3a]**

B. pannonicus Kummer & Sendtn. var. *reptans* subvar. *stolonifer* (Borbás) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932). **[3a]**

B. parilicus Petr., Kozuh. & Ehrend., in press (1993). **[8]**

B. perennis Vill., *Pl. Dauph.* 2. 122 (1887). **[5a]**

B. pindicolus Hausskn. (1885), known only from herbarium label. No publication found. **[6a]**

B. pindicus Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53-54 (1899).**[6a]**

B. pseudo-arvensis Koel., *Gram.* 241 (1802). **[5a]**

B. pseudoasper Schur, *Enum. Pl. Transsilv.* 804 (1866). **[1a]**

B. ramosus Huds., *Fl. Anglica,* ed. I. 40 (1762). **[1a]**

B. ramosus Huds. var. *benekenii* (Lge.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 576 (1901). **[1b]**

B. ramosus Huds. var. *eu-ramosus*, Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1) 575 (1901). **[1a]**

B. repens Borbás, l.c. 335 (1878). Hackel, *Öesterr. Bot. Z.* 29: 205 (1879). **[3a]**

B. riparius Rehm., *Notiz. Veg. Gest. Schwarz. Meer.* 83 (1872). **[6a]**

B. riparius Rehm. subsp. *barcensis* (Simonk.) Soó, *Acta Bot. Acad. Sci. Hung.* 17 (1-2): 115 (1971). **[6b]**

B. riparius Rehm. subsp. *macedonicus* (Degen & Dörfler) Soó, *Acta Bot. Acad. Sci Hung.* 17 (1-2): 115 (1971). **[6c]**

B. sphacioticus Gand., *Fl. Crète*: 101 (1916). **[10]**

B. stenophyllus Link, *Enum. Pl. Hort. Berol.* 1: 94 (1821). **[5c]**

B. tomentellus Boiss., *Diagn. Pl. Orient. Nov. Ser.* 1 (7): 126 (1846). **[10]**

B. tomentellus Boiss. var. *hispidus* Boiss., *Diagn. Pl. Orient. Nov. Ser.* 3 (4) 140 (1859). **[10]**

B. transsilvanicus Schur, *Öesterr. Bot. Z.* 10: 227 (1860), non Steudel. **[6a]**

B. transsilvanicus Steud. var. *angustifolius* Sagorski, *Mitth. Thüring. Bot. Vereins* 16: 34 (1901). **[2c]**

B. transsilvanicus Steud. var. *montenegrinus* Sagorski, *Mitth. Thüring. Bot. Vereins* 16: 34 (1901). **[5e]**

B. vernalis Pancic, *Öesterr. Bot. Z.* 29: 205 (1879). **[3b]**

Festuca L.

Festuca aspera Mert. & Koch, *Deutschl. Fl.* 1: 673 (1823). **[1a]**

F. erecta Wallr., *Sched. crit.* 35 (1822). **[5a]**

F. hirta Seenus, *Reise*, 59 (1805). **[5a]**

F. inermis (Leyss.) Lam. & DC., *Fl. France*, 3rd edition, 3: 49 (1805). **[11]**

F. leyssieri Moench, *Fl. Hass.* 82 (1777). **[11]**

F. montana Savi, *Fl. Pis.* 1. 118 (1798). **[5a]**

F. poaeformis Pers., *Syn.* 1. 94 (1805). **[11]**

F. speciosa Schreber, *Spicilegium,* 59 (1771). **[11]**

Schedonorus Beauv.

Schedonorus asper (Murr.) Fr., *Bot. Not.*, 131 (1843). **[1a]**

S. benekeni Lange, *Fl. Danica*, fasc. 48: 5, t. 2826 (1871). **[1b]**

S. erectus Fries, *Bot. Not.* 131 (1843). **[5a]**

S. inermis (Leyss.) Pal. Beauv., *Ess. Agrosts.* 99: 177 (1812). **[11]**

S. serotinus (Beneken) Rostr., in Lange *Haandb. Danske Fl.*, 3rd edition, 103 (1864). **[1a]**

Zerna Panzer

Zerna aspera (Murr.) Panzer, *Denkschr. Königl. Akad. Wiss. München,* 296 (1814). **[1a]**

Z. benekenii (Lge.) Lindm., *Svensk Fanerog.* 101 (1918). **[1b]**

Z. cappadocica (Boiss. & Balansa) Nevskii, *Acta Univ. Asiae Mediae. Bot.* 17: 17 (1934), *quoad nomen.* **[9a]**

Z. erecta Panzer, *Denkschr. Königl. Akad. Wiss. München,* 297 (1814). **[5a]**

Z. inermis (Leyss.) Lindm., *Svensk Fanerog.* 101 (1918). **[11]**

Z. monoclada (Domin) Holub, *Novit. Bot. Delect. Seminun Horti. Bot. Univ. Carol. Prag.* 9: 160 (1960). **[3c]**

Z. ramosa (Huds.) Lindm., *Svensk Fanerog.* 101 (1918). **[1a]**

Z. ramosa (Huds.) Lindm. subsp. *benekenii* (Lge.) Tsvelev, *Novit. Syst. Pl. Vasc.* (Leningrad) 7: 53 (1971). **[1b]**

Z. riparia (Rehm.) Nevskii, *Acta Univ. Asiae Mediae. Bot.* 17: 17 (1934). **[6a]**

Z. riparia (Rehm.) Nevskii subsp. *barcensis* (Simonk.) Holub, *Folia Geobot. Phytotax.* 5: 440 (1970). **[6b]**

Z. tomentella (Boiss.) Nevskii, *Acta Univ. Asiae Mediae Bot.* 17: 17 (1934). **[10]**

Z. tomentella (Boiss.) Nevskii subsp. *cappadocica* (Boiss. & Balansa) Tsvelev, *Novit. Syst. Pl. Vasc.* (Leningrad) 7: 56 (1971). **[9a]**

Chapter 4 Leaf Anatomy

4.1 Introduction

Anatomical investigations of the leaf blade in grasses represent a broadly accepted source of valuable taxonomic information, also providing important characters with specific diagnostic value, which can be associated with an ecological adaptation to the environmental conditions in specific habitats.

Some botanists (Stebler & Schroeter 1889; McAlpine 1890; Pée-Laby 1898) have recognised the fact that the anatomical structure of the leaves represents a valuable aid for the identification of many grasses especially when, as happens during a great part of the year, one has only the vegetative organs to work with; in this situation the transverse sections of the leaf would be the only means of distinguishing correctly very nearly related taxa. This statement seems, on my experience, to be somewhat exaggerated, since on examination, the transverse sections of leaves of closely related species of perennial brome-grasses are very similar, if not practically identical. This is more the case when the species have a very similar habitat: when the habitat is dissimilar, they often have different leaf structure but in these cases the taxa concerned may often be recognised without the need to examine the leaf section.

The extensive work carried out in this field of agrostology has been published in a vast amount of literature with a lack of uniformity on definitions and descriptions. A significant attempt to improve the situation was carried out by Metcalfe (1960). A further contribution was presented by Ellis (1976, 1979), who produced an important system to standardise and simplify the comparison of the leaf anatomy in grasses.

The object of the present research has been twofold:

1) to find diagnostic characters which might be related to form/function in response to certain environmental conditions and to show taxonomic differences.
2) to corroborate Metcalfe's statements (1960) viz. that:
    a) leaves from different nodes on an individual plant exhibit structural variations.
    b) leaves from plants belonging to a single species grown in different habitats also vary within limits.

My procedure for a comparative study of leaf anatomy followed Ellis' conventions (1976, 1979).

Research carried out on these perennial brome-grasses rested mainly on the use of fresh leaves from specimens growing in the green-house at the University of Edinburgh, and also on herbarium specimens in those situations where living plants were not available, so as to cover the whole spectrum of the section *Pnigma* in Europe (see Material and Methods). I have investigated plants growing under unnatural i.e., cultivated conditions, so that the anatomical structure of the leaves might appear to be different from those growing under natural conditions in a natural habitat. Some future research could be done to discover what changes, if any, are produced in the structure of the leaf by controlled changes in the environment.

The species selected for the purpose of this study were:

B. ramosus (BR) and *B. benekenii* (BB) in the *B. ramosus* group, *B. erectus* (BE) in the *B. erectus* group, *B. cappadocicus* (BC) and *B. tomentellus* (BT) in the *B. riparius* group, and *B. inermis* (BI).

4.2 Material and Methods

As mentioned before, there were two sources of material used for the current investigation, fresh leaves and herbarium specimens in those situations where I did not have a source of fresh material. For anatomical studies, better quality sections were obtained with fresh leaves. Good success in using herbarium material requires previous hydration of the tissues, which sometimes is not easy, and does not offer technically satisfactory results. In each case, the different methods were identical, except the pre-treatment given to dry specimens which will be described later.

The leaf below the flag leaf was selected for a standard procedure. All the sections were taken from half way between the base and the apex of the leaf, because leaves grow from a basal meristem and therefore the apex is mature while the base is still immature. Intermediate parts of the leaf represent a gradual transition from immature to mature characters (Metcalfe 1960; Ellis 1976). Accession numbers used are cited in Appendix 4.1. Material of these accessions is maintained either as seed material in Dr. P.M. Smith's *Bromus* collection (University of Edinburgh) or as voucher specimens in the Royal Botanic Garden in Edinburgh. The counts of stomata were carried out on ten transverse sections, leaf margin to leaf margin of each species, i.e., a transect of the opposed abaxial and adaxial surfaces.

Transverse sections were taken following Rahman's procedure (1988), who based his investigations on Johansen's wax method (1940). However, some modifications were necessary depending on the nature of the material used .

i) Preparation

Three to five segments, each 5 mm long, were cut with a sharp razor blade. The dried material was also cut into segments and gently boiled in water with some drops of washing powder, to recover its natural shape and size. The duration of boiling varied from 15 minutes to an hour. Segments were fixed in 20 ml vials containing F.A.A.

solution. Each vial with its corresponding label was capped and stored for at least 24 hours.

F.A.A. solution

70% alcohol	90 ml
Glacial Acetic acid	5 ml
40% Formaldehyde	5 ml

ii) Rinsing

The pieces were transferred to conical flasks with cold water for 15 minutes, occasionally shaking by hand. Several changes of water were made to remove the F.A.A.

iii) Dehydration

The aim was to remove water from the tissues. The segments were treated with ten different concentrations of alcohol and Tertiary butyl alcohol (T.B.A.) (2-methyl-propan 2-ol).

10% alcohol	1 1/2 h
20% alcohol	1 1/2 h
30% alcohol	1 1/2 h
50% alcohol	1 1/2 h
70% alcohol	2 h
Johansen solution 1	2 h
Johansen solution 2	2 h
Johansen solution 3	2 h
Johansen solution 4	2 h
Johansen solution 5	2 h

Johansen solutions

Solution	Distilled H_2O	95% Ethyl alcohol	T.B.A.	100% Ethyl alcohol
1	50 ml	40 ml	10 ml	
2	30 ml	50 ml	20 ml	
3	15 ml	50 ml	35 ml	
4		45 ml	55 ml	
5			75 ml	25 ml

The segments were left in T.B.A. for 2 hours, followed by two changes, and a third one overnight. Treatments with Johansen solutions and T.B.A. were applied in the vacuum embedder.

I agree with Rahman (1988) that when required, specimens were left in one of the dehydration and/or infiltration series for a much longer duration that indicated, and no harm was found.

iv) Infiltration

For this procedure it was necessary to use an oven adequate for anatomical investigations. The material was transferred to a mixture of equal parts of paraffin oil and T.B.A., in which it remained for at least an hour or somewhat longer. The vials in the oven were 3/4 full of melted Paraplast (Sigma Chemical Co., P3808) and later left to stand until the Paraplast was slightly solidified but not cooled completely. The material resting in the T.B.A./paraffin oil mixture was poured onto the slightly solidified wax, and the vial was placed back in the oven. Thus, the segments slowly sunk through the melting Paraplast until rested on the bottom of the container. Like Rahman (1988), I obtained better results by leaving the material in the mixture overnight, instead of 1 hour (Johansen 1940). The entire mixture of Paraplast, oil and what traces of alcohol remained were poured off and replaced with pure melted wax. This process was repeated twice during the next 6 hours, discharging each change of Paraplast.

v) Embedding

The contents of the vial were poured into suitable receptacles. Brass embedding frames were used instead of folder paper trays. I found them easier to manipulate than the latter (Johansen 1940; Rahman 1988). Melted Paraplast was added from the stock container if necessary and with quick manipulation, the segments were arranged in order with the help of a needle previously heated in a gas flame. I arranged not more than three segments per tray, to avoid overlapping and leave plenty of space between neighbouring pieces. As soon as the tray could be moved without disturbing the material, it was transferred to a vessel with cold water. Water did not cover the tray, but just came to below the top edges of the frame. Once the wax became sufficiently firm, it was splashed by hand and then removed from the brass frame. The blocks were left in the water for at least 1/2 hour until thoroughly cooled. It is important to emphasise the rapid cooling of the wax. If the process is too slow, the Paraplast may crystallise, making it difficult to obtain goods results with the sectioning.

vi) Microtoming

A piece of tissue was removed from the block of material by cutting it with the help of a scalpel and made ready for sectioning. Rotary microtome (Automatic Rotary Microtome: R. & J. Beck Ltd., England) was used. It is essential if the ribbon is to be straight that the face of the block containing the tissue must be parallel with the razor blade. For that reason, the holder must be adjusted until the edges of the block and razor coincide. Sections were cut at thicknesses of 12-15 μm but best sections were obtained at 12 μm. Ribbons were cut approximately 10 cm long and were ready to be mounted.

vii) Mounting Ribbons

Several segments of the ribbon (number varying according to the size), were placed on a slide previously smeared with egg albumen and a few drops of water to make them stick. The process was carried out with the help of a scalpel or a needle. The slide was left on a warming plate heated at 40-45°C. The ribbons flattened out progressively with the heat, and the wrinkles in the paraffin disappeared. The slides were left on the warming plate for 15 minutes until all the water evaporated and the ribbons were firmly adhered to the surface to avoid detachment during the de-waxing process. At this stage, the slides were put inside a drawer on a piece of kitchen paper and left to dry overnight.

viii) De-waxing

Before the sections were stained, the paraffin had to be removed. The slides were placed in staining jars containing one rack each to hold the slides. Several solutions were used. The rack was transferred from one jar to the next one and left there according to the time indicated.

1. Xylene	15 min
2. Xylene	5 min
3. Xylene + absolute alcohol (1:1)	10 min
4. Absolute alcohol	10 min
5. Absolute alcohol	10 min

ix) Staining

The slides were placed in a jar with safranin and left in the solution for 24 hours. After the tissues had been stained, the rack was taken through the following series of solutions, to ensure dehydration.

1. Methylated spirit	5 min
2. Absolute alcohol	10 min
3. Absolute alcohol	10 min

I decided not to use fast green as a later staining agent due to its powerful effect and hazardous manipulation; it dyed the tissues wholly and strongly green. I found this messy and that it contributed nothing to the findings. Instead I opted for safranin as the only staining product, obtaining very clean and neat results. Rahman (1988) used fast green after the absolute alcohol and left the material in it for 5-20 seconds, varying with the thickness of the sections. This treatment was followed by three consecutive changes of absolute alcohol, 10 seconds for the first two and 5 seconds for the last.

Safranin

To make 408 ml: Dissolve 4 g of the dye in 200 ml Methyl Cellosolve. When solution is complete, 100 ml each of 95% alcohol and distilled water are added, followed by 4 g Sodium Acetate and 8 cc Formalin.

x) Mounting

The slides were removed from the absolute alcohol and the excess of alcohol was allowed to drip off. The sections were mounted in Euparal (Agar Scientific, R1344) and covered with a cover slip. The slides were left on the warming plate at least for 2 days at 45°C. After this period, the slides were ready for a further examination under the binocular microscope.

xi) Photographing

Photographs were taken with Olympus OM-2 camera attached to a Vickers Photoplan microscope, recorded on Kodak Technical Pan film and processed in Kodak HC110 developer, dilution B (1:32) for 5 minutes at 20 °C. The magnifications are indicated in each case.

4.3 Results

To provide a basic understanding of the leaf anatomy in transverse sections of the perennial brome-grasses, I will first describe the general range of morphology observed in all the species studied.

Outline of the lamina (in section)

Expanded, flat or undulating gently; sometimes U-shaped or V-shaped.

Adaxial and abaxial longitudinal ribs and furrows

Slight shallow furrows, wide open or narrow in the form of steep-sided grooves between all vascular bundles; sometimes no ribs and furrows present, with the surface smooth or slightly undulating. Abaxial ribs and furrows do not occur in these species.

Keel structure

Developed and associated with sclerenchyma; emergent abaxially and varying among taxa; one vascular bundle comprising the keel, exceptionally three.

Vascular bundles

Different orders alternate with one another, all of them are rounded in outline. The vascular tissue in the third order vascular bundle consists of a few strands; xylem and phloem elements are easily distinguishable in the second order group; conspicuously larger metaxylem vessels or lysigenous cavities are not observed; sclerenchyma arrangement is usually the same as for the first order bundles. The median vascular bundle of the first order contains large metaxylem vessels whose walls can be slightly or distinctly thickened, and occurring on either side of protoxylem elements; lysigenous cavities can be present or absent; protoxylem adjoins the inner parenchyma sheath.

Vascular bundle sheaths

Double; the outer sheath is round in the three categories of bundles; complete or incomplete due to the interruption of sclerenchymatous girders abaxially and/or adaxially. Frequently the bundle sheath presents extensions on one or both sides comprised of parenchyma cells and extended to adjacent sclerenchymatous strands; the nature of the extensions varies among different taxa, and represents a useful diagnostic character for taxonomic purposes. The inner sheath is complete, entirely surrounding the xylem and phloem; the cells comprising the sheath are relatively large with inner tangential and radial walls heavily thickened, with a small lumen, or not conspicuously thickened; sometimes the cells exhibiting irregular outlines, relatively small with uniformly thickened walls.

Sclerenchyma

The function of all the sclerenchyma present in the leaf is undoubtedly to provide mechanical support for the softer tissues. This can be present abaxially and/or adaxially either in contact with the bundle sheath, referred as **girder** or separated from the bundle sheath by parenchyma or mesophyll, termed **strand.** The presence/absence of sclerenchyma, distribution and nature constitute taxonomic characters which vary among different taxa. Sclerenchyma is always associated with first and second order vascular bundles, never found in third order bundles. Sclerenchyma in the leaf margin comprises the only mechanical tissue in relation to the margin of the lamina. It occurs in the form of an edging rod or band i.e., not in contact with the lateral bundle, and may consist of only a couple of relatively small fibres, or be well developed of several/many cells.

Mesophyll

This consists mainly of assimilatory tissue i.e., chlorenchyma. It is more or less homogeneous, cells not arranged in any definite pattern in relation to the vascular bundle; it is referred to as the festucoid type (Metcalfe 1960; Ellis 1976).

Bulliform cells

These occur in the adaxial surface only, either at the bases of furrows or along the lamina; corresponding to the fan-shaped type (Metcalfe 1960; Ellis 1979); each cell of the group with outer tangential walls shorter than the inner tangential wall; median cell of the group appreciably larger than the remainder. The size and outline of the cells vary among different taxa, from relatively small, tortuous/regularly smooth in outline to very large, with regular or irregular contours.

Stomata

Stomata complexes are long and narrow with parallel-sided subsidiary cells. They correspond to the low-domed shape type (Metcalfe 1960; Ellis 1979).

Macrohairs

Unicellular, hard, stiff hairs usually with thickened walls; no specialised cells associated with the base of macrohairs; irregularly distributed on both sides of the lamina, sometimes very abundant.

Epidermis

Cuticle not obvious, clearly very thin; epidermal cells of variable form, often arched sideways and the cell becoming papillose or expanded externally into prickles and papillae. Commonly the epidermal cells which adjoin the bands of mechanical tissue become smaller and have thicker walls than the remaining cells; in fact they take the

appearance of sclerenchyma cells and generally their outer wall is thicker than in the other epidermal cells.
The anatomical characters selected for comparative purposes are listed in table 4.1, conjointly with the relevant states for each one.

Intra-individual anatomical variations have been observed in relation to the size, degree of development and number of vascular bundles associated with the keel in different leaves of the same species. Lower leaves of *B. benekenii* present a prominent keel with three vascular bundles, the median bundle larger and two subsidiary smaller. In the upper leaves, the conspicuous keel has only the median vascular bundle associated (fig. 4.1). Another example of such anatomical variation is shown in *B. erectus* (fig. 4.2). Different authors have reported the existence of two kind of leaves in this taxon, narrow basal leaves and upper broader leaves. Both present the same overall anatomical pattern, differing in the amount of sclerenchyma fibres in relation to the bundles. I therefore agree with Metcalfe in stating that leaves from different nodes on an individual plant exhibit structural variation.

Information derived from the distribution of sclerenchyma associated with the vascular bundles can be of both ecological and taxonomic interest. In order to investigate intra-individual variation, I examined six samples of *B. erectus* collected from different localities and carefully compared them. The difference in the amount of this mechanical tissue was reflected in the median vascular bundle (see figure 4.3). One extreme exhibited a large proportion of sclerenchymatous fibres on the keel in comparison with the other sextreme specimen which had very few sclerenchyma in the same position.

Table 4.1. List of anatomical characters selected with their corresponding states.

Character state	BR	BB	BI	BE	BT	BC
Adaxial furrows absent, i.e., lamina surface smooth or only slightly undulating	X					
Adaxial furrows present:						
a) slightly shallow, i.e., less than ¼ of the leaf thickness		X	X			
b) medium furrows, i.e., ¼ to ½ the leaf thickness				X	X	
c) deep furrows, i.e., more than ½ the leaf thickness						X
Sclerenchyma present in association with the leaf margin:						
a) very small sclerenchyma, consists of a couple of fibres		X				
b) relatively small	X			X		
c) well developed			X		X	X
Bundle sheath lacking of adaxial and/or abaxial parenchymatous extensions	X	X	X			X
Bundle sheath presenting adaxial and/or abaxial parenchymatous extensions				X	X	
Extensions consist of large, thin-walled colourless cells				X adax.	X adax.	

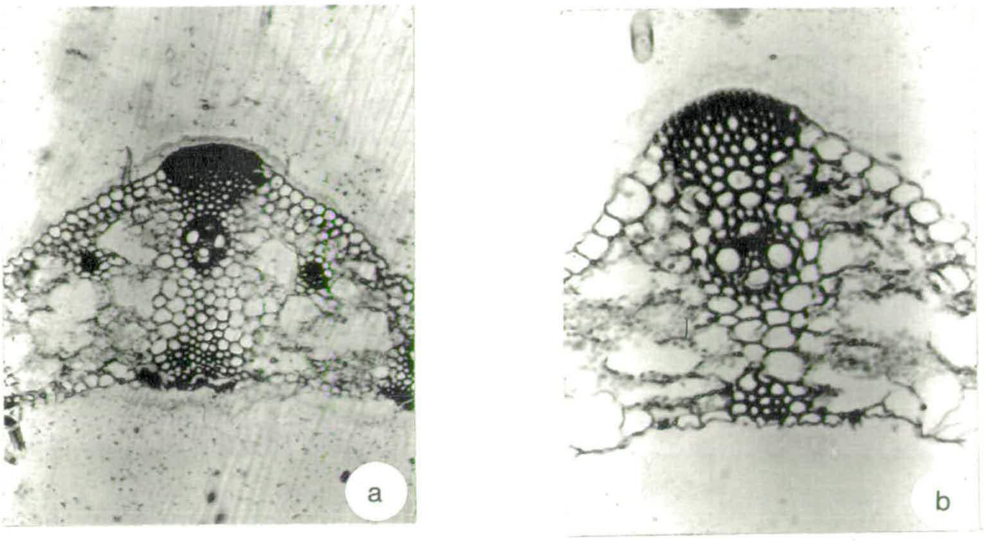
Table 4.1 continued

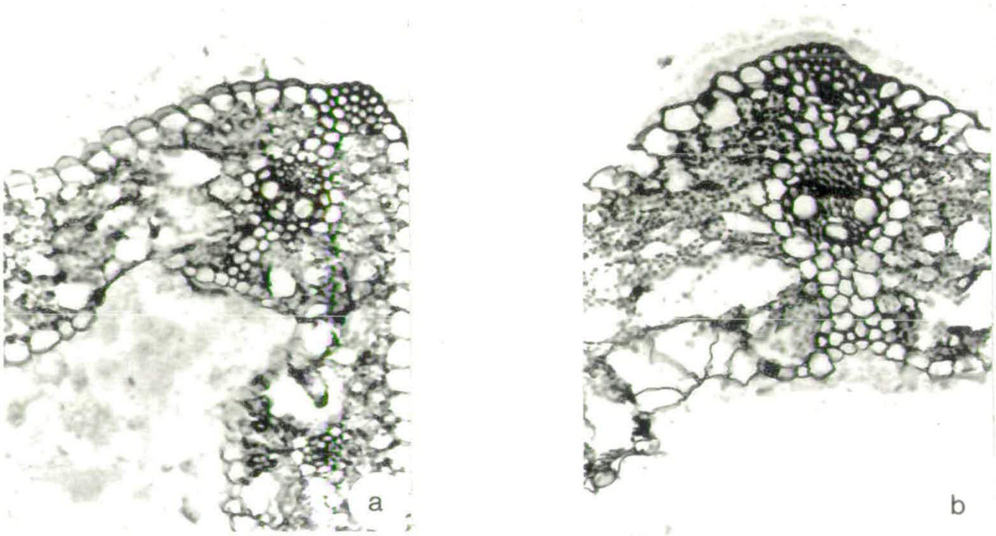
Character state	BR	BB	BI	BE	BT	BC
Extensions consist of colourless cells gradually decreasing in size as walls increase in thickness and eventually merge into the sclerenchyma strand				X abax.	X abax.	
Abaxial strand present above the basic type of vascular bundle:						
a) small	X			X	X	
b) well developed				X		
Abaxial girder present above the basic type of vascular bundle:						
a) small						
b) well developed		X	X		X	X
Adaxial strand present below the basic type of vascular bundle:						
a) minute, consisting of only a few sclerenchymatous fibres				X	X	
b) small						
c) well developed						
Adaxial girder present below the basic type of vascular bundle:						
a) minute, consisting of only a few sclerenchymatous fibres	X					
b) small		X	X			
c) well developed						X

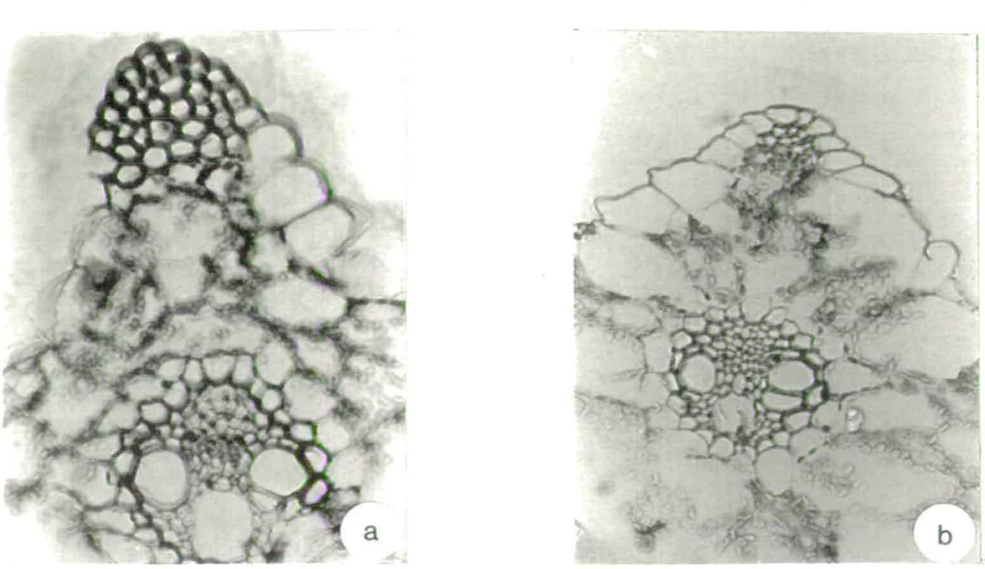
Fig. 4.1. (a) Lower leaf of *B. benekenii* with a prominent keel and three vascular bundles, one large and two subsidiary smaller. Mag. x41; (b) upper leaf with only one main vascular bundle associated with the keel. Mag. x102 (Accession number 1693).

Fig. 4.2. Keel areas of (a) lower, narrower basal leaf in *B. erectus*. Mag. x102; (b) upper, broader leaf in the same taxon. The main difference between them is quantitative, in the amount of fibres associated with the main vascular bundle. Mag. x102 (Accession number 1694).

Fig. 4.3. (a) Leaf of *B. erectus* showing a large proportion of sclerenchymatous fibres abaxially. Mag. x204 (Accession number 1656); (b) leaf of *B. erectus* from a different locality where the sclerenchyma is very inconspicuous. Mag. x204 (Accession number 1710).


a
b


a
b


a
b

This example corroborates Metcalfe's statement that leaves from plants belonging to a single species growing in different habitats may also vary. Clearly this is a caveat for taxonomic use.

The study of transverse sections of leaves from different species has nevertheless shown some taxonomic differences. The distribution of sclerenchyma as well as the occurrence of stomata, both reflected slight variations. The amount of sclerenchyma tissue that is present varies from species to species. It is reported to be especially well developed in grasses from dry, arid localities (Metcalfe 1960). It constitutes a mechanical support for the softer tissues without which a grass leaf could not withstand physical strains and stresses. It is found more abundantly on the abaxial (lower) side of the lamina than on the adaxial (upper) where it can be present as a few sclerenchyma fibres. *B. cappadocicus* grows in very exposed, windy areas and probably in relation to dry conditions; the leaves are rolled up with a cylindrical outline during a great part of their life (fig. 4.4). In many sections they reveal a massive support of sclerenchyma fibres over all the vascular bundles, which might constitute the best arrangement as a strengthening tissue. No doubt this offers superior resistance to Euler buckling - a potential problem with effectively cylindrical hollow forms in plant vegetative structures (Niklas 1992). In comparison, *B. ramosus* produces flat leaves and occurs in moist, often sheltered forest edge habitats (fig. 4.5). The number of sclerenchyma fibres is far less striking. As a supporting tissue, we can explain its taxonomic variations from this analysis of form in relation to function and habitat.

The particular distribution of stomata has often been strongly associated with particular environments - where the plant is deemed to be adapted to dry conditions. In my own studies I have observed that when leaves are either rolled up, folded or flat with abundant hairs, as is the case in dry, wind-swept localities, the adaxial (upper) surface exhibits deep furrows where the stomata are confined, sometimes also protected by

Fig. 4.4. Rolled leaf of *B. cappadocicus*. Numerous sclerenchymatous fibres are developed as supporting tissue. Mag. x41 (Accession number 15768)

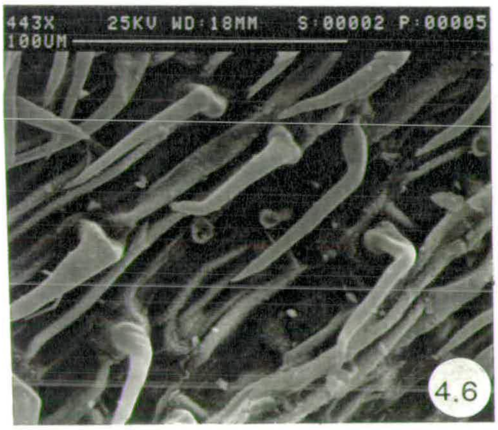
Fig. 4.5. Flat leaf in *B. ramosus*: the amount of sclerenchyma is reduced. Mag. x102 (Accession number 1684)

Fig. 4.6. Surface of the leaf in *B. tomentellus* with furrows where the stomata are located and protected by abundant hairs. (Accession number 19846)

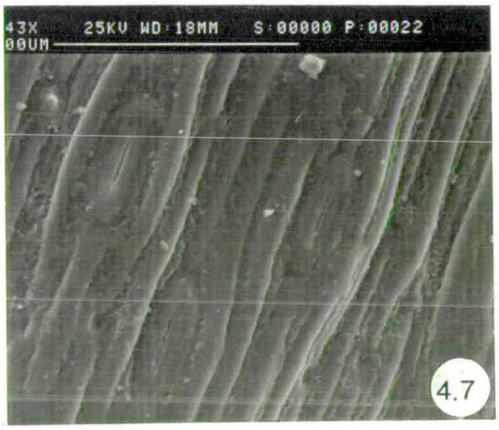
Fig. 4.7. Surface of the leaf in *B. riparius* showing stomata distributed along the epidermis. No furrows or hairs are present. (Accession number 22304)

4.4

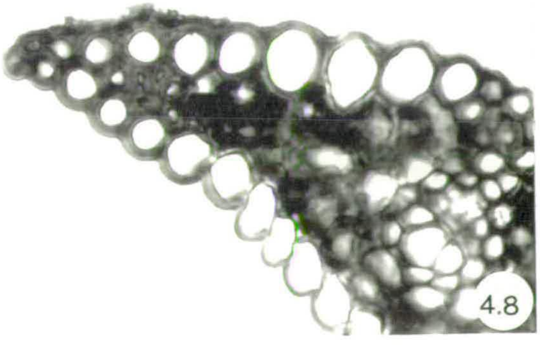
4.5


443X 25KV WD:18MM S:00002 P:00005
100UM

4.6


43X 25KV WD:18MM S:00000 P:00022
00UM

4.7



4.8

numerous hairs, although they also occur in the abaxial (lower) (fig. 4.6). Flat leaves present no corrugated adaxial surface, both surfaces being essentially similar. In these cases, stomata are located along the epidermis, lacking any special protection (figure 4.7). The above photographs were taken with the Scanning Electron Microscope. The methodology is explained in chapter 6, sect. 6.4.1.2.

Redmann (1985) carried out an investigation on different grasses from a range of ecological conditions. He summarised the relationship of leaf type to habitats as follows:

i) Flat, amphistomatous leaves (stomata on both surfaces) only in relative moist sites (e.g., *Bromus pumpellianus*, *Phragmites communis, Agropyron subsecundum*)

ii) Flat, epistomatous leaves (stomata on the upper surface) in moist, often shaded, forest edge habitats (e.g., *Bromus ciliatus, Elymus innovatus*).

iii) Rolling or folding amphistomatous leaves in relatively dry sites (e.g., *Poa arida, Calamagrostis montanensis*).

iv) Rolling or folding epistomatous leaves in relatively dry habitats (e.g., *Stipa comata, Oryzopsis pungens*).

v) Permanently rolled amphistomatous leaves in typical sand-dune habitats (e.g., *Oryzopsis hymenoides*).

vi) Permanently rolled epistomatous leaves in dry habitats (e.g., *Stipa richardsonii, Festuca scrabella*).

Stomatal occurrence on each side of the lamina was here analysed in a range of *Bromus* species from different habitats. These findings (table 4.2) are in line with the predictions of Redmann 1985 except as asterisked (*)

Table 4.2. Leaf characteristics of *Bromus* § *Pnigma* species from a range of different habitats.

Species	Accession n°	Mean and range of stomatal n° in adaxial transect (A)	Mean and range of stomatal n° in abaxial transect (B)	Ratio stomata A/B	Leaf type[1]	Habitat
B. ramosus	1684	10 (8-12)	1.25 (0-4)	8	Fe	Bank of rivers, woods, hedges and shady road sides
B. benekenii	1693	19.5 (15-23)	0.65 (0-2)	30	Fe	Woods and hedges
B. erectus	1711	12.75 (9-16)	2.65 (1-5)	4.81	Fa*	Meadows, dry grasslands and grassy slopes
B. tomentellus	19846	7.8 (4-11)	3.8 (2-7)	2.05	Fa*	Dry hills, rocky, sandy steppes and mountains
B. cappadocicus	15768	10.3 (8-12)	5.6 (3-7)	1.83	PRa	Dry hills, rocky, sandy steppes and mountains
B. inermis	1697	20.25 (16-23)	10 (8-12)	2.025	Fa*	Grassy meadows, dry slopes, alluvial soils

[1] Fe = Flat, epistomatous; Fa = Flat, amphistomatous; PRa = Permanently rolled or folded, amphistomatous

B. ramosus and *B. benekenii* exhibit flat leaves, clearly largely epistomatous (stomata on the upper surface). These occur in moist, often shaded, forest edge habitats. The high ratio for *B. benekenii* (A/B=30) could be attributed to only small problems with transpiration/water loss.

B. erectus has expanded leaves, amphistomatous (stomata on both surfaces) with shallow and narrow furrows. The stomata are located adaxially in the flanks of the furrows, in a more protected area, and abaxially along the epidermis. It grows in meadows, dry grassland and on grassy slopes, often on well drained chalk or limestone substrates.

An interesting comparison can be drawn between *B. tomentellus* and *B. cappadocicus*. Both taxa grow under quite similar ecological parameters: dry, windy and sunny spots where the water supply may be irregular; these outer factors favour very strong transpiration. Each one, differently and individually, seem to have evolved some adaptations to prevent the loss of water through this process. *B. tomentellus* presents flat leaves with stomata sunk on both epidermes and protected by abundant hairs (fig. 4.6). By contrast, *B. cappadocicus* exhibits rolling leaves, with stomata also distributed abaxially and adaxially. The amount of sclerenchyma tissue in *B. tomentellus* is scarcely notable when compared with *B. cappadocicus* where its mechanical role is obviously much more significant, in the water economy of the plant (fig. 4.4). More numerous vascular bundles enable the leaf to roll up perhaps for long periods, so reducing the area loosing water, while being mechanically resistant to bucking while in the rolled condition.

B. inermis exhibits expanded leaves, with numerous sclerenchymatous fibres along the leaf margin (fig. 4.8) and slight furrows adaxially; the stomata are found on both epidermes. It occurs in open, dry plains.

4.4 Conclusions

The characters observed in transverse sections of the lamina in several taxa of perennial *Bromus,* particularly the distribution of sclerenchyma and occurrence of stomata, all provided significant information. The former exhibits specific diagnostic value from the taxonomic standpoint between species, although the differences are more quantitative than qualitative. Its contribution as a mechanical tissue shows also some ecological interest. Sclerenchyma was observed in great amount in those grasses with rolling leaves, presumably adapted to areas where the windy and dry conditions exert strong influence. See chapter 9, section 9.3.3.2. for further discussion.

The distribution of stomata in relation to environment and shape of leaf shows some variations. A significant example is presented in two taxa, *B. cappadocicus* and *B. tomentellus.* Both exhibit an amphistomatous condition and grow in very similar habitats. This corroborates Parkhurst's statement (1978), that the character of having amphistomatous leaves is more frequent in both xeric and hydric habitats, thus disproving the old and equivocal assumption that under xeromorphic conditions, the stomata were considered to be confined to the upper surface only, hence enclosed during rolling (Warming 1909; Weaver & Clements 1929; McDougall 1949).

The provisional definition of four taxonomic groups (*B. ramosus* agg., *B. erectus* agg., *B. riparius* agg. and *B. inermis*) at the beginning of this study, according to their morphological, biological characters and apparent affinity are largely supported by the results obtained from this anatomical investigation.

The *B. ramosus* group has broad, flat leaves, with the stomata distributed on the upper surface along the epidermis; the amount of sclerenchyma is not strikingly significant. All these characteristics may well represent an adaptation with the habitat where the species occur, i.e., in moist, often shaded, forest margins.

In the *B. riparius* group is possible to draw two adaptive lines, both in concordance with their ecological distribution in dry hills, sandy steppes and mountains. *B. cappadocicus* has rolling leaves, with sclerenchyma well developed as a supporting tissue; stomata occur on both sides, although adaxially they are found in protected areas along very deep furrows. In *B. tomentellus* the sclerenchyma is less developed as are the furrows also, but the stomata are probably very much protected by numerous, long hairs.

B. inermis and *B. erectus* seem to occupy an intermediate position. Both present adaxial furrows, deeper in *B. erectus,* where they contain the stomata, and stomata also occur on the abaxial surface. The amount of sclerenchyma is not very significant, although in *B. inermis*, mechanical strength of leaf edge might present frictional damage from the leaves nearby, in this turf-forming grass. Both grow in meadows, dry grasslands and grassy slopes.

It must be stressed that we cannot explain all the features by relating them to outer factors, although some may be so explained, or at least understood, in this way. Others can be accidentally functional/non functional and they are outside the rationale of any particular adaptation-form connection. All characters are accidental in origin: if they persist they are either functional or selectively neutral. If apparently non-functional, it is of course possible that they once had a function, now not known.

Chapter 5 Cytological and Reproductive Studies

5.1 Cytological Studies

5.1.1 Introduction

The research carried out on a cytological basis for the perennial brome-grasses is discussed in this chapter as a compilation or review of the main research done on *Bromus* § *Pnigma* hitherto, rather than an emphasis on my own results, for the reasons to be explained later. The degree of similarity between two taxa in respect of the number, size, and morphology of their chromosomes along with other evidence - such as, external morphology, anatomy and histology - may provide meaningful information for the clarification of the phylogenetic relationship between them.

The genus *Bromus,* like the majority of festucoid grasses, has the basic haploid number $x = 7$ from which several polyploid series have derived (Avdulov 1931; Stebbins & Crampton 1961). Stebbins (1982) suggested that this number derived by dysploid increase from the basic number $x = 6$ which is believed to be the original basic number for the family Poaceae. This dysploid increase probably happened during the differentiation of the subfamily Festucoideae from other subfamilies. In the genus *Bromus* there is clear evidences supporting the number $x = 7$ as the basic number of the series; thus, it can be stated that the ancestral plants with $2n = 14$ have a ploidy of 2x.

The size of the chromosomes in *Bromus* varies from medium to large (Stebbins 1981). The smallest mean is present in sect. *Neobromus* (= subg. *Neobromus*) and sect. *Ceratochloa* (= subg. *Ceratochloa*) in comparison with species in sect. *Pnigma* (= subg. *Festucaria*) and sect. *Genea* (= subg. *Stenobromus*) which have the largest chromosomes. There is no published record of the chromosome size in sect. *Bromus*.

Particularly in sect. *Pnigma,* the length varies between species. Thus *B. inermis* presents the smallest chromosomes while diploid species from the New World have larger chromosomes (Stebbins 1981). *Pnigma* brome-grasses in Europe are characterised by a predominance of high levels of polyploidy, such as hexaploids, octoploids and decaploids, with few diploid taxa. The situation for their counterparts in the New World is quite the reverse. The American brome-grass flora is composed predominantly of diploids with a few tetraploids. Armstrong (1973, 1979, 1983, 1990) made some attempts to cross species of *Pnigma* from Europe with species from North America, and also between Eurasian species. Results are shown in table 5.1. The implication of this research involving taxa from both continents will be discussed closely in chapter 11, where the pattern of evolution for the whole group will be presented.

It has been observed in several cases that allopolyploids have smaller chromosomes and lower DNA content than expected (Darlington 1956; Martínez & Ginzo 1985; Bennett 1987; Poggio & Hunziker 1986; Poggio & Naranjo 1990) i.e., presuming that the allopolyploid DNA equals the sum of DNA from both parents added together. Studies carried out in S. American species of *Bromus* sect. *Pnigma* confirmed this observation on the variation of DNA content of polyploids in relation to the diploids (Naranjo et al. 1990). Two alternative interpretations have been offered to explain allopolyploid taxa having less DNA per basic genome than the ancestral parents. Either they once possessed lower DNA content (Darlington 1956), or saltatory changes occurred in the genome (DNA reduction) at the diploid or polyploid level (Grant 1987).

The number of chromosomes with nuclear organisers, identified as satellite chromosomes by several authors, has been reported in this group of grasses (Schulz-Schaeffer 1960; Kozuharov et al. 1981; Armstrong 1982).

Table 5.1. Chromosome number of hybrids between Eurasian species and between Old and New World species in *Bromus* section *Pnigma*.

Species	Chromosome number	Author
Eurasian × American		
4x ***B. benekenii*** × 8x ***B. pumpellianus***	42	Armstrong 1983
		"
American × Eurasian		"
4x ***B. pacificus*** × 4x ***B. benekenii***	28	"
" "× 10x ***B. riparius***	49	"
4x ***B. richardsonii*** × 4x ***B. benekenii***	28	"

Table 5.1 continued

Species	Chromosome number	Author
Eurasian × Eurasian		
B. riparius × ***B. inermis***	63	Schulz-Schaeffer 1960
4x ***B. erectus*** × 8x ***B. inermis***	41, 42	Armstrong 1973
4x ***B. erectus*** × 4x ***B. inermis***	28	Armstrong 1979
4x ***B. erectus*** × 8x ***B. inermis***	21	Armstrong 1979
4x ***B. benekenii*** × 8x ***B. inermis***	42	Armstrong 1983
" " × 4x ***B. inermis***	28	"
" " × 4x ***B. erectus***	28	"
" " × 10x ***B. riparius***	49	"
10x ***B. riparius*** × 8x ***B. inermis***	63	Armstrong 1990

Kozuharov et al. (1981) pointed out that the number varies between taxa at the same ploidy level, and so does not always correspond to the basic chromosome number.

Evolution in the genus seems to have involved polyploidy and hybridisation within and/or between the different sections (= subgenera), which has given rise to species with complex genomic constitutions (Stebbins 1981). An evaluation of the complexity of the *Pnigma* brome-grasses will be discussed in sect. 5.3.

5.1.2 Materials and Methods

Two sources of material were used in the cytological study, viz. root-tips and shoot meristems. Both came from living specimens growing in the greenhouse at the University of Edinburgh. The range of temperature was 15-30°C, the diurnal fluctuation varying with the time of the year. No artificial light was used. In the selection of taxa to study, I chose representatives of the four main groups, *B. ramosus, B. erectus, B. riparius* and *B. inermis,* but it was not possible to cover the whole range of putative species due to the lack of viable caryopses. The plants, when mature, were pressed, mounted and deposited in the Royal Botanic Garden Edinburgh (E). The investigation was carried out from July until the beginning of October.

Cytological research on *Bromus* may result in frustration; other researchers have experienced the same problem (Armstrong, pers. comm. 1989; Sales 1991). The chief obstacle lay in the difficulty to obtain good spreads, especially with highly polyploid taxa. For unknown reasons, the chromosomes tangled together, frustrating spreading and making counts uncertain and time consuming. *Bromus* chromosomes are simply very "difficult".

5.1.2.1 Root-tips

i) Germination

20-25 caryopses were germinated in Petri dishes with filter paper on the top and bottom lid. These were kept slightly damp and subjected to different combinations of light and temperature, in order to find the conditions maximising germination. These combinations were:

1) 13°C constant and darkness in a growth room. This is a warm summer night temperature in mid-temperate latitudes. It was used by Armstrong (pers. comm. 1989) and Sales (1991).
2) 13°C and continuous light.
3) Room temperature (± 24°C) and normal daylight and darkness.
4) 13°C in total darkness until germination started, then transfer to room temperature (± 24°C) and so to a normal cycle of light.

Initially, none of these conditions seemed to offer any positive result. The immediate problem to overcome was the failure of the seeds to germinate. The addition of gibberellic acid (0.05N) helped to take the seeds out of a dormancy stage and promote the beginning of the germination. Other researchers (Nakamura 1962) found an improvement in the germination of *Bromus* seeds when they were treated with gibberellic acid. Incorporating this dormancy-breaking factor in all trials, I found the fourth combination gave the best results. The degree of enhancement was reflected in a high proportion of germination (95%) compared with the initial low frequency of germination (10%) before treating the seeds with gibberellic acid. The other combinations did not reach an acceptable level of success. It seems as if the double treatment - lower temperature/gibberellic acid - enhances germination. Once germination started, the caryopses were transferred to pots in the green house. Thereafter, vigorously growing seedlings of approximately 14 cm height were taken out and their root tips cut to give a length of 1 cm (see later section for pre-treatment and staining methods).

The number of cells observed in division was generally very low. According to Armstrong (pers. comm. 1989), the times of the day when the numbers of divisions are at their highest are 9-10 a.m. and 3-4 p.m. He associated this observation with the fact that a cyclical pattern sometimes develops. Better results in the Edinburgh conditions came from sampling the material in the morning (9-10 a.m.). The weather seemed also to contribute to the variable incidence of cell divisions in these root tips. In my own observations, on sunny days the number of divisions was higher than on dark and wet days. In a further range of trials, with the continued aim of promoting further divisions, pots were transferred to the mist propagation unit in the greenhouse and left there for three days. This last treatment seemed to provide better results although it was still not totally satisfactory. The basis of the effect is not known and it does not seen to have been reported before. Throughout this work, the frequency of dividing cells remained less than I wished.

ii) Pre-treatment

Pre-treatment is very helpful for root tip mitoses, and with other meristematic tissues in plants (Dyer 1979). Tissues are pre-treated in various ways to stop divisions at metaphase, by inhibiting the further development of the spindle, resulting in an accumulation of divisions at metaphase with the chromosomes scattered through the cytoplasm. For this purpose, several chemical agents were tested and compared, adopting other researchers' treatments. Root-tips were placed in a vial containing one of the solutions. These are listed in table 5.2, which also shows the duration and conditions of each procedure. The best results were obtained with α-bromo-naphthalene at 2-4°C for 24 hours, although even then the results were not entirely satisfactory.

Table 5.2. List of chemical agents used for the pre-treatment of root tips in cytological studies. The range of t° and duration of the treatment is specified in each case.

Reagent	Concentration	Time	Temperature
Colchicine	0.05%	4 h, 6 h, 24 h	22-24 °C
		4 h, 6 h, 24 h	2-4 °C
Cold pre-treatment		16-24 h	2-4 °C
8-hydroxy quinoline	0.002 M	4 h, 6 h, 24 h	22-24 °C
		4 h, 6 h, 24 h	2-4 °C
α-bromo naphthalene		4 h, 6 h, 24 h	22-24 °C
		4 h, 6 h, 24 h	2-4 °C
p-dichloro benzene		4 h, 6 h, 24 h	22-24 °C
		4 h, 6 h, 24 h	2-4 °C

Nevertheless, I observed that a long, cold pre-treatment favours a higher degree of condensation of the chromosomes, an effect quite vital for successful later spreading, particularly when chromosomes exhibit such long arms as in these perennial brome-grasses.

iii) Fixation

The purposes of fixation are:

- to coagulate the constituents of the cell without disturbance of their structure - in effect to kill the cell with the smallest possible sign of death.
- to provide conditions that may intensify the subsequent staining process.

The fixative used in this study was Carnoy's fixative II (ethanol: acetic acid: chloroform, 6: 3: 1), as found to be the most widely used by other researchers. The root-tips were transferred to a vial and left for at least one hour at room temperature.

iv) Hydrolysis /Maceration

When the Feulgen technique is used for staining the tissues, it is necessary to hydrolyse the material. This exposes the aldehyde groups of the nucleic acid which will react with the leuco-basic fuchsin of the Schiff's reagent (Sigma, S5133). The result is a violet colouration specific for DNA and thus for the chromosomes. Further, the hydrolysis softens or even macerates the tissues, making squashing easier. Material to be hydrolysed was placed, after fixation, in a vial containing 5N HCl for 30 minutes. An alternative was to use 1N HCl, placing the hydrolysis vial in a water bath at 60°C for 12 minutes. I opted for the first procedure; it was less hazardous, not involving the manipulation of hot acid, and worked equally well.

v) Enzymatic Treatment

Enzymatic treatment is a further means of promoting successful tissue squashes. The best results were obtained with equal proportions of Cellulase 4% (BDH, 39074/2C) and Pectinase 4% (Sigma, 2401). Pectinase attacks the middle lamella, so promoting cell separation. Cellulase attacks cellulose and promotes cell flatness after squashing. The material was left in the enzymatic mixture for 10-15 minutes. It was found that after longer periods of treatment, e.g., 1/2 hour, excessive disintegration of the tissues became apparent due to a considerable fragility of the material.

vi) Squashing

A root tip approximately 2 mm long was cut off from the fixed, hydrolysed root and the rest was discarded. The tip was placed on the middle of a microscope slide in a large drop of acetic acid (45%). The slide was transferred onto a sheet of white filter paper to make the tip more easily visible. With the help of a brass rod, the tissue was gently tapped until eventually macerated and the cells had spread into a single layer. Then a coverslip was put on it and the gentle pressure from its weight spread the cells further. A layer of filter paper was put on top of the coverslip and gently pressed. This had the aim of pushing all the cells into more or less the same focal plane, spreading them further and spreading out any metaphase figures. The paper also sucks up the excess of acetic acid from the edge of the coverslip.

I did not make permanent preparations. Instead, I opted for an alternative system, photographing the material immediately after the counting and discarding the slide once the process was finished. In retrospect, this was an error because no photographic record of the cytological study is now available, due to a failure in the microscope used to photograph the evidence. This was a considerable calamity in my work. It was subsequently found when they were sent to the laboratory to be processed that the films had not been exposed to the light. Because of restricted availability of time, it was not feasible to repeat all the counts. As mentioned in the introduction, chromosome numbers from my own research are therefore not accompanied by the relevant photographic records. Thus it was not possible to analyse the complete karyotype - size and morphology of the chromosomes - for the taxa studied. This is unfortunate because my eventual preparations, using the finally selected method, were good.

Slides prepared with the squash method can be studied under the microscope without additional treatment. If at any time I decided to store them for a further observation, I kept them in the fridge, sealed around the cover-slip edges with nail varnish. In this way, the preparation lasted for a couple of days although progressively tended to spoil through evaporation. The only effective procedure to maintain cytological material indefinitely is through an adequate and permanent technique which, with some chagrin, I strongly recommend for an accurate study of the karyotype.

5.1.2.2 Shoot Meristem

Observations on somatic chromosomes were also made from young shoot tissues. The technique adapted from Ali Önder (1978) is now described. The lowest node on the shoot base, just above the soil level was identified. In *Bromus* this young node is a purplish-red colour and the section approximately 1 cm above it is white. A portion of the shoot above this node, approximately 2 cm long, was excised in order to have a reasonably convenient length of shoot to handle easily throughout the subsequent process (fig. 5.1). The lower part, including roots, was removed by an oblique cut on or immediately below the node (see figs. 5.1.a-5.1.b). This cut permits contact of the cells of the inner meristematic region with the pre-treatment chemical. Then several layers of outer leaves of the shoot were removed (fig. 5.1.c) until the very delicate

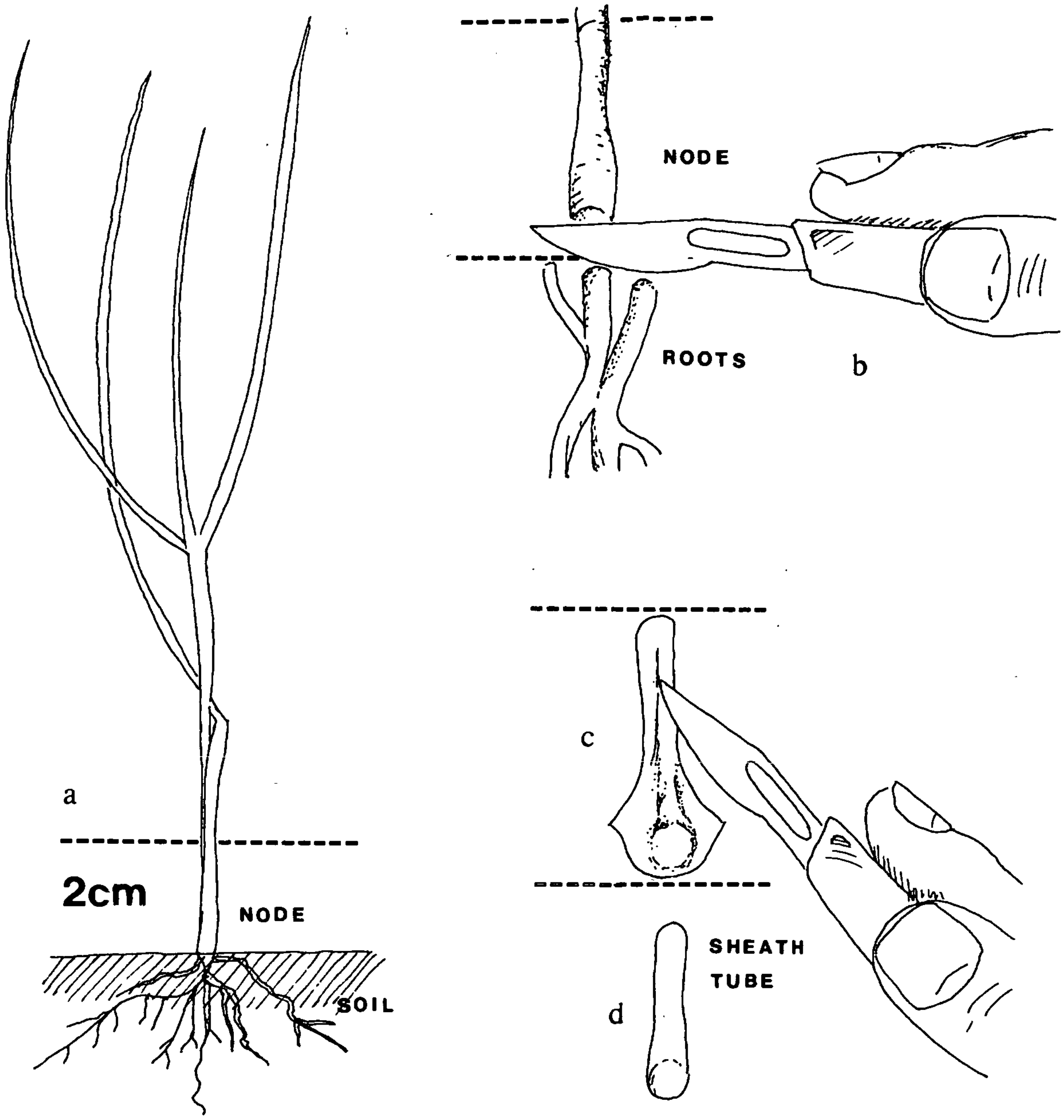


Fig. 5.1. Shoot meristem.

Figs. 5.1.a-5.1.b. Selection of the lower part of the shoot for further examination.

Fig. 5.1.c. Removal of the outer leaves of the shoot.

Fig. 5.1.d. The "sheath tube" ready for treatment.

"sheath tube" is exposed (fig. 5.1.d). Though "sheath tube" is Ali Önder's term, in fact the material is the young stem (stem in a very juvenile state).

The whole process was carried out with the aid of a dissecting microscope. After following the surgical exposure and detachment of "sheath tubes" described above, specimens were pre-treated, fixed, macerated and squashed according to the technique described before. Ali Önder (1978) based his research on *Festuca ovina* (Gramineae). Unfortunately, my own results were not satisfactory at all. For unknown reasons, the chromosomes showed distortions. These distortions were that the chromosomes were often broken, and figures were insufficiently intact for study. I also found that the arms sometimes showed local swellings. For this reason, all the effective study was carried out using root-tips. It was more economical in plant material.

5.1.3 Results

A great amount of literature exists on the past research done on the cytology of *Bromus*. Chromosome counts for relevant species of section *Pnigma* in chronological order, obtained by diverse authors, are shown in table 5.3. Most of the counts seem to be similar, although great caution must be exercised in the interpretation of this data, especially in those situations where the citation of the voucher specimens has been omitted. The taxa studied may often have been wrongly identified, especially in this crucial group, as I have observed myself in particular situations. My own data are shown in table 5.4.

Table 5.3. Compilation of the main research done on the cytology of *Bromus* § *Pnigma*. Results are presented in chronological order for each cytotype.

Species	Chromosome number (2n)	Country of material origin	Author
B. ramosus	14	Unknown	Stälin 1929
	28	Unknown	Kozuharov & Petrova 1976 (in Majovsky et al. 1970 *)
	"	Bulgaria	Kozuharov et al. 1981
	"	Holland	Armstrong 1984
	42	Unpublished	Stebbins in Löve & Löve 1961
	"	Czechoslovakia	Hindakova 1978
	"	Bulgaria	Kozuharov et al. 1981
	56	Spain	LLoret & Cardona 1988
Bromopsis ramosa subsp. ***ramosa***	42	Former U.S.S.R.	Sokolvoskaya & Probatova 1979
Bromus benekenii	28	Unknown	Polya 1950
	"	.Czechoslovakia	Petrova in Prokudin et al. 1977
	"	Former U.S.S.R	Hindakova in Majovsky et al.1978
		Greece	Strid & Franzen 1981
	"	Bulgaria	Kozuharov et al. 1981

Bromus benekenii	28	Czechoslovakia, Germany	Armstrong 1983
	"	Poland	Pogan et al. 1985
	"	Former U.S.S.R.	Armstrong 1987
		Poland	Pogan & Wcislo 1990
B. ramosus subsp. ***benekenii***	28	Czechoslovakia	Hindakova in Majovsky et al. 1970
Bromopsis benekenii	28	Former U.S.S.R.	Roos 1975
B. ramosa subsp. ***benekenii***	28	Former U.S.S.R.	Sokolvoskaya & Probatova 1979
B. erectus	28	Hungary	Armstrong 1973
	"	Czechoslovakia	Hindakova in Majovsky et al. 1974
	"	Hungary, Germany	Armstrong 1983
	42	Unknown	Avdulov 1931
	"	Turkey	Hill 1965
	"	Spain	Lloret & Cardona 1988
	42 + 8	Unknown	Schulz-Schaeffer 1956
	56	Unknown	Kattermann 1931 (in *)
	"	Finland	Schulz-Schaeffer 1960
	"	Unknown	Hanna 1961

B. erectus	56	Iran	Hill 1965
		Czechoslovakia	Hindakova in Majovsky et al. 1974
	"	Unknown	Kozuharov & Petrova 1976 (in *)
	"	France	Natarajan 1977
	"	France	Natarajan 1978
	"	Unknown	Buttler 1985
	"	Spain	LLoret & Cardona 1988
	59	Unknown	Hanna 1961
	65	Unknown	Hanna 1961
	70	Unknown	Hanna 1961
	"	Afghanistan	Hill 1965
	"	Bulgaria	Kozuharov et al. 1981
B. erectus subsp. ***erectus***	42	France	Verlaque & Vignal 1993
	56	France	Verlaque & Vignal 1993
	70	France	Verlaque & Vignal 1993
B. erectus var. ***eu-erectus***	56	Unknown	Avdulov 1931
Bromopsis erecta	42	Former U.S.S.R.	Slyusarenko in Prokudin 1977

Bromopsis erecta	56	Former U.S.S.R.	Roos 1975
Bromus erectus subsp. ***pannonicus***	28	Hungary	Baksay 1956
B. pannonicus subsp. ***monocladus***	28	Czechoslovakia	Hindakova in Majovsky et al. 1970
	"	France	Chas & Kerguelen1992
B. monoclados subsp. ***monoclados***	28	Hungary	Baksay 1956
B. monoclados subsp. ***pannonicus***	28	Hungary	Baksay 1956
B. moellendorffianus	14	Bulgaria	Petrova et al. 1993
B. erectus subsp. ***transsilvanicus***	56	Bulgaria	S.Z.-Borsos 1971
B. transsilvanicus	28	Unknown	Kozuharov & Petrova 1976 (in *)
	56	Hungary	Schulz- Schaeffer 1960
B. inermis	28	Unknown	Elliott 1949
	"	Unknown	Hill & Carnahan 1957
	"	Former U.S.S.R.	Armstrong 1983
	"	Former U.S.S.R.	Armstrong 1987
	42	U.S.A.	Knobloch 1943
	"	Spain	LLoret & Cardona 1988
	54	Unknown	Hanna 1961

B. inermis	56	U.S.A.	Nielsen 1939
	"	U.S.A.	Knobloch 1943
	"	U.S.A.	Elliot 1949
	"	Unknown	Schulz-Schaeffer & Makarian 1957
	"	Germany	Schulz-Schaeffer 1960
	"	Unknown	Hanna 1961
	"	Poland and Rumania	Rychlewski 1970
	"	Bulgaria	Kozuharov et al. 1981
	"	Cultivars Tempo, Baylor	Armstrong 1983
	"	Former U.S.S.R.	Armstrong 1987
	"	Cutivar Saratoga	Armstrong 1990
	"	Poland	Pogan & Wcislo 1990
	70	U.S.A.	Nielsen 1939
Bromopsis inermis	28	Former U.S.S.R.	Roos 1975
	56	Former U.S.S.R.	Sokolvoskaya & Probatova 1967
	"	Former U.S.S.R.	Roos 1975
	"	Former U.S.S.R.	Petrova in Prokudin et al. 1977

Bromus inermis subsp. ***inermis***	56	Canada	Bowden 1960
B. riparius	69	Former U.S.S.R.	Armstrong 1983
	70	Former U.S.S.R.	Elliott 1949
	"	Former U.S.S.R.	Schulz-Schaeffer 1960
	"	Former U.S.S.R.	Armstrong 1984
	"	Russian cultivar Krasnodar	Armstrong 1990
	70 + 1	Bulgaria	Kozuharov et al. 1981
	70 + 4	Bulagaria	Kozuharov et al. 1981
	70 + 6	Bulgaria	Kozuharov et al. 1981
Bromopsis riparia	56	Former U.S.S.R.	Petrova in Prokudin et al. 1977
	"	Former U.S.S.R.	Slyusarenko in Prokudin et al. 1977
	70	Former U.S.S.R.	Roos 1975
Bromus fibrosus	14	Unknown	Kozuharov & Petrova 1976 (in *)
	59	Unknown	Kozuharov & Petrova 1976 (in *)
	70	Unknown	Kozuharov & Petrova 1976 (in *)
B. cappadocicus	28 + 2	Unknown	Schulz-Schaeffer 1956
	42	Unknown	Stälin 1929

B. cappadocicus	56	Unknown	Schulz-Schaeffer & Makarian 1957
	"	Grecee	Strid 1983
B. cappadocicus subsp. ***lacmonicus***	42	Greece	Strid & Franzen 1981
B. lacmonicus	56, 56+ 3	Bulgaria	Kozuharov et al. 1981
Bromopsis cappadocica	14	Former U.S.S.R.	Petrova in Prokudin et al. 1981
	"	Former U.S.S.R.	Slyusarenko in Prokudin et al 1981
B. barcensis	14	Unknown	Kozuharov & Petrova 1976
	28	Bulgaria	Kozuharov et al. 1981
B. macedonicus	70, 70 + 1	Bulgaria	Kozuharov et al. 1981
B. moesiacus	14	Bulgaria	Petrova et al. 1993
B. orbelicus	70	Bulgaria	Kozuharov et al. 1981
B. parilicus	14	Bulgaria	Kozuharov et al. 1981
B. tomentellus	14	Turkey	Petrova et al. 1993
	28	Former U.S.S.R.	Schulz-Schaeffer 1960

Table 5.4. Results of my own cytological research on Eurasian *Bromus* section *Pnigma.*

Species	Accession number	Voucher specimen	Country	Chromosome number
B. benekenii	1692	(E)	Germany	28
	1693	(E)	Germany	28
	1734	(E)	U.S.S.R.	42
B. erectus	1744	(E)	Spain	42
	1745	(E)	Yugoslavia	56
	1798	(E)	U.S.S.R.	68
B. inermis	1743	(E)	France	56
	1730	(E)	Czechoslovakia	49
	1768	(E)	U.S.S.R.	56
B. riparius	1748	(E)	Germany	63
	1748	(E)	Germany	66
	1773	(E)	U.S.S.R.	70
	1770	(E)	U.S.S.R.	69

5.1.4 Discussion of Cytological Results

The inferred ploidy for my results agrees mostly with the research done by previous authors. There is however evidence of occasional aneuploidy in my data which seems to have occurred in three different specimens, either by gain or loss of chromosomes, *B. riparius* (1748), 2n = 66 (= 9x + 3?), *B. erectus* (1798), 2n = 68 (= 10x - 2?) and *B. riparius* (1770), 2n = 69 (= 10x - 1?).

Polyploids are generally more tolerant of aneuploidy than are diploids (Dyer, pers. comm.) - based largely on the literature on wheat aneuploids.

It is interesting to point out the fact that in *B. erectus* (1748), two plants from the same pot were recorded having different chromosome number, 63 and 66. There are some cases in the literature where aneuploid individuals have also been reported from the same population, e.g., *B. lacmonicus* 2n = 56, 56 + 3 (Kozuharov et al. 1981), 4x *B. erectus* × 8x *B. inermis* 2n = 41, 42 (Armstrong 1973).

5.2 Reproductive Studies

5.2.1 Introduction

I attempted crosses of living material as soon as I had them established in the greenhouse. These crosses (in my final year of work) have been available, in robust growing form, for too short a time for the necessary cytological examinations. Nevertheless the plants exist, and I discuss them here.

5.2.2 Material and Methods

The material used for this study was living perennial brome-grasses growing in the greenhouse. In all the crosses the genotypes belonged to different populations.

For the crossing purpose, I partially adopted the technique of Beddows & Davis (1938), quite old but very simple and well described. Pollinations were done at random, using the plants which were in flower at that particular time. The most appropriate hours were early in the morning, between 8 to 10 a.m., when the florets had just opened with the anthers hanging out. It is important to carry out the emasculation when the anthers are still immature, showing a bright yellow colour. If the process is done when they are fully mature, there is a chance of breaking them with the consequence of possible self-pollination. If there was a risk of the latter as the result of faulty removal, the floret was discarded. One should not penetrate too far down into the base of the floret because of the risk of damaging the stigmas. The florets were done in sequence from the uppermost to the lowest.

Two methods were used: manual and so-called "automatic pollination".

Manual pollination

The pollen from the parental spikelet was collected on a piece of glossy, dark paper. The smooth surface makes the pollen more visible and facilitates transfer on to the stigmas. A small artist's paint brush was used to transfer the pollen. After using the brush, it was dipped in 90% alcohol to kill the remaining pollen and ensure fairly rapid drying. Each fresh lot of pollen needs a clean brush. The inflorescence that had been emasculated was covered with a bag made out of lens tissue. A bamboo cane of suitable length was inserted near the selected inflorescence, acting as a support for the bag. The edges of the lens tissue were sealed with staples. Each bag was numbered. The process of pollination was repeated over 2-3 days to ensure the maximum frequency of fertilisation.

"Automatic pollination"

The arrangements were similar to the manual process, except that the pollen was not collected. The emasculation was done as described above. Both spikelets, the donor of pollen and the one which had been emasculated, were covered under the same bag.

Two bamboo canes inserted in the respective pots helped to hold the bag on each side. It was customary to shake all paired units during or soon after the anther dehiscence to ensure pollen dispersal. The advantage of automatic pollination is that it avoids the time-consuming hand-pollination. The drawbacks of this method are that its accuracy depends on perfect emasculation and that it is not possible to notice errors as in the case of hand pollination units which are opened each day.

5.2.3 Results

Twelve crosses were carried out; only seven produced seeds. These were grown and four produced mature plants. The crossing results are shown in table 5.5.

5.2.4 Discussion of Reproductive Studies

For the interpretation of the rate of success/failure of the different crosses it is important to take into account the differences in the methodology used.

B. inermis × *B. inermis*

Five attempts to cross different specimens of *B. inermis* were made. One cross succeeded well, producing 21 seeds, the rest failed or produced only one seed which never developed into a mature plant. The successful cross was the result of automatic pollination. The achievement of adult plants demonstrates that in this case the method was satisfactory and there exists no genetic incompatibility between the genotypes. In the second and third crosses, hand pollination was carried out and no seeds were formed, indicating either a possible ineffectiveness in the method, or genetic incompatibility. The fourth and fifth crosses were also done by hand pollination. Although 2 seeds were produced, one in each case, they never reached an adult form, which possibly shows that genetic incompatibility exists between these genotypes.

Table 5.5. Crossing results between Eurasian species of *Bromus* section *Pnigma* (Accession numbers in brackets).

Cross	Method	Florets pollinated	Mature seeds	Adult plant
1) ***B. inermis*** (1054) × ***B. inermis*** (1730)	"Automatic pollination"	25	21	Yes
2) ***B. inermis*** (1755) × ***B. inermis*** (1364)	Manual pollination	12	0	No
3) ***B. inermis*** (1755) × ***B. inermis*** (1735)	"	22	0	No
4) ***B. inermis*** (1755) × ***B. inermis*** (1764)	"	17	1	No
5) ***B. inermis*** (1755) × ***B. inermis*** (1735)	"	31	1	No
6) ***B. riparius*** (1766) × ***B. inermis*** (1743)	"	25	2	Yes
7) ***B. riparius*** (1766) × ***B. inermis*** (1764)	"	39	2	No

Table 5.5 continued

Cross	Method	Florets pollinated	Mature seeds	Adult plant
8) ***B. inermis*** (1768) × ***B. riparius*** (1766)	Manual pollination	25	2	Yes
9) ***B. inermis*** (1735) × ***B. riparius*** (1748)	"	36	0	No
10) ***B. inermis*** (1735) × ***B. erectus*** (1746)	"	43	0	No
11) ***B. erectus*** (1746) × ***B. inermis*** (1768)	"	13	10	Yes
12) ***B. inermis*** (1735) × ***B. variegatus*** (1789)	"	26	0	No

The facts that *B. inermis* (1755) was used in the four trials, and that in spite of a high number of flowers being pollinated, only two seeds were formed, might indicate that this species is infertile.

B. riparius × *B. inermis*

Hand pollination was carried out and in both cases seeds were produced. In the first cross the seeds grew to maturity, but in the second cross failed to develop further. This may indicate genetic incompatibility in the latter. In the case of cross 7, neither parent is of known chromosome number. Table 5.3 reveals considerable reported variation of somatic numbers in both species. Failure to form adult plants may result from chromosomal disturbances.

B. inermis × *B. riparius*

Although both crosses were done by hand pollination, only the first one succeeded, forming two seeds which grew to maturity. This could be explained by a genetic compatibility between the genotypes in the former and a failure in the method used or genetic incompatibility (note the unusual non-euploid chromosome number in *B. inermis* (1748) table 5.4)) in the latter.

B. inermis × *B. erectus*

No seeds were formed. The failure may be related to the method carried out (hand pollination) or genetic incompatibility between these two genotypes. Further, the maternal species *B. inermis* (1735) is involved as a male parent in the unsuccessful crosses 3 and 5 (table 5.5). It may be infertile for some unknown reason.

B. erectus × *B. inermis*

Ten seeds were collected and grown into maturity. This rate of success could be achieved through the association of two factors, effectiveness in the hand pollination and the absence of genetic incompatibility. Both crosses involving *B. inermis* (1768) (8 and 11) successfully produced adult plants, and it has a known euploid somatic number (table 5.4).

B. inermis × *B. variegatus*

Either or both, failure in the method and genetic incompatibility, prevents the development of seeds. *B. inermis* (1735) was the only available female parent: as in other tests, it is again here involved in a reproductive failure.

As observed above, sometimes the use of hand pollination could explain the lack of seeds (i.e., crosses 9 and 10), possibly because of damage to the stigmas when brushing them with pollen. Perhaps the lower amount of manipulation in automatic pollination better preserves the integrity of the reproductive apparatus. A second important factor might be parental genetic incompatibility, i.e., crosses 4 and 5. Some crosses, i.e., 1 and 6, form seeds which grow into adult plants. However without further information, which is not available, such seeds might result from agamospermy or accidental selfing. Morphology of the plants when full grown needs to be inspected for maternal similarity, to indicate such possibilities. Failure to produce seeds, in this relatively small trial does not necessarily means genetic incompatibility between parents; one or other parent or both may be partially or wholly infertile or stigmas and pollen may have been incompletely developed, or even these particular parents may have been incomplete interfertile but be exceptions. The present contribution does not provide any definitive knowledge of possible hybridity or incompatibility. A longer study is necessary.

The effect of hand pollination *versus* automatic pollination is unknown. More research should is needed to be able to establish any kind of correlation.

5.3 General Discussion

In sect. *Pnigma*, diploids and polyploids are very similar in external morphology. Simultaneously, different levels of polyploidy have been recorded within the same taxon (see table 5.3). In general an increase in polyploid level coincides with a decrease in fertility (Fukuda 1967; Asay & Dewey 1976) and in some species this is accompanied by an increase in vegetative vigour (Jones & Carroll 1962; Rowe 1967; Dewey 1979). It would be of great interest in a further study to analyse and compare diverse cytotypes reported in any of the rhizomatous perennial brome-grasses and observe if cytotypes with a lower level of ploidy are predominantly sexually reproducing, whereas those with higher polyploidy exhibit more vigorous vegetative propagation - as it has been reported in *Agrostis stolonifera* (Björkman 1954). The distribution of different cytotypes might also be related to the level of disturbance of the habitat (Kik et al. 1992). If results obtained correlated with all the factors mentioned, this would contribute enormously to the understanding of the pattern of adaptive radiation presented in the group. Unfortunately, from my reviews of the literature, material of known cytotypes is rarely kept for subsequent biological investigation. Too often, the somatic number was the only goal.

As mentioned in the introduction, the chromosome length varies between species. I observed that the chromosome length of *B. ramosus* and *B. benekenii* is considerably greater than in the rest of the taxa studied. These results agree with Armstrong's evidence (1983) for the same group. He suggested the subdivision of sect. *Pnigma* into two groups of species which can be separated on the basis of chromosome and satellite size. He carried out some crosses (table 5.1) and the results obtained led him to these conclusions: the larger satellite contributed by the male parent in these crosses could be identified in the F_1 hybrids; the longest chromosomes of *B. benekenii* were longer than the longest chromosomes of *B. inermis*, *B. pumpellianus*, *B. erectus*, *B. variegatus* and *B. riparius*. He observed that all American species studied to date, except *B. pumpellianus,* have been shown to possess only pinhead (small) satellites (Wilton 1965; Armstrong 1981). In Europe, *B. benekenii* and *B. ramosus* are the only species known to have pinhead satellites. Armstrong (1983) suggested that the *B. benekenii - B. ramosus* complex may be related to the North-American diploid-tetraploid group. Another line of evidence lies in the fact that the chromosomes of *B. benekenii* and some American species are similar in length, while the remainder of European species studied present smaller chromosomes.

Armstrong suggested dividing sect. *Pnigma s.lat.* into two sections corresponding to two evolutionary lines, based on the morphology of the chromosomes only:

- sect. *Bromopsis* Dumort. characterised by a strong interspecific sterility, low levels of polyploidy, including the European species with larger chromosomes, small satellites (*B. benekenii* and *B. ramosus*), and the American species except *B. pumpellianus.*
- sect. *Pnigma* Dumort. *s.s.* containing the European species which possess smaller chromosomes, big satellites and exhibit higher level of polyploidy, and the North-American *B. pumpellianus.*

I agree with the two evolutionary pathways suggested by Armstrong. However, I do not support the attempt to group the taxa in two different sections based only on cytological observations and ignoring other important features, such as the external morphology, ecological affinities and geographic distribution. For this reason I believe they should remain in sect. *Pnigma.* More evidence from other sources is needed, particularly chloroplast DNA restriction-site variation. It has been very useful in inferring phylogenetic relationships in other polyploid complexes (chapter 11, sect. 11.2). In addition studies of isozyme variation patterns are required. Many more species should be studied before definite conclusions and possible subdivisions of the section can be drawn. There are too few substantial phenetic differences between the taxa to warrant sectional distinction. I regard these two groups of species as simply that - "species groups".

The Eurasian species, except for the complex *B. ramosus - B. benekenii*, are characterised by their allogamy (self-incompatibility) and interfecundity. They differ clearly from the rest of *Bromus* here studied which is autogamous and intersterile (Armstrong, loc. cit.; Stebbins 1981; McKone 1985; Sitjas 1989). From personal observations in the greenhouse and outdoors, I conclude that the complex *B. ramosus -B. benekenii* is autogamous (self-compatible), reflected in their spikelets carrying successfully numerous caryopses (98% success). By contrast, specimens of *B. riparius, B. erectus* and *B. inermis,* the rate of fertility was extraordinarily low, with most of the spikelets empty of seeds (3-5% success), which agrees with their status as an allogamous (self-incompatible) group.

A question which can be posed is what is the significance of experimental hybrids if the same species are not interfertile in nature. According to Armstrong (1977, 1983, 1984), the genomic homology seems to be very important between different taxa in this group, with an intricate differentiation (1981, 1987), and it seems to be almost absent in other *Bromus*. Another answer to the problem lies in their strong geographic differentiation. In contrast to the autogamous, sympatric § *Bromus* taxa, the allogamous taxa of *Pnigma* have an allopatric distribution (Kozuharov et al. 1981); this restricts considerably the possibility of interspecific hybridisation *in situ* and so replaces their weak genetic barriers of isolation (lost maybe with polyploidy) (Verlaque & Vignal 1993). Some reproductive barriers have been reported, e.g., in *B. inermis* the opening of flowers is in the morning from 7.00-10.00 h, while in *B. erectus* and *B. riparius* it occurs from 15.00-20.00 h (Sitjas 1989). The experimental crosses carried out in the greenhouse do no support such observations. Flowering periods were all similar (early morning), in all species grown. In nature, hybrids do not seem to have been detected or at least reported in the literature. Perhaps they have just been overlooked: in a critical group this is possible.

In perennial herbs there is a correlation between the potential for vegetative reproduction, in particular by rhizomes or stolons, and high rates of polyploidy. This correlation is evident in the family Gramineae (Stebbins 1971). As observed in the literature, the aggressive rhizomatous *B. inermis* and the less creeping but rhizomatous *B. riparius*, both exhibit a high polyploid level, $2n = 8x$ and $2n = 8x$, $10x$ respectively. Brilliantly discussed by Stebbins (1971), polyploids in their initial stages depend upon favourable conditions for their survival and perpetuation but once they have become successful, they are more competitive and aggressive than related diploids. Initially most polyploids, in particular those which have irregular meiosis, must pass through a "bottle-neck" of semi-sterility. They will be more capable of confronting this situation if they are long-lived perennials instead of short-lived annuals. This circumstance will be positively reinforced if they can spread vigorously by means of rhizomes and stolons. Given the long duration of the individuals, there is a longer period over which the generation of more fertile offspring, which would be automatically selected, can take place.

All the cytological research done to date contributes to an understanding of the evolutionary relationship pattern between the perennial brome-grasses, which slowly begins to take shape. However much more work must be done to achieve a final clarification of the complicated network which seems to have operated in this group. It would seem that only some of the Eurasian germ-plasm has so far penetrated the New World, there diversifying (chapter 11, sect. 11.3.2).

Chapter 6 An investigation of the Sheath Characters

6.1 Introduction

There is no great difference in the reproductive morphology of the *B. erectus* group when compared with *B. ramosus* or the complex around *B. riparius*. Fundamental form is similar. All three groups contain species with loose panicles and species with congested panicles. There is also broad similarity in the photosynthetic surfaces although leaf-blades may be broad to narrow to varying degree in all three groups. The differences between the groups which seem most marked are those connected with the anchorage to the substrate and with survival/perennation capacity. Sometimes some of these features are undervalued by taxonomists because they are "merely" vegetative or are poorly presented in badly collected specimens (chapter 8). Yet these characters may be the most important in the resolution of these taxa by Natural Selection, and therefore they may help us to understand adaptive radiation in the group as a whole (see chapter 11 for further discussion). I term this type of character **Pivotal**. They may be, if truly and significantly adaptive, the clues to the diversification achieved at pivotal times of evolution. Perhaps they may show us, at periods of change when taxa originate or become extinct, adapting to this niche or another niche, how the balance of advantage swings one way rather than another. Therefore, it is logical to examine possible pivotal characters, those at least that are manifested to us, and to consider very closely if and how their form may be related to function and habitat.

6.2 Structural Differences in Three Groups

The anchorage and survival/perennation features referred to above comprise first, the nature of the habit exhibited and second the nature of the accumulation of dead sheath material around the bottom of the emergent stems. These sheaths differ between different groups of brome-grasses. In the present study, taxa are caespitose or tufted, shortly rhizomatous or extensively rhizomatous. In terms of sheath form they have dead sheaths which are, on one hand, intact, or broken up somewhat but into parallel fibres or, on the other hand, decay into a network of reticulating fibres. Table 6.1 shows how taxa can be arranged according these sheath and anchorage features. In several European keys the sheath morphology has been used by different authors as the main feature to split up *Bromus* § *Pnigma* into different groups (Hayek 1933; Nevskii & Sochava 1963; Smith 1980), although no further study referred to the possible connection between the form and function in these three types of sheath has been carried out.

Caespitose *versus* rhizomatous habits present clearly different attributes when vegetative propagation is considered. The former grow by seed that when established, form tufts which grow expanding radially and they may eventually fuse together to the eye, but which corresponds to a mosaic of separate genotypes. Sometimes densely tufted or mat forming areas may decrease in size, either locally or temporally; thus, they will start degenerating centrally leaving the way open for other plants to grow (Rodwell 1992). This may be due to nutrient starvation or to autotoxicity. Benedict (1941) studied the reasons for the natural thinning of *B. inermis* and established that a toxic substance was produced by the roots of this species, reducing seedling growth. Rhizomatous grasses on the other hand form large areas of turf (= sod), genetically uniform, and one or few genotypes can spread very aggressively into any territory locally available without waiting for a complete sexual cycle. They have been deliberately introduced in many areas because their value in land reclamation and coastal defence (Raybould et al. 1991), where they can stabilise sandy substrates. The age of some rhizomatous extensions in *Festuca* has been estimated at 850 years (Harberd 1961). They are now up to 240 yards in diameter. Resistant to grazing, they present a quick system for repairing trampling damage.

Table 6.1. Grouping of the perennial brome-grasses on the basis of the sheath decay, anchorage system and the type of habitat (M= Moist; S= Shaded; E= Exposed)

Sheath type	Anchorage system	
	Rhizomatous	Densely or loosely tufted, sometimes with tufts connected by very short rhizomes
Intact or partially breaking into parallel fibres	***B. inermis*** (E) ***B. caprinus*** (E) ***B. condensatus*** subsp. ***moellendorffianus*** (E) ***B condensatus*** subsp. ***condensatus*** (E) ***B. condensatus*** subsp. ***microtrichus*** (E) ***B. pannonicus*** subsp. ***pannonicus*** (E) ***B. pannonicus*** subsp. ***vernalis*** (E) ***B. pannonicus*** subsp. ***monocladus*** (E) ***B. erectus*** subsp. ***aurouzensis*** (E) ***B. erectus*** subsp. ***montenegrinus*** (E)	***B. ramosus*** subsp. ***ramosus*** (M, S) ***B. ramosus*** subsp. ***benekenii*** (M, S) ***B. erectus*** subsp. ***erectus*** (E) ***B. erectus*** subsp. ***laxus*** (E) ***B. erectus*** subsp. ***longiflorus*** (E)

Table 6.1 continued Sheath type	Anchorage system	
	Rhizomatous	Caespitose or loosely tufted connected by short rhizomes
Sheath forming a reticulum	***B. riparius*** subsp. ***riparius*** (E) ***B. riparius*** subsp. ***barcensis*** (E) ***B. riparius*** subsp. ***macedonicus*** (E) ***B. tomentellus*** (E) ***B. cappadocicus*** subsp. ***crassipes*** (E)	***B. moesiacus*** (E) ***B. cappadocicus*** subsp. ***cappadocicus*** (E) ***B. cappadocicus*** subsp. ***lacmonicus*** (E) ***B. parilicus*** (E)

Tufted grasses are more vulnerable to trampling, and recover more slowly. Both rhizomatous and deeply caespitose grasses are well provided with a system of anchorage against mechanical removal, wind damage etc. even in soils where the substrate is sandy and mobile.

It would seem, *a priori*, on these arguments, that the rhizomatous brome-grasses might have exploited the opportunity to survive, diversify and extend territory in the heavily grazed grassland communities opening in Eurasia after the forest clearance of the later post-glacial periods (post-Atlantic period e.g.). By contrast the caespitose species may, on these *a priori* considerations, have been restricted to, or diversified into shaded woodland and wood margins, moist slopes - perhaps montane, where grazing pressure might be lower, water supply more substantial and more certain, and the chances of dislodgement modest. But as table 6.1 shows some of the tufted plants are often found not in moist, shaded habitats, but in very exposed ones. Thus plants of *B. erectus* and most of the *B. riparius* group can be found commonly in very dry areas, often in very cold, open montane habitats, or very dry (seasonally hot and cold) open grass steppes and rocky, gravelly, sandy ruderal areas. Here the temperatures are variable, the water supply irregular or seasonally limited, the soil dry and mobile, and there is some grazing pressure. These habitats present problems if they are to be colonised.

Analysing three contrasting taxonomic groups, with these considerations in mind, I noted that the morphology of the dead sheaths around the stem bases differs markedly. Dead tissues may potentially discharge one or several functions. Let us seek possible explanations which connect forms with their possible functional significance, and with the habitat. In this way, it may be possible to understand the directions in which adaptive radiation of the perennial brome-grasses has proceeded (chapter 11). Perhaps also, therefore, it may help identify and understand pivotal characters, as I have defined them.

6.3 Morphology

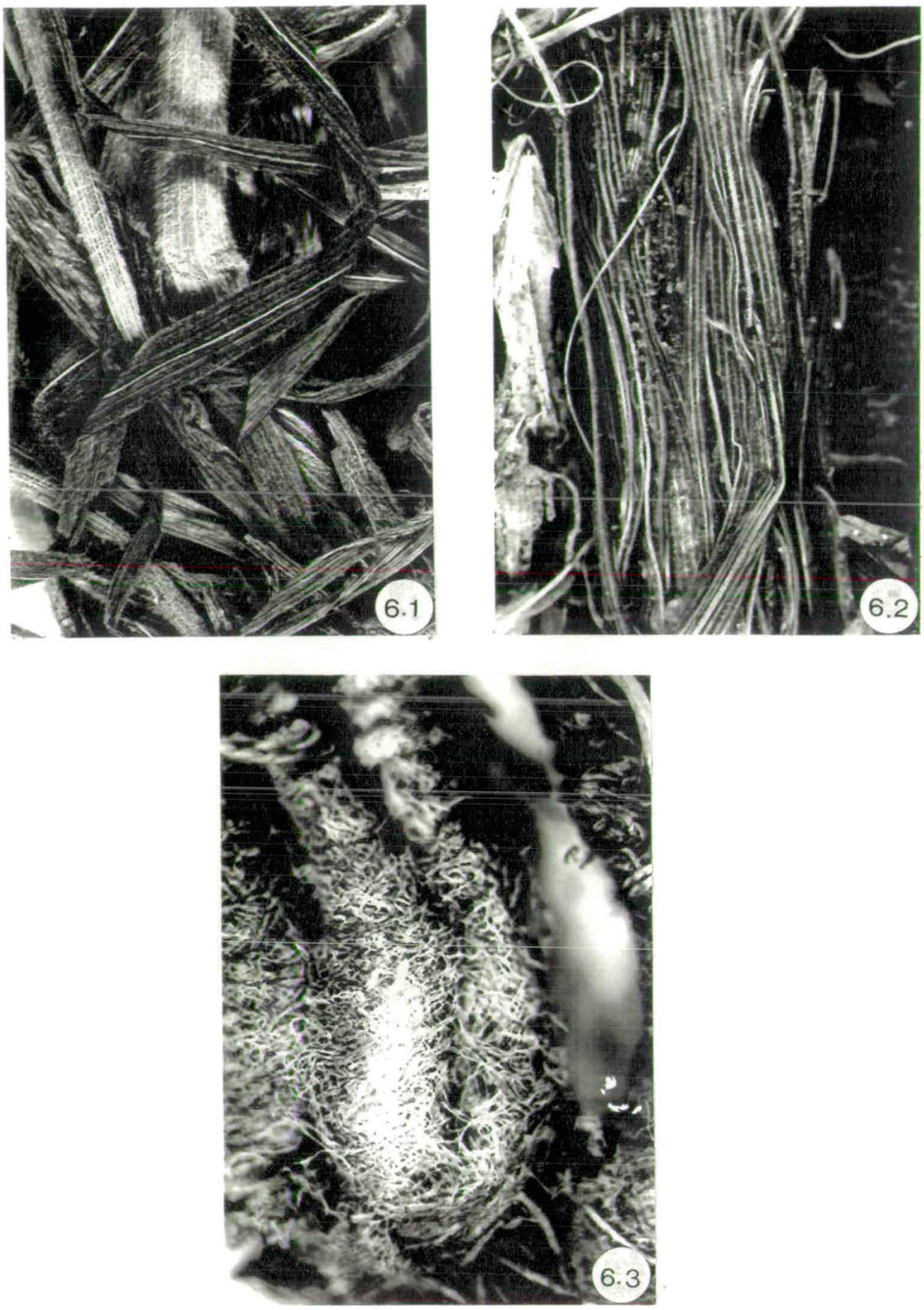
In European and Southeast-Asian *Bromus* § *Pnigma*, the sheaths may exhibit three patterns of decay: sheaths which (1) remain intact around the bottom of the emergent stems, or (2) break up into parallel fibres, or (3) sheaths which decay into a network of reticulating fibres. The three sheath decay syndromes are illustrated in figs. 6.1, 6.2 and 6.3 respectively.

6.4 The Basis of the Sheath Morphological Differences

Vascular strand differences were suspected governing the pattern of decay. These were investigated.

6.4.1 Materials and Methods

The source of material used in the study of sheath characters were herbarium specimens. The procedure for the study of sheath morphology was similar to the one adopted for anatomical studies of leaves (chapter 4, sect. 4.2), except for some alterations now described. The initial step for preparing the fragments consisted in placing them in a mixture of any of the common household bleaching solutions containing about 5% sodium hypochlorite and water (1:2) respectively. After 1/2 hour approximately, most of the tissue joining different veins would disintegrate, thus allowing the venation patterns to show more clearly. The material was not left longer than an hour because it then disintegrated totally, making a further study unsuccessful. From this stage, it was important to carry out a very delicate manipulation of the segments as they were so frangible, if appropriate results were to be obtained. After bleaching, sheath material was carefully transferred to conical flasks filled with cold distilled water.



Figs. 6.1-6.3. Overall morphology of three types of sheath.

Fig. 6.1. Intact sheath of *B. ramosus*. Mag. x1.81 (Accession number 16256)

Fig. 6.2. Sheath splitting into fibres in *B. erectus*. Mag. x1.81 (Accession number 290)

Fig. 6.3. Reticular sheath in *B. riparius*. Mag. x1.81 (Accession number 423)

Several changes of water were made to remove the bleaching agent. Some of the standard procedures for anatomical studies - rinsing and dehydration - were also used here (chapter 4, sect. 4.2). Once the material was dehydrated, it was stained directly. The segments were transferred to small vials containing safranin and left to stain as indicated in chapter 4 sect. 4.2. Once ready, i.e., with clearly stained vascular tissue they were mounted in Euparal (Agar Scientific, R1344) and covered with a cover slip.

Fragments of the three types of sheath were processed and studied at two different morphological levels viz. light microscopy and Scanning Electron Microscopy (S.E.M.). By using both techniques it was possible to compare the underlying venation pattern.

6.4.1.1 Light Microscopy

Sheath fragments were studied and photographed with an Olympus OM-2n camera attached to a Vickers Photoplan microscope. See p. 29 for further details on the photographic techniques.

6.4.1.2 Scanning Electron Microscopy (S.E.M.)

Small pieces (5 mm × 3 mm) of the sheath material to be investigated were mounted on aluminium S.E.M. specimen stubs (Agar Scientific, Ltd) by means of double sided adhesive tape. Position and identity of the material was previously recorded. Silver conductive paint (Electrodag 915, Acheson colloids, Plymouth) was used to make electrical connections between the specimen and the stub surface. The specimens and the stub surface were then coated with about 10 nm of gold; this was carried out in an Emscope gold sputter coating unit (Emscope Laboratories, Ashford, Kent, UK) for 2 minutes at 20 mA in an argon atmosphere (0.1 Torr.). The stubs were viewed using a Stereoscan S250 MK1 scanning electron microscope [Leica UK

Ltd (Formerly Cambridge Instruments) Cambridge, UK] at an accelerating voltage of 5-25 KV. Electron micrographs were recorded on Kodak TMax 100 film, and processed in Kodak HC110 developer, dilution B (1:32) for 7 minutes at 20°C

6.4.2 Results

6.4.2.1 Sheath Anatomy Revealed by Light Microscopy of Processed Dried Material

Results derived from this study clearly showed the three vascular arrangements observed externally. Photographs taken of various taxa are shown in figs. 6.4-6.6.

6.4.2.2 Scanning Electron Microscopy Examination of Dried Sheaths

The use of this second method provided very precise, accurate, clear results which corroborated the results obtained with light microscopy. As observed in fig. 6.7, the tissue which connects different parallel fibres remains intact, keeping the fibres united. Fig. 6.8 shows the gradual splitting of the fibres. The third type of sheath decaying into a reticulum is characteristic of the *B. riparius* group. Here different fibres are anastomosed, with the internal tissue joining them gradually disintegrating. As a result, a perfect reticulum is formed (fig. 6.9).

6.4.3 Conclusion

The possible connection between the pattern of venation and habit of decay in sheaths of perennial brome-grasses seems to be confirmed by the results obtained. The use of both techniques, light microscopy and Scanning Electron Microscopy (S.E.M.) showed in great detail the internal structure which defines and underlies the three patterns of sheath decay, previously discussed on the basis of their distinctive anatomy. A further preliminary experimental study on sheath morphology carried out (and presented in the next section) corroborated these observations. There are two fundamental venation types viz., *ramosus* type and *erectus-riparius* type. The *riparius* type is clearly an extreme form of the *erectus* type. The critical difference in the decay pattern relates to the tissue in between the veins. Why this behaves differently in these grasses, i.e., remaining wholly intact or disappearing totally or partially is not revealed by these pictures. Transverse sections or tests of tensile strength might reveal whether differences of thickness or tissue type are involved.

6.5 Functional Differences of these Sheath Types

The most interesting question referred to these three types of sheaths concerns the possible functional difference between them. As pivotal features these might explain the resolution of the taxa in an evolutionary sense. Functional differences might be related to water trapping, protection from frost or possibly a trap for water-borne (alluvium) or wind-blown (loess) soils (Smith 1991). Of course any or all these functions might be discharged simultaneously, or there may be no function whatever.

6.6 Investigation of Sheath Properties

Water trapping ability by the dead sheath mass might aid both water acquisition and water conservation. Perhaps the uptake of water and/or its rate of loss differ between different sheath types. Possibly the insulatory capacity of the sheath types for frost protection of young basal meristems could vary. Soil trapping ability may be important in environments where the soils are mobile - whether in water or wind. Retaining as much substrate as possible around the stem base may promote water conservation as well as frustrate root exposure and possible damage, disease or dislodgement. Water retention and soil trapping properties would usefully reinforce each other.

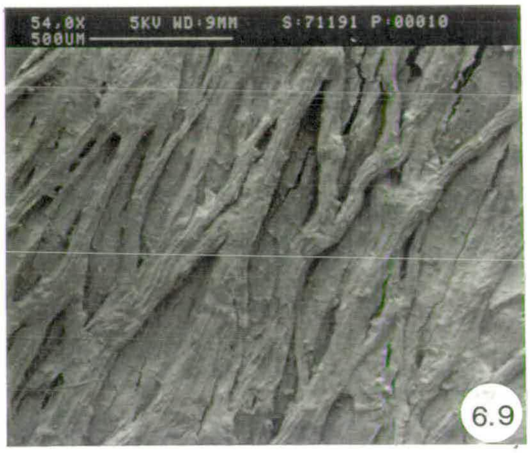
Two of these possibilities were investigated in a preliminary way, the third - frost will be tested in the future.

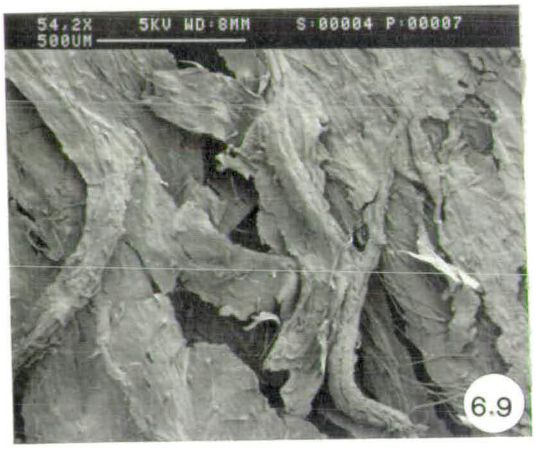
Figs. 6.4-6.6. Light microscopic views of three types of sheath.

Fig. 6.4. *B. ramosus* sheath. Note the thickness of the parallel fibres composing a solid structure remaining unchanged after decaying. Mag. x389

Fig. 6.5. *B. erectus* sheath. Note the progressive splitting of the fibres which are relatively thin. Mag. x389

Fig. 6.6. Reticular sheath in *B. riparius*. The fibres are anastomosed forming a reticulum. Mag. x389





Figs. 6.7-6.9. Scanning Electron Microscope (S.E.M.) photographs of three types of sheaths. Magnifications are indicated by bars.

Fig. 6.7. Intact sheath of *B. ramosus*.

Fig. 6.8. *B. erectus* sheath. Note the progressive splitting of the fibres.

Fig. 6.9. Reticular sheath of *B. riparius*. Note the development of the reticulum: the connecting material between the anastomosing vascular bundles progressively disappears.

As previously mentioned, there are three main types of sheath found in the perennial brome-grasses of Europe: basal sheaths remaining intact, sheaths partially decaying into persistent, parallel fibres and sheaths decaying into persistent fibrous reticulum. The basis of the two experiments now described below was to clarify the possible functional difference which could be related to water absorption, and soil trapping. In the first experiment, dry stem bases were used to quantify the percentage of water taken up in each case as well as the percentage of water lost from the sheath at different intervals of time. In the second experiment, plastic models resembling the three types of sheath were used to quantify the amount of soil trapped, when placed in a current of air containing soil particles.

6.6.1 Materials and Methods

6.6.1.1 Water Absorption and Loss

The types of plant material used were:

***B. ramosus* (RAM)**

Loose tufted. Sheaths remaining intact.

***B. erectus* (EREC)**

Densely tufted or sometimes with loose tufts connected by short/long rhizomes. Sheaths decaying into parallel fibres. This could be considered as a variant of the below type.

***B. riparius* (RIP)**

Rhizomatous with short or long rhizomes. Sheath disintegrating in a reticulum.

One stem base was removed from a herbarium specimen of each species and weighed. These were soaked in water (under vacuum) until fully saturated. Following this treatment the stem bases were blotted dried and re-weighed to determine the amount of water soaked up. Specimens were left at room temperature and humidity, and the amount of water lost through evaporation was determined by re-weighing at the following intervals: 1/2 h, 1.5 h, 3.5 h, 6.5 h and 20 h. Each experiment was repeated ten times with each stem base.

B. inermis is strongly rhizomatous. The sheaths remain intact although they do not accumulate at the base of the stem basis as it occurs in the three groups discussed above. A full explanation of this character will be presented in section 6.7.

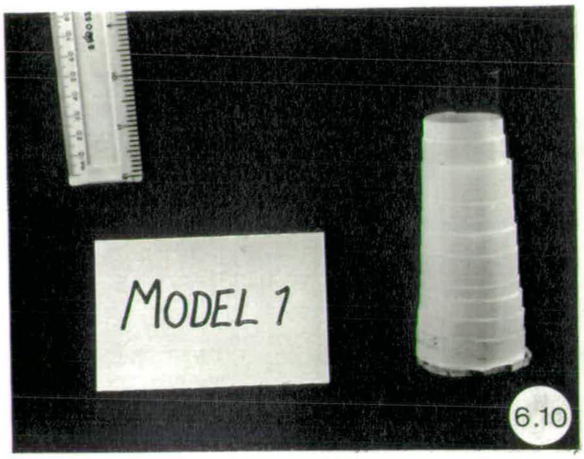
6.6.1.2 Soil Trapping

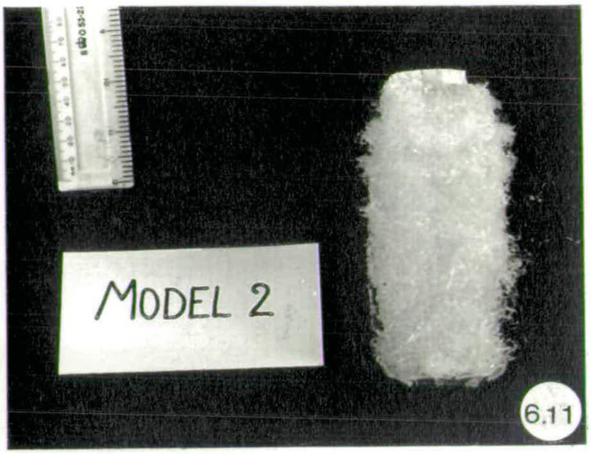
For the design of the models for soil trapping studies, white plastic card was used. Each model was carefully engineered, so that the outline area in the path of the wind current was constant. This area is not the same as the drag coefficient, (cd) = actual force/ 1/2 ρ u^2 A, regarded by Grace (1977) as a useful measure of the bluffness of a body. This is because the area in outline does not take account of the surface roughness projected forward from the models. This was different in each case, but was not easily quantifiable. It is the drag coefficient, differing between the three models, which probably connects very closely with their different soil trap properties.

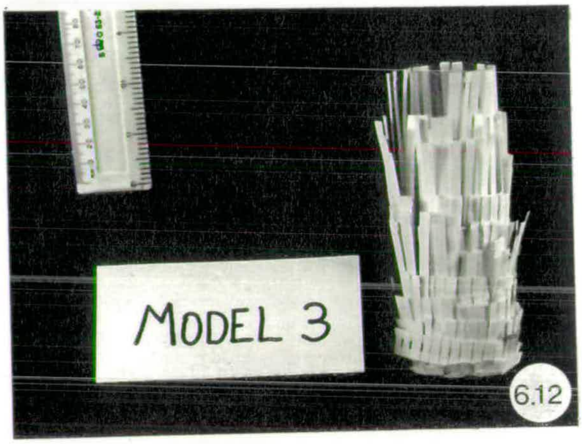
Model type 1. This was a series of overlapping plastic tubes (ten in total) of different heights, resembling the solid, intact sheaths. Each piece of card was glued longitudinally to make these tubes (fig. 6.10).

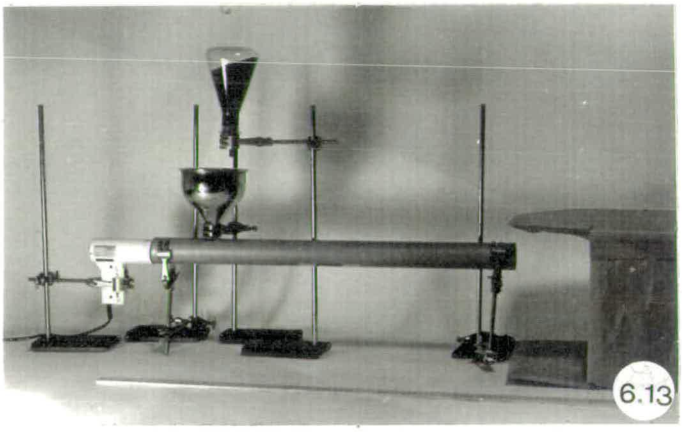
Model type 2. Plastic scouring pads were used as reticular material. This model resembles the reticular sheath. The central tube, as in model 1, represents the base of the stem (fig. 6.11).

Model type 3. This model resembles model 1 except that the model sheaths were cut in vertical strips, simulating the parallel fibres described earlier for *B. erectus* (fig. 6.12).









Figs. 6.10-6.12. Model design for the soil trapping experiment

Fig. 6.10. Model representing the intact sheath of *B. ramosus*.

Fig. 6.11. Model representing the reticular sheath in *B. riparius*.

Fig. 6.12. Model representing the sheath splitting into parallel fibres in *B. erectus*.

Fig. 6.13. Blowing machine designed for the soil trapping experiment.

Each model had a standard plastic base plate with a small retaining annular lip, into which it fitted tightly. Soil adherent to the model, including that deposited on the standard base plate, was weighed. Loamy garden soil previously dried, powdered and sieved to remove the particles larger than 0.2 mm diameter, was blown through a blowing machine especially devised for this purpose (fig. 6.13). The standard amount of soil blown each time was 400 g. The models were weighed before and after the treatment. Each experiment was repeated ten times with each model. Models were carefully cleaned in between each replicate test.

6.6.2 Results from Experiments

6.6.2.1 Water Absorption

Raw data in Appendix 6.1.

Table 6.2. Absorption of H_2O (% of dry weight). Each value is the mean of 10 replicates ± se. Values between columns followed by different letter differ significantly (P = 0.05) by one way analysis of variance (t-Test).

RAM	EREC	RIP
405 ± 1.35 **a**	334 ± 2.34 **b**	273.11 ± 1.94 **c**

Within the limits of this experiment, it looks as though between species differences are indeed biologically significant; it seems that water absorption is very much more efficient in RAM (fig. 6.14). This would fit with the continuity of old sheath tissue in this species (like blotting paper). The blotting paper effect of EREC is interrupted by splits and breaks, and it is non-existent in RIP which presents merely a reticulum of hard, woody threads (mainly old xylem). Data from only <u>one</u> stem-base in each case are presented here. Only two specimens (one poorly formed) per species were available for test, so certainly these data need extending. However, combining the data from each specimen within each species, then comparing between species variation, still showed significant differences between the three species.

6.6.2.2 Water Loss

Raw data in Appendix 6.2.

Table 6.3. Loss of water (as % of wet weight at start). Each value is the mean of 10 replicates ± se.

Time	RAM	EREC	RIP
1/2 h	3.018 ± 0.023	7.155 ± 0.032	2.495 ± 0.03
1.5 h	9.283 ± 0.089	19.949 ± 0.010	8.178 ± 0.033
3.5 h	22.329 ± 0.148	41.896 ± 0.010	25.1 ± 0.025
6.5 h	40.072 ± 0.041	52.446 ± 0.05	33.975 ± 0.044
20 h	76.351 ± 0.033	62.224 ± 0.023	58.093 ± 0.032

The confidence limits of these points are satisfactorily narrow and show the means of observations at each sampling time to be significantly different. RIP and RAM lose water quickly at first, later more slowly. EREC loses water quickly at first, later slowly. All three after 20 hours are much the same, having lost 60-80% of their water (fig. 6.15). All are fast, then slow, but EREC shows the greatest difference between these two phases. It is not simply possible to attribute massive overall significances to the statistically different figures produced. This is because only three stem bases were available for use and this is to limited a sample to be relied upon. Any three individual specimens might show statistically significant differences; more specimens are needed before any clear picture emerges.

6.6.2.3 Soil Trapping

Raw data in Appendix 6.3.

Table 6.4. Soil trapping. Each value is the mean of 10 replicates ± se. Values between columns followed by different letter differ significantly (P = 0.05) by one way analysis of variance (t-Test). These figures are mean percentages showing the percentage of the soil blown at the model that was trapped by it.

RAM	EREC	RIP
0.345 ± 0.027 **a**	4.522 ± 0.126 **b**	6.092 ± 0.135 **c**

The surface or texture characteristic of RAM relative to RIP and EREC and *vice versa* therefore seems to constitute a significant difference in soil trapping efficiency. RAM is a relatively ineffective soil trapper. RIP and EREC are both very much more effective, but slightly different from each other (fig. 6.16).

6.6.3 Discussion

The results obtained from the first experiment (i.e., water absorption/water loss) showed little of significance. No great difference was found between the three sheath types, though RAM was best at absorption. Nevertheless, this property may not seem to be very relevant to this group, keeping in mind the type of habitat where it occurs (see chapter 11, sect. 11.3). This leads me to the conclusion that the functional difference, if there is one, is not related to water trapping or retention. Results derived from the second experiment (i.e., soil trapping), on the other hand, provided some possibly significant information. The amount of soil trapped by the reticular model (RIP type) was very considerably higher than by the intact model. This may be an indication of the functional significance of the sheath morphology. This investigation is yet to be completed but the results so far are suggestive.

Fig. 6.14. Graph showing the amount of water (% of dry weight) absorbed by each stem base. Bars = 95% confidence limits.

Fig. 6.15. Graph showing the amount of water (% of wet weight at start) lost by each stem base at different intervals of time: (■) *B. ramosus*, (□) *B. erectus* and (◆) *B. riparius*.

Fig. 6.16. Graph showing the amount of soil (% of soil blown) retained by each model. Bars = 95% confidence limits.

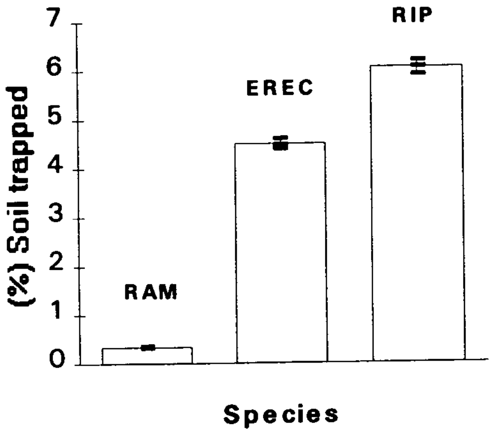


Fig. 6.14

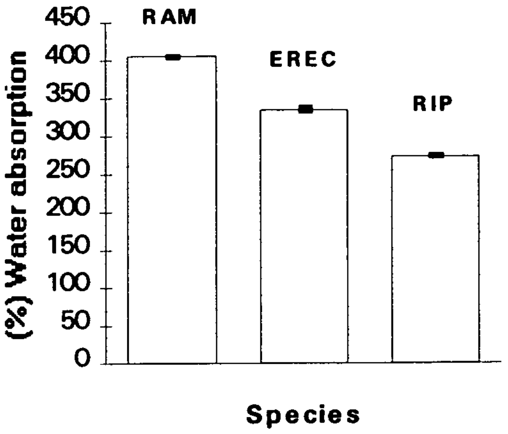


Fig. 6.16

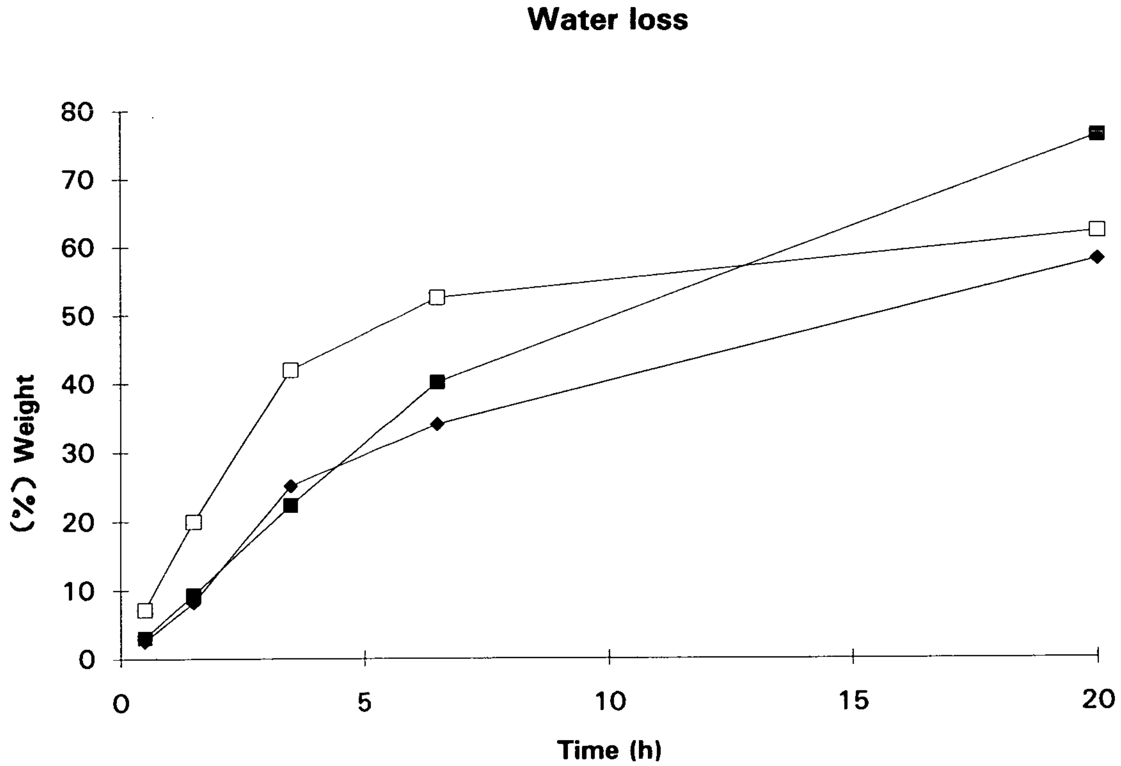


Fig. 6.15

RAM type sheaths seem to absorb water well, perhaps at the cost of not being good soil trappers. RIP type sheaths are associated with high soil trapping, but absorb water poorly. EREC sheaths seem to be intermediate.

Perhaps there is a trade-off evolutionarily. Either the old sheath can trap soil well, but absorb water poorly (RIP), or trap soil badly but absorb water well (RAM), or be reasonable at both (EREC). Different mutations for sheath decay have presumably been fixed in two cases (RIP and EREC), also for the venation pattern of the sheaths. These more or less effective mutations may well have been fixed at different times, or in different places, or both. On current information, it seems likely that the soil trap differences do indeed indicate a functional significance of the sheath morphology diversity.

Different kinds of sheath (used as states of a pivotal taxonomic character) are thus likely to have different functional characteristics. Thus, they may be pivotal characters also in explaining the evolutionary divergence of different species groups.

Time and materials did not permit tests of frost resistance. Simple tests with thermocouples are planned for the future.

6.7 Conclusions on Pivotal Stages of the Sheaths and Related Characters

An analysis of the habitat of the group brome-grasses with reticular sheath type shows a distribution mainly in dry hills, rocky and sandy steppes and mountain slopes (Smith 1980). My own investigations confirm this. In Europe, this group occurs in the Balkan peninsula and elsewhere it is found in Asia Minor, S.W. Asia and Central Asia. As a consequence of the destruction of woodlands, frequently the higher mountain zones are either nearly bare rock or have vegetation of a grassland type (Turrill 1929). Especially in Greece, plateau formation is rare in the mountains and steep exposed slopes are very common. There are also frequent, strong winds which denude them of soil (Turrill 1929). The soil cover is often mobile and ephemeral. These austere conditions may have comprised a selection pressure, encouraging these brome-grasses to evolve a particular system of anchorage for the colonisation of new niches in the course of their adaptive radiation. The main operating factor identified here seems to be the wind. Aeolian soils are derived from wind-borne material and are exemplified by sand-dunes, and the fine grain deposits known as loess. The thickest and most extensive loess blankets occur in China, Soviet Central Asia, the Ukrainian, Central and Western Europe, the Great Plains of North America and Argentina (Pye 1987) (figs. 6.17 and 6.18). Where native grassland exists in these areas (hardlly at all in Europe), the caespitose habit is commonest, as for instance in the native bunch grasses of N. America prairie.

Pollen and fauna evidence indicates that the loess accumulated under relatively cold and dry conditions with steppe vegetation (Pye 1987). Like many other transported soils, it is generally very fertile, containing plenty of calcium, potash and phosphorus. The size of the particles which form loess varies in the range of 0.07 to 0.01 mm (Russell 1961). It has the most continuous distribution of any one type of soil within the Balkan peninsula and in areas with considerable temperature extremes and irregular water supply, is usually covered with some type of steppe (Turrill 1929).

This situation can be compared with the formation of "phytogenic" hillocks in dry, open desert regions and sand beaches where the vegetation is subject to the action of violent winds. Batanouny & Batanouny (1968) showed that quite small plants of *Aristida* can initiate hillock formations. Plants impede air flow and this impedance causes wind-blown dust and sand to be deposited round its base as well as, eventually, water-borne materials. They carried out an interesting study on the formation of "phytogenic" hillocks in desert areas.

Among other characteristics of plants forming these deposits of sand, they pointed out the presence of intricately branching shoot systems, effective in reducing the wind velocity, and so causing the air burden - soil particles - to be deposited around the plant body. Anything that roughens the surface or increases the contact area of the plant, should increase soil deposition (Agnews & Haines 1960). Another important morphological feature characteristic of plants forming hillocks is the ability to produce adventitious roots from the buried vegetative organs (Batanouny & Batanouny 1968). These seem to offer an advantageous plant-soil-water relationship.

Hillocks, even small ones, may increase the area of dew layer available near the plant. If adventitious roots are formed in the hillock, this may be an important extra source of water. Hillocks will contain litter derived from the buried vegetative parts and also from old sheath material. High organic status in a generally mineralised wind-blown soil reduces loss of rain water by permeation, as a consequence of the high water-retaining capacity of the soil (Batanouny & Batanouny 1968). This in turn is derived from the highly colloidal organic material present. At the same time, hillocks may cool faster when elevated above general soil level. So, dew condenses preferentially around plants forming hillocks. They refer to external dew (in the air) and internal (within the hillock) dew which occurs as the temperature gradient is favourable for an upward movement of water from the warm and wetter deep layers. Abd El Rahman et al. (1966) suggested the vapour movement and condensation due to temperature gradients may take place on the root surface itself and thus water may be absorbed directly without any soil resistance.

Fig. 6.17. The global distribution of major loess occurrences (After Pye (1984a), *Prog. Phys. Geog.* 8: 76-217).

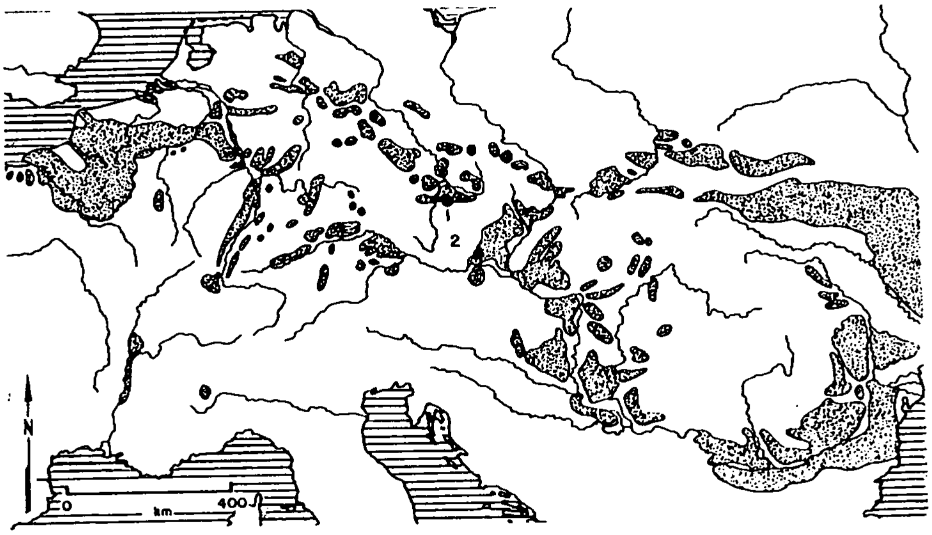


Fig. 6.18. Distribution of loess in Europe (After Haesaerts (1985), *Bull. Ass. Franç. Étude Quat* 2-3: 105-115).

Taking all these factors into consideration, it seems that the development of adventitious roots may be indicative of a direct link with such water supply. None of these physiological relationships have yet been demonstrated in reticular sheath brome-grasses. However, all of them have a well developed system of adventitious roots (fig. 6.19), and they are hillocks generates, as I have shown. As a consequence, all the characteristics defined previously may be applicable to these grasses.

An important aspect to take into account in the group of brome-grasses with a reticular sheath type is the finer structure of the sheath itself. It is relevant not only to impedance or increased "bluffness", but also to soil-trapping. In dry, open areas, the wind will blow particles of soil which will be deposited around the plant because the sheath acts as a rough, high surface-area obstacle that checks the velocity of the wind. But, unless the soil is trapped in somehow, it will not stay permanently around the plant and it will be blown away again.

The structure of the reticular sheaths corresponds to a complex series of fibres, finely dichotomised and interlaced, forming an intricate network with very small orifices through which the air can circulate easily; hence the network may well act as an effective trapping device, not merely stopping, for the wind-blown material. The nature of winds characteristics in the Balkan peninsula, strong and persistent, together with the type of soils (loess) as well as the particle size of the wind-blown material, seem to fit with the structure and distribution of the reticulate sheath type described previously. The small orifices between fibres can retain these particles of soil easily (fig. 6.20) Furthermore, rain or other precipitation seeping into the network may lodge the soil in and around the plants stem base even more firmly and intimately as the sheath material accretes over the years. Though water is not obviously retained better by reticular sheaths, so far as my scanty data go, this soil accretion may be a significant effect, specially when sheaths are wet.

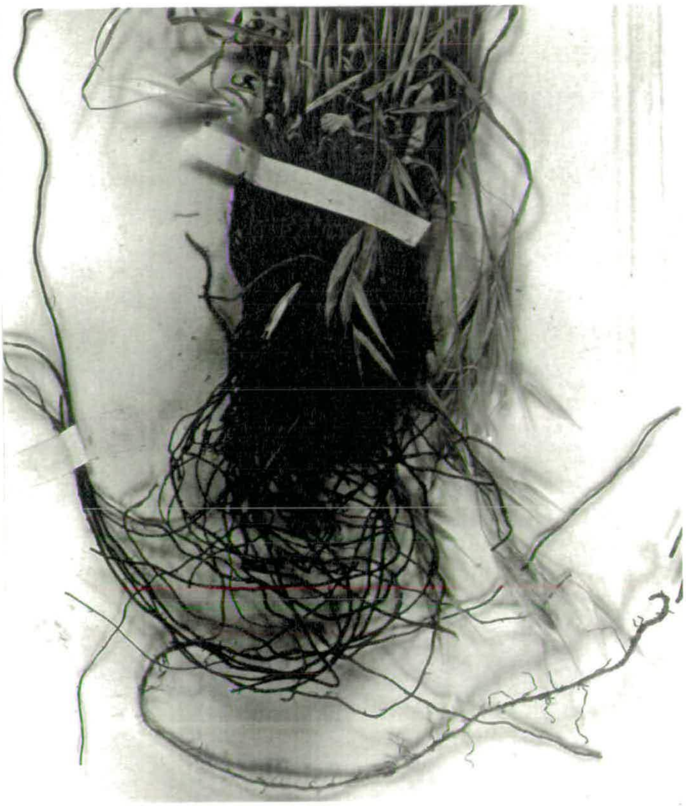


Fig. 6.19. Root system in *B. tomentellus*. Note the numerous adventitious roots developed. Mag.x0.60

Fig. 6.20. Close up of the reticular sheath. Note the small particles of soil adhering to it. Mag. x2.90

My own observations of this group in Bulgaria showed the stem bases partially buried in the ground and covered with soil, corroborating the trapping property here associated with the reticular sheaths.

A soil conservation method which has been developed in the semi-arid parts of America, where the need for controlling wind-blown material is well-recognised, is the "stubble-mulch" cultivation (Russell 1961). In the wheat-growing areas after harvesting, the stubble is typically left anchored in the surface. Thus, the wind velocity at ground level decreases because of the resistance of the stubble, reducing the chance of moving sand grains. This method is relevant to the natural strategy carried out by the reticular sheath brome-grasses. In both cases, the aim is to retain the soil grains transported by the wind. Of course, all perennial grasses with persistent, natural stubble would possess such properties: the reticulum would, however, seem to be the most additional effective soil trap of any seen.

Another important ecological consequence to bear in mind is derived from the mechanical effect which wind exercises on vegetation. The damage resulting from the impacting of wind blown particles is increasingly being assessed by plant physiologists (Van Gardingen et al. 1991). The more or less permanent bases of the perennial brome-grasses suffer abrasion longer than any other feature of the plant. Powerful winds are characteristic of the Balkan peninsula and as a consequence, these grasses need protection which can be achieved in two ways, keeping the dead, old sheaths around the stem and also covering them with soil, retained by the reticular sheaths, so they get protected from the abrasive effect of newly blowing loess.

The possible explanation of the relation of form-function in this group of plants seems therefore to be directly related to the physical and ecological conditions where they grow. The fact of trapping soil around their base, in the first place, reduces the chance of being uprooted as a consequence of the effect of strong winds; secondly, as mentioned previously, the loess forms one of the richest soils in the world (Turrill 1929), thus contributing an important source of mineral elements to be used by plants. In the introduction of this chapter, I defined pivotal characters as those which are critical in times of evolution and change during the capture of a niche. They may confer an advantage so that the new niche opportunity swings towards one particular taxon or group of taxa rather than others. Thus the character itself is selected, and fixed. This represents a close, evolutionarily pivotal relationship between two factors, form and function, allowing the possessor plants to colonise and dominate niches in the course of their adaptive radiation. This study of the structure of the reticular sheath related to the ecological and physical conditions where these grasses grow seem to demonstrate an adaptation to particular conditions, viz. powerful winds, unstable habitats and irregular water supply - thus enabling plants to survive and exploit one particular niche. These plants contrast with other brome-grass groups, such as those containing *B. ramosus* or *B. erectus* where these pressures are weaker or absent in their niches.

As mentioned in sect. 6.6.1.1, *B. inermis* is an aggressive rhizomatous plant. The sheaths, although remaining intact when dead, they do not accumulate as in the *B. ramous* group, and do not form a compact series of numerous layers enveloping the emergent stems. This could be associated with its crawling capacity. Once the plant has reached an adult form, a newly emerging shoot will be produced near the old one rather than be regenerated at more or less the same place. Consequently, individual stems will grow, sometimes protected only by one dead sheath. This sheath is of a juvenile, prophyllar leaf, characteristic of the innovation from which the new stem grows. The situation is very different from the extravaginal stem and tiller production typical of the *B. riparius* group. The stem production area is always mobile in *B. inermis*. An observation of the type of localities where it grows, conjointly with the habitat feature, could clarify this possible form/function relationship associated with the sheaths, if it is real. As compared with the *B. erectus* and *B. riparius* groups, any soil trap problem would need to be linked to the normal ecogeographic distribution of the *B. inermis* group - meadows, steppes, semi-arid places, and most significant, riverside sands (= alluvium). It might be expected that the sheaths may contribute some property of soil trapping, but it seems unlikely. Perhaps, in *B. inermis*, other features of the plant can act as a soil binder. The densely vegetative cover could retard erosion by cushioning the beating force of the wind and rain, increasing the absorptive capacity of the soil and holding it against both water and wind. More probably, a soil trapping ability is a feature of the rhizomes, rather than the sheaths. *B. inermis* is a sod former, associated with its aggressive creeping rhizomes. It is widely cultivated in the United States as a pasture grass, and also is used extensively in soil conservation (Wagnon 1952). It can resist flooding and trampling. Perhaps its characteristic long rhizomes are associated, evolutionarily with alluvium - a substrate of much more uniform texture than the rocky, gravelly, sandy, loamy, heterogenium typically inhabited by *B. riparius* and the *B. erectus* groups.

The sheath investigation carried out arose from the taxonomic importance derived from sheath morphology in these grasses. It seems that sheath morphology represents an example where the use of particular characters may bring into light some unexplored associated features. Taxonomists should, in my view, try to understand the characters they favour.

Interestingly, the model of sheath decay forming a reticulum is not exclusive to the *B. riparius* group. It occurs in other groups of grasses, e.g., the *Sesleria tenuifolia* complex. This is found in Italy, W. Yugoslavia and N. Albania (Deyl 1980) and grows in limestone rocks. The pattern of distribution fits accurately with the European area occupied by the *B. riparius* group along the Balkan peninsula. It seems that the same mutation was fixed here in a different genus of the family Gramineae during the colonisation of quite similar niches.

Strgar (1982) carried out an investigation on transverse sections and the venation pattern which governs this type of sheath. He found that this morphological feature constituted the only reliable character for the delimitation of the groups *Calcaria* and *Tenuifolia* in the genus *Sesleria*. This observation reflects a parallel situation to *Pnigma* brome-grasses where the sheath morphology is extraordinarily helpful for the delimitation of three groups previously described.

In other groups of *Bromus* the pattern of sheath decay produces numerous parallel fibres. *B. auleticus* is a perennial brome-grass native in South America: "It grows in steppes in Argentina and Uruguay and it prospers in sandy or sandy-wet soils; it is more resistant to cold, drought and strong winds than *B. brevis* and *B. unioloides*" (Cámara-Fernandez 1970). Coincidentally, this region in S. America is defined as one of the major loess occurrences in terms of global distribution (fig. 6.17). In addition the morphology of the old sheath in *B. speciosus* is characteristically of stiff, hard bristles. Originally from S. Africa, it grows on steep, moist mountains slopes, occasionally in the shade along streams (Gibbs Russell et al. 1991). It would be extraordinarily interesting to carry out research on the factor(s) which may determine the occurrence of sheaths splitting into parallel fibres instead of a reticular type in other parts of the world, bearing in mind the fact that they grow under the same conditions as their counterparts in the Balkan peninsula.

The venation pattern in sheaths has been studied recently in a different group of grasses (Broome, pers. comm.). Sheaths of species of *Poa* sect. *Bolbophorum* in Europe are parallel veined. The character of leaf sheath venation and stem base structure were added to the morphological characters and a new classification was produced by both traditional and by numerical means.

It is interesting that pivotal characters can function when the tissue is dead. The permanence of dead elements, i.e., senesced but permanently attached features round plants, can be more than just a protective system again abrasion by wind or a soil trapping mechanism. In particular, persistent dead as well as young live shoots are directly related to the survival of some salt marsh grasses. Wijte & Gallagher (1991) carried out a study about the permanence of both types of shoots in *Spartina alterniflora* Loisel. This is a perennial grass dominating high-salinity marshes of the Atlantic coastline. Reserves of non-structural organic matter stored in living underground parts of the grass during and at the end of the growing season (Gallagher 1983), are important for over-wintering and spring re-growth (Gallagher & Howarth 1987). Both shoot elements, living and dead, were found to conduct sufficient oxygen to the over-wintering roots and rhizomes to support aerobic respiration. When both live and dead shoots were removed in December, the plants did not survive the winter. However, the presence of either live or dead shoots enabled the plants to survive.

An interesting example which reinforces the important role carried out by "dead elements" was discussed by Niklas (1992). Clasping leaf sheaths may be the principal supporting elements not only early in the ontogeny of the monocot shoot, but much later, as in arborescent monocots, such as the palms, where the vascular system of dead clasping leaf bases may continue to provide structural reinforcement as the shoot system matures and ages. Since monocots lack secondary growth, they provide us with a mechanical design alternative to plants that produce secondary wood.

The sheath characters, studied in this chapter and here considered evolutionary "pivotal" are also, by this interpretation, among the most significant in taxonomic terms and so may reasonably be weighted more heavily than others.

6.8 Another Example of a Pivotal Character

An interesting, though very different example of a soil-trapping/humus trapping adaptation is found in the case of *Platycerium* Devaux (Stag's horn fern), a genus of epiphytic ferns which is found in forests, on trees and steep sided rocks in Malaysia, Australia and S. America. It is characterised by its dimorphic foliage. It has erect or pendent "foliage-leaves", which habitually bear the sori, and also "nest-leaves" which after dying persist in a rigid, scarious condition as collector of humus and moisture (Bell & Woodcock 1983). Thus, these plants create their rooting medium by intercepting falling litter. The sterile fronds form a substratum catchment (Benzing 1990), representing a system of soil trapping for the nutrition as well as the anchorage of the fern on the tree. This can be compared with reticular sheath brome-grasses, both growing in environments where the soil is mobile. Bower (1928) remarked of *Platycerium*: "This genus owes its systematic permanence to the very distinctive vegetative character which it presents". This statement closely parallels the concept linking morphology, taxonomy and adaptive radiation which is here summarised as pivotal character.

Chapter 7 Macromorphological Characters

Taxonomy, concerned with organisms and their classification, deals with characters. A general definition of a character is (Davis & Heywood 1963): "any attribute (or descriptive phrase) referring to form, structure and behaviour which the taxonomist separates from the whole organism for a particular purpose such as comparison or interpretation". Nevertheless, it is the expression or states of the specific character that taxonomists use, e.g., leaf length, number of basal branches etc. The selection of some features with a practical use for the identification, characterisation and delimitation of species is in large extent an intuitive process, based on my experience acquired with time through the study of a large amount of specimens.

In identification and characterization the taxonomist always seeks to employ diagnostic or key characters, i.e., those of limited occurrence, selected so that their use alone is sufficient for reaching a correct diagnosis (Davis & Heywood 1963). A good character must obviously be one that is little influenced by environmental changes, its manifestation being fairly constant.

For practical reasons all the measurements carried out in this study were standardised. The best specimen was always selected. Only those measurements which could be vague have been discussed. A hand lens and a ruler served for this purpose.

Stem width

The widest section of stem was measured, mostly coinciding with the basal part of the same.

Basal leaf blade

One of the lower leaves near the base was selected.

Cauline leaf blade

The first leaf above the basal leaf was selected.

Panicle length

This was measured from the lowest to the uppermost node.

Floret

The lowest one, in contact with the glumes, was always chosen.

Rachilla internode length

This was measured from the point of insertion on its own floret to the top where it joins the upper floret.

Glumes length

This length was represented by the distance from the basal annular strangulation on each glume to its apex.

Lemma length

It was measured from the rounded base to the hyaline apex.

Lemma width

Only the opaque surface was measured, excluding the lateral hyaline margins, and coinciding with the widest area.

Awn length

The measured length was the distance from the insertion point on the lemma, below the apex, to the awn tip.

Palea length

Paleas were not mechanically separated from the lemma for this measurement. The length indicated the distance from the contact point with the lemma up to the palea apex.

In the list below, those characters used in my taxonomic accounts of the perennial *Bromus* comprising the section *Pnigma* are listed and briefly discussed, some being mainly diagnostic, others presenting overlapping values and carrying less useful information for a taxonomic separation. All these characters with their corresponding states were used for the numerical analysis of the perennial brome-grasses (Appendix 10.1). In this Appendix are listed the full variation ranges for each of these characters and the codifications for taximetric analysis. The character variation ranges are of course also a feature of the formal discussion (p. 128 ff.). The codifications themselves are now discussed. The codification principles are discussed in chapter 10, sect. 10.2.2.

Habit

As discussed in chapter 8, this feature has been neglected frequently as a result of inadequate collection. All the perennial brome-grasses included in this study form tufts, either loose with no joining rhizomes, occasionally dense connected by very short rhizomes (1-2 cm), or loose tufts joined by relatively short (2.1-4 cm), or very long (more than 4 cm, up to 8 cm) rhizomes. Morphologically they are an important character and their occurrence is taxonomically useful for the distinction between different taxa.

Stem height and width

Both characters seem to be directly related. Although they can show some degree of plasticity, in particular cases they are helpful and conjointly with other features are useful for separation at the subspecific level. Three main height states are observed: up to 50 cm; 50.1-90 cm, and more than 90 cm reaching 150 cm. The width states are: up to 1.5 mm; 1.6-3 mm and more than 3 mm.

Morphology of the basal sheaths

A discussion of this macrofeature is presented in chapter 6. My main subdivision of the perennial brome-grasses comprising the section *Pnigma* has been primarily on the basis of the pattern of sheath decay, sheaths remaining intact, splitting into parallel fibres, and sheaths decaying forming a reticulum.

Leaf length, width and form

The first two parameters exhibit overlapping values between taxa, particularly when compared at the subspecific level, and they are easily susceptible to environmental modifications. The length shows two main states, up to 20 cm and more than 20 cm long. The states of width are, up to 1.5 mm and more than 3 mm, frequently reaching 7 mm wide; within species the variation is often 1.6-3 mm.

Three forms define the leaf in perennial *Bromus* - flat, conduplicate and involute. It is an important and constant taxonomic character, especially in involute leaves, showing a correlation with particular ecological conditions.

Leaf and sheath indumentum

The different variants of leaf vesture in this group of grasses are, glabrous, ciliate along the margins, scattered hairs, densely hairy, giving a velvety appearance and minutely pubescent. The sheath indumentum varies from glabrous to minutely pubescent or with scattered hairs to densely lanate and easily observable. In some cases it can be a quite striking and good diagnostic character, e.g., when it shows a velvety appearance. I must however point out that in some botanical keys, particularly in the past, many infraspecific taxa were "created" based only on the indumentum character. The quantity of hair should often be seen as a manifestation of continuous intraspecific variation and not taken as an absolute diagnostic element, often of minor taxonomic entities that are, frequently, dubious.

Ligule length

This does not seem to be an important key character. There is variation, but it seems not to be correlated with other diagnostic features. Two main states can be established, up to 1 mm, very short and scale-like, or more than 1 mm.

Flag leaf length and width

Overlapping values in these parameters between two taxa occur. Consequently they are not very useful. The magnitude of the flag leaf is up to or more than 10 cm long, and up to or more than 2.5 mm wide.

Panicle length and shape

Several contributing factors are involved. There exists great variation in the former parameter, ranging from 8.6 cm-15 cm as the intermediate value, up to 8.5 cm in one extreme or more than 15 cm, in the opposite extreme. Three main morphological types of panicles occur in *Bromus* § *Pnigma* at maturity: erect-oblong, drooping-effuse or spreading-deltoid. They can stay more or less the same from youth to maturity or vary at maturity.

Number of basal panicle branches/pedicels

Some degree of differentiation exists between subspecies in this character, but it can not be taken as an absolute diagnostic feature. The states are 1-3, 4-6 and more than 6.

Panicle branches/pedicels mechanical strength and length

Both conjointly determine the shape of the panicle, particularly the former, either when the panicle branches or pedicels are very stiff or, by contrast, fine and tortuous at maturity. They are useful taxonomic characters generally at the infraspecific level. Two states are quantified, the shortest panicle branche/pedicel at the lowest node with values of up to 2.5 cm, more than 4.6 cm, and an intermediate variation of 2.6-4.5 cm, and the longest panicle branche/pedicel at the lowest node, being up to 4.5 cm, 4.6-6.5 cm, and more than 6.5 cm.

Spikelet length and shape

The length represents a good diagnostic parameter between species and subspecies. It shows an intermediate state of 2.1-3.5 cm, minimum up to 2 cm and not less than 3.6 cm. Contrarily, the shape seems not to be a key character. The spikelets in a young state tend to be narrowly ovate, becoming more broadly ovate at maturity.

Spikelet number

This character is associated with the shape of the panicle, conjointly with the panicle branches and pedicels. It is a fairly good taxonomic feature for the distinction of subspecies. Some panicles are relatively poorly spiculated, bearing 8-13 spikelets, others have more than 23 spikelets, up to 60, and as an intermediate state there are panicles with 14-23 spikelets.

Floret number

Although sometimes it is difficult to quantify the number - because the disarticulation of the upper florets has occurred - some degree of variation exists when comparing at the subspecific level. The states are up to 5, or exceeding 5.

Rachilla internode length and indumentum

This does not seem to be a key character. The possible states, up to or more than 1 mm are dubious. Variation is continuous and seems to correlate with nothing else. The vesture varies from glabrous to finely hairy, exceptionally with numerous, short or long hairs.

Glumes length and shape

Both characters are strongly correlated with the lemma dimensions. They are taxonomically very useful. The states of length in both glumes are: up to 9.5 mm and more than 9.5 mm for the lower glume, and up to 11 mm and more than 11 mm for the upper one. The shape represents a very constant feature for the lower glume, being narrowly lanceolate. By contrast, the upper glume varies from narrowly lanceolate to broadly lanceolate.

Lemma length, width and shape

The lemma, although with such small scale differences, is frequently neglected since the evidence requires precise measurement under strong magnification. It is however very valuable for diagnostic purposes, particularly at the subspecific level. Three length states are observed, up to 11.5 mm, 11.6-14 mm, and more than 14 mm. The width, although a little meticulous to quantify, is represented by two states, up to 2 mm and more than 2 mm. Three main shapes are observed in the lemma of this group of grasses: oblong-lanceolate, ovate-lanceolate and narrowly lanceolate, derived from the length/width ratio.

Lemma and glume indumentum

In very few cases, the presence of hairs is a constant, diagnostic element. On a regular basis, the degree of hairiness varies notably in the same taxon. When hairs are present in the lemma they can be scanty and scattered, sometimes restricted to the lower half, adpressed, they can also extend reaching almost the apex, sub-patent, or be numerous, covering the totality of the surface of the lemma. The glumes are mainly glabrous, occasionally presenting scattered, very few hairs

Hyaline margins width

The width of the hyaline margins is complementary with the shape and coloration, of glumes and lemmas, being narrow or very broad.

Glumes and lemma colour

On a regular basis not much variation is observed, although in specific situations can be used to aid separation at the subspecific level. The majority of glumes and lemmas are pale green, though in some cases the degree varies to very pale green-yellowish, giving a shining and delicate appearance. The purple-flecked colour also occurs but it is very variable.

Vein number

This is a fairly constant character in perennial brome-grasses. In particular occasions shows some degree of variation between subspecies. The number of veins for the lower glume is one, with three for the upper glume. The characteristic number in the lemmas is 3, though a variation to 5, 3 very prominent and 2 more obscure disappearing towards the bottom of the lemma, is also observed.

Awn length and orientation

The former does not seem to be a good diagnostic feature. By contrast, the orientation can be characteristic. The states are: absent; up to 5 mm and longer than 5 mm. The orientation is indicated by straight awns, slightly out-curved or strongly divaricate.

Palea length

This is always shorter than the lemma, but it is not a key character. There is great overlap between the taxa I recognise. Three states are quantified, up to 10 mm, more than 12 mm and an intermediate state of 10.1-12 mm. The keels can present small, obscure teeth or relatively well developed ones.

Stamen length

Although frequently is not possible to record it, some degree of variation is observed between groups of species. Two main states seem to exist, up to 4.5 mm and more than 4.5 mm.

Caryopsis length

The caryopsis is lacking in the majority of the specimens, making its study difficult. Here is another point for note by collectors. Mature caryopses in other *Bromus* groups (e.g., section *Bromus*, see Smith & Sales 1993) give numerous taxonomic characters. In section *Pnigma*, collecting of caryopses (i.e., mature fruiting material) seems, for some unknown reason, to be unusual.

Chapter 8 The Importance of Stem Base and Rhizomes

The main purpose of this short chapter is to emphasise the importance of habit characters in grasses. This also applies in general to any group of plants. Habit defines, in conjunction with other features, the biology of plants, but is frequently ignored by collectors and writers of botanical keys, accounts and descriptions.

It has not been unusual in the past and also in present times to come across poorly collected specimens, where basal parts have been discarded or never gathered as a consequence of cutting/tearing them above the soil surface. Much information can potentially be derived from the habit of plants, which may aid in understanding their pattern of adaptive radiation. Poor collection certainly derives partly from the under-emphasis of the significance of the features in keys and descriptions, but of course the opposite relationship also exists. It is a vicious circle, but is still really astonishing to me to observe how poorly collected underground features are in herbarium material of many perennial plants.

The group of brome-grasses included in this study exhibit a perennial condition, persisting for few to many years. Perennial grasses can be caespitose, rhizomatous or stoloniferous. Culms growing in dense clumps due to branching at the base are said to be densely **tufted** or **caespitose**. The term **tussock** is applied to a group of culms that are densely caespitose (Gould & Shaw 1983). It seems to mean the same as tuft. Culm branches at the base may produce erect lateral **shoots**; horizontal, above-ground **stolons**; or subterranean **rhizomes**.

Lateral shoots of cultivated crop and pasture plants are frequently referred to as **tillers** or **suckers**. The former term is used for wheat and other cereals, and the latter for corn and sorghum (Booth 1964; Gould & Shaw 1983). In most grasses the basal branches are called **innovations**. In any case they develop adventitious roots, and thus are sustained by their own independent root system. They may break off and become established as individual plants (Booth 1964; Langer 1979). In perennial species many of these innovations are sterile, remaining in a vegetative state and not forming a culm. They can contribute to increase size of the population. The lateral shoots (innovations) may be **intravaginal** or **extravaginal** (Gould & Shaw 1983; Hubbard 1984; Clark & Fisher 1986; Nicora & Rúgolo de Agrasar 1987). In the former the young shoot grows up within the enclosing leaf sheath, forming dense tufts; in the latter the buds of the young shoots grow through the bases of the enveloping leaf sheaths, breaking through them and forming loose tufts, stolons or rhizomes (Langer 1979; Hubbard 1984). Intravaginal branching is the more common condition (Gould & Shaw, 1983), although it is not unusual for both types to occur on a single plant (Etter 1951; Langer 1979; Gould & Shaw 1983) - a situation very frequent in the Poideae. In the group of *Pnigma* brome-grasses the lateral shoots show an extravaginal development.

Buds at the base of culms may also develop as stolons or rhizomes (Langer 1979). Frequently in many keys and descriptions, both these terms have been treated as synonymous, although they represent significantly different concepts. Stolons are modified stems creeping above the surface of the soil, with regular internodes and nodes, upon which adventitious roots, flowering shoots and leaves are borne. The ability of stolons to form roots at the nodes enables the plant to spread and establish, but also it constitutes a form of asexual reproduction when the stolons are broken. Rhizomes on the other hand are modified, underground stems, with internodes and nodes, developing small, thin, brownish or whitish scale-like leaves at the same point. Anatomically, stolons may be intermediate between culms and rhizomes (Weatherwax 1970). Both constitute an effective means of colonisation of new areas. Rhizomes sometimes are incorrectly called "rootstocks". This term is confusing and ambiguous and requires clarification. The term rootstock has been used for the primary unbranched root in a young plant, further, it may have the unfortunate connotation of root homology (Booth 1964; Gould & Shaw 1983). Undoubtedly the rhizome has both spread and survival functions. It is commonly starch-rich.

Plants originating from rhizomes are sturdy, well connected to food and water, and so better able to contend with environmental conditions than young seedlings (Booth 1964). The development of rhizomes in most of the taxa belonging to the *Pnigma* group is possibly of great significance in the adaptive radiation (chapter 11).

The presence or absence of stolons and rhizomes represents an important feature for species differentiation and a real biological distinction, although it is not always easy to distinguish between short rhizomes and underground tillers or short stolons and decumbent stems. This is especially the case in young plants.

In the *Pnigma* brome-grasses we find taxa whose habit involves the culms growing in dense clumps and emitting very short rhizomes. There are however some others which develop loose tufts connected by very long rhizomes. Sometimes the presence/absence and length of rhizomes constitute a key character for the distinction of taxa. In situations where the specimen has been incompletely collected, the identification of the taxon will simply not be possible. Cope (1982) also referred to the problems derived from an incomplete collection of material in the field. Difficulties with identification are strongly associated with the condition of herbarium material. In the field the distinction between tufted and rhizomatous species is quite clear, but in herbarium specimens the rhizomes are seldom collected and the tufted species are rarely represented by more than a single culm. It is an intractable problem in the section *Pnigma* brome-grasses.

I therefore wish to encourage plant collectors, and the writers of botanical keys, accounts and descriptions to bear in mind the importance of the characteristic habit of any plant. From the taxonomic, as well as the ecological and evolutionary point of view, all specimens should be collected entirely, including the basal parts which contain great informative value. We must not ignore certain features as a result of negligent collection. Vegetative and reproductive morphological characters contribute conjointly to the full understanding of the biology of any and every species. Both may play a key role in explaining the pattern of adaptive radiation presented. Specific cases of difficulty will be commented upon in the formal observations for certain taxa (chapter 9, section 9.3).

Chapter 9 Herbarium and Type Specimens

9.1 Concept of Taxonomic Categories

9.1.1 Introduction

Different ranks from section to subspecies have been used in this revision of the perennial brome-grasses. Some fundamental ideas about taxonomic categories, which I had in mind while attributing different ranks to taxa, are expressed here.

9.1.2 The Section Concept

Infrageneric classification should be considered if it is a practical need when two groups are distinct but not obviously generically distinct, or when in doubt as to whether to accord generic rank to a group. The structure and biodiversity of very large, diverse genera is more easily communicated if infrageneric groupings are possible, even if they are no more than informal species groups!

The main dispute in the attribution of infrageneric rank to the different groups defined in *Bromus* lies mainly in whether it should be a generic, subgeneric or sectional classification (chapter 2, table 2.1). Stebbins (1981) believed that subdivisions in *Bromus* should be recognised as subgenera rather than sections. His main criteria for a rejection of a sectional classification is based on his estimation of the strong separation between all the groups. There is much yet to be determined about the actual genetic and evolutionary affinities of the infrageneric taxa recognised in *Bromus,* however. Recent investigations on the chloroplast DNA between the *Ceratochloa* and *Pnigma* sections (Pillay & Hilu 1990) have revealed a closer relationship between them than was previously thought (chapter 11, section 11.2). An annual species of section *Bromus* (*B. arvensis)* can be crossed with many of the perennial species of section *Pnigma* (Armstrong 1990). This also reveals a closer affinity between sections than would be implied by subgeneric status, as I conceive it.

More multidisciplinary data is needed to clarify the degree of relationship between the different groups, but as a working hypothesis, I have accepted the circumscription of *Bromus* into sections. It seems to me that the numerous features that unite species groups of *Bromus s.l.,* from morphological to serological (Fairbrothers & Johnson 1961; Smith 1969a, b) and genetical (Cugnac & Camus 1944; Smith 1968) are more striking that the relatively minor features in which they differ. For my own work, totally within *Pnigma*, the sectional/subgeneric argument is, in any case, of marginal relevance only.

9.1.3 A Species Concept

There is perhaps no other subject in biology which has given rise to so much controversy as the species concept, and it still represents a perennial problem for systematists and evolutionary biologists. All the voluminous amount of literature written about the topic reflects extraordinarily the disagreement among authors.
Some parameters involved in different viewpoints can be expressed as follows:

Objectivity *versus* subjectivity
Arbitrariness *versus* non-arbitrariness
Logical in theory *versus* impractical in use
Morphological definition *versus* biological i.e., genetical definition

Species are important because they represent an important, biologically real level of integration in living nature (Mayr 1957), but their perception is very subjective. The following historical survey of different species concepts clearly shows this situation.

Typological or Essential Species Concept

Species can be recognised by their essential (i.e., of the essence) nature or essential characters, and these are expressed in their morphology. This species concept, going back to Plato (his *edos*) and Aristotle(his essence), was the concept that Linnaeus had, as well as his followers. This early concept of species was based on the belief that each species was created in its present form. The number of species on earth was the same number that had been created by God since the beginning of time. The only task of the taxonomist was to discover and distinguish between the various entities created. Nevertheless, Linnaeus was not blind to the evidence of evolutionary change. Greene (1912) clearly documented Linnaeus' belief in the common descent of certain species. In practical terms and with important conceptual variations, such as the constancy in the number of species, it represents the morphological species concept, still broadly used by taxonomists. According to this idea, a species is recognised by an intrinsic difference reflected in its morphology (Mayr 1992), which makes this species clearly different from any all other species.

As Mayr (1969) emphasised correctly, this static concept ignores the fact that species are not merely classes of objects, but are formed of natural populations of individuals which show an internal organisation and a changeable diversity based on genetic, ethological and ecological properties.

Darwin looked at the species from a viewpoint different from that of Linnaeus. As his idea of evolution became more patent, so grew his conviction that it would be impossible to delimit species objectively: "In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow (Darwin 1859).

Nominalistic Species Concept

For the nominalists, only individuals exist, the species being seen as the product of the human imagination. They ignore the fact that species are the product of evolution and not a human invention. This idea was popular in France in the 18th century. Anyone who accepts evolution must reject the nominalistic species concept.

Biological Species Concept

A new species concept arose in rejection of the simple morphological species idea, based on degree of phenetic difference. This new concept viewed the species as a reproductive community, with interactions among their individuals at a given locality. A precise definition: "Species are groups of interbreeding natural populations that are reproductively isolated from other such communities (Mayr 1957; Mayr 1992). Since the Modern Synthesis (Huxley 1942), the biological species concept based on the principle of interfertility seems to have provided a common framework to evolutionary biologists, geneticists and systematists.

Mayr is a zoologist and his concept arises from the study of organisms that mostly do not hybridise and are not vegetatively iterative. The application of the biological species concept in botany leads to difficulties, though the power of the reproductive isolation factor is not denied. For instance, blocks of cross-incompatible individuals exist in nature (e.g., *Glyceria*). Conceptually they are Mayrian biological species, despite being morphologically unremarkable and unrecognisable, as well as ecologically the same. Species that are not perceptibly different serve no obvious function in communication - a prime purpose of taxonomy: though they may have biological significance. Naming them may confuse rather than clarify general understanding. In practice, a common-sense consideration of all evidence, not just morphological, not just genetic, would lead to a workable compromise. In relatively few cases, as yet, is genetic information complete enough to be sure of the limits of biological species.

A standard species definition does not exist. There is more than one species concept and it is futile to search for one unifying definition; concepts vary depending on their purposes. I agree with Endler (1989) in observing that it is unproductive and often positively misleading to apply one species concept to meet all circumstances. The perception of the species varies among authors. The practising taxonomist will define the species on the basis of the observable morphological differences in the herbarium material used in the study, and sometimes with complementary experimental work. For the geneticist, species represent a genetic unit consisting of a large, intercommunicating gene pool. The ecologist in the field will perceive the species as a population of individuals and will manifest special interest in the grade of competition or interdependence in a particular habitat.

My personal taxonomic yardstick was based on a highly individual mixture of elements. The use of morphological differences helped me to define species in particular situations. In other circumstances, my species delimitation was the result of combining diverse parameters: cytological, morphological, anatomical, ecological and geographical data, to the extent that they were available.

My own feeling is that since the species by its nature is a complex entity, it requires a multidimensional study based on the inference of the highest possible number of available sources for its delimitation, accepting the fact that the rank will be determined in the end by a purely arbitrary decision. Numerical valuations are not inherently different! Dendrogram interpretation is not a "hard" science! The more information is deployed in arriving at rank attribution, the more likely it is that the attribution will be non-controversial and stand the test of time.

9.1.4 A Subspecies Concept

Bearing in mind the intrinsic subjectivity in species circumscription, the same situation occurs at the subspecific level.

Davis and Heywood (1963) stated: "The subspecies has been widely accepted in a sense similar to that of Du Rietz and Rothmaler, i.e., as a considerable segment of a species with a distinct area and more or less distinct morphology, often showing intergradation, and clearly fulfils a useful purpose". This pragmatic idea was the foundation of the subspecies concept in this study. Subspecies represent a recognisable distinct part of a species with differential characters consistently correlated, and they show a distinctive geographical or ecological distribution. Smith (1973) has commented on the relationships between ecotypes and subspecies, including situations where Man is providing the selective pressure. Such subspecies might well be polytopic, but not of phenetically minor peculiarity nor of random occurrence, as would be the case with a variety.

9.2. Sources of Plant material

The formal taxonomic description of four groups in the next section was based primarily on herbarium material, with much provided by the following herbaria in Europe: Berlin (B), Natural British Museum (BM), Budapest (BP), Copenhagen (C), Edinburgh (E), Florence (FI), Geneva (G), Gothenburg (GB), Jena (JE), Kew (K), Munich (M), Madrid (MA), Paris (P), Stockholm (S), Sofia (SOM) and Vienna (W, WU). The total of specimens studied was in excess of 3000.

A large collection of living specimens growing at the University of Edinburgh was a fundamental part in the leaf anatomy (chapter 4) and reproductive studies (chapter 5). The source of seeds shown and grown into adult forms was provided by several Botanical Gardens in Europe and America. A totality of 331 accession numbers were grown. They are referred to specifically where necessary. The seed and voucher collection is stored at Edinburgh (E). Field observations, particularly in Bulgaria, were also carried out.

9.3 Four Groups of European Bromus § Pnigma

Here follows an introductory key relevant to four groups of *Bromus* species that I have recognised.

1) Basal sheaths decaying into persistent fibrous reticulum ***B. riparius* group** (p.207)

1) Basal sheaths remaining intact or decaying into persistent, parallel fibres, not forming a reticulum

  2) Vigorously creeping rhizomes, often up to 1 m. Awn absent or very short, up to 0.5 mm ***B. inermis* group** (p.250)

  2) Densely/loosely tufted or rhizomatous with very short rhizomes, (1-2 cm) or longer (up to 8 cm). Awn always present, longer than 0.5 mm

    3) Basal sheaths remaining intact ***B. ramosus* group** (p.128)

    3) Basal sheaths decaying into parallel fibres ***B. erectus* group** (p.152)

9.3.1 B. ramosus Group

9.3.1.1 Account of the Taxa

B. ramosus Hudson, *Fl. Anglica*. ed. I. 40 (1762).

Perennial, loosely tufted, erect grass. Stems (50)-70-150-(220) cm tall, (1.5)-2-5.5-(7.5) mm wide, glabrous below with short patent hairs above, 4-6-(7) noded, invested at the base by 2-10-(15) light or dark brown, intact, dead leaf sheaths. Sheaths of the uppermost leaves with numerous, very long, retrorse hairs or shortly hairy, sometimes glabrous. Leaf blade 15-55 cm × 4-15 mm, glabrous or sometimes with long hairs along margins and abaxial surface; the adaxial surface glabrous or with long, fine, scattered hairs, dark green, flat, acuminate or finely pointed; ligule (1)-2-5-(6) mm, membranous, variously entire to erose; auricles 0.2-1.5 mm or absent. Flag leaf 10-40 cm × 2.5-9.5-(11.5) mm. Panicle varying from multilateral, wide, erect to nodding or unilateral, erect, narrow when young, becoming effuse, very lax, drooping or nodding in the upper part at maturity, (7)-10-35 cm long from the lowest to the uppermost node, with 2-5 branches at the lowest node, ascending, divaricate at a right angle with the stem or forming an acute angle with the main axis; the shortest (0.5)-1-9 cm, the longest 2-13 cm, with a long ciliate or glabrous scale, sometimes with scattered short hairs. Spikelets 2-3.5 cm, bearing 3-8-(10) florets; florets of the spikelet tardily or early disarticulating. Glumes glabrous or with fine, adpressed hairs near margins, subequal, green or purple-tipped, the pigment sometimes strong, rough-keeled; the lower 5.5-9.5-(11) mm, narrowly lanceolate, abruptly pointed, the upper 6-11.5 mm, oblong-lanceolate, mucronate or very shortly awned. Lemma 9.5-14.5 mm × 1.5-2.5 mm, with fine, long, adpressed hairs below, glabrous above or with long hairs sub-patent at the sides above, oblong-lanceolate, green or purplish-tipped, with 2 small teeth at the base of the awn. Awn (2)-3.5-7.5-(10) mm, straight, rough. Palea 8-10 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers 2-4 mm. Caryopsis 7.5-10 mm, dark brown to glossy orange-brown.

Key to two subspecies of ***B. ramosus***:

Panicle multilateral, effuse, very lax, drooping at maturity. Lowest node of the panicle with 2 branches, occasionally 3, with a long ciliate basal scale. Lemma 11.5-14.5 mm × 2-2.5 mm, with fine, long, adpressed hairs restricted to the base and margins in the lower half.

subsp. ***ramosus***

Panicle unilateral, erect, nodding in the upper part at maturity. Lowest node of the panicle with 3-5 branches, occasionally 2, with a glabrous basal scale, sometimes weakly hairy. Lemma 9.5-12.5-(14) mm × 1.5-2 mm with fine, adpressed hairs below, longer and sub-patent on the upper margins up to the apex

subsp. ***benekenii*** (Lge.) Lindb.

1a) *B. ramosus* (Huds.) subsp. ***ramosus***[1]

Perennial, loosely tufted. Stems (70)-73-150-(220) cm tall, robust, (2.5)-3-5.5-(7.5) mm wide. Basal leaf sheaths intact, investing the emergent stem. Sheaths of the uppermost leaves with numerous, very long, retrorse hairs. Leaf blade 23.5-55 cm × (4.5)-5.5-15 mm, glabrous, scabrid abaxially, the adaxial surface glabrous or with scattered, long hairs, flat, acuminate; ligule (1.5)-2-5-(6) mm; auricles 0.2-1.5 mm, sometimes absent. Flag leaf 15-40 cm × 4-9.5-(11.5) mm. Panicle multilateral, erect, wide when young, becoming effuse, very lax, drooping at maturity, 15-35 cm long

[1] Divided into many branches

from the lowest to the uppermost node, with 2 branches at the lowest node, occasionally 3, divaricating at a right angle with the main axis at maturity; the shortest 1.5-9 cm, the longest 4-13 cm, presenting a long ciliate basal scale. Spikelets 2.5-3.5 cm, bearing (4)-6-8-(10) florets tardily disarticulating. Glumes glabrous, occasionally with scattered hairs near margins, green or weakly purple-flecked; the lower 5.5-9.5-(11) mm, narrowly lanceolate, the upper 6-11.5-(12) mm, oblong-lanceolate. Lemma 11.5-14.5 mm × 2-2.5 mm, with fine, sometimes stiff, adpressed hairs restricted to the base and margins in the lower half, oblong-lanceolate, green or purple-flecked. Awn (2.5)-4-7.5-(10) mm, straight, rough. Palea (7.5)-8.5-10 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers (2)-2.7-4 mm. Caryopsis (7.5)-8-10 mm. Flowering in June-July, fruiting in August. Geographical distribution in fig. 9.3.1.1.

Habitats: Mixed woodlands; shady ground by stream; at wood edge in deep shade; shaded roadside bank; in oak-ash wood on rough slope; woodland by the river; wet bank in *Quercus* woodland; damp edge of grassland; among rocks by burn in open woodland; calcareous; 14-1900 m.

Type: I have not been able to track the type. Possibly Hudson's herbarium was destroyed. Therefore I choose a specimen from England as a neotype, which in my view fairly represents Hudson's concept of this species.

Neotype (fig. 9.3.1.2): "Leigh Wood, North Somerset, 5.6.1884, James W. White" (S!).

Fig. 9.3.1.1. Geographical distribution of *B. ramosus* subsp. *ramosus* (▲), *B. ramosus* subsp. *benekenii* (Δ) and apparent intermediates between both taxa (●)

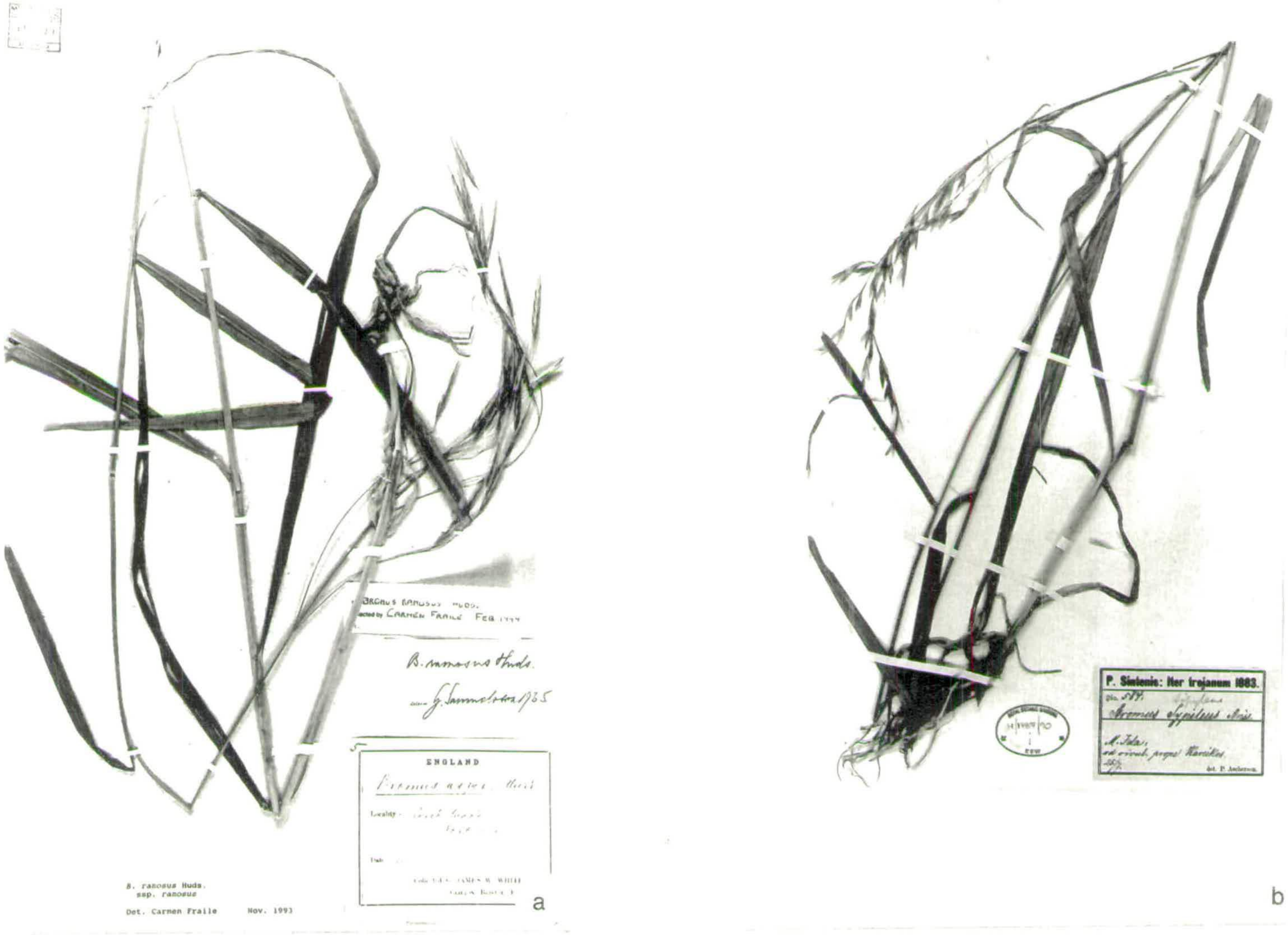


Fig. 9.3.1.2. (a) Neotype of *B. ramosus* Huds. and (b) Type of *B. sipyleus* Boiss. Mag. x0.32

Synonyms: *B. ramosus* Huds., *Fl. Angl.* ed. 1. 40 (1762); *B. asper* Murr., *Prodr. Stirp. Gotting.* 42 (1770); *B. nemorosus* Vill., *Pl. Dauph.* 2: 117 (1787); *Zerna aspera* (Murr.) Panzer, *Denkschr. Königl. Akad. Wiss. München,* 296 (1814); *Festuca aspera* Mert. & Koch, *Deutschl. Fl.* 1: 673 (1823); *Bromus asper* Murr. var. *angustifolius* Nees ex Royle, *Bot. Him.* 3: 417 (1839), *nom. nud.*; *Schedonorus asper* (Murr.) Fr., *Bot. Noti.* 131 (1843); *S. serotinus* (Beneken) Rostr., in Lange *Haandb. Danske Fl.*, ed. 3, 103 (1864). *Bromus pseudoasper* Schur, *Enum. Pl. Transsilv.* 804 (1866); *B. ramosus* Huds. var. *eu-ramosus*, Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 575 (1901); *Zerna ramosa* (Huds.) Lindm., *Svensk Fanerog.* 101 (1918); *Bromopsis ramosa* (Huds.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973).

Icones: Lange, *Fl. Danica,* fasc. 8, tab. 1382 (1763); Javorka & Csapody, *Icon. Fl. Hung.*, tab. 379, pp. 44 (1934); Hubbard, *Grasses*, pp. 70 (1984).

Selection of specimens

Scandinavia

Sweden

Gotland, Paroecia fide prope templum, 27.8.1930, *Fries*, s.n (BM, K); Skane, Alnarp, 9.8.1932, *Asplund,* s.n. (K, S); Sk. Alnarp, 25.7.1876, *Humbla*, s.n (S); Gotland, Fide vid Kyha, 27.5.1930, *Fries*, s.n (S); Sk. Alnarp, 8.1903, *Larsson*, s.n (S); Sk. Alnarps, 1903, *Vifell*, s.n (S); Scania, Oved, prope Lavausjo, 27.7.1924, *Holmberg*, s.n (S); Gotl, Eksta, Djupvik, 20.8.1916, *Johansson*, s.n (S).

Western, central and eastern Europe

Austria

Ratikon, Drei Schwestern-Gruppe, Waldrand, Flysch, 800 m, 2.8.1973, *Polatschek*, s.n (W); Austria-inferior, in silvis caeduis ad rivum in valle Hainbachtal in silva

Vindobonensi, 12.11.1913, *Spreitzenhofer*, s.n (BM, E, K, W); Oberosterreich, Salzkammergut, Traunsee, Gschliefbach, 3.7.1915, *Ronniger*, s.n (W); Oberosterreich, Salzkammergut, Traunsee, Gschliefwald, 14.8.1920, *Ronniger*, s.n (W); Niederosterreich, Feldholzern am Bisamberg, 6.7.1912, *Korb*, s.n (W); Niederosterreich, Wienerwald, Lavibwaldern, 7.8.1911, *Korb*, s.n (W); Austria inferior, Haltertal prope Hutteldorf ad Vindobonan, *Heimerl*, s.n (BM, E, K, W).

Belgium

Namur, Heure, bois de Saumot, bois clairiere a l'exp.s., sur calcaire, 1.8.1977, *Duvigneaud*, 77 B 677 (B, MA); Heure, bois, 18.7.1910, *Mairlot Theux*, s.n. (MA).

Czechoslovakia

Slovakia occidentalis, Montes Strazovska hornatina, convale rivuli ad pedem meridionalem montis Maly Rokos sept.-occid, 400-450 m, 23.7.1967, *Holub & Mesicek*, s.n (BM, MA, W).

Denmark

Lolland, Lindelse Skov., 14.7.1944, *Dahl*, s.n (BM); South of Aarhus, Marselisborg, beech wood, 1.9.1964, *Larsen & Pedersen*, s.n (BM).

France

Pyrenees-Atlantiques, 800 m, 11.7.1979, *Charpin & Jeanmonod*, 15544 (E); Haute Savoie, Mont Paleve pres Veirier, 600 m, 1.8.1912, *Ekman*, s.n (S); (Nord) Mareshes, 28.6.1938, s.n (K).

Germany

Gockersgraben in Guttenbergerwald bei Wurzburg, Keuper, 250 m, 20.7.1902, *Rost*, s.n (E, WU); Mittelfranken, Kr. Hersbruck, 13.7.1946, *Starcs*, 3416 (S); Willinger Berg (b.Stadl-Ilm), 16.7.1911, *Bornmüller*, s.n (B); Erfurt, Steiger, 7.84, *Ruvalph*, s.n (B); Gockersgraben im Guttenbergerwald, Keuper, 250 m, 20.7.1902, *Rost*, s.n (E, WU); Ehersberg bei Weimar, 8.1874, *Haussknecht*, s.n (WU); Rosenburgh, Bonn a Rh., 30.7.1907, *Vestergran*, s.n (S).

Hungary

Inter pagos Izbeg et Pomaz, sylvis umbrosissimis, solo argilloso, 250 m, 12.7.1901, *Degen*, s.n. (BM, K).

Luxembourg

Between Ueberseyren & Beyren, beech forest, 27.7.1957, *Young, Reichling, Ettlinger & Jungblut*, s.n (BM).

Poland

Silesia Inferior, silva foliosa ad Kozielno apud Zabkowice Sl, 27.7.1966, *Pender*, s.n (W).

Switzerland

Kanton Waadt, Les Plans sur Bex, 23.7.1972, *Scholz*, s.n (B); Stachelberg, ex subalpinis, 3-5000', 8.1857, *Ball*, s.n (E).

Iberian peninsula

Portugal

Estremadura, Alcobaca, sebes sombreadas, 40 m, 30.6.1962, *Rainha*, 5652 (MA).

Spain

Huesca, Castejon de Sos, valle y rio Esera, shady ground by stream, 950 m, 27.7.1955, *Sandwith*, s.n (BM); Navarra, Orbaizeta, hayedo, 900 m, 21.8.1985, *Aizpuru & Catalan*, s.n (MA); Catalogne, Montagne de Cabrera, 1900 m, 7.1910, *Sennen*, s.n (MA); Catalogne, Massif du Tibidabo, 9.7.1911, *Sennen*, s.n (MA); Cataluña, Pont de Molins, fourres, 6.7.1908, *Sennen*, s.n (MA); Barcelona, Montserrat, 9.1914, *Caballero*, s.n (MA); Navarra, Romanzado, bosque mixto, 530 m, 17.6.1984, *Aizpuru & Catalan*, s.n (MA); Granada, Guejar, Sierra Nevada, 21.8.48, s.n (MA).

Mediterranean Europe

Greece

Pindus Mts,Visikhori, stream, 3300 ft, 3.8.1961, *Cambridge Univ. Exp.*, s.n (K).

Italy

Palermo, al Parco, sylvaticis, 5, *Todaro* s.n (BM, E); Reg. Marche, Prov. Ascoli Piceno, 1020 m, wet bank in *Quercus* woodland, 17.7.1985, *Jury, Watson, Webb & Jackson*, 6501 (BM); M. Cerreto, vers. sett., 27.6.1912, *Pampanini*, s.n (FI).

Ireland

Galway, Headford, 6.1832, s.n (BM); V.C. H 23 Westmeath, 28.6.1952, *Drummond*, 850 (MA); Clanre, Lisdoovarna, 23.7.1933, *Nilsson & Degelius*, s.n (S); V.C. H 12 Wexford grid 03/81, wood NE of Banclody, 4.9.1962, *McCallum & Webster*, s.n (BM).

Great Britain

England

V.C. 60 Lancashire west, Shrang End nr Yealand, 8.1884, *Wilson*, s.n (BM); V.C. 56 Nottinghamshire, 90 ft, 26.7.1963, *Bowden & Hillman*, 451 (BM); Dorset, W. Adder wood, 1.8.1944, *Dunston*, s.n (K); Surrey, Petersham, woodland, 11.7.1964, *Blake*, 22298 (K); V.C. 66 roadside Force, Durham, Teesdale, 4.7.1961, *Raven*, 16256 (BM); Surrey, Mickleham, edge of wood, 23.7.1952, *Melderis & Bangerter*, 133 (S); Northsomerset, Leighwood, 5.7.1884, *White*, s.n (S); V.C. 16 West Kent, Kemsing, wood edge in deep shade, 1.7.1972, *Jermy*, 9517 (S); Sussex, near Storrington, woods at the foot of the Downs, 8 feet high, 28.7.1913, *Littlebury*, s.n (BM).

Scotland

Wasterness, Rahoy, L. Sunart, 9.8.1884, *Ex. Herb. E. F. Linton* (Legi ipse), s.n (BM); V.C. 72, Dumfries, Mouswald, woodland, 6.8.1957, *Bangerter & Milne-Redhead*, 347 (BM); V.C. 95, Elgin, Darnaway Forest, damp edge of grassland, 28.6.1953, *Melderis*, 261 (BM); V.C. 103 Mull, Tobermory, Rubha nan Gall, wood, 22.8.1967, *Melderis*, 2128 (BM); V.C. 103 Mull, Aros House woods, among rocks by burn in open woodland, 30.6.1969, B. M. Mull Survey, 3611 (BM); V.C. 108 W. Sutherland, near Inchnadamph on limestone, 15.7.1908, *Marshall*, s.n (BM); V.C. 103, Mull Tobermory village, bank of Tobermory river, 21.8.1967, *Melderis*, 2073 (BM).

Wales

Near Brecon, 23.7.1883, *Ley*, s.n (BM).

1b) ***B. ramosus*** subsp. ***benekenii***[1] (Lange) Lindb., *Finska Vet. - Soc. Forhandl.* 38, 13: 10 (1906).

Perennial, loosely tufted. Stems (50)-70-130-(145) cm tall, (1.5)-2-4.5-(5.5) mm wide. Basal leaf sheaths intact, investing the emergent stem. Sheaths of the uppermost leaves almost glabrous or shortly hairy. Leaf blade 15-35.5 cm × 4-10 mm, glabrous or with scattered hairs along the margins abaxially, the adaxial surface with scattered, long, fine hairs, flat, finely pointed. Flag leaf 10-28-(36) cm × (2)-2.5-7.5 mm; ligule (1)-2-4 mm; auricles (0.1)-0.3-0.7 mm, sometimes absent. Panicle unilateral, narrow, erect when young, becoming looser, nodding in the upper part at maturity, (7)-10-20-(28) cm long from the lowest to the uppermost node, with 3-5 branches, occasionally 2, forming an acute angle with the main axis; the shortest (0.5)-1-3-(4) cm, the longest 2-5-(7) cm, with a glabrous basal scale, sometimes weakly hairy. Spikelet 2-3 cm, bearing 3-4 florets early disarticulating. Glumes with fine, long hairs near the margins, occasionally glabrous; the lower 6-8.5 mm, narrowly lanceolate, the upper 8.5-11.5 mm, oblong-lanceolate.

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[1] Ferdinand Beneken (1800-1859), pharmacist and prestigious horticulturist

Lemma 9.5-12.5-(14) mm × 1.5-2 mm, with fine, long, adpressed hairs below, longer and sub-patent on the upper margins up to the apex, narrowly lanceolate, green or slightly purple-flecked. Awn (2)-3.5-7-(8) mm, straight, rough. Palea 8-9.5 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers (1.5)-2-3.5 mm. Caryopsis (7)-7.5-8.5-(9) mm. Flowering in June-July, fruiting in August. Geographical distribution in fig. 9.3.1.1.

Habitats: Beech wood on slopes; shadowy deciduous and mixed woods; under *Corylus* in clearing in *Picea* forest; limestone; soil neutral and slightly calcareous; soil organic pH = 5; granitic; 90-1700 m.

Type: Described from Denmark: "in insula Lolland" E. Rostrup (C); Iso. (FI).

Synonyms: *Schedonorus benekeni* Lange, *Fl. Danica*, fasc. 48: 5, t. 2826 (1871); *B. benekeni* (Lge.) Trimen, *J. Bot.* 10: 333 (1872); *B. asper* Murr. var. *benekenii* Syme, *Sowerby Engl. Bot.* 11: 157 (1872); *B. ramosus* Huds. var. *benekenii* (Lge.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 576 (1901); *Zerna benekenii* (Lge.) Lindm., *Svensk Fanerog.* 101 (1918); *Z. ramosa* (Huds.) Lindm. subsp. *benekenii* (Lge.) Tsvelev, *Novit. Syst. Pl. Vasc.* (Leningrad) 7: 53 (1971); *Bromopsis benekenii* (Lge.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973); *B. ramosa* (Huds.) Holub subsp. *benekenii* (Lge.) Tsvelev, *Fl. Part. Europ. S.S.S.R.* 1: 175 (1974).

Icones: Lange, *Fl. Dan.*, fasc. 16, tab. 2826 (1871); Javorka & Csapody, *Icon. Fl. Hung.*, tab. 380, pp. 44 (1934); Hubbard, *Grasses*, pp. 68 (1984).

Selection of specimens

Scandinavia

Norway

Prope Christianiam, Par. Asker, 9.8.1890, *Dyring*, s.n (BM, MA); Lier, 18.7.1869, *Blytt*, s.n (BM); Sondmore, Hjorundfjord, Ronningen, 31.7.1918, *Dahl*, s.n (S); Christiania, Bergsfjiel, *Blytt*, s.n (BM).

Sweden

Sodermanland, Toro, 4.8.1929, *Asplund*, s.n (B, MA); Skane, Sodra Mellby, Stenshuvud, Carpinus-Skog vaster om berget, 7.7.1954, *Asplund*, s.n (S); Ostergotland, Omberg, Vastra Vaggar Vaversunda parish, 8.7.1951, *Smith*, s.n (BM); Gotlandia, Harsne, 7.7.80, *Kahe*, s.n (S); Gotl, Lojsta, Stanga glott, 7.1870, *Krok*, s.n (S); Gotl. Etelhen s-n, en hasselhage nara jeruvagutationen, 2.7.1895, *Roman*, s.n (S); Vastergotland, Kinnekulle, 14.6.1914, *Hulphers*, s.n (S); Upland, Estuna, Hammarudden., 2.7.1953, *Smith*, s.n (BM); Vastergotland, par. Skallsjo, Oskarshojd, 8.1897, *Thedenius*, s.n (E); Ostergotland, Omberg, par. V. Tollstad, Makersbergen, 5.7.1950, *Smith*, s.n (BM); Scania, Lommma, Alnarps parks, 13.6.1938, *Norman*, s.n (E).

Western, central and eastern Europe

Austria

Nieder-Osterreich, Waldern bei Perchtoldschorf, 20.6.1923, *Vetter*, s.n (W); Kaisersteinbruch bei Bruck, Leitha, Ungarn, 22.6.1905, *Vetter*, s.n (W); Niederosterreich, Feldholzern am Risamberg, 6.7.1912, *Korb*, s.n (W); Osterreich, Niederosterreich, Weinviertel, 220 m, 20.6.1973, *Krendl*, s.n (W); Klostertal, Dalaas/Mason, Kalk, 900-1000 m, 15.6.-3.7.1971, *Polatschek*, s.n (W); Walgau, Ruine Ramschwag b. Nenzing, wiesen und Waldgurtel um die Ruine, 18.7.1971, *Seipka*, s.n (W); Klostertal, Verwall, Kalk u. silikat, 1480-ca 1150 m, 15.6.-3.7.1971, *Polatschek*, s.n (W); Austria inferior, silvis in valle Weixeltal prope Oppidum Baden, solo calc, 300 m, 24.7.1971, *Hayek*, s.n (S); Wien III, Schonbrunn, 10.6.1904, *Ronniger*, s.n (W).

Belgium

Liege, Pailhe, lisiere de bois condrusien neutrophile, riche en *Fraxinus excelsior*, 230 m, 14.8.1985, *Lambinon*, 85/378 (B, MA); Namur, Heure, bois de Saumont, lisiere forestiere, sur calcaire, exp.s, 8.1977, *Duvigneaud*, 77 B 677 (B, MA); Furfooz, bois, 22.6.1958, *Castagne*, s.n (MA).

Czechoslovakia

Harta, Fuchshubel, 430 m, 18.6.1909, *Cy.*, s.n (BM, E, S); Moravia centr, Brno, Blansko, prope Macocha, fagineis, 350 m. 8.7.1925, *Sirjaev & Sirjaev*, s.n (K, S, W, WU); Waldhang am Fuchshubel, Harta, 430 m, 26.6.1905, *Cypers*, s.n (WU); Com Neutra, Ghymes, montis Varhegy, silvaticis, 26.6.27, *Rechinger*, s.n (S); Vsetin, dumetis montis Recevna, 8.7.1803, *Rubela*, s.n (B).

Denmark

Falster, Kohaven, Kykjobing D. 37, 16.7.1942, *Dahl*, s.n (BM); Allinde Lille Skov, beechwood on chalky boulder clay, 24.6.1950, *Tutin*, 5013 (BM).

France

Aubrac, bosques, 22.8.1815, *Sennen*, s.n, (MA); Dans les coupes du bois des Fourches, 8.7.1851, *Parisot*, s.n (BM); Cote d'Or, Combe de Malgorge pres Changey, 3.8.1875, *Bomet*, s.n (K); Dep. Haut-Rhin, Foret de la Hardt, coupe sur sol neutre a legerement calcaire, 242 m, 3 et 13.6.1986, *Rastetter*, s.n (MA); Gallia, Pyren. Orient, Haute Ariege, *Aymeric*, s.n (S).

Germany

Wurzsburg, Waldlichtung auf der Hohe des Unglucksbergs, Guttenbergerwald, Keuper, 300 m, 13.7.1902, *Rost*, s.n (E, WU); Laasitzer Bergland, Laasche, 7.7.1917, *Weder*, s.n (B); Baden, Heidelberg, 7.1907, *Vesterzren*, s.n (S); Frankischer Jura, Hangbuchenwald, 450-500 m, 5.6.66, *Scholz & Hiepko*, 95, (B); Bavaria, silvis prope

Nürnberg, 10.6.1902, *Kaulfuss*, s.n (S); Munchen, Pallach, 23.7.1929, *Ekman*, s.n (S); Guttenbergerwald bei Wurzburg, 13.6.1902, *Rost*, s.n (B).

Hungary

Herkulesbad, 7., *Golopencza*, s.n (BM, K, W); In fagetis montium Budensium (Harshegy Pilishegy), solo calcareo, 200-400 m, 6.1900, *Degen*, *Flatt* & *Thaisz*, s.n (E, K, W, WU); In sylvis umbrosissimis inter pagos Izbeg et Pomaz, solo argilloso, 250 m, 12.7.1901, *Degen*, s.n (E, W, WU); Ungaria meridional, silvis prope Nagy Nyarad, 13.7.67, *Janka*, s.n (B); Budapest, Zugliget, 30.6.1941, *Pamyouf*, s.n (S).

Luxembourg

A l'Est de Dahlem, *Querceto-carpinetum* sur marnes liasiques, 330 m, 6.8.1954, *Reichling*, s.n (K); Between Uebersyren and Beyren, beech wood, 27.7.1957, *Reichling*, s.n (BM); Between Ueberseyren & Beyren, beech forest, 28.7.1957, *Young*, s.n (BM).

Poland

Lublin, Walde bei Wrutkow, 21.6.1918, *Hayek*, s.n (WU); Pokrzywna ad Glucholazy, silva mixta, 18.7.1957, *Krawiecova*, s.n (B).

Rumania

Crisana, distr. Arad., *Querceto* cerris vallis Cladova, solo granitico, 160 m, 14.7.1941, *Borza*, *Buia* & *Pteancu*, s.n (W, WU); Transsilvania, distr. Alba, in Coryleto, 1100 m, 6.8.1969, *Gergely*, s.n (S).

Switzerland

Pays de Gruyere, Monbovon, 772 m, 30.6.04, *Jaquet*, s.n (WU); Einer tiefen Schlucht unter Rotbuchen und Rottannen bei Albeuve in der Gruyere auf dem linken Ufer der Sarine in Canton Freiburg (Schweiz), Himbeer- und Brombeergebusch, kalk, 850-900 m, 19.8.1906, *Kneucker*, s.n (E, K, MA, WU); Kt. Aargau, Zurischen Aarau und Wasserfluh, Buchenwald, 5.6.1921, *Samuelsson*, s.n (S).

Former U.S.S.R.

Mosqua, silva pr. Mjtisczi, 5.7.1902, *Syrejsczikow*, s.n (S, WU); Tula, silva frondosa pr. Melechowka, 18.7.1902, *Zinger*, s.n (S, WU); Serpuchov, prope pag. Luzhki, 18.8.1945, *Mikeschin & Makarov*, s.n (WU); Ucrania, Distr. Bila Fzerkva, silva, 5.7.1922, *Polonska*, s.n (S); Harjumaa, parish of Juri, shadowy deciduous and mixed woods, 17.7.1930, *Uksip*, s.n (S); Latvia, prov. Vidzeme, Priekuli, 27.7.1923, *Starcs*, 3460 (B, S); Voronesch prov, Pravlovi Distr, Kozlovka, 25.6.1913, *Orlov*, s.n (S).

Iberian peninsula

Spain

Jaen, Siles, Barranco de las Acebedas, 1280 m, 5.8.1984, *Soriano*, s.n (MA); M. Port de Benasque, sylva prope hospitium gallicum, 8.1831, *Endress*, s.n (K, W); Asturias, Valgrande, in fagetis abundantissimus, 900 m, 28.7.1958, s.n (E); Navarra, Isaba, Barranco Aztaparreta, Hayedo abetal sobre calizas, 1100-1500 m, 4.8.1987, *Seguinolaza*, *Uribe-Edularne* & *Uruitre*, s.n. (MA); Prov Oviedo, Picos de Europa, Oberhalb von Pandetrave, Faguswald, 1570 m, 8.9.85, 254-77-85-10 (B); Salamanca, Linares de Riofrio, Las Honfrias, 5.7.1979, *Amich* y *Rico* (MA).

Mediterranean Europe

Albania

Distrit of Korce, dry beech woods, 550 ft, 26.8.1935, *Alston & Sandwith*, 2698 (K, S).

Bulgaria

Smolyan, under *Corylus* in clearing in *Picea* forest, 1500 m, 16.8.1988, *Jury & Thornton-Wood*, 9784 (BM, MA); M. Vitosa, fageto, 1320 m, 13.8.1953, *Vihodcevsky*, s.n (B, E, MA, S, W); In graminosis m. Vitosa, cupra pagrin Bojana, 20.7.1930, *Stojanoff*, s.n (S). Biosphere Reserve "Chervenata stena", edge of *Fagus* woodland, shade, 1530 m, 27.7.1993, *Fraile*, 34 (E); Papovi livadi, beside the road, exposed, 1550 m, 29.7.1993, *Fraile*, 39 (E).

Greece

Pindus Mts, Scamnelli, limestone rocks, 4400 ft, 9.8.1961, *Cam. Univ. Exp.*, s.n (K); Pindus Mts, Scamnelli, in deep limestone pavement, little light, 4500 ft, 9.8.1961, *Camb. Univ. Exp.*, s.n (K).

Italy

Firenze, Etruria, in silvis abietinis hinc inde, solo siliceo-humoso, 950-1000 m, 31.7.1912, *Fiori*, s.n (BM, FI, K, WU); Reg. Trentino bei Piere di Ledro, 4.7.1977, *Scholz*, s.n (B); Vallombrosa lungo la via pel Saltino, 7.1901, *Fiori*, s.n (FI); Gargano, Foresta umbrosa, calcare, 850 m, 20.5.1913, *Fiori*, s.n (FI); Calabria-Sila, Fossiata (Longobucco), granitico, 1350 m, 29.7.-3.8.1918, *Fiori*, s.n (FI).

Former Yugoslavia

Hercegovina, silv. subalp. montis Velez planina, 3.7., *Murbeck*, s.n (WU); Hercegovina, in silv. subalp. montis Velez planina, 27.7., *Murbeck*, s.n (S).

Great Britain

England

Surrey, Effingham Hill, beech wood on chalk, 7.7.1971, *Hubbard*, 17.7.71 (B, K); V.C. 17, Surrey, two places near Polesden Lacey, 31.7.1966, *Lousley* (Leg. ipse), s.n (BM); London, Kensington Gardens, 4.8.1871, *Trimen*, s.n (BM); V.C. 20 Tring Urban parish, Herts, Stubbing's Wood, 23.6.1959, *Dandy*, 1368 (BM); V.C. 33 E. Gloucester, Painswick, beech wood, 3.7.1982, *Pankhurst*, 80/50 (BM); North of Painswick Beacon, in beech wood on oolite, 3.7.1932, *Shaw.*, s.n (K); V.C. 33 E. Gloucester, Painswick, beech wood near Pitchcombe, 14.6.1901, *Marshall*, s.n (BM); V.C. 17, Surrey, Compton, track under beech, 21.6.1977, *Pankhurst*, 77/37 (BM).

Scotland

V.C. 89, Killiecrankie, under planted *Fagus,* 28.7.1974, *Mullin*, 27/9111629 (BM); Perthshire, Craig Hall, Blairgowrie, deeply wooded limestone gorge, 29.8.1976, *Copping*, 174482 (K).

Wales

Monmouth, woods, Piercefield Park near Chepstow, limestone, 3-400 ft, 22.6.1878, *Ley*, s.n (BM); Monmouthshire, woods Wynd cliff, near Tintern, limestone, 600 ft, 22.6.1878, *Ley*, s.n (BM).

Apparent intermediates between *B. ramosus* Huds. subsp. *ramosus* and *B. ramosus* Huds. subsp. *benekenii* (Lange) Lindb. (fig. 9.3.1.1)

Austria

Klostertal, Buchenwald, Flysch, 800 m, 22.8.1980, *Polatschek*, s.n. (W).

Sweden

Sk. Kallaberg, 8.1881, *Wallengren*, s.n (S); Sk. Alnarp, 7.1884, *Palmér*, s.n (S).

Switzerland

Zurich, champ d'essai de la station federale du controle des semences a Zurich, sol argileux, 460 m, 24.6.1890, *Stebler & Schroter*, 142 (K, S).

9.3.1.2 Assessment of the Taxonomic Status of B. ramosus-benekenii and Aggregates

9.3.1.2.1 Résumé of Taxonomic History

These two taxa have received different treatments according to diverse authors.

B. ramosus was described by Hudson in 1762 in the first edition of his *Flora Anglica*. Linnaeus in his "Mantissa" pp. 34 (1767) applied the same name *B. ramosus* to an entirely different plant (now *Brachypodium ramosum* Roemer & Schultes = *B. retusum* (Pers.) Beauv.), and probably from a mistaken deference to the great naturalist, Hudson in the second edition of his *Flora Anglica* (1778) abandoned the name *B. ramosus* and called the British plant *B. nemoralis*. Other botanists gave it various appellations: Murray (1770) applied the name *B. asper*; Solander named it *B. serotinus* in 1773, although this name was never published (Trimen 1872). Grenier and Godron (1856) defined three species under the section *Festucaria* (= § *Pnigma*), one of them was *B. asper* Murray which later was treated as a synonym of *B. ramosus*. Subsequent authors, such as Steudel (1855), Schur (1866) and Nyman (1889) included *B. asper* in their respective treatments of this group. It was Richter in 1890 who determined the synonymy and priority of the taxon *B. ramosus* with *B. asper*, and re-established that binomial.

B. benekeni (Lge.) Trimen was described by Lange in 1871 under the binomial of *Schedonorus benekeni* in *Flora Danica.* Later, Trimen (1872) treated it as a species of *Bromus*, keeping the rule of priority. It was from that time that the status and relationship of these taxa began to be unclear. The publication of Ascherson and Graebner (1901) could be regarded as the origin of the controversy about the attribution of rank- which is still not resolved. These two authors treated *B. benekenii* as a variety of *B. ramosus*. Hegi in 1906 gave *B. benekenii* the rank of a variety of *B.*

ramosus, as also did Stoyanov and Stefanov (1925). Hayek (1933) treated it as a subspecies. In the most recent European Floras, such as *The Flora U.S.S.R.* (Nevskii & Sochava 1963), *Flora Republicii Socialiste România* (Todor 1972), *Flora Europaea* (Smith 1980) and *Flora d' Italia* (Pignatti 1982) both taxa are recognised as species. The prevailing modern tendency has been to split them into two species. However, due to the close similarity, their taxonomic status as species seems to me very dubious (see sect. 9.3.1.3 for further discussion).

B. ramosus Huds. subsp. ***sipyleus*** (Boiss.) C. Fraile, *comb. nov.*

B. sipyleus was described by Boissier in 1854 in his *Diagn. Pl. Orient. Nov. Ser.* 1 (13): 65 (1854). In two major accounts, Flora of Pakistan (Cope 1982) and *Flora of Turkey* (Smith 1985), this taxon was viewed as an endemic of the E. Mediterranean related to *B. ramosus*. A detailed study of the type and other few authentically named specimens (K!) (fig. 9.3.1.2) show a great similarity to *B. ramosus* subsp. *benekenii* in terms of the architecture of the panicle, and glabrous scale, differing from it in the indumentum of the sheath and the completely glabrous lemma. It seems to me to be an outlier of the *B benekenii* complex, and a subspecific rank appears to be well justified.

9.3.1.2.2 Macromorphological Review

One of the main features which characterises *B. ramosus* subsp. *benekenii* is the relative delicacy (relative smallness and apparent physical weakness) of the spikelet which is occasioned by the width of the lemma (narrow, 1.5-2 mm) and the presence of marginal, long, fine, sub-patent hairs well developed up to the apex. In *B. ramosus* subsp. *ramosus* the appearance of the spikelets is more coarse, with a broader lemma (2-2.5 mm) and the presence of stiff, adpressed hairs restricted to the base and margins in the lower half.

The number of the lowest branches in the panicle of both taxa, subspecies *ramosus* and subspecies *benekenii* (2 and 3-5 respectively), is not an absolute diagnostic character. In my comprehensive analysis of the latter I have observed specimens with all the features which define this taxon but where the number of branches was 2. I have also seen living specimens in Scotland otherwise typical of *B. ramosus* subsp. *ramosus* with 3 branches.

The shape of the panicle represents a morphological character which differentiates both taxa. Subspecies *benekenii* develops unilateral, erect, narrow, panicles which become looser, nodding in the upper part at maturity, with the basal branches forming an acute angle with the main stem. In contrast, subspecies *ramosus* has multilateral, wide, erect to nodding panicles, becoming effuse, very lax, drooping at maturity, with the basal branches divaricate at a right angle with the stem.

9.3.1.2.3 Micromorphological Review

One reproductive character, very particular for each taxon, is the time of disarticulation of the spikelet. In *B. ramosus* subsp. *benekenii* it seems to be early while in *B. ramosus* subsp. *ramosus* it is tardy, the florets remaining attached for a longer time to the spikelet axis. This difference is accounted for by the nature of the rachilla and callus scar. In the subspecies *benekenii* the central tissue of the callus scar is scanty; the rachilla is thus effectively hollow and its vascular bundles are less well developed (fig. 9.3.1.3). The subspecies *ramosus* has considerable central tissue in the callus scar, the rachilla is effectively solid and exhibits three very well developed vascular bundles. The persistence and strength of these vascular bundles seem to comprise a strong mechanism for attachment of the floret to the rachilla (fig. 9.3.1.4).

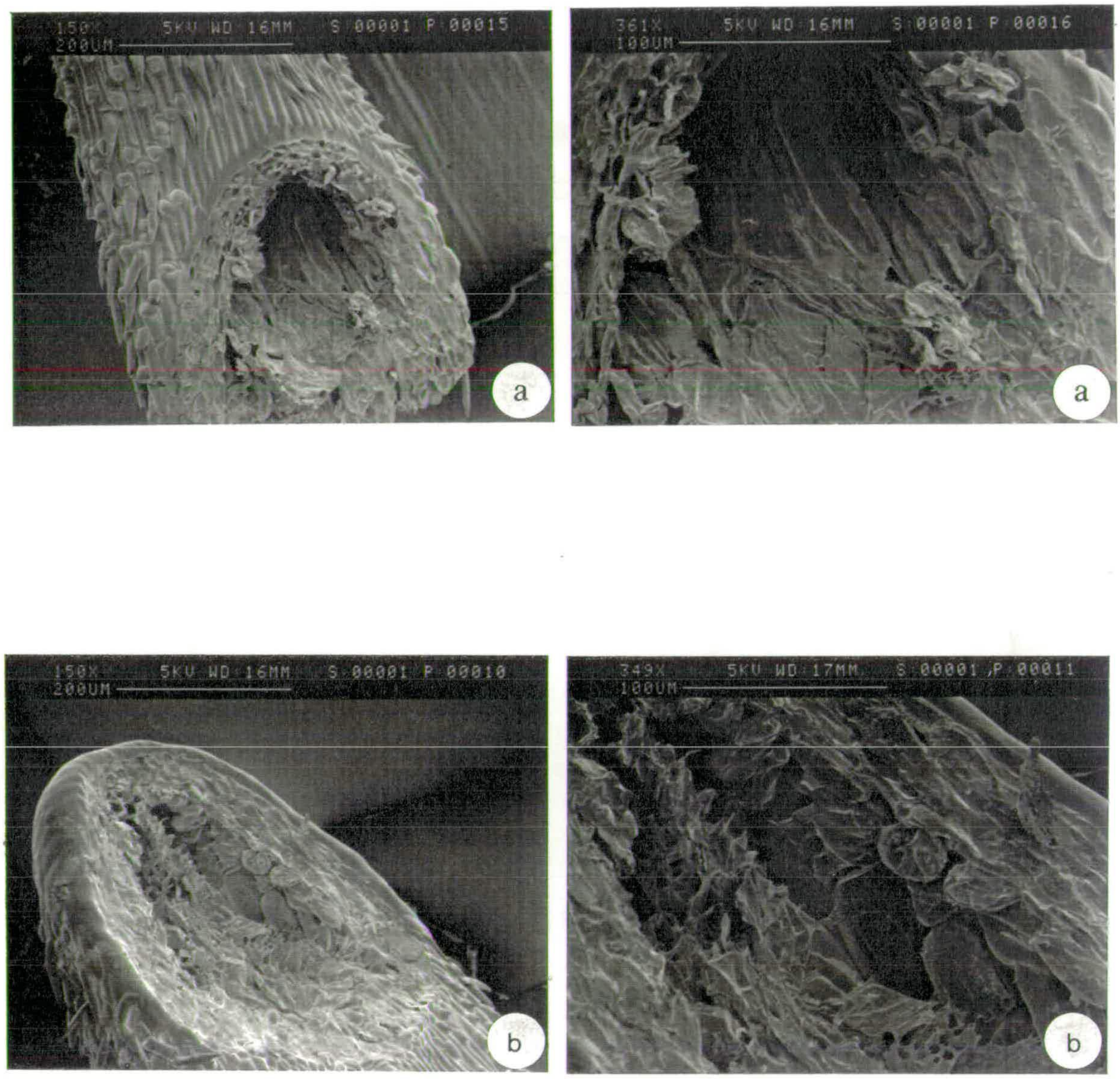

Fig. 9.3.1.3. S.E.M. results of the system of attachment in florets of subspecies *benekenii*. Note the internal hollow in the rachilla with only three main vascular bundles (a), and the poorly developed central tissue in the callus scar (b). Magnifications are indicated by bars

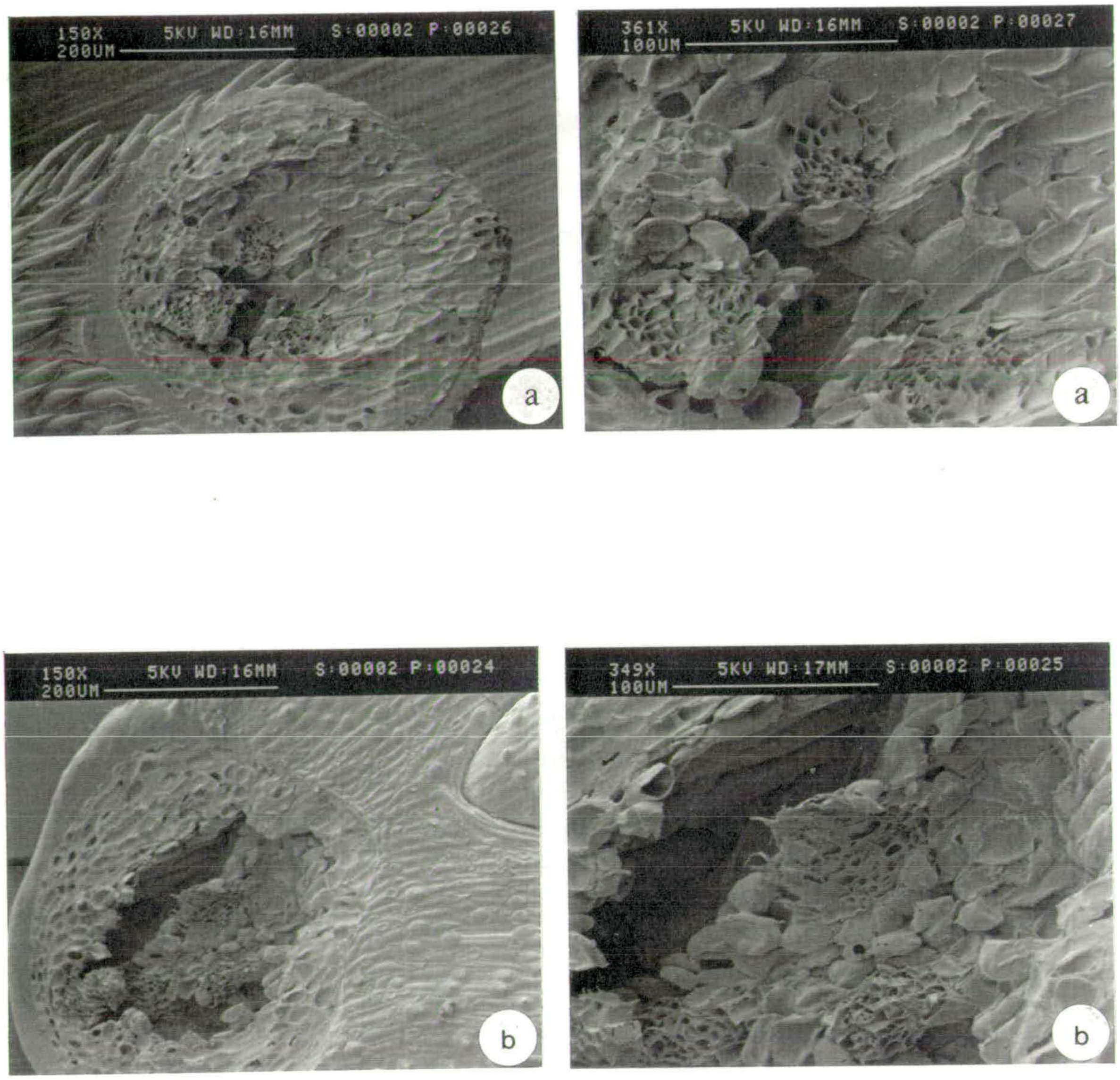

Fig. 9.3.1.4. S.E.M. results of the system of attachment in florets of subspecies *ramosus*. Note the well developed vascular bundles in the rachilla (a), and central tissue in the callus scar (b). Magnifications are indicated by bars.

This difference in the time of disarticulation could have important biological-reproductive consequences for the spreading and survival of the colony. The significance is unknown, and more research is needed.

9.3.1.2.4 Ecological and Geographical Distribution

In terms of ecological distribution, both taxa seem to have the same inclination for shady woods although *B. ramosus* subsp. *ramosus* seems to be more characteristic of humid environments, such as the bank of rivers and moist woodlands. The degree of soil pH tolerance varies also among these two subspecies (chapter 11, sect. 11.3).

An observation detected in the analysis of both taxa is the tendency towards a geographically based variation in size, in certain morphological characters. Thus, specimens of the subsp. *benekenii* from Austria are quite subsp. *ramosus*-like, coarse, with very broad leaves, thick stems and longer panicles - in contradistinction to specimens from Sweden which are smaller, with a fragile appearance recollecting typical *B. ramosus* subsp. *benekenii*. The same tendency is shown in the subspecies *ramosus*. Thus, specimens from England are characterised by their essentially large size parts, coarse look with broad leaves, long panicles and thick stems while specimens from Sweden are more subspecies *benekenii*-like. This particular observation may be related to different environmental aspects, such as day length, variations in temperature, or humidity.

The geographical distribution of these taxa in Europe is shown on the map (fig. 9.3.1.1). They are almost coincident throughout the range of *B. ramosus* subsp. *ramosus* but *B. ramosus* subsp. *benekenii* is more widely distributed in these largely central and western areas and has a substantial extension to the East.

As a result of the analysis of many specimens over a very wide geographical range, I have found intermediate forms which connect these two taxa (fig. 9.3.1.1). Thus, the boundaries between them may be unreal and they could represent extremes of a continuous pattern of variation.

9.3.1.3 Conclusions

My choice of a subspecific rank of both taxa is based on the following reasoning: They have attributes in common while others are very specific for each taxon, like the "delicacy" of the lemma and structure of the panicle, both these characteristic of *B. ramosus* subsp. *benekenii.* However, there is not a sufficient degree of morphological differentiation to treat them as different species. I have also found apparent intermediate forms which connect these two putative taxa. Regarding the pattern of geographic distribution the "benekenoid" morphology seems to be northern and central Europe (mainly) while the "ramosoid" morphology is more central to western Europe, although it exhibits some overlapping distribution related to both taxa. A name for the variants is needed, for communication and as a focus for further observation, but I think it is unlikely that they are separate species.

9.3.2 B. erectus Group

9.3.2.1 Account of the Taxa

B. condensatus Hackel, *Öesterr. Bot. Z.* 29: 209 (1879).

Perennial, with isolated, compact or loose tufts connected by thin rhizomes, 1-3.5 cm long. Ascending to erect stems, 16-70 cm tall, (0.4)-0.5-1.8-(2) mm wide, glabrous, occasionally finely hairy. Leaf sheaths varying from densely lanate, with greyish hairs to minutely pubescent or glabrous, sometimes with scattered, long, retrorse hairs; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous or shortly hairy, linear, conduplicate or involute, occasionally flat; the basal 3.5-16-(17) cm × 0.5-1-(1.5) mm, the cauline 3-14.5-(20) cm × 0.4-1-(1.5) mm; ligule (0.3)-0.5-1.3-(1.4) mm. Flag leaf 3-14 cm × 0.3-0.8-(1.5) mm. Panicle erect, narrowly ovate, compact when young, becoming broadly ovate at maturity, (1.5)-3-8.5-(10.5) cm long from the lowest to the uppermost node, bearing (5)-6-23-(31) spikelets. Panicle branches very slender, straight, sometimes curved upwards, 1-5-(6) at the lowest node; the shortest 0.5-1.5-(2) cm, the longest 0.8-3.5 cm. Spikelets (1)-1.5-2.5-(3) cm, narrowly ovate when young, more broadly ovate at maturity, with 3-7 florets; rachilla (0.9)-1-2.5 mm, glabrous. Glumes and lemmas with narrow or broad hyaline margins, broader towards the apex, sometimes purple-flecked. Glumes subequal, the lower (4.7)-6-9-(10) mm, narrowly lanceolate, the upper (6)-7.5-10-(12) mm, narrowly or broadly lanceolate. Lemma (7)-8-12 mm × 1.4-2.5 mm, glabrous or with fine, short, adpressed hairs, narrowly lanceolate to widely ovate-lanceolate. Awn (0.7)-1-5-(5.5) mm, straight. Palea 7-9-(10) mm, shorter than the lemma. Stamens 3, anthers (3.5)-4-6 mm. Caryopsis 5.8-8.5 mm.

Key to three subspecies of ***B. condensatus*** Hackel:

1) Spikelet 2-2.5-(3) cm long. Lemma (10)-10.5-12 mm × 1.5-2.5 mm, ovate-lanceolate with broad hyaline margins, especially towards the apex, 3 prominent nerves, 2 more obscure disappearing only towards the bottom of the lemma. Awn (2.5)-4-5.5 mm. Sheaths glabrous or with long, scattered, retrorse hairs. Rhizomes 2-3.5 cm.

B. condensatus Hackel subsp. ***moellendorffianus*** (Aschers. & Graebn.) C. Fraile

1) Spikelet (1)-1.5-2-(2.5) cm long. Lemma (7)-8-10-(11.5) mm × 1.4-2 mm, smooth, shiny, giving a delicate appearance to the spikelet, narrowly lanceolate with narrow hyaline margins. Awn (0.7)-1-5 mm. Sheaths densely lanate or minutely pubescent, occasionally glabrous. Rhizomes 1.5-3 cm.

2) Basal leaf sheaths densely lanate. Panicle bearing (5)-11-23-(31) spikelets. Lemma (8)-9-10-(11.5) mm × 1.7-2 mm. Awn (0.7)-1-3-(5) mm.

B. condensatus Hackel subsp. ***condensatus***

2) Basal leaf sheaths minutely pubescent, occasionally glabrous. Panicle bearing 6-14 spikelets. Lemma (7)-8-9-(10.5) mm × 1.4-1.9-(-2) mm. Awn (1.2)-2-5 mm.

B. condensatus Hackel subsp. ***microtrichus*** Borbás

2a) *B. condensatus* Hackel subsp. *condensatus*[1]

Perennial, with compact tufts connected by narrow rhizomes, 1.5-3 cm long. Ascending to erect, slender stems, 20-55 cm tall, (0.4)-0.6-1-(1.5) mm wide, glabrous, occasionally finely hairy. Leaf sheaths densely lanate, with greyish hairs giving a velvety appearance; lowest sheaths decaying into parallel fibres, eventually entwined with each other. Basal and cauline leaf blades shortly hairy, linear, involute; the basal 5-16 cm × 0.5-1.3 mm, the cauline 4.5-13.5-(16.5) cm × 0.4-1-(1.5) mm; ligule (0.3)-0.5-0.7-(1.4) mm. Flag leaf (3.5)-4-14 cm × 0.3-0.8-(1) mm. Panicle erect, narrowly ovate, compact when young, becoming slightly looser at maturity, (2.5)-6-7.5-(10.5) cm long from the lowest to the uppermost node, bearing (5)-11-23-(31) spikelets. The short internodes of the panicle and the high number of spikelets generate the compact appearance of the inflorescence. Panicle branches finely scabrous, very slender, 2-5 at the lowest node, the shortest 0.7-1.5-(1.7) cm, the longest 1.8-2.5-(3.5) cm. Spikelets narrowly ovate when young, more broadly ovate at maturity, small, (1.5)-1.7-2-(2.5) cm, with 3-7 florets; rachilla 1-1.6-(2) mm, glabrous. Glumes and lemmas very pale green-yellowish, sometimes purple- flecked, with narrow hyaline margins, smooth, shiny, giving a delicate appearance to the spikelets. Glumes subequal, the lower (5)-7-8-(8.3) mm, the upper 7.5-10 mm. Lemma (8)-9-10-(11.5) mm × 1.7-2 mm, narrowly lanceolate. Awn (0.7)-1-3-(5) mm, straight. Palea (6.5)-8-9-(10) mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers 4.2-5.5 mm. Caryopsis 6-7.3 mm. Flowering in May, fruiting in June. Geographical distribution in fig. 9.3.2.1.

Habitats: Dry grassland; stony places; dry, South exposed slopes in *Castanea*; serpentine; chalk; 300-1000 m.

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[1] Condensed inflorescence

Type: This taxon was described by Hackel in 1879. The type has proved elusive. I do not believe it exists. In his description, Hackel cited Bozen (Bolzano) as a characteristic locality for this taxon. I have selected a well-collected, widely available specimen of Sauter as a neotype, because of its geographical distribution (Bozen) and its well manifested morphological characters which seem to me to define *B. condensatus*, for instance the densely lanate sheath and condensed panicle.

Neotype selected here (fig. 9.3.2.2): Described from Italy: "Tirolia australis, Bozen, ad saxa porphyrica montis Kalvarienberg", Sauter (in Flora Exciccata Austro-Hungarica, Nr. 3943) (K!); Iso. (BM!, C!, E!, FI!, GB!, JE!, P!, W!).

Synonyms: *B. condensatus* Hackel, *Öesterr. Bot. Z.* 29: 209 (1879); *B. erectus* Huds. var. *insubrica* Stebler, *Futterpfl. 2. 2 Aufl.* 29 (1895) *vgl. Schw. Gräs.-Samml.* 237; *B. erectus* Huds. var. *condensatus* (Hackel) Fiori, *Fl. Anal. Ital.* 1: 98 (1896); *B. erectus* Huds. subsp. *condensatus* (Hackel) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 585 (1901); *B. erectus* Huds. subsp. *australis* (Griseb.) Hackel var. *condensatus* Hackel, in Bornm. *Mitth. Thüring. Bot. Vereins,* 29: 64 (1912); *B. erectus* Huds. subsp. *australis* (Griseb.) Hackel var. *pomöensis* Teyb., *Öesterr. Bot. Z.* 70: 246 (1921); *B. condensatus* Hackel var. *pomöensis* (Teyb.) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932); *Bromopsis condensata* (Hackel) Holub, *Folia Geobot. Phytotax.* 8 (2): 167 (1973).

Selection of specimens

Italy

Gargniano, 11.8.1901, *Bornmüller*, s.n. (W); Lago di Garda, 8.6.1911, *Ronniger*, s.n. (W); Sorrento Peninsula, Valle d. Ferriera, 16.6.1954, *Larsen*, 88 (JE); Lago d'Iseo, Tavernola, 28.5.1911, *Ronniger*, s.n. (W); Gargniano, Maderno, 8.6.1901, *Haussknecht,* s.n. (JE); Aquascria, Menaggio, 20.5.1907, *Ronniger*, s.n. (W); Lago d'

Fig. 9.3.2.1. Geographical distribution of *B. condensatus* subsp. *condensatus* (▲) and *B. condensatus* subsp. *microtrichus* (□).

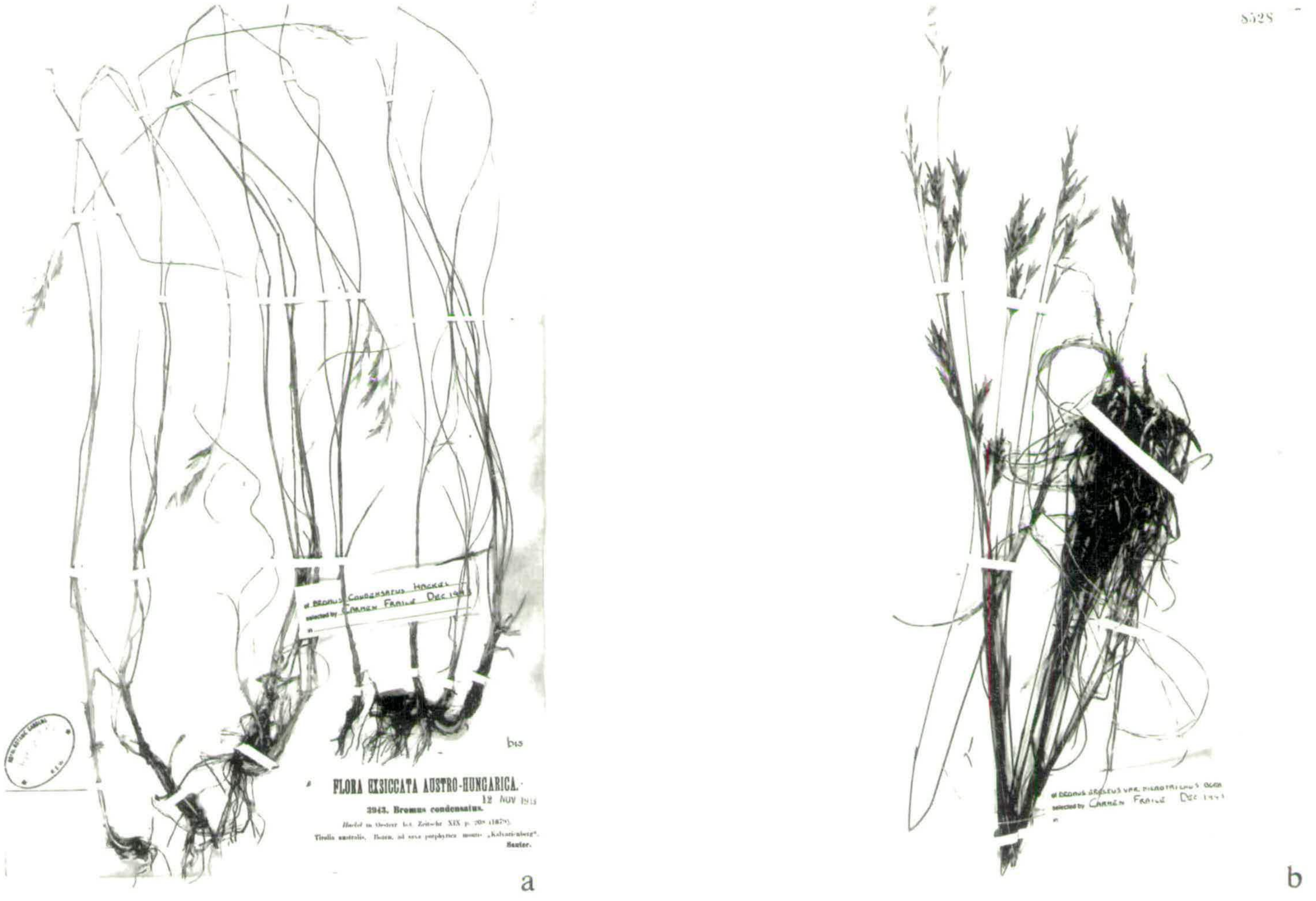

Fig. 9.3.2.2. (a) Neotype of *B. condensatus* Hackel and (b) Neotype of *B. condensatus* Hackel subsp. *microtrichus* Borbás Mag. x0.32

Iseo, Marone-Pisogne, 27.5.1911, *Ronniger*, s.n. (W).

Switzerland

Lugano, S. Salvadore-Cap., 3.6.1895, *Bornmüller*, s.n. (W); Luganer See, Monte Bré, 29.5.1909, *Kneucker*, 772 (W).

Former Yugoslavia

Scoglio Pomo., 3-9.6.1911, *Teyber.*, s.n. (W), sub *B. erectus* Huds. subsp. *australis* (Griseb.) Hackel var. *pomöensis* Teyb.

2b) ***B. condensatus*** Hackel subsp. ***microtrichus***[1] Borbás in Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 580 (1901).

Perennial, with compact tufts, connected by narrow rhizomes, 1.5-3 cm long. Ascending to erect stems, 16-50 cm tall, 0.5-1 mm wide, glabrous. Leaf sheaths minutely pubescent, occasionally glabrous; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades, glabrous, linear, involute; the basal 3.5-13.5 cm × 0.5-0.9 mm, the cauline 3-11 cm × 0.4-0.7-(1) mm; ligule (0.3)-0.5-1.3 mm. Flag leaf 3-8.5 cm × 0.3-0.6 mm. Panicle erect, compact, narrowly ovate when young, becoming more broadly ovate at maturity, (1.5)-3-8.5 cm long from the lowest to the uppermost node, with 6-14 spikelets. Panicle branches shortly scabrous, very slender, 1-4 at the lowest node, the shortest 0.5-13-(1.8) cm, the longest 0.8-2.5-(3.5) cm. Spikelets narrowly ovate when young, slightly broader at maturity, small, (1)-1.5-1.8-(2) cm, bearing (3)-4-6 florets; rachilla (0.9)-1-1.6 mm, glabrous. Glumes and lemmas glabrous, rarely hairy, with narrow hyaline margins, smooth, shiny, giving a delicate appearance to the spikelet, sometimes strongly purple-flecked. Glumes subequal, the lower (4.7)-6-7.5-(8) mm, the upper (6)-8-9-(9.8) mm. Lemma (7)-8-9-(10.5) mm × 1.4-1.9-(2) mm, narrowly lanceolate. Awn (1.2)-2-5 mm, straight.

[1] Small hairs

Palea 6-8-(9) mm, shorter than the lemma. Stamens 3, anthers (3.5)-4-4.2 mm. Caryopsis 5.8-7 mm. Flowering in May, fruiting in June. Geographical distribution in fig. 9.3.2.1.

Habitats: Stony slopes; meadows; woodland; chalk; 150-1700 m.

Type: It has proved impossible to track down a type specimen. It may have been destroyed. I therefore turn to authentic material. In the account of *B. microtrichus*, Ascherson & Graebner (1901) cited a specimen from Croatia: "Zeng: Vratnik (Borbás)" which I have selected as a neotype

Neotype selected here (fig. 9.3.2.2): Described from Croatia: "Monte Vratnik Segniae, 28.7.1883, Borbás" (W!).

Synonyms

B. erectus Huds. var. *microtrichus* Borbás, *Hirc Fl. okoli bakarske,* 138 (1884); *Öesterr. Bot. Z.* 35: 124 (1885); *B. condensatus* Hackel var. *microtrichus* (Borbás) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932); *B. condensatus* Hackel var. *microtrichus* Borbás subvar. *australis* (Griseb.) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932); *B. condensatus* Hackel var. *microtrichus* Borbás subvar. *cilifer* (Beck) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 206 (1932); *B. erectus* Huds. var. *istrianus* Belli, name known only from herbarium label. No publication found.

Selection of specimens

Hungary

Cott. Brocica, 19.7.1881, *Borbás*, s.n. (W).

Italy

Lucania, Trigento, 13.6.1907, *Guadagno*, s.n. (W); Val di Ledro bei Riva, 11.6.1908, *Velter*, s.n. (W); Divaccia, 6.6.1935, *Ronniger*, s.n. (W).

Former Yugoslavia

Skusari, 27.4.1914, *Dörfler*, 17 (W); Ragusa, 11.5.1911, *Bornmüller*, s.n. (B); Istrien, Mte Spaccalo, Triest, 23.5.1880, *Beck*, s.n. (W); Croatia, Buccari, 13.5.94, *Beck*, s.n. (W); Dalmatien, Montenegro, Bucovicasattel, 27.5.1910, *Ronniger*, s.n. (W); Inter Fiume et Buccari, 16.6.1903, *Degen*, 221 (W); Slovénie, Veliko Gradisce, 20.5.1976, *Mortin*, 8909 (B); Luissinpiccolo, 22.5.1911, *Bornmüller*, s.n. (B); Istrien, Monte Maggiore, 31.5.1890, *Richter*, s.n. (W); Istrien, Mte Maggiore, 960 m, 20.6.1909, *Belli*, s.n. (W), sub. *B. erectus* Huds.var. *istrianus* Belli.

Apparent intermediates between *B. condensatus* Hackel subsp. *condensatus* and *B. condensatus* Hackel subsp. *microtrichus* Borbás (fig. 9.3.2.3)

Italy

Riva, 3.6.1905, *Bornmüller*, s.n (B, JE, W); Colline argillose di Casciana Fra Pontedera e Sienna, 28.5.1871, *Levier*, s.n. (GB).

Former Yugoslavia

Gravosa, Anunciata, 200 m, 1.5.97, *Baenitz*, s.n (E, GB, JE, W); Dalmatien, Spalato, 19.5.1926, *Korb*, s.n (W); Insel Cherso, 9.7.1930, *Morton*, s.n. (W).

Fig. 9.3.2.3. Geographical distribution of apparent intermediates between *B. condensatus* subsp. *condensatus* and *B. condensatus* subsp. *microtrichus* (○).

2c) *B. condensatus* Hackel subsp. ***moellendorffianus***[1] (Aschers. & Graebn.) C. Fraile, *comb. nov.*

Perennial, with isolated loose tufts connected by long, thin rhizomes, 2-3.5 cm. Ascending to erect stems, 38.5-70 cm tall, 1-1.8-(2) mm wide, glabrous. Leaf sheaths glabrous or with long, scattered, retrorse hairs; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades ciliate, linear, conduplicate, occasionally flat; the basal (6)-8.5-12-(17) cm × 0.5-1-(1.5) mm; the cauline 7-14.5-(20.5) cm × 0.5-1 mm; ligule (0.3)-0.5-1 mm. Flag leaf (4)-7-10-(14.5) cm × 0.3-0.6-(1.5) mm. Panicle narrowly ovate, compact when young, becoming more broadly ovate at maturity, 4-7.5-(8.5) cm long from the lowest to the uppermost node, with (5)-6-13-(23) spikelets. Panicle branches shortly scabrous, straight, slender, sometimes curved upwards, mainly the lowest, (1)-2-4-(6) at the lowest node; the shortest (0.4)-0.5-1.5-(2) cm, the longest (1.5)-1.8-3.5 cm. Spikelets from narrowly ovate when young to more broadly ovate at maturity, 2-2.5-(3) cm long, bearing 4-6-(7) florets; rachilla (1.2)-1.5-2.5 mm, glabrous. Glumes and lemmas frequently purple-flecked, with broad hyaline margins, broader towards the apex. Glumes glabrous, subequal, the lower (6.5)-7-9-(10) mm, narrowly lanceolate, the upper (8)-9-10-(12) mm, broadly lanceolate. Lemma (10)-10.5-12 mm × 1.5-2.5 mm, glabrous, sometimes with fine, short, adpressed hairs, ovate-lanceolate, 3 prominent nerves, 2 more obscure, disappearing only towards the bottom of the lemma. Awn (2.5)-4-5.5 mm, straight. Palea 7-9 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers 4.5-6 mm. Caryopsis 6.7-8.5 mm. Flowering in May, fruiting in June-August. Geographical distribution in fig. 9.3.2.4.

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[1] Otto von Moellendorff, German consul in Kowno (Former U.S.S.R.)

Habitats: Dry, rocky ground; alpine meadows; grassy places; coniferous woodland; in loess near woodland margins; calcareous; serpentine; argillaceous soil; 50-1600 m.

Type: This taxon was described by Ascherson and Graebner in 1901. The type was probably destroyed during the Second World War bombing of Berlin and I have been unable to find it. In their account, they cite a specimen of *Bromus erectus* Huds. subsp. *moellendorffianus* from Bosnia: "Travnik: Castell (Brandis in Schultz Herb. norm., nov.ser. Nr. 2795). I have seen this specimen and for this reason choose it as a neotype.

Neotype selected here (fig. 9.3.2.5): Described from Bosnia: "Castell-Puticevo, 20 Junii 1890, Leg. Brandis (in Schulz Herb. norm., nov. ser. Nr. 2795) (W!); Iso. (BM!)

Synonyms: *B. erectus* Huds. subsp. *moellendorffianus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 582 (1901); *B. transsilvanicus* Steud. var. *angustifolius* Sagorski, *Mitth. Thüring. Bot. Vereins,* 16: 34 (1901); *B. moellendorffianus* (Aschers. & Graebn.) Hayek, *Prodr. Fl. Penins. Balcan.* 3: 208 (1933); *Bromopsis moellendorffiana* (Aschers. & Graebn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973).

Selection of specimens

Austria

Inneres Zillertal, Mayrhofen, Kalk, 27.6.-1.7.1978, *Polatschek*, s.n. (W).

Hungary

Lovasberény, 6.6.1937, *Boros*, s.n. (W); Martonvásár, 4.6.1947, *Boros*, s.n. (W).

Fig. 9.3.2.4. Geographical distribution of *B. condensatus* subsp. *moellendorffianus* (●)

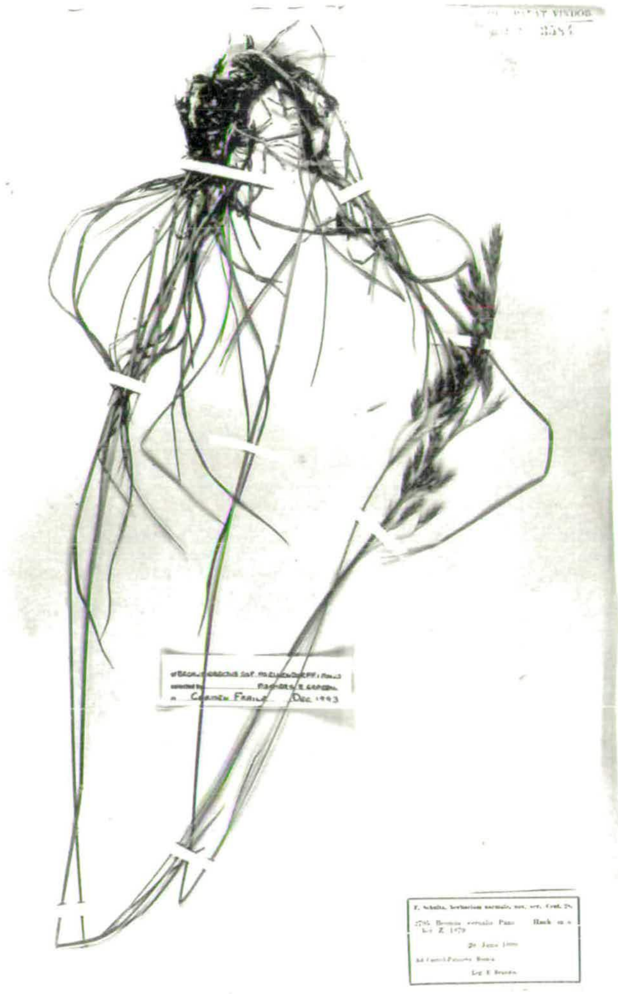

Fig. 9.3.2.5. Neotype of *B. erectus* Hackel. subsp. *moellendorffianus* Aschers. & Graebn. Mag. x0.32

Italy

Alta Valle Tiberina, 4.6.1935, *Sermoli*, s.n. (W); Mouli, Castellammare, 1906, *Cavara*, s.n. (W).

Rumania

Banatus, Timis-Torontal, 3.6.1941, *Bujorean,* 2161 (C).

Switzerland

Zürich, pentes de l'Uetliberg, molasse, 460 m, 15.6.1887, *Stebler & Schröter*, 93 (W).

Former Yugoslavia

Dalmatien, Cattaro, 9.6.1926, *Korb*, s.n. (W); Dalmatien, Insel Arbe, 10.6.1913, *Ronniger*, s.n. (W); Herzegovina, Velez Planina, 1000 m, 7.1901, *Sagorski,* s.n. (JE), sub. *B. transsilvanicus* Steud. var. *angustifolius* Sagorski; Montenegro, Montes Rumija, 28.6.1977, *Cernoch*, 32746 (B); Dalmatica, Cattaro, 6.1905, *Sagorski*, s.n. (JE); Herzergovina, Neverinje, 7.1902, *Sagorski*, s.n. (B).

B. pannonicus Kummer & Sendtn., *Flora*, 32: 757 (1849).

Perennial, with very loose tufts connected by long, narrow rhizomes, 2-5-(6) cm. Ascending to erect stems, 10-80 cm tall, (0.5)-1-2 mm wide, glabrous or very shortly hairy. Leaf sheath vesture varying from densely lanate, with long, greyish hairs giving a velvety appearance, to puberulous with scattered, long, patent hairs, sometimes glabrous; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous, with scattered hairs along the margins or puberulous or densely lanate on both sides, linear, flat, sometimes conduplicate or rolled up towards the apex; the basal (4.5)-7-14-(22) cm × 0.8-3 mm, the cauline 4.5-15-(24) cm × (0.5)-1.5-2.5-(3) mm; ligule (0.3)-0.5-1-(2) mm, sometimes very short with two long, lateral, membranous teeth. Flag leaf (3)-7-12.5-(20) cm × 0.5-1.5 mm. Panicle erect, compact, ovate in outline when young, becoming erect, very loose, deltoid or just slightly looser, (2.5)-4.5-10-(12) cm from the lowest to the uppermost node, bearing (6)-8-26-(31) spikelets. Panicle branches shortly scabrous, straight, slender, sometimes slightly tortuous or almost patent, 2-6 at the lowest node; the shortest 0.5-2.5-(4) cm, the longest (1)-1.5-4.5 cm. Spikelets 1.5-2.5-(3) cm, narrowly ovate when young to broadly ovate at maturity, with 4-7-(8) florets; rachilla (1)-1.5-2.5-(3) mm, glabrous. Glumes and lemmas with broad hyaline margins, very pale green, sometimes purple-flecked. Glumes subequal, the lower (5.4)-6.5-9.5-(10) mm, the upper (7.3)-7.5-11.5-(12) mm. Lemma (8.5)-9.5-12 mm × 1.5-2.2-(2.6) mm, glabrous or hairy with fine, short, adpressed hairs. Awn (1)-2.7-5.5 mm, straight. Palea (4.5)-5-9.5-(11) mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers (1.7)-3-5.5-(6.1) mm. Caryopsis 6.8-8.5 mm.

Key to three subspecies of ***B. pannonicus*** Kummer & Sendtn.:

1) Leaf sheaths and blades densely lanate, giving a velvety appearance. Panicle erect, compact, narrowly ovate to lanceolate when young, scarcely varying at maturity, and becoming slightly looser, (2.5)-5.5-7-(12) cm long from the lowest to the uppermost node. Low-growing plant, stems up to 45 cm tall.

B. pannonicus Kummer & Sendtn. subsp. ***vernalis*** (Pancic) C. Fraile

1) Not with the above combination of characters.

2) Panicle ovate, compact, scarcely varying at maturity, and becoming a little looser. Leaf blades and sheaths shortly puberulous or with scattered, long, patent hairs. Spikelet 1.5-2.5-(3) cm, bearing 4-7-(8) florets. Lemma broadly lanceolate, with 3 prominent nerves and 2 more obscure, disappearing only towards the bottom of the lemma.

B. pannonicus Kummer & Sendtn. subsp. ***pannonicus***

2) Panicle narrowly ovate, varying significantly from compact when young to erect, very loose and deltoid at maturity. Leaf sheaths glabrous, sometimes with very short, retrorse hairs. Leaf blades glabrous. Spikelet 2-2.8 cm, bearing (4)-5-6 florets. Lemma and glumes very pale green, sometimes quite translucent with broad hyaline margins throughout their length, giving a glossy appearance to the spikelets.

B. pannonicus Kummer & Sendtn. subsp. ***monocladus*** (Domin) P.M. Smith

3a) *B. pannonicus* Kummer & Sendtn. subsp. ***pannonicus***

Perennial, with very loose tufts connected by long rhizomes, 2-4.5-(6) cm. Ascending to erect stems, 30-80 cm tall, 1-1.7 mm wide, glabrous. Leaf sheaths shortly puberulous or with scattered, long, patent hairs, rarely glabrous; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades puberulous or with scattered hairs along the margins, flat, the basal (4.5)-9-12-(22) cm × 0.8-2.5 mm, the cauline 4.5-12.5-(24) cm × (0.5)-1-2-(2.5) mm; ligule (0.3)-0.5-1-(2) mm. Flag leaf (3.5)-7-10-(20) cm × 0.5-1-(1.5) mm. Panicle ovate, compact, scarcely varying at maturity and becoming slightly looser, (2.5)-5.5-9.5-(12) cm long from the lowest to the uppermost node, bearing (6)-8-16-(31) spikelets. Panicle branches shortly scabrous, slender, straight, 2-5-(6) at the lowest node, the shortest 0.5-2.5-(3) cm, the longest (1)-2-5 cm. Spikelets from narrowly ovate when young to more broadly ovate at maturity, 1.5-2.5-(3) cm long, with 4-7-(8) florets; rachilla 1-2-(3) mm. Glumes and lemmas with very broad hyaline margins, frequently purple-flecked. Glumes subequal, the lower (5.4)-6.5-8.5-(10) mm, narrowly lanceolate, the upper 7.5-11.5-(12) mm, more ovate lanceolate. Lemma (8.5)-9.5-12 mm × 1.5-2.2-(2.6) mm, glabrous, occasionally hairy, with fine, short adpressed hairs, broadly lanceolate, with 3 prominent nerves and 2 more obscure, disappearing only towards the bottom of the lemma. Awn (1.3)-3-5.5 mm, straight, frequently purple-flecked.

Palea 7.5-9.5-(11) mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers 4.6-5.5-(6.1) mm. Caryopsis 7-8.5 mm. Flowering in May-June, fruiting in July. Geographical distribution in fig. 9.3.2.6.

Habitats: Rocky, alpine grassy areas; chalk; calcareous and dolomitic soils; 150-1910 m.

Type (fig. 9.3.2.7): Described from Bosnia: "In declivibus aridis et saxosis a Travnik versus pagum Bukovizza, Majo florens (2500-3000'). (76 b.) (M!).

Synonyms: *B. pannonicus* Kummer & Sendtn., *Flora* 32: 757 (1849); *B. erectus* Huds. var. *pannonicus* Aschers. & Kanitz, *Cat. Corm. et Anthoph. Serbiae, Bosniae,* 12 (1877); *B. erectus* Huds. var. *pycnotrichus* Borbás, *Math. Term. Közlem,* 15, 9: 334 (1878); *B. repens* Borbás, l.c. 335 (1878). Hackel, *Öesterr. Bot. Z.* 29: 205 (1879); *B. pannonicus* Kummer & Sendtn. var. *reptans* Borbás, Faldmiv. Erdek., 11. (1882); *B. pannonicus* Kummer & Sendtn. var. *hercegovinus* (Beck) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932); *B. pannonicus* Kummer & Sendtn. var. *hirtiflorus* (Maly) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932). *B. pannonicus* Kummer & Sendtn. var. *reptans* subvar. *stolonifer* (Borbás) Hayek, *Repert. Spec. Nov. Regni Veg. Beih.* 30 (3): 208 (1932); *B. erectus* Huds. var. *pannonicifolius* Prod., *Bul. St. Sect. Biol. Acad. R.P.R,* 9 (4): 292 (1957); *Bromopsis pannonica* (Kummer & Sendtn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973).

Selection of specimens

Hungary

Kom. Pest. Nagymavos, 7.6.63, *Bisse*, s.n. (JE); Comit Pest. Adlersberg, 7.6.85, *Degen*, s.n. (JE); Budapest, 26.5.1912, *Vetter*, s.n. (W); Ofen, Adlersberg, 26.5.1912, *Korb*, s.n. (W).

Fig. 9.3.2.6. Geographical distribution of *B. pannonicus* subsp. *pannonicus* (Δ), *B. pannonicus* subsp. *vernalis* (■), apparent intermediates between these two subspecies (□), *B. pannonicus* subsp. *monocladus* (●) and *B. caprinus* (▲)

Fig. 9.3.2.7. (a) Type of *B. pannonicus* Kummer & Sendtn. and (b) Type of *B. erectus* Huds. var. *vernalis* Pancic Mag. x0.32

Former Yugoslavia

Croatia litoralis, Monte Velnac supra Carlopago, 14.6.1905, *Kocsis*, s.n. (W); Njegus, calcareis, 17.7.97, *Sagorski*, s.n. (W); Sarajevo, Kastellberg, 8.6.1910, *Sagorski*, s.n. (BP, JE); Hercegovina, Velez planina, 1450 m, 5.7, *Sagorski*, s.n. (BP, JE); Hercegovina, Neverinje, Ost-Velez, 1450 m, 20.6.11, *Sagorski*, s.n. (JE, W). Croatia, m. Velnac ad Carlopago, 6.1906, *Sagorski*, s.n. (JE).

3b) ***B. pannonicus*** Kummer & Sendtn. subsp. ***vernalis***[1] (Pancic) C. Fraile, *comb. et stat. nov.*

Perennial, with loose tufts connected by long rhizomes, 2-5 cm. Ascending to erect stems, low-growing plant, 10-45 cm tall, (0.5)-1-1.5-(1.6) mm wide, very shortly hairy. Leaf sheaths densely lanate, with long, greyish hairs, giving a velvety appearance; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades flat except near the inrolled apex, densely lanate on both sides; the basal (4.5)-7-9-(16.5) cm × (1)-1.5-3 mm, the cauline (4.5)-9-12-(18) cm × (0.8)-1-2-(3) mm; ligule up to 0.3 mm, very short. Flag leaf (3)-7-12.5-(15) cm × 0.5-1.5 mm. Panicle simple, erect, compact, narrowly ovate to lanceolate when young, scarcely varying at maturity, and becoming somewhat looser, (2.5)-5.5-7-(12) cm long from the lowest to the uppermost node, with (7)-8-18-(27) spikelets. Panicle branches very shortly scabrous, sometimes glabrous, straight, slender, 2-4-(5) at the lowest node, the shortest (0.5)-1.5-2.5-(4) cm, the longest (1.5)-3-3.5-(4.5) cm. Spikelets from narrowly lanceolate-ovate when young, to more broadly ovate at maturity, (1.5)-1.8-2.5 cm, bearing 4-7-(8) florets; rachilla (1)-1.5-2.1-(2.5) mm, glabrous. Glumes and lemmas very pale green-yellowish, sometimes slightly purple-flecked, shiny, with very broad hyaline margins throughout, giving a delicateappearance to the spikelets.

[1] Pertaining to spring

Glumes glabrous, subequal, the lower (5.7)-6.6-8-(9) mm, the upper (7.3)-8.5-10-(11.5) mm. Lemma (8.5)-10-11.5 mm × 1.5-2 mm, glabrous, with two very small apical teeth. Awn (1)-3-4.5-(5.5) mm, straight. Palea (4.5)-5-9-(10) mm, shorter than the lemma, very short hairs along the keels. Stamens 3, anthers (1.7)-3-4 mm. Caryopsis 6.8-7.5 mm. Flowering in June, fruiting in July. Geographical distribution in fig. 9.3.2.6.

Habitats: Rocky places; grassy areas; serpentine; calcareous soils.

Type (fig. 9.3.2.7): Described from Serbia: "Rupestrib. Serpentinacesi ad Broja ne Serb. merid. Maj. 1850, Verz. d. Serb. Phaner. n° 1721" (W!).

Synonyms: *B. erectus* Huds. var. *vernalis* Pancic, *Verh. Zool.-Bot. Ges. Wien,* 6: 592 (1856); *B. vernalis* Pancic, *Öesterr. Bot. Z.* 29: 205 (1879).

Selection of specimens

Hungary

Ráros, patris, 9.5.1871, *Borbás*, s.n. (W).

Former Yugoslavia

Serbia, Brgjani prope Garnji, Milanovac, calc., 4.1897, *Adamovic*, s.n. (W); Serbia, Brgjani (Milanovac), serpent., 4.1893, *Adamovic*, s.n. (JE, W); Serb. Centr., Brgjani, *Reuter*, s.n. (JE); Serbia merid., Brojane, rupestrib. serpentinacei, 5.1850, *Pancic*, s.n. (W); Serbien, Brgjanska klissura, 4.94, *Dimitrijevic.*, s.n. (GB).

Apparent intermediates between *B. pannonicus* Kummer & Sendtn. subsp. *pannonicus* and *B. pannonicus* Kummer & Sendtn. subsp. *vernalis* (Pancic) C. Fraile (fig. 9.3.2.6)

Hungary

Budam, graminosis, solo calc., 100 m, *Borbás*, 1070, (BM, BP, C, GB, JE, K, PC, W); Montis Nagyszénahegy, Szent-Iván, in declivibus graminosis aridis, solo dolomitico, 150 m, 21.6.1899, *Degen*, 222 (BM, E, GB, JE, K, W).

3c) *B. pannonicus* Kummer & Sendtn. subsp. *monocladus*[1] (Domin) P. M. Smith, *Bot. J. Linn. Soc.* 76: 360 (1978).

Perennial, with loose tufts connected by long rhizomes, 3-5 cm. Ascending to erect stems, 42.5-80 cm tall, (1.1)-1.5-2 mm wide, glabrous. Leaf sheaths glabrous, sometimes with very short, retrorse hairs; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous, narrow, flat, sometimes conduplicate mainly near the apex, the basal 8-14 cm × 1-2 mm, the cauline 8-15 cm × 1.5-2.5 mm; ligule very short with two long, lateral, membranous teeth. Flag leaf 7.5-11.5 cm × 0.3-1.3 mm. Panicle simple, erect, narrowly ovate, compact in outline when young, becoming very loose, deltoid at maturity, some times unilateral, 4.5-10 cm long from the lowest to the uppermost node, bearing 10-26 spikelets. Pedicels shortly scabrous, very slender, from erect to slightly curved, almost patent, 2-6 at the lowest node, the shortest 0.5-2 cm, the longest 1.5-4.5 cm. Spikelets narrowly ovate-cuneate when young, more broadly ovate at maturity, 2-2.8 cm long, with (4)-5-6 florets; rachilla 1.5-2.5 mm, glabrous. Glumes and lemmas very pale green, sometimes quite

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[1] One branch, shoot

translucent, with broad hyaline margins throughout most of their length, becoming very narrow towards the apex, giving a glossy appearance to the spikelets. Glumes subequal, the lower 6.7-9.5 mm, the upper 8.6-11.2 mm. Lemma 10-12 mm × 1.6-2 mm, glabrous, weakly purple-flecked. Awn 2.7-4.5 mm, straight. Palea 8.5-9.5-(10) mm, shorter than the lemma, with very short hairs along the keels. Stamens 3, anthers 4.5-5.2 mm. Caryopsis not seen. Flowering May-June, fruiting time unknown. Geographical distribution in fig. 9.3.2.6.

Habitats: Meadows; open, rocky places often in between *Fagus*; dolomitic soils; 560-718 m.

Type: Described from Czechoslovakia: "Slovakia austro-occidentali in monte dolomitico Rokos dicto in graminosis montanis praesertim e *Sesleria calcaria, Carice humile* et *Festuca amethystina* constitutis, altitudine 680-730 m.s.m., Domin, 5.7. 1930".

Synonyms: *B. monocladus* Domin, *Mem. Soc. Sci. Boheme* 14, 14: 1-2 (1932); *Zerna monoclada* (Domin) Holub, *Novit. Bot. Delect. Seminum Horti. Bot. Univ. Carol. Prag.* 9: 160 (1960); *B. pannonicus* Kummer & Sendtn. var. *monoclados* (Domin) Soó, *Acta Bot. Acad. Sci. Hung.* 17: 115-125 (1971); *Bromopsis monoclada* (Domin) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973); *Bromopsis pannonica* (Kummer & Sendtn.) Holub subsp. *monoclada* (Domin) Holub, *Folia Geobot. Phytotax.* 18 (2): 205 (1983).

Selection of specimens

Czechoslovakia

Slovakia occidentalis, Montes Strázovská, pratis saxosis, solo dolomitico, 718 m, 25.6.1956, *Pouzar*, s.n. (C, W); Montes Povázsky (distr. Nové Mesto nad Váhom), locis apertis, substrato dolomitico, 560 m, 27.5.1969, *Dvåkovå, Smejkal & Vicherek*, 1595 (C, JE, K, W).

4) ***B. caprinus***[1] Kerner ex Hackel, *Öesterr. Bot. Z.* 29: 209 (1879).

Perennial, with loose tufts connected by narrow rhizomes, 2-3 cm long. Ascending to erect stems, glabrous, 20-75 cm tall, (1.1)-1.5-1.8-(2.2) mm wide. Leaf sheaths densely lanate, with long, greyish hairs, giving a velvety appearance; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades densely velutinous, linear, involute, sometimes flat; the basal (9.5)-10.5-21-(22.5) cm × (0.5)-0.8-2 mm, the cauline 9-16-(27.5) cm × 0.7-2.5-(2.8) mm; ligule (0.3)-0.5-1-(1.2) mm. Flag leaf 6.5-14.5-(17.5) cm × 0.6-0.7-(2.4) mm. Panicle simple, erect, narrowly ovate to lanceolate when young, becoming broadly ovate, lax at maturity, (5.5)-9.5-13.5 cm long from the lowest to the uppermost node, multispiculate, with (9)-17-21-(35) spikelets. Pedicels shortly scabrous, robust, straight, rarely slender, (2)-4-5-(11) at the lowest node; the shortest (0.3)-0.5-1-(2.7) cm, the longest (2)-3-5.5 cm. Spikelets 2-2.6-(2.8) cm long, narrowly-ovate when young, more broadly at maturity, bearing 4-7 florets; rachilla (0.7)-1.2-2-(2.2) mm, glabrous. Glumes and lemmas with broad hyaline margins towards the apex. Glumes subequal, the lower (7)-8-10-(10.5) mm, narrowly lanceolate, the upper (9)-10-11-(12) mm, more broadly lanceolate. Lemma 11-12-(13) mm × (1.5)-1.8-2.3-(2.4) mm, glabrous, rarely hairy, finely scabrous on the nerves, especially below, oblong-lanceolate, with two small apical teeth at the apex. Awn (1.7)-3-6 mm, straight. Palea 9-10-(12) mm, shorter than the lemma, shortly serrate-scabrous along the keels. Stamens 3, anthers 3-5.3 mm. Caryopsis 8-10 mm. Flowering in May, fruiting in June. Geographical distribution in fig. 9.3.2.6.

[1] From the island of Capri (Italy)

Habitats: Very dry, sunny places; stony and calcareous soils; 200-1450 m.

Type: Described from Italy: "Ex sem. spont. leg. Kerner ins. Capri, 6.1878, Stein"; Iso. (FI).

Synonyms: *B. caprearum* Hackel, *Öesterr. Bot. Z.* 29: 209 (1879); *B. erectus* Huds. var. *caprinus* (Kerner ex Hackel) Fiori, *Fl. Anal. Ital.* 1: 98 (1896); *B. erectus* Huds. var. *stabianus* Guadagno, *Bull. Orto Bot. Regia Univ. Napoli*, 3: 85 (1913).

Selection of specimens

Italy

Capo di Sorrento, 6.1937, *Bornmüller*, s.n. (B); Campania, Supra Sarno, calcareis, 200-300 m, 25.5.1909, *Pellanda*, s.n. (FI); Campania, Supra Sarno, luoghi rupestri, 200 m, 3.6.1908, *Pellanda*, s.n. (JE, W); Capri, 7.6.1907, *Briquet*, s.n. (W); Capri, 20.4.1898, *Haussknecht*, s.n. (JE); Campania, prov. di Salerno, herbosis et rupestribus, calcareo, 200-400 m, 22.5.1909, *Pellanda*, 1420 (BM, FI, K); Castellammare, 2.1902, *Guadagno*, s.n. (W); Campania, Salerno, apricis aridis, 200-300 m, 20.5.1912, *Pellanda*, s.n. (B); Ins. Capri, 1878, *Hackel*, s.n (W).

B. erectus Hudson, *Fl. Angl.* 39. (1762).

Perennial, with very dense or loose tufts, connected by short or long rhizomes, 1-8 cm. Stems 30-110 cm tall, (1.2)-1.5-3-(4) mm wide, glabrous. Leaf sheaths glabrous or with scattered, long, mainly retrorse hairs, occasionally very abundant; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous, sometimes densely hairy, margins scabrous or ciliate, flat or conduplicate, occasionally involute, varying from relatively narrow to very broad and long, especially the cauline, with very prominent midrib and nerves; the basal 7-38 cm ×

0.5-3.3-(5) mm, the cauline (7.5)-10-40 cm × (0.5)-0.8-5.5 mm; ligule 0.2-1.5-(2.5) mm. Flag leaf (3.5)-5-33.5 cm × 0.6-4.5-(5.5) mm. Panicle scarcely varying from youth to maturity, long-ovate, dense, compact or slightly looser, sometimes very broadly ovate, dense, ± contracted when young, becoming effuse, very lax, spreading and deltoid at maturity, (3.5)-6-25 cm long from the lowest to the uppermost node, bearing (7)-11-47 spikelets. Panicle branches or pedicels shortly scabrous, erect, straight, slender or stiff, robust, sometimes becoming very lax and tortuous at maturity, (2)-3-7 at the lowest node; the shortest 0.5-3.5-(5.5) cm, the longest 1-5.5-(8) cm. Spikelets (1.5)-2-3.5-(5.3) cm long, narrowly, long-ovate when young, becoming more broadly ovate at maturity, with 3-8-(11) florets; rachilla (1)-1.5-2-(3) mm, glabrous or shortly hairy. Glumes and lemmas glabrous, occasionally hairy, with broad hyaline margins, sometimes shiny, pale green or purple-flecked. Glumes subequal, the lower (6)-7-11.5 mm, narrowly lanceolate, the upper 7-13.5-(15) mm, broadly or narrowly lanceolate. Lemma 9.2-15-(18) mm × (1.5)-2-2.4-(2.8) mm, glabrous, occasionally hairy, narrowly lanceolate to oblong-lanceolate. Awn 2-6 mm, straight. Palea (5)-9-12 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers (3)-4-6.5 mm. Caryopsis 7.3-9.5 mm.

Key to five subspecies of ***B. erectus*** Huds.:

1) Plant very robust, stems up to 110 cm tall. Cauline leaf blades 12-40 cm × (1.8)-2.5-5.5 mm wide, flat, with very prominent midrib and nerves. Panicle 9.5-25 cm long from the lowest to the uppermost node, effuse, very lax, spreading, deltoid at maturity. At least two or more than two basal panicle branches or pedicels distinctly longer than their spikelets, very slender, erect, when young, becoming very lax and tortuous at maturity. Rhizomes very short, 1-2 cm.

B. erectus Huds. subsp. ***laxus*** (Hornem.) C. Fraile

1) Low growing plant, stems 35.5-50-(75) cm tall. Cauline leaf blades flat, rarely with rolled margins, 4.5-12.5 cm × 1-2.5 mm. Panicle (3.5)-6-9 cm long from the lowest to the uppermost node, erect, more contracted when young, but scarcely varying from youth to maturity. The basal panicle branches or pedicels shorter than their spikelets, slender, straight. Rhizomes very long, 3-8 cm.

B. erectus Huds. subsp. ***aurouzensis*** C. Fraile

2) Basal and cauline leaves linear, involute, occasionally conduplicate, 0.5-1.5 mm wide. Panicle erect, compact, unilateral in outline, scarcely varying from youth to maturity. Glumes and lemma glabrous, very narrowly lanceolate; glumes very unequal, the lower 9.5-11 mm, the upper 12.5-13.5 mm; lemma 14-15 mm × 2-2.3 mm, very long. Awn 5-6 mm, straight. Rhizomes 2-4 cm.

B. erectus Huds. subsp. ***montenegrinus*** (Sagorski) C. Fraile

2) Basal and cauline leaves linear, flat, sometimes conduplicate, (0.5)-0.8-4.2-(4.5) mm wide. Panicle erect, stiff, narrowly ovate, dense when young, becoming looser at maturity. Glumes narrowly lanceolate, subequal, the lower (6.5)-7-10.5-(11.5) mm, the upper (8.5)-9-12-(13) mm. Lemma 10.5-14.5 mm × (1.7)-2-2.3-(2.6) mm, glabrous, occasionally hairy, oblong-lanceolate. Awn (2)-3.5-5-(6) mm, straight. Rhizomes very short, 1-2 cm.

3) Stems up to 100 cm tall. Panicle large, dense, compact, 8.5-13.5-(18) cm long from the lowest to the uppermost node, with erect, stiff, robust panicle branches and pedicels when young and at maturity; at least two distinctly longer than the spikelet. Spikelet (2)-3-3.5 cm long, bearing 4-7-(11) florets.

B. erectus Huds. subsp. ***longiflorus*** (Willd. ex Spreng.) Arcangeli

3) Stems up to 70, rarely 80 cm tall. Panicle (5.5)-8-10-(11.5) cm long from the lowest to the uppermost node, with erect, slender panicle branches and pedicels when young and at maturity, rarely longer than the spikelet. Spikelet (1.5)-2-3 cm long, bearing 4-6-(8) florets.

B. erectus Huds. subsp. ***erectus***

5a) *B. erectus* Huds. subsp. ***erectus***

Perennial, with very dense tufts connected by very short, narrow rhizomes, 1-2 cm long. Ascending to erect stems, 30-70-(80) cm tall, (1.2)-1.5-2-(2.5) mm wide, glabrous. Leaf sheaths with scattered, long hairs sometimes very abundant; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous or with scattered hairs along the margins, sometimes densely hairy, flat or conduplicate; the basal 8-15-(20) cm × 1-2-(4) mm, the cauline (7.5)-10-12.5-(22) cm × (0.5)-0.8-3 mm; ligule 0.2-1 mm. Flag leaf (7)-9.5-11-(15) cm × 1-2-(3.5) mm. Panicle stiff, erect, long-ovate when young, becoming looser at maturity, (5.5)-8-10-(11.5) cm long from the lowest to the uppermost node, with (9)-19-25 spikelets. Panicle branches and pedicels slender, erect, glabrous or shortly scabrous, (2)-3-6 at the lowest node; the shortest 0.5-1.5-(3) cm, the longest 1-2.5-(4.5) cm. Spikelets (1.5)-2-3 cm, narrowly lanceolate when young, more broadly ovate at maturity, bearing 4-6-(8) florets; rachilla (1)-1.7-2 mm, glabrous. Glumes and lemmas glabrous, occasionally hairy, with broad hyaline margins, sometimes purple-flecked. Glumes subequal, the lower (6.5)-7-9-(10) mm, narrowly lanceolate, the upper (8.5)-10-11-(12) mm, more broadly lanceolate. Lemma 10.5-12-(13.5) mm × (1.7)-2-2.3 mm, narrowly lanceolate to oblong-lanceolate. Awn 2-4.5-(5) mm, straight. Palea 9-10-(11.5) mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers (4.5)-5-5.5-(6) mm. Caryopsis 7.3 mm. Flowering June-July, fruiting in August. Geographical distribution in fig. 9.3.2.8.

Habitats: Meadows; dry coastal slopes; sunny, rocky places; mixed woodland with beech, pine and fir; dry, stony slopes; abundant on dry rocky ground; open *Juniperus-Corylus* scrub; chalk cuttings by the roadside; chalk hill-slopes; limestone ledges; gently sloping grassy banks; calcareous; 110-2000 m.

Type: Described from England: "(England, Kent), in cretaceis circa Rochester, Dartford et Gravesend, in Cantio, Hudson" (Holo. destroyed).

Lectotype selected here (fig. 9.3.2.9): "*B. erectus* Huds. determined by himself. I. p. 39. II. p. 49. Scheuch. t. 5. 13" (BM!).

Synonyms: *B. erectus* Huds., *Fl. Angl. ed.* 1. 39 (1762); *B. odoratus* Gouan, *Hort. Monsp.* 11 (1768); *B. arvensis* Poll., *Pl. Palat.* 1. 113 (1776); *B. angustifolius* Schrk., *Baier Fl.* 366 (1789); *Festuca montana* Savi, *Fl. Pis.* 1. 118 (1798); *B. pseudo-arvensis* Koel., *Gram.* 241 (1802); *Festuca hirta* Seenus, *Reise*, 59 (1805); *Bromus glaucus* Lapeyr., *Hist. Arbr. Pyr.* 633 (1813); *Zerna erecta* Panzer, *Denkschr. Königl. Akad. Wiss. München,* 297 (1814); *Festuca erecta* Wallr., *Sched. crit.* 35 (1822); *Schedonorus erectus* Fries, *Bot. Notis.* 131 (1843); *Bromopsis erecta* (Huds.) Four., Ann. *Soc. Linn. Lyon*, 17: 187 (1869); *B. agrestis* All., *Fl. Ped.* 2. 249 (1875); *B. erectus* Huds. var. *glabriflorus* Borbás., *Öesterr. Bot. Z.* 32: 135 (1882); *B. erectus* Huds. var. *hackelii* Borbás, *Földmiv. érdek.* 11 (1882). *Öesterr. Bot. Z.* 32: 135 (1882); *B. perennis* Vill., *Pl. Dauph.* 2. 122 (1887); *B. erectus* Huds. subsp. *eu-erectus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901); *B. eu-erectus* var. *villosus* (Mart. & Koch) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901); *B. eu-erectus* subvar. *planifolius* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901); *B. eu-erectus* var. *fasciculatus* Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 586 (1901).

Selection of specimens

Austria

Seleskopf/Sesvenna - Grappe, Bündnerschiefer, 1650 m, 30.7.1969, *Polatschek*, s.n. (W); Nieder-Österreich, Hoheneich, Waldviertal, 14.6.1992, *Vetter*, 290 (W); Alpenostrand, Abhänge oberh., Gainfahrn, 28.5.1916, *Ronniger*, s.n. (W).

France

Coteaux au Vinaigrier près Nice, 8.5.1861, *Bourgeau*, 290 (W); Dept. Aveyron, dry stony slopes below the road (N.9), 27.5.1962, *Brummitt*, *Gibbs & Ratter*, 179 (E).

Great Britain

Surrey, Purley, on chalk down near main path, 26.5.1953, *Cannon & Herbert*, 2040, (C); Cumbria, Westmorland, Kendal golf course, on limestone ledges, 11.6.1981, *Halliday*, 54/81 (C).

Hungary

In praedio Ràkos versus Kispest ad Budapestinum, solo arenoso, 110 m, *Flatt & Thaisz.*, 223 (W); Visegrad, Nagymaros, 31.5.1963, *Schneider*, s.n. (JE).

Italy

Vallombrosa, 3.7.1902, *Fiori*, s.n. (FI); Impruneta, serpentini, 26.6.1943, *Corradi*, s.n. (FI); Alto Adige, Val Gardena, Piceto ericetoso sopra casa, 1550 m, 20.7.1931, *Chiarugi*, s.n. (FI).

Poland

Galicia orient., in agro Leopolitano, 12.1896, *Piotrowski*, s.n. (W).

Rumania

Municip. Bacâu, in pratis siccis, 200 m, 12.6.1971, *Barabas & Mititeleu*, 315 (JE).

Sweden

Skane Ålnus, 15.6.1926, *Tufvesson*, s.n. (C); Gotland, Visby, 15.6.1882, *Lénström*, s.n. (E).

Former U.S.S.R.

Prov. Leningrad, distr. Gatczina, in declivitae sicca calcarea prope marginem australi-occidentalem, 16.6.1971, *Tzvelev*, 5321 (W).

Former Yugoslavia

Tnebavic - Sarajevo, abundant on dry rocky grownd, 13.7.1960, *McCallum Welch*, 4038 (E).

Icones: Javorka & Csapody, *Icon. Fl. Hung.*, tab. 383, pp. 45 (1934); Todor, *Fl. Rep. Soc. Rom.*, fasc. 12, tab. 58, pp. 304 (1972); Hubbard, *Grasses*, pp. 72 (1984).

5b) ***B. erectus*** Huds. subsp. ***aurouzensis***[1] C. Fraile, *subsp. nov.*

Diagnosis: A subsp. ***erecto*** rhizomatibus longioribus, culmo breviore, ramis basalibus paniculae 2, raro 5, spiculis lemmatibusque angustioribus, maturitate immutabilibus differt.

Gramen perenne, culmis brevibus in caespites rhizomatibus longis junctis. Paniculae simplices. Spiculae longo-oblongae, juventute et maturitate similes, (4)-5-6-(7) florae. Glumae et lemmata glabri, pallide virides, nitidi, ergo spiculae faciei delicatae.

Perennial with loose tufts connected by long rhizomes, 3-8 cm. Ascending to erect stems, 35.5-50-(75) cm tall, 1.5-2-(2.5) mm wide, glabrous. Leaf sheaths glabrous, rarely with scattered, short hairs; lowest sheaths decaying into parallel fibres.

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[1] From Aurouze (France)

Fig. 9.3.2.8. Geographical distribution of *B. erectus* subsp. *erectus* (Δ) and *B. erectus* subsp. *aurouzensis* (●)

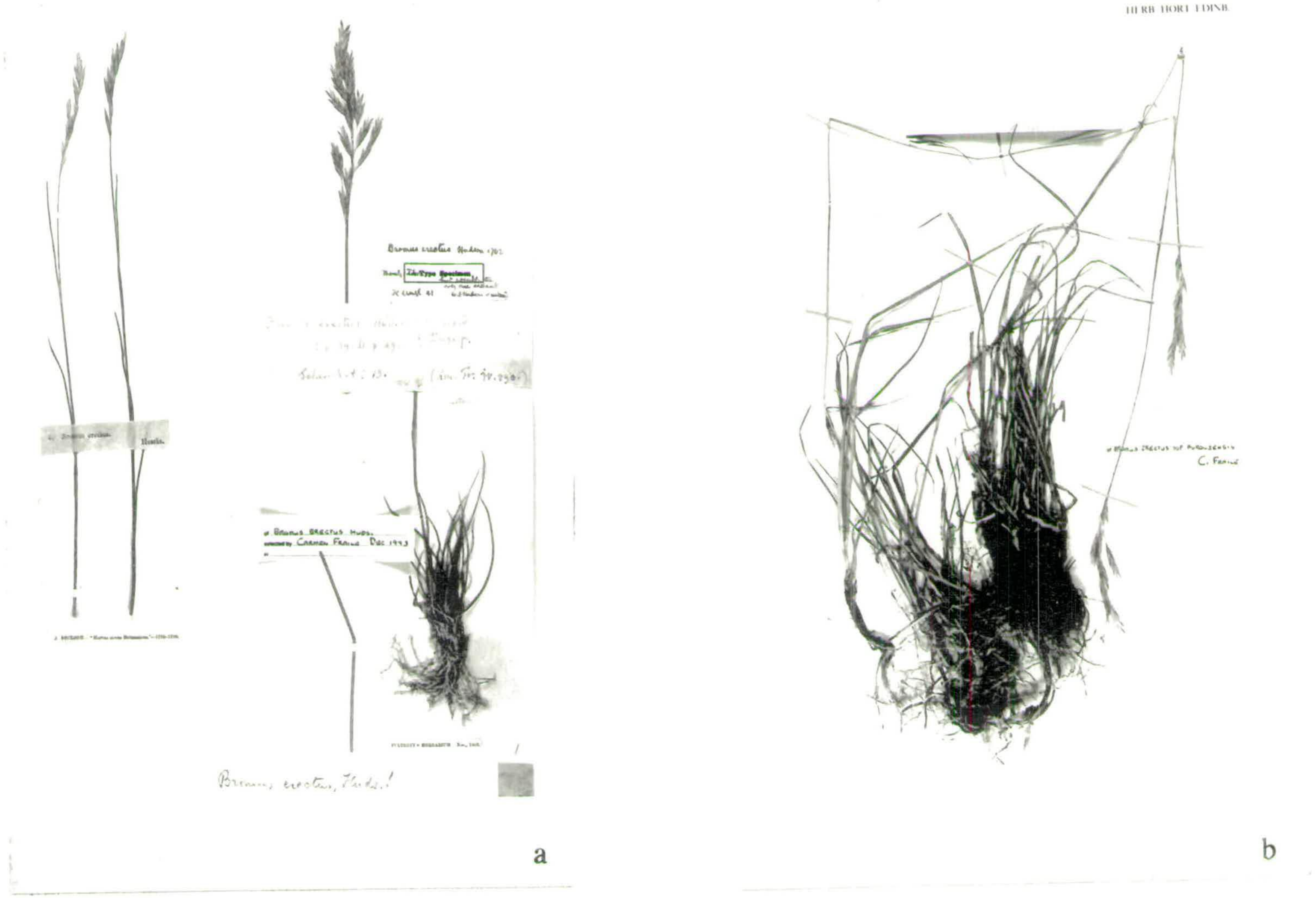

Fig. 9.3.2.9. (a) Lectotype of *B. erectus* Huds. and (b) Type of *B. erectus* Huds. subsp. *aurouzensis* C. Fraile Mag. x0.32

Basal and cauline leaf blades glabrous or with scattered hairs along the margins, flat, rarely with rolled margins; the basal 5-15 cm × 1-2.5 mm, the cauline 4.5-12.5 cm × 1-2.5 mm; ligule (0.3)-0.5-1.5 mm. Flag leaf (3.5)-5-10 cm × 0.5-1.5-(2) mm. Panicle simple, somewhat more contracted when young, but scarcely varying from youth to maturity, (3.5)-6-9 cm long from the lowest to the uppermost node, bearing 7-15-(20) spikelets. Pedicels glabrous or shortly scabrous, slender, straight, 2, very rarely 5 at the lowest node; the shortest 0.5-2.5 cm, the longest 1.5-3 cm. Spikelets 2-3.5 cm, oblong-lanceolate when young, scarcely varying at maturity, with (4)-5-6-(7) florets; rachilla 1.5-2-(2.5) mm, glabrous, occasionally with very short hairs. Glumes and lemmas glabrous, pale green, somehow shiny, giving a delicate appearance to the spikelets. Glumes subequal, narrow hyaline margins, the lower 6-8-(9.5) mm, narrowly lanceolate, the upper 7-10 mm, narrowly lanceolate or oblong-lanceolate. Lemma 9.2-12 mm × 1.8-2 mm, narrowly lanceolate to oblong lanceolate, narrow hyaline margins, becoming slightly broader at the apex. Awn 2-4.5 mm, straight. Palea shorter than the lemma, 8-10 mm, with short hairs along the keels. Stamens 3, anthers 3.8-5.5 mm. Caryopsis not seen. Flowering in June-July, fruiting time unknown. Geographical distribution in fig. 9.3.2.8.

Habitats: Open soily scree beside road, on a moraine; grassy slopes; damp area; in fagetis, upper mountainous region; limestone; 1650-2000 m.

Type (fig. 9.3.2.9): Described from France:"Hautes Alpes, Montagne de l'Aurouze, bas de la Combe d' Aurouze a l'est du Roe des Hirondelles, 1750 m, 16.7.1991, E. Chas" (E!).

Selection of specimens

France

Pyrenäen, Pic. de Césiré, 2000 m, 15.7.1925, *Konniger*, s.n. (W); Ex Pyrenaeis centralibus, juxta Gavarnie, 8.1880, *Ball*, s.n. (E).

Spain

Picos de Europa, Peña Vieja, beside Refugio Aliva, 1650 m, 28.8.56, *Dresser*, P/306 (E); Encinillas, prov. Burgos, in fagetis reg. mont. sup., 18.10.1852, *Herb. Joh. Lange*, s.n. (E); Picos de Europa, Pido, gently sloping grassy bank, limestone, 1700 m, 29.8.56, *Dresser*, P/399 (E); Distr. Logroño/Soria, Sierra de la Urbión, grassy slopes, damp areas, 1700 m, 17.7.1960, *Dresser*, 683 (E).

Observations: This taxon was recorded by Chas & Kerguelen (1992) as a new species for the French flora, and identified as *B. pannonicus* subsp. *monocladus*. Very kindly both authors sent in 1991 a duplicate to Dr. P.M. Smith in Edinburgh, who transferred it to me, being related to my current research. After a close study of this and other specimens and after a complete taxonomic delimitation of the *B. pannonicus* subgroup, all the evidence suggests the existence of a new taxon in the *B. erectus* group with a pattern of distribution in the South of France and North of Spain. The chromosome number has also been reported, 2n = 28 (Chas & Kerguelen 1992). Its taxonomic status is discussed in the next section.

5c) ***B. erectus*** Huds. subsp. ***laxus*** (Hornem.) C. Fraile, *comb. et stat. nov.*

Perennial, with dense tufts connected by short rhizomes, 1-2 cm long. Ascending to erect stems, glabrous, very robust, 40-110 cm tall, (1.7)-2-2.5-(4) mm wide. Leaf sheaths glabrous, rarely with scattered hairs; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous, margins scabrous or rarely ciliated, flat, occasionally conduplicate, varying from relatively narrow to very broad and long, especially the cauline, with prominent midrib and nerves; the basal 7-23-(24) cm × (1)-2-2.5-(5) mm, the cauline 12-40 cm × (1.8)-2.5-5.5 mm; ligule 0.5-1-(2.5) mm. Flag leaf 10.5-33.5 cm × (0.7)-1-4.5-(5.5) mm. Panicle from very broadly ovate, dense, ± contracted when young, becoming effuse, very lax, spreading and deltoid at maturity, large, 9.5-25 cm long from the lowest to the uppermost node, multispiculate, bearing 12-47 spikelets. Panicle branches and pedicels shortly scabrous, 4-angled, slender, erect when young, becoming very lax and tortuous at maturity, (2)-3-7 at the lowest node, the shortest (0.5)-1.5-3.5-(5.5) cm, the longest 4.5-5.5-(8) cm. Spikelets (2.7)-3.3-3.5-(5.3) cm long, narrowly ovate when young, becoming very broadly ovate-cuneate later, with (5)-7-8-(11) florets, well distanced from each other at maturity, gaping, especially the upper forming an angle of 45° with the rachilla; rachilla (1)-1.5-2-(2.6) mm, glabrous. Glumes and lemmas very shiny, pale green, with broad hyaline margins, broader towards the apex. Glumes subequal, the lower (8)-8.5-11.5 mm, narrowly lanceolate, the upper (9)-10.5-11.5-(15) mm, more broadly lanceolate. Lemma 12-14-(18) mm × (1.5)-2-2.4-(2.8) mm, glabrous, sometimes finely hairy, oblong-lanceolate, with two small apical teeth. Awn 2.5-5-(5.5) mm, straight. Palea (9)-10-11-(12) mm, shorter than the lemma, very shortly serrate-scabrous along the keels. Stamens 3, anthers 4-6.5 mm. Caryopsis 8-9.5 mm. Flowering in May-June, fruiting in July. Geographical distribution in fig. 9.3.2.10.

Habitats: Rocky, grassy places; calcareous soils; 50-700 m.

Type: No type material nor authentically named specimens have come to hand, despite rigorous searching. I do not think any exist. Nevertheless the taxon as I have recognised it fits well with Hornemann's description of *B. laxus* (1815) and the illustration of this in Reichenbach (1850). I choose this illustration as the type (see observations below).

Neotype selected here (fig. 9.3.2.11): (Illustration) *B. laxus* Hornem. ex Reichenb., *Icon. Fl. Germ. et Helvet.* fasc.1, pp. 146, tab. 291 (1850).

Synonyms: *B. laxus* Hornemann, *Hort. Hafn.* 2: 954 (1815); *B. angustifolius* Hornemann, *Hort. Hafn. Suppl.* 13 (1819), non Marschall; *B. stenophyllus* Link, *Enum. Pl. Hort. Berol.* 1: 94 (1821); *B. erectus* Huds. var. *laxus* (Hornem.) Döll, *Fl. Bad.* 1: 144 (1857); *B. erectus* Huds. subsp. *stenophyllus* (Link) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 583 (1901); *B. erectus* Huds. var. *stenophyllus* (Link) Fiori, *Nuov. Fl. Anal. Ital.* 1: 146 (1923).

Observations: The taxon described here was named before *B. stenophyllus* Link which basionym would otherwise have priority. Its rank or status has varied according to different authors (Aschers. & Graebn. 1901; Hegi 1906; Fiori 1923; Hayek 1933; Zangheri 1976; Smith 1980; Pignatti 1982). Link (1821) based his original description on *B. angustifolius* Hornemann (1819), which in turn was described as follows: *"panicula nutante spiculis 14-floris linearibus, aristis glume dimidio brevioribus, foliis anguste linearibus glabris. Hab. in Caucaso? . D. intro. 1815"*. All the features seem to fit well with the taxon considered here, except the leaves which paradoxically can indeed be relatively narrow (2.5 mm) to extraordinarily broad, up to 5.5 mm. The epithet "stenophyllus" itself also means "narrow blade", and does not wholly accurately describe this taxon. The same author, Hornemann, described a new taxon in 1815 under the epithet *B. laxus* as follows: *"panicula florente nutante, spiculis pendulis compressis linearibus pubescentibus, arista glumis breviore, fol. laxis pubescentibus ciliatis. Hab... D. intro. 1813. Subhoc nomine"*. Effectively, I am stating that, in my opinion, Hornemann named two taxa where there is only one. For this taxon, the name *laxus* has priority.

The illustration of *B. laxus* Hornem. by Reichenbach in *Fl. Germanicae et Helveticae* (1850) reproduces precisely the concept of this brome-grass described above. Thus, I have adopted the accurately descriptive name *B. laxus* Hornem. referring to a robust *Bromus* perennial of erectoid affinity, with a large panicle, replacing the equivocal name of *B. stenophyllus* Link.

Selection of specimens

Austria

Niederoesterreich, Wienerwald, 1.7.1919, *Korb*, s.n. (W).

Germany

Blocksberg, Kalk, 700 m, 25.5.1876, *Bohatsch*, s.n. (BP); Pasing, 6.1915, *Ganz*, s.n. (W).

Italy

Gardone, graminosis olivesis, 6.1901, *Haussknecht*, s.n. (JE); Maderno, apricis silvat., 1.6.1901, *Haussknecht*, s.n. (JE); Maderno, saxos., 17.5.1901, *Haussknecht*, s.n. (JE).

Former Yugoslavia

Dalmatia, Cattaro, 50 m, 18.5.97, *Baenitz*, s.n. (E, JE).

Fig. 9.3.2.10. Geographical distribution of *B. erectus* subsp. *laxus* (□), *B. erectus* subsp. *longiflorus* (■) and *B. erectus* subsp. *montenegrinus* (●)

Fig. 9.3.2.11. Neotype of *B. laxus* Hornem. Mag. x0.53

5d) ***B. erectus*** Huds. subsp. ***longiflorus***[1] (Willd. ex Spreng.) Arcangeli, *Compendio della Flora Italiana...* (1894).

Perennial, with dense tufts connected by very short rhizomes, 1-2 cm. Ascending to erect stems, robust, glabrous, 40-100 cm tall, (2)-2.2-3 mm wide. Leaf sheaths with scattered, long, mainly retrorse hairs, occasionally glabrous; lowest sheaths decaying into parallel fibres. Basal and cauline leaf blades glabrous or with scattered hairs, margins scabrid, glabrous or ciliate, flat, sometimes conduplicate, prominent midrib and nerves, the basal 7.5-38 cm × (0.8)-1.3-3.3 mm, the cauline 11-22.5-(23.5) cm × 1.3-4.2-(4.5) mm; ligule (0.2)-0.5-1.5-(2) mm. Flag leaf (10.5)-12-17-(25) cm × 1-2-(4.5) mm. Panicle scarcely varying from youth to maturity, long-ovate, dense, compact, 8.5-13.5-(18) cm long from the lowest to the uppermost node, multispiculate, with 11-44 spikelets. Panicle branches and pedicels shortly scabrous, 4-angled, erect, stiff, robust, (3)-4-6-(7) at the lowest node, the shortest 0.5-2-(2.8) cm, the longest 3.5-5.5-(6.3) cm. Spikelets (2)-3-3.5 cm, narrowly ovate when young, broader at maturity, bearing 4-7-(11) florets; rachilla 1.5-2-(3) mm, glabrous or with short hairs. Glumes and lemmas with broad hyaline margins, pale green, giving a silvery appearance to the spikelets. Glumes subequal, narrowly lanceolate, the lower (7.5)-9-10.5-(11.5) mm, the upper 9-12-(13) mm. Lemma (11)-11.5-14.5 mm × 2-2.3-(2.6) mm, glabrous, occasionally finely hairy, oblong-lanceolate, purple-flecked, with 3 prominent nerves, 2 more obscure, gradually disappearing towards the bottom of the lemma. Awn (2.2)-3.5-5-(6) mm, straight. Palea (5)-9-11-(12) mm, shorter than the lemma, shortly serrate-scabrous along the keels. Stamens 3, anthers (3)-5.3-5.5-(5.8) mm. Caryopsis 8-9.5 mm. Floweringin May-June, fruiting in July. Geographical distribution in fig. 9.3.2.10.

[1] Long-flowered

Habitats: Ruderal; coniferous forest; scree slopes; meadows; hard limestone, calcareous and siliceous soils; 300-1400 m.

Type: I have not been able to track the type. Possibly it was destroyed during the Second World War bombing of Berlin in 1945. Therefore I choose a neotype.

Neotype selected here (fig. 9.3.2.12): Described from Germany: "Zell am see, Bachufer im Orte. Dichtrasig. 12.8.48, Reiter" (W!).

Synonyms: *B. longiflorus* Willd., *Enum. Pl. Suppl.* 6 (1813), nom. nud., ex Spreng. *Pl. Pugill.* 2: 23 (1815); *B. erectus* Huds. var. *longiflorus* Parl., *Fl. Ital.* 1: 413 (1848); *B. eu-erectus* subsp. *longiflorus* (Willd.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 588 (1901); *Bromopsis erecta* (Huds.) Four. subsp. *longiflora* (Willd. ex Spreng.) Dostal, *Folia Mus. Rerum. Nat. Bohemiae Occid., Bot.*, 2: 16 (1984).

Selection of specimens

Austria

TuxerAlpen, Brenner, silikat, 1400 m, 7.1966, *Polatschek*, s.n. (W).

Czechoslovakia

Moravia Centr., Brno, declivbus substepposis, 300 m, 25.5.1927, *Podpera*, 484 (C, W); Kloboucky, Bucovice, pratis ad fontem, 22.5.1921, *Podpera*, s.n. (C).

Italy

Bellagio, 21.5.1874, *Herb. Joh. Lange*, s.n. (C).

Former Yugoslavia

Dalmatien, Mte. Marian, Spalato, 19.5.1910, *Ronniger*, s.n. (W).

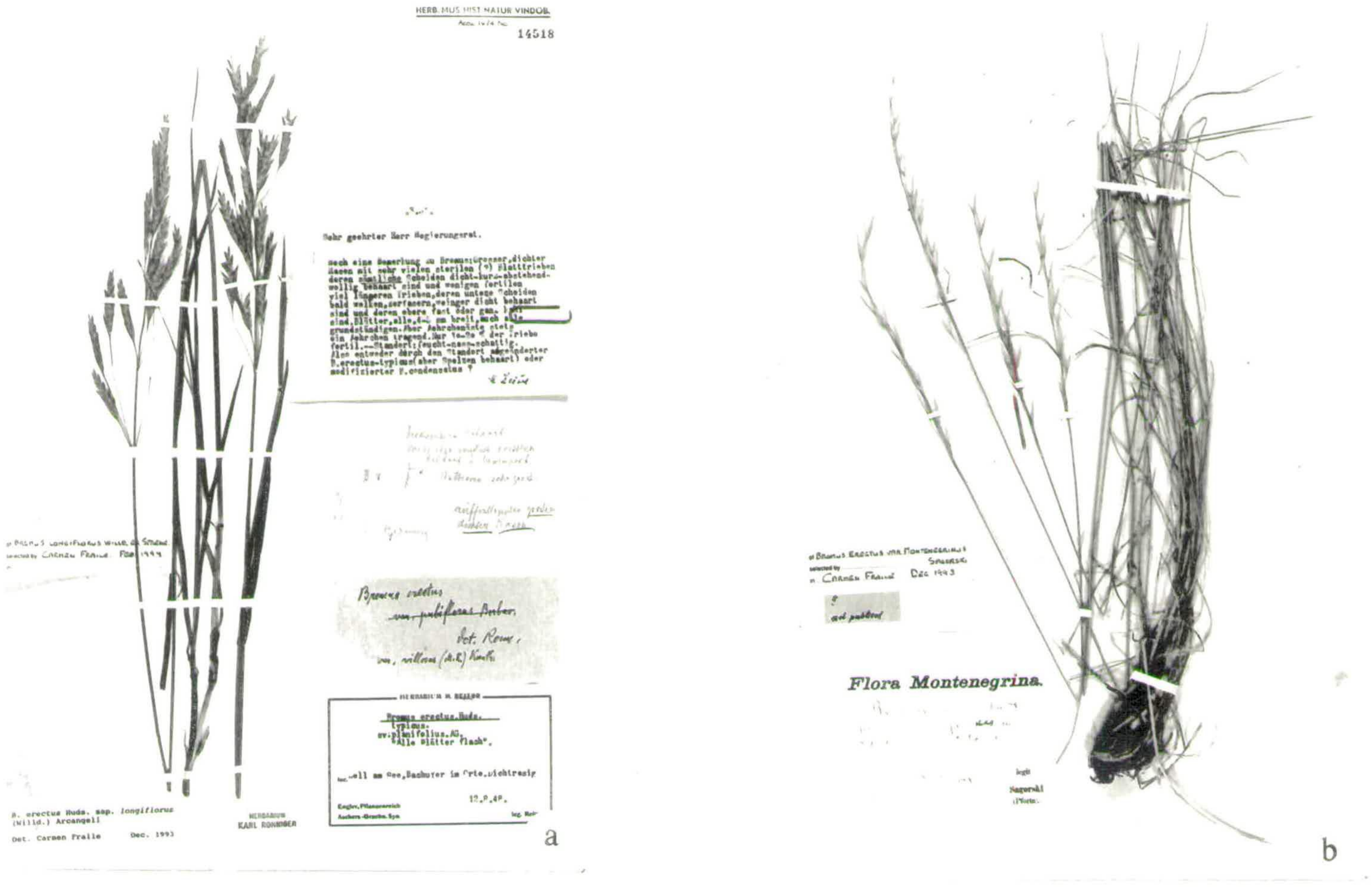

Fig. 9.3.2.12. (a) Neotype of *B. longiflorus* Willd. and (b) Type of *B. trassilvanicus* Steud. var. *montenegrinus* Sagorski Mag. x0.32

5e) ***B. erectus*** Huds. subsp. ***montenegrinus***[1] (Sagorski) C. Fraile, *comb. et stat. nov.* Perennial, with loose tufts connected by narrow rhizomes, 2-4 cm long. Ascending to erect stems, glabrous, 70.5-80 cm tall, 1.8-2 mm wide. Leaf sheaths glabrous; lowest sheaths breaking into parallel fibres at maturity. Basal and cauline leaf blades glabrous, linear, involute, occasionally conduplicate; the basal 7-16 cm × 0.5-1 mm, the cauline 12-16 cm × 0.5-1.5 mm; ligule scale-like, very short. Flag leaf 13-17.5 cm × 0. 6-1 mm. Panicle simple, erect, compact, scarcely varying from youth to maturity, unilateral in outline, 10-13 cm long from the lowest to the uppermost node, bearing 11-16 spikelets. Pedicels very shortly scabrous, straight, robust, 3-4 at the lowest node; the shortest 1.3-2.5 cm, the longest 4.5-7 cm. Spikelets 2.8-3.1 cm long, ovate when young, broader at maturity, with 3-4 florets; rachilla 2 mm, glabrous. Glumes and lemmas glabrous, very narrowly lanceolate, with narrow hyaline margins. Glumes very unequal, the lower 9.5-11 mm, the upper 12.5-13.5 mm. Lemma 14-15 mm × 2-2.3 mm, glabrous, smooth, with narrow hyaline margins. Awn 5-6 mm, straight. Palea 9.5-12 mm, much shorter than the lemma, very shortly serrate-scabrous along the keels. Stamens 3, anthers 6 mm. Caryopsis 8-9 mm. Flowering in June, fruiting in July. Geographical distribution in fig. 9.3.2.10.

Habitat: Calcareous soils.

Type (fig. 9.3.2.12): Described from Montenegro: "vidit et comprobavit Hackel, in calcareis ad Njegus, Julio 98, Sagorski" (B!); Iso. (JE!).

Synonyms: *B. transsilvanicus* Steud. var. *montenegrinus* Sagorski. *Mitt. Thüring. Bot. Vereins,* 16: 34 (1901); *B. erectus* Huds. var. *transsilvanicus* subvar. *montenegrinus* (Sagorski) Hayek, *Repert. Spec. Nov. Regni Beih.* 30 (3): 207 (1932).

[1] From Montenegro (Former Yugoslavia)

Selection of specimens

Former Yugoslavia

Njegus, 7.98, *Sagorski*, s.n. (JE).

9.3.2.2 Discussion

Undoubtedly, of the grasses comprising the section *Pnigma*, the highest grade of morphological complexity and difficulty in the delimitation and identification of taxa is represented in the *B. erectus* group. The long-existing taxonomic ambiguities which characterise the taxa are manifested by the long synonymy attributed to most of these brome-grasses that have long, erect panicles and sheaths splitting into parallel fibres. It has long been a refractory group needing clarification. This group constitutes a good example of polytypy. Many more taxa have been described than really exist, often based on minor variants. Only after a prolonged, careful, meticulous, and difficult study of numerous herbarium specimens (nearly 1500), I have felt confident in presenting (above) a new taxonomic account for the *B. erectus* group. Some taxa seem to be relatively simply and clearly defined, while for others, the resolution of taxonomic boundaries has sometimes seemed to call for the judgement of Salomon.

Twelve taxa have been defined, all of them with a distinct pattern of distribution in Europe. My intuitive view of the morphological diversification and the relationship occurring among the component taxa is now explained. My taxonomic analysis has confirmed the working hypothesis (p.1) of four taxonomic groups.

The *B. condensatus* group is readily characterised by its strikingly small spikelets, and very narrow, conduplicate or involute leaves. There are three component subspecies, *B. condensatus* Hackel subsp. *condensatus*, *B. condensatus*

Hackel subsp. *microtrichus* Borbás and *B. condensatus* Hackel subsp. *moellendorffianus* (Aschers. & Graebn.) C. Fraile. The first two show great similarity, differing mainly in the indumentum of the sheaths, densely lanate in the subspecies *condensatus* and minutely pubescent in the subspecies *microtrichus*, the size of the spikelets, being smaller in the subspecies *microtrichus*. The pattern of distribution is shown in fig. 9.3.2.1. Apparent intermediate forms have also been observed (fig. 9.3.2.3). After much thought, I believe that a subspecific taxonomic separation is undoubtedly the most appropriate approach.

B. condensatus Hackel subsp. *moellendorffianus* (Aschers. & Graebn.) C. Fraile is a critical, confusing taxon. Many authors have included it in their taxonomic studies under different treatments. Significantly, no one has referred to the type specimen: probably it was destroyed during the second World War. Consequently, an unclear definition has accompanied this taxon for many years, since it was described by Ascherson & Graebner in 1901. The neotype selected here (pp. 162) shows great similarity with the *B. condensatus* types - small spikelets, and very narrow leaves, although its broader pattern of distribution (fig. 9.3.2.4) and diagnostic phenotypic characters suggest it to be a subspecies.

I find that the presence of rhizomes is a feature of all the taxa of the *B. erectus* group, including the subspecies *erectus*, which although short, change significantly the traditional image of a densely caespitose plant. Within the complex, very long rhizomes characterise the *B. pannonicus* group, and three subspecies have been defined, *B. pannonicus* Kummer & Sendtn. subsp. *vernalis* (Pancic) C. Fraile, *B. pannonicus* Kummer & Sendtn. subsp. *pannonicus*, and *B. pannonicus* Kummer & Sendtn. subsp. *monocladus* (Domin) P.M. Smith.

B. pannonicus Kummer & Sendtn. subsp. *vernalis* (Pancic) C. Fraile develops long rhizomes, up to 5 cm long. It is a low growing plant with densely lanate sheaths and leaf blades. Some apparent intermediates between this subspecies and the subspecies *pannonicus* have been observed (fig. 9.3.2.6). This finding in conjunction with a localised geographical distribution, points to subspecific status, rather than specific distinction.

B. pannonicus Kummer & Sendtn. subsp. *monocladus* (Domin) P.M. Smith and *B. pannonicus* Kummer & Sendtn. subsp. *pannonicus* display an overall similarity, although they differ mainly in the indumentum of sheaths and leaves, which are glabrous throughout in the subspecies *monocladus* and puberulous in the subspecies *pannonicus*. Other distinctions include the shape of the panicle - very loose, spreading, deltoid at maturity in the former and compact, erect in the latter. The patterns of distribution (fig. 9.3.2.6) also offer a clear distinction between both. There are several phenotypic distinctions, with an overall resemblance, and distinctive distributions. These facts lead me to propose subspecific rank.

B. caprinus Kerner ex Hackel comprises plants with densely lanate sheaths, involute leaves and lax, spreading panicles, described so far as an endemic species from the Italian island of Capri and neighbouring territory of Sorrento. Phenotypically it is very distinctive and this, together with the geographical distribution (fig. 9.3.2.6), suggest to me that the specific status is justifiable.

B. erectus described by Hudson in 1762 from England, does not show any great morphological complexity in the British Isles, where it is found growing on chalk and limestone substrata. However, on the continent of Europe, various related and polymorphic taxa have led me to the delimitation of four subspecies, *B. erectus* Huds. subsp. *aurouzensis* C. Fraile, *B. erectus* Huds. subsp. *longiflorus* (Willd.

exSpreng.) Arcangeli, *B. erectus* Huds. subsp. *laxus* (Hornem.) C. Fraile and *B. erectus* Huds. subsp. *montenegrinus* (Sagorski) C. Fraile.

B. erectus Huds. subsp. *aurouzensis* C. Fraile shares quite similar features with the subspecies *erectus* but also presents some very distinctive morphological and biological characters. It is a low growing plant characterised by its, long, narrowly-oblong spikelets and panicles, scarcely varying from youth to maturity, narrower lemmas than the subspecies *erectus*, with only 2 basal panicle branches, very rarely 5. The most striking feature is the long rhizomes, up to 8 cm, differing from the shortly rhizomatous subspecies *erectus* with rhizomes 1-2 cm. The geographical distribution, as far as it can be ascertained at this stage, corresponds to the South of France and North of Spain (fig. 9.3.2.8). All these features seem to justify subspecific rank.

Subspecies *laxus* and subspecies *longiflorus* are typically tall plants, with long, thick stems, big panicles and wide leaves. The former at maturity, develops very large panicles with panicle branches or pedicels distinctly longer than the spikelets, eventually becoming very lax and tortuous. Curiously, the width of the leaves varies from relatively narrow to very wide, up to 5.5 mm. No other feature varies in concert with the leaf width, as far as I have been able to detect. Subspecies *longiflorus*, although developing relatively large, dense panicles, has stiff panicle branches and pedicels that remain quite close to the main stem. My assessment is that both taxa show an overall similarity while also presenting morphological differences. The diagnostic phenotypic features are consistently associated, and the patterns of distribution are characteristic (fig. 9.3.2.10). For these reasons I believe that subspecific taxonomic separation is appropriate.

B. erectus Huds. subsp. *montenegrinus* (Sagorski) C. Fraile has been described so far only from Montenegro (Former Yugoslavia). It develops loose tufts connected by long rhizomes, very long, narrowly lanceolate glumes and lemmas, long awns and its narrow, unilateral panicle in outline. Phenetically it is distinctive, and together with the geographical distribution (fig. 9.3.2.10) this again suggests to me that subpecific rank is justifiable.

A general key comprising the taxa of the *B. erectus* group is shown in p. 202

The highly polymorphic nature of the taxa which comprise the *B. erectus* group may perhaps rest on high rates of hybridisation and backcrossing among the different taxa, thus generating considerable morphological variation and so complicating species delimitation and the taxonomy of this group. Unfortunately, experimental evidence is at present lacking. Taxonomic firmness needs to precede experimentalism, later being revised. It would be extremely interesting to establish theoretical models of hybridisation to explain the evolutionary pathways in this group, as a complement of the taxonomical account here presented. Of course it would be naive to suggest that all or most of this proposed hybridisation is current, or that it happened in the past all at the time. Some degree of isolation is implied to account for the persistence of what are, in my view, relatively similar and probably closely related taxa. These possibilities are discussed later (chapter 11, sect. 11.3.1).

General key for all the taxa comprising the *B. erectus* group.

1) Plant very robust, stems up to 110 cm tall. Cauline leaf blades flat, occasionally conduplicate, varying from relatively narrow to very broad and long, 12-40 cm × (1.8)-2.5-5.5 mm, with very prominent midrib and nerves. Panicle very large, 9.5-25 cm long from the lowest to the uppermost node, effuse, very lax, spreading, deltoid at maturity; at least two or more than two, panicle branches or pedicels distinctly longer than their spikelet, very slender, erect when young, becoming lax and tortuous at maturity.

B. erectus Huds. subsp. ***laxus*** (Hornem.) C. Fraile

1) Not with the above combination of characters.

2) Stems very thin, 1 mm wide, rarely up to 1.5 mm. Leaf sheaths densely lanate or minutely pubescent, occasionally glabrous. Basal and cauline leaf blades linear, involute, 0.4-1.3-(1.5) mm. Spikelets (1)-1.5-2-(2.5) cm, very small, shiny, smooth, giving a delicate appearance.

3) Leaf sheaths densely lanate, with shaggy, greyish hairs. Panicle bearing (5)-11-23-(31) spikelets. Glumes subequal, the lower (5)-7-8-(8.3) mm, the upper 7.5-10 mm. Lemma (8)-9-10-(11.5) mm × 1.7-2 mm. Awn (0.7)-1-3-(5) mm.

B. condensatus Hackel subsp. ***condensatus***

3) Leaf sheaths minutely pubescent, occasionally glabrous. Panicle bearing 6-14 spikelets. Glumes subequal, the lower (4.7)-6-7.5-(8) mm, the upper (6)-8-9-(9.8) mm. Lemma (7)-8-9-(10.5) mm × 1.4-1.9-(2) mm. Awn (1.2)-2-5 mm.

B. condensatus Hackel subsp. **microtrichus** Borbás

2) Stems more than 1 mm wide. Leaf sheath glabrous or with scattered, long hairs, or densely lanate. Basal and cauline leaf blades flat, broad, occasionally conduplicate and narrow, 0.5-4.2 mm. Spikelets longer than 2 cm.

4) Leaf sheaths densely lanate, with long, greyish hairs, giving a velvety appearance.

5) Low growing plant, stems up to 45 cm tall. Leaf blades densely lanate on both sides, flat, except near the inrolled apex. Panicle erect, compact, narrowly ovate to lanceolate when young, scarcely varying at maturity, and becoming somewhat looser, (2.5)-5.5-7-(12) cm long from the lowest to the uppermost node.

B. pannonicus Kummer & Sendtn. subsp. **vernalis** (Pancic) C. Fraile

5) Stems up to 75 cm tall. Leaf blades densely velutinous, linear, mainly involute, sometimes flat. Panicle erect, narrowly ovate to lanceolate when young, becoming lax, broadly ovate at maturity, (5.5)-9.5-13.5 cm long from the lowest to the uppermost node.

B. caprinus Kerner ex Hackel

4) Leaf sheath glabrous or with scattered hairs, never lanate.

6) Basal and cauline leaves linear, conduplicate or involute, 0.5-1.5 mm wide. Panicle 4-13 cm long from the lowest to the uppermost node, bearing 5-16-(23) spikelets, (1)-2-4-(6) panicle branches or pedicels at the lowest node. Rhizomes 2-4 cm.

7) Panicle erect, compact, unilateral in outline, scarcely varying from youth to maturity. Glumes and lemmas glabrous, very narrowly lanceolate; glumes very unequal, the lower 9.5-11 mm, the upper 12.5-13.5 mm; lemma 14-15 mm × 2-2.3 mm. Awn 5-6 mm.

B. erectus Huds. subsp. ***montenegrinus*** (Sagorski) C. Fraile

7) Panicle narrowly ovate, compact when young, becoming more broadly ovate at maturity. Glumes glabrous, subequal, the lower (6.5)-7-9-(10) mm, narrowly lanceolate, the upper (8)-9-10-(12) mm, broadly lanceolate. Lemma (10)-10.5-12 mm × 1.5-2.5 mm, glabrous, sometimes with fine, short, adpressed hairs, ovate-lanceolate. Awn (2.5)-4-5.5 mm.

B. condensatus Hackel subsp. ***moellendorffianus*** (Aschers. & Graebn.) C. Fraile

6) Basal and cauline leaves linear, flat, sometimes conduplicate or with rolled margins, wider than 1.5 mm. Panicle (2.5)-4.5-13.5-(18) cm long from the lowest to the uppermost node, bearing (4)-5-44 spikelets, with 2-6-(7) panicle branches or pedicels at the lowest node. Rhizomes 2-8 cm.

8) Panicle erect, stiff, long ovate, scarcely varying from youth to maturity, becoming looser at maturity. Glumes glabrous, occasionally hairy, narrowly lanceolate, subequal, the lower (6.5)-7-10.5-(11.5) mm, the upper (8.5)-9-12-(13) mm. Lemma 10.5-14.5 mm × (1.7)-2-2.3-(2.6) mm, narrowly lanceolate to oblong-lanceolate. Awn (2)-3.5-5-(6) mm, straight. Rhizomes very short, 1-2 cm.

9) Stems up to 100 cm tall. Panicle large, dense, compact, 8.5-13.5-(18) cm long from the lowest to the uppermost node, with erect, stiff, robust panicle branches and pedicels, when young and at maturity; at least two distinctly longer than their spikelet. Spikelet (2)-3-3.5 cm long, bearing 4-7-(11) florets.

B. erectus Huds. subsp. ***longiflorus*** (Willd. ex Spreng.) Arcangeli

9) Stems up to 70, rarely 80 cm tall. Panicle (5.5)-8-10-(11.5) cm long from the lowest to the uppermost node, with erect, slender panicle branches and pedicels when young and at maturity, rarely longer than their spikelets. Spikelet (1.5)-2-3 cm long, bearing 4-6-8 florets.

B. erectus Huds. subsp. ***erectus***

8) Panicle erect, compact, narrowly ovate when young, scarcely varying at maturity or becoming very loose, deltoid. Glumes glabrous, subequal, the lower (5.4)-6-9.5-(10) mm, narrowly lanceolate, the upper 7-11.5-(12) mm, more broadly lanceolate. Lemma glabrous, occasionally with fine, short, adpressed hairs, (8.5)-9.2-12 mm × 1.5-2-(2.6) mm. Awn (1.3)-2-5.5 mm, straight. Rhizomes very long, 2-8 cm.

10) Low growing plant, stems 35.5-50-(75) cm tall. Panicle with 2, very rarely 5 pedicels. Spikelet 2-3.5 cm, oblong-lanceolate, scarecely varying from youth to maturity. Very long rhizomes, 3-8 cm.

B. erectus Huds. subsp. ***aurouzensis*** C. Fraile

10) Stems 30-80 cm tall. Panicle with 2-6 basal panicle branches or pedicels. Spikelet 1.5-2.8-(3) cm, narrowly ovate when young, to more broadly ovate at maturity. Rhizomes 2-5-(6) cm.

11) Panicle narrowly ovate, compact when young, varying significantly and becoming very loose, deltoid at maturity. Leaf sheaths glabrous, sometimes with very short, retrorse hairs. Leaf blades glabrous. Spikelet 2-2.8 cm, bearing (4)-5-6 florets. Glummes and lemmas very pale green, sometimes quite translucent, with broad hyaline margins throughout most of their length, giving a glossy appearance to the spikelets.

B. pannonicus Kummer & Sendtn. subsp. ***monocladus*** (Domin) P.M. Smith

11) Panicle ovate, compact, scarcely varying at maturity and becoming slightly looser. Leaf blades and sheaths shortly puberulous or with scattered, long, patent hairs. Spikelet 1.5-2.5-(3) cm, bearing 4-7-(8) florets. Lemma broadly lanceolate, with 3 prominent nerves and 2 more obscure, disappearing only towards the bottom of the lemma.

B. pannonicus Kummer & Sendtn. subsp. ***pannonicus***

9.3.3 B. riparius Group

9.3.3.1 Account of the Taxa

B. riparius Rehmann, *Notiz. Veg. Gest. Schwarz. Meer.* 83 (1872).

Perennial, rhizomatous, rhizomes 2-5-(8) cm long. Ascending to erect stems, (27.5)-35-85 cm tall, 0.5-4 mm wide, glabrous. Leaf sheath indumentum varying from glabrous to densely covered with short hairs or with long, patent hairs or finely puberulous; basal sheaths decaying into persistent, reticulate fibres. Basal and cauline leaves glabrous, sparsely pilose or finely tomentose, flat, sometimes with inrolled margins; the basal 7-20 cm × 1.5-5 mm, the cauline 7.5-27.5 cm × (1)-1.5-5 mm; ligule 0.5-2 mm. Flag leaf 6.5-26 cm × 1-2-(4.5) mm. Panicle varying from narrowly ovate, compact when young, becoming broadly ovate, looser or widely spreading, deltoid at maturity, (6)-7-12-(18) cm long from the lowest to the uppermost node, bearing 6-23-(28) spikelets. Panicle branches shortly scabrid or glabrous, erect, stiff, 2-6 at the lowest node; the shortest 1-4-(5) cm, the longest (2.7)-3-6.5-(7.5) cm. Spikelets narrowly ovate to lanceolate when young, becoming broadly ovate or cuneate at maturity, 2-3.5-(4.5) cm long, with (3)-5-9-(10) florets; rachilla (1)-1.5-3-(3.8) mm. Glumes and lemmas glabrous or covered with silky, short, adpressed hairs, frequently purple-flecked. Glumes subequal, the lower (6.5)-7-11.5-(12) mm, narrowly lanceolate, the upper (9)-11-13-(15) mm, broadly lanceolate. Lemma (10)-11.5-14-(18) mm × (1.5)-2-2.8 mm, oblong-lanceolate, with broad hyaline margins forming 2 apical teeth, sometimes with 5 nerves, 3 very prominent and 2 more obscure disappearing only towards the bottom of the lemma. Awn (2)-3.6-6.5-(9) mm, subapical, straight or slightly out-curved. Palea 9-12-(13) mm, with short, fine hairs along the keels. Stamens 3, anthers (3.8)-4.5-7.5 mm. Caryopsis 8.5-10.2 mm.

Key to three subspecies of ***B. riparius*** Rehm.:

1) Leaf sheaths densely covered with short, erect hairs. Basal leaves 9.5-15 cm × 3.5-5 mm, slightly tomentose. Panicle broadly deltoid, spreading. Glumes and lemmas moistly hairy, with soft, adpressed hairs, pale green-yellowish, shiny, giving a golden appearance to the spikelets.

subsp. ***macedonicus*** (Degen & Dörfler) Soó

1) Leaf sheaths glabrous or with few, scattered, sometimes numerous long hairs. Basal leaves 7-20 cm × 1.5-3-(3.5) mm, glabrous, scabrid or pilose, with hairs along the margins. Panicle broadly ovate, loose at maturity. Glumes and lemmas glabrous or with silky, short, adpressed hairs, frequently purple flecked.

2) Stems (1.5)-2.5-3-(3.5) mm wide. Panicle (7)-9.5-12-(18) cm long from the lowest to the uppermost node, with (10)-14-23-(28) spikelets, (2)-3-6 pedicels at the lowest node. Basal leaves 8.5-22 cm long, flat. Lemma (10)-11.5-14 mm × (2)-2.5-2.8 mm, ovate-lanceolate. Long rhizomes, 2-5-(8) cm.

subsp. ***barcensis*** (Simonk.) Soó

2) Stems 0.5-1.5-(1.8) mm wide. Panicle (6)-7-8.5-(12) cm long from the lowest to the uppermost node, with 6-12-(25) spikelets, 2-4 panicle branches at the lowest node. Basal leaves 7-14.5 cm long, flat, sometimes with inrolled margins. Lemma (11.5)-12-14-(18) mm × (1.5)-2-2.5 mm, oblong-lanceolate. Rhizomes 2-4 cm.

subsp. ***riparius***

6a) *B. riparius* Rehm. subsp. ***riparius***[1]

Perennial, rhizomatous, rhizomes 2-4 cm long. Ascending to erect stems, (27.5)-40-60-(95) cm tall, 0.5-1.5-(1.8) mm wide, glabrous. Leaf sheaths glabrous or with numerous patent hairs, the lowest decaying into fibres forming a reticulum. Basal and cauline leaves glabrous, scabrid or sparsely pilose with scattered cilia along the margins, flat, sometimes with inrolled margins, the basal 7-14.5 cm × 1.5-3 mm, the cauline 7.5-21 cm × 1.5-4.5 mm; ligule 0.5-2 mm. Flag leaf 6.5-16.8 cm × 1-2.2-(2.5) mm. Panicle narrowly ovate, compact when young, becoming broadly ovate, looser at maturity, (6)-7-8.5-(12) cm long from the lowest to the uppermost node, bearing 6-12-(25) spikelets. Panicle branches shortly scabrous, erect, 2-4 at the lowest node; the shortest (2)-2.2-3-(5) cm, the longest (2.7)-4.7-6.5-(6.7) cm. Spikelets lanceolate when young, becoming cuneate after anthesis, (2.3)-2.5-3.5-(4.5) cm long, with (3)-4-9-(10) florets; rachilla (1.5)-2.5-3-(3.8) mm, hairy. Glumes and lemma glabrous, occasionally purple-flecked. Glumes subequal, the lower (6.5)-8.5-10.5-(12) mm, narrowly lanceolate, the upper (9)-11-13-(15) mm, broadly lanceolate. Lemma (11.5)-12-14-(18) mm × (1.5)-2-2.5 mm, oblong-lanceolate, broad hyaline margins forming 2 apical teeth, with 5 nerves, 3 very prominent, 2 more obscure disappearing only towards the bottom of the lemma. Awn (2.5)-5-6-(9) mm, subapical, straight or slightly out-curved. Palea shorter than the lemma, 9.5-12-(13) mm, with short hairs along the keels. Stamens 3, anthers (3.8)-5.5-6-(6.2) mm. Caryopsis 8.5-9.5 mm. Flowering in June, fruiting in July. Geographical distribution in fig. 9.3.3.1.

Habitats: Alpine pastures with some rocky outcrops; stony meadows; rocky slopes at and above timber line; damp meadows; gentle slopes and stony alpine pastures; flooded meadow near the bank of river; limestone; 50-2180 m.

[1] Frequenting banks of streams or rivers

Type (fig. 9.3.3.2): Described from the former USSR: "auf dürrem, steinigen Boden des Peresyp bei Odessa und auf Granitfelsen der Bohinsel Konstantynówska in Menge" (BM!); Iso. (K!), (W!).

Synonyms: *B. riparius* Rehm., *Notiz. Veg. Gest. Schwarz. Meer.* 83 (1872); *Bromus fibrosus* Hackel, *Öesterr. Bot. Z.* 29: 209 (1879), based on *B. transsilvanicus* Schur, *Öesterr. Bot. Z.* 10: 227 (1860), non Steudel; *B. pindicolus* Hausskn. (1885), known only from herbarium label. No publication found; *B. fibrosus* Hackel var. *contractus* Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53 (1899); *B. pindicus* Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53-54 (1899); *B. erectus* Huds. subsp. *fibrosus* (Hackel) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 578 (1901); *B. fibrosus* Hackel subsp. *eu-fibrosus* Hayek, *Prodr. Fl. Pen. Balcan.* 3: 205 (1933); *Zerna riparia* (Rehm.) Nevskii, *Acta Univ. Asiae Mediae. Bot.* 17: 17 (1934); *Bromopsis pindica* (Hausskn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973); *Bromopsis riparia* (Rehm.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973); *Bromopsis riparia* (Rehm.) Holub subsp. *fibrosa* (Hackel) Tsvelev, *Fedorov Fl. Evr. Casti* S.S.S.R., 1: 176 (1974).

Icones: Javorka & Csapody, *Icon. Fl. Hung.*, tab. 382, pp. 44 (1934); Todor, *Fl. Rep. Soc. Rom, fasc.* 12, tab. 59, pp. 308 (1972); Smith, *Fl. Turkey,* fasc. 9, tab. 12, pp. 293 (1985).

Selection of specimens

Bulgaria

Backovo, in submontanis, 7.1907, *Stríbrny,* s.n. (W); "Rakovo dere", beside the road, dry, exposed, 1600 m, 26.7.93, *Fraile,* 25 (E); Beglika, on stony hill, exposed, 1600 m, 26.7.93, *Fraile,* 30 (E); "Chervenata stena", stony, exposed area, beside a comunity of *Pinus nigra,* 1450 m, 27.7.93, *Fraile,* 31 (E); Trigrad, beside the road on a rocky hill, 1200 m, 28.7.93, *Fraile*, 36 (E); Trigrad, on a steep slope, 1230 m, 28.7.93, *Fraile*, 37 (E); Popovi livadi, mountainous meadows, stony, 2000 m, 29.7.93, *Fraile*, 40 (E).

Greece

Mt Falakron, damp meadows gentle slopes and stony alpine pastures around of the snow hole, limestone, 2100-2150 m, 1.7.1981, *Stamatiadou*, 22304 (C); Sterea Ellas, Giona-Massiv, Kalfelswände, 1800-2000 m, 25.6.1982, *Hagemann, Scholz & Schwarz*, 423 (B); Pindus Tymphaeus, Malakasi in Saturigin., 7.1885, *Haussknecht*, s.n. (BM, JE, K), sub. *B. pindicolus* Haussknecht.

Rumania

Krassó-Szöreny: Kazán ad Orsovan, *Degen*, 3944 (WU); Deliblát-Fehértelep, in desertis aren., 28.5.1917, *Jávorka et Timkó*, s.n. (S).

Former U.S.S.R

Staryj Oskol, steppum pratosum "Jamskaja", loco elevato, 19.6.1970, *Krylova*, s.n. (E).

Observations: *B. pindicus* (Hausskn.) has been accounted by diverse authors (Halacsy 1904; Hayek 1933; Smith 1980) as an endemic species from N.C. of Greece in the *B. erectus* group. An analysis of the type specimen (BM!) showed some important findings. The original specific name was *B. pindicolus* (Hausskn.) instead of *B. pindicus*. A close study of the sheath revealed it to be formed of a reticulum, although in a very early stage in spite of being an adult plant. This may indicate the existence of diverse patterns of reticular sheath. I therefore believe that both names, *B. pindicolus* (Hausskn.) and *B. pindicus* (Hausskn.) apply to the same taxon. The former is dated from 1885 and the later from 1899. Presumably, when Haussknecht published the type description 14 years after finding the specimen, he mixed up the names. *B. pindicus*, the only published name, nevertheless has the priority, should the taxon be recognised as a species.

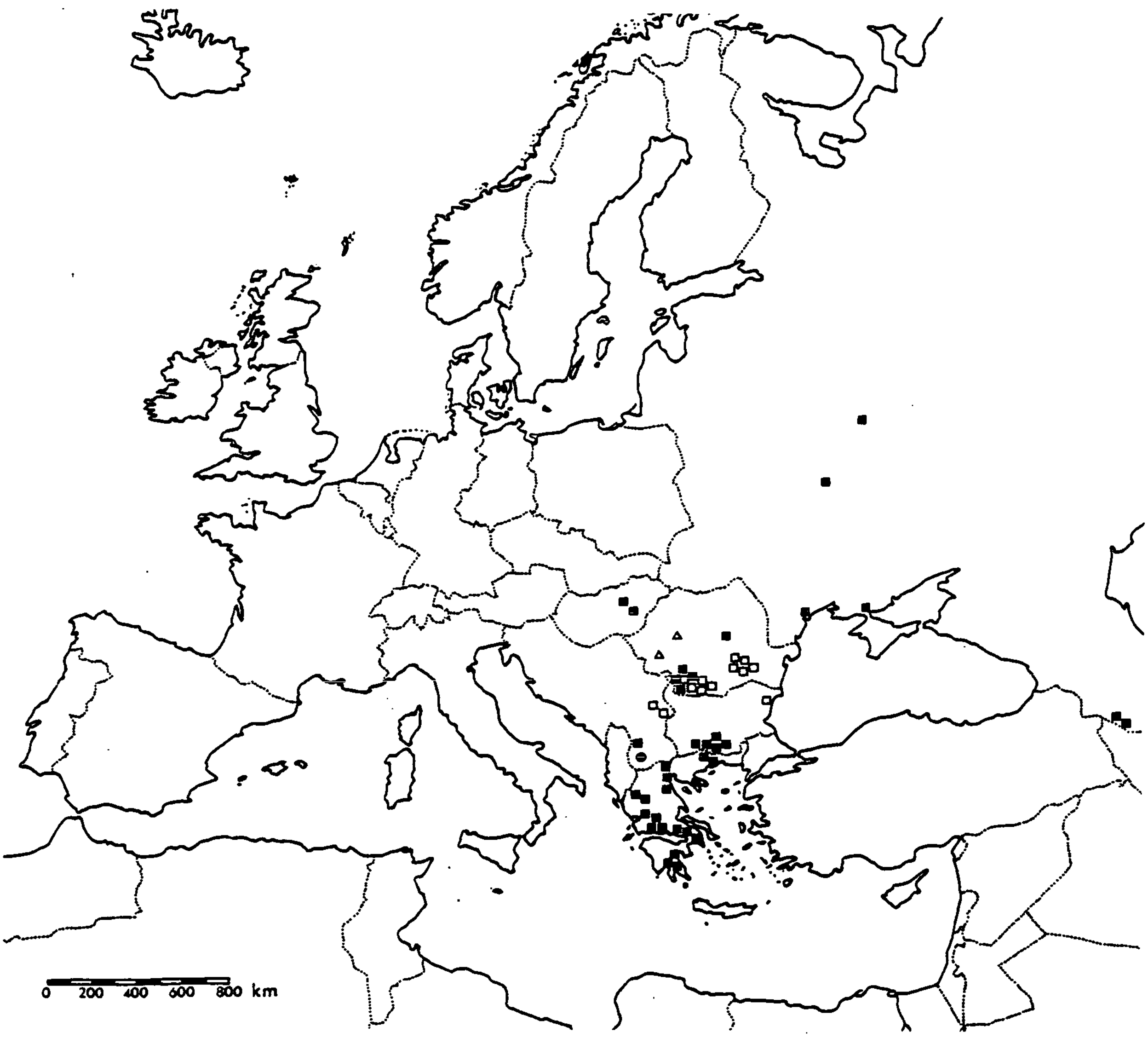

Fig. 9.3.3.1. Geographical distribution of *B. riparius* subsp. *riparius* (■), *B. riparius* subsp. *barcensis* (□), apparent intermediates between these two subspecies (Δ) and *B. riparius* subsp. *macedonicus* (●)

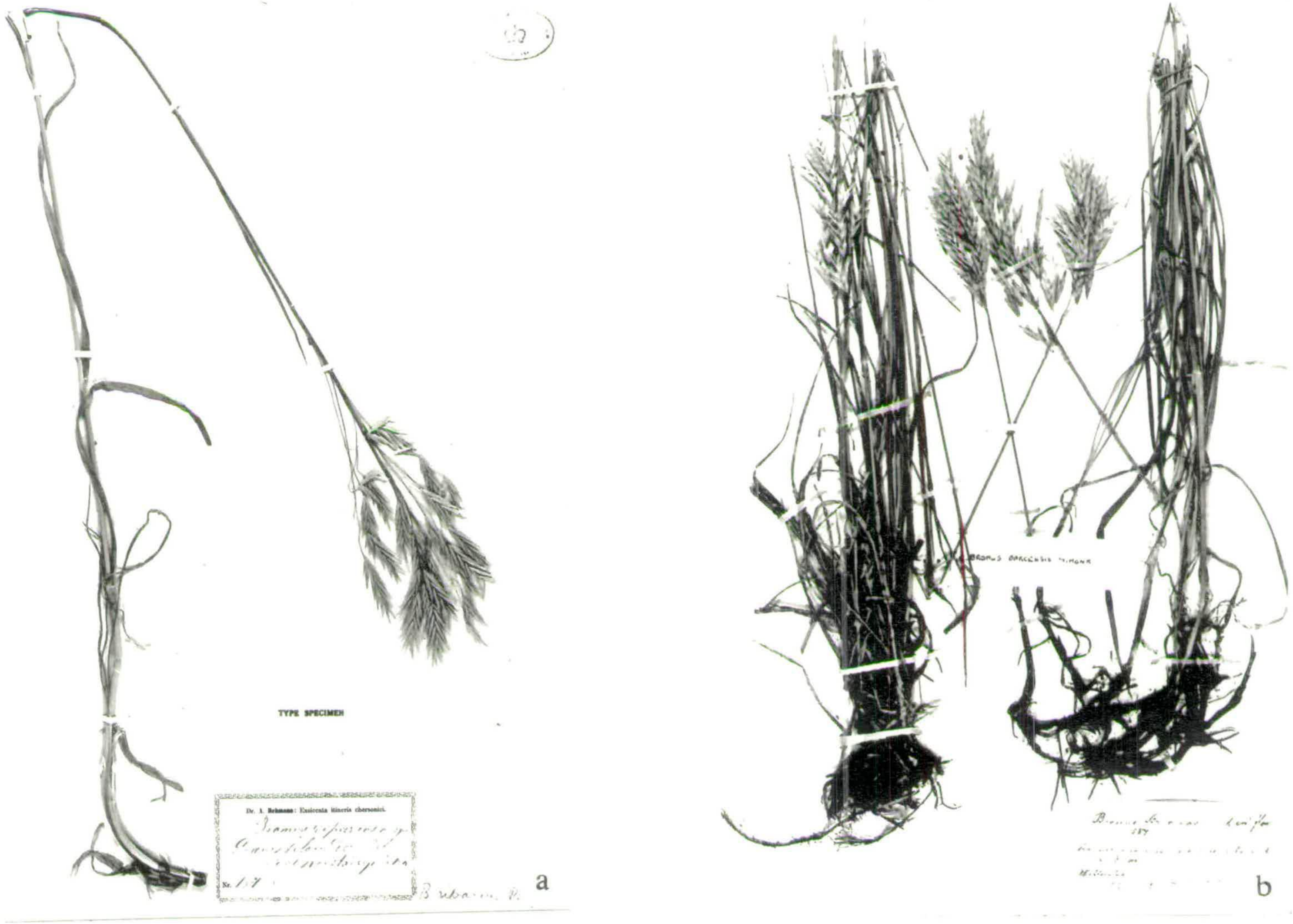

Fig. 9.3.3.2. (a) Type of *B. riparius* Rehm. and (b) Type of *B. barcensis* Simonk. Mag. x0.32

6b) *B. riparius* Rehm. subsp. ***barcensis***[1] (Simonkai) Soó, *Acta Bot. Acad. Scient. Hung.* 17 (1-2): 115 (1971).

Perennial, with loose tufts connected by long rhizomes, 2-5-(8) cm. Ascending to erect stems, 37.5-85 cm tall, (1.5)-2.5-3-(3.5) mm wide, glabrous. Leaf sheaths glabrous, occasionally with few scattered long hairs; basal sheaths decaying into persistent, reticulate fibres. Basal and cauline leaves pilose or mostly glabrous with scattered long hairs along the margins, flat, sometimes conduplicate, the basal 8.5-22 cm × 1.5-3-(3.5) mm, the cauline 7.5-27.5 cm × (1)-2.5-3-(5.5) mm; ligule (0.5)-1-1.5-(2) mm. Flag leaf 9.5-26 cm × (1)-1.5-2-(4.5) mm. Panicle simple, initially ovate, compact, later becoming looser, spreading, (7)-9.5-12-(18) cm long from the lowest to the uppermost node, bearing (10)-14-23-(28) spikelets. Pedicels shortly scabrid, erect, stiff, (2)-3-6 at the lowest node, the shortest 1-3-(4.5) cm, the longest (3.5)-4-5.5-(7.5) cm. Spikelets narrowly ovate when young, becoming broadly ovate at maturity, (2.5)-3-3.5-(4) cm, with numerous florets, 5-8-(9); rachilla 1.5-2.5 mm, with abundant short hairs. Glumes and lemmas glabrous or covered with silky, short, adpressed hairs, frequently purple-flecked, with broad hyaline margins, especially towards the apex. Glumes subequal, the lower (7)-8.5-10 mm, narrowly lanceolate, the upper (9.5)-11-11.5 mm, broadly lanceolate. Lemma (10)-11.5-14 mm × (2)-2.5-2.8 mm, ovate-lanceolate, with 2 apical membranous teeth. Awn (3.6)-4.5-6.5 mm, subapical, straight. Palea (9.5)-10.5-11.5 mm, shorter than the lemma, with fine, short hairs along the keels. Stamens 3, anthers 4.5-7.5 mm. Caryopsis 9.5-10.2 mm. Flowering in May, fruiting in June. Geographical distribution in fig. 9.3.3.1.

Habitats: Steppe; meadows; rocky slopes; subalpine; calcareous; 50-1400 m.

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[1] From Bárcaság, small town in Rumania

Type (fig. 9.3.3.2): Described from Rumania: "Transssilvania: in apricis calcariis montis Czenk ad Brassó, 1886 jul 6." (BP!).

Synonyms: *B. barcensis* Simonk. *Enum. Fl. Transs.* 584 (1886); *B. fibrosus* Hackel var. *barcensis* (Simonk.) Jav., *Magyar Fl.* 1, 1: 108 (1924); *B. fibrosus* Hackel subsp. *barcensis* (Simonk.) Hayek, *Fl. Pen. Balc.* 3: 205 (1933); *B. erectus* Huds. subsp. *barcensis* (Simonk.) Aschers. & Graebn., *Syn. Mitteleur. Fl.* 2 (1): 579 (1901); *Zerna riparia* (Rehm.) Nevskii subsp. *barcensis* (Simonk.) Holub, *Folia Geobot. Phytotax.* 5: 440 (1970); *Bromopsis riparia* (Rehm.) Holub subsp. *barcensis* (Simonk.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973).

Icones: Todor, *Fl. Rep. Soc. Rom.*, fasc. 12, tab. 59, pp. 308 (1972).

Selection of specimens

Bulgaria

Black sea coast, Balcick, 2n = 70, 27.5.1976, *Petrova*, 2629 (WU).

Rumania

Monte Rius, in loco classico, 7.8.90, *Römer*, s.n. (WU); Mtis Tampa, in declivibus saxosis calcareis, 600-700 m, 2.7.1912, *Nyárády,* 229 (WU); Zinne, 7-800 m, 27.6.1912, *Bornmüller*, s.n. (B); Brassó, in apricis calcariis, 6.7.1886, *Simonkai*, s.n. (BP); Mtis Czenk, in graminosis, solo calcareo, 960 m, 15.7.1901, *Degen*, 220 (W).

Former Yugoslavia

Basora, Pirot, 6.1882, *Jovanovié*, s.n. (W); Mte. Bassora, subalpinis, 5.3., *Bierbach*, s.n. (MA); Mte Kapaorik, 5.3., *Bierbach*, s.n. (JE).

Apparent intermediates between *B. riparius* Rehm. subsp. *riparius* and *B. riparius* Rehm. subsp. *barcensis* (Simonk.) Soó (fig. 9.3.3.1)

Bulgaria

Three specimens, Cyrillic: 10.6.1951, s.n. (SOM); 28.7.1956, s.n. (SOM); 19.6.1954, s.n. (SOM).

Rumania

Banatus, distr. Caras-Severin, declivibus, saxosis, solo calc., 80 m, 29.5.1923, *Borza & Nijárády*, s.n. (BM, K, W, WU); In rupibus calcareis ad pagum Remete, 30.5-20.6.1889, s.n. (B).

6c) *B. riparius* Rehm. subsp. ***macedonicus***[1] (Degen & Dörfler) Soó, *Acta Bot. Acad. Sci. Hung.* 17 (1-2): 115 (1971).

Rhizomatous, with loose tufts connected by long rhizomes, 3-4 cm. Ascending to erect stems, 30-80 cm tall, 2.8-4 mm wide, glabrous. Leaf sheaths densely covered with short, erect hairs, the lowest decaying into fibres forming a reticulum. Basal and cauline leaves slightly tomentose, flat, sometimes with inrolled margins; the basal 9.5-15 cm × 3.5-5 mm, the cauline 8-16.5 cm × 1.5-5 mm; ligule very short 0.5 mm. Flag leaf 10-13 cm × 1-1.5 mm. Panicle simple, broadly deltoid, spreading, 7-10 cm long from the lowest to the uppermost node, with 10-11 spikelets. Pedicels glabrous, erect, stiff, 3-4 at the lowest node, the shortest 2-4 cm, the longest 3-6 cm. Spikelets from narrowly lanceolate when young to broadly ovate-cuneate at maturity, 2-3.5 cm long, multiflowered, bearing 6-8 florets; rachilla (1)-2-2.5 mm, finely hairy. Glumes

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[1] From Macedonia (former Yugoslavia)

and lemmas mostly hairy with soft, adpressed hairs, pale green-yellowish, shiny, giving a golden appearance to the spikelets. Glumes glabrous or with scattered, few fine hairs, subequal, the lower 8.5-11.5 mm, narrowly lanceolate, the upper 11-12.5 mm, broadly lanceolate. Lemma 12.5-14 mm × 2.2-2.6 mm, presenting broad hyaline margins and fine, adpressed hairs, ovate-lanceolate. Awn 4.2-6.5 mm, straight. Palea 9-10 mm, shorter than the lemma, with short hairs along the keels. Stamens 3, anthers 5.5-6.3 mm. Caryopsis not seen. Flowering in June-July, fruiting time unknown. Geographical distribution in fig. 9.3.3.1.

Habitat: Rocky places.

Type (fig. 9.3.3.3): Described from Macedonia: "Macedon. Centr. in petrosis prope Allchar, 19.6., Dörfler" (W!); Iso (W!, WU!).

Synonyms: *B. fibrosus* Hackel subsp. *macedonicus* Degen & Dörfler, *Akad. Wiss. Wien, Math.- Naturwiss. Kl., Denkschr.* 64: 741 (1897); ? *B. macedonicus* auct. Kozuh., Petr. & Ehrend., *Bot. Jahrb. Syst.* 102 (1-4): 382 (1981), sub. *B. orbelicus* Petr., Kozuh. & Ehrend., in press (1993).

Selection of specimens

Former Yugoslavia

Macedon. Centr, in petrosis prope Allchar, 19.6, *Dörfler*, 396 (W, WU).

Fig. 9.3.3.3. Type of *B. riparius* Rehm. subsp. *macedonicus* (Deg. & Dörfler) Soó. Mag. x0.32

7) ***B. moesiacus*** Velenovsky, *Fl. Bulg.* 616 (1891).

Perennial, caespitose. Ascending to erect stems, low growing plant, 20-30 cm tall, 0.6-1.1 mm wide, finely hairy. Leaf sheaths puberulous, frequently covered with scattered long cilia; the lowest sheaths decaying into fibres forming a very compact reticulum. Basal and cauline leaves minutely pubescent with scattered long cilia along margins, flat, occasionally conduplicate; the basal 3.5-12 cm × 1.5-3 mm, the cauline 5-11.5 cm × 1.2-4 mm; ligule very short, 0.5-1.5 mm. Flag leaf 3.5-8.5 cm × 1-2.5 mm. Panicle varying from ovoid, compact when young to deltoid, wide open, spreading at maturity, 4-9 cm long from the lowest to the uppermost node, multispiculate, bearing 10-35 spikelets. Panicle branches very fine, puberulous, initially erect, later becoming slightly tortuous, sometimes patent at maturity, 2 branches at the lowest node, presenting short cilia on the scale; the shortest 1.2-3 cm, the longest 2-3.5 cm. Spikelets from narrowly lanceolate when young to more broadly ovate-cuneate at maturity, quite small, 1-2 cm, with 4-6 florets; rachilla 1.3-2.5 mm, hairy. Glumes and lemmas covered with silky, fine, adpressed hairs, giving a delicate appearance to the spikelets, frequently purple-flecked, 3 nerves very prominent. Glumes subequal, narrowly lanceolate, narrow hyaline magins, the lower 5.6-6.5 mm, the upper 7.5-8.5 mm. Lemma 8-10 mm × 1.5-1.9 mm, small, oblong-lanceolate, broad hyaline margins, especially at the apex, forming 2 apical teeth. Awn 3.5-6 mm, straight, frequently purple-flecked. Palea 7.5-9.5 mm, shorter than the lemma, with long hairs along the keels. Stamens 3, anthers 3.5-4.5 mm. Caryopsis 7-8 mm. Flowering in June, fruiting time unknown. Geographical distribution in fig. 9.3.3.4.

Habitats: Rocky steppes; meadows; limestone; 900-1400 m.

Type: Described from Bulgaria: "In collibus aridis calcareis ad Krapec ad radicem merid. m. Vitoša a. 1890. legit. amic. Škorpil".

Synonyms: *B. erectus* Huds. *var. moesiacus* (Velen.) Stoy. & Stefanov, *Fl. Bulg.*, 3rd edition, 160 (1948); *Bromopsis moesiaca* (Velen.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973).

Icones: Velchev, *Atlas of the endemic plants of Bulgaria*, pp. 179 (1992).

Selection of specimens

Bulgaria

Golo Bardo, in ruderatis circa cacum, solo calcareo, 1400 m, 14.6.1954, *Bondev*, 773 (B); Golo Bardo Mt., 2n=14, 17.7.1972, *Kozuharov*, 221401 (WU); Vitosha Mt., 2n=14, 11.5.1973, *Kozuharov*, 23170 (WU); Vitosha Mt., 2n=14, 25.5.1975, *Kozuharov*, 25253 (WU); Vitosha Mt., 2n=14, 9.12.1972, *Kozuharov*, 221753 (WU); Mt. Mecer, in graminosis et in rupibus calcareis, 900-1200 m, 18.6.1933, *Stoyanov*, s.n. (S).

8) *B. parilicus*[1] Petrova, Kozuharov & Ehrendorfer, in press (1993).

Perennial, with relatively loose tufts connected by short rhizomes, 1-2 cm. Ascending to erect stems, 45-50 cm tall, 0.7-1.5 mm wide, very thin, glabrous. Leaf sheaths glabrous, the lowest decaying into fibres forming a reticulum. Basal and cauline leaves glabrous, linear, involute; the basal 8.5-12 cm × 0.5-1 mm, the cauline 6.5-10 cm × 0.5-1-(1.5) mm; ligule 0.2-0.5 mm. Flag leaf 3-6 cm × 0.3-0.5 mm. Panicle simple, varying from ovoid, compact when young to more broadly ovoid, looser at maturity, 5-6.5-(7) cm long from the lower to the uppermost node, bearing 7-9 spikelets. Pedicels shortly rough, initially straight, nooding later, very thin, 2 at the lowest node, which frequently presents few cilia on the scale; the shortest 2-3.5 cm

[1] From "Parilski dol" (Bulgaria)

the longest 3.5-4 cm. Spikelets narrowly lanceolate when young, becoming more broadly ovate at maturity, 2.5-3 cm long, with 4-5 florets; rachilla 2-2.5 mm, glabrous. Glumes and lemmas glabrous, narrowly lanceolate, with narrow hyaline margins. Glumes subequal, the lower 8.5-9.5 mm, the upper 10-12 mm. Lemma 12-14 mm × 1.5-2 mm, glabrous. Awn 6-6.5 mm, straight. Palea shorter than the lemma, 10-12.5 mm, with short hairs along the keels. Stamens 3, anthers 3.5-4.3 mm. Caryopsis not seen. Flowering in June-July, fruiting time unknown. Geographical distribution in fig. 9.3.3.4

Habitats: stony, dry slopes.

Type: Described from Bulgaria: "Bulgaria australis, Mt. Slavjanka (Alibotusch), in declivibus convaliis lapidosus siccis supra pagum Paril, ad loco dicto " Parilski dol", 27.7.1977. Leg. S. Kozuharov".

Selection of specimens

Bulgaria

Two specimens, Cyrillic: 26.6.1969, 69641 (SOM); 25.7.1969, 191084 (SOM).

Fig. 9.3.3.4. Geographical distribution of *B. moesiacus* (■) and *B. parilicus* (□)

B. cappadocicus Boissier & Balansa, *Bull. Soc. Bot. France,* 4: 306 (1857).

Perennial, with loose tufts connected by rhizomes, 1-7 cm long. Stems 30-60-(90) cm tall, 1-2.5 mm wide, glabrous or finely hairy. Leaf sheaths glabrous or puberulous covered with patent, stiff hairs or puberulous with scattered long cilia, the lowest decaying into persistent reticular fibres enveloping stem bases. Basal and cauline leaves glabrous or minutely pubescent, sometimes with scattered long cilia along the margins and nerves, linear, involute, somewhat rigid, occasionally flat, presenting rolled margins; the basal 4.5-18 cm × 0.5-3 mm, the cauline 5-15 cm × 0.5-2.3 mm; ligule 0.5-2 mm. Flag leaf 3.5-13 cm × 0.4-1.5 mm. Panicle lanceolate, compact when young, becoming slightly looser or broadly deltoid, spreading at maturity, 3.5-10 cm long from the lowest to the uppermost node, bearing 5-20 spikelets. Panicle branches glabrous or shortly scabrous, straight, rigid or relatively fine, sometimes becoming tortuous at maturity, 2-6 at the lowest node, presenting occasionally few cilia on the scale; the shortest 1.5-3.5-(4) cm, the longest 2.5-5.5-(6) cm. Spikelets from narrowly ovate when young to more broadly ovate-cuneate at maturity, 2-3.7 cm, with 5-7-(8) florets; rachilla 1.3-3 mm, covered with numerous short or long hairs, sometimes glabrous. Glumes and lemmas densely hairy or with scattered fine hairs, broad or narrow hyaline margins, sometimes purple-flecked. Glumes narrowly or broadly lanceolate, the lower 5.5-13 mm, the upper (7.5)-8-15 mm. Lemma 10-14-(16) mm × 2-2.6-(2.7) mm, narrowly lanceolate or ovate-lanceolate, with 2 short apical teeth. Awn 3-8.5 mm, subapical, straight or weakly outwardly curved, sometimes strongly divaricate at maturity. Palea 7.5-10.5-(12) mm. Stamens 3, anthers 5-7.2 mm. Caryopsis 8.3-9.5 mm.

Key to three subspecies of ***B. cappadocicus*** Boiss. & Balansa:

1) Leaf sheaths glabrous. Spikelet 2.8-3.7 cm. Glumes and lemmas narrowly lanceolate, with narrow hyaline margins. Glumes subequal, the lower 8.2-13 mm,

the upper 9.7-15 mm. Lemma 12-14-(16) mm × 2-2.5 mm, narrowly lanceolate. Awn 4.5-8.5 mm, strongly divaricate at maturity.

subsp. ***cappadocicus***

1) Leaf sheaths puberulous, with scattered long cilia or covered with patent hairs, sometimes glabrous. Spikelet 2-3.7 cm. Glumes broadly lanceolate, with broad or narrow hyaline margins, the lower 5.5-10 mm, the upper (7.5)-8-12 mm. Lemma 10-13 mm × 2-2.6-(2.7) mm, ovate-lanceolate. Awn 3-8.5 mm, straight or slightly outwardly curved at maturity.

2) Panicle broadly deltoid, spreading, 3.5-8.5-(9.5) cm long from the lowest to the uppermost node, 2-6 branches at the lowest node. Glumes and lemmas with abundant, long, silky, sub-patent hairs, very pale green-yellowish, sometimes slightly purple-flecked, very broad hyaline margins, giving a delicate-golden appearance to the spikelets. Glumes almost equal, the lower 6-9.5 mm, the upper (7.5)-8.5-9.5-(10) mm. Awn 3-5.5 mm.

subsp. ***crassipes*** (Halácsy) C. Fraile

2) Panicle very compact when young, slightly looser at maturity, 4.5-10 cm long from the lowest to the uppermost node, 2-4 pedicels at the lowest node. Glumes and lemmas densely hairy or presenting few, fine, relatively short hairs, rarely glabrous. Glumes subequal, the lower 5.5-10 mm, the upper 8-12 mm. Awn 3-8.5 mm.

subsp. ***lacmonicus*** (Hausskn.) P.M. Smith

9a) *B. cappadocicus* Boiss. & Balansa subsp. ***cappadocicus***[1]

Perennial, with dense tufts connected by rhizomes, 1-2 cm long. Stems 27.5-55.5 cm tall, 1.2-1.5-(1.6) mm wide, glabrous. Leaf sheaths glabrous; basal sheaths decaying into persistent reticulate fibres enveloping stem bases. Basal and cauline leaves glabrous, linear, involute; the basal 4.5-18 cm × 0.5-1 mm, the cauline 7-10.5 cm × 0.6-1.4 mm; ligule very short, 0.5-1-(1.5) mm. Flag leaf 4-8 cm × 0.4-0.8 mm. Panicle simple, dense, compact when young, becoming looser at maturity, 4.5-8.5 cm long from the lowest to the uppermost node, bearing 8-13-(15) spikelets. Pedicels glabrous or shortly scabrous, straight, relatively fine, sometimes slightly tortuous after anthesis, 2-3 at the lowest node; the shortest 1.5-3.5 cm, the longest 2.5-4.5 cm. Spikelets from narrowly ovate-lanceolate when young to very broad ovate-cuneate at maturity, with each floret expanding laterally, 2.8-3.7 cm long, with 5-7 florets; rachilla 1.3-3 mm glabrous or finely hairy. Glumes and lemmas glabrous, occasionally presenting very short, scarce hairs, narrowly lanceolate, with narrow hyaline margins. Glumes subequal, the lower 8.2-13 mm, the upper 9.7-15 mm. Lemma 12-14-(16) mm × 2-2.5 mm, frequently purple-flecked. Awn 4.5-8.5 mm, subapical, strongly divaricate at maturity. Palea 8-10.5-(12) mm, shorter than lemma. Stamens 3, anthers 5.5 mm long. Caryopsis 9.5 mm. Flowering in June, fruiting in July. Geographical distribution in fig. 9.3.3.5.

Habitats: North-east facing grassy alpine and subalpine meadows; rocky slopes; rocky meadows; limestone; 1350-2212 m.

Type (fig. 9.3.3.6): Described from Turkey: "Très abondant sur toutes les collines de la Cappadoce, de 1000 à 1500 mètres d'altitude, Balansa 841" Holo. (G!); Iso. (K! W!).

[1] From Cappadocia (Turkey)

Fig. 9.3.3.5. Geographical distribution of *B. cappadocicus* subsp. *cappadocicus* (■), *B. tomentellus* (▲), apparent intermediates between these two taxa (□), *B. cappadocicus* subsp. *lacmonicus* (Δ) and *B. cappadocicus* subsp. *crassipes* (●)

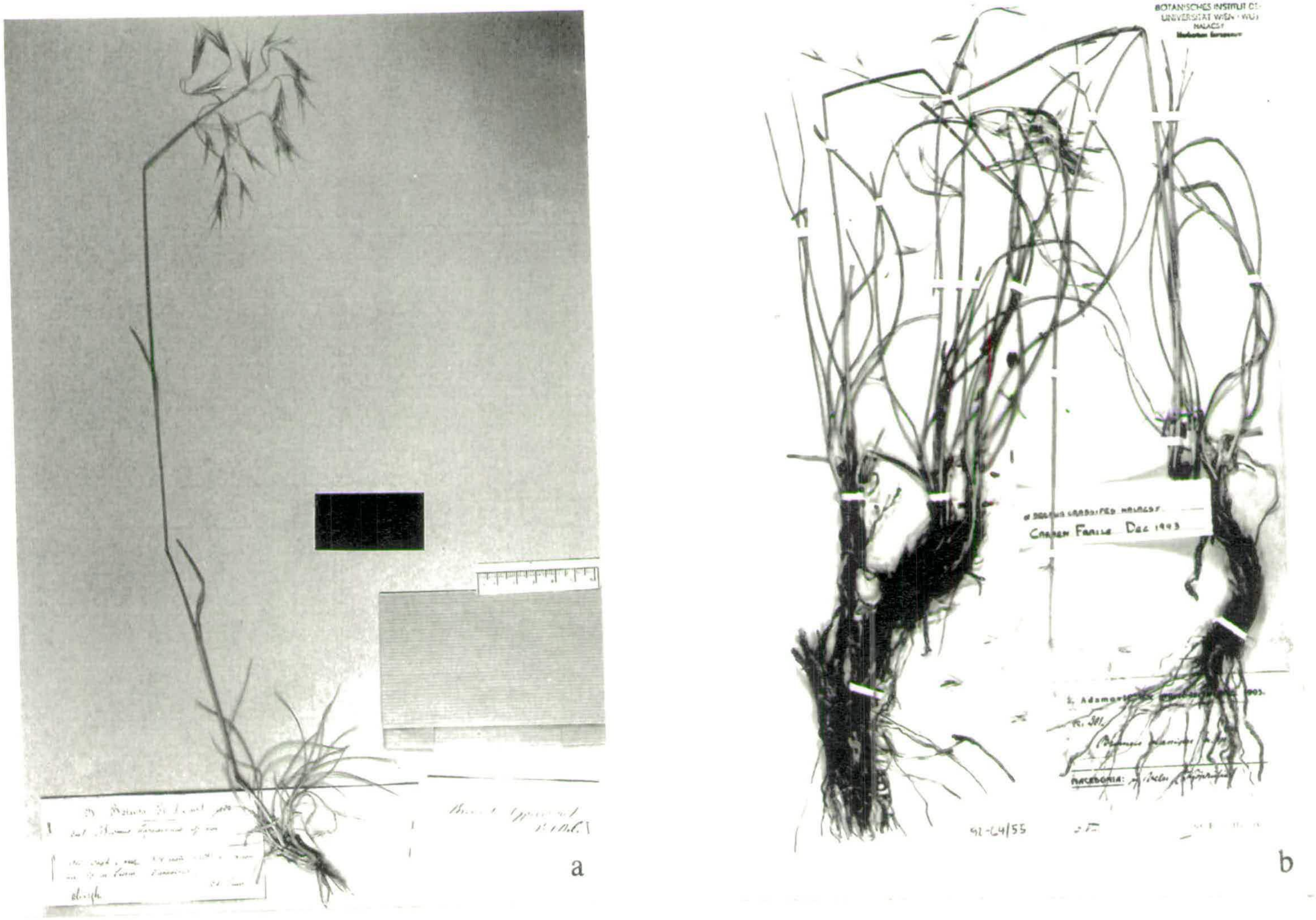

Fig. 9.3.3.6. (a) Type of *B. cappadocicus* Boiss. & Balansa and (b) Type of *B. crassipes* Halacsy Mag. x0.32

Synonyms: *B. cappadocicus* Boiss. & Balansa, *Bull. Soc. Bot. France*, 4: 306 (1857); *Zerna cappadocica* (Boiss. & Balansa) Nevskii, *Acta Univ. Asiae Mediae Bot.* 17: 17 (1934) quoad nomen; *Z. tomentella* (Boiss.) Nevskii subsp. *cappadocica* (Boiss. & Balansa) Tsvelev, *Novit. Syst. Pl. Vasc. (Leningrad)* 7: 56 (1971); *Bromopsis cappadocica* (Boiss. & Balansa) Holub, *Folia Geobot. Phytotax.* 8 (2): 167 (1973); *B. tomentella* (Boiss.) Holub subsp. *cappadocica* (Boiss. & Balansa) Tsvelev, *Zlaki S.S.S.R.:* 217 (1976).

Icones: Smith, *Fl. Turkey*, fasc. 9, tab. 12, pp. 293 (1985).

Selection of specimens

Albania

Tomor range, Abbas Ali, rubbly limestone slopes, 650 ft., 14.8.1935, *Alston & Sandwith*, 2492 (BM, K).

Greece

Mt Menikion, rocky subalpine meadows, limestone, 1350-1600 m, 23.7.79, *Strid & Papanicolau*, 15768 (B); Mt Orvilos (Ali Botus), grassy meadows on calcareous ground, 1800-2000 m, 25.7.1977, *Strid & Georgiadou*, 13334 (B); Mt Orvilos (Ali Botus), alpine pastures and rocky places, limestone, 2000-2200 m, 23.7.81, *Strid & al.*, 19419 (C); Mt Menikion (Boz Dagh of Serre), grassy subalpine meadows, limestone, 1500-1600 m, *Strid & al.*, 18630 (B); Mons Orvilos, in pascuis alpinis Sesleriae dumis Juniperorum inspersis, solo calcareo, 1750-2212 m, 21.8.78, *Greuter*, 16643 (B); Montis Meniki (Boz dag Serron), in pascuis et clivis graminosis petrosis boreo orientem spectantibus, solo calcareo, 1550-1850 m, 20.7.78, *Greuter*, 16144 (C).

9b) ***B. cappadocicus*** Boiss. & Balansa subsp. ***crassipes***[1] (Halácsy) C. Fraile, *comb. et stat. nov.*

Perennial, with loose tufts connected by long rhizomes, 3-7 cm. Stems 30-50-(90) cm tall, 1-2.5 mm wide, finely hairy, sometimes glabrous. Leaf sheaths puberulous, covered with patent, stiff hairs; the lowest decaying into fibres eventually forming a reticulum. Basal and cauline leaves minutely pubescent with scattered long cilia along the margins and nerves, linear, involute, somewhat rigid, occasionally flat presenting inrolled margins; the basal 4.5-12 cm × 1-3 mm, the cauline 5-11 cm × 1-2.3 mm; ligule short, 0.6-1-(1.8) mm. Flag leaf 3.5-6 cm × 0.7-1 mm. Panicle broadly deltoid, spreading, 3.5-8.5-(9.5) cm long from the lowest to the uppermost node, bearing 5-20 spikelets. Panicle branches shortly hairy, straight initially, becoming tortuous at maturity, 2-6 at the lowest node, with few cilia on the scale; the shortest (2)-2.5-3.5-(4) cm, the longest (3)-4.5-5-(6) cm. Spikelets from narrowly ovate when young to more broadly ovate at maturity, 2.5-3.7 cm long, with 6-7-(8) florets; rachilla (1.5)-2-2.5 mm long, covered with numerous long, fine hairs. Glumes and lemmas with abundant, long, sub-patent, silky hairs, very pale green-yellowish, sometimes slightly purple-flecked, very broad hyaline margins, giving a delicate-golden appearance to the spikelets. Glumes broadly lanceolate, almost equal, the lower 6-9.5 mm, the upper (7.5)-8.5-9.5-(10) mm. Lemma 10-12 mm × 2.2-2.6 mm, ovate-lanceolate, with 2 short, apical teeth. Awn 3-5.5 mm, subapical, straight or slightly outwardly curved. Palea 8.5-10 mm, shorter than the lemma, numerous, fine, quite long hairs along the keels. Stamens 3, anthers 5-7.2 mm. Caryopsis 8.3-8.5 mm. Flowering in May, fruiting in June-July. Geographical distribution in fig. 9.3.3.5.

[1] Thick foot

The name refers to the long rhizomes, forming a dense mass

Habitats: Dry, rocky slopes; dry hills; 300-500 m.

Type (fig. 9.3.3.6): Described from former Yugoslavia: "Macedonia: pr. Veles (Kjoprülü), 6.7., N° 981, Halácsy" (WU!).

Synonyms: *B. crassipes* Halacsy, *Öesterr. Bot. Z.* 56: 282 (1906); *B. cappadocicus* Boiss. & Balansa var. *velutinus* Bornm., *Bot. Jahrb. Engler* 61, 140: 172 (1928).

Selection of specimens

Former Yugoslavia

Kisela-voda, in decliv. lapidosis apricis, 300 m, 30.5.1917, *Bornm.*, 2267 (B); Kisela-voda, in decliv. aridis, 300-400 m, 1.6.1918, *Bornm.*, 5264 (B); Sveti Gjorge, in collibus aridis, 3.6.1918, *Borm.*, 5263 (B); Macedonia, in declivibus siccis, 10.5.1976, *Rechinger*, 54389 (B).

9c) *B. cappadocicus* Boiss. & Balansa subsp. ***lacmonicus*** (Haussknecht) P.M. Smith, *Bot. J. Linn. Soc.* 76: 360 (1978).

Perennial, with loose tufts connected by rhizomes, 1-2-(4) cm long. Stems 32.5-60 cm tall, 1-1.7 mm wide, glabrous. Leaf sheaths puberulous with scattered long cilia or sometimes glabrous; basal sheaths decaying into persistent, reticular fibres enveloping stem bases. Basal and cauline leaves glabrous or minutely pubescent, linear, involute, somewhat rigid, occasionally flat, presenting inrolled margins; the basal 6.5-17 cm × 0.8-1.5-(2) mm, the cauline 5-15 cm × 0.5-2 mm; ligule 1-2 mm. Flag leaf 3.5-13 cm × 0.7-1.5 mm. Panicle simple, very compact when young, slightly looser at maturity, stiff, 4.5-10 cm long from the lowest to the uppermost node, bearing 8-13-(14) spikelets. Pedicels glabrous or shortly scabrous, straight, rigid, 2-4 at the lowest node; the shortest 1.5-3-(4) cm, the longest 1.8-5.5 cm; upper branches very short, giving depauperate appearance to the panicle. Spikelets narrowly ovate when young to more broadly ovate-cuneate at maturity, 2-2.8-(3) cm long, with 5-6 florets; rachilla 1.5-3 mm with numerous short or long hairs. Glumes and lemmas densely hairy or presenting few, fine, relatively short hairs, rarely glabrous, narrow hyaline margins. Glumes subequal, broadly lanceolate, the lower 5.5-10 mm, the upper 8-12 mm. Lemma 10.5-13 mm × 2-2.5-(2.7) mm, ovate-lanceolate, with 2 very short apical teeth. Awn 3-8.5 mm, subapical, straight or slightly outwardly curved. Palea 7.5-9.5-(12) mm, shorter than lemma, keels presenting short, fine hairs. Stamens 3, anthers 5.1-7 mm. Caryopsis 8.7-9.5 mm. Flowering in June, fruiting in July. Geographical distribution in fig. 9.3.3.5.

Habitats: Alpine, subalpine meadows; dry meadows and steep rocky slopes with patches of *Fagus* forests; Eastern facing slopes; rocky pine clearing; wet meadows along rivulets on a South facing slope; West facing rocky steppes; grazed slopes with scrub in ravines; limestone and siliceous-serpentine soils;1000-2300 m.

Type (fig. 9.3.3.7): Described from Greece: "Pindus Timphaeus: in summo montis Zygos (Laknon veter.) supra Metzovo, alt. 4500-5000', substratu silicico-serpentino, dieb. Jul., C. Haussknecht" (JE!).

Synonyms: *B. lacmonicus* Hausskn., *Mitth. Thüring. Bot. Vereins,* 13-14: 53 (1899); *B. erectus* Huds. subsp. *fibrosus* (Hackel) Aschers. & Graebn. var. *lacmonicus* (Hausskn.) Stoy. & Stefanov, *Fl. Bulg.*, 3rd edition, 160 (1948); *Bromopsis lacmonica* (Hausskn.) Holub, *Folia Geobot. Phytotax.* 8 (2): 168 (1973).

Selection of specimens

Albania

District Gjinokastrë, Mali Lunxheriës Range, rocky limestone slopes, 5000 ft., 12.7.1933, *Alston & Sandwith*, 2198 (BM, K).

Bulgaria

Kamiko supra vic. Belidiehan, in pascuis saxosis, solo calcario, 5.7.1954, *Velcev*, 514 (W).

Greece

Nomos u. Esparchie kozani, Vourinos, Serpentinfels, 1886 m, 8.7.89, *Höner & Potthoff*, 1269 and 890 (B); Montis Pinovo, in fissuris et scansilibus rupium calcarearum praeruptarum umbrosarum, 1600 m, 20.8.1976, *Greuter*, 14629 (B); Askion (Siniatsikon) Massiv, Gipfelplateau anstehender Fels, Kalkgestein, 2100 m, 22.8.1983, *Hagemann, Ketelhut & Wolf*, 1324 (B); Mt tzena (Kozuf), wet meadows along rivulets on a S. facing slope, 1650 m, 23.8.1981, *Andersson & Franzén*, 809 (B); Vourinos Massiv, steile Felswände, W-exponiert, Serpentingestein, 1450 m, 19.8.1983, *Hagemann, Ketelhut & Wolf*, 1107 (B); Montis Vourinon, in apertis saxosis pinetorum, in declivibus orientalibus substr. serpent., 1200-1400 m, 5.7.1956, *Rechinger*, 17501 (B); Montis Zygos (Lakmon veter.), substratu silicico-serpentino, 4500-5000', Jul., *Haussknecht*, s.n. (JE).

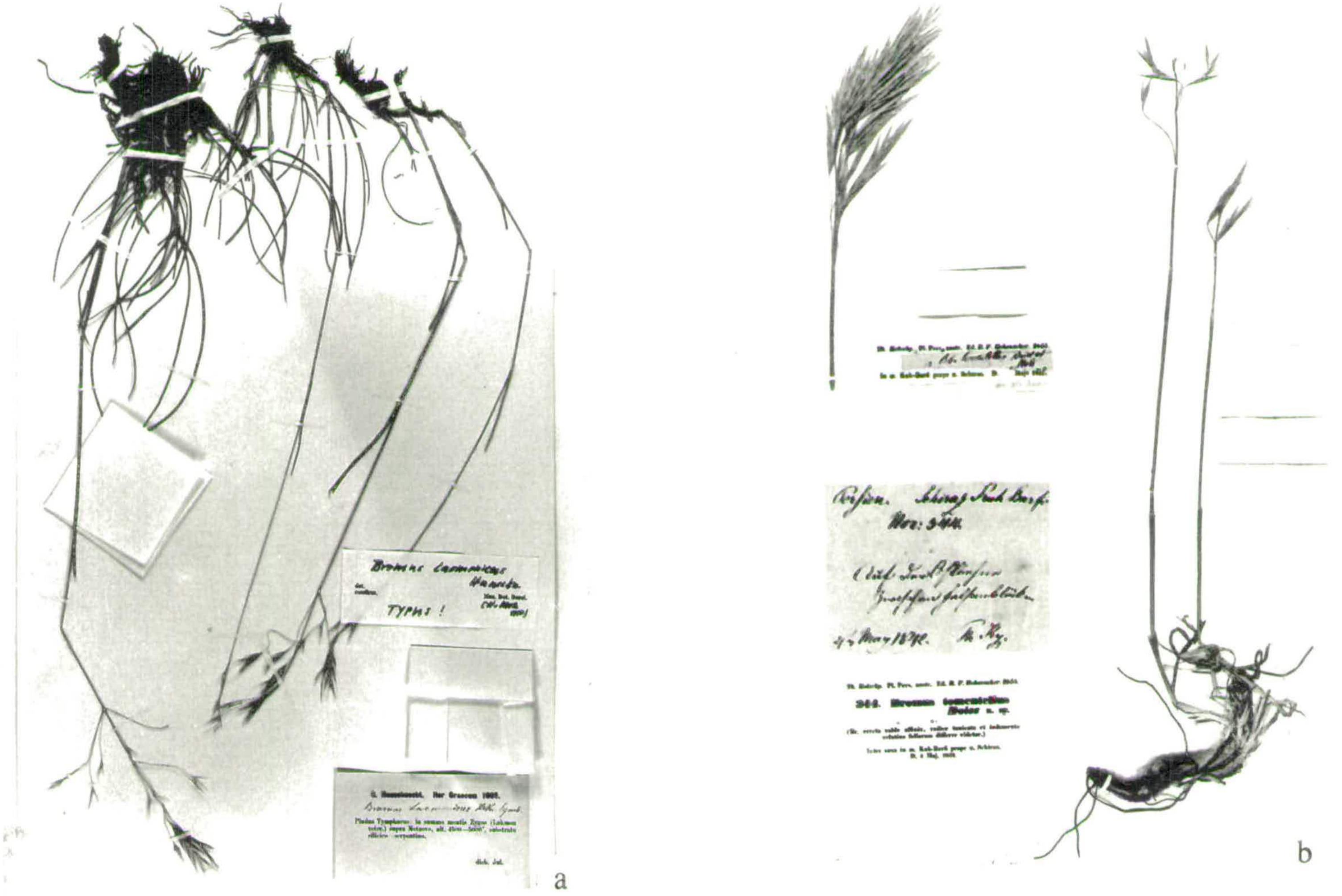

Fig. 9.3.3.7. (a) Type of *B. cappadocicus* subsp. *lacmonicus* (Hausskn.) P.M. Smith and (b) Type of *B. tomentellus* Boiss. Mag. x0.32

10) ***B. tomentellus*[1]** Boissier, *Diagn. Pl. Orient. Nov. Ser.* 1 (7): 126 (1846).

Perennial, with dense tufts connected by rhizomes, 2.5-3 cm long. Stems 20-60 cm tall, 0.5-0.7-(1.5) mm wide, glabrous or shortly hairy. Leaf sheaths densely covered with fine, short, soft hairs and sparse long cilia, sometimes simply pubescent; basal sheaths decaying into persistent, reticulate fibres enveloping stem bases. Basal leaves 5.5-12 cm × 2-2.5-(3.5) mm, densely tomentose, with scattered long cilia along margins, flat, prominent white nerves abaxially, cauline leaves 3.2-18.5 cm × 1-2.5 mm, with similar vesture, conduplicate, occasionally involute; ligule (0.5)-1-2-(2.5) mm. Flag leaf (1.8)-2.3-9 cm × (1)-1.2-2-(2.5) cm. Panicle ovoid-ellipsoid, more contracted when young, but scarcely varying from youth to maturity, 3-8.5 cm long from the lowest to the uppermost node, bearing 5-8 spikelets. Panicle branches shortly pubescent or glabrous, straight, 2 at the lowest node; the shortest 1-1.5-(3.5) cm, the longest 1.2-6 cm, both mostly shorter than the spikelets. Spikelets lanceolate when young becoming cuneate at maturity, (2.4)-2.8-3.5 cm long, with 5-7-(8) florets. Glumes glabrous, subequal, narrowly lanceolate, slightly broad hyaline margins, the lower 7-12 mm, the upper 8.5-15 mm. Lemma 11-15 mm × 2-2.5 mm, glabrous or densely hairy, oblong-lanceolate, slightly broad hyaline margins, with 3 prominent scabrous nerves, 2 more obscure disappearing only towards the bottom of the lemma. Awn (3)-6-7 mm long, straight, subapical, sometimes weakly divaricate. Palea (11)-11.5-12-(12.5) mm, shorter than lemma, finely hairy along the keels. Stamens 3, anthers 3-6.2 mm. Caryopsis 7.5 mm. Flowering in May, fruiting in June-July. Geographical distribution in fig. 9.3.3.5.

Habitats: Stony slopes; limestone-clay; 150-1800 m.

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[1] Minutely tomentose

Type (fig. 9.3.3.7): Described from Iran: "Inter saxa in m. Kuh-Barfi prope Schiras. D. 4 Maj. 1842", based on Kotschy n°. 344 (BM!); Iso.(BM!, K!, W!).

Synonyms: *B. tomentellus* Boiss. var. *hispidus* Boiss., *Diagn. Pl. Orient. Nov. Ser.* 3 (4): 140 (1859); *B. sphacioticus* Gand., *Fl. Crète*: 101 (1916); *Zerna tomentella* (Boiss.) Nevskii, *Acta Univ. Asiae Mediae Bot.* 17: 17 (1934); *Bromopsis tomentella* (Boiss.) Holub, *Folia Geobot. Phytotax.* 8 (2): 169 (1973).

Icones: Cope, *Fl. Iranica*, fasc. 70, tab. 21 (19820); Smith, *Fl. Turkey*, fasc. 9, tab. 12, pp. 293 (1985).

Selection of specimens

Crete

Milopotamos: N-Hang des Berges, Melidhomaskala, Kalgeröllhalde, 1550-1715 m, 27.5.1983, *Greuter & Risse*, 19846 (B); Kreta, Ida, 31.5.1904, *Dörfler*, 687 (WU); Kydonias: Levka Ori, 1200-1500 m, 26.6.1979, *Strid & Papanicolau*, 15097 (C); In rupestribus, 5000', 5.1846, *Heldreich*, s.n. (K); Ida, 5000', 27.5.1846, *Heldreich*, s.n. (W).

Former U.S.S.R

Tauria merid. Sudak, 150 m, 9.5.1969, *Smirnow*, s.n. (W).

Apparent intermediates between *B. tomentellus* Boiss. and *B. cappadocicus* Boiss. & Balansa subsp. *cappadocicus* (fig. 9.3.3.5)

Asian Turkey

B3 Eskigehiri 2m. East of Sivrihisar, rocky limestone slopes, 1100 m, 12.6.1965, *Coode & Jones*, 2246 (K); B2 Usak, chalk slope, 800 m, 14.6.1965, *Coode & Jones*, 2395 (K).

Europe

Crimea

Distr. Simferol, in forest steppe zone, calcareous, 330 m, 5.6.1959, *Davis*, 33556 (K).

9.3.3.2 Notes on Ecology of the B. riparius Group

The evolutionary adaptation of grasses, like that of any other groups of plants, involves particular physiological, anatomical, and morphological characteristics. For example, vascular bundles and mesophyll cell arrangement are related to the type of photosynthetic pathway (Black et al. 1973; Hattersley & Watson 1975). A prevailing characteristic in the group of brome-grasses with a reticular sheath is the existence in some of its taxa of narrow and rolling leaves, with sclerenchymatous fibres in great amount, acting as a mechanical tissue (see chapter 4, sect. 4.3). The anatomy and mechanism of leaf rolling in grasses has been studied for over a century, creating a lot of controversy (Tschirch 1882; Shields 1951); it has been related to the loss of turgor in the bulliform cells presented on the adaxial (upper) surface, also known as "motor cells" (Bews 1929). However rolling can occur in leaves that lack bulliform cells (Shields 1951). In spite of numerous studies and resulting theories (Tschirch 1882; Brandis 1907; Goossens & Theron 1934; Breakwell 1915; Shields 1951) the nature of the rolling mechanism has not been determined.

The combination of both elements - form and function - seems to be directly related in rolling leaves. Before progressing with these considerations, it is useful to recollect some ecological aspects concerning these brome-grasses. Their pattern of distribution, as discussed in section 9.3.3.1, corresponds to mountain slopes, dry hills and rocky, sandy steppes, all of them under the effect of strong winds, distinctive in the Balkan peninsula (Turrill 1929). Hence it may constitute a group of grasses which seems to show certain correlated adaptations to xeric habitats.

The leaf rolling process, especially in the Gramineae, has been mentioned as a way of decreasing transpiration rate of water-stressed plants (Parker 1968; Oppenheimer 1960). O'Toole & Cruz (1979) in a study carried out on *Oryza sativa*, quantified this effect and also investigated the effect of wind velocity on the process of leaf rolling. They showed a direct relationship between leaf-rolling and a decrease of transpiration rate, and also that the effect of leaf rolling became more pronounced as wind speed was increased. There seems no doubt that the functional significance traditionally attributed to leaf rolling is, in fact, genuine. This study accounts for the effect that exposure to winds exert on the leaves of these grasses in their only European redoubt - the Balkan peninsula. Naturally, windy steppes of Turkey and adjacent S.W. Asia, where some of the taxa are also distributed, would also have the same properties.

The process of rolling has been interpreted as a xeromorphic adaptation for reducing transpiration by "protecting " the stomata - which were considered to be distributed on the adaxial (upper) surface. Parkhurst (1978) after studying four families (not including grasses) concluded that the condition of amphistomatous leaves (stomata on both surfaces) is more frequent in xeric and hydric habitats. Redmann (1985) also confirmed it, but in grasses (chapter 4, section 4.3). A detailed study of leaves belonging to two different taxa in this group of brome-grasses (*B.*

tomentellus and *B. cappadocicus* subsp. *cappadocicus*), showed that stomata occurred on both sides. They were located in longitudinal furrows protected by hairs in the former (chapter 4, fig. 4.6).

The principal of Optimal Design (Parkhurst & Loucks 1972) could be applicable to this situation: "natural selection leads to organisms having a combination of form and function optimal for growth and reproduction in the environments in which they live". Although this concept is interesting and helpful, I find the use of word "design" curious in a scientific, evolutionary context. I would also point out that the optimum phenotypes are rarely achieved because of non-available mutations, evolutionary inertia (the load of conservative, canalised features - to some extent genetically linked) and interference from interacting factors.

Thus, leaf rolling represents an effective means to conserve water during periods of water deficit, a condition quite frequent in the mountain regions along the Balkan peninsula, combined with the effect of strong winds - both - creating at least periodically, quite xeromorphic conditions for the growth of these brome-grasses. Narrow leaves are more efficient heat exchangers and less likely to overheat when exposed to drought and high irradiance (Parkhurst & Loucks 1972; Gates 1980). This, of course, is only to the extent that the majority of stomata are adaxial. In these *Bromus* species - both sides have stomata, so rolling does indeed reduce stomatal exposure.

A point I wish to emphasise in connection with the pattern of variation I have described in the *B. riparius* group (section 9.3.3.1), is that given the above ecological analysis, it would be unusual if narrow (i.e., inrollable, inrolling) leaves were a character restricted to one taxon in the group. One might suppose, given the functional significance, necessary mutations may have been fixed several times in the past of this evolving complex, not just once. Alternatively, as once established functional gene complex, it would be inherited by directly descended successor organisms in the same or related habitats. Inrolled leaves occur in three taxa of *B. cappadocicus* (subspecies *cappadocicus,* subspecies *lacmonicus* and subspecies *crassipes*), all of them closely related, and in the separated species *B. parilicus*, which has been considered as a possible progenitor of this group (Kozuharov et al. 1981). This may indicate the inheritance, rather than the separate generation, of the inrolled leaf feature in this case.

9.3.3.3 Discussion

In the introduction (chapter 1), I defined critical groups as those which may show some internal noda of variation but in which any taxonomic subgroups are difficult to determine; sometimes it is not possible to make clear-cut demarcations which will define well consolidated taxa. The *B. riparius* group can be classified as such, showing a great polymorphism. In Europe it occurs throughout the Balkan peninsula, although some of the integrating taxa extend along the Ukraine and Anatolia to Central Asia, outside the geographical context of this current study. In *Flora Europaea* (Smith 1980), 3 species and 2 subspecies were recognised. The group includes perennial brome-grasses of different level of polyploidy (chapter 5, table 5.3). All of them show the same kind of reticular sheath, corresponding to a complex series of fibres finely dichotomised and interlaced forming an intricate network when they decay. The system of anchorage presented, in particular that incorporating the reticular sheath, seems to be directly related to some ecological-physiological factors (discussed in chapter 6).

The most recent study of this group was carried out by Scholz (1991) in *Mountain Flora of Greece*, although his analysis did not include all the taxa previously mentioned. Scholz encountered the same problem as I have when he tried to assess the rank of the taxa comprising this critical group. Thus, he stated: "*B. tomentellus* is closely related to the more widely distributed *B. cappadocicus* with several races or subspecies of intermediate characters, e.g., *B. fibrosus* Hackel subsp. *macedonicus* Degen & Dörfler", and also: "...*B. cappadocicus* is a polymorphic species extending from the Balkan peninsula to Iran. In Greece two subspecies can be tentatively recognised; they are connected by intermediates and not always clearly distinguishable from *B. riparius*". After the careful analysis of 1000 specimens, I believe, I have detected a pattern of adaptive radiation manifested by this group of brome-grasses with reticular sheaths, as well as determining a taxonomic rank for all the taxa comprising the same. Here I give my reasoning.

Geographically I find it is possible to distinguish two groups, one with a northern-central-southwestern distribution containing *B. riparius, B. barcensis, B. macedonicus, B. crassipes* and *B. moesiacus* elements, and the other group comprising *B. cappadocicus, B. tomentellus, B. lacmonicus* and *B. parilicus* elements, extending from the S.E. of Europe towards Asia, with the exception of the last two taxa. There are conflicting overlapping areas, with intermediate forms which seem to exist. I shall now analyse each group.

B. riparius Rehm. subsp. *barcensis* (Simonk.) Soó has been described as related to *B. riparius* Rehm. subsp. *riparius,* and characterised by its long, multispiculate panicles, broad stems and long leaves. Its pattern of distribution extends from Bulgaria to Rumania and Yugoslavia (fig. 9.3.3.1). *B. riparius* Rehm. subsp. *riparius* has shorter panicles, fewer spikelets, thinner stems and shorter leaves. As in the previous group, both taxa also manifest great phenotypic similarity. I do not believe it is practicable to draw a boundary line consistently between them - apparent intermediate forms underlie this observation (fig. 9.3.3.1). So, in my view, recognition of separate species does not appear to be well justified, but geography points to subspecific status.

B. riparius Rehm. subsp. *macedonicus* (Degen & Dörfler) Soó is reported from the former Yugoslavia and characterised by its spreading, broadly deltoid panicles, long and broad leaves, tomentose sheaths and leaves. These phenotypic features are very consistent and characteristic for this taxon, as is the geographical distribution (fig. 9.3.3.1), and I believe that subspecific taxonomic separation is again the most adequate approach. Some confusion has risen related to this taxon and its rank. Kozuharov et al. (1981), in a preliminary account and following cytological evidence, used the specific epithet *macedonicus* to name it. In a latter paper (1993), they have opted for the name *B. orbelicus*. Although described from Yugoslavia, some populations have been found in Bulgaria by the same authors. As I have not had an opportunity to analyse the type specimen of *B. orbelicus* Petrova et al., I am unable to interpret these authors' views concerning its relationship, biological or nomenclatural, to *B. macedonicus*.

B. moesiacus Velen. has been found only in the limestone hills of W. Bulgaria, and those of E. Yugoslavia in the limestone area of Mt. Kopaonik, "Srebrenaz" (Kozuharov et al. 1981). It seems to be a taxon which has coherent phenotypic features and can reasonably be treated as a distinct species. It has been counted as diploid, and it may thus be an important element in the phylogeny of the *B. riparius* group. It is characterised by its multispiculate panicles, small spikelets, minutely pubescent, flat, occasionally conduplicate leaves, and compact basal fibrous reticulum surrounding the emergent stem. I have not been able to see the type but the materials I have studied certainly appear to be of this taxon and to be fairly homogeneous - not a common feature in these brome-grasses.

B. cappadocicus Boiss. & Balansa subsp. *crassipes* (Halácsy) C. Fraile, although clearly part of the *B. cappadocicus* complex, is distributed only in the former Yugoslavia (fig. 9.3.3.5). It exhibits great overall similarity with the other two taxa, especially with *B. cappadocicus* Boiss. & Balansa subsp. *lacmonicus* but its particular, consistent phenotypic features, as well as its range of distribution, suggest it to be a subspecies. It is characterised by a broadly deltoid, spreading panicle, puberulous sheaths and densely hirsute lemmas. I hope it will be searched for in neighbouring territories, eventually.

The second group defined previously and also found in the Balkan peninsula contains *B. cappadocicus, B. tomentellus*, *B. lacmonicus* and *B. parilicus* as its elements, extending from the Southeast of Europe towards Asia, except for the last two taxa.

B. tomentellus Boiss. and *B. cappadocicus* Boiss. & Balansa subsp. *cappadocicus* have been defined here as two separate species with an overlapping pattern of distribution in S. Asia. *B. tomentellus* extends further East to Iran - this extension being the bulk of its distribution. In Europe it has only been recorded from Crete (fig. 9.3.3.5). In contrast, the subspecies *cappadocicus* extends widely throughout Albania, Greece and Eastern Asia. *B. tomentellus* Boiss. is characterised mainly by its flat, sometimes involute leaf blades, densely tomentose with sparse long cilia along the margins. *B. cappadocicus* Boiss. & Balansa subsp. *cappadocicus* shows glabrous, linear, involute leaf blades. Both taxa seem to have their phenotypic features best defined in the extreme areas of their range of distribution; however, it is interesting to point out that in Turkey and in Europe (Crimea) both taxa overlap. Apparent intermediates have arisen there, characterised by narrow, involute, tomentose leaf blades, as well as very short, dense panicles. These plants are thus manifesting some features of each "species". Both taxa can still be found showing slight phenotypic differences pointed out previously. The existence of these intermediate forms hardly contributes to the easy establishment of discernible gaps in the morphological variation between these two closely related taxa, *B. tomentellus* Boiss. and *B. cappadocicus* Boiss. & Balansa subsp. *cappadocicus*. Nevertheless, in general I think these two taxa show enough consistent difference to be recognised as parts of separated species (see below).

A third taxon attributed to this group is *B. cappadocicus* Boiss. & Balansa subsp. *lacmonicus* (Hausskn.) P.M. Smith, with an endemic distribution reported from S. Bulgaria, Albania to Greece (fig. 9.3.3.5). It is characterised by its linear, rigid, involute basal leaf blades, depauperate appearance of the panicles and densely hirsute lemmas, sometimes only with few, fine hairs. Scholz (1991) "tentatively" recognised this taxon as a subspecies of *B. cappadocicus*. Each of these two taxa exhibits some small, but characteristic phenotypic features, but it is not possible to draw a clear-cut line between them. They belong to a group sharing a great morphological similarity, exhibiting also an overlapping distributional pattern.

I am unwilling to recognise *B. tomentellus* Boiss. and *B. cappadocicus* Boiss. & Balansa as conspecific subspecies because they are distinct in at least some parts of their range, and they have at least in Europe a different geographical distribution. It is a convenient judgement, not without expediency - I believe more attention from collectors and experimenters (both needed) will come if specific status is maintained. They may be "young" species, as yet incompletely differentiated. Internal variants, such as the subspecies *lacmonicus*, would sit uncomfortably as varieties, were the species themselves to be relegated to subspecies rank.

B. parilicus Petrova, Kozuharov & Ehrendorfer, is an endemic taxon reported only from Slavjanka Mt. (Alibotush Mt.) on the border between Bulgaria and Greece so far (Petrova et al. 1993). It has been counted as diploid, and, according to the same authors, it could be regarded as an ancestral cytodeme of the series. Phenetically it is very distinctive, with its fragile appearance, very thin stems, thin leaves, long and narrowly lanceolate glumes and lemmas. These features, together with the geographical distribution (fig. 9.3.3.4), suggest that the specific rank may well be justified.

A general key for the whole group is presented in pp. 246.

The pattern of adaptive radiation followed by the perennial *B. riparius* group could be generally interpreted as now follows. The nine taxa show great phenotypic similarity, to the extent that, in the absence of the basal elements, such as leaves and sheaths, it is very difficult, sometimes impossible to establish an adequate identification. The phenotypic closeness is accompanied by an ecological affinity, with an establishment in exposed, well drained habitats - e.g., rocky slopes, dry meadows, alpine and subalpine steppes. The reticular sheath type shared by all can be interpreted as the result of an effective combination between the form and function elements, in colonisation and adaptation to these particular ecological niches - niches characteristic in the Balkan peninsula (chapter 6). This is a group of plants displaying great overall morphological similarity, although it shows also some slight internal phenotypic heterogeneity, and perhaps taxonomic "lumpiness". But it also could be assessed, in truth, as a smooth and rather progressive transformation of these varying phenotypic properties. As time continues, enough morphological change, arising from reproductive isolation, will perhaps accumulate, so that, it may be possible to designate several parts of this complex as species or lower taxa, but the isolation may never be insufficient, and perhaps will be frustrated by man. Perhaps this is happening already. For now, all I can accept is the imperfect resolution of the 9 taxa as described earlier. It is not a resoundingly clear classification, but I think it is a pragmatic one. All taxonomy is provisional.

Mayr (1969), Stebbins (1950) and others have pointed out that geographic isolation leads to reproductive isolation, which in turn leads to the consolidation and further development of general phenotypic differences between two recently divergent species. This seems to be the situation for the putative taxa in this study of the *B. riparius* group. They may represent different evolving lines in a process of speciation initiated but not yet consolidated or certain, and certainly not completed. We are perhaps spectators of an evolutionary, speciative process which may not be completed for 10,000 generations - or more.

General key for all the taxa comprising the *B. riparius* group.

1) Leaf sheaths puberulous covered with patent, stiff hairs. Basal and cauline leaves minutely pubescent, ciliate, linear, involute, somewhat rigid, occasionally flat with inrolled margins. Panicle broadly deltoid, spreading. Glumes and lemmas with abundant, long, sub-patent, silky, hairs, very pale green-yellowish, sometimes weakly purple-flecked, giving a delicate-golden appearance to the spikelets. Rhizomatous, with long rhizomes, 3-7 cm.

B. cappadocicus Boiss. & Balansa subsp. ***crassipes*** (Halácsy) C. Fraile

1) Not with the above combination of characters.

2) Basal leaves flat, occasionally conduplicate or with inrolled margins, 1.5-5 mm wide. indumentum varying from finely tomentose to minutely pubescent or glabrous to sparse pilose.

3) Low growing plant, stems 20-30 cm tall. The lowest sheaths decaying into fibres forming a very compact reticulum. Panicle branches very fine, initially erect, becoming slightly tortuous later, sometimes patent at maturity, 2 at the lowest node. Spikelets quite small, 1-2 cm. Lemma 8-10 mm.

B. moesiacus Velen.

3) Stems up to 85 cm tall. The lowest sheaths decaying into fibres forming a loose reticulum. Panicle branches or pedicels erect, robust, 2-6 at the lowest node. Spikelets bigger, (2.3)-2.5-3.5-(4.5) cm. Lemma (10)-11-15-(18) mm.

4) Leaf sheaths densely covered with fine, short hairs, sometimes also sparse long cilia. Leaves 5.5-15 cm long, slightly or densely tomentose. Awn (3)-4.2-7 mm, straight, sometimes slightly divaricate.

5) Stems 30-80 cm tall. Panicle 7-10 cm long from the lowest to the uppermost node, broadly deltoid, spreading, 3-4 pedicels at the lowest node. Spikelets bearing 6-8 florets. Basal leaves 9.5-15 cm × 3.5-5 mm, slightly tomentose.

B. riparius Rehm. subsp. ***macedonicus*** (Degen & Dörfler) Soó

5) Stems 20-60 cm tall. Panicle 3-8.5 cm long from the lowest to the uppermost node, erect, ovoid-ellipsoid, more contracted when young, but scarcely varying from youth to maturity, 2 branches at the lowest node. Spikelets bearing 5-7-(8) florets. Basal leaves 5.5-12 cm × 2-2.5-(3.5) mm, densely tomentose.

B. tomentellus Boiss.

4) Leaf sheaths glabrous or with scattered, long hairs, sometimes numerous. Basal leaves glabrous, scabrid, sometimes with hairs along margins or sparsely pilose, 7-20 cm long. Awn (2.5)-4.5-6.5-(9) mm, straight.

6) Stems (1.5)-2.5-3-(3.5) mm wide. Panicle (7)-9.5-12-(18) cm long from the lowest to the uppermost node, bearing (10)-14-23-(28) spikelets, (2)-3-6 pedicels at the lowest node. Basal leaves 8.5-22 cm long, flat, sometimes conduplicate. Lemma (10)-11.5-14 mm × (2)-2.5-2.8 mm, ovate-lanceolate. Rhizomes 2-5-(8) cm.

B. riparius Rehm. subsp. ***barcensis*** (Simonk.) Soó

6) Stems 0.5-1.5-(1.8) mm wide. Panicle (6)-7-8.5-(12) cm long from the lowest to the uppermost node, 6-12-(25) spikelets, 2-4 panicle branches at the lowest node. Basal leaves 7-14.5 cm long. Lemma (11.5)-12-14-(18) mm × (1.5)-2-2.5 mm, oblong-lanceolate. Rhizomes 2-4 cm.

B. riparius Rehm. subsp. ***riparius***

2) Basal leaves linear, involute, 0.5-3 mm broad, occasionally flat with inrolled margins, glabrous or shortly puberulous, sometimes with scattered long cilia along the margins.

7) Stems very thin, 0.7-1.5 mm wide. Basal leaves 8.5-12 cm × 0.5-1 mm, very thin. Panicle 5-6.5-(7) cm long from the lowest to the uppermost node, very fine pedicels, 2 at the lowest node, which frequently presents few cilia on the scale. Glumes and lemmas narrowly lanceolate; the lower glume 8.5-9.5 mm, the upper 10-12 mm; lemma 12-14 mm × 1.5-2 mm. Awn 6-6.5 mm.

B. parilicus Petrova, Kozuharov & Ehrendorfer

7) Stems wider than 1 mm. Basal leaves 4.5-18 cm × 0.5-1.5-(2) mm. Panicle 4.5-10 cm long from the lowest to the uppermost node, relatively fine or rigid pedicels, 2-4 at the lowest node. Glumes and lemmas narrowly or broadly lanceolate; the lower glume 5.5-13 mm, the upper glume 8-15 mm; lemma 10.5-14-(16) mm × 2-2.5-(2.7) mm. Awn 3-8.5 mm.

8) Panicle 4.5-10 cm long from the lowest to the uppermost node, 2-4 stright, rigid pedicels at the lowest node. Spikelet 2-2.8-(3) cm. Florets densely hairy or with few, relatively short hairs, rarely glabrous. Glumes broadly lanceolate, the lower 5.5-10 mm, the upper 8-12 mm. Lemma 10.5-13 mm × 2-2.5-(2.7) mm, ovate-lanceolate. Awn 3-8.5 mm, straight or slightly outwardly curved at maturity.

B. cappadocicus Boiss. & Balansa subsp. ***lacmonicus*** (Hausskn.) P.M. Smith

8) Panicle 4.5-8.5 cm long from the lowest to the uppermost node, 2-3 pedicels at the lowest node, straight, sometimes relatively tortuous after anthesis. Spikelet 2.8-3.7 cm. Florets glabrous, occasionally with short, very fine hairs. Glumes and lemmas narrowly lanceolate; lower glume 8.2-13 mm, upper glume 9.7-15 mm. Lemma 12-14-(16) mm × 2-2.5 mm. Awn 4.5-8.5 mm, strongly divaricate at maturity.

B. cappadocicus Boiss. & Balansa subsp. ***cappadocicus***

9.3.4 B. inermis Group

9.3.4.1 Account of the Taxa

11) ***B. inermis***[1] Leysser, *Fl. Halensis*, 16 (1761).

Perennial, with vigorously creeping rhizomes, often up to 1 m. Erect stems, 50-110 cm tall, 2.3-3.8 mm wide, glabrous. Leaf sheaths glabrous or shortly hairy, the lowest remaining intact. Basal and cauline leaf blades glabrous, scabrous margins, sometimes with short, scattered, fine hairs; the basal 10-22.5 cm × 3-5-(7.5) mm, the cauline 13-30 cm × 4.5-8 mm; ligule (1)-1.5-2 mm. Flag leaf 10-11-(20) cm × 3-4.5-(6) mm. Panicle erect, oblong, compact when young, becoming looser, spreading at maturity, 7.5-17 cm long from the lowest to the uppermost node, bearing numerous spikelets, 15-60. Panicle branches shortly scabrous, erect, spreading, 2-9 at the lowest node; the shortest 1-1.5-(3) cm, the longest (2)-3-5 cm. Spikelets 1.5-2-(3) cm, oblong-lanceolate when young, broader at maturity, with (4)-5-6-(8) florets; rachilla 1.5-2 mm, glabrous or shortly hairy. Glumes and lemmas glabrous, with broad hyaline margins, especially towards the apex, pale green or weakly purple-flecked. Glumes subequal, oblong-lanceolate, the lower 5.5-6.5-(8) mm, the upper 7-9 mm. Lemma (8.5)-9.5-11.5 mm × 2-2.3-(2.6) mm, obtuse or shallowly emarginate, ovoid-lanceolate. Awn absent or very short up to 0.5 mm. Palea shorter than the lemma, 8-9 mm, very shortly scabrous-ciliate along the keels. Stamens 3, anthers 4-5 mm. Caryopsis 6-7 mm. Flowering in June-July, fruiting in August. Geographical distribution in fig. 9.3.4.1.

[1] Unarmed, without spines, prickles

The name refers to the (usual) absence of the awn

Fig. 9.3.4.1. Geographical distribution of *B. inermis*

Habitats: Steppes; grassy meadows; dry slopes; rocky, sandy soil; alluvial; 95-700 m. In E. Europe, particularly in the former U.S.S.R., it shows great economic importance, being widely cultivated for forage. The main properties rest on the resistance to shortage of moisture and low temperatures, modest requirements as regards soil conditions, and immunity to fungal diseases.

Type: Described from Germany: "...in Fürstengarten, in den Pulverweiden, Halle, Leysser" (LINN).

Synonyms: *B. inermis* Leyss., *Fl. Hal.* 16 (1761); *Festuca speciosa* Schreber, *Spicilegium,* 59 (1771); *F. leyssieri* Moench, *Fl. Hass.* 82 (1777); *Bromus litoreus* Reich., *Nachtr.* 259 (1802); *Festuca inermis* (Leyss.) Lam. & DC., *Fl. France*, 3rd edition, 3: 49 (1805); *F. poaeformis* Pers., *Syn.* 1. 94 (1805); *Schedonorus inermis* (Leyss.) Pal. Beauv., *Ess. Agrosts.* 99: 177 (1812); *Bromus inermis* Leyss. var *aristatus* Schur, *Enum. Pl. Transsilv.* 805 (1866); *Zerna inermis* (Leyss.) Lindm., *Svensk Fanerog.* 101 (1918); *Bromopsis inermis* (Leyss.) Holub, *Folia Geobot. Phytotax.* 8 (2): 158 (1973).

Icones: Todor, *Fl. Rep. Soc. Rom.*, fasc. 12, tab. 59, pp. 308 (1972).

Observations: *B. inermis* Leyss., although native to Europe, has been introduced into the United States and is one of the most valuable forage grasses. Some controversy has arisen about the rank of *B. pumpellianus* Scribn., an American representative, in relation to the Eurasian *B. inermis*. The former has sometimes been considered as a subspecies of the widely distributed *B. inermis* (which is in turn related to some other Asiatic species sometimes treated as subspecies under *B. pumpellianus*). Although outside the confines of this study, it seems to me that a subspecific rank for *B. pumpellianus* would be appropriate and indicative of the closeness between both taxa. Morphologically the main difference relies on the grade of pubescence. *B. inermis* presents glabrous florets, leaves and nodes in the stem; also the awn is absent or very short (up to 0.5 mm). *B. pumpellianus* has very hairy florets, leaves and nodes; the awn is longer, up to 3 mm. There exist differences in the geographical distribution. Hybrids have also been reported (Elliott 1949a, 1949b). In *Grasses of the Soviet Union* (Tsvelev 1983), several varieties of *B. inermis* (= *Bromopsis inermis*) are mentioned: var. *aristatus* (= *aristata* (Schur) Tsvel.); var. *pellitus* (= *pellita* (Beck) Tsvel.); var. *hirtus* (= *hirta* (Drob.) Tsvel.); var. *malzevii* (Drob.) Tsvelv. It seems to be a very interesting polymorphic species, though mainly if not wholly at varietal level, but as I have not had the opportunity to analyse specimens of these varieties, and they have no European distribution, I have excluded them from my account. *B. inermis* is widely distributed and well known in Europe: I have cited relatively very few specimens mainly because the taxon is in no way critical or puzzling in my view.

Selection of specimens

Austria

Breslau, St. Vincenz-Kirchhofes, 120 m, 26.6.96, *Baenitz*, s.n. (E); Graz, St. Leonhard, solo alluviali, 360 m, 6.1909, *Fritsch*, 921 (E).

Czechoslovakia

Burberg, Kaaden, 28.6.1909, *Stelzhamer*, 309 (E).

Germany

Frankfurt, Mainufer, 95 m, 11.6.1900, *Dürer*, 161 (E).

Hungary

Budapest, Alluvialsand, 100 m, 15.6.1905, *Degen*, 596 (E); Hárshegy, declivibus dumetosis, solo calc., 300 m, 14.6.1904, *Torday*, s.n. (E).

Rumania

Transsilvania, distr. Cojocna, graminosis, solo argilloso, 420 m, 24.6.1923, *Nyárády & Bujorean*, 349 (E).

Sweden

Öestergötland, Alvastra, 11.7.1945, *Kjellmert*, s.n. (E).

Former U.S.S.R.

Mosqua, distr. Zvenigorod, in declive arenoso ad fluvium, 28.6.1969, *Makarov*, 119 (E).

Chapter 10 Taximetric Analysis

10.1 Introduction

The need for some system of classification is a process which mankind carries out instinctively and which has been performed from his very beginning, for an accurate recognition of food, animals, tools, etc. In a botanical context, Linnaeus through his main works, *Genera Plantarum* (1737 with later editions) and *Species Plantarum* (1753 with later editions) classified plants according to his artificial "sexual system". This system was popular largely because of its simplicity but was also severely criticised. Among the main critics of Linnaeus' work was M. Adanson, who is most remembered for emphasising the idea that in classification, a great range of characters covering all aspects of the plant should be used, not placing greater emphasis on some than on others. This constitutes an empirical approach. On this basis - of using all the characters with equal importance and so reducing subjectivity to a minimum in making correlations - is based the concept of numerical taxonomy proposed by Sokal & Sneath (1963) in their text book *Principles of Numerical Taxonomy*, and some years later in an updated and rewritten version *Numerical Taxonomy* (Sneath & Sokal 1973). It was defined by the same authors as "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities.

The traditional taxonomist makes intuitive or subjective decisions concerning similarity, based upon experience and skill. The numerical taxonomist bases his comparisons on an estimate of a defined measure of similarity, which is objective. It (numerical taxonomy) is not a theory, but merely a way of summarising information in an intelligible form (Dunn & Everitt 1982). Numerical taxonomy in the broad sense includes both numerical phenetics and numerical evolutionary (cladistic) methods. The latter bases the clustering on maximising the apparent shared derived characters (synapomorphies). Nevertheless, the difficulty of pinpointing primitive and derived characters exists, and the value of this phylogenetic system is subject to some controversy. The method used in this study was an assessment of the morphological (phenetic) similarities between taxa of *Bromus* § *Pnigma*. Rahman (1988) used UPGMA clustering strategy for a comparative study with his own classificatory treatment of the genus *Panicum* (Gramineae). Some previous UPGMA work has also been carried out on the perennial *Bromus* § *Pnigma* in South America (Naranjo et al. 1990). The UPGMA algorithm computes the average similarity or dissimilarity of a candidate OTU to an extant cluster equally, regardless of its structural subdivision (Sneath & Sokal 1973). It is probably the most frequently used clustering strategy (Consaul et al. 1991; Sales 1991; Aiken et al. 1993). It is thus an average linking clustering, which avoids the bunching of OTUs which is a feature of complete linkage clustering, and also the straggly clusters of single (nearest neighbour) linkage trees. I wanted to produce a dendrogram output, not simply a pictorial cluster, because of the dendrogram's hierarchical quality which I believe has more taxonomic relevance.

10.2 Materials & Methods

10.2.1 Character Assessment

The total number of qualitative and quantitative characters used in perennial brome-grasses for the description and delimitation of each taxon were discussed in chapter 7, and these were also used for this taximetric purpose.

10.2.2 Coding Characters

Each qualitative character was split into 2 to 4 characters states with the aim of covering the maximum variation occurring in the totality of the taxa studied. Where two character states were present in a taxon, (OTU - operational taxonomic unit), the one more widely occurring in the majority of the specimens studied for this particular OTU was recorded. Quantitative characters were reduced to ranges of mean values, based on 20 measurements per taxon when enough material was available, then coded and scored for each OTU. See Appendix 10.1 for the character codings, and chapter 7 for a discussion of these character codings.

10.2.3 Creating the Computer Data File

Cluster analysis by the hierarchical method UPGMA (Unweighted Pair-Group Method Using Arithmetical Averages) was used. It seems to have become well established among those taxonomists using numerical studies. The analysis follows a two step process: first similarity coefficients are calculated between paired OTUs; second hierarchical clusters of OTUs are created based on their similarity coefficients and the information is displayed as a dendrogram. The proximity between two clusters is defined by the average of the similarity coefficients between all the elements that make one and the other. Gower's similarity coefficient was chosen. The entire study was carried out using the program Hierarchy in the statistical package GENSTAT 5 on the Castle system (University of Edinburgh Amdahl main frame computer). OTUs were indicated at the start of the row by a three digit number, e.g., 001 for the first one. Where there was no data available, an asterisk was typed. The data was entered in lines, each line representing all the characters observed for one OTU (Raw data matrix in Appendix 10.2).

10.2.4 Running the Analysis

Different combinations of characters and OTUs were used, so obtaining various dendrograms. To assess the importance and type of characters used to infer the relationships between taxa, several tests were tried:

a) the totality of OTUs (24) and characters (44).

b) 24 OTUs and the most biologically and morphologically significant characters, i.e., using residual weighting characters (Appendix 11.3).

c) 9 OTUs representing the taxa which comprise the *B. riparius* group and 44 characters.

d) 12 OTUs integrating the *B. erectus* group and 44 characters.

e) 22 OTUs representing the three main groups, *B. erectus, B. riparius, B. inermis* and the same characters used in test **b**. These selected characters are simply those that I regarded intuitively as "good", i.e., predictive, biologically significant characters.

10.3 Results

Test a: Relationship between all taxa in the sect. *Pnigma* (44 characters were used). See fig 10.1.

The relationship of two main groups (I and II) occurs at 75%. The main taxa comprising group I are brought together at 78%, and 80% in the group II. Groups of subspecies from the same taxon are distinguished at relatively high levels of similarity, i.e., two subspecies of *B. riparius* at 93%, and respect to the third one, subspecies *macedonicus* at 90%; subspecies *longiflorus* and subspecies *laxus* at 92%; two subspecies of *B. ramosus* at 93%, and subspecies *condensatus* and subspecies *microtrichus* at 93%.

Test b: Relationship between all taxa comprising sect. *Pnigma* after residual weighting of characters (21 characters only used). See fig. 10.2.

Two groups (I and II) are distinguished at 77% similarity. The main subdivision seems to be associated to the overall size of the plant. Thus, those taxa defined as robust, with broad leaves, long panicles, e.g., subspecies *barcensis*, subspecies *ramosus* are grouped together (VI) at 83% of similarity. The second group (I) comprises taxa with a fragile appearance, presenting thin, involute leaves and show a relationship at 85%. With a higher level of relationship, 87%, lies the subgroup V. The subgroups XVI and XVII share a similarity at 90%, containing taxa with sheaths splitting into parallel fibres and reticular sheaths respectively, except the subspecies *vernalis* in the second group, which has sheaths splitting into fibres.

Test c: Relationship between all taxa in the B. *riparius* group (44 characters were used). See fig 10.3.

Two main groups (I and II) show 73% of similarity. A further subdivision differentiates *B. moesiacus* from a third group (III) at 77%. The subspecies of the *B. riparius* group are brought together at 90% of similarity. Except for these, the rest of the taxa seem to have been grouped on the basis of underestimating some features and exalting some others which are not biologically or morphologically significant.

Test d: Relationship between all taxa in the *B. erectus* group (44 characters were used). Fig. 10.4.

Two subspecies, *laxus* and *longiflorus*, are differentiated from the remaining taxa at 75%. Two big subgroups (V and VI) show a closer relationship at 82.5%. The subspecies *condensatus* and the subspecies *microtrichus* are brought together at 90%. My overall impression is that except for two of the subspecies of *B. condensatus* and the subspecies *laxus* and subspecies *longiflorus*, the latter being very robust taxa and differentiated from the rest of the group, relationship between the remaining taxa has been established on not very significant grounds, either biologically or morphologically.

Test e: Relationship between three main groups, *B. erectus*, *B. inermis* and *B. riparius* after weighting of characters (21 characters only used). Fig. 10.5.

Figs. 10.1.-10.5. Dendrograms

Fig. 10.1. Dendrogram of the relationships between all 24 OTUs when 44 characters are used.

Fig. 10.2. Dendrogram of the relationships between all 24 OTUs when 21 characters are used.

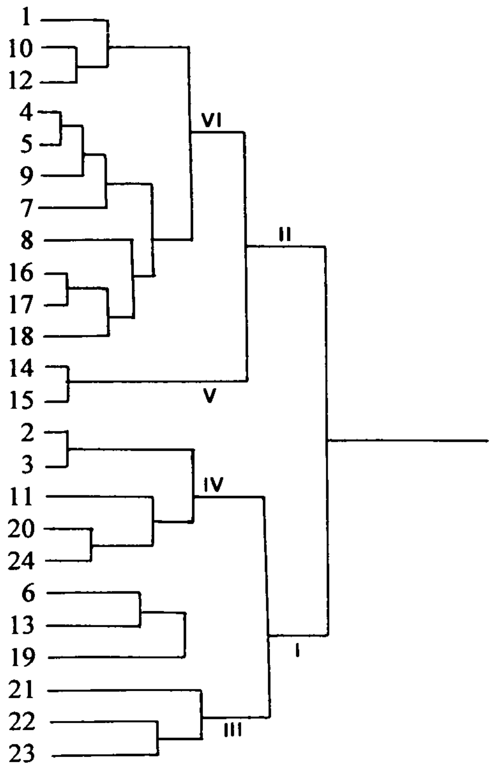
Fig. 10.3. Dendrogram of the relationships between 9 OTUs when 44 characters are used.

Fig. 10.4. Dendrogram of the relationships between 12 OTUs when 44 characters are used.

Fig. 10.5. Dendrogram of the relationships between 22 OTUs when 21 characters are used.

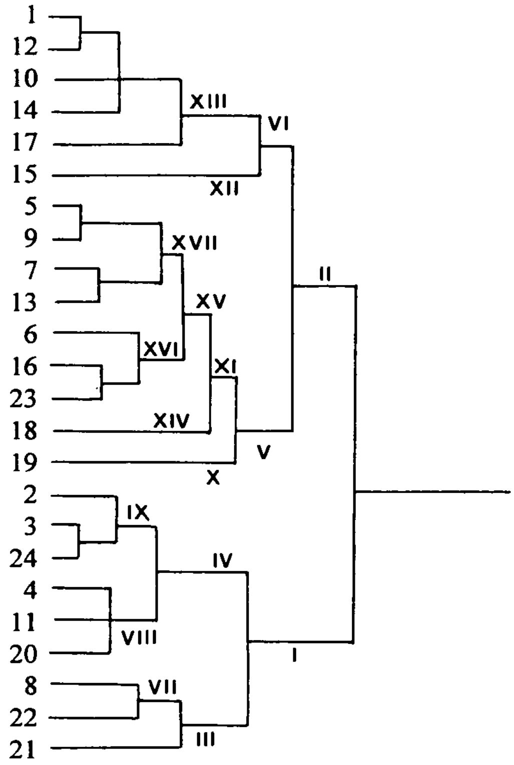
Fig. 10.1. Dendrogram

** Levels 90.0 85.0 80.0 75.0 70.0 65.0 60.0



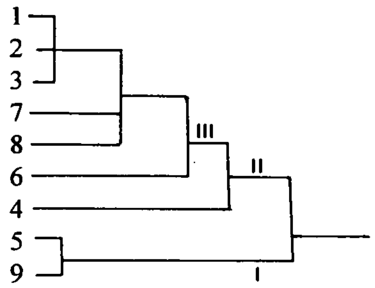
1) *B. inermis*
10) *B. erectus* subsp. *laxus*
12) *B. erectus* subsp. *longiflorus*
4) *B. condensatus* subsp. *moellendorffianus*
5) *B. pannonicus* subsp. *pannonicus*
9) *B. erectus* subsp. *erectus*
7) *B. pannonicus* subsp. *monocladus*
8) *B. caprinus*
16) *B. riparius* subsp. *riparius*
17) *B. riparius* subsp. *barcensis*
18) *B. riparius* subsp. *macedonicus*
14) *B. ramosus* subsp. *ramosus*
15) *B. ramosus* subsp. *benekenii*
2) *B. condensatus* subsp. *condensatus*
3) *B. condensatus* subsp. *microtrichus*
11) *B. erectus* subsp. *montenegrinus*
20) *B. cappadocicus* subsp. *cappadocicus*
24) *B. parilicus*
6) *B. pannonicus* subsp. *vernalis*
13) *B. erectus* subsp. *aurouzensis*
19) *B. moesiacus*
21) *B. cappadocicus* subsp. *crassipes*
22) *B. cappadocicus* subsp. *lacmonicus*
23) *B. tomentellus*

Fig. 10.2. Dendrogram
** Levels 95.0 90.0 85.0 80.0 75.0 70.0 65.0 60.0



1) *B. inermis*
12) *B. erectus* subsp. *longiflorus*
10) *B. erectus* subsp. *laxus*
14) *B. ramosus* subsp. *ramosus*
17) *B. riparius* subsp. *barcensis*
15) *B. ramosus* subsp. *benekenii*
5) *B. pannonicus* subsp. *pannonicus*
9) *B. erectus* subsp. *erectus*
7) *B. pannonicus* subsp. *monocladus*
13) *B. erectus* subsp. *aurouzensis*
6) *B. pannonicus* subsp. *vernalis*
16) *B. riparius* subsp. *riparius*
23) *B. tomentellus*
18) *B. riparius* subsp. *macedonicus*
19) *B. moesiacus*
2) *B. condensatus* subsp. *condensatus*
3) *B. condensatus* subsp. *microtrichus*
24) *B. parilicus*
4) *B. condensatus* subsp. *moellendorffianus*
11) *B. erectus* subsp. *montenegrinus*
20) *B. cappadocicus* subsp. *cappadocicus*
8) *B. caprinus*
22) *B. cappadocicus* subsp. *lacmonicus*
21) *B. cappadocicus* subsp. *crassipes*

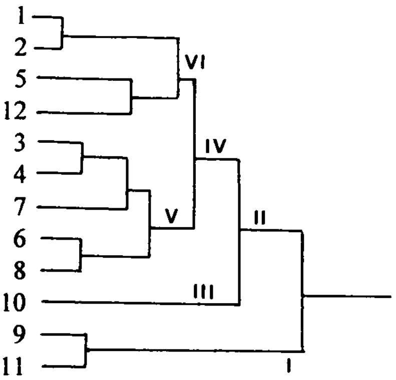
Fig. 10.3. Dendrogram
** Levels 85.0 80.0 75.0 70.0 65.0 60.0 55.0



1) *B. riparius* subsp. *riparius*
2) *B. riparius* subsp. *barcensis*
3) *B. riparius* subsp. *macedonicus*
7) *B. cappadocicus* subsp. *lacmonicus*
8) *B. tomentellus*
6) *B. cappadocicus* subsp. *crassipes*
4) *B. moesiacus*
5) *B. cappadocicus* subsp. *cappadocicus*
9) *B. parilicus*

Fig. 10.4. Dendrogram

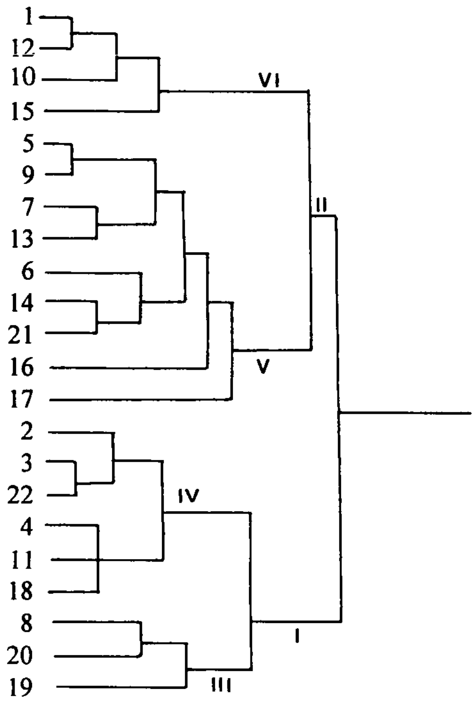
** Levels 87.5 82.5 77.5 72.5 67.5 62.5 57.5



1) *B. condensatus* subsp. *condensatus*
2) *B. condensatus* subsp. *microtrichus*
5) *B. pannonicus* subsp. *vernalis*
12) *B. erectus* subsp. *aurouzensis*
3) *B. condensatus* subsp. *moellendorffianus*
4) *B. pannonicus* subsp. *pannonicus*
7) *B. caprinus*
6) *B. pannonicus* subsp. *monocladus*
8) *B. erectus* subsp. *erectus*
10) *B. erectus* subsp. *montenegrinus*
9) *B. erectus* subsp. *laxus*
11) *B. erectus* subsp. *longiflorus*

Fig. 10.5. Dendrogram

** Levels 95.0 90.0 85.0 80.0 75.0 70.0 65.0 60.0



1) *B. inermis*
12) *B. erectus* subsp. *longiflorus*
10) *B. erectus* subsp. *laxus*
15) *B. ramosus* subsp. *barcensis*
5) *B. pannonicus* subsp. *pannonicus*
9) *B. erectus* subsp. *erectus*
7) *B. pannonicus* subsp. *monocladus*
13) *B. erectus* subsp. *aurouzensis*
6) *B. pannonicus* subsp. *vernalis*
14) *B. riparius* subsp. *riparius*
21) *B. tomentellus*
16) *B. riparius* subsp. *macedonicus*
17) *B. moesiacus*
2) *B. condensatus* subsp. *condensatus*
3) *B. condensatus* subsp. *microtrichus*
22) *B. parilicus*
4) *B. condensatus* subsp. *moellendorffianus*
11) *B. erectus* subsp. *montenegrinus*
18) *B. cappadocicus* subsp. *cappadocicus*
8) *B. caprinus*
20) *B. cappadocicus* subsp. *lacmonicus*
19) *B. cappadocicus* subsp. *crassipes*

The groups I, II are distinguished at 80% of similarity. In the group I, two subgroups (III and IV) are recognised at 86%, in the group II at 81%. The principal taxa of subgroup VI show a closer relationship at 92%. Results are identical to test **b**, except for the exclusion of subspecies *ramosus* and subspecies *benekenii*. Three groups are brought together at 80%. For the group comprising all the "big" taxa, similarity occurs at 91-92%, higher than in test **b** at 85%.

10.4 Discussion

The use of all the characters without a previous selection of those defined as being diagnostic, either from a biological or morphological point of view (tests a, c, d), comprises *a priori* equal weighting. They seem to bring more subspecies from the same taxon to higher levels of relationship than when the characters are weighted via *a posteriori* selection (tests b.e).

In some particular cases, not very surprisingly, very close taxa (close by my intuitive reasoning) are grouped together (e.g., subspecies *condensatus* and subspecies *microtrichus* in test a and d). By contrast, taxa from different (fide Fraile) groups also show a close relationship (e.g., *B. caprinus* from the *B. erectus* group with respect to three subspecies of *B. riparius* group in test a). In order to solve some of these contradictions (if possible), more data should be analysed to be able to achieve a more "perfect" system of relationship. I find, in general, little overall consistency or usefulness in these dendrogram classifications.

On the basis of my experience, I am not utterly convinced about the advantages that numerical taxonomy can offer with respect to conventional taxonomy. I conceive the study as a mere curiosity which should be used to contrast with some other sources of information, but without a full commitment to the results obtained by applying this methodology. The intuitive view of the taxonomist, achieved through experimenting and meticulous observation of a large amount of specimens to understand the range of variation and species delimitation, should prevail over the limited information manipulated by this hierarchical system. Perhaps the characteristic appearance of taxa/individual specimens to which, with experience, I react, has not been adequately communicated to the computer by the characters chosen, or by their coding - though I did my best. Further, ecological and geographical considerations, evaluated by me, are not in the data suites compiled for taximetric analysis. It was my feeling that they should not be, not being primary features of the plant material itself.

In relation to the objectivity which is associated with these methods of organising data, is relevant to keep in mind that a human mind has been associated with:

a) the design of the computer program
b) the selection of material for study
c) the selection of characters
d) the interpretation of the output.

Is it still appropriate to talk about an objective system? I am dubious. Other choices might have brought forth different results.

It is not my intention to seek to discredit this taximetric method as Ross (1964) conceived it, and who stated: "Numerical Taxonomy is an excursion into futility", but I must declare my reservations about its contribution as I have experienced it. More characters may have been necessary. In seeking to explain the clash between my intuitive classification and the output from the UPGMA process I suggest that the following factors may be involved:

first, it might be that my codification obscured some of the variation which I have intuitively and, perhaps, unconscious evaluated; perhaps also the use of 20 selected (well collected, well grown, complete) specimens for the codifications have created some distortion. Second, the taximetric equal weighting of the characters may be responsible for some of the difference, although my test **b** which was of characters which I had personally weighted ought to have revealed this it did not. Third, it has to be recognised that in reaching my intuitive conclusions I considered some factors and relevant evidence which the computer did not have. Among these factors are features of ecology, geographical distribution and cytology. Fourth and finally, I think it is probable that my intuitive evaluation contains elements of evolutionary interpretation which were quite uncodifable in the UPGMA program. It may be that using the same data in the cladistic program (PAUP for instance) might produce a result more compatible with my intuitive classification. This can be tested in future.

One conclusion that may be possible from the dendrograms is that the UPGMA program here generates something like the same confusing output as has characterised the last century of orthodox study. This group of plants is no easy fox for any taxonomic marksman to shoot!

Chapter 11 Diversification and Evolutionary Pathways of Bromus § Pnigma

11.1 Speciation and Evolution

The origin of evolutionary theory can be associated with the theological and philosophical traditions rooted in Judeo-Christian thinking more than 2000 years ago. The belief in an unchanging universe and invariable life forms was based on a full acceptance of the Creation as described in Genesis. Through centuries, the Divine Plan of nature was an unquestioned idea perceived by philosophers and theologians. Nevertheless, towards the 13th century some gradual changes were perceived. Saint Augustine and Saint Thomas Aquinas were largely responsible for laying the theological ground for evolutionary ideas. The universe and the living creatures in it kept evolving after Creation, but only in accordance with the Divine Plan.

During the Renaissance, the development of physical sciences, mathematics, chemistry, physics, geology and astronomy concluded in a search for natural laws to explain natural phenomena, thus replacing the Divine Plan. It was Charles Darwin, with the publication *On the Origin of Species* in 1859 who made a profound impact on biology. His theory of Natural Selection as the mechanism responsible for evolutionary change in organisms, constitutes the cornerstone of modern biological science. The recognition of genetics as a strong foundation for evolutionary theory was supported by the amalgamation of the data and concepts of taxonomy, embryology, biogeography and other disciplines, which constituted the so called "Neo-Darwinian" theory in the 1930s and 1940s. Nowadays most biologists agree that the three major causes of evolution, mutation, genetic recombination and natural selection with isolation are complementary to each other. In the field of botany the development of the evolutionary theory crystallised with G. Ledyard Stebbins' seminal work of synthesis: *Variation and Evolution in Plants* (1950), which presented the process of evolution operating in plants.

Modern views of evolution account for the pace and scale of evolutionary changes by involving two faces, one essentially gradualist and one involving rapid adaptive radiation, the punctuational.

The gradualist theory is based on a gradual accumulation of selectively favourable genetic variation in spatially isolated populations, leading to genetically incompatible groups descended from an ancestral gene pool, i.e., a continuous anagenetic transformation of populations.

The punctuated equilibrium theory was developed by Eldredge & Gould (1972). It emphasises rapid pace of speciation based more on a random process of mutation and genetic drift than on selection, with the origin of new species by the splitting of one or more subpopulations into reproductively isolated groups, that ultimately may replace the ancestral populations.

Among the weak points of the gradual divergence theory as the major speciation pattern, is its emphasis on the existence of transitional forms that connect the ancestral and descendant species. The real facts show that these transitional forms are often missing in living and fossil groups. The second alternative, punctuated equilibrium, states that the absence of transitional, or intermediate forms in most of the fossil record is related to the fact they have not occurred. Thus, an apparent pattern of relatively brief times of speciation episodes happened, which were separated by very long periods during which little significant change occurred.

The latter has been broadly recognised by the majority of the scientific community as the leading process in speciation. As stated by Eldredge & Gould recently (1993): "Punctuated equilibrium has finally obtained an unambiguous and incontrovertible majority - that is, our theory is now 21 years old.....and it has been accepted by most of our colleagues (a more conventional form of majority) as a valuable addition to evolutionary theory".

One essential corollary in the study of the diversification among any group of plants is the pattern of adaptive radiation, defined as the rapid proliferation which usually comes in bursts, of many new kind of organisms diverging from a single ancestral group (Stanley 1979).

A main aim of this study on perennial brome-grasses is to elucidate the pattern of adaptive radiation followed in the colonisation of new niches since their origin, and which will be discussed in this chapter.

11.2 Adaptive Radiation in Bromus

Due to the lack of fossil record and the extinction of all ancestral forms from which the current taxa derived, the relationship between all the different sections must be speculative.

According to Stebbins (1981), the most primitive, now extinct *Bromus* species probably originated in western Eurasia during the Miocene. I believe it may have happened earlier, in the Oligocene (see sect. 11.3. for further discussion). During the Pliocene, the differentiation of sect. *Neobromus* (= subg. *Neobromus*), *Ceratochloa* (= subg. *Ceratochloa*) and *Pnigma* (= subg. *Festucaria*) probably occurred, with a consecutive spreading of the representatives of the first two sections to N. America and then to S. America (Stebbins 1981). The initial spread of sect.

Pnigma (= subg. *Festucaria*) to Africa and Americas possibly occurred also during this period (Stebbins 1981).

A logical development in the evolution of the primitive *Bromus* stock seem to have three major steps (Sales 1991):

1) the replacement of this primitive stock, now extinct, by modern perennials.
2) the differentiation of annual species.
3) the development of strong weedy tendencies in many of these annuals.

It seems unlikely to me that any of the present § *Pnigma* groups of species are the ancestors of modern species in the annual groups in sections *Bromus*, *Genea*, *Boissiera* and *Nevskiella*. Nevertheless, on the basis of the three evolutionary steps, Stebbins (1981) believes it is highly probable that during the Pleistocene four groups of annual species, sect. *Bromus* (= subg. *Bromus*), sect. *Genea* (= subg. *Stenobromus*), sect. *Boissiera* (= subg. *Boissiera*) and sect. *Nevskiella* (= subg. *Nevskiella*) derived from the perennial sect. *Pnigma* (= subg. *Festucaria*). It seems more likely that some of these annual sections existed before the Pleistocene dramas, though their modern species may of course have evolved in the Pleistocene interglacials or post-glacially (Smith, pers. comm.). Some of them may have become weedy comparatively recently, though we should not fall into the error of thinking that "weedy" habitats did not exist before Man discovered agriculture! *B. secalinus* and *B. hordaceus* - representing very distinctive part of § *Bromus* - are both early recognisable in British post-glacial fossils (Godwin 1956).

The profound changes in both biota and climate, which took place in Eurasia during the Pleistocene glaciations placed an enormous pressure on these groups of grasses. Elevation of mountaining ranges and high plateaux of Central Asia derived in the acquisition of very severe continental type of climate, characterised by extreme seasonal fluctuations of temperature. The evolution of bovine ungulate, heavy grazers, exerted strong pressures and, consequently, the selection and evolution of species capable to coexist with them, like strongly rhizomatous *B. inermis* or annuals in sect. *Genea* and *Bromus.* The perennial taxa of sect. *Pnigma* probably started building up their high chromosome numbers (Stebbins 1981).

Chloroplast DNA (cpDNA), being evolutionary highly conserved, has been used to assess phylogenetic relationships between polyploid species of sect. *Ceratochloa* (= subg. *Ceratochloa*) and species of sect. *Pnigma* (= subg. *Festucaria*) (Pillay & Hilu 1990). The low genetic distance values obtained between taxa from the two sections do not support Stebbins' statement (1981), that the relationships between both sections (= subgenera) are obscure and that consequently a recent common origin is difficult to image. This recent DNA study has contributed to a partial elucidation of the various evolutionary patterns occurring in *Bromus.* Further exploration in the remaining groups is needed.

For a summary of the proposed pattern of adaptive radiation in the genus see fig. 11.1.

11.3 Adaptive Radiation in § Pnigma

To understand the pattern of adaptive radiation presented by this group of perennial brome-grasses, it would be pertinent to raise the following question: how are abilities for colonisation and rapid geographic expansion correlated with general features of life-form, reproduction, chromosome system, habitat requirements, etc.? A spectrum of features occurring in perennial *Bromus* was analysed with the aim of providing an answer to the above question.

As presented in chapter 1, I defined four phenetic groups in this study which, I have come to believe, represent four distinctive evolutionary lines inside the section *Pnigma.* These four groups were analysed in a morphological, anatomical, cytological, biogeographical and numerical comparison, for an attempt in detecting different directional trends of evolution occurring in this group of grasses.

Morphology of the inflorescence

Two very different types of panicles can be differentiated in perennial *Bromus*:

a) effuse, drooping panicles characteristic of the *B. ramosus* group in Europe and *Bromus* § *Pnigma* from North America.

b) congested, erect panicles presented in the remainder groups.

It is generally accepted that the first type is less advanced than the second kind (Scholz 1975; Smith 1991). The large, drooping panicles are strongly linked with a woodland or woodland-margin habitat, which occurs in the *B. ramosus* group. In contrast, congested, erect panicles seem to be associated with more and different types of habitats - dry, open, exposed. This congestion can be achieved by diverse means, such as shorter internodes in the panicle axis as well as in the branches.

The evolution of the two lines of panicle shape appears to represent first, a response to the kind of habitat. The *B. erectus, B. inermis* and *B. riparius* groups - especially the latter, grow in very exposed areas, subjected to the influence of strong winds. The more congested panicles have a switch form, and although they are shaken by wind against neighbouring stems, they will not suffer the breaking off of loose, outlying parts, or not to the extent of loose, effuse types. Perhaps more importantly, there can be less damage of the reproductive structures at a time when they are particularly fragile. When the water supply is irregular and its use is an important factor for the physiology of the plant, as happens in dry habitats, the switch form feature offers a rapid speed of growth of the panicle, as well as a higher number of spikelets contained in the inflorescence. There is little non-reproductive tissue in the inflorescence. The fruits are enclosed to some degree and kept well protected, e.g., from desiccation.

On the contrary, the *B. ramosus* group occurs in woodlands or woodland-margins, where environmental factors are steadier (less exposed, shadier, wetter places). Mechanical damage of the larger, drooping panicles by wind abrasion is considerably lower, and danger of caryopsis damage is reduced. Water supply is normally quite regular for the normal development of the plant. However, in a large effuse panicle there are fewer caryopses per gram of tissue - this is more costly and slower to produce.

The liberation and dispersal of the fruits seems also to have a connection with the morphological pattern of the panicle. Drooping panicles take advantage of the gravitational force to liberate their caryopses. Bearing in mind the environment where the *B. ramosus* group occurs, forests and forest-margins, wind liberation and dispersal probably is relatively unsuccessful in this habitat where wind currents are few or weak. Congested panicles meanwhile seem to show an adaptation for the dispersion of the fruits, developing long, sometimes strongly divaricate awns as they mature, e.g., *B. cappadocicus*, and encouraging removal by passing animals. *B. erectus* presents heavy seeds (Lloyd 1964; Lloyd & Pigott 1967), which are awned and readily caught in animal hairs or on clothing (Rodwell 1992). In congested panicles the dispersion of the caryopses can also occur through mechanical abrasion of one plant by another nearby as they mature (Smith 1991) - the adult form is less switch-like than when young.

Panicle shape may thus be an useful indicator of different trends of adaptation/evolution within the section.

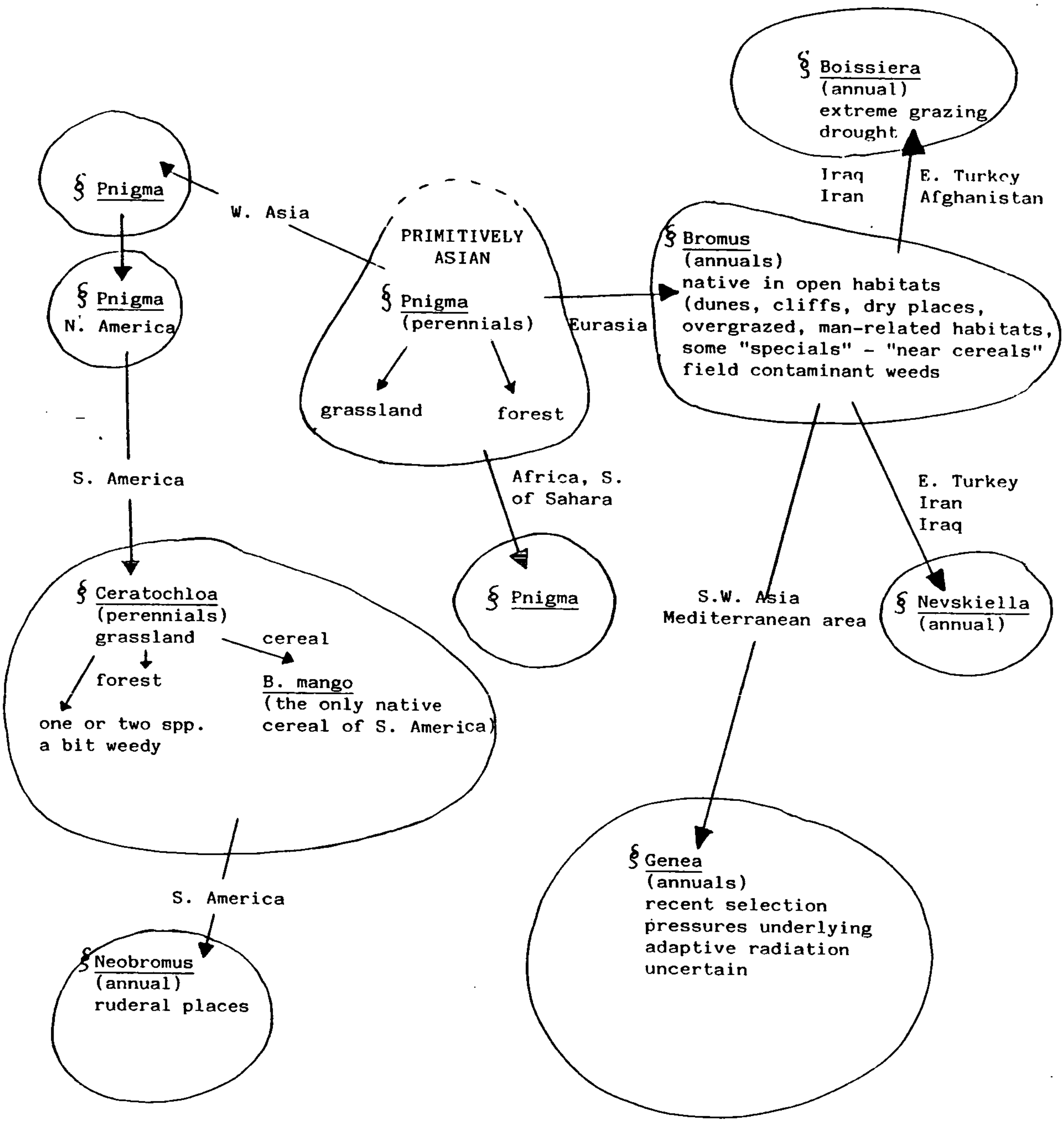


Fig. 11.1. Adaptive radiation in *Bromus* according to P.M. Smith in Sales (1991)

Sheath persistence

The main subdivision of perennial brome-grasses in four groups partly coincides with three patterns of sheath decay: sheaths which (1) remain intact around the bottom of the emergent stems, e.g., the *B. ramosus, B. inermis* groups, or (2) broken up somewhat but into parallel fibres, e.g., the *B. erectus* group, or on the other hand, sheaths (3) which decay into a network of reticulating fibres, e.g., the *B. riparius* group. The morphology of the dead sheaths around the stems bases thus differs markedly. Dead tissues might potentially discharge one or several functions; these functions were discussed and some of them tested in chapter 6 .

The water absorption property is much more efficient in the *B. ramosus* group, where the old sheaths seem to act like blotting paper. However, in the physical environments where this group occurs, wetter and shadier places, water-use efficiency is unlikely to be a crucial parameter for the development of the plant. The blotting-paper "property" of the intact sheaths, may not indicate an evident correlation between both factors, form and function, but be a selectively neutral, perhaps ancestral state of the character. Certainly it is the simplest form of sheath.

The *B. riparius* group grows in very windy, dry, exposed areas where soils are mobile. This reticular sheath pattern may exhibit a connection with these particular parameters. In the *B. erectus* group, the sheath morphology is a simpler version of the reticular type, splitting in some parallel fibres. This group is found also in exposed, but milder areas, where the external factors do not impose the same level of stress as in the *B. riparius* group. These sheaths may accumulate soil but in less quantity than the previous group.

B. inermis is associated with permanently or periodically very dry, grassy places, riverside sands and steppes. Being a sod-forming plant, the soil trapping property seems to have been transferred to the creeping rhizomes (see chapter 6, sect. 6.7) which have acquired an efficient function as soil binders.

The possibility of frost protection carried out by old sheaths round the emergent stems will constitute future work.

Different kinds of sheaths are thus quite likely to discharge diverse functions. Form appears partially at least connected with function and consequently with the habitat.

Habit characteristics

The life-form which characterises all taxa comprising sect. *Pnigma* is perennial, although they differ in their habit features. On this basis, three kinds of habit have been observed in perennial brome-grasses:

- densely or loosely tufted, sometimes tufts connected by very short rhizomes. *B. ramosus* group, and some taxa in the *B. erectus* group.
- shortly/long rhizomatous - *B. riparius* group, and some taxa in the *B. erectus* group.
- Strongly rhizomatous - *B. inermis* group.

For annual plants, it is extremely important to ensure, apart from some long distance dispersal, the local continuation of the population in the next season (Sales 1991). Contrarily, perenniality in principle works in favour of a long life-span. Grazing seems to act as a pressuring factor towards the development of different vegetative means of reproduction. *B. erectus* is palatable to sheep, cattle and rabbits; when grazing is intensive, the size of the community decreases although its reversible expansion is achieved by a vigorous and rapid vegetative expansion (Tansley & Adamson 1926; Wells 1971). *B. riparius*, due to its rapid recovery after grazing, has been successfully used as pasture in Alberta (Knowles et al. 1993). The regrowth comes from existing tiller bases and being so vigorous, it can extend the grazing season (Knowles, in Armstrong 1990). A similar situation is reflected in *B. inermis*, a clone-forming, aggressive rhizomatous grass species. It is native to Eurasia but is now widely cultivated and escaped in N. America. The regrowth is initiated from crown and rhizome beneath the soil surface (Knowles et al. 1993). Its powerful creeping nature may conceivably be related to its wider distribution compared to any other taxa in the section. Apart from its physiological capacity to extend its area, it would be able to exploit soil transport by man better than some other taxa. *B. inermis* apparently gets its initial start wherever man has disturbed the soil (Wagnon 1952).

In stable, primitive habitats, as occur in woodlands where the *B. ramosus* group is characteristic, grazing pressure is almost non-existent. These grasses have not been required to develop any particular vegetative means of reproduction to guarantee the establishment or recovery after damage in the community.

Because of their modular organisation, perennial grasses can regenerate and expand by replacing old tillers with new ones. At the same time a decline in population size can be quickly compensated by an increase in tillering (Jónsdóttir 1991). In my own observations, all taxa studied have considerable tillering ability, with the exception of the *B. ramosus* group, being a feature of advantage in grazed, exposed areas. The development of a vigorous vegetative system of reproduction has contributed to the expansion of a great majority of the perennial *Bromus* species in the colonisation of new niches and in particular in those situations where the pressuring factors, i.e., grazing, failure of sexual reproduction, could have led them to extinction instead.

All these vegetative features offer very useful pointers towards an understanding of the main evolutionary trends developed in each group.

Leaf morphology

A comparative study on leaf anatomy was discussed in chapter 4. Basically two main morphological types of leaf occur in sect. *Pnigma,* both strongly connected with physical parameters:

- flat, broad leaves are indicative of high and regular water availability and shady places. The characteristic habitats where they are found correspond to sheltered or permanently wet ones.
- narrow, linear, frequently rolled leaves do not offer great wind resistance, thus being harder to tear. Although they grow in dry, exposed habitats, the rolling capacity avoids high water loss.

For a discussion on stomatal distribution see pp. 36. Leaves of the second form are frequently indurated to some degree, and this probably contributes to grazing resistance.

Geographical/ ecological distribution

The four distinct and natural groups defined in this study have followed different evolutionary pathways and show preferential areas of distribution:

- **B. *ramosus*** agg.: western-nordic, distributed mainly in C.-N. and W. Europe, N. Africa, and migrating from eastern Eurasia to western Europe.
- **B. *erectus*** agg.: rather mesophilous, it extends from S.E. to C. and W. Europe. It belongs to the W. Balkan-C. and W. European element, migrating also from eastern Eurasia to western Europe.
- **B. *riparius*** agg.: xerophilous, with western Eurasia to central Asia migration. It ranges from the Balkan peninsula through Ukraine and Anatolia to Iran. It is considered as a member of the E. Balkan-S.W. Asiatic element.
- **B. *inermis*** agg.: distributed along C. and N. Europe, N. Asia, N. America, and migrating from western Eurasia to western and northen Europe.

Some evolutionary trends have been observed in relation to each group, showing particular ecological affinities and different polyploid levels.

The *B. ramosus* group manifests great taxonomic and ecological stability, individuals persisting on woody slopes for many years (Smith, pers. comm.). However, the effect of soil acidification in deciduous forest in S. Sweden during the last 40 to 50 years has been stronger in the subsp. *ramosus* than in the subsp. *benekenii* (Brunet & Neymark 1992). The former seems to be most sensitive to low pH and is almost restricted to soils with pH 5.5-7. *B. ramosus* subsp. *benekenii* is not found below a pH of 4.5. It would appear that two related niches seem to accommodate these two subspecific taxa.

The xerophilous *B. riparius* group is connected mainly with limestone and occurs along the Balkan peninsula, with a progressive extension towards central Asia. It is characterised by the great polymorphism of its taxa. Two evolutionary lines have been recognised in Bulgaria (Kozuharov et al. 1981) (see next section).

The *B. erectus* group (mesophilous) prefers limestone rocks, and shows a more western distribution. In a recent study (Verlaque & Vignal 1993) some cytotypes of this group from S.W. Europe were investigated, and found to have some biogeographical specificities. The octoploid race (2n = 56) is distributed in the mesic European grassland. The high rate of germination and pollen fertility of this race explains the extension of this cytotype in all Europe, to the exclusion of the other two. The hexaploid (2n = 42) and decaploid races (2n = 70) are found in some localities on the southern limit of the European area, with a specific location in sparse mountains grass-lands up to 700 m.

This detailed study by Verlaque & Vignal (1993) constitutes a fine example of the numerous investigations on local populations which are needed for a better clarification of different evolutionary trends within species in perennial brome-grasses.

Chromosome/breeding system

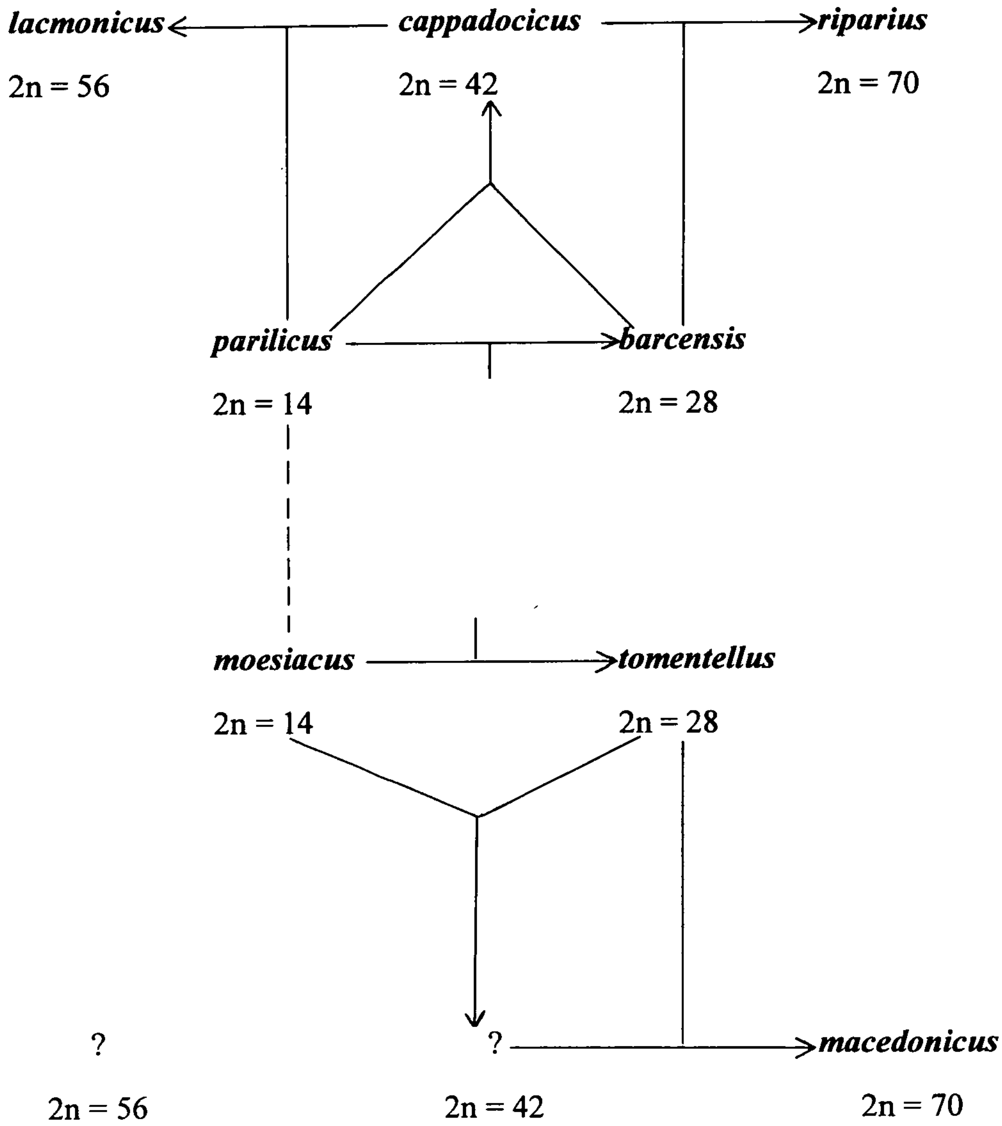
Section *Pnigma* comprises mainly polyploid taxa with a few, locally distributed, diploid species. Polyploidy is widely recognised as being an important process in plant evolution (Stebbins 1971), and seems to have had noticeable influence in the evolution of the four groups. So far, only two diploid taxa are known in the Euroasiatic context of the section - *B. moesiacus* and *B. parilicus*. The rest are polyploids, and in the majority of the taxa several cytotypes have been found.

The direction of evolution in a group can emerge from the comparison between diploids and polyploids with respect to cytogenetic characteristics, geographic distribution and morphology (Stebbins 1975). Kozuharov et al. (1981) made an attempt to clarify the different evolutionary lines occurring in the *B. riparius* group in Bulgaria (fig. 11.2). It may constitute an important step in the progressive clarification of the adaptive radiation pattern, combining cytological, ecological and morphological features. I must however express my doubts in relation to some of the taxa studied. For example, *B. barcensis* has been recorded as diploid (2n = 14, Kozuharov & Petrova 1976) and as tetraploid (2n = 28, Kozuharov et al. 1981). The chromosome level for *B. riparius* is decaploid (2n = 70, Kozuharov et al. 1981). According to the same authors, an increase in ploidy level is generally followed by an increase in plant dimensions. In my own concept, *B. barcensis* differs from *B. riparius* in being more robust, with longer panicles and a higher number of spikelets. A re-examination of the voucher specimen of *B. barcensis* originally studied by these authors reveals that it does not fit with my concept of this taxon. On the basis of these arguments it would be curious if *B. barcensis* with greater dimensions shows a lower degree of polyploidy than *B. riparius*. Moreover, the considerable differences in morphology between *B. parilicus* and *B. barcensis* make it difficult to believe that the former is a progenitor of the latter.

My data (chapter 5, table 5.4) are not sufficient to complete the evolutionary pattern initiated by Kozuharov et al. (1981). Many more studies must be carried out, particularly the completion of a detailed cytological analysis of all the taxa. Nevertheless I think my analysis is indicative of the evolutionary trends.

Polyploidy has been probably an important factor in the expansion of the groups. The diploid species, *B. moesiacus* and *B. parilicus*, are both endemic to Bulgaria and show a very curtailed distribution. The former is a local endemic, strongly isolated in a deep and rather humid valley (Kozuharov et al. 1981); the latter shows a main distribution in the lower mountain belt and the hills of the Thracian plain (Kozuharov et al. 1981). A comparison of the pattern of dispersion of both diploid taxa with that of the other polyploid species in the group of perennial brome-grasses, reveals the broader geographical area occupied by the polyploids, which seem to be more successful invaders than these diploids. In the past it was postulated that polyploidy was directly associated with a greater ability to withstand severe ecological conditions, such as cold or drought (Tischler 1935; Löve & Löve 1949). Polyploidy has a direct effect on the nuclear volume increase in structural and developmental characteristics; also an indirect effect, producing new and wider range of allelic combinations acquired by hybridisation, and consequently a greater ability to invade and colonise new or disturbed areas beyond the limit of their diploid progenitors.

Fig. 11.2. Diagram illustrating probable relationships between taxa of the *B. riparius* group in Bulgaria, with two parallel polyploid series in the *B. lacmonicus* and *B. moesiacus* lines. Question marks refer to postulated hypothetical cytodemes (Kozuharov et al. 1981).



As discussed in chapter 5, sect. 5.3 an increase in polyploidy seems to be correlated with an increase in vegetative vigour. Most of the taxa studied exhibit quite vigorous, in some instances very aggressive, systems of vegetative reproduction, e.g., *B. inermis*. This is a factor of great consequence, particularly associated with local expansion and always accompanied by seed dispersion.

Perennial brome-grasses have expanded successfully throughout other continents, e.g., N. Africa and N.-S. America. Species in N. America are predominantly diploid together with a very few tetraploids. Eurasian species, however, are characterised mainly by high levels of polyploidy. With the exception of *B. pumpellianus*, all American species and two Eurasian species, *B. ramosus* and *B. benekenii*, have pinhead (small) chromosome satellites (Wilton 1965; Armstrong 1981) and large chromosomes (Armstrong 1981). Other Eurasian species have larger satellites (Schulz-Schaeffer 1960; Armstrong 1973) and small chromosomes (Armstrong 1983). These observations led Armstrong (1983) to establish two evolutionary lines within the sect. *Pnigma* (see chapter 5, sect. 5.3).

The general morphology and growth habit of the *B. ramosus* group shows certain affinity with the N. American diploid-tetraploid complex; they are short-lived non-rhizomatous and generally highly self-fertile. Stebbins (1981) emphasised that *Bromus* species with smaller chromosomes should be regarded as more primitive than those having larger ones. In the family Festucoideae a general evolutionary trend towards increasing chromosome size has taken place (Avdulov 1931; Stebbins 1981). Some evidence for this observation can be found in *Bromus*. Armstrong (1977) noted that the chromosomes of the annual species *B. arvensis* (sect. *Bromus*) are considerably larger than those of *B. erectus* and *B. inermis* (sect. *Pnigma*). The DNA values per genome of these species indicate that there is twice as much DNA in the *B. arvensis* genome (Bennett & Smith 1976). The significance of this observation rests on the fact that a chromosome size difference is directly proportional to DNA content (Baetcke et al. 1967), such that species with larger chromosomes possess more DNA per genome than those with smaller chromosomes. Comparative DNA measurements among brome-grasses species in sect. *Pnigma* have not been made, but it would be expected that in *B. ramosus*, having bigger chromosomes, their DNA value per genome is larger than *B. erectus*, *B. inermis* and *B. riparius* with smaller chromosomes. A possible explanation of the larger chromosome size in North America in those species of sect. *Pnigma* which resemble some European counterparts, may lie in the migration of ancestral taxa of the *B. ramosus* group to the New World which had already acquired large chromosomes in Europe before migrating. This could also imply that this new evolutionary step occurred before the build up of the polyploid complexes in smaller chromosomes (Armstrong 1983).

Interspecific crosses between Eurasian and American species of sect. *Pnigma* have been carried out (chapter 5, table 5.1). Results indicated a low level of pairing affinity and recombination between *B. benekenii* and *B. erectus* chromosomes and between *B. ramosus* and *B. variegatus*, *B. erectus* or *B. inermis*. These results lead to the conclusion that large and small chromosome species have probably followed different evolutionary pathways. Some degree of differentiation was found between *B. benekenii-B. ramosus* and N. American species (Armstrong 1984). One possible explanation could rest on the length of isolation that both groups have had from each other, with the possibility of extinction of close relatives among the American group (Armstrong 1984).

All this cytological evidence corroborates the internal diversification occurring in perennial *Bromus* and clarifies the different relationships among the taxa.

11.3.1 Colonisation and Migration in Europe

Going back to the question raised in sect. 11.3, and after a comparative study of different elements of perennial *Bromus*, a positive correlation can now be established between diverse lines of adaptive radiation occurring in the four natural groups defined, and the diversification of morphological, biological and cytological parameters discussed in detail, all of them contributing to the colonisation and expansion of these groups away from their centre of origin.

The combination and interpretation of the information reviewed above have led me to propose the following, speculative, evolutionary scheme (see fig. 11.3).

According to Stebbins (1981) the differentiation of sect. *Pnigma* (= subg. *Festucaria*) from a now extinguished genetic stock of *Bromus*, probably occurred during the Pliocene in western Asia. I also believe it may have happened in western Asia but earlier, in the Miocene. Stebbins did not recognise any internal diversification in this section which, I think existed and is discussed next. Two main evolutionary lines could have emerged, differing chronologically. The older perhaps sometime during the Miocene led to a diploid ancestral complex which evolved large chromosomes. In a second evolutionary step, one line diverged from this diploid ancestral, migrating from western Eurasia to western Europe founding the *B. ramosus* group; a second line, from the same ancestral group, could migrate later, reaching N. America during the Pliocene. Consequently, the *B. ramosus* group and the N. American *Bromus* § *Pnigma* would on this plan have a common origin. There are great similarities between both groups, discussed in the next section. I believe that the *B. ramosus* group and the N. American *Pnigma* brome-grasses are older than the other three groups of perennial brome-grasses in Europe, having associated features which may reflect primitive status: effuse, drooping panicles, preference for woodlands and great stability/clarity from the taxonomic point of view. The adaptive radiation seems to be more ancient. The species are more clearly demarcated.

The explanation for the derived character of larger chromosomes in the *B. ramosus* group and their American counterparts could be associated with the diploid ancestor, which achieved this feature in a primary step.

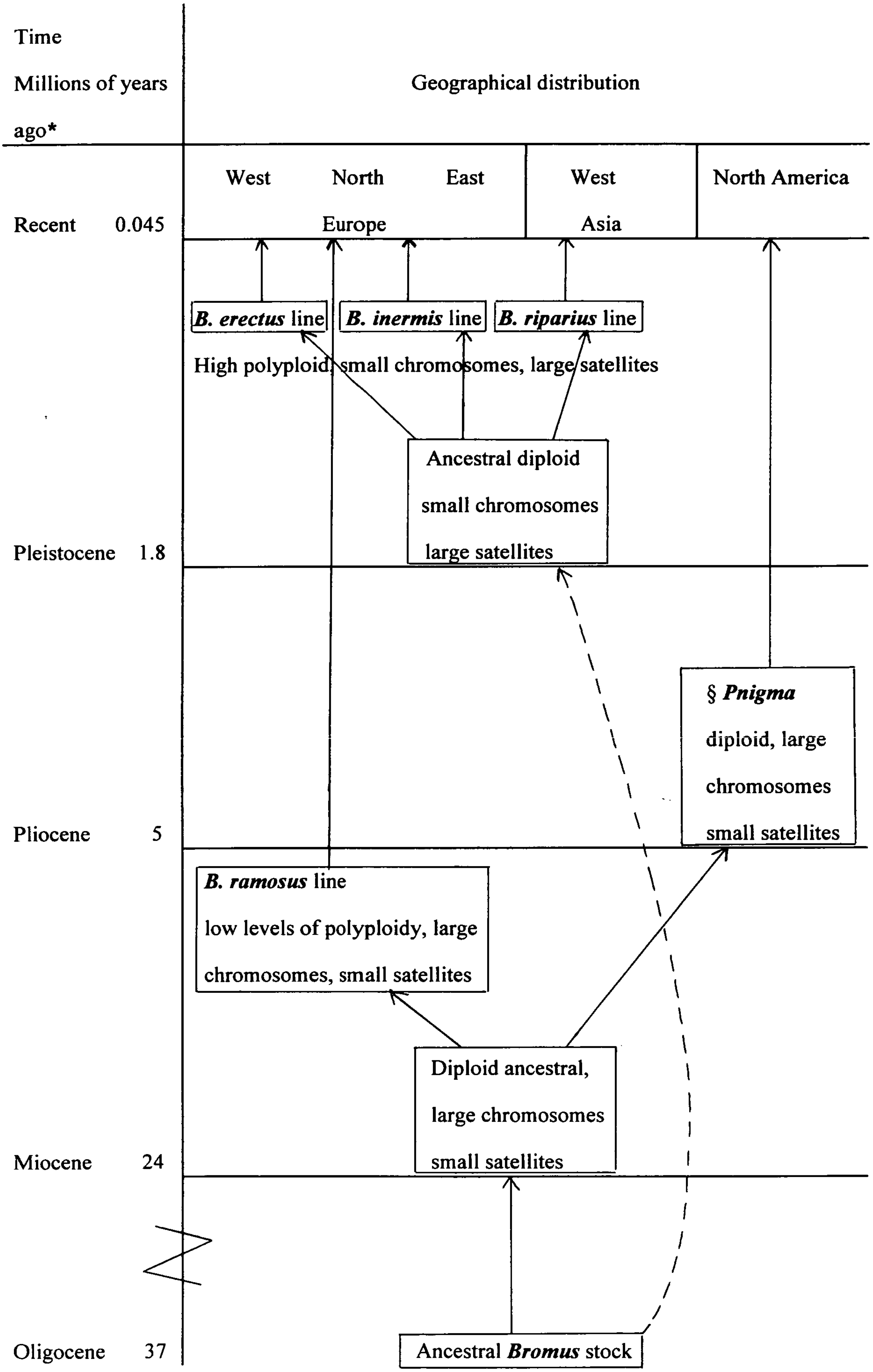
It is important to analyse the type of past vegetation dominating Europe for a better understanding of the evolutionary trends associated with the *B. ramosus* group. During the Pliocene period the general vegetation in the Balkan peninsula, as in the rest of Europe, was probably forest similar to that which exists today in the few places where man has not interfered (Turrill 1927).

The *B. erectus*, *B. riparius* and *B. inermis* groups possibly emerged later during the Pleistocene. From a now extinct ancestor, which possibly was diploid, had small chromosomes and large satellites, three evolutionary, highly polyploid lines could have evolved, showing three different gradients of migration: one from western Eurasia to western Europe representing the *B. erectus* group, a second migratory line from western Eurasia to central Asia, leading to the *B. riparius* group, and a third line from western Eurasia to western and northern Europe, resulting in the *B. inermis* group. The ancestral diploid could have derived from the primitive *Bromus* stock. It is feasible to believe that there were also intermediate forms which also became extinguished.

An element of extreme importance in the particular evolutionary trend of the *B. riparius* group is the loess soil characteristic in the Balkan peninsula. It might have happened that this line of adaptive radiation produced plants able to deal with different kinds of pressure, like drought, strong winds, mobile soils which were features conferring the evolutionary opportunity described. The appearance of this particular kind of environment prevailing in the Balkan peninsula surely stimulated a new direction of adaptive radiation, and thus plants diverged from their original forms and physiology. In the colonisation of new niches, it was of vital importance that this group opportunistically developed the reticular sheath, a crucial element in their success.

The *B. inermis* group, native to Europe, has also been introduced in North and South America. The extreme hardiness, drought resistance, long-lived perennial habit and very crucially, the aggressive growth of this group have enabled it to become very widespread.

The dry, exposed and disturbed habitats in which the three groups of the second evolving line are found, could indicate a progression into the more challenging niches made available. These taxa appear to show the most recent adaptive radiation in these brome-grasses. Their differentiation might have occurred in three divergent lines. The taxa which comprise each group, particularly the *B. erectus* and *B. riparius* group, display taxonomic unclarity. They seem to be still in the process of evolving. The majority show great polymorphism, with many intermediate forms and intricate connections frustrating the establishment of clear cut boundaries and which have led to great taxonomic confusion.


Time
Millions of years ago*
Geographical distribution
West
North
East
Europe
West
Asia
North America
Recent 0.045
Pleistocene 1.8
Pliocene 5
Miocene 24
Oligocene 37
B. erectus line
B. inermis line
B. riparius line
High polyploid, small chromosomes, large satellites
Ancestral diploid
small chromosomes
large satellites
§ ***Pnigma***
diploid, large
chromosomes
small satellites
B. ramosus line
low levels of polyploidy, large
chromosomes, small satellites
Diploid ancestral,
large chromosomes
small satellites
Ancestral ***Bromus*** stock

This hypothesis agrees with that of Stebbins (1981) which established western Eurasia as the centre of differentiation of the genus *Bromus* and sect. *Pnigma* (= subg. *Festucaria*). The reasons are various. The Balkan peninsula, very rich in endemic taxa, would constitute a primordial area of speciation for perennial *Bromus*, particularly for the *B. riparius* group. It would appear to be a centre of diversity. It contains some primitive diploid species, and these could be related to the putative ancestors of the polyploid series. At the end of the Pliocene, the coming of the Ice Age affected N. and C. Europe in a drastic manner. The Balkan peninsula did not completely escape all climatic changes, but actual glaciation was extremely local, being limited to some of the highest mountains (Turrill 1929). This coincides with the concept that big massifs, as the Rhodopes in S. Bulgaria may have been the centre of active form-differentiation, acting also as refugia for numerous plants pushed southwards by the action of the ice in the N. of Europe. Primitive types may have accumulated there and the pressure of new climatic/edaphic/biotic circumstances, no doubt with some niche release following extinctions, created evolutionary opportunity. The plants are found in habitats which are not associated with human introduction: none of them have weedy tendencies or are otherwise crop-related. Like Stebbins (1981), I found significant the fact that central Eurasia could possibly be the centre of origin for the subfamily Festucoideae to which *Bromus* belongs (Hartley 1973). Another observation is that sect. *Pnigma* (= subg. *Festucaria*) is the only section (= subgenus) having a range of distribution coextensive with that of the entire genus, containing species that are found in all the geographic regions to which *Bromus* is native (Stebbins 1981).

I emphasise that this is only a working hypothesis, for there are too many gaps that must be related to conjecture rather than real facts. Nonetheless, without a degree of speculation, hypotheses cannot be framed and, later tested.

11.3.2 Colonisation by § Pnigma in the New World

It must be emphasised that all the ideas discussed in this section are merely speculative. I recognise that the scope of my research has been limited to *Bromus* § *Pnigma* with a distributional pattern in Europe.

For understanding the possible adaptive radiation pattern of perennial *Bromus* in the New World, some observations on the taxa in this continent are relevant.

Section *Pnigma* in N. America is mainly represented by loosely tufted, short-lived perennials, with long, drooping panicles associated with stable habitats, and quite similar to their counterparts in the Old World, the *B. ramosus* group. Many are plants of woodland slopes, too.

There are two possible hypotheses in explaining the migration pattern adopted by the ancestors of the N. American *Bromus* § *Pnigma.* They could have crossed from Asia to the New World in the late Pleistocene, through the Bering bridge. Its emergence occurred several times during this period. Rising sea level seems to have submerged fully the Alaska-Siberia land connection as early as 15,000 years BP (before present, the present being defined as 1950 for radiocarbon dating) (Hopkins 1982). Macrofossils of plants and insects show that the late Pleistocene was treeless, implying prevalence of steppe-like conditions, which differed from present-day tundra (Matthews, Jr. 1982). Many areas in Beringia show a record of aeolian activity, with large active dunes and loess deposits (Hopkins 1982). These biotic and environmental conditions prevailing during the late Pleistocene do not seem to accommodate the putatively perennial ancestral *Bromus* (*ramosus*-like). Its living American descendants, in my theory, occur in damp, shady woodlands.

Another hypothesis would indicate that the ancestors of the N. American brome-grasses probably entered from Asia during the Miocene/Pliocene epochs, being the only time when the Bering bridge was forested, at least in part (Wolfe 1972). Bearing in mind the habitat where the actual representatives grow in the New World (forests, forest-margins and shady slopes), this second hypothesis seems to be more plausible. The colonisers differed slightly from their Eurasian counterparts and followed a different evolutionary trend. Fossil evidence dated from the Pleistocene was found in Canada, possibly corresponding to a leaf fragment of *Bromus* (Penhallow 1890). This second hypothesis disagrees with Stebbins' observation that the initial spread of sect. *Pnigma* (= subg. *Festucaria*) to Africa and Americas possibly happened during the Pliocene. I believe that migration to the New World may well have occurred slightly earlier, in the Miocene and reaching N. America during the Pliocene epochs. This observation agrees with the occurrence of one episode of the origin and migration of New World § *Pnigma* from a primitive genetic stock of *Bromus* discussed on pp. 282. This stock would represent the "*ramosus*" line, and would accommodate quite precisely and synchronise the events just discussed. Thus the ultimate origin of *Bromus* might have been in the Oligocene.

I cannot accept that the occurrences of most perennial *Bromus* § *Pnigma* species in N. America are the result of early or recent human introduction. Their current habitats, open woods, shady ravines and woodlands-margins are, beyond doubt, not associated with man's influence. Morphologically, ecologically and cytologically they resemble the *B. ramosus* group. Although now internally diversified, they could have derived from a primitive germ-plasm with an Old World origin which crossed through Beringia and stabilised, colonising quite similar niches. This would have been well before human colonisation of the New World. The time when man could walk from Northeast Asia into Alaska was almost any time during late Pleistocene.

The locations where good evidence of early man occurs are all dated later than 25000 BP (Jennings 1978).

Perennial brome-grasses in S. America are associated with very distinctive types of habitats, varying notably from the ecological niches in N. America. The studies developed on the group in this part of the New World are as yet very scanty, particularly on a cytological basis, although so far diploid taxa have not been reported. The distribution of *Bromus* in northern S. America coincides with the Andean zone and, apart from rare exceptions, it is found in the cold thermic belt, between 2000 and 3000 m (Pinto-Escobar 1981).

In more southern regions, the habitat varies dramatically, being mainly semi-desert and dry grass steppes in the sub-Andean region. One species in particular, *B. auleticus*, is found in sandy soils in Argentina. Morphologically, the similarity to *B. erectus* is striking. They share erect, very contracted panicles, and sheaths splitting into fibres, although to a greater degree in *B. auleticus*. Some authors (Doell, loc. cit.; Arechavaleta 1897, in Nicora & Rúgolo de Agrasar 1987) defined it as a variety of *B. erectus* Hudson. As many of the taxa in this area are used as forage, and it would be plausible in principle to regard the S. American distribution as associated with human introduction from N. America. I find this difficult to believe. It seems unlikely that a primitive genetic stock could cross with man to N. America from Europe and diversify, exploiting new, but quite similar niches, later expanding in the South, reaching S. America, but leave no trace of itself in the North. This would have implied tremendous genetic changes, leading to a genetic diversification and reflected in particular morphological characters, like the transformation of long, drooping or nodding panicles into erect, very contracted forms, and the shift from stable habitats, like forest, dense, moist shade sites to grasslands, semi-desert areas under strong grazing pressure.

There is a simpler explanation. A much more recent "*auleticus*" invasion in S. America, directly from the Old World, could easily have happened. In the Old World, groups like *B. erectus* seem to have associated with a more recent adaptive radiation, which would explain a possible later arrival in part of S. America through man's influence.

11.4 Conclusion

The correlation of form-function in the perennial brome-grasses seems to me to be positive after the study and comparison of a large number of parameters, from a morphological to an ecological basis, geographical and cytological. The patterns observed are significant, i.e., a deeper study on the sheath morphology has brought into light a better understanding of the biology of these grasses and clarification of the pattern of adaptive radiation.

The initial intuitive subdivision of *Bromus* § *Pnigma* into four main groups has been confirmed through a large spectrum of evidence, showing in many cases a plausible relation to form and function. More work is needed, as was stated in various chapters to "solve" some of the questions left unanswered, and will most probably be achieved via a comparative investigation. Taxonomy should be interpreted in terms of adaptive radiation, keeping in mind that our results will reflect the panorama occurring in nature over a particular length of time, and be a changing manifestation of a continuing evolutionary process.

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Appendix 4.1. Accession number details of material used for anatomy and experimental investigations.

Species	Accession number	Origin/ collector / Herbarium
B. ramosus	1684	Belgium
B. ramosus	16256	England/ Raven/ (BM)
B. benekenii	1693	Germany
B. erectus	1694	Germany
B. erectus	1710	France
B. erectus	1656	Hungary
B. erectus	290	France/ Bourgeau/ (W)
B. tomentellus	19846	Crete/ Greuter & Risse/ (B)
B. cappadocicus	15768	Greece/ Strid & Papanicolau/ (B)
B. inermis	1697	Germany
B. riparius	423	Greece/ Scholz & Schwarz/ (B)
B. riparius	22304	Greece/ Stamatiadou/ (C)

Appendix 6.1 Raw data from water absorption experiment.

RAM	EREC	RIP
402.2	344.4	275.4
410	334.1	260.6
407.6	326.6	269.3
399.4	322	270
405	336.8	278.6
411.1	329.7	280.1
401.7	340.1	279.3
399.8	342.3	268.1
406.3	339.7	273.4
409.1	328.9	276.3

Appendix 6.2. Raw data from water loss experiment.

Time	RAM	EREC	RIP
0.5	3.08	7.23	2.57
0.5	2.96	7.16	2.62
0.5	3.03	7.25	2.35
0.5	3	7.13	2.5
0.5	3.01	7.2	2.46
0.5	2.88	7.21	2.38
0.5	3.1	7.18	2.53
0.5	2.95	6.99	2.63
0.5	3.12	7.24	2.49
0.5	3.05	6.96	2.42
1.5	9.49	20.11	8.23
1.5	8.84	20.08	8.09
1.5	9.62	20.16	8.32
1.5	9.35	19.98	8
1.5	9.16	20.01	8.16
1.5	9.46	20.04	8.3
1.5	9.58	19.98	8.06
1.5	9.2	19.01	8.14
1.5	9.32	19.99	8.27
1.5	8.81	20.13	8.21
3.5	22.62	42.03	25.12
3.5	21.59	41.99	25.19

3.5	22.8	42.09	24.98
3.5	22.58	41.77	25.07
3.5	22.13	42	25.2
3.5	22.57	41	25.03
3.5	22.78	41.97	25.17
3.5	22.15	42.03	25.16
3.5	22.57	42.1	24.99
3.5	21.5	41.98	25.09
6.5	40.07	52.54	33.98
6.5	40.29	52.49	33.82
6.5	40.15	52.59	34.09
6.5	39.87	52.09	34.12
6.5	40.16	52.51	33.8
6.5	40	52.46	34.07
6.5	39.97	52.18	33.81
6.5	40.22	52.39	34.15
6.5	39.95	52.61	33.86
6.5	40.04	52.6	34.05
20	76.42	62.25	59.01
20	76.37	62.23	58.84
20	76.6	62.18	59.1
20	76.34	62.09	58.93
20	76.21	62.29	59.06
20	76.39	62.2	59.04
20	76.32	62.12	58.82
20	76.26	62.28	58.97
20	76.29	62.3	59.11
20	76.31	62.3	59.05

Appendix 6.3. Raw data from soil trapping experiment.

RAM	EREC	RIP
0.47	4.25	5.71
0.39	4.83	6.63
0.45	5.2	5.78
0.22	4.23	5.26
0.27	4.56	5.91
0.26	5.01	6.2
0.38	4.38	6.46
0.42	3.99	6.38
0.28	4.65	6.09
0.31	4.12	6.5

Appendix 10.1. List of characters, size ranges (in brackets) and characters states used in the taximetric analysis (chapter 10, sect. 10.2.2).

Rhizome length	absent	0
(1-8-(100) cm)	1-2 cm	1
	2.1-4 cm	2
	more than 4 cm	3
Stem height	up to 50 cm	0
(16-150-(220) cm)	50.1-90 cm	1
	more than 90 cm	2
Stem width	up to 1.5 mm	0
((0.4)-0.5-5.5-(7.5) mm)	1.6-3 mm	1
	more than 3 mm	2
Stem indumentum	glabrous	0
	hairy	1
Sheath decay	intact	0
	parallel fibres	1
	reticulum	2
Sheath indumentum	glabrous	0
	minutely pubescent	1
	scattered hairs	2
	densely lanate	3
Basal leaves		
- length	up to 20 cm	0
(3.5-38 cm)	more than 20 cm	1
- width	up to 1.5 mm	0
(0.5-5-(7.5) mm)	1.6-3 mm	1
	more than 3 mm	2

- form	flat	0
	conduplicate	1
	involute	2
- indumentum	glabrous	0
	ciliate at margins	1
	scattered hairs	2
	densely hairy	3
	minutely pubescent	4
Cauline leaves		
- length	up to 20 cm	0
(3-40 cm)	more than 20 cm	1
- width	up to 1.5 mm	0
(0.5-5.5-(8) mm)	1.6-3 mm	1
	more than 3 mm	2
- form	flat	0
	conduplicate	1
	involute	2
- indumentum	glabrous	0
	ciliate at margins	1
	scattered hairs	2
	densely hairy	3
	minutely pubescent	4
Ligule length	up to 1 mm	0
(0.2-5-(6) mm)	more than 1 mm	1
Flag leaf		
- length	up to 10 cm	0
(3-40 cm)	more than 10 cm	1
- width	up to 2.5 mm	0

(0.3-9.5-(11.5) mm)	more than 2.5 mm	1
Panicle length	up to 8.5 cm	0
((1.5)-3-35 cm)	8.6-15 cm	1
	more than 15 cm	2
Panicle shape		
- panicle shape at maturity	erect-oblong	0
	drooping-effuse	1
	spreading-deltoid	2
- panicle shape constancy	stays the same	0
	varies at maturity	1
Number of panicle basal	1-3	0
branches	4-6	1
(1-9)	more than 6	2
Panicle branches length		
- shortest	up to 2.5 cm	0
(0.5-9 cm)	2.6-4.5 cm	1
	more than 4.5 cm	2
- longest	up to 4.5 cm	0
(0.8-13 cm)	4.6-6.5 cm	1
	more than 6.5 cm	2
Panicle branches roughness	glabrous	0
	shortly scabrous	1
Spikelet length	up to 2 cm	0
((1)-1.5-3.7-(5.3) cm)	2.1-3.5 cm	1
	more than 3.5 cm	2
Number of spikelets	8-13	0
(5-60)	14-23	1
	more than 23	2

Number of florets	up to 5	0
(3-9-(11))	more than 5	1
Rachilla length	up to 1 mm	0
((0.9)-1-3-(3.8))	more than 1 mm	1
Rachilla indumentum	glabrous	0
	finely hairy	1
	densely hairy	2
Glumes length		
- lower glume	up to 9.5 mm	0
((4.7)-5.5-13 mm)	more than 9.5 mm	1
- upper glume	up to 11 mm	0
(6-15 mm)	more than 11 mm	1
Upper glume shape	narrowly lanceolate	0
	broadly lanceolate	1
Glume hyaline margins	narrow	0
	broad	1
Lemma		
- length	up to 11.5 mm	0
((7)-8-15-(18) mm)	11.6-14 mm	1
	more than 14 mm	2
- width	up to 2 mm	0
(1.4-2.8 mm)	more than 2 mm	1
- shape	oblong-lanceolate	0
	ovoid-lanceolate	1
	narrowly-lanceolate	2
Lemma indumentum	glabrous	0
	scattered, few hairs	1

	hairs restricted to the lower half, adpressed	2
	hairs reaching the apex, sub-patent	3
	numerous	4
Lemma hyaline margins	narrow	0
	broad	1
Number of veins in the lemma (3-5)	3	0
	more than 3	1
Awn ((0.5)-1-8.5 mm)	absent	0
	up to 5 mm	1
	more than 5 mm	2
Awn orientation	straight	0
	slightly out-curved	1
	strongly divaricate	2
Palea length ((4.5)-5-12-(13) mm)	up to 10 mm	0
	10.1-12 mm	1
	more than 12 mm	2
Palea keels	small, obscure teeth	0
	relatively well developed teeth	1
Stamen length ((1.7)-2-7.5 mm)	up to 4.5 mm	0
	more than 4.5 mm	1

Appendix 10.2. Raw data matrix of 24 OTUs and measurements of 44 of their characters (chapter 10, sect. 10.2.3).

```
001220120012001011101220111111001101101200013*0
002100002200220131001010010110001000020101 11200
003000002000201110001010010110000000002000110200
004110001100110100001010011110001111111100121200
005110010201020120000110111111011111111110121301
006001010301030131000010011110000100001100 10300
007110010001000101021110011110011110001200 11300
008110112301230131001110011110101111001101 21200
009110010001000121001110001110001111021201 11100
010210110012001101121221112110111111100121011100
011110002000200101000110211010010021020110 21200
012210120012001121000110111110111111101211 11100
013010010101011100000100011110000010000100 11300
014220120212021021111202211 1**01102100020120002
015220020212021021111211111 0**0110100202012000 3
016100010112011221001011111111110111010 1121210
017110110211021201001110111112111111011111121301
018120020302030221021111111111111111011001 21201
019001010402041220021101010111000000001201 20001
020100002000200200001001012110110011320011 21120
021011012401240220021011102112001111011101 21304
022110002401241210001110111112111011010001 2*111
023101010301031220000000111112110111101011 21200
024000002000200200001001011010010010020021 2*000
```

Appendix 10.3. List of the most biologically and morphologically significant characters selected in the taximetric analysis (chapter 10, sect. 10.2.4).

Rhizome length	absent	0
	1-2 cm	1
	2.1-4 cm	2
	more than 4cm	3
Stem height	up to 50 cm	0
	50.1-90 cm	1
	more than 90 cm	2
Stem width	up to 1.5 mm	0
	1.6-3 mm	1
	more than 3 mm	2
Sheath decay	intact	0
	parallel fibres	1
	reticulum	2
Sheath indumentum	glabrous	0
	minutely pubescent	1
	scattered hairs	2
	densely lanate	3

Basal leaves:		
- length	up to 20 cm	0
	more than 20 cm	1
- width	up to 1.5 mm	0
	1.6-3 mm	1
	more than 3 mm	2
- form	flat	0
	conduplicate	1
	involute	2
- indumentum	glabrous	0
	ciliate at margins	1
	scattered hairs	2
	densely hairy	3
	minutely pubescent	4
Cauline leaves		
- length	up to 20 cm	0
	more than 20 cm	1
- width	up to 1.5 mm	0
	1.6-3 mm	1
	more than 3 mm	2
- form	flat	0
	conduplicate	1
	involute	2
- indumentum	glabrous	0
	ciliate at margins	1
	scattered hairs	2
	densely hairy	3
	minutely pubescent	4

Panicle shape		
- panicle shape at maturity	erect-oblong	0
	drooping-effuse	1
	spreading-deltoid	2
Panicle length	up to 8.5 cm	0
	8.6-15 cm	1
	more than 15 cm	2
Spikelet length	up to 2 cm	0
	2.1-3.5 cm	1
	more than 3.5 cm	2
Number of spikelets	8-13	0
	14-23	1
	more than 23	2
Lemma		
- length	up to 11.5 mm	0
	11.6-14 mm	1
	more than 14 mm	2
- width	up to 2 mm	0
	more than 2 mm	1
- shape	oblong-lanceolate	0
	ovato-lanceolate	1
	narrowly-lanceolate	2
Lemma indumentum	glabrous	0
	scattered, few hairs	1
	hairs restricted to the lower half, adpressed	2
	hairsreaching the apex, sub-patent	3
	numerous	4