THE *BROMUS MOLLIS* AGGREGATE IN BRITAIN

By PHILIP SMITH

Department of Botany, University of Edinburgh

ABSTRACT

Experimental studies on taxa within the *Bromus mollis* aggregate (sensu Tutin) have revealed that plants referable to *B. thominii* sensu Tutin are hybrid derivatives of crosses between *B. mollis* L. and *B. lepidus* Holmberg. The name *B.* × *pseudothominii* Philip Smith (hybr. nov.) is given to this material. It is demonstrated that the selection pressures favouring the persistence of these hybrid forms are associated with their success in contaminating sown pasture grass seed. The name *B. thominii* Hardouin should be applied to a dune species which is shown to be genetically and serologically distinct from inland forms of *B. thominii* sensu Tutin. It is proposed to include the dune material, together with *B. mollis* sensu stricto and *B. ferronii* Mabille, in a single species for which the correct name is *B. hordeaceus* L. Subspecific rank is given to these component taxa of *B. hordeaceus*, which therefore become: *B. hordeaceus* subsp. *hordeaceus* (syn. *B. mollis* L.); *B. hordeaceus* subsp. *thominii* (Hardouin) Hylander; and *B. hordeaceus* subsp. *ferronii* (Mabille) Philip Smith.

INTRODUCTION

Tutin (1962) includes *Bromus mollis* L., *B. thominii* Hardouin and *B. ferronii* Mabille in his conception of the *B. mollis* aggregate. These plants are closely similar morphologically, and seem to have strong affinities with at least three other taxa, namely *B. molliformis* Lloyd, *B. interruptus* (Hackel) Druce and *B. lepidus* Holmberg. Variation in the field in the *B. mollis* agg. is frequently puzzling since all variants of *B. mollis* and '*B. thominii*' often grow together in the same sward, and their taxonomic separation is sometimes apparently arbitrary. Though several features are used to distinguish them (Tutin 1962), in practice the variation in lemma and spikelet sizes is the only character which can be used to discriminate between the two taxa. Both *B. mollis* and '*B. thominii*' are ruderal plants of inland areas, sometimes found in maritime habitats, but *B. ferronii* is a cliff-top plant of very restricted distribution. It is known only from a few localities in the south and west of Britain, and western France. *B. mollis* and '*B. thominii*' appear to be widely distributed in Europe and western Asia and are introduced in most other parts of the world, often becoming well established.

An enquiry into the treatment of these taxa by different authors reveals a wide variety of opinions as to their taxonomic rank and nomenclature. Difficulties also arise because the application of two Linnaean names, *B. mollis* and *B. hordeaceus*, is uncertain. Discussion of Linnaeus' interpretation in the literature (e.g. Munro 1861; Hackel 1884; Holmberg 1924) has further confused the position.

My investigations into these problems, as part of a large-scale experimental treatment of the genus *Bromus*, were begun in 1961, and the present account relates to my first results bearing on the *B. mollis* aggregate. Experimental work with *B. interruptus* is not yet complete, and the relationship of this curious species to the rest of the British bromes will be discussed in a subsequent paper. The results of my work require some nomenclatural changes which are presented first so that the correct names can be used through the rest of the paper.

FORMAL TAXONOMY OF THE MATERIAL

Nomenclature and synonymy

Results of examining the bromes of the Linnaean herbarium in London (**LINN**) (Smith 1965) indicate that while the modern conception of the species *B. mollis* L. (e.g. in Hubbard 1954, and Tutin 1962) is correct, it is not certain what Linnaeus meant by his name *B. hordeaceus* (*Species Plantarum* ed. 1, 1753). Munro (1861), Hackel (1884) and Holmberg

(1924) have each provided partial explanations of Linnaeus' meaning, which are unfortunately based on mutual misunderstandings and are incorrect. By comparing the Linnaean treatments of *Bromus* in the *Flora Suecica* ed. 1 (1745), *Species Plantarum* eds. 1 and 2 (1753 and 1762) and *Flora Suecica* ed. 2 (1755), one can trace a sequence of change in Linnaeus' ideas about these plants (Smith 1965). Comparison with the Linnaean herbarium provides further information.

Linnaeus' criteria for distinguishing species of *Bromus* are restricted to laxness of panicle, gross spikelet shape, spikelet indumentum and whether the awns are straight or reflexed. Using them he had no difficulty in distinguishing a lax-panicled plant which he named *B. secalinus* from a plant with an erect, dense panicle which he named *B. hordeaceus* L. (*Flora Suecica* ed. 1, 1745). This treatment is repeated in the first edition of the *Species Plantarum* (1753), which is the earliest place of valid publication. In *Flora Suecica* ed. 2 (1755) Linnaeus transferred *B. hordeaceus* to the status of variety β of *B. secalinus*, retaining the epithet '*hordeaceus*'. (A printer's error makes it appear as β; since *B. secalinus* already had one variety, it should correctly have been var. γ.) Linnaeus explains this change: '*Bromus hordeaceus in hortis satus transit in Bromum secalinum, cujus varietas est, ex solo arido et duro pygmaeus.*' Clearly cultivation of a depauperate accession of *B. hordeaceus* L. in the richer soil of a garden had produced a specimen approaching the vigour of *B. secalinus*.

A further evolution of Linnaeus' treatment of these bromes is marked in *Species Plantarum* ed. 2 (1762) which is the last evidence we have of Linnaeus' intentions. '*Var.* β *hordeaceus*' still appears under *Bromus secalinus*, and there is a new entry—*B. mollis.* From the Linnaean phrase name: '*Bromus panicula erectiuscula, spicis ovatis aristis rectis, foliis mollissime villosis*' it is highly likely that the plant referred to is a soft brome, at present called *B. mollis* L. His description is expanded by a footnote: '*Similis B. secalino sed albido-pubescens. Genicula crassiora, cylindrica, subtus inprimis valde hirsuta. Folia utrinque mollis sima vaginis striatis. Panicula brevius pedicellata.*'

Of the six sheets of *Bromus* in the Linnaean herbarium referable to the *B. mollis* agg. sensu Tutin (Smith 1965), sheet 93.5 bears two specimens labelled *B. mollis* by Linnaeus (*fide* Spencer Savage in the Linnean Society's *Catalogue of the Linnaean Herbarium*). Sheet 93.7 bears a depauperate tussock of a soft brome which though totally unlike *B. secalinus* has been so labelled by Linnaeus. This plant has been named '*B. nanus*' by Weigel.

Together with evidence from his published accounts these specimens indicate that both *B. mollis* L. and *B. hordeaceus* L. applied to a plant within the *B. mollis* agg. sensu Tutin. Linnaeus transferred *B. hordeaceus* to varietal rank beneath *B. secalinus* after cultivation of a specimen resembling that on sheet 93.7. It is possible that this plant was his original collection. This explanation is supported by all the alterations of synonymy throughout the four Linnaean works cited (Smith 1965).

If *B. hordeaceus* L. and *B. mollis* L. are conspecific, the former is the earlier and thus the correct name of the species.

The genotypically depauperate material from dunes described later in this paper appears to be correctly named *B. thominii* Hardouin, judging from material collected and named by Hardouin in the herbaria at Kew (**K**) and Paris (**P**). Some of this material is illustrated in Plate 14*a*. *B. thominii* Hardouin replaced the earlier hononym *B. arenarius* Thomine-Desmazures (1824) non Labillardière (1804). No type of either *B. thominii* or *B. arenarius* Thomine-Desmazures was cited in the original descriptions. Thomine's herbarium material seems to have been lost. His figure (Thomine-Desmazures 1824) plainly indicates material similar to Hardouin's *B. thominii*. Wendelbo (1956) indicated that he thought *B. thominii* sensu Tutin (Tutin 1962) differed from French material collected and named by Hardouin.

The depauperacy of Linnaeus' *B. hordeaceus* has been used by many taxonomists as an indication that the name should apply to small plants like *B. thominii* Hardouin, and not to *B. mollis* L. If the depauperacy was only phenotypic and resulted from growth in hard, dry soils as Linnaeus reported (*Flora Suecica* ed. 2, 1755), then genetically dwarfed material should not be included in *B. hordeaceus* L., if it is regarded as specifically distinct from more robust specimens (i.e. *B. mollis* L.). The evidence in this paper that plants from sand dunes are genetically depauperate is reinforced by the work of Holmberg (1924), Nilsson (1931, 1937) and Wilson (1956). The two earlier workers regarded this material as specifically distinct and mistakenly named it *B. hordeaceus* L. The evidence above requires that, if such distinct status is accorded to these plants, then the name must be *B. thominii* Hardouin.

Weigel published the name *B. nanus* in 1772 (*Observationes Botanicae*) and refers Linnaeus' sheet 93.7 (**LINN**) to it. Weigel's conception of this species probably included depauperate material of a number of related species. Sheet 93.7 material probably grew in an exposed place, in black, well-drained soil. It has rather short lemmas and short, weakly divaricate awns, and would be referred to *B. hordeaceus* subsp. *thominii* in the key given below.

As explained above, if all these bromes are included in one species, then the name *B. hordeaceus* has priority over *B. mollis*. In view of the differences between the taxa, discussed in the rest of the paper, I believe that *B. mollis* L. (as in Hubbard 1954, and Tutin 1962), *B. thominii* Hardouin non sensu Tutin, and *B. ferronii* Mabille are best regarded as subspecies of a single species. Hylander (1945) has also concluded that the dwarfed form from dunes should be regarded as a subspecies in this group, basing his conclusion on Nilsson's (1931, 1937) genetic work, which is discussed below. He has already made the necessary combination: *B. hordeaceus* L. subsp. *thominii* (Hardouin) Hylander.

My conclusions from the evidence presented below are that *B. lepidus* is a distinct species, and that *B. thominii* sensu Tutin is a collection of hybrid derivatives (nothomorphs) which are, however, so common that a suitable binomial is needed for reference. The name *B.* × *pseudothominii* Philip Smith is therefore proposed. Clearly it is very difficult to describe the limits of what is by definition a segregating hybrid complex. Some variants of *B.* × *pseudothominii* are very close to pure *B. lepidus*, others resemble pure *B. hordeaceus* subsp. *hordeaceus*. The evidence of the artificial hybridizations reported in this paper, and of field collections, indicate that the commonest variants resemble *B. hordeaceus* more closely than they do *B. lepidus*. The key is written with this fact in mind. In most bromes there is variation in the development of spikelet indumentum from pubescence to glabrosity and this is acknowledged by the recognition of taxonomic forms and varieties based on the indumentum variation alone. It is an equivocal point as to whether the hairy spikelet form of the typically glabrous *B. lepidus* is a genuine expression of intraspecific variation, or whether it may result from a flow of genes for hairiness from *B. hordeaceus*. The same problem exists for glabrous spikelet varieties of *B. hordeaceus*. It is not possible to know whether the types of these varieties are pure intraspecific variants or the products of introgressive hybridization and therefore synonyms of *B.*×*pseudothominii*. It is likely that such varieties contain genetic material from both sources and therefore it seems wiser to regard them as only *pro parte* synonyms of *B.* × *pseudothominii*.

The correct nomenclature of the material considered in this paper, together with a selected synonymy, is listed below.

B. HORDEACEUS L., *Sp. Pl.*, 77 (1753).

subsp. HORDEACEUS
B. mollis L., *Sp. Pl.* ed. 2, 112 (1762).

subsp. THOMINII (Hardouin) Hylander, *Upps. Univ. Årsskr*, **1**, (7) 84 (1945).
?*B. nanus* Weigel, *Obs. Botan.* 8 (1772).
B. arenarius Thomine-Desmazures, *Mém. Soc. Linn. Calvados* **1824**, 40 (1824) non Labill., *Nov. Holl. Pfl.* **1**, 23 (1804).
B. thominii Hardouin, *Congrès Sc. Fr.* **1**, 56 (1833) non sensu Tutin in Clapham et al., *Flora of the British Isles*, ed. 2, 1152 (1962).

subsp. **ferronii** (Mabille) Philip Smith, **comb nov.**
B. ferronii Mabille, *Act. Soc. Linn. Bord.*, **25**, 612 (1864).

B. LEPIDUS Holmberg, *Bot. Notiser*, **1924**, 326 (1924).
B. gracilis Krösche, *Feddes Rep.* **19**, 329 (1924) non Leysser, *Fl. Hal.* 16 (1761).
B. britannicus I. A. Williams, *J. Bot. Lond.*, **67**, 65 (1929).

Bromus × pseudothominii Philip Smith, **hybr. nov.**
B. mollis L. var. *leiostachys* Hartman, *Handb. Skand. Fl.* ed. 2, 33 (1832) pro parte.
B. gracilis Krösche, var. *micromollis* Krösche, *Feddes Rep.* **19**, 329 (1924) pro parte.
B. lepidus Holmberg, f. *lasiolepis* Holmberg, *Bot. Notiser* **1924**, 326 (1924) pro parte.
B. thominii sensu Tutin in Clapham *et al.*, *Flora of the British Isles* ed. 2, 1152 (1962) non Hardouin, *Congrès Sc. Fr.*, **1**, 56 (1833).

Annuum vel bienne. Culmi graciles, erecti, 20–70 cm alti, vaginis foliisque pubescentibus. Panicula laxa vel contracta, erecta, 1–10 cm longa. Spiculae lanceolatae, glabrae vel pubescentes, 10–15 mm longae, breviter pedicellatae. Glumae inaequales, prominenter nervosae, inferior lanceolata, superior ovato-lanceolata. Lemma chartaceum, ovato-lanceolatum, 6·5–8 mm longum, palea longius, prominenter nervosum, marginibus angustis hyalinis plerumque obtuse angulosum. Arista recta, 3–7 mm longa. Palea bicarinata, nervis ciliatis. Antherae 0·2–1·5 mm longae. Caryopsis palea aequilonga.

A *B. hordeaceo* subsp. *hordeaceo* lemmate breviore saepe marginibus acutius angulosis differt.

A *B. hordeaceo* subsp. *thominii* culmo altiore erecto panicula majore laxiore, plurispiculataque differt.

A *B. lepido* lemmate longiore marginibus obtusius angulosis, parte hyalina angustiore, palea caryopsim aequante differt.

Holotypus: Roadside near Queen Elizabeth Hospital, Birmingham, England. Coll. 1962, *P. Smith* 458. In Herbarium of the Royal Botanic Garden, Edinburgh (E).

Key to taxa

1. Awns stout, recurved in fruit. Lemmas 6·5–8·5 mm long, bluntly angled. Spikelets densely hairy, in a dense panicle. (Coastal cliffs).
2. *B. hordeaceus* subsp. *ferronii*

Awns straight, or if weakly divaricate then the culms prostrate or procumbent. Lemmas 4·5–11 mm long, sharply or bluntly angled. Spikelets hairy or glabrous 2

2. Lemmas 4·5–6·5 mm long, margins sharply angled with a broad hyaline margin. Awns weak. Grain exceeding palea.
4. *B. lepidus*

Lemmas 6·5–11 mm long. 3

3. Culms 1–8 (–12) cm, prostrate or procumbent to ascending. Lemmas 6·5–7·5 mm long. Awns sometimes divaricate in fruit. Grain shorter than palea. (Sand dunes).
3. *B. hordeaceus* subsp. *thominii*

Culms 3–80 cm, normally erect. Lemmas 6·5–11 mm long. Awns straight, erect. Grain shorter than or equalling the palea. 4

4. Lemmas 6·5–8 mm long, usually glabrous, with broad or narrow, normally bluntly angled, hyaline margins. Grain usually equalling the palea.
5. *B.* × *pseudothominii*

Lemmas 8–11 mm long, usually hairy, with narrow, bluntly angled hyaline margins Grain shorter than the palea.
1. *B. hordeaceus* subsp. *hordeaceus*

Descriptions

1. B. HORDEACEUS L.
subsp. HORDEACEUS

Annual or biennial, 3–80 cm. Culms erect or rarely ascending, usually stout, but slender in depauperate material. Panicles 5–10 cm, erect, lax or rather dense, or reduced to a single spikelet. Spikelets 12–25 × 4–6 mm, usually hairy, lanceolate. Glumes unequal, lower lanceolate, upper ovate. Lemmas 8–11 mm, ovate, bluntly angled, with a narrow hyaline margin. Awn stout, straight, erect, 4–11 mm long. Palea shorter than lemma. Anthers 0·2–2·0 mm. Grain shorter than palea. ($2n=28$).

Europe, W. Asia, N. Africa. Introduced and naturalized in many parts of the world.

2. B. HORDEACEUS L.
subsp. **ferronii** (Mabille) Philip Smith

Annual or biennial, 2–15 (-20) cm. Culms erect or ascending, usually stout. Panicles 2–5 cm, erect, dense, often simple, sometimes reduced to a single spikelet. Spikelets 8–18 × 3–6 mm, densely hairy, ovate-oblong. Glumes unequal, lower lanceolate, upper broadly ovate. Lemmas 6·5–8·5 mm, rather broad, bluntly angled, with a narrow hyaline margin. Awn stout, flattened at base, recurved in fruit, 2–5·5 mm long. Palea shorter than lemma. Anthers 0·2–1·5 mm. Grain shorter than palea. ($2n=28$).

W. Europe. Cliff-tops.

3. B. HORDEACEUS L.
subsp. THOMINII (Hardouin) Hylander.

Annual, 1–8 (–12) cm. Culms prostrate, procumbent or ascending. Panicles 1–3 cm, erect, dense, often simple, or reduced to a single spikelet. Spikelets 8–12 × 2–3 mm, hairy or glabrous, lanceolate. Glumes unequal, lower lanceolate, upper ovate. Lemmas 6·5–7·5 mm, ovate, bluntly angled, with a narrow hyaline margin. Awn weakly divaricate in fruit, 3–7 mm long. Palea shorter than lemma. Anthers ca. 1·0 mm. Grain shorter than palea. ($2n=28$).

W. Europe, probably elsewhere. On coastal dunes and similar habitats inland.

4. B. LEPIDUS Holmberg.

Annual or biennial, 4–70 cm. Culms erect, often rather slender. Panicles 2–10 cm, erect, rather narrow, lax or dense, or reduced to a single spikelet. Spikelets 5–15 × 2–4 mm, usually glabrous and glossy, lanceolate. Florets tightly imbricate at first and giving a green and white striped appearance to the spikelet, later slightly divaricate. Glumes unequal, ovate with broad hyaline margins. Lemmas (4·5–) 5·5–6·5 mm, ovate or broadly ovate, sharply angled, with a broad hyaline margin. Awn straight, erect, weak, setaceous, 2–5·5 mm long. Palea shorter than lemma. Anthers 0·5–2 mm. Grain exceeding palea, rarely exceeding lemma. ($2n=28$).

Introduced in Britain in ruderal habitats, perhaps also introduced in W. Europe. Native distribution unknown.

5. **B.** × **pseudothominii** Philip Smith (*Bromus hordeaceus* L. × *Bromus lepidus* Holmberg)

Annual or biennial, 20–70 cm. Culms erect. Panicles 1–10 cm, erect, lax or dense, sometimes reduced to a single spikelet. Spikelets 10–15 × 3–4 mm, hairy or glabrous, lanceolate. Glumes unequal, lower lanceolate, upper ovate-lanceolate. Lemmas 6·5–8 mm, usually bluntly angled, with a narrow hyaline margin. Awn straight, erect, 3–7 mm long. Anthers 0·2–1·5 mm. Grain usually equalling the palea. ($2n=28$).

Europe, probably elsewhere.

MATERIALS AND METHODS

(*i*) *Seed sources*

The accessions of *Bromus* species used in this work originate from a wide geographical area. British material used in serological and genetic experiments is listed in an Appendix. Morphological studies were made on plants from many parts of the world, but especially from Britain. The Flora of Warwickshire *Bromus* collection was placed at my disposal, and I am indebted to Messrs. Anton Nielsens, of Vejle, Denmark, for samples of Danish-produced forage grass seeds. All accessions used in experiments are being maintained in a living condition, together with voucher specimens, in the author's *Bromus* collection at the Department of Botany, University of Edinburgh.

(*ii*) *Morphological studies*

The herbaria of the Department of Botany, University of Birmingham (**BIRM**), of the Birmingham Natural History Society (Midland Institute, Birmingham), and of the Royal Botanic Gardens, Kew (**K**), have been extensively consulted to determine the limits of natural variation. The Birmingham collections included the recent Flora of Warwickshire material, so that an up-to-date idea of field variation was obtained. Specimens have been received on loan from the herbaria of Oregon State University, Corvallis (**OSC**), the Naturhistorisches Museum, Vienna (**W**), and the Muséum National d'Histoire Naturelle, Paris (**P**). I am indebted to the Curators of these institutions for their co-operation.

Data from herbarium material was used to construct scatter diagrams to demonstrate the extent of variation in some selected morphological features. Owing to the paucity of collections of *B. ferronii*, there has been a deficiency in the amount of *B. ferronii* material available for scoring.

(*iii*) *Karyological and Genetic Studies*

The chromosome numbers of cultivated accessions were determined. Attempts at hybridization were made using a variety of techniques. Crossing technique proved to be an obstacle to progress and most success was achieved using the laborious method of hand pollination described by Beddows & Davies (1938). Since the plants are all self-compatible, as was evident from good seed-setting in enclosed panicles, emasculation was essential. Maternal panicles were enclosed in pergamene bags.

(*iv*) *Ecological Studies*

Enquiries were restricted to observations of the various habitats in which the taxa were commonly found, and how they were associated with one another. Further information was supplied by analysis of the ecological records of the Flora of Warwickshire survey.

(*v*) *Serological Studies*

Serological techniques have been used in an attempt to determine the relationships between the taxa principally involved in this account. Although it has not yet been possible to apply these methods to *B. hordeaceus* L., *B. lepidus* and *B.* × *pseudothominii* as comprehensively as is desirable, the preliminary results seem to contribute valuable corroboration to my hypothesis of the evolution of this group of species developed from other criteria. Serological methods applied to many other bromes in this section of the genus (Smith 1965) have proved to be a valuable adjunct to morphological and cytological methods in determining patristic relationships. Hence the present data are presented with confidence.

The serological techniques adopted were basically those of Gell, Hawkes & Wright (1960), involving the use of double diffusion and immuno-electrophoretic analysis of the plant proteins, in agar gels. In their work on *Solanum*, tuber proteins were used, but in the present work the seed proteins were employed. Storage proteins seem to offer the best material for serological comparison, since greater inter-specific differences may be expected in them than in proteins concerned with activities such as photosynthesis, which are perhaps fundamentally similar in all green plants. Kloz (1960) has demonstrated the greater inter-specific differentiation of the storage proteins in a study of *Phaseolus* species. Kloz surmises that the reasons for this may be that the storage proteins are phylogenetically older, but it is hard to find evidence for this view. It seems more likely that storage proteins in seeds are under particularly severe selective pressure from the environment because during the critical establishment phase when the survival capacity of a plant is most searchingly tested, variation in the composition, size and shape of stored protein molecules might well affect the success or failure of a plant competing with others. Since storage protein acts largely as an amino-acid reserve, the precise sequence of the residues may not be so rigidly fixed as in enzymes carrying out specific tasks in green tissues. So it may be that selective forces have a wider range of viable mutant molecules to operate on, and hence produce a comparatively rapid divergence between species.

Storage proteins seem therefore to be the plant serologists' material of choice, and have the merit of being available in high concentration at a particular stage in the life of the organism. Kloz (1960) was working with globulins, whereas the storage protein of grasses comprises the prolamine and glutelin fractions of the seeds.

Unfortunately, the solvents of prolamine and glutelin proteins (ethanol and alkaline solutions respectively) cause non-specific precipitation of the serum proteins in the antisera used to determine interspecific differences in protein precipitation. Therefore in the present work it was necessary to restrict the serological analysis to the water and saline soluble fractions, i.e. the albumins and globulins. It must be borne in mind that serological differences which may be demonstrated in these are likely to be smaller than the differences which exist in the prolamine and glutelin fractions.

0·8 per cent. saline extracts of finely ground, dehusked seeds of *Bromus* species were compared by raising antisera to them in rabbits. Courses of up to nine injections of the extracts were administered over a period of about six weeks. The earlier injections were of a 1:1 mixture of a 1 per cent. protein solution (the antigen solution) and Freund's adjuvant (Freund & Bonanto 1944) and were intramuscular. Later injections were of unadulterated saline extract into the marginal veins of the ears, or into the muscle of the thighs. 100–150 mg. of plant protein was injected during the course of the immunization.

The blood serum, containing antibodies to *Bromus* proteins, was used to analyse the antigen content of extracts of the seeds. The antiserum and the antigens were allowed to diffuse towards one another in 0·6 per cent. agar gel, buffered at pH 8·6 by barbital-HCl buffer (Michaelis 1930). Lines of precipitated protein ('precipitin') representing the reaction of the antibodies with antigens were developed after 24 hour incubation at 30°C. The differences in pattern produced by the reaction of antigen preparations from different species were regarded as taxonomic criteria. For immuno-electrophoresis, the seed extracts were electrophoresed in agar buffered at pH 9·4 (barbital-HCl) for eight hours (1·2V/cm, 20mA). After this time the antiserum was allowed to diffuse towards the now separated antigenic proteins, to produce an immuno-electropherogram. After 24 hour incubation, the precipitin lines, each representing an antigen-antibody complex, were sufficiently well-developed to be observed and drawn. After a further three days' development, the buffer salts and soluble proteins were washed out of the agar, and the agar itself was dried on a glass plate, protected by a piece of filter paper. When drying was complete the paper was removed and the pattern of lines was stained in 0·2 per cent. Ponceau S in 30 per cent. trichloracetic acid. After further drying, contact prints or photographs could be made from the finished preparations.

RESULTS

(*i*) *Morphological*

The distinguishing features of the taxa in the *B. mollis* agg. sensu Tutin (1962) and of the related species *B. lepidus* are listed in Table 1. Plate 14*b* shows the gross differences in floret size and shape between *B. hordeaceus*, *B. lepidus* and '*B. thominii*' sensu Tutin (*B.* × *pseudothominii*). Herbarium material was scored for these features and the results are presented on a scatter diagram (Fig. 1). Recent Warwickshire material is plotted separately in Fig. 2. Floret characters were measured on the lowest floret in the uppermost spikelet of the panicle. Some of the features showed no consistent pattern of variation, and have thus been omitted from the scatter diagrams. Anther-length varied widely within each taxon, as did stem-width. Spikelet-width and -length appeared very strongly correlated with lemma-length, while awn-length showed a lower correlation. As suggested by Tutin (1962) *B. hordeaceus* subsp. *ferronii* has quite wide spikelets, but my measurements showed that they were no wider than the spikelets of some specimens of *B. hordeaceus* subsp. *hordeaceus.*

TABLE 1. Distinguishing features of *B. hordeaceus* subsp. *hordeaceus*, subsp. *thominii*, subsp. *ferronii*, *B.* × *pseudothominii* and *B. lepidus*
(All measurements are in millimetres. Stem width was measured 1·5 cm below the first node of the inflorescence.)

Character	B. hordeaceus				
	subsp. hordeaceus	*subsp.* thominii	*subsp.* ferronii	B. × pseudo-thominii	B. lepidus
1. *lemma-length*	8–11	6·5–7·5	6·5–8·5	6·5–8	(4·5–)5·5–6·5
2. *awn-length*	4–11 straight	3–7 weakly divaricate	2–5·5 recurved	3–7 straight	2–5·5 straight
3. *spikelet-length*	12–25	8–12	8–18	10–15	5–15
4. *spikelet-width*	4–6	2–3	3–6	3–4	2–4
5. *anther-length*	0·2–2	ca. 1·0	0·2–1·5	0·2–1·5	0·5–2
6. *stem-width*	0·5–1·5	0·5–1	0·5–1·25	0·5–1·25	0·5–1
7. *spikelet indumentum*	usually hairy	hairy or glabrous	densely hairy	hairy or glabrous	hairy or glabrous
8. *hyaline lemma-margin*	narrow	narrow	narrow	usually narrow	broad
9. *lemma shoulder*	bluntly angled	bluntly angled	bluntly angled	bluntly angled	sharply angled
10. *length of grain relative to palea*	grain shorter	grain shorter	grain shorter	grain about equal to palea	grain longer

In both scatter diagrams it will be seen that the spread of points exceeds the variation range quoted by Tutin (1962) and by Hubbard (1954) for these features, emphasizing the extreme morphological variability of the group as a whole. Though few plants of subsp. *ferronii* were scored (none, of course, from Warwickshire) they probably fall into quite a distinct group with dense panicles, recurved awns and densely hairy lemmas. They do not appear to be as distinct from *B. hordeaceus* subsp. *hordeaceus* as is *B. lepidus*, though both subsp. *hordeaceus* and *B. lepidus* are connected by a whole range of variants which approach the Tutin definition of '*B. thominii*', but which intergrade into both the former taxa. The indicated distribution of spikelet pubescence is consistent—a gradual increase of hairiness with increasing lemma size. The existence of names for hairy and glabrous variants of all the taxa concerned, except subsp. *ferronii*, accords with this finding.

It seems reasonable to postulate from these scatter diagrams that some hybridization may be occurring between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*, which is either obscuring a discrete taxon '*B. thominii*', or which may be the sole source of bromes so named. The consistent spread of spikelet hairiness from *B. hordeaceus* subsp. *hordeaceus* to *B. lepidus* may indicate introgression of genes for hairiness from subsp. *hordeaceus* into *B. lepidus*, and factors for glabrosity in the reverse direction.

(*ii*) *Ecological*

Field collecting has indicated that pure stands of both *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* can be found but that mixed populations of both these taxa and '*B. thominii*' are more frequent. Often the herbarium sheets examined proved to bear mixed gatherings of two or three of these taxa. *B. hordeaceus* subsp. *hordeaceus* collections often included material with shorter lemmas, referable to '*B. thominii*' sensu Tutin. Pure stands of *B. hordeaceus* subsp. *hordeaceus* were found in woods, in hayfields and occasionally on roadsides. Pure stands of *B. lepidus* were almost invariably associated with sown grassland of one sort or another, for example, sown sheep pasture, lawns, and newly sown roadside verges and embankments. In these latter habitats, *B. lepidus* was quite commonly found mixed with '*B. thominii*' and sometimes with *B. hordeaceus* subsp. *hordeaceus* as a third component of the brome flora. A mixed population of *B. lepidus* and '*B. thominii*'-type variants grows on an area of the Knocking Hoe National Nature Reserve in Bedfordshire, parts of which were sown after the war (J. G. Dony, personal communication).

A curious population growing in disturbed soil on a cereal field margin at Ufton, Warwickshire, was scored for various morphological features, and the results are plotted in Fig. 3. Variation in lemma-size, sharpness of lemma shoulder, and spikelet hairiness place the plants of this population in a position intermediate between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. No *B. lepidus* could be found nearby at the time of sampling, but several large patches of *B. hordeaceus* subsp. *hordeaceus* grew within thirty metres of this population. According to the key in Tutin (1962) such plants would be referable to '*B. thominii*', but the recognition of such intermediate populations as a separate species requires some experimental validation.

Material of '*B. thominii*' accession 121 was found to segregate slightly in experimental cultivation, producing some plants with shorter lemmas in the second experimental generation. Such segregation supports the idea that '*B. thominii*' populations are composed of plants of hybrid origin. Most samples of '*B. thominii*' came true from seed, however, and showed no variation between generations which could be attributed to segregation.

Further insight into the ecological position of the taxa in Britain comes from an analysis of the copious ecological records of the new Flora of Warwickshire survey (Hawkes & Readett 1963). Fig. 4 represents the distribution of the three taxa, *B. hordeaceus* subsp. *hordeaceus*, *B. lepidus* and '*B. thominii*' sensu Tutin, in the sixteen habitats in which they have so far been recorded. It can be seen that while all three taxa are commonest on roadsides, in the other habitats their distribution appears most interesting. In cultivated land *B. lepidus* is commonest, followed by '*B. thominii*', with *B. hordeaceus* subsp. *hordeaceus* a poor third. *B. lepidus* and '*B. thominii*' are much commoner in pasture land than is *B. hordeaceus* subsp. *hordeaceus*, while in rough grassland *B. lepidus* is much less common than '*B. thominii*' and *B. hordeaceus*. *B. lepidus* is commonest on waste ground, and, where *B. lepidus* is not recorded from a ruderal habitat, '*B. thominii*' is commoner than *B. hordeaceus* subsp. *hordeaceus*. It is perhaps worth emphasizing that the identifications on which these ecological records are founded were all supported by specimens from the various collectors, and were confirmed by the author, in collaboration with the Flora Identification Panel.

From these data it appears that both *B. lepidus* and '*B. thominii*' are associated with artificially sown grassland. Both are poor pasture grasses which are never deliberately sown in Britain, so that the most likely reason for their distribution seems to be that they occur as contaminants in the seeds which are deliberately sown. To investigate this hypothesis, samples of commercial grass seeds have been inspected for contamination by bromes. These samples were purchased from seed firms in Britain, and a valuable collection of Danish strains, both cleaned and uncleaned samples, was made available by the firm of Anton Nielsens, Vejle. *Bromus* seeds found in imported cleaned seed of Danish *Festuca pratensis* Huds. were referable to *B. lepidus* and '*B. thominii*', while in an uncleaned sample of *F. pratensis* from another producer, *B. hordeaceus* subsp. *hordeaceus* seed was seen. Clearly this shows that the seed size and shape of *B. lepidus* and '*B. thominii*' are so similar to those of meadow fescue that seed cleaning methods do not remove them, though the larger seeds of *B. hordeaceus* subsp. *hordeaceus* are removed with less difficulty. *B. lepidus* has also been found in uncleaned seed of Chewings Fescue (*Festuca rubra* subsp. *commutata* Gaud.), and in cheap, cleaned lawn grass seed consisting largely of *Lolium perenne* L. One

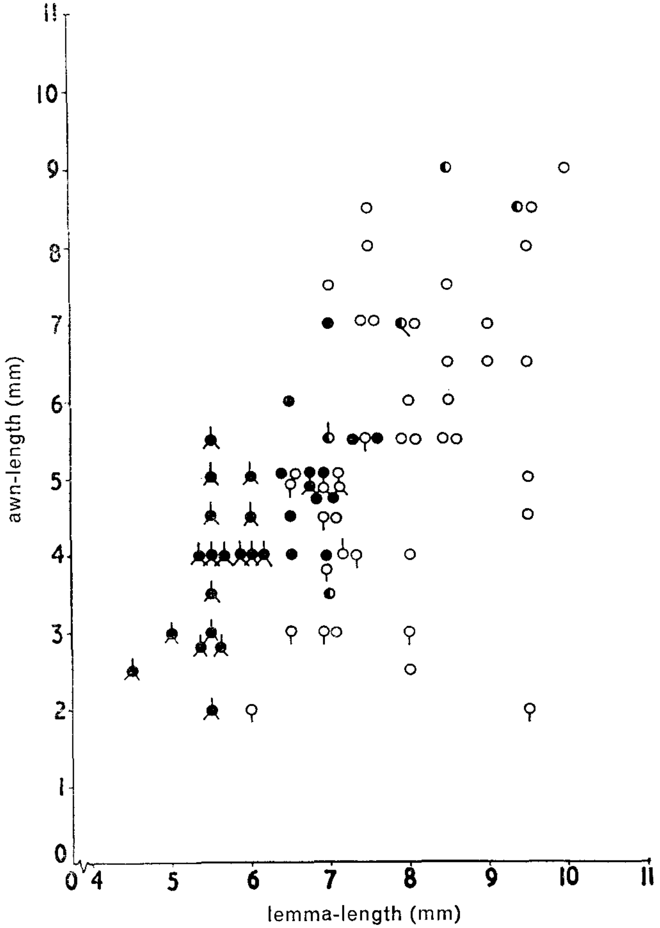

Fig. 1. Scatter diagram of the *B. mollis* agg. sensu Tutin, and *B. lepidus*, compiled from herbarium material.

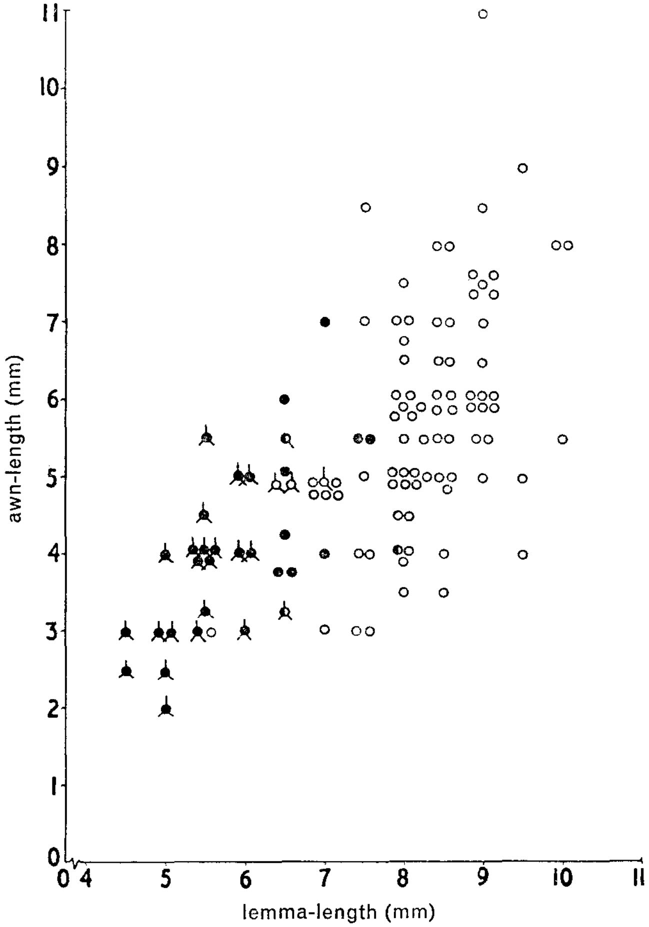

Fig. 2. Scatter diagram of recent Warwickshire collections of the *B. mollis* agg. sensu Tutin, and *B. lepidus*.

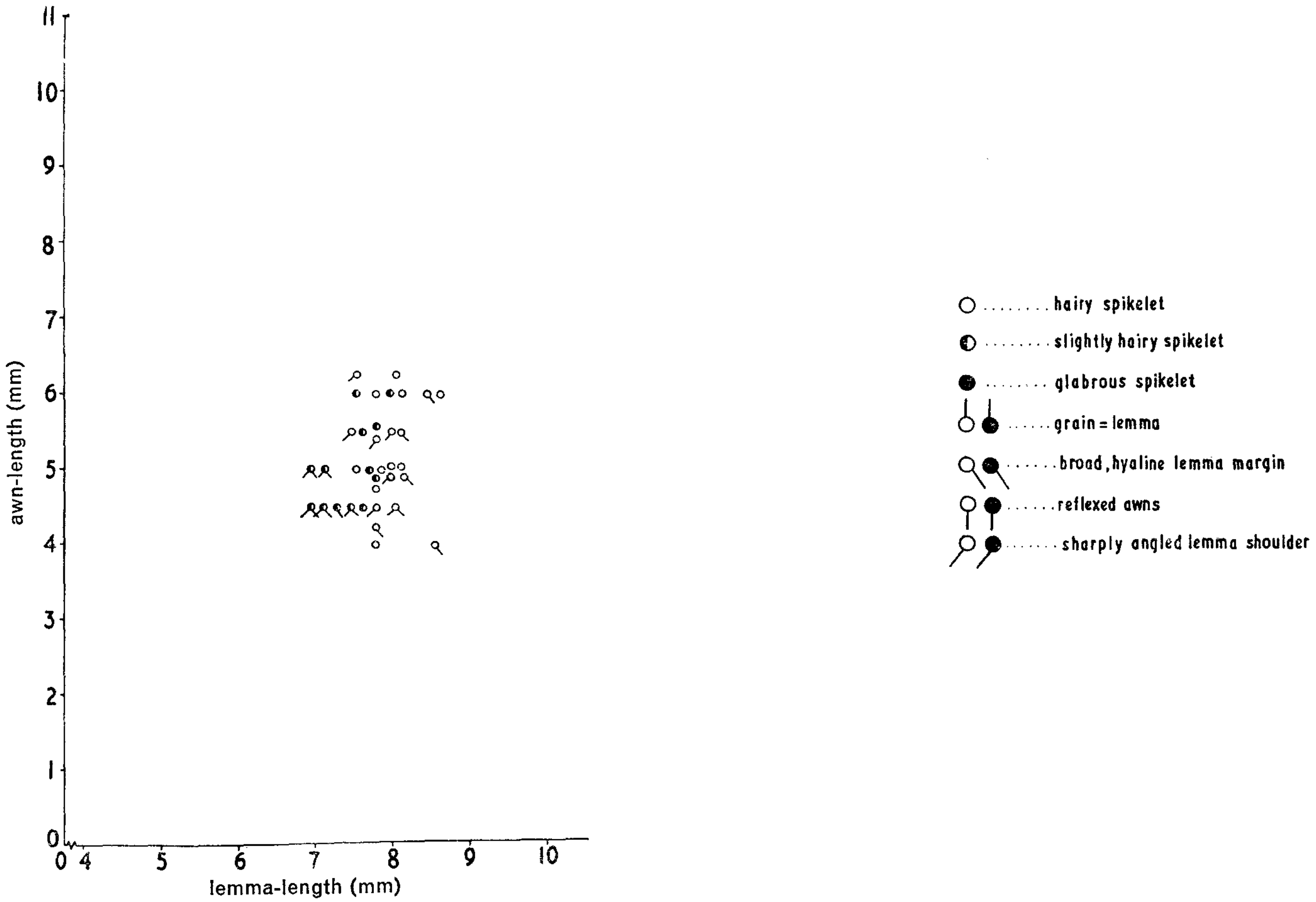

Fig. 3. Scatter diagram of *B. mollis* agg. population from Ufton, Warwickshire.

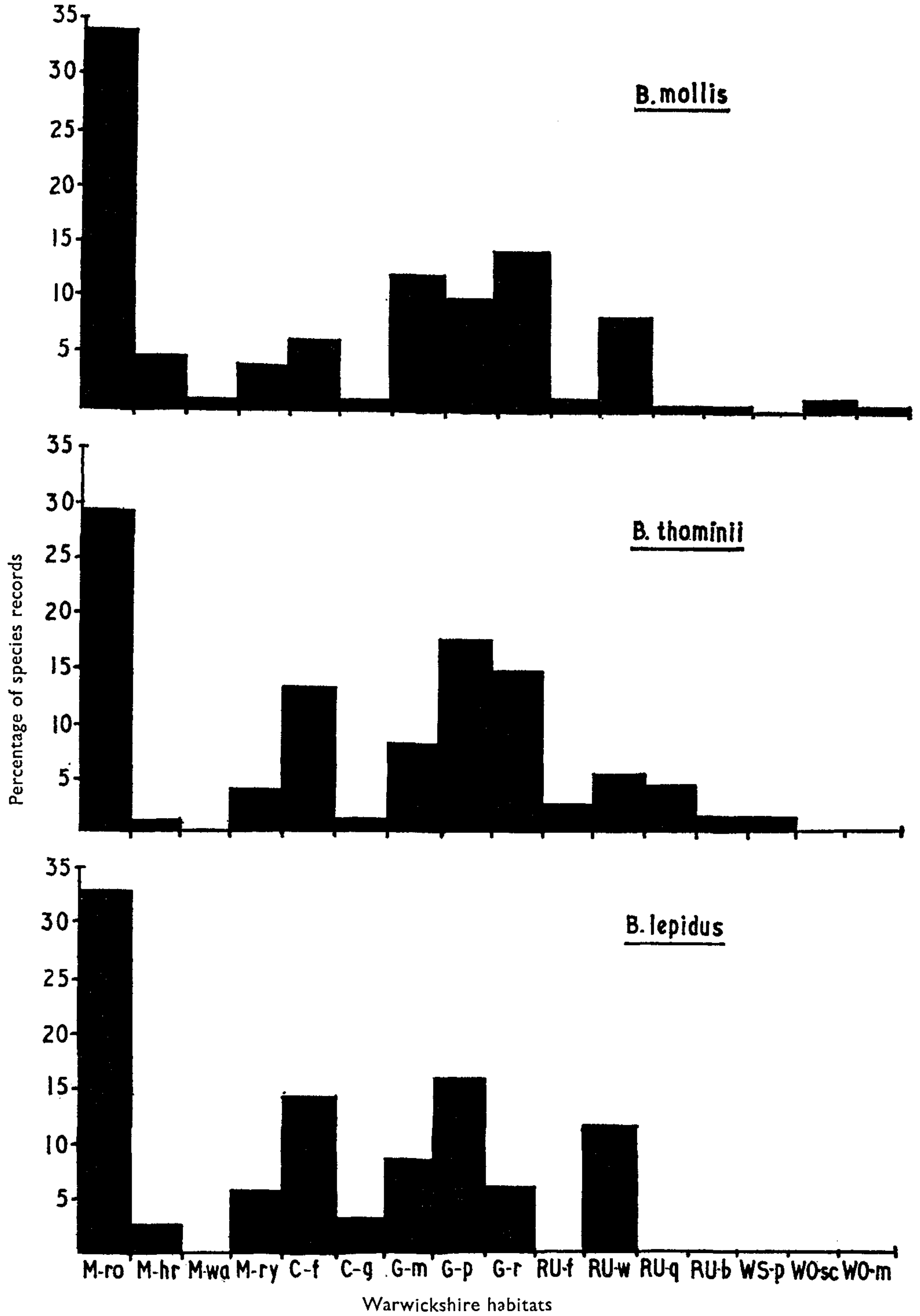

Fig. 4. Histogram of distribution of *B. hordeaceus* subsp. *hordeaceus*, B. *thominii* sensu Tutin and *B. lepidus* in all Warwickshire habitats in which they have been recorded. The percentages are of the total number of records of each taxon in the Flora of Warwickshire Survey. Key to abbreviations:

M-ro—roadside
M-hr—hedgerow
M-wa—wall
M-ry—railway embankment or cutting
C-f—cultivated field
C-g—garden

G-m—meadow
G-p—pasture
G-r—rough grassland
RU-f—farmyard
RU-w—waste ground

RU-q—quarry
RU-b—brick or marl pit
WS-p—pondside
WO-sc—scrub or derelict wood
WO-m—mixed wood

landscaped site in the University of Birmingham grounds, which bore a rich brome flora of three taxa, *B. lepidus*, *B. hordeaceus* subsp. *hordeaceus* and '*B. thominii*', with all spikelet indumentum variants, was found to have originated from a sown mixture including an impure source of *Festuca longifolia* Thuill. Investigation of other samples of cleaned *F. longifolia* revealed *B. lepidus* as a contaminant.

Beddows (1953) shows that large-scale importations of rye-grass and other grass seed into Britain date from about 1831, so that *B. lepidus* and '*B. thominii*' may have entered Britain in quantity from about this time. The earliest British collection of *B. lepidus* is dated 1836. Early agricultural literature on grass husbandry (*e.g.* Sturrock 1865; Everitt 1897) indicates that imported grass seed was very impure and needed considerable cleaning. Britain is now a major producer of grass seed, and advice on this very specialized trade is given to farmers by the National Institute of Agricultural Botany, Cambridge. A series of *Herbage Seed Growers' Leaflets* has been produced and additionally a series of *Seed Notes. Seed Notes No. 72* shows that *Bromus* is a recognized weed in rye-grass and fescue crops, and the *Herbage Seed Growers' Leaflet No. 2* advises farmers to remove from the field and field margins any rogue grasses whose seed may be difficult to remove from the crop.

It seems clear that *B. lepidus* and '*B. thominii*' owe much of their British distribution to the practice of sowing grass seeds in pastures and on roadsides. British Certified Seed, or its foreign equivalent, of very high purity is commonly used, and in this brome contamination is at a minimum, though still present. However, much cheap seed is used by roadside contractors and local councils, and this is often impure.

Methods of seed cleaning by screening for seed size will explain the strong tendency for small-seeded bromes to occur on cultivated ground among sown grasses of similar seed size. *B. hordeaceus* subsp. *hordeaceus* can more easily be removed, and this species seems more commonly established on old roadsides and hayfields than either *B. lepidus* or '*B. thominii*'. Some seed contamination by *B. hordeaceus* subsp. *hordeaceus* is rendered possible by the occasional maturation of smaller seeds in the upper part of the spikelet.

The above discussion relates only to the inland members of this aggregate of species, but it is a common observation that '*B. thominii*' occurs, often abundantly, on coastal dunes where there is no likelihood of artificial sowing. *B. lepidus* is uncommon here, moreover. *B. hordeaceus* subsp. *hordeaceus* occurs on coastal cliffs and on some dunes. It is sometimes depauperate and occasionally has procumbent culms, but these characters have not been found to persist in cultivation (Wilson 1956). '*B. thominii*' from sand dunes has a rather distinct morphology not manifested in the scatter diagrams owing to lack of material. These plants, which are here regarded as *B. hordeaceus* subsp. *thominii*, are usually very small and often prostrate or procumbent, with small, dense paucispiculate panicles. The awns often become divaricate. Experiments revealed that these features were maintained in cultivation, recalling the similar experience of Nilsson (1937) and Wilson (1956). The dune material used came from the Ynys-Las dune system in Cardiganshire and from Burry Port, Carmarthenshire.

(*iii*) *Serological*

Using antisera raised to two accessions of *B. hordeaceus* subsp. *hordeaceus* (Nos. 13 and 21 in appendix), the albumin and globulin fractions of the seed proteins of taxa within the *B. mollis* aggregate (sensu Tutin) and *B. lepidus* were studied and compared. Both double diffusion and immunoelectrophoretic analysis of the antigen components in the saline extracts gave compatible results. The precipitin spectra obtained are illustrated in Pl. 15*b* and *c*.

The homologous reaction of *B. hordeaceus* subsp. *hordeaceus* with its own antiserum cannot be distinguished from that of *B. lepidus* nor from inland accessions of '*B. thominii*'. Other *Bromus* species tested, most of which do not form part of the present investigation, gave reactions varying from similar to very different from the homologous reaction, with the exception of *B. interruptus* which resembled *B. hordeaceus* subsp. *hordeaceus* completely in its serological behaviour. *B. hordeaceus* subsp. *ferronii* and subsp. *thominii* from dunes both showed slight though persistent differences from the homologous reaction. In both these taxa, one antigen line is lacking and the main antigen moves more slowly in electrophoresis than that of the homologous reaction, and that of *B. lepidus* and inland '*B. thominii*'.

These immunological differences were detected by the antibody-forming mechanisms of four adult rabbits.

(*iv*) *Karyological and Genetic*

B. hordeaceus (all subspecies), *B. lepidus* and '*B. thominii*' were found to have a somatic chromosome number of $2n=28$ and are tetraploid. Using the technique described by Beddows & Davies (1938) it was possible to establish a number of hybrids of *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. These hybrids resembled '*B. thominii*' sensu Tutin in all their morphological features, and were almost completely fertile. A typical hybrid panicle is shown in Pl. 15*a*. The F_2 generation, raised from the seeds of the hybrids, proved to be highly variable and to include types which would be referable to *B. hordeaceus* subsp. *hordeaceus*, *B. lepidus* and '*B. thominii*'. Plate 14*c* illustrates some of the variations in floret size which were produced. Hairy and glabrous spikelets occurred throughout the range of variation.

A fully fertile hybrid of *B. hordeaceus* subsp. *hordeaceus* and subsp. *ferronii* was also obtained, which was morphologically intermediate between the parents.

Discussion and conclusions

Morphological studies suggested that plants referable to *B. thominii* sensu Tutin might be the result of hybridization between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. Field observations showed the common occurrence of mixed populations of all three taxa in fields and on roadsides. *B. hordeaceus* subsp. *ferronii* and '*B. thominii*' from coastal dunes seemed rather more distinct, but inland '*B. thominii*' and *B. lepidus* were shown to be associated with sown grassland. Examination of grass seed samples revealed that both occurred as contaminants in the sown seed of various species of pasture grass. Their seed-size so closely matches that of a number of rye-grasses and fescues that they cannot readily be separated by normal mechanical methods. A similar situation has been reported in the weed *Camelina* by Tedin (1925). Contamination of the seed must occur in the production field, though examination of the uncleaned seed purity records at the National Institute of Agricultural Botany failed to demonstrate the expected high contamination. This may readily be explained. Firstly, the sample sizes used by the N.I.A.B. testers may be too small to reveal the comparatively small number of brome seeds required to initiate substantial contaminating populations. Secondly, it seems likely that the records of contamination by '*Bromus mollis*' (*B. hordeaceus* subsp. *hordeaceus*), of which there are a good many, actually refer also to the smaller seeded bromes. Thirdly, the incidence of contamination may be a regional or climatic variable depending on methods of cultivation and cleaning and on the amount of effort expended in certifying the seed. In the present work it was obvious that seed of Danish origin and seed from southern Britain were frequently significantly contaminated with small-seeded bromes. Gooch (1963) shows from an analysis of purity records of imported Danish meadow fescue grass that 69·8 per cent. of samples were contaminated with '*Bromus mollis*' (*B. hordeaceus* subsp. *hordeaceus*), while 40·7 per cent. of creeping red fescue samples were contaminated. A contaminated sample was one which contained at least one contaminant seed in the portion analysed (though the size of this sample is not defined). Contamination of rye-grass by *B. hordeaceus* subsp. *hordeaceus* was found in only 7–8 per cent. of Danish samples. In samples of English origin, Gooch found *B. hordeaceus* subsp. *hordeaceus* contamination in 17·1 per cent. of samples of *Lolium perenne*, and 20·4 per cent. of samples of *Festuca pratensis*. *B. hordeaceus* contamination was almost twice as frequent in samples from western counties of England as in those from eastern areas. Astonishingly high incidence of contamination—76·4 per cent. and 96·5 per cent. respectively—was recorded in Irish samples of Italian and perennial rye-grass.

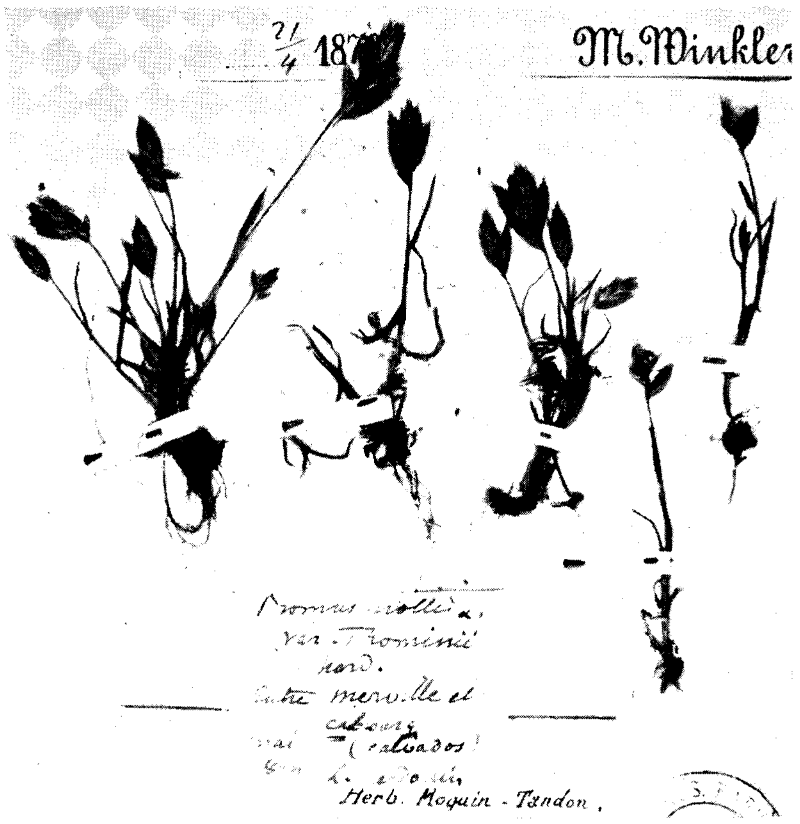

PLATE 14a—Authentic material of *B. thominii* Hardouin (collected and named by Hardouin), in herb. Muséum National d'Histoire Naturelle, Paris (**P**).

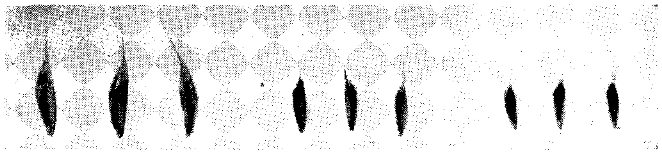

PLATE 14b—Florets of *B. hordeaceus* subsp. *hordeaceus* (left); *B. thominii* sensu Tutin (centre); and *B. lepidus* (right).

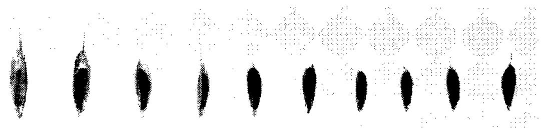

PLATE 14c—Range of variation in florets of the F_2 generation of the cross *B. hordeaceus* subsp. *hordeaceus* × *B. lepidus*.

[*facing page 340*

PLATE 15a—Panicle of artificial F_1 hybrid of *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*.

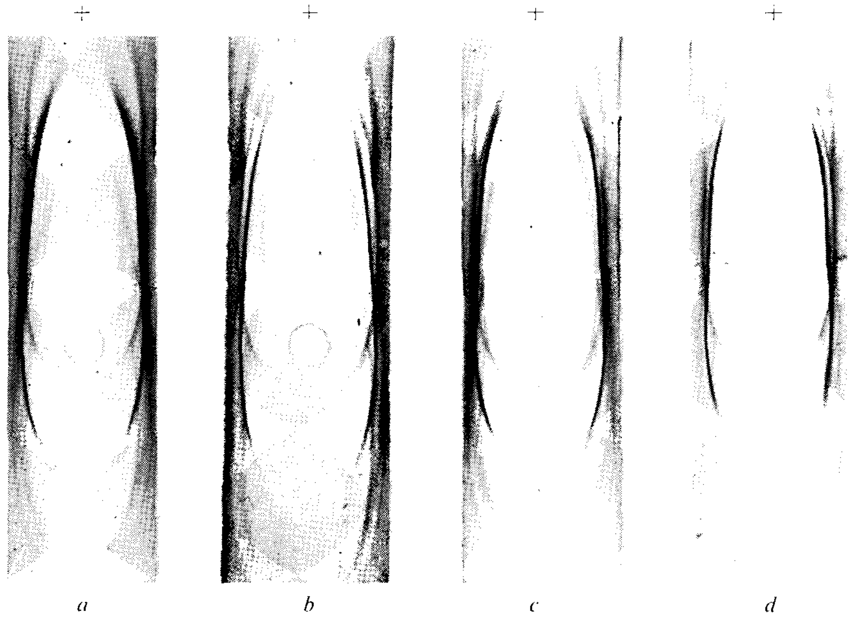

PLATE 15b—Immunoelectropherograms of seed protein extracts of: (*a*) *B. hordeaceus* subsp. *hordeaceus*; (*b*) *B. thominii* sensu Tutin; (*c*) *B. lepidus*; (*d*) *B. hordeaceus* subsp. *thominii* (Hard.) Hylander.

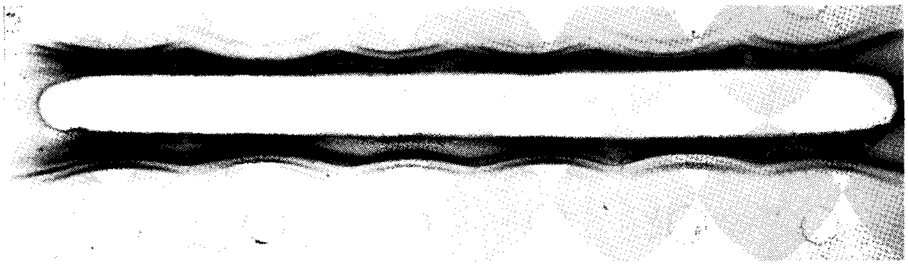

PLATE 15c—Double diffusion spectra of seed protein extracts of: TOP (left to right) *B. thominii* sensu Tutin; *B. hordeaceus* subsp. *hordeaceus*; *B. hordeaceus* subsp. *thominii* (Hard.) Hylander; *B. thominii* sensu Tutin; *B. interruptus*; *B. hordeaceus* subsp. *thominii*. BOTTOM (left to right) *B. thominii* sensu Tutin; *B. lepidus*; *B. hordeaceus* subsp. *thominii*; *B. thominii* sensu Tutin; *B. hordeaceus* subsp. *ferronii*; *B. hordeaceus* subsp. *thominii*. Note missing inner lines from *B. hordeaceus* subspp. *thominii* and *ferronii*.

Thus there seems to be abundant evidence of the origin of the small-seeded annual brome populations from contaminated seed in sown grassland.

Serological evidence showed that *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* were indistinguishable in terms of their seed albumins and globulins, implying therefore a very close patristic relationship. Inland '*B. thominii*' was also indistinguishable, thus supporting the idea that it may result from hybridization, and possibly introgression, between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. *B. hordeaceus* subsp. *ferronii* and subsp. *thominii* sensu stricto were slightly different, which agrees with their morphological and ecological distinctness from the typically inland forms.

Genetic evidence showed that *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* were interfertile tetraploids, thus genetically closely related, and that they could hybridize to produce highly fertile progeny indistinguishable in morphology from inland material of '*B. thominii*'.

It is therefore suggested that inland '*B. thominii*' in Britain results from the hybridization of *B. hordeaceus* subsp. *hordeaceus* with *B. lepidus*. It seems highly likely that such hybridization has been followed by back-crossing of the hybrids to the parents to some extent, a process which would contribute a further range of intermediates to the initial hybrid populations. This introgression hypothesis is supported by the distribution of hairy-spikelet variants in *B. lepidus*, and of glabrous-spikelet variants in *B. hordeaceus* subsp. *hordeaceus*. In each case the spikelet- and lemma-size of these variants is at the extreme end of the variation range which approaches the other taxon. Only rarely are glabrous-spikelet variants of *B hordeaceus* subsp. *hordeaceus* found with lemma-length in the upper end of the species range. Small-lemma, hairy-spikelet variants of *B. lepidus* have not been seen during this investigation. The hybridization may not have taken place originally in Britain, but wherever in Eurasia *B. lepidus* is native and is sympatric with *B. hordeaceus*. Certainly neither *B. lepidus* nor '*B. thominii*' give the appearance of being native in Britain, since they are not well-established in any natural community. Their populations are ephemeral and they are quickly ousted from the sown grassland in which they are most commonly found by the intended components of the seed mixtures applied. *B. hordeaceus* subsp. *hordeaceus* on the other hand, while also a ruderal plant, seems much more persistent wherever it grows, and tends to spread rather than to disappear. In old hayfields it often seems to be a permanent feature of the flora. Although both *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* are predominantly self-fertilizing in Britain, Beddows (1936) concluded that the wide variation exhibited by the former could be explained only on the basis of some degree of outbreeding. Observations during the present work indicated that both species sometimes shed pollen, and it is possible that elsewhere both species may normally be outcrossing. The variation generated by hybridization would produce a range of types which would eventually become stabilized by a resumption of selfing (Stebbins 1950). This would explain the wide variation range which exists between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. The success of the hybrid derivatives, at least in Britain and probably elsewhere where agricultural practices are similar, appears to be a result of the ease with which they contaminate grass seed crops, and so persist with the intended harvest. This type of adaptation in response to 'artificial natural selection' has been frequent in *Bromus*, as witnessed by the cereal field contaminants *B. secalinus* and *B. arduennensis* Dumort., as well as by other species yet to be considered. These are all examples of the effectiveness of the facultative inbreeding system in changing environments, and of the unconscious selection by Man of weed as well as crop plants.

With the coastal populations of *B. hordeaceus* subsp. *thominii*, the explanation of origin by hybridization and possible introgression from *B. lepidus* is not satisfactory. They are well-established in natural communities, and have been, in many cases, observed for over 150 years, and are clearly not established by artificial sowing. The persistence of their morphological peculiarities in cultivation and their serological distinctness from the rest of the *B. hordeaceus* subsp. *hordeaceus*-*B. lepidus*-'*B. thominii*' complex indicates that they have a different evolutionary history. Genetic evidence of their distinctness has been reported by Holmberg (1924) who described a naturally occurring plant as a hybrid of *B. hordeaceus* subsp. *thominii* and *B. hordeaceus* subsp. *hordeaceus*. The plant was only 50 per cent. fertile. Nilsson (1931; 1937) produced artificial hybrids of the same parentage and found that fertility increased very markedly after comparatively few generations. Presumed hybrids of these taxa appear regularly in the literature and they have been named *B.* × *jansenii* A. Camus (Camus 1957) in another report indicating partial sterility. Wilson (1956), in an attempted artificial hybridization, failed to get any seed in a small trial. Spatial isolation, and possibly disruptive and stabilizing selection, are the presumed causes of the ecological and genetical peculiarities of these dune plants. Because of these distinctions it seems best to regard them as ecotypes of *B. hordeaceus*. On dunes, the course of genecotypic adaptation, if this is in fact the explanation, has been in the direction of small size of plants, with prostrate or procumbent culms, a tendency to broad short lemmas and small seeds, and rather dense small panicles. The prostrate or procumbent habit is a familiar development in seaside plants, while the broad lemmas may perhaps be a photosynthetic compensating mechanism since the leaves are short-lived. It is the small lemma and seed size which is of particular systematic interest. Perhaps the genetically fixed 'depauperation' was initially disadvantageous in terms of the number of seeds maturing, but was followed by selection of variants with a larger number of smaller seeds. As well as making most use of possibly limiting nutrient supplies, biotypes with smaller more numerous seeds might have the developmental advantage of faster maturation in conditions of imminent drought. The isolation of these gene-pools on dunes would naturally offer the opportunity for divergence in seed protein complement such as has been demonstrated.

Some ecotypic adaptation may have occurred in the bromes inhabitating areas used for grass seed production, but owing to the rarity of variants of *B. hordeaceus* subsp. *hordeaceus* with sufficiently small seeds, and the inconstancy of the selection pressure on any particular gene complement, it has probably been insignificant. Where the crop and weed seed sizes are more closely similar at the outset, genecotypic adaptation is probably the major means of evolutionary change towards the size and shape of the crop seed. Such adaptation is presumably the cause underlying the contamination of rye fields by *B. secalinus* and of *Triticum spelta* L. by *B. arduennensis*. In the present instance, where the seed sizes of *B. hordeaceus* subsp. *hordeaceus* and the crop grasses are rather different, only hybrids combining the characters of a very small-seeded brome could have exploited this niche. A further factor promoting genecotypic adaptation in cereal field contaminants is the regular harvesting of seed with resowing of some fraction of it. The cereal field ecotypes were common enough to persist through these generations of crops and so progressively become better and better adapted. The incidence of subsp. *hordeaceus* variants with seeds small enough to escape removal in the normal seed cleaning techniques is very low, if they exist at all, and so the chance of their reappearing in another generation of the crop plant grown for seed multiplication is minimal. Probably they would be dispersed in the part of the crop sold commercially, and so not be subject to further selection.

Bromus hordeaceus subsp. *ferronii* appears to have serological and ecological peculiarities and its morphological features were found to persist in cultivation. It is interfertile with subsp. *hordeaceus* and most of its characteristics—dense hairiness, short, stout culms and recurved awns—can be interpreted as ecotypic adaptations to the cliff-top environment. Awn recurvature in bromes seems to be xeromorphic feature, and the hairiness may also be so explained, or else be of some protection against grazing.

For an ecotype it may seem to have a rather restricted geographical distribution. There is no reason, however, why an ecotype need be present in all the possible places where its particular environment occurs. Baker (1953) has cited an excellent example of the restriction of morphologically striking apomicts of *Limonium binervosum* (G.E.Sm.) C. E. Salmon to particular localities in south-west England and West Wales. The habitat is similar but the particular apomict in each one differs in morphology sufficiently to have been recognized as distinct species by some taxonomists. *B. hordeaceus* subsp. *ferronii* may illustrate a similar phenomenon in an autogamously reproducing group.

The close morphological resemblance of material of *B. hordeaceus* subspp. *hordeaceus*, *thominii* and *ferronii*, supported by the nature of their serological and genetical resemblances appears to expose them as subspecific variants within a single species. Accordingly this is the course which has been followed in the taxonomic treatment given earlier. The material formerly named '*B. thominii*', which has been shown above to be a hybrid complex between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*, is so common and conspicuous that some reference name seems desirable. The name *B.* × *pseudothominii* Philip Smith has therefore been proposed for it. Though *B. lepidus* is shown to be interfertile with *B. hordeaceus*, and to have an indistinguishable serological spectrum, its specific status is maintained since it contributes to the hybridization as an independent and distinct source of genes, and has a very characteristic morphology, which suggests that at least one of its diploid ancestors is not shared by *B. hordeaceus*.

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APPENDIX

Accessions of *Bromus* mentioned in the account. Voucher material at Dept. of Botany, University of Edinburgh. Flora of Warwickshire material at **BIRM.**

Species	Acc. no.	Origin
Bromus hordeaceus subsp. *hordeaceus*	13	England, Warwickshire; Edgbaston, Birmingham 15. Vincent Drive roadside. P. Smith, 457, 1962.
,,	21	England, Worcestershire; Queensway, Halesowen, Old allotment. P. Smith 503, 1962.
,,	26	England, Warwickshire; Quinton, Birmingham. Roadside. P. Smith 494, 1962.
,,	474	Flora of Warwickshire accession. Myton Farm, near Warwick. On a roadside. 1963.
Bromus hordeaceus subsp. *thominii*	429	Wales, Cardiganshire; Ynys-Las, sand dunes on the Dyfi estuary. P. Smith 671, 1963.
,,	510	Wales, Carmarthenshire; Burry Port. Sand dunes near the Old Harbour. P. Smith 813, 1965.
Bromus hordeaceus subsp. *ferronii*	462b	Wales, Anglesey; South Stack, on a wall top. Coll. J. B. Phipps. 1963.
B. lepidus	31	England, Worcestershire; Halesowen by-pass. Roadside embankment. P. Smith 502, 1962.
	92	Flora of Warwickshire accession. S.E. of Willoughby. Railway embankment. 1959.
B. × *pseudothominii*	116	Flora of Warwickshire accession. S.E. of Barford. Farmyard. 1962.
	121	Flora of Warwickshire accession. Green Lane, E. of Cloudesley Bush. Farmyard. 1962.

The panicle illustrated (Plate 15a) is from a hybrid between *B. hordeaceus* subsp. *hordeaceus* 26 and *B. lepidus* 31.