A new subspecies of *Bromus hordeaceus* L. (Poaceae)

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ABSTRACT

A new subspecies of *Bromus hordeaceus* is described and named subsp. *longipedicellatus*. It has long pedicels and branches and thus resembles *B. commutatus*, but the lemmas are papery which is a feature of the *B. hordeaceus* group and its anthers are longer. The grass is fertile and comes true from seed. The reliability of various taxonomic characters in *Bromus* is discussed.

KEYWORDS: *B. commutatus*, *B. racemosus*, diagnostic characters, taxonomy.

INTRODUCTION

In 1977 L. J. Margetts found an odd *Bromus* in Cornwall that had long branches and long pedicels but also papery lemmas. He sent it to C. E. Hubbard at Kew who suggested that it might be '(?) *B. commutatus* × *B. mollis* or *B. commutatus* var. *pubens*' (pers. comm. Hubbard to L. J. Margetts 1978). Margetts later found it in Devon and further specimens all from one site in Devon were determined as *B. commutatus* by P. J. O. Trist (pers. comm. to L. J. Margetts 1987), H. J. M. Bowen (pers. comm.,1998) and T. A. Cope (pers. comm., 1998); as '(?) *B. racemosus* × *B. commutatus* + *B. hordeaceus*' by T. A. Cope (pers. comm. 1993); as '(?) *B. commutatus* var *pubens*' by R. M. Payne (pers. comm. to L. J. Margetts 1997) and A. Copping (pers. comm., 1997); as '(?) *B. hordeaceus* × *B. commutatus*' by C. Stace (pers. comm., 1998) and T. B. Ryves (pers. comm.,1998); as 'a new var. or ssp. of *B. hordeaceus*' by M. Kerguélen (pers. comm., 1998); as 'a new taxon unnoticed until now with close affinities to *B. hordeaceus* by H. Scholz (pers. comm., 1999); and as 'an unusual variant of normal *B. hordeaceus* by T. A. Cope (pers. comm., 1999).

Specimens of the grass were also sent to F. Llamas in Spain, F. Sales in Portugal, P. W. Stahlman in U.S.A., E. Pavlick in Canada, and E. Edgar in New Zealand. None of them reported that they recognised the grass.

To determine its identity, in 1997 a comparative morphological study was commenced on this puzzling grass and on the potentially related taxa *B. hordeaceus* subsp. *hordeaceus, B. racemosus, B commutatus* Schrad. and *B. commutatus* var. *pubens* Wats. Botanists were requested to send material for examination (Spalton pers. comm. to several botanists 1997, 1999, 2000), which many of them did. At the same time herbarium specimens were examined and the grasses were cultivated. The grass was given a provisional working name of '*longipedicellatus*'.

METHODS

A total of 3021 specimens of *Bromus* were studied: 1232 were fresh or recently collected specimens and 1789 were herbarium specimens from **BDD**, **BM**, **BRISTM**, **BTN**, **DBN**, **E**, **GL**, **GLAM**, **HAMU**, **HCCMS**, **K**, **LTR**, **MANCH**, **NMW**, **OLDM**, **OXF**, **RAMM**, **RNG**, **SLBI**, **SUN**, **TCD**, **TOR**, and **WARMS**. 2308 specimens were analysed morphometrically: 775 of '*longipedicellatus*',1201 of *B. hordeaceus* subsp. *hordeaceus*, 183 of *B. racemosus*, 130 of *B. commutatus s. s.* and 109 of *B. commutatus* var. *pubens*.

Before the main morphological study, there was a pilot investigation of spikelet and floret structure and development. Spikelets were collected at different times and at different stages of development and all florets in each spikelet were opened and examined. It was found that anther length became progressively smaller from the lowest floret towards the apex of the spikelet.

Chasmogamy usually only occurred in the lowest two or three florets and these rarely contained fruit. In the other florets filament development was poor or absent and cleistogamy and fruit formation was very rapid with the dehisced anthers being distorted and pushed out by the developing fruit. In each panicle cleistogamous anthers varied widely in length but undehisced chasmogamous anthers from the lowest florets did not. Smith (1972) and Clapham *et al.* (1962) pointed out that cleistogamy changes anther size and according to Smith & Sales (1993) only intact (undehisced) anthers should be measured. Pollen was also measured, but it varied widely in size and too much to separate these taxa.

In the main study, culm height was first measured. In multi-culmed specimens the heights of mature culms were averaged. Panicle length was measured from the node of the lowest branch or pedicel to the apex of the terminal spikelet. Branches were measured from their node to the base of their terminal spikelets. Pedicels were measured, and the pedicel and branch lengths were also compared with the length of the spikelet that each of them bore. Nine spikelets from each panicle were measured, three near the apex, three near the basal node and three from the middle region and the measurements were averaged. Immature and atypical spikelets were ignored. Under lateral lighting with a hand lens, it was noted whether a substantial majority of the lemmas had veins that were protruding.

Some spikelets were removed and, whether fresh or dried, were soaked for two hours in water containing a wetting agent. Soaking was to restore tissue, to facilitate dissection and produce a more uniform condition for testing lemma texture. The lengths of the lowest lemmas and of the lowest rhachilla-segments were measured. Mature undehisced anthers in the lowest florets were measured and if the lowest florets were empty (indicating that chasmogamous anthers had already been extruded and dropped) this was noted. Fruit development was always recorded and quantified by the length of the developing fruit.

Lemma texture was assessed on a slide under a binocular microscope by holding the lemma at the base or by the awn and probing it with a blunt needle. If necessary, previously soaked lemmas of *B. commutatus* and *B. hordeaceus* were used as comparative controls. Papery lemmas were thin and fragile and readily collapsed or bent under pressure. Leathery lemmas were thicker and stiffer and therefore more resistant to pressure, and when they eventually give way it was over a wider area and the lemma would resume its shape when the pressure was removed. In doubtful cases additional lemmas were tested. If fruit was formed or was being formed it had to be removed before assessing lemma texture.

Graticules in 30× binocular and 1000× monocular microscopes were used for all fine measurements. Measurements in the text and in Tables 1 and 2 are range measurements obtained with some extremes eliminated but the number of these extremes was never allowed to exceed 2% from the upper and 2% from the lower limits. If there was any evidence of immaturity the data were not recorded. If a spikelet was not fully developed, the upper glume appeared longer than usual in comparison with the length of the spikelet. Immaturity was confirmed if under a high-power microscope the anther cuticle was fragile and partially translucent and the pollen grains lacked full content.

A character often used to pick out *Bromus* species in the field is the crowded or lax nature of the panicle, and this was the first character which drew attention to '*longipedicellatus*'. In Stace (1997), plants with a ±dense panicle usually with all pedicels shorter than spikelets and with papery lemmas are referred to *B. hordeaceus*, and plants with ±lax panicles with at least some pedicels longer than spikelets and with rather coriaceous lemmas are referred to *B. racemosus* and *B. commutatus*. A somewhat similar wording was used by Smith (1980) and by Clapham *et al.* (1987). It is often difficult to decide whether a panicle is lax or dense and some plants of *B. hordeaceus* often had one or two pedicels that were longer than the spikelets. Furthermore, lax panicles frequently had long branches with or without long pedicels.

It was considered that the characters for determining lax panicles should be revised to recognise the contribution of branching to laxness. After evaluating various possibilities including the method used by Kerguélen (1995) in France, mentioned in Table 2, it was found that the panicle of '*longipedicellatus*' could best be distinguished from that of subsp. *hordeaceus* by having at least four pedicels and branches that are longer than the spikelets that they bear (branches measured to the base of the terminal spikelet) When other diagnostic characters were also taken into consideration there were few indeterminates. This formula also separated *B. commutatus* and most

FIGURE 1. Panicle of *Bromus hordeaceus* L. subsp. *longipedicellatus* L. M. Spalton. L. M. Spalton 1926, v.c. 12, N. Hants, Hurstbourne Priors, SU445452, 20 May 2000. Scale bar = 1 cm.

specimens of *B. racemosus* from subsp. *hordeaceus*. It is suggested that this empirical formula, while not perfect, is more satisfactory than the present descriptions of laxness and denseness that the Floras have had to use (Table 2).

In 1999 and 2000, the grasses were cultivated in Cardiganshire, in Devon (two stations), in Suffolk and, to a lesser extent, in Lancashire and Norfolk. Seed sources were as follows: '*longipedicellatus*' from ten sites in Devon; subsp. *hordeaceus* from two sites in Devon; and *B. racemosus* from one in Devon; *B commutatus* from two sites in Somerset; and *B. commutatus* var *pubens* from Anglesey and Suffolk. Seed was sown in September (when these plants germinate in the wild) in John Innes Compost in four or six inch pots, germinated initially under glass and then placed outside for autumn growth and over-wintering. However, in one station the plants remained under glass throughout. Some seedlings were also pricked out on to ordinary garden soil and seed was also sown directly into the soil. From March 2000 one third of the plants of '*longipedicellatus*' and of subsp. *hordeaceus* were enriched by doses of a fertiliser (Liquid Growmore).

TABLE 1. MORPHOLOGICAL DATA ON THE FIVE *BROMUS* TAXA

Character	*B. hordeaceus* subsp. *hordeaceus*	*B. hordeaceus* subsp. *longipedicellatus*	*B. racemosus*	*B. commutatus* var. *pubens*	*B. commutatus s.s.*
Indumentum of young, lower leaf sheath	usually villous	variable and intermediate between subsp. *hordeaceus* and *racemosus*	usually long slender patent hairs, often indeterminate	variable from *commutatus* to *longipedicellatus* types	stiff thick patent hairs
Culm height	to 80 cm	80–75 cm	20–105 cm	60–120 cm	60–150 cm
Panicle structure	usually dense, not more than 3 pedicels and branches exceeding the length of their spikelets	lax; at least 4 pedicels and branches exceeding the length of their spikelets	narrow; usually at least 4 pedicels and branches exceeding the length of their spikelets	lax; at least 4 pedicels and branches exceeding the length of their spikelets	as for var. *pubens* but very spreading, some pedicels or branches more than 8 cm long
Panicle length	1–10 cm	10–20 cm	4–20 cm	8–20 cm	10–25 cm
Spikelet length	11–20 mm	13–21 mm	11–18 mm	15–28 mm	15–30 mm
Lemma texture	papery	papery	leathery	± leathery	leathery
Lemma length	7–10·5 mm	7·5–10·5 mm	7–9 mm	7·5–11 mm	7·5–11 mm
Lemma indumentum	pubescent or glabrous	pubescent (rarely glabrous)	glabrous	pubescent	glabrous
Shape of lemma margin	indeterminate	indeterminate	usually smoothly curved	often intermediate	usually broadly angled
Lower rachilla-segment length	0·8–1·4 mm	0·8–1·5 mm	0·9–1·6 mm	1–1·7 mm	1·1–1·8 mm
Lowest floret Undehisced anther length	1–2·6 mm	2·2–3·8 mm	1·5–3·5 mm	1·3–2·5 mm	1·3–2·5 mm

RESULTS

The morphological data are summarised in Table 1. Lemma length is only of limited value to separate these taxa but smaller lemmas do indicate *B. lepidus*. The lemmas of *B. hordeaceus*, '*longipedicellatus*', *B.* × *pseudothominei* and *B. lepidus* were of papery texture and those of *B. racemosus*, *B. commutatus, B. secalinus*, and *B. pseudosecalinus* were leathery. This difference in texture is of fundamental importance to distinguish these two groups of grasses. In dried material the veins of thin and papery lemmas tend to protrude but they do not in leathery lemmas.

Lemmas of subsp. *hordeaceus* are usually pubescent but in this study 6·1% were glabrous; lemmas of '*longipedicellatus*' were also pubescent but only 0·4% were glabrous. Lemmas of *B. commutatus* were glabrous but those of *B. commutatus* var. *pubens* were pubescent and this grass, which is more frequent than *B. commutatus s. s.*, can be confused with '*longipedicellatus*'. Pubescence was not found on the lemmas of *B racemosus* and this was a good character for distinguishing it. Glabrous lemmas in all the taxa were often scabrid. The margin of the lemma in *B. racemosus* was smoothly curved and that of *B. commutatus* broadly angled; this was a confirmatory character but often the difference was not clear. This character was of no diagnostic value in *B. commutatus* var. *pubens* or in the *B. hordeaceus* group but a sharply angled margin was indicative of *B. lepidus*.

The stiff, rather thick patent hairs on the lower leaf-sheath of young fresh *B. commutatus* were very distinctive. In subsp. *hordeaceus* the indumentum was usually villous but in '*longipedicellatus*', *B. racemosus* and in most specimens of *B. commutatus* var. *pubens* it was

TABLE 2. DIAGNOSTIC CHARACTERS OF *BROMUS HORDEACEUS* SUBSP. *HORDEACEUS* AND SUBSP. *LONGIPEDICELLATUS*

Taxon	Source	Culm height	Panicle length	Panicle structure	Anther length
Subsp. *longipedicellatus*	L. M. Spalton	80–175 cm	10–20 cm	at least 4 pedicels and branches exceeding the length of their spikelets	2·2–3·8 mm #
Subsp. *hordeaceus*	L. M. Spalton	up to 80 cm	1–10 cm	up to 3 pedicels and branches exceeding the length of their spikelets	1–2·6 mm
	Clapham *et al.* (1981)	3–80 cm	(3–)5–10 cm	pedicels mostly shorter than spikelets	usually <1 mm
	Hubbard (1968)	10–100 cm	1.5–16* cm	pedicels 2–10 mm	0·2–2 mm
	Kerguélen (1995)	1–100 cm	5–10 cm	pedicels and branches < 2·5 cm	0·2–2 mm
	Smith (1980)	3–80 cm	(3–)5–10 cm	pedicels mostly shorter than spikelets	0·2–2 mm,
	Stace (1997)	up to 80 cm	up to 10 (–16*) cm	usually with all pedicels shorter than spikelets	0·5–1·5(–2) mm

* may include subsp. *longipedicellatus*. # Undehisced anthers from lowest florets only.

intermediate. The lengths of the lower rhachilla-segments were found to be unreliable for distinguishing these taxa. These segments also elongated as fruit began to form.

In cultivated and in wild plants chasmogamy occurred in all taxa and was most frequent in subsp. *hordeaceus* and '*longipedicellatus*', but fertilisation was still mainly by cleistogamy. Fertilisation and fruiting was most rapid in subsp. *hordeaceus*. Chasmogamous anthers were only found in the lowest florets and were quickly extruded, dehisced and dropped. Within the other florets, the anthers dehisced internally, cleistogamy occurred and these florets remained closed until fruiting. In this study the anther measurements for subsp. *hordeaceus* differed from those published elsewhere (Table 2). The anther lengths of *B. commutatus* (1·3–2·5 mm in Table 1) were also different to the '1–1·5 mm' in Stace (1997) and Clapham *et al.* (1987), 'c. 1·5 mm' in Smith (1980) and '1·5–2 mm' in Hubbard (1968). This may be because dehisced anthers had been included.

The important characters distinguishing '*longipedicellatus*' from subsp. *hordeaceus* are summarised in Table 2.

In the cultivation experiments enrichment of '*longipedicellatus*' and subsp. *hordeaceus* pots with fertiliser did not increase culm height, nor the lengths of panicles, pedicels or branches. It is likely that had these grasses been grown in nutrient-poor soil a different result would have been obtained. However, the length of the spikelets of '*longipedicellatus*' increased by 26% and the enriched spikelets contained more florets The length of the lemmas only increased by 7%. Enrichment of subsp. *hordeaceus* pots produced somewhat similar results but the sample was too small to justify quantification. Smith (1972) had also found that spikelet size is susceptible to soil nutrient status and that more florets are produced in rich soil. Stace (1997), Clapham *et al.* (1987) and Smith (1980) did not use spikelet length in their keys to identify B. *hordeaceus*, but spikelet length is employed to separate *B. racemosus* from *B. commutatus* (Table 1). Smith (1972) had also found that lemma size was not much affected by richness of the substrate.

The cultivation experiments showed that '*longipedicellatus*' was fertile and that it came true from seed. At the main Devon station in May and June 2000 additional plants of '*longipedicellatus*' were collected from the six marked sites where the seeds for cultivation had been obtained in 1999. The cultivated plants of '*longipedicellatus*' were very carefully compared with these newly collected wild plants and with the herbarium specimens collected from these sites in 1999. No significant differences were found (Table 3).

TABLE 3. COMPARISON OF WILD PARENT AND CULTIVATED PROGENY OF *BROMUS HORDEACEUS* SUBSP. *LONGIPEDICELLATUS*

Locality	Culm height, cm	Panicle length, mm	No. pedicels > their spikelets	No. branches > their spikelets	No. pedicels and branches	Spikelet length, mm	Lemma length, mm	Undehisced anther length, mm
Tiverton, wild (n=1)	115	14·1	8·0	3·0	11·0	19·0	9·1	3·4
Tiverton, cultivated (n=13)	141	14·7	7·1	2·3	9·4	21·0	9·2	3·6
Exeter, wild (n=1)	110	16·0	5·0	2·0	7·0	18·0	9·8	2·8
Exeter, cultivated (n=12)	127	15·8	6·2	1·1	7·3	19·3	10·2	2·9
Kennford, wild (n=1)	140	16·3	5·0	2·0	7·0	18·0	9·5	3·2
Kennford, cultivated (n=11)	147	15·9	4·4	3·1	7·5	19·9	9·2	2·9
Dartington, wild (n=1)	129	13·5	6·0	-	6·0	18·0	9·0	3·1
Dartington, cultivated (n=6)	121	13·1	5·7	-	5·7	17·6	9·3	2·9
Bicton, wild (n=1)	135	18·0	6·0	2·0	8·0	20·0	10·5	3·5
Bicton, cultivated (n=10)	122	16·4	4·1	2·3	6·4	19·1	11·0	3·3
Hams Barton, wild (n=1)	172	15·0	3·0	4·0	7·0	14·1	8·8	-
Hams Barton, cultivated (n=11)	161	14·3	3·8	4·1	7·9	14·3	9·0	3·5

Figures presented are the measurements from the single wild parents and mean of the cultivated progeny. Parent plants were collected as follows: Tiverton, road lay-by SX996143, 5 May 1999. Exeter, bank above road SX962916, 9 May 1999. Kennford, road verge, SX918875, 15 May 1999. Dartington, disturbed ground, SX787621, 21 May 1999. Bicton, disturbed ground SX072868, 22 May 1999. Hams Barton, edge of wheat field, SX882801, 26 May 1999.

DISCUSSION

The '*longipedicellatus*' taxon was thus found to differ from the other taxa investigated. It is most closely related to *B. hordeaceus* subsp. *hordeaceus*, but differs in its long culms, long panicles with long pedicels and/or long branches and long chasmogamous undehisced anthers. It superficially resembles *B. commutatus* var. *pubens* in being 80–175 cm tall with panicles 10–20 cm long but its lemmas are papery and like *B. racemosus* and *B. arvensis* it has long chasmogamous anthers. As the grass is clearly a distinct taxon it is it is named *Bromus hordeaceus* subsp. *longipedicellatus*.

Bromus hordeaceus L. subsp. ***longipedicellatus*** L. M. Spalton, ***subsp. nov.***
Varietas robusta. Caules 80–175 cm. Paniculae 10–20 cm, quattuor minimum pedicellis aut ramis longitudinem spicularum suarum excedentibus (ramis ad basem spiculae terminalis mensis). Lemmae 7·5–10·5 mm, pubescentes, texturae papyraceae, venis in siccitate extantibus. Antherae adhuc intactae infimorum florum 2·2–3·8 mm, ceterae breviores.

A robust grass with culms 80–175 cm long. Panicles 10–20 cm long with at least 4 pedicels or branches exceeding the length of their spikelets (branches measured to the base of the terminal spikelet). Lemmas 7·5–10·5 mm long, of papery texture, with protruding veins when dried, pubescent or rarely glabrous. Undehisced anthers from the lowest florets 2·2–3·8 mm long, other anthers smaller.

HOLOTYPUS: South Devon, v.c. 3, Aveton Gifford (SX691474), grassy bank on thin soil above road, 23 May 1999, *L. M. Spalton s.n.* (**BM**).

Subsp. *longipedicellatus* is found on road verges and banks, on waysides, on the edges of arable fields (especially wheat), on waste ground and less frequently in pasture. On road verges it is in flower from the beginning of May and is very soon cut during roadside trimming. When in fruit (and when dried) the spikelets lie close to the culm so the panicle no longer appears to be lax.

Subsp. *longipedicellatus* has been confirmed in 46 vice-counties of England, eight of Wales, six of Scotland and one of Ireland. Out of 1789 herbarium specimens that were examined only 28 were subsp. *longipedicellatus*, the earliest of which was collected by G. H. Douglas in Torbay, Devon in 1926 (**TOR**). This suggests that, whatever the origin of subsp. *longipedicellatus*, it may have spread rapidly in England and Wales. It is probable that the grass may have been disseminated as a contaminant of *Lolium perenne* seed in agricultural and amenity grass seed mixtures or of wheat seed.

Subsp. *longipedicellatus* might have resulted from a gene transfer from *B. hordeaceus* into *B. racemosus* or *B. arvensis* with *hordeaceus* genes becoming dominant. *B. commutatus* var. *pubens* has pubescent, less leathery (though still papery) lemmas, a variable indumentum of the lower leaf-sheath and an earlier flowering time than *B. commutatus* and it might contain genes from *hordeaceus*. On the rare occasions when B. *racemosus* and *B. commutatus* share the same habitat, intermediates are produced. There are many problems in the genus and DNA or isoenzyme studies might resolve at least some of them. A new key to the genus *Bromus* in Britain will be produced when additional research has been completed.

An important consequence of the recognition of subsp. *longipedicellatus* is that the descriptions of *B. hordeaceus* and subsp. *hordeaceus* now require revision because *B. hordeaceus* cannot be reliably separated from *B. racemosus* and *B. commutatus* by panicles that are dense or lax. The following descriptions are proposed:

Bromus hordeaceus L.: Culms usually erect 2–175 cm. Panicle dense or lax, 1–20 cm, sometimes only 1 spikelet. Lemmas 6·5–10·5 mm, papery with protruding veins when dried, pubescent or glabrous. Undehisced anthers from the lowest florets 1–3·8 mm.

***Bromus hordeaceus* subsp. *hordeaceus*:** culms erect or ascending to 80 cm. Panicle 1–10 cm, dense or somewhat lax with not more than 3 pedicels or branches exceeding the length of their spikelets. Lemmas 7–10·5 mm, papery with protruding veins when dried, pubescent or glabrous. Undehisced anthers from the lowest florets 1–2·6 mm.

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