BROMUS L. SECT. *BROMUS*: TAXONOMY AND RELATIONSHIP OF SOME SPECIES WITH SMALL SPIKELETS.

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An artificial group of twelve brome-grasses with small-spikelets is reviewed. Descriptions, comments on their distinctive features, keys, diagnosis, citations and illustrations are provided. Form/function and evolutionary relationships are discussed and four affinity groups are recognized. The possible origin of *B. lepidus* and *B. brachystachys* is discussed.

INTRODUCTION

This paper is about critical taxa, with small spikelets, in *Bromus* section *Bromus*. This group of critical taxa is avowedly 'artificial' as a whole, though it contains some 'natural' parts. Our criterion for including a taxon is: having all or a significant part of its lemma length variation within the limits 4–7mm. The species included in this study are listed in Table 1. *Bromus racemosus* L., in its robuster manifestations, certainly has an evolutionary link with species with large or very large spikelets (e.g. *B. commutatus* Schrad., *B. secalinus* L. and *B. grossus* Desf.), but we have excluded these simply because we focus here on small-spikelet features *per se*. We also omit *B. oostachys* Bornm. partly because we believe this extinct species, known only from its type specimen, would add an unnecessary, unrelated complication at this stage.

Many of the species here studied are hard to identify because their diagnostic characters are difficult to communicate in written descriptions (Smith, 1973). Though individual character states may often be only subtly different, they may contribute to a collective appearance or facies which is quite striking. Additional problems are the variations of size and occasional congestion of florets and spikelets that are associated with different habitats or states of maturity, i.e. plastic developmental variation. These circumstances have encouraged taxonomists to resort to characters, for instance of lemma shape or texture, which have the merit of conservatism but the demerit of being hard to describe.

Several consequences follow these difficulties. One is the common confusion of discrete taxa. Another is the tendency for collectors to overlook at least some of them, leading to uncertainties of distribution or even of continued existence. A third consequence is the unworkability of many keys, because the subtle but real distinctions of the species are often not used in them. A final outcome is the obscurity of evolutionary pattern and relationships in brome-grasses with small spikelets.

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Though the species of *Bromus* sect. *Bromus* are scarcely of major economic interest, at least at present, many of these taxa are weeds, and some of them are known contaminants of grass seed crops or otherwise commensal with man (Smith 1968, 1986). The fact that some of them are, or appear to be, recent extinctions or are apparently rare, lends them a general evolutionary interest. Further, the necessarily partial treatments in Floras create needs for overall reviews of critical species and a continuing scrutiny of the biology of the group as a whole. For instance, some specific distinctions have only recently been established by exceptional observers, e.g. Scholz (1972) on *B. brachysta-chys* and *B. pseudobrachystachys*. Confusion of these two species, for example, frustrates attempts to use Marshall Ward's (1902) interesting work on cross-infectivity of fungal parasites. Our study reveals that some at least of his '*B. brachystachys*' was *B. pseudobrachystachys*. His work may repay reinterpretation by mycologists.

The work here presented cannot be a 'final' view of these taxa, for they are mostly inadequately collected, and it is the authors' conviction that there are brome-grasses, even in Europe (Sales & Smith, 1990), awaiting discovery.

ENUMERATION AND CONSPECTUS OF SPECIES INCLUDED

The nomenclatural details of the taxa are discussed, with an indication of what is known of ploidy and distribution. In cases where it is thought helpful, new accounts or illustrations are cited. Where the published geographical range is thereby extended, specimens are cited. There are some notes about the general state of herbarium holdings in some cases.

B. arvensis L., Sp. Pl. 77 (1753).
(Fig. 6c, d: Luxembourg, 18 vii 1954, *Reichling* (BM).
2n=14. S and SC Europe and contiguous Asia. Field margins. Including *B. arvensis* subsp. *segetalis* H. Scholz in Willdenowia 6: 145 (1970). (Syn. '*B. billottii*' (Kerner) Asch. & Graebn.) A weed of cereal fields. This taxon has probably been under-recorded.

B. brachystachys Hornung in Flora 16: 417–421 (1833).
(Fig. 2a, b, c: Germany, Aschersleben, 25 vi 1906, *Preusse* s.n. (G))
2n=? Saxony, Aschersleben and district, in fields and waste places. (Figs 1a, 4a, b: Sweden, Uppsala, grown in the garden, ex Fries Herb. Norm. Scand XV, 96 (K)).

B. hordeaceus L., Sp. Pl. 77 (1753).
Subsp. *ferronii* (Mabille) P.M. Smith in Watsonia 6: 327–344 (1968).
2n=28. W Europe. Maritime cliffs.
Subsp. *thominii* (Hardouin) Bram-Blanquet, Orig. Dev. Fl. Massif Central 113, 1923.
2n=28. W Europe. Sand dunes.

B. x pseudothominii P.M. Smith in Watsonia 6: 327–344 (1968).
(*B. lepidus* x *B. hordeaceus* subsp. *hordeaceus*).
2n=28. Widely distributed in anthropogenic habitats in Europe, W Asia. Part of the *B. hordeaceus* complex. Smaller, more congested spikelets than *B. tigridis*.

B. lepidus Holmberg in Bot. Notiser 326 (1924).

Fig. 1c: England, Derbyshire, 23 vi 1956, *P.H. Davis* (E); Fig. 2d, e: England, Gloucs, Woodchester. *H.P. Reeder* s.n. sub *racemoso* (K).

2n=28. Europe, in sown grassland. Distribution imperfectly known.

Specimen recently found in the Cairo Herbarium (CAI): Egypt, Raafaran Palace, Cairo, as a weed, vi 1929, *M. Hassib* s.n.

B. lusitanicus Sales & P.M. Smith in Edin. J. Bot. 47: 361–366 (1990).

Fig. 5a, b.

2n= 14 Known from the type only: Portugal, Souzelas, near Coimbra, vi 1983. *F. Sales* s.n. (holo. E, iso. K).

B. psammophilus P.M. Smith in Notes R. B. G. Edinb. 42: 491–501 (1985).

Figs 1c, 4c, d.

2n=? Known only from the type: S Turkey, C5 Icel, Tarsus, dunes, 3 vi 1973, *T. Uslu* 36425, sub *B. briziformis* (holo. E).

B. pseudobrachystachys Scholz in Bot. Jb. Syst. 91: 462–469 (1972).

Fig. 3a: Turkey, C5 Icel. vi 1855, *Balansa* 752 (BM); Fig. 3b: Iraq, Khalis 22 iv 1960, *Wheeler Haines* 1660 (E); Figs 1d, 3c: Palestine, Dead Sea, 18 iv 1921, *Meyers & Dinsmore* 1299b (E).

(Syn. *B. brachystachys* auct. orient. non Hornung)

2n=? S.W. Asia, moist areas.

B. pseudosecalinus P.M. Smith in Fedde, Rep. 77: 61–64 (1969).

Fig. 6a, 6b: Wales, Montgomeryshire, Bettws, 5 vii 1955, *Milne-Redhead* 6657 sub *B secalino* var *hirsuto* (K).

2n=14. Europe, waste places and sown grassland, hayfields.

B. racemosus L., Sp. Pl. (ed. 2) 114 (1762).

Fig. 5c, d: England, Oxford, Pixey Mead near King's Weir, 16 vi 1978, *Pankhurst* 78/161 (BM).

2n=28. Europe, W Asia. Water-meadows, waste places.

B. scoparius L., Cent. Pl. 1: 6 (1755).

2n=14. Europe, N Africa, W Asia. Waste places and as a weed. Generally well collected and identified but with depauperate material often undetected in mixed gatherings with *B. hordeaceus* and *B. rubens*.

B. tigridis Boiss. & Nöe, Diagn. Plant. Nov. II (4) (1859).

Fig. 1b: Palestine, Dead Sea, Beth-Hoglah, 26 iii 1912, *Meyers & Dinsmore* 9299 (E).

Fig. 3d, e, f: Palestine, Gilead et Auraniticae, Tell el Kadi, 11 v 1911, *Meyers & Dinsmore* 85299! (S). This is the type specimen of *B. palaestinus* Meld.

(Syn. *B. aegyptiacus* Tausch., *B. palaestinus* Meld.)

2n=? E Mediterranean, Egypt, Iraq, Iran, Turkey (C6 Gazientep, Nurdag: bei Fevzipah, Felder unter Triften, 7 ix 1981, *H. Ern* 6855 (B)).
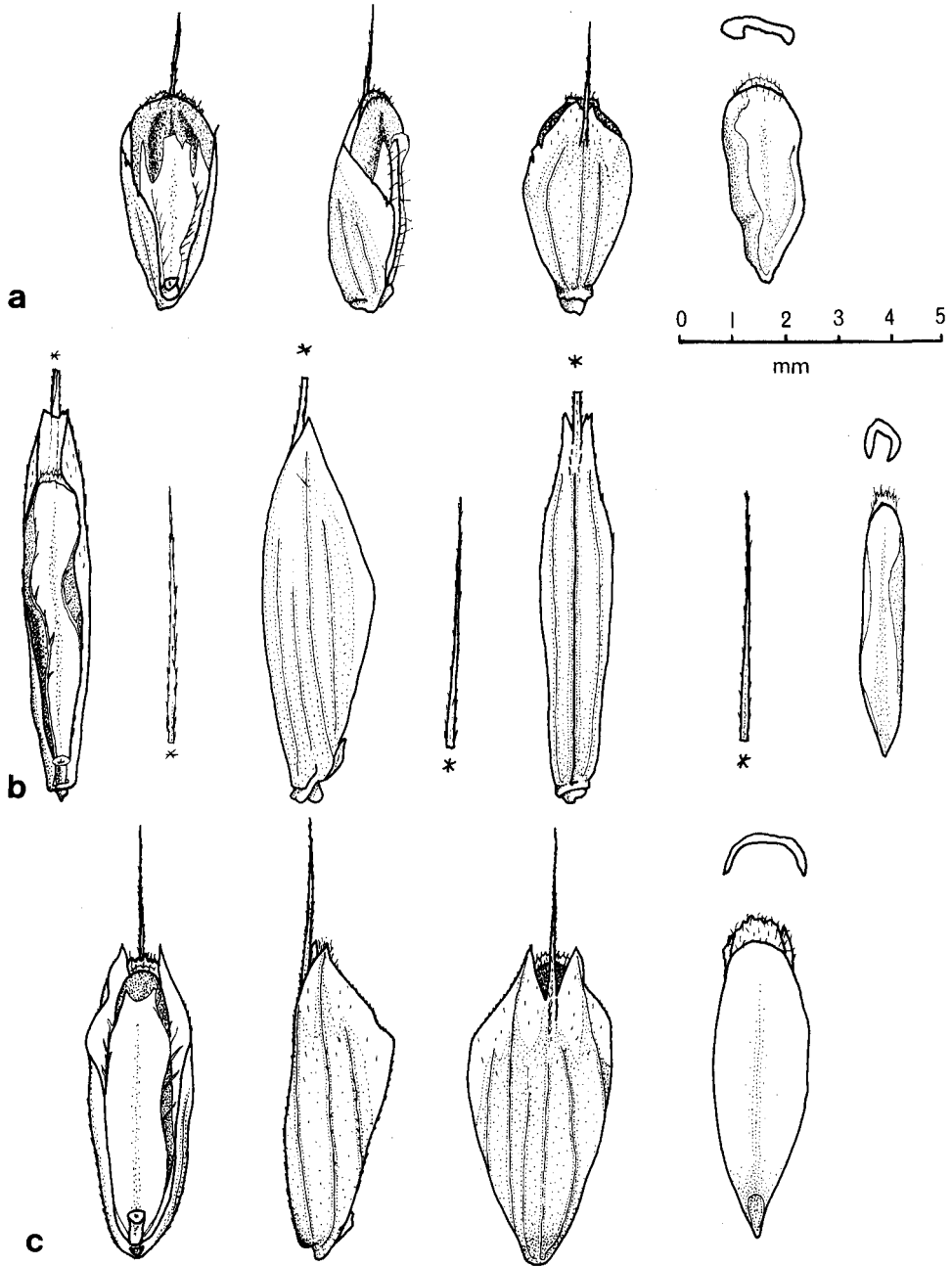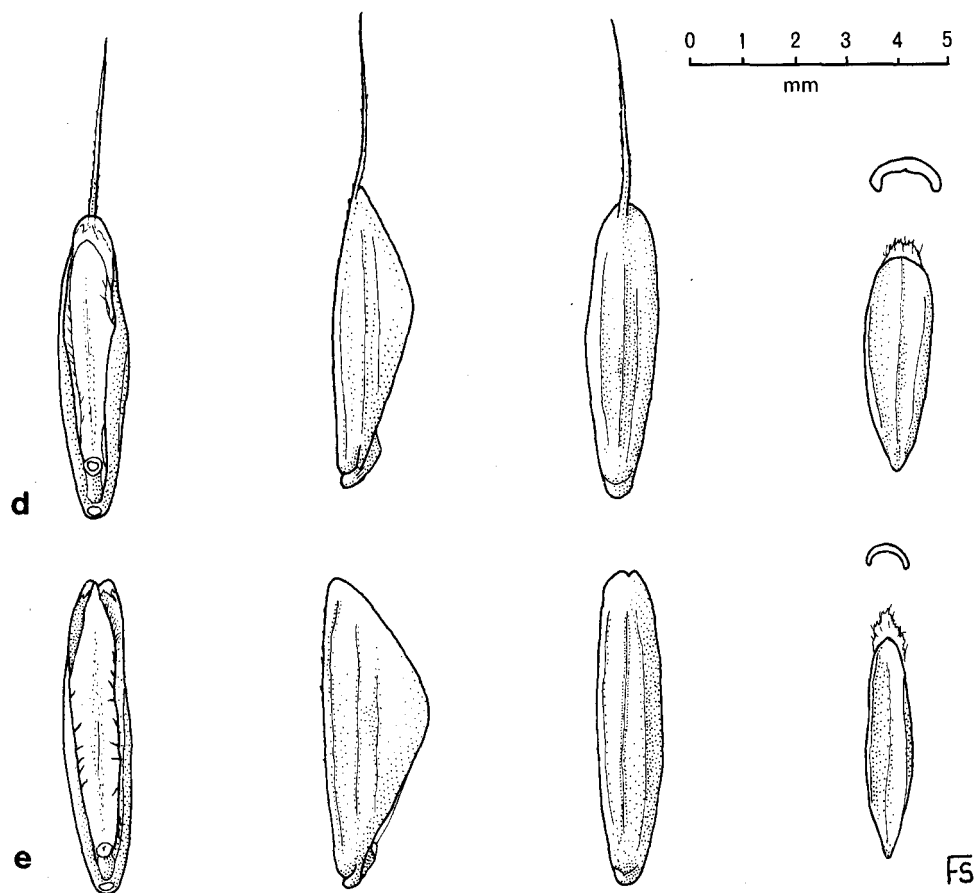
FIG. 1 (above and oppposite). Ventral, lateral and dorsal views of florets, and ventral and transectional views of caryopses of: a, *Bromus brachystachys*; b, *B. tigridis*; c, *B. lepidus*; d, *B. pseudobrachystachys*; e, *B. psammophilus*.

MORPHOLOGY OF SMALL-SPIKELET BROME-GRASSES

(a) DIAGNOSTIC FEATURES

Full, formal descriptions of similar taxa which are, by definition, liable to be confused, can paradoxically reinforce the problem by demonstrating their resemblance. Accordingly, the chief *diagnostic* features are here presented, in tabular form (Table 1), along with references to the best published illustrations. Table 1 can of course be used in conjunction with Figs 1–6.

(b) GENERAL

There are essentially no vegetative characters by which the taxa here discussed may safely and consistently be distinguished. They all have the standard features of brome-grasses – tubular sheaths (i.e. with connate margins), membranous ligules, and flat leaf blades. All these organs can be glabrous, or variously hairy. Long patent hairs are characteristic of the sheaths of seedling and juvenile specimens of *B. scoparius*, but are not always produced. Some variants of *B. hordeaceus*, notably subsp. *ferronii*, have densely lanuginose sheaths, but this character is continuously variable and hence hard

Table 1. Diagnostic features of some small-spikelet bromegrasses.

Note: Panicle branch lengths quoted are for the longest branch (*including* spikelet) at the lowest node of the panicle. The lemma and awn characters quoted are of a basal floret of a mature spikelet. The striate lemma drying pattern consists of longitudinal ridges and grooves associated with veins.

	Panicle	Panicle Branches		Spikelet	Lemma		Awn Characters	Anther	Caryopsis
	length; type (cm)	robustness, attitude	length (cm)	length (mm)	length (mm) marginal angle	texture; drying pattern		length (mm)	relative length; transection
arvensis	7-23(-36); broad, effuse, very loose	medium, ascending or patent	4-6(-8)	9-11(-25)	7-8(-9); obscure, blunt	± chartaceous, striate	fine, straight or weakly spreading; lowest shortest	3.5-5	≤ lemma and palea; thin, flat or feebly grooved
arvensis subsp. *segetalis*	7-15; broad, effuse, very loose	medium, ascending or patent	2-6	13-15	6(-6.5); obscure, blunt	± chartaceous, weakly striate	fine, straight or flexuous; lowest shortest	3-3.5	≤ lemma and palea; thick, flat
brachystachys	6.5-11(-18); broad, loose, pyramidal	stiff, robust, patent or ascending	(3-)4-6(-12)	(7-)8-9(-11)	(3.5-)4-4.5(-4.7); very distinct	chartaceous-translucent, striate	fine, weak, straight; lowest shortest	2-2.5	> palea ≥ lemma
hordeaceus subsp. *ferronii*	2-5; oblong-ovoid, dense	robust, ascending or patent	0.25-1.5	8-18	6.5-8; blunt	chartaceous, striate	robust, spreading or patent; lowest shortest	0.2-1.5	< palea
hordeaceus subsp. *thominii*	1-3; ovoid, contracted with few spikelets	robust, ascending or erect	0.25-0.7	8-12	6.5-7.5; blunt	chartaceous, striate	fine, often spreading or patent; lowest shortest	0.5-1	< palea
× *pseudothominii*	1-10; ovoid, usually dense	fine, ascending or erect	0.7-1.5	10-15	6.5-8; blunt	chartaceous, striate	fine, straight; all ± equal	0.2-1.5	< palea
lepidus	2-10; narrowly ovoid, oblong, usually dense	fine, ascending or erect	0.5-1.5	5-15	5.5-6.5; very distinct	chartaceous-translucent, striate	very fine, hair-like, straight; lowest shortest	0.5-2	> palea ≥ lemma
lusitanicus	4.5-(8-10)-13; narrowly oblong	fine, ascending-erect, later nodding	(0.4-)2-7	12-15	7-8; blunt	corneous, smooth or irregularly folded	fine, straight; all ± equal	1.5-2	± = palea
psammophilus	7; broadly pyramidal, loose	stiff, robust, ascending	5	10-15	5.5-6; very distinct	sub-chartaceous, striate	N/A	2-2.5	< palea
pseudo brachystachys	7.5-10(-17); broadly pyramidal to narrowly oblong	fine, ascending or erect	2-4	5-12	4-5; distinct	chartaceous, striate	fine, straight; all ± equal	(1.25-)1.5-2(-2.5)	< palea
pseudosecalinus	3.5-(8-10)-11; narrowly ovoid-oblong	fine, erect or ascending	(0.8-)1-3	8-12	5-6; blunt	corneous, smooth or irregularly folded	fine, straight; lowest ≤ the upper awns	1.7-2	± = palea
racemosus	4.5-(8-12)-14; narrowly ovoid oblong	fine, erect or ascending	1.5-2.5	12-16	6.5-8; obscure or absent	corneous, smooth or irregularly folded	fine, straight; lowest usually shortest	1.5-2.5	< palea
scoparius	1.7; ovoid, dense	stiff, robust, erect or ascending	0.3-1	(10-)15-17(-20)	(7-)8(-10); obscure	chartaceous, striate	fine, spreading or patent; all ± equal, equalling or exceeding lemma	0.25-0.5	≤ palea
ugridis	5-12; ovoid-oblong, loose or contracted	fine, erect or ascending	1-6	1-15(-17)	6-7; distinct	chartaceous, striate	fine, straight or slightly spreading; all ± equal, exceeding lemma	2-2.2	< palea

to define. There are sheath hair differences between *B. brachystachys* and *B. pseudo-brachystachys* (Scholz, 1972) but at least as field characters they are somewhat obscure.

Many reproductive characters, by contrast, vary discontinuously, and some are conservative to a useful degree, offering a good opportunity for taxonomic circumscription. Among these the most notable are glume and lemma size, shape and texture; extent and form of the hyaline margin of the lemma; awn length, form, attitude – variation in all these between the florets of a single spikelet; spikelet form; palea length, (absolute and relative to the lemma); anther length; caryopsis length (absolute and relative to the palea) and mature form, especially in transverse section. Rather less useful, because more complex in origin, less discontinuous, harder to circumscribe and more plastic, are panicle characters – of size, shape and density.

The bases on which these characters are here rated as more or less conservative are, first, a familiarity with thousands of specimens of the taxa from a wide range of habitats and time of collection, and also from the widest possible geographical area; second, a close knowledge of the plastic and developmental changes peculiar to each character, obtained from cultivating all the extant taxa in a diversity of environments.

(c) THE CHARACTERS
(i) Glume and lemma size, shape and texture
Glume and lemma form and size are closely correlated. The glume forms of discrete taxa show consistent differences, mainly as a function of width, but these are simply too small and subtle to be very effective in identification. However, because in *Bromus* the glumes persist after maturity, they can be of some value when dealing with old or badly preserved specimens. Lemma form has extra value arising from the additional features of awn insertion, and of the upper margin ('shoulder'). All these features are highly conservative. Normally, lemmas of florets up to the middle of the spikelet are about equal in size to the lowest, those above showing a gradual decline. Sudden decline in size (and fertility) may sometimes indicate some degree of genotypic heterodiaspory, but it can also accompany insect damage or interruptions of water supply.

All lemma measurements quoted by the authors (Table 1) relate to lowest lemmas of well-formed flowering or fruiting spikelets and are, in our experience, rarely transgressed. Young spikelets should be ignored (see b (iii)).

Lemma shapes, although difficult to communicate, are valuable aids to identification and diagnosis. The useful variation arises from the depth of the apical sinus, the depth of insertion of the awn (these two never being the same), the shape of the lemma in its upper third – the 'shoulder' area, and the width of the hyaline margin. So characteristic and consistent are these features in brome-grass taxa, within the limits quoted, that it is hard to believe that they are not functional. Floret form and function in *Bromus* is receiving attention in another series of papers (Smith, 1989). To exemplify these features we may contrast the sharply angled upper lemma margin of *Bromus lepidus* (Figs 1c, 2d), which is also broadly hyaline well down its length, with the more rounded, bluntly angled, narrowly hyaline margin of *Bromus tigridis* (Fig. 1b). Genetic control of the lemma shoulder hyaline margin shape in *B. lepidus* is implied by its more rounded, narrower form in hybrids with *B. hordeaceus* L. (Smith, 1968). The apical sinus is
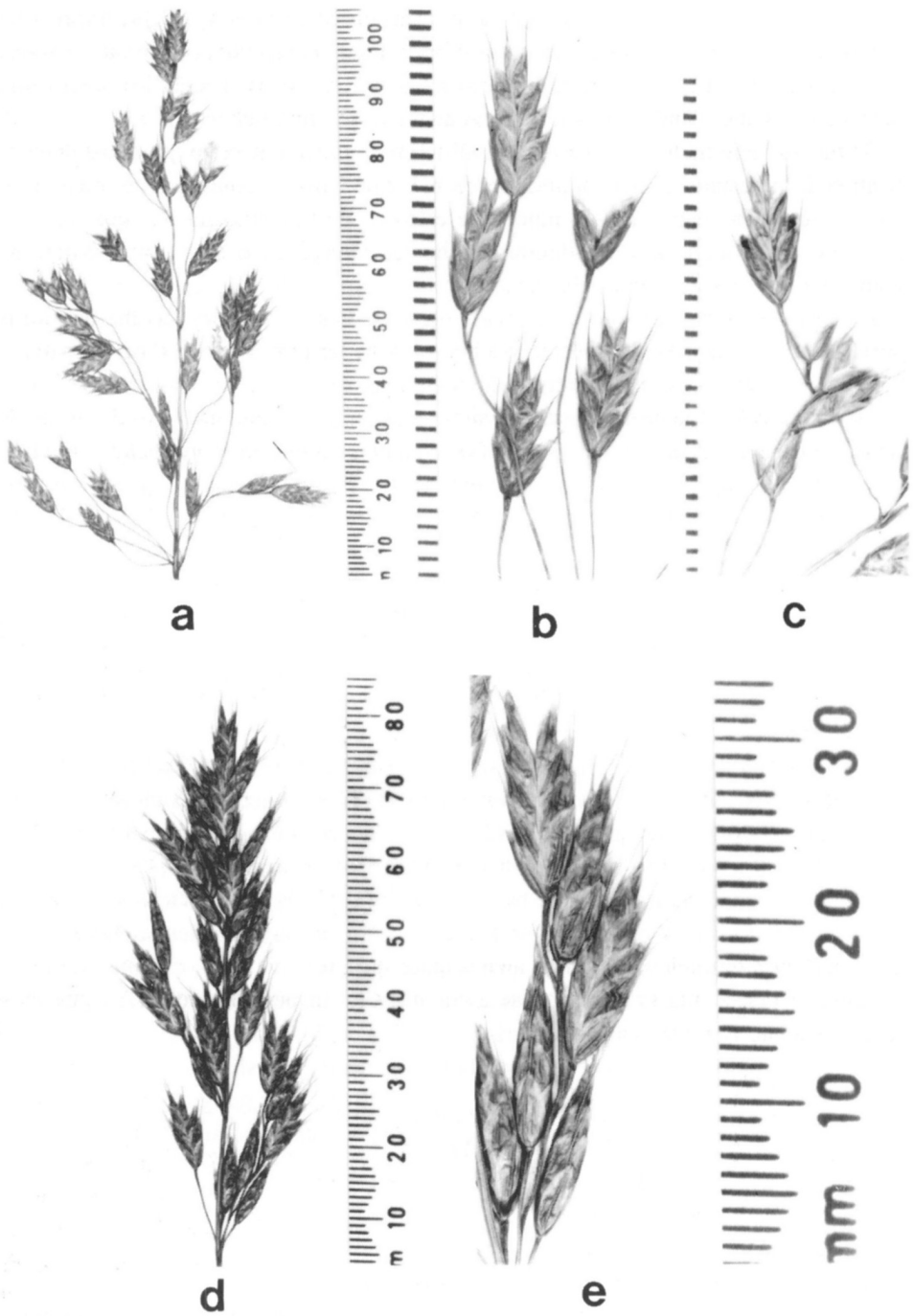
C

FIG. 2. *Bromus brachystachys*: a, panicle; b & c, spikelet details. *B. lepidus*: d, panicle; e, spikelet details. (Scale in mm).

typically acutely triangular in *Bromus*, but in some it can sometimes be shallow or absent, as in *B. pseudobrachystachys* and *B. psammophilus*. The lemma sinus is a fragile area, sometimes ripping to the point of awn insertion, and so giving a false impression unless the observer is careful. An example of awn insertion diversity comprising a useful identificatory feature is the difference between *B. brachystachys* (rarely less than 1 mm below lemma apex) and *B. pseudobrachystachys* (c. 0.5 mm below apex).

Glume and lemma texture, hardest of all to communicate save by practical demonstration, is of considerable taxonomic value, being both highly conservative and persistent in herbarium material. Differences arise from two fundamental features, viz. the thinness of the tissue and the degree of abaxial emergence of the veins. When the interfascicular tissue, mainly chlorenchyma, is relatively thick and the veins scarcely raised (e.g. as in *B. racemosus*, *B. pseudosecalinus* and *B. lusitanicus*) the texture is sometimes described as coriaceous. We believe a better term is 'horny' or 'corneous'. Corneous lemmas are quite tough. Irregular foldings on drying often run perpendicular to the veins. When the interfascicular tissue is relatively thin, and the veins prominently raised (e.g. in *B. hordeaceus*, *B. scoparius*, *B. lepidus* and *B. brachystachys*), the best description is 'papery' or chartaceous. Such lemmas are more easily ripped. Folds on drying are parallel to the veins. Assessment of texture is best made first by eye, then by probing with a needle. Inevitably, experience is helpful.

A further, highly conservative, and striking feature correlated with the thinness of the lemma should be noted. When there is a substantial area of hyaline tissue in a thin lemma, it becomes essentially translucent. Thus in both *B. lepidus* and *B. brachystachys* the mature grain can often be seen as a brown structure through much of the lemma.

(ii) Awn characters

Awns are straight and stiffly erect in most material here reviewed; in a few cases they twist at the base and then become to some degree spreading or, more rarely, recurved (see Table 1). In *B. lepidus* and *B. brachystachys* the awns are erect but weak and very fine (in *B. lepidus* almost hair-like), often breaking. In *B. psammophilus*, there is no awn.

The awns of most of the fertile florets are normally of about the same length, though in some cases (e.g. *B. tigridis*) middle and upper lemmas may have longer awns (Fig. 3 e, f). In *B. brachystachys* the lowest awn is quite short relative to the remainder, though because of occasional breakage these awns must be inspected carefully. Uppermost awns are somewhat vestigialized.

(iii) Spikelet form

All the taxa reviewed here have spikelets of initially circular section, tapering to the top, the young florets being tightly and regularly imbricated. There may be as many as fifteen fertile florets in robust forms of *B. tigridis*, but the norm for all these taxa is about six. Floret number is a plastic character, as therefore is spikelet length. We have detected no sign of any functional synaptospermy. In *B. pseudosecalinus* the abscission of the grain is late: florets may remain unshed for a long period.

The mature spikelet becomes somewhat compressed laterally, as the rachilla internodes curve, forcing apart the mature florets, and the grain, inrolling to some degree,
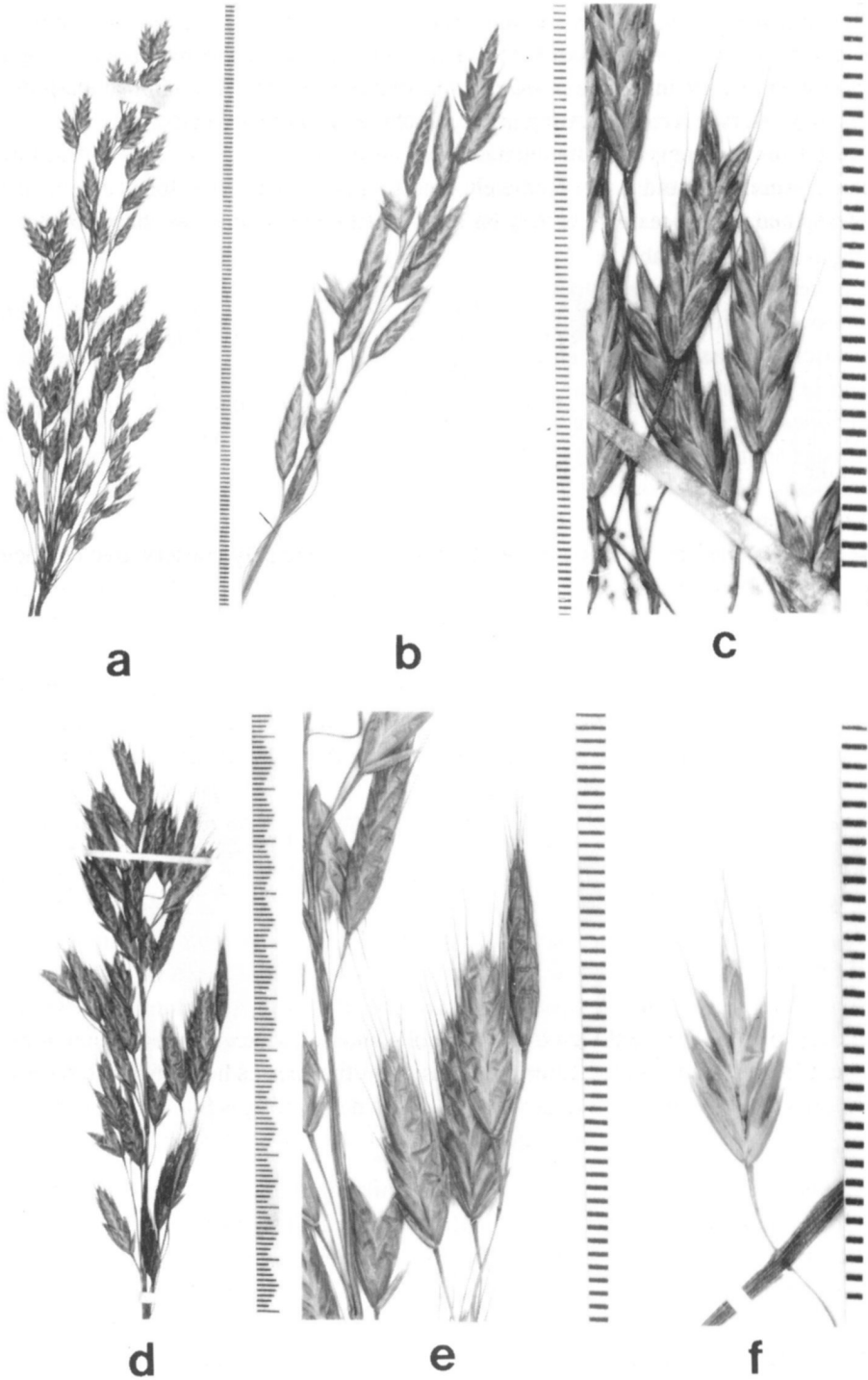
FIG. 3. *Bromus pseudobrachystachys*: a & b, panicles; c, spikelet details. *B. tigridis*: d, panicle; e & f, spikelets. (Scale in mm).

draws together the previously gaping margins of the lemma. The lemma and palea are glued to the mature grain (Smith 1989). In *B. pseudosecalinus* the inrolling of the grain is accompanied by inrolling of the lemma margins, so that the lemma margins of contiguous florets cease to overlap and the rachilla is clearly revealed.

Young spikelets have a characteristic appearance caused by the glumes and/or lower floret or pair of florets almost completely investing the as yet poorly formed upper parts of the spikelet. Such material is very hard to identify and is rarely worth collecting.

(iv) Palea length

Paleas are typically somewhat shorter than the lemmas in these taxa, and a little longer than the mature grain. The apex of the palea becomes associated with the hairy appendage of the grain. In *B. arvensis* the palea normally almost equals the lemma. *B. lepidus* and *B. brachystachys* are unusual in that the mature grain is longer than the palea, emerging above it quite perceptibly (Fig. 1a, c). In a few specimens the grain exceeds even the lemma.

(v) Anther length

The length of mature anthers is generally a useful, reasonably conservative character. One has to be aware of atypically short anthers that may be formed late in the growing season. Fortunately the intact, mature anther dries out to something close to its length when alive, so is useful in herbarium specimens.

Some short-spikelet brome-grasses have anthers quite long in relation to other floret organs. In *B. arvensis* and *B. brachystachys* they can approach or exceed half the length of the lemma: in some specimens, these large anthers are clearly exserted. In the small-spikelet plants of the *B. hordeaceus* group and in *B. scoparius*, the anthers are usually small or very small, and seem never to be exserted during their maturity. Particularly in *B. lepidus* and *B. brachystachys*, it is usual for the dead anthers to be pushed out at the top of the florets by the swelling caryopsis: there is scarcely space for them within.

(vi) Caryopsis form

The relative lengths of caryopses have been mentioned already in b(iv), and their tendency to become centrally grooved in b(iii). Almost all species in this section produce grains which inroll to some degree at maturity: all the species here reviewed have thin caryopses in which any incurvature is clear. Extreme inrolling is found quite commonly in *B. pseudosecalinus*. Thickening of the caryopsis is seen in *B. arvensis* subsp. *segetalis*.

(vii) Panicle form

Less conservative than the features discussed above, characters of the panicle can vary confusingly during development and in different environmental constraints. 'Dense' versus 'loose' are therefore subjective descriptions which are difficult to use precisely. Few normally loose-panicled species do not occasionally manifest dense panicles in the juvenile state or when growing in poor soil. Similarly, dense-panicled taxa normally produce looser panicles when grown in shade, or on later-flowering tillers. Extreme cases create no difficulty: *B. arvensis* has large effuse, open panicles when well grown,

rather shorter, narrower but still open ones when immature or depauperate. Similarly, *B. scoparius* typically has a dense, ovoid panicle: if very well supplied with water and nutrient, it reacts either by simply growing larger, or by becoming verticillate, with two or more groups of densely crowded spikelets.

Panicles which are typically between these extremes give particular difficulty to the identifier when they present a *narrow* form, which may appear *superficially* dense. It is a good indication that the material is of a taxon normally producing open panicles when any one or two panicle branches or pedicels are longer than the spikelets they bear. In a few cases late changes in panicle form offers useful clues to identity. *B. pseudosecalinus* panicles sometimes become secund. In *B. brachystachys* the branches stiffen and often become patent.

KEY TO BROMUS TAXA WITH LEMMAS 4–7mm

1a. Awns absent; lemmas sub-rhombic; panicle open, stiff _____ **B. psammophilus**
1b. Awns present; lemmas and panicles various _____ 2

2a. Panicles open, effuse, rhomboid or pyramidal, at least half as broad as long; anthers usually about half the length of the lemma _____ 3
2b. Panicles denser, narrower; anthers less than half the length of the lemma _____ 6

3a. Panicle branches robust, stiff; mature grain exceeding the palea; mature lemmas commonly translucent, with broadly hyaline margins _____ **B. brachystachys**
3b. Panicle branches fine, flexible; mature grain shorter than the palea; mature lemmas more or less opaque, with narrow hyaline margins _____ 4

4a. Lemmas not more than 5.5mm, green _____ **B. pseudobrachystachys**
4b. Lemmas 6–9mm, frequently bicoloured _____ 5

5a. Grains thin, usually flat; lemmas 7–9mm; mature florets imbricate, soon falling
B. arvensis
5b. Grains thickened, feebly incurved; lemmas c. 6mm; mature florets divaricate to sub-patent, falling tardily _____ **B. arvensis** subsp. **segetalis**

6a. Lemmas 4–6.5mm _____ 7
6b. Lemmas 6.5 mm or more _____ 8

7a. Awns very delicate, almost hair-like; grain equalling or exceeding the palea; lemmas 5.5–6.5 mm, very sharply angled, with a broadly hyaline margin that makes the young spikelets appear green-white variegated _____ **B. lepidus**
7b. Awns fine but stiff; grain shorter than palea; lemmas 4–5.5mm, not as above
B. pseudobrachystachys

8a. Awns divaricate or spreading, sometimes twisted at the base _____ 9
8b. Awns, straight or flexuous _____ 11

9a. Lemmas c.2mm wide; grain narrowly elliptical, c.1mm wide; panicle always very dense _____ **B. scoparius**

9b. Lemmas 3–5 mm wide; grain oblanceolate, more than 1mm wide; panicle dense
    or loose _____ 10

10a. Awns stout, basally flattened, divaricate, patent or recurved; spikelets densely
    pilose _____ **B. hordeaceus** subsp. **ferronii**
10b. Awns feeble, ± terete at the base, weakly spreading; spikelets hairy or glabrous
    B. hordeaceus subsp. **thominii**

11a. Mature lemmas and glumes chartaceous, with parallel nerves becoming
    prominent when dry _____ 12
11b. Mature lemmas and glumes corneous, smooth or with irregular transverse folds
    when dry _____ 13

12a. Panicles dense; awns weak, shorter than the lemma **B. hordeaceus** subsp. **thominii**
12b. Panicles usually loose, occasionally dense; awns robust, stiff, as long as or
    longer than the lemma _____ **B. tigridis**

13a. Lemmas 5.5–6.5mm; awns 2–6 mm; palea equalling the lemma; grain usually
    obviously inrolled _____ **B. pseudosecalinus**
13b. Lemmas 6.5–8mm; awns 7–9mm; palea shorter than the lemma; grain flat or
    feebly incurved _____ 14

14a. Spikelets narrowly ovate, 10–15 x 3–5mm; rachilla internodes 1mm; lemma
    with a curved back, and an acute tip; grain shorter than palea _____ **B. racemosus**
14b. Spikelets lanceolate-attenuate, 12–18 x 5.5–6.5mm; rachilla internodes 1.5mm;
    lemma with a straight back which angles towards the obtuse tip; grain equalling
    the palea _____ **B. lusitanicus**

PROBABLE AFFINITIES OF SMALL-SPIKELET BROME-GRASSES

Table 2 groups the species here discussed into what appear to us to be natural groups,
i.e. groups of species which are more closely related to each other, evolutionarily, than
to other species or groups. Since the most recent general discussion of the affinities of
species in section *Bromus* (Scholz, 1970; Smith, 1972), new taxa have been detected,
and others have been much more clearly defined and diagnosed.

Table 2. Four affinity groups of small-spikelet brome-grasses
    Group 1: *B. psammophilus, B. pseudobrachystachys, B. tigridis.*
    Group 2a: *B. brachystachys, B. lepidus*
    Group 2b: *B. arvensis*
    Group 2c: *B. hordeaceus*
    Group 3: *B. scoparius*
    Group 4: *B. lusitanicus, B. pseudosecalinus, B. racemosus*

Group 1
These taxa are from the SW Asian–NW African area. They have chartaceous glumes
and lemmas and, except for *B. psammophilus*, well-developed, straight, erect awns –
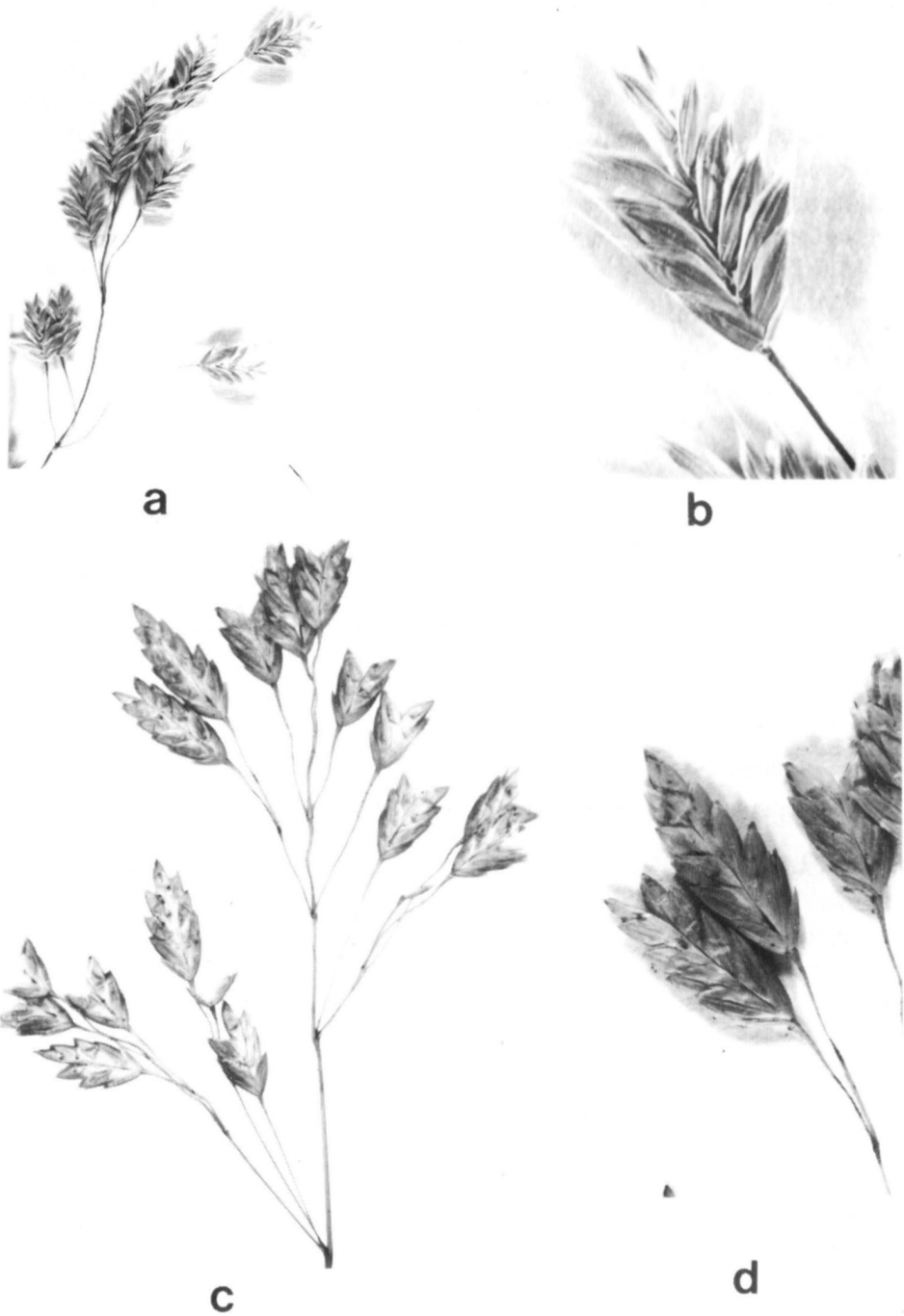
FIG. 4: *Bromus brachystachys*: a, panicle; b, spikelet detail to show the extreme congestion of florets which sometimes characterize late flowering tillers. *B. psammophilus*: c, panicle; d, spikelet details.

characters which we regard as important because they are conservative. The awns arise quite near the lemma apex, which is shortly bidentate or entire. The lemma-drying character (see Table 1), which they also share, is probably a consequence of the papery nature of the lemmas. All have opaque lemmas with bluntly but clearly angled, narrowly hyaline margins, and reasonably large anthers. The somewhat inrolled grain is shorter than the palea, which in turn is shorter than the lemma. The florets are quickly shed when they are mature and variable in this group: they tend to be open and loose (but very stiff in *B. psammophilus*), but there are more congested forms in *B. pseudobrachys-tachys* and *B. tigridis*, that do not seem to be caused by poor growing conditions. Chromosome numbers would undoubtedly add to our understanding of these species.

Group 2

These taxa are mainly Eurasian and Mediterranean, though *B. brachystachys* is known only from Saxony and the native distribution of *B. lepidus* is uncertain (Smith, 1986). All have chartaceous glumes and lemmas (*B. arvensis* sometimes rather tougher than the others), and straight, mostly erect awns. Lemma form and opacity, quantitative features of the florets and panicle architecture are all variable in this group.

Group 2a

Though differing sharply in inflorescence form, even taking atypical developmental forms (Fig. 4a,b) into account, *B. brachystachys* and *B. lepidus* share some unique floret features. These include the sharp angle of the lemma, the great area of its hyaline tip and margin, the translucent mature lemma (glossy in young, glabrous *B. lepidus*), and the relatively large, flattish grains, which commonly exceed the palea. In *B. lepidus* the grains can exceed even the lemma in rare cases. The grain seems 'too large' for the floret. Additionally, these species have very fine, short and fragile awns arising clearly below the lemma sinus. The green vein area extending into the apical teeth of the *B. lepidus* specimen shown in Fig. 2c is an unusual character in *Bromus* – sometimes seen in *B. brachystachys* (Scholz, 1972). Both species have relatively large anthers, though *B. lepidus* often has tiny ones (probably in cleistogamous genotypes).

The karyotype of *B. lepidus* has been studied many times (see Smith, 1968): it seems always to be tetraploid (2n=28). The chromosome number of *B. brachystachys* is unknown. Since it has not even been recorded since 1936 and the most recent confirmed specimens date from the early years of the century, its ploidy is unlikely to be directly detectable. On the expectation that very closely related taxa have correlated ploidy and stomatal sizes (Wagnon, 1952; Borrino & Powell, 1988), one might expect larger guard cells in tetraploids than in diploids. We find that guard cells of *B. brachystachys* and of *B. lepidus* show no substantial or very consistent size differences. It is not possible to interpret this finding with any confidence.

Group 2b

Bromus arvensis (2n=14) is a clear-cut taxon with no obvious very closely similar relative. Though it has a characteristically large, open panicle, like *B. brachystachys* though normally much larger, the branches are fine and flexible. The anthers are relatively large, another similarity with *B. brachystachys*. *B. arvensis* lacks the 'over-
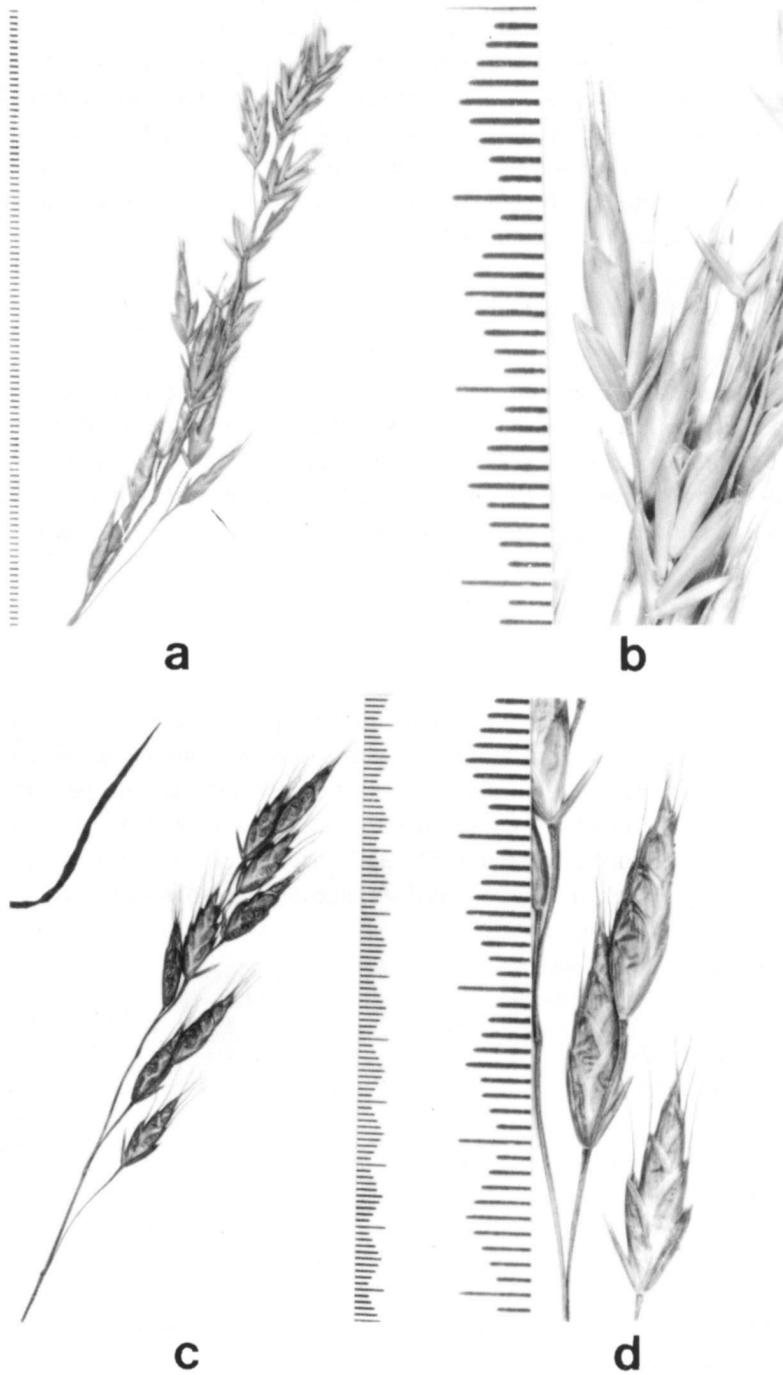
FIG. 5: *Bromus lusitanicus*: a, panicle; b, spikelet detail. *B. racemosus*: c, panicle; d, spikelet detail. (Scale in mm).

sized' caryopsis feature of *B. brachystachys*, though its palea normally equals the lemma in length. *B. arvensis* glumes and lemmas have a papery texture, akin but not identical to those of *B. brachystachys* and *B. lepidus*, but are opaque, often green or brown-purple variegated. Awns of *B. arvensis* are normally quite well developed, except for some genotypes of the cereal mimic subspecies *segetalis*, whereas *B. lepidus* and *B. brachystachys* have rather feeble awns, and are unlike subsp. *segetalis* in other respects.

It seems reasonable therefore to group *B. arvensis* quite close to *B. brachystachys*, though at one remove.

Group 2c

Bromus hordeaceus (2n=28) has both large and small spikelet versions (Smith, 1968). Its small spikelet manifestations, particularly those in subsp. *thominii* or attributed to x *pseudothominii*, show strong resemblances to *B. lepidus* – in spikelet and form, texture and partly anthropogenic habitats. Glume and lemma veins are more prominent on drying than in Group 2b species. Anthers are usually short or very short and panicles normally contracted or very dense, thus further recalling *B. lepidus* morphology. Nevertheless the relative lengths of lemma, palea and caryopsis are unlike those of *lepidus/brachystachys-arvensis* (except in *hordeaceus* x *lepidus* hybrids – Smith, 1968). The panicle contraction and relatively wider lemmas, with more gaping margins, further indicate difference from *B. arvensis* and *B. brachystachys*.

Group 3

B. scoparius (2n=14) has dense panicles, tiny anthers, opaque, papery glumes and lemmas, with veins prominent on drying. In these features it approaches *B. hordeaceus*. However, its panicles are so dense that the panicle branches and pedicels are not normally visible. Furthermore, the lemmas and caryopses are very narrow and the latter are thin and are outcurved when dry. The awn arises distinctly below the lemma apex and is spreading, patent or even recurved – features seen also in some subspecies of *B. hordeaceus*.

Group 4

These three species are very closely similar, and almost certainly closely related evolutionarily. They share the features of corneous glume and lemma texture, the irregular foldings of the lemmas, narrow, congested panicles yet with a number of fine, relatively long panicle branches or pedicels. All have fine, straight, erect awns. Caryopses are equal to or shorter than the palea which is only a little shorter than the lemma. Tightly imbricate when young, lemmas of the mature floret seem in death almost to tighten their grip on the lemma above, the margins sometimes spreading out a little in *B. racemosus* (2n=28) or, in *B. pseudosecalinus* (2n=14) inrolling tightly so that the rachilla is exposed.

Of all these groups, Group 4 species are most likely to be overlooked in mixed gatherings, confused with each other or with collections of *B. hordeaceus* and *B. lepidus*. They are known largely from anthropogenic habitats in Europe, but this may not be a reflection of their true geographical or ecological distribution.
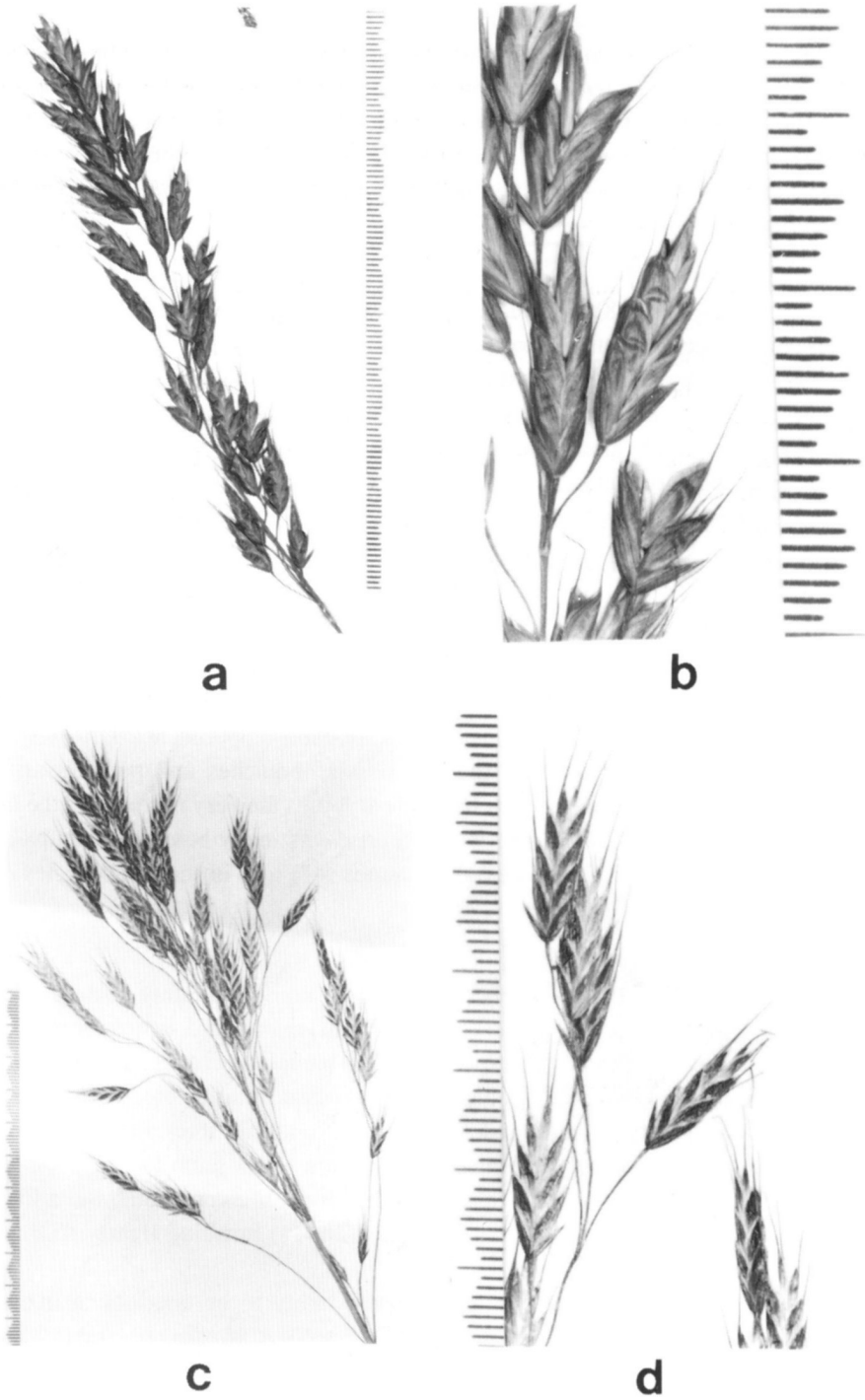
FIG. 6: *Bromus pseudosecalinus*: a, panicle; b, spikelet details. *B. arvensis*: c, panicle; d, spikelet details. (Scale in mm).

FORM, FUNCTION AND ADAPTIVE RADIATION

Until genome relationships have been established, and/or a rational basis is established for determining the primitive and advanced states of significant characters, there is little objective evidence for or against any evolutionary scheme seeking to explain the similarities commented on in the previous section. Also, our knowledge of the distribution, karyology and genetics needs to be greatly extended. Given the identification/recognition problems, we are not likely even to have discovered all the taxa that exist in these groups. Nevertheless it may be helpful to contribute some suggestions at this stage of our understanding, that may perhaps stimulate further work in all these areas.

It is not implied here that species in the four groups are related just because they have small spikelets: rather it is believed that the reduction in size may show convergent evolution in a number of separate lines (see Fig. 8). The functional significance or advantage of the small-spikelet character itself would seem to be the most rapid production of the maximum number of propagules per unit of photosynthate. The smallness of the propagules promotes easier dispersal, though as the size diminishes, the lower provision of stored reserves in the caryopsis is likely to reduce viability and/or success of ecesis. It is notable that in the smallest of these small-spikelet bromes (*B. brachystachys, B. pseudobrachystachys, B. lepidus, B. scoparius*), the caryopses are proportionally larger than lemmas and paleas compared with others in the group. Of these four species, lemmas and paleas are flimsiest (most vestigialized) in *B. brachystachys* and *B. lepidus*. Speed and profligacy of seed production are features of annual, opportunist plants. They may often mark advancement, comprising recent adaptations to the widening opportunities for such plants in post-glacial Eurasia. If so, these small-spikelet taxa, at least those found mostly in anthropogenic habitats, would seem generally to be the most highly evolved species in section *Bromus*. The grass crop mimics *B. arvensis* subsp. *segetalis* and *B. pseudosecalinus*, would seem also to be very recent (Smith, 1969; Scholz, 1970).

It is not clear what, if any, functional significance attaches to the striking lemma texture differences shown by these taxa.

Awn vestigialization in *B. brachystachys* and *B. lepidus* is correlated with thin, translucent lemmas that would seem to be an advanced feature, given that grasses believed generally to be primitive have opaque lemmas, more leaf-like in texture. The weakness of awns here, as occasionally seen in *B. pseudosecalinus*, may indicate that human activity is exploited in dispersal. The loss of awns in *B. psammophilus* is hard to interpret in a functional or evolutionary sense, because the taxon is as yet so little known. However, its inflated lemmas may suggest wind dispersal rather than ectozoic, i.e. awn-related dispersal, a feature seen also in *B. briziformis* Fisch. & Meyer.

Curved awns should be regarded as more advanced than straight ones: most perennial brome-grasses have straight awns, and the curvature on drying (sometimes with a basal twist) is caused by a flattening of the awn base which is not characteristic of the lemma vein of which the awn is the emergent, distal end. The outspreading exposes extra photosynthetic surface to light, perhaps useful when the leaves wither early. It may also discourage grazing, though the awns are soft when young. Certainly the outcurved awns
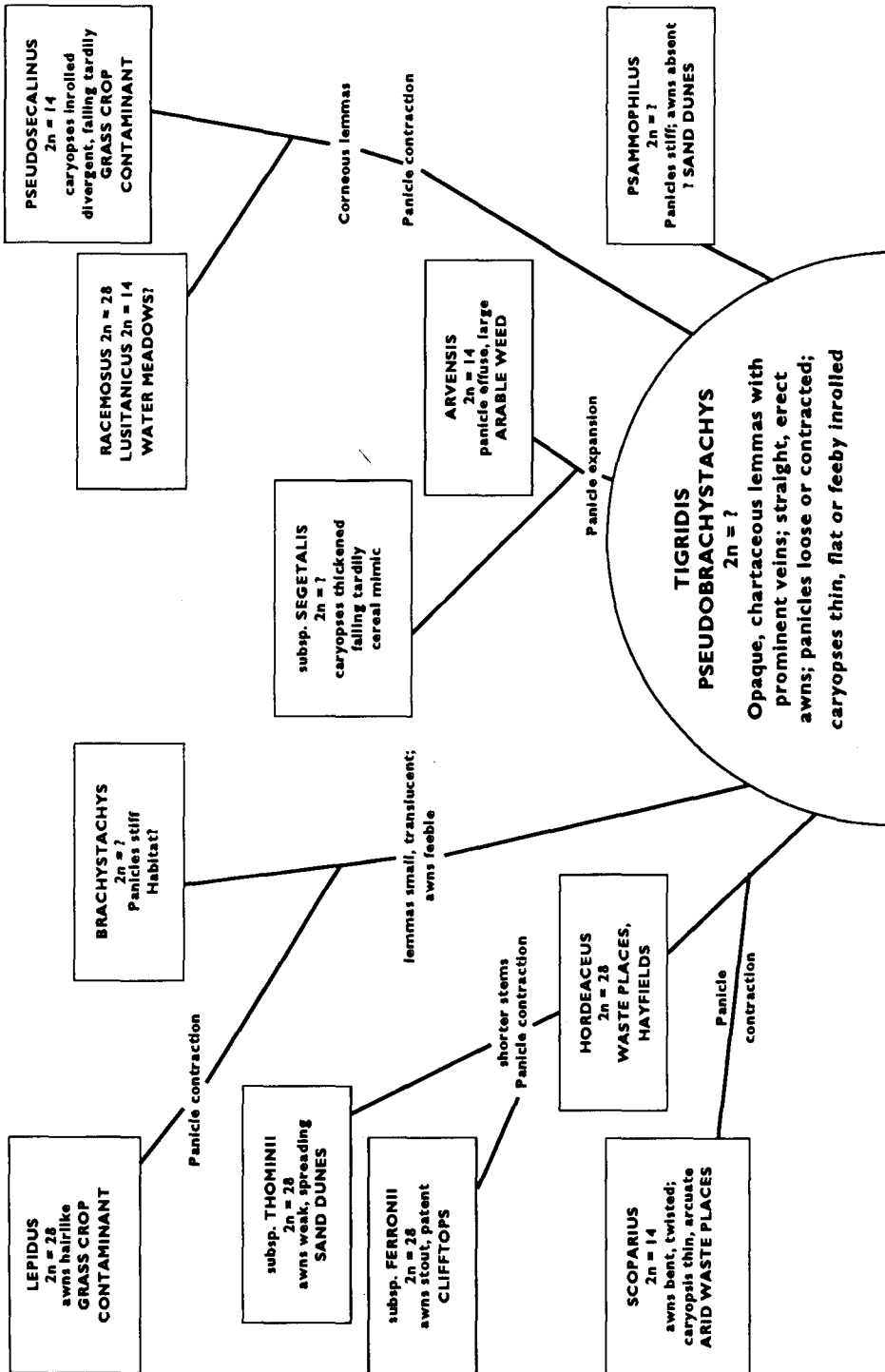
FIG. 7: Diagram summarizing probable lines of adaptive radiation in small-spikelet brome-grasses. Species or species groups furthest from the presumed primitive stock (represented in this sample by *B. tigridis* and *B. pseudobrachystachys*) are those deemed most advanced.
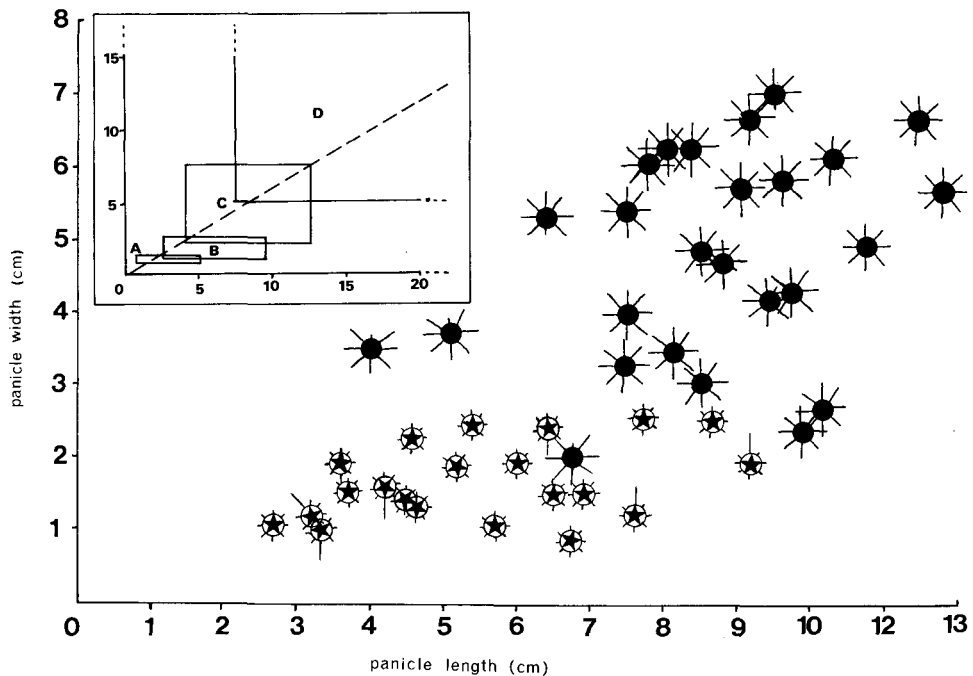
FIG. 8: Scatter diagram of *Bromus lepidus* and *B. brachystachys* specimens. Inset: Extrapolated correlates along the regression line of x (panicle width) on y (panicle length) show the possible characteristics of hypothetical diploid taxa A and D putatively parental to allotetraploid B (*B. lepidus*) and taxon C (*B. brachystachys* – ploidy unknown). Taxon A has the characteristics of some forms of *B. pseudobrachystachys* and *B. hordeaceus* and Taxon D has characteristics of *B. arvensis*.

promote mechanical dislodgement of mature caryopses by chance external friction. Outcurved caryopses, often seen in *B. scoparius*, have the effect of making the awns spread out further, thus promoting external contact. A similar form is shown by *B. fasciculatus* C. Presl of sect. *Genea* (Sales, 1991). These species are not closely related, but grow in similar, dry open habitats. Both are commonly short, stiff grasses, vibrating rapidly in the wind. The mature florets appear to be aided in liberation by mechanical abrasion of one panicle by another. In both cases the dissected caryopses are distinctly arcuate.

Anther-length diversity is hard to interpret functionally apart from the likely association of very short anthers with cleistogamy. On this basis, the relatively long-anther taxa (*B. brachystachys, B. arvensis, B. pseudosecalinus, B. psammophilus, B. racemosus, B. tigridis*) may be chasmogamous and hence to some degree more allogamous than others.

Possible functional significance of panicle forms was recently discussed by Smith (1991).

In Eurasia, especially in SW Asia and the Mediterranean area, permanently semi-desert or ephemeral, arid, open habitats like anthropogenic grazed grassland have extended particularly over the last 5,000 years (Scholz, 1975). They developed from more or less

open woodland with consistent water supply, modest grazing and low wind speed. The formation of such arid habitats with a short growing season, because of water deficits and high soil temperatures, offered an opportunity for niche diversification, and hence adaptive radiation, to several existing species of brome-grasses. Grasses of open woodland, typically with effuse, spreading or drooping panicles, probably produced relatively late in season, seem to have evolved into grasses with smaller, less-branched panicles that can reproduce more quickly in the uncertain, treacherous, niches of the arid habitats. Congested panicles offer less surface area to drying conditions while retaining high reproductive capacity. Evolution of dense-panicle forms, with small spikelets probably occurred in parallel in several species of brome-grasses.

Figure 7 represents a possible 'adaptive radiation' interpretation of the similarities of the small-spikelet brome-grasses here reviewed. It rests on form/function/habitat advancement ideas offered above. The suggestions in Fig. 7 can for the most part be tested by experimental taxonomic methods and cytogenetic study, which must await reasonable living materials, and by assiduous field observation and collection.

Given the extinction of *B. brachystachys*, it will take rather more effort to verify the suggestion that *B. brachystachys* is a diploid parent of *B. lepidus*. This verification may not be wholly impossible in the near future (Fig. 8). Figure 8 shows, on a conventional scatter diagram, the relativities of *B. brachystachys* and *B. lepidus*. Also shown is an extrapolation of the main component of variation which may indicate the position, hence perhaps some of the features, of the putative second parent (A) of *B. lepidus* (B) should *B. brachystachys* (C) be one of its diploid progenitors. Some forms of *B. pseudobrachystachys* would seem to be candidates. Similarly, another extrapolation (D) shows features of the second parent of *B. brachystachys*, supposing *B. brachystachys* to have a species like A or B (*B. lepidus*) as a progenitor. In most respects, potential ancestor D would resemble *B. arvensis* (cf. Scholz, 1972).

These possibilities of evolutionary links between these taxa may soon be experimentally testable. Nevertheless, any such tests will rest ultimately on securing the better collection of living small-spikelet brome-grasses which we hope this paper will stimulate.

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D