TAXONOMY AND NOMENCLATURE OF THE BROME-GRASSES (Bromus L. s. l.)

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ABSTRACT. The limits of the genus *Bromus* s.l. (Gramineae) are examined and its relationships to *Megalachne* Steud. and to *Littledalea* Hemsl. are considered. Infrageneric elements in *Bromus* are defined and their better known species are enumerated. Available names for the genus and each of its parts are reviewed and those appropriate to generic, subgeneric and sectional treatment are indicated. Nomenclatural types are cited. Sectional rank is thought most appropriate for the infrageneric elements within *Bromus* s.l.

INTRODUCTION

Bromus L. *sensu lato* is a well-defined, natural group of annual and perennial grasses, with a very wide geographical distribution. Within the group there is a considerable degree of heterogeneity which has resulted in many different taxonomic treatments. *Bromus* has been split up variously into sub-genera, sections and subsections, and occasionally some of these have been elevated to generic rank. Variation in the nomenclature of the group is staggering. Authors agreeing about the rank of the taxa to be recognised have seldom used the same names for them. The result is that a large number of names, originally applied at generic, subgeneric or sectional level, are still being applied rather carelessly to taxa of different rank. Curiously, the actual number of generic subdivisions recognised in *Bromus* with whatever name or rank, is quite small, rarely exceeding eight or ten.

The aim of the present note is to define the genus *Bromus* L. in the wide sense, together with its parts, and to review the available names which have accumulated over the centuries. The correct name which should be assigned for each recognisable taxon at generic, subgeneric and sectional rank is deduced. The taxa themselves are defined and their species provisionally enumerated. Lectotypes are cited in each case. Finally, considerations favouring sectional treatment of the groups of plants included in *Bromus* L. *s.l.*, are put forward.

Interesting contributions to the tortuous study of *Bromus* nomenclature, with or without the offering of a taxonomic treatment, have been made by Holmberg (1924), Stapf (1928), Nevski (1934), Henrard (1941), Wagnon (1952) and Tournay (1961).

1. DEFINITION OF THE GENUS BROMUS L. *s.l.*

A number of genera have been considered to be close relatives of *Bromus*, and these have sometimes been incorporated in it. These are included in the lists which follow. One such genus, *Boissiera* Hochst. ex Steud. has only recently been recognised as a member of *Bromus* s.l. (Smith 1969a). Certain other genera have similarly been regarded as part of *Bromus* in the past, or have been thought to be fairly closely related to it. Such taxa are *Littledalea* Hemsl. and *Megalachne* Steud.

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Of these two latter taxa, *Megalachne*, a genus endemic to Juan Fernandez, can easily be shown to have only a low affinity with *Bromus*. It appears more closely related to *Festuca* L. than to *Bromus*. *Megalachne* has a festucoid type embryo, as defined by Reeder (1957), but unlike *Bromus*, it possesses compound starch grains. There is only a low level of serological correspondence between the seed proteins of *M. fernandeziana* (Phil.) Skottsb. and those of all *Bromus* species so far used for comparison (Smith unpubl.). The morphological similarities between the florets of *Megalachne* and those of brome-grasses assigned to the *Ceratochloa* group (see below) probably account for the idea of an affinity between the two genera. Both have compressed, keeled glumes and lemmas, with hyaline margins. *Megalachne* differs in having a tuft of white hairs at the base of the lemmas and terminal awns on the lemmas. Caryopses were lacking from Philippi's original material and are hence not described by him or by Bentham and Hooker in *Genera Plantarum*. They are, in fact, similar to caryopses of species of the *Ceratochloa* group, being bilaterally compressed, often with prominent bands of whitish endosperm visible through the translucent pericarp. There are hairs at the apex but not a true appendage as in *Bromus*. There are three stigmas, whereas in *Ceratochloa* there are merely three small knobs at the summit of the grain.

The morphological resemblances of *Megalachne* and *Bromus* s.l. are hence somewhat trivial, while the differences are in more important characters. Pilger (1920) has assigned this curious taxon to *Bromus*, but the evidence of morphology, starch grains and serology makes this unacceptable. *Megalachne* is a distinct genus.

Littledalea Hemsl. is a strikingly distinct genus of perennial grasses from China and Tibet. Having the general facies of *Bromus*, it possesses large, ligulate, papery lemmas, with erose tips. None of the seven or nine nerves is produced into an awn. The spikelets are broadly cuneiform. The ovary and caryopsis are surmounted by a hairy appendage resembling that of *Bromus*, and the two feathery styles emerge from it laterally. *Littledalea* has simple starch grains and overlapping sheaths.

At present it seems to the writer that *Littledalea* is a discrete genus, pending the accumulation of more evidence of its similarity or otherwise to *Bromus*. In many ways it appears more primitive than *Bromus*, combining many of the features which might have been expected in the early bromes. It would be premature to claim *Littledalea* as a representative of a morphological stage previous to the origin of the genus *Bromus* until more evidence is available. The genus is now under active investigation with this aim in view.

Many other species mistakenly have been included in *Bromus* s.l. in the past, and are now widely recognised as members of other genera. *Festuca gigantea* (L.) Vill. was once considered to be a brome by many authors, including Linnaeus, but the superficiality of the resemblance is now well known. There seems to be an effective genetic barrier between species of *Bromus* and *Festuca* (Smith 1969b). *Bromus* s.l. may be recognised by the following features:

> Annual or perennial grasses of diverse vegetative morphology; ligules membranous; sheaths connate; inflorescence a panicle; spikelets hermaphodite with one to many similar florets; lemmas exceeding the glumes; glumes persistent at maturity; glumes and lemmas few- or many-nerved,

awned or awnless; awns, when present, always subterminal; lodicules entire; caryopsis usually adherent to the palea, and tightly enclosed within the lemma; hilum narrow, elongate; hairy appendage surmounting the ovary and grain on which the stigmas are borne laterally.

Starch grains simple; basic chromosome number apparently always seven.

The groups commonly recognised within the above generic limits are briefly diagnosed below. The names of species included are the specific epithets appropriate to inclusion within *Bromus* L. The list is not exhaustive. Obvious synonyms are omitted.

Group I

Annual grasses; spikelets lanceolate or ovate-lanceolate, more or less terete or slightly compressed; lower glume 3–5-, upper glume 5–7-nerved; lemmas rounded on the back, with a shallow terminal notch, sometimes lacking; awns single, straight and erect or divaricate, equalling or slightly exceeding the lemmas in length, rarely absent.

Native distribution: Europe, Mediterranean area, Asia.

Species included: *abolinii* Drobov; *adoensis* Hochst.; *aegyptiacus* Tausch.; *anatolicus* Boiss. & Heldr.; *alopecuroides* Poir.; *arenarius* Labill.; *arvensis* L.; *brachystachys* Horn.; *brizaeformis* F. & M.; *commutatus* Schrad.; *degenii* Pénzes; *gedrosianus* Pénzes; *grossus* Desf. ex DC.; *hordeaceus* L.; *intermedius* Guss.; *interruptus* (Hack.) Druce; *japonicus* Thunb.; *javorkae* Pénzes; *lanceolatus* Roth; *lepidus* Holmberg; x *litvinovii* Roshev.; *molliformis* Lloyd; *oostachys* Bornm.; *oxyodon* Schrenk; *palaestinus* Meld.; *pectinatus* Thunb.; *pseudosecalinus* P. Smith; x *pseudothominii* P. Smith; *racemosus* L.; *scoparius* L.; *secalinus* L.; *sewerzowii* Regel; *squarrosus* L.; *szaboi* Pénzes; *tuzsonii* Pénzes; *tytthanthus* Nevski; *ugamicus* Drobov.

Group II

As "group I" except as follows: having a deep sinus at the apex of the lemma, with the resulting pair of apical teeth long, narrow, rather hard and awn-like, the true awn arising below the sinus (the lemma might be thought to be three-awned on casual inspection); lemma with a marked marginal tooth (pointed or rounded) on either side, about $\frac{1}{3}$ down from the apex.

Native distribution: the Ardennes. Possibly extinct?

Species included: *bromoideus* (Lej.) Crép.

Group III

As "group I" except as follows: spikelets compressed; lemmas with several irregular apical notches below which arise usually three awns; lower lemmas often with a single awn, upper lemmas usually with three; lateral awns often weaker than central awn and occasionally vestigial, sometimes all three awns are equally robust; awns flattened and strongly recurved at maturity.

Native distribution: SW Asia, eastern Mediterranean area.

Species included: *danthoniae* Trin.

GROUP IV

As "group I" except as follows: spikelets terete; rhachilla internode long, up to about ½ the length of the lemma; lower lemmas 5-awned, below an irregularly toothed apex, upper lemmas 5–9-awned; awns flattened, and recurved at maturity.

Native distribution: Central and SW Asia, eastern Mediterranean area.

Species included: *pumilio* (Trin.) P. Smith.

GROUP V

Annual grasses; spikelets lanceolate only when young, later cuneiform, wider at the top; lower glume 1-, upper glume 3-nerved; awns single, long, usually flattened and rough.

Native distribution: Europe, Mediterranean area, W Asia.

Species included: *diandrus* Roth; *fasciculatus* Presl.; *flabellatus* Hack. ex Boiss.; *haussknechtii* Boiss.; *madritensis* L.; *rigidus* Roth; *rubens* L.; *sericeus* Drobov; *sterilis* L.; *tectorum* L.

GROUP VI

Perennial grasses, forming sods or tufts; spikelets narrow, more or less lanceolate, terete; lower glume 1(–3)-nerved, upper glume 3(–5)-nerved; lemmas rounded or slightly keeled on the back, sometimes unevenly hairy; awns single, usually shorter than the lemmas, rarely weak or absent.

Native distribution: Eurasia, Africa and Madagascar; North and South America.

Species included: *adjaricus* Somm. & Lev.; *albidus* M. Bieb.; *angrenicus* Drobov; *anomalus* Rupr. ex Fourn.; *armenus* Boiss.; *arrhenatheroides* Baker; *attenuatus* Swallen; *auleticus* Trin. ex Nees; *avenoides* Baker; *benekenii* (Lange) Trimen; *biebersteinii* Roem. & Schultz; *cappadocicus* Boiss. & Bal.; *ciliatus* L.; *cognatus* Steud.; *densus* Swallen; *dissitiflorus* Baker; *dolichocarpus* Wagnon; *erectus* Huds.; *exaltatus* Bernh.; *fibrosus* Hack.; *frigidus* Boiss. & Hausskn.; *frondosus* (Shear) Woot. & Standl.; *grandis* (Shear) Hitchc.; *himalaicus* Stapf; *inermis* Leyss.; *irkutensis* Kom.; *kalmii* Gray; *kopetdagensis* Drobov; *korotkyi* Drobov; *lanatipes* (Shear) Rydb.; *laevipes* Shear; *latiglumis* Hitchc.; *macranthus* E. Desv.; *orcuttianus* Vasey; *ornans* Kom.; *pacificus* Shear; *pamiricus* Drobov; *paulsenii* Hack.; *pinetorum* Swallen; *porteri* (Coult.) Nash; *pseudolaevipes* Wagnon; *pubescens* Muhl. ex Wild.; *pumpellianus* Scribn.; *purgans* L.; *ramosus* Huds.; *richardsonii* Link; *riparius* Rehm.; *runssorensis* K. Schum.; *scabridus* Hook. f.; *sclerophyllus* Boiss.; *suksdorfii* Vasey; *texensis* (Shear) Hitchc.; *thysanoglottis* Soderstr. & Beam.; *tomentellus* Boiss.; *tomentosus* Trin.; *turkestanicus* Drobov; *tyttholepis* Nevski; *variegatus* M. Bieb.; *vogulicus* Socszava; *vulgaris* (Hook) Shear.

GROUP VII

Perennial, tuft-forming grasses; spikelets ovate or ovate-lanceolate, strongly compressed; lower glume 3–5-, upper glume 5–7-nerved; lemmas strongly keeled on the back; awn single, usually short, often absent.

Native distribution: North, Central and South America.

Species included: *aleutensis* Trin.; *arizonicus* (Shear) Stebbins; *breviaristatus* Buckl.; *carinatus* Hook. & Arn.; *coloratus* Steud.; *haenkeanus* Kunth; *laciniatus* Beal; *mango* E. Desv.; *marginatus* Nees; *maritimus* (Piper) Hitchc.; *pitensis* H.B.K.; *polyanthus* Scribn.; *sitchensis* Trin.; *stamineus* E. Desv.; *unioloides* H.B.K.; *valdivianus* Phil.; *willdenowii* Kunth.

Group VIII

Annual grasses; spikelets few-flowered, small (up to 10 mm long) terete when young, later somewhat compressed, ovate-lanceolate, becoming cuneiform (wider above) when mature; glumes narrow, the lower 1-nerved, the upper 3-nerved; lemma rounded on the back; awn single, slender and straight, 4–6 times as long as the lemma.

Native distribution: Central Asia, Iran, Afghanistan.

Species included: *gracillimus* Bunge.

Group IX

Annual grasses; spikelets narrowly elliptic; lower glume 1-nerved, upper glume 3–5-nerved; lemmas with a deep apical sinus and two long, narrow teeth; awn single, longer than the lemma, twisted below the middle and spreading at maturity.

Native distribution: Pacific seaboard countries of North, Central and South America.

Species included: *trinii* E. Desv.

2. Treatment of the brome-grasses as a single genus

Plants falling into several of the above mentioned groups were included by Linnaeus in his genus *Bromus* (*Species Plantarum* 1753). Linnaeus' concept of the genus at that date was quite a wide one, and hence the name *Bromus* is quite suitable for a genus including all or most of the grasses included in Groups I–IX. The genus *Forasaccus* Bub. (1901) has a similar circumscription and definition.

The question which now arises is to which subsidiary group the name *Bromus* L. should be applied, if these groups were to be regarded as individual genera. The answer depends on which species is regarded as the type of Linnaeus' genus *Bromus*. Several species have been considered as representative of Linnaeus' concept of the "natural character" (Stearn, 1957) of the genus. *B. secalinus* L. was chosen by Shear (1900), Britton & Brown (1913) and Britton (1918). *Bromus sterilis* L. was selected by Hichcock & Green (1929) and Phillips (1951). Wagnon (1952) argues that *B. arvensis* L. should be the lectotype, and his conclusion is accepted by Soderstrom and Beaman (1968).

Wagnon indicates the arbitrary nature of Shear's decision in 1900 (also admitted by Shear) in simply choosing the first *Bromus* species in *Species Plantarum* ed. 1 (1753). He then selects *B. arvensis* on criteria scarcely less

arbitrary. The synonyms quoted in *Hortus Cliffortianus* (1737) and *Flora Lapponica* (1737) which are contemporaneous with the first edition of Linnaeus' *Genera Plantarum*, are applied to *B. arvensis* in 1753 (*Species Plantarum*). Wagnon therefore claims that *B. arvensis* was thought most typical of the genus by Linnaeus. This seems unlikely to the present writer, and does less than justice to Linnaeus' generic concepts!

The references to figures of *Bromus* L. in *Genera Plantarum* (1737) indicate that Linnaeus had, from the first, a concept of the genus based on more than one species. There is an asterisk against the name *Bromus* indicating that the plant or plants were known to Linnaeus in the living state. Monti's figure 32, which is cited, is of a spikelet almost certainly of *B. squarrosus* L. Scheuchzer's figures on his plate 5 (of *Agrostographia sive Graminum* etc., 1719) are of various bromes, with the exception of number 2. Figure 10 is referable to *B. arvensis* L. or *B. commutatus* Schrad., figure 11 to *B. squarrosus* L., and figure 12 to *B. secalinus* L. The figure cited from Dillenius ("*Dill. gen.* 3") is of an immature spikelet belonging to some species in "Group I". Although covering a range of species, Linnaeus' original conception of the genus therefore seems to be a taxon resembling "Group I".

The single species of *Bromus* mentioned in *Flora Lapponica* (1737) is later (*Species Plantarum* 1753) referred to by the name *B. arvensis*. The subsequent species (no. 28) becomes *B. secalinus* in 1753, but is ascribed to *Festuca* in *Flora Lapponica*. By 1745, Linnaeus had evidently adopted "no. 28" (*B. secalinus*) as most representative of his genus, because he puts it first in the first edition of *Flora Suecica* (1745). He quotes the Swedish local name for the plant—"Roglosta"—which is still used for *B. secalinus*, and gives a habitat note—"*Inter segetes*". In *Flora Suecica* (ed. 1.) "no. 27" of *Flora Lapponica* (to be named *B. arvensis* in 1753) is relegated to second place. The common name "Renlosta" is cited, and Linnaeus indicates that this is a plant of field margins.

Therefore, between 1737 and 1745 Linnaeus deliberately reversed the position of the first two species he refers to his genus *Bromus*, together with all their synonyms and references. This must suggest that he considered *B. secalinus* better indicated the character of his genus. This conclusion is strengthened by his treatment of *Bromus* in *Species Plantarum* (1753). *B. secalinus* still occupies first place, while *B. arvensis* is further down the list, after three other species in two distinct groups (*B. purgans*, *B. ciliatus* and *B. sterilis*). Though Linnaeus widens his generic concept here, he retains *B. secalinus* in first place.

Hence there seems to be abundant evidence in Linnaeus' published works that *B. secalinus* was the brome he knew best and thought most indicative of his genus *Bromus*. He was sufficiently interested by this species to carry out experimental taxonomic observations on it, the results of which appear in the second edition of *Flora Suecica* in 1755 (see Smith 1968). Of all the species known to Linnaeus, *B. secalinus* comes nearest to obeying his rule (*Critica Botanica* 246, 1737) that what we now call a generitype should be "the best known and officinal plant".

Bromus secalinus should undoubtedly, therefore, be considered the lectotype of *Bromus* L. and consequently (Article 22, Code of Nomenclature) any genus containing it must be named *Bromus*, and so must any subgenus or section of *Bromus* in which it is included.

This correct name for a genus containing *B. secalinus* L. was used, for example, by Fries (1843), Shear (1900), Tutin (1962) and Hubbard (1969) although their concepts of the size and limits of the genus differ considerably. The correct use of the name *Bromus* for an infrageneric taxon including *B. secalinus* is less widespread. *Bromus* subgenus *Bromus* was recognised and so named by Nyman (1855) and Shear (1900), but not by Ovadiahu-Yavin (1969) who uses the name *Zeobromus*. *Bromus* section *Bromus* was recognised and correctly named by Soderstrom and Beaman (1968) but not by Hitchcock & Chase (1951) who use the name *Bromium* Dum.

3. Nomenclatural history of *Bromus s.l.*

The following lists give details of the names applied to the groups of brome-grasses defined above, at generic, subgeneric and sectional rank. The species included are referred to by the specific epithet appropriate to their inclusion in the genus *Bromus*. If the section or subgenus proposed for the bromes enumerated was referred by the authority to a genus other than *Bromus*, the name of the other genus appears in brackets before the species list. The list of generic names omits many extremely heterogeneous genera, described by early authors, which included only one or two species now referable to *Bromus* s.l. as defined above. They are too numerous to list, and are no longer of any significance. One exception, which is included because it has been an unusually persistent name associated with brome-grasses, is *Schedonorus* Beauv., which included only one brome species.

(a) *Sectional Names in Bromus s.l.*

Author	Date	Sectional Name	Species Included
Dumortier	1823	*Genea*	*sterilis, tectorum, rigens, rigidus.*
,,	,,	*Bromopsis*	*giganteus, asper.*
,,	,,	*Pnigma*	*erectus, inermis.*
,,	,,	*Bromium*	*mollis, affinis, racemosus, elongatus, arvensis, agrarius, patulus, diffusus, gaudini, secalinus, squarrosus, nitidus, grossus.*
Dumortier	1827	*Bromotypus*	*squarrosus, mollis, racemosus, nitidus, diffusus, elongatus, brevisetus, secalinus, grossus, patulus, arvensis.*
Ledebour	1829	*Zerna*	*tectorum, inermis.*
Bertolini	1833	*Bromi secalini*	*secalinus, racemosus, arvensis, squarrosus, mollis, intermedius, lanceolatus, scoparius.*
,,	,,	*Bromi festucacei*	*giganteus, asper, inermis, erectus.*
,,	,,	*Bromi genuini*	*sterilis, scaberrimus, maximus, tectorum, rubens, fasciculatus.*
Koch	1837	*Libertia* Weihe	*bromoideus.*
Drejer	1838	*Bromochloa*	(*Festuca*) *asper, erectus, giganteus.*

Fries	1843	*Perennes*	(*Schedonorus*) *inermis, asper, erectus.*
,,	,,	*Annui*	(*Schedonorus*) *sterilis, tectorum.*
Koch	1843	*Serrafalcus* Parl.	*secalinus, commutatus, racemosus, mollis, confertus, brachystachys, arvensis, patulus, squarrosus.*
Grisebach	1844	*Zeobromus*	*mollis, racemosus, scoparius, squarrosus, patulus, macrostachys*
,,	,,	*Schoenodorus*	*asper, erectus, inermis.*
,,	,,	*Stenobromus*	*maximus, madritensis, tectorum, sterilis.*
Cosson & Germain	1845	*Perennes*	*asper, erectus.*
,,	,,	*Annui*	*sterilis, tectorum, arvensis, secalinus, mollis, racemosus.*
Fries	1845	*Festucacei*	(*Schedonorus*) *inermis, asper, erectus.*
,,	,,	*Vulpioidei*	(*Schedonorus*) *sterilis, tectorum.*
Grisebach in Ledebour	1853	*Schedonorus* Fries	*asper, erectus, variegatus, tomentosus, albidus, inermis, latifolius, subulatus, ciliatus, sterilis, tectorum, maximus, rubens, madritensis.*
,,	,,	*Ceratochloa* Beauv.	*purgans, aleutensis, sitchensis.*
,,	,,	*Zeobromus*	*mollis, racemosus, arvensis, squarrosus, macrostachys, danthoniae, patulus, secalinus, brizaeformis.*
Cosson & Durieu	1855	*Eubromus*	*sterilis, madritensis, rigidus, tectorum, rubens, fasciculatus.*
,,	,,	*Festucoides*	*erectus.*
Grenier & Godron	1856	*Festucaria*	*asper, erectus, inermis.*
Kirschleger	1857	*Trespa*	*sterilis, tectorum.*
Jessen	1863	*Steriles*	(*Festuca* subg. *Annuae*) *sterilis, tectorum.*
Husnot	1898	*Euserrafalcus*	(*Serrafalcus*) *secalinus, patulus, arvensis, racemosus, mollis, hordeaceus, molliformis, intermedius squarrosus, macrostachys.*
,,	,,	*Michelaria*	(*Serrafalcus*) *bromoideus.*
,,	,,	*Festucaria*	*asper, erectus, inermis.*
Koch	1907	*Michelaria* (Dum.) Brand	*bromoideus.*
Rouy	1913	*Secalini*	*secalinus.*
,,	,,	*Euserrafalcus*	*arvensis, racemosus, commutatus, mollis, thominii, lloydianus, intermedius, patulus, squarrosus, macrostachys.*

Holmberg	1924	*Macrantheri*	*arvensis, brachystachys.*
,,	,,	*Brachyantheri*	*japonicus, squarrosus, secalinus, racemosus, commutatus, mollis, hordeaceus, lepidus, scoparius, intermedius, macrostachys.*
Nevski	1934	*Aphaneroneuron*	*arvensis, brachystachys, japonicus, squarrosus, secalinus, racemosus, commutatus.*
,,	,,	*Sapheneuron*	*mollis, lepidus, scoparius, intermedius, macrostachys, tytthanthus, severtzovii, oxydon.*
,,	,,	*Triniusia* Steud.	*danthoniae.*
Hitchcock	1935	*Neobromus* Shear	*trinii.*
Tournay	1961	*Nevskiella* Krecz. & Vved.	*gracillimus.*

(b) *Subgeneric Names in Bromus s.l.*

Author	Date	Subgeneric Name	Species Included
Nyman	1855	*Schedonorus*	*giganteus, asper, pannonicus, erectus, variegatus, inermis, maximus, rigidus, madritensis, rubens, tectorum, sterilis, longipilus, fasciculatus.*
Hackel	1887	*Festucoides*	*erectus, inermis, catharticus.*
,,	,,	*Stenobromus*	*tectorum, sterilis.*
,,	,,	*Zeobromus*	*secalinus, arvensis, mollis, danthoniae.*
,,	,,	*Libertia* Lejeune	*bromoideus.*
,,	,,	*Ceratochloa*	*unioloides, mango.*
Shear	1900	*Neobromus*	*trinii.*
,,	,,	*Zerna* Panz.	*orcuttianus, purgans, pacificus, porteri, kalmii, vulgaris, ciliatus, richardsonii, suksdorfii, ramosus, laevipes, pumpellianus, erectus, inermis.*
			porteri, kalmii, vulgaris, ciliatus, inermis.
,,	,,	*Ceratochloa* Beauv.	*polyanthus, aleutensis, laciniatus, carinatus, sitchensis, marginatus, unioloides, subvelutinus.*
Rouy	1912	*Eubromus* Godr.	*distichus, tectorum, villosus, madritensis, rubens.*
Kreczetovich & Vvedensky	1934	*Nevskiella*	*gracillimus.*
Pénzes	1936	*Triniusia* Steud.	*danthoniae, pseudodanthoniae.*

(c) *Generic Names applied within Bromus s.l.*

Author	Date	Generic Name	Species Included
Ehrhart	1789	*Lasiopoa*	*asper.*
Palisot de Beauvois	1812	*Ceratochloa*	*unioloides.*
,,	,,	*Schedonorus*	*elatior, altissima, arundinacea, aurata, aurea, calamaria, curvata, dumetorum, eskia, gerardi, glauca, inermis, littoralis, lolicea, ingrescens, pilosa, poaeformis, pratensis, pulchella, rhetica, scheuchzeri, serotina, sylvatica, tenella, varia, violacea, poacurvata.*
Panzer	1813	*Zerna*	*asper, giganteus, madritensis, macrostachys, tectorum, sterilis, erectus, ligusticus,* (*Festuca myurus, bromoides* and *distachyos*).
Dumortier	1823	*Michelaria*	*bromoideus.*
Lejeune	1824 – 1825	*Libertia*	*bromoideus.*
Parlatore	1840	*Serrafalcus*	*racemosus, velutinus, mollis, intermedius, lanceolatus, scoparius.*
Sprengel	1840	*Aechmophora* Spreng. ex Steud.	*bromoideus.*
Fries	1843	*Schedonorus*	*inermus, asper, erectus, sterilis tectorum.*
Koch, C.	1848	*Anisantha*	*pontica.*
Steudel	1854	*Triniusa*	*danthoniae, flavescens.*
Hochstetter	1894	*Boissiera* Hochst. ex Steud.	*pumilio.*
Kreczetovich & Vvedensky	1934	*Nevskiella*	*gracillimus.*
Nevski	1934	*Trisetobromus*	*trinii.*

4. Correct names for taxa within Bromus *s.l.*

The correct generic, subgeneric or sectional names for Groups I–IX can be chosen from the lists above, in accordance with the provisions of the *Code of Nomenclature*. The correct name for a genus or a subdivision of a genus is the earliest legitimate name validly published in that rank. For each of Groups I–IX, the correct name in each rank is the earliest legitimate, validly published name the type species of which is included in that particular Group.

(a) Names for Group I

As previously indicated, the name for any genus or infrageneric taxon including *B. secalinus*, the type species of *Bromus* L., must be *Bromus.*

Thus if Group I is recognised as a genus its name is *Bromus* L. If it is considered to be a subgenus of *Bromus* L., then the correct combination is *Bromus* L. subgenus *Bromus*. At the sectional level, if thought appropriate for Group I, the name must be *Bromus* L. section *Bromus*.

(b) Names for Group II

The correct generic name is *Michelaria* Dumortier (1823). If this group is regarded as a subgenus of *Bromus*, the correct name is *Libertia* (Weihe ex Koch) Hackel. Lejeune's *Libertia* (pro. gen.) is a homonym of the conserved name *Libertia* Spreng. (Iridaceae). At sectional level, the correct name for Group II is *Libertia* Weihe ex Koch.

The type of all these names is the sole species referable to group II. This is *Bromus bromoideus* (Lej.) Crépin. This plant was first noted as conspecific with *Briza subaristata* by Beauvois (Ess. Agrost., p. 85, and plate XVII, fig. 7, 1812), who included it in his heterogeneous genus *Calotheca*. Following Michel's rediscovery of the plant in 1822, Lejeune named it *Calotheca bromoidea* (*Messager des Sciences et des Arts du royaume de Pays Bas*, Sept. 1823). Dumortier regarded *Calotheca* as an insufficiently natural genus for so distinct a plant and so re-named it *Michelaria bromoidea* (Obs. Gram. Belg., 1823), with a reference to Lejeune's prior publication. Dumortier also suggested *Bromus arduennensis* as a provisional name, which was later validly published by Kunth (Enum. I: 416, 1833). The aptness of this name for an Ardennes endemic with such obvious brome-like qualities has ensured its wide and long-lasting adoption. The correct name for the plant as a *Bromus* species is *Bromus bromoideus* (Lej.) Crépin (*Bull. Soc. roy. bot. Belg.* 6: 399, 1867). The basionym is *Calotheca bromoidea* Lej.

(c) Names for Group III

Treated as a genus, Group III must be named *Triniusa* Steud. As a subgenus of *Bromus*, the appropriate name is *Triniusa* (Steud.) Pénzes. *Triniusia* is an orthographic variant of *Triniusa*. At sectional level, the correct name is *Triniusa* (Steud.) Nevski. The type is *B. danthoniae* Trin. in C.A. Meyer, Verz. Pfl. Cauc. 24 (1831) (*Triniusa danthonia* Steud., Syn. Pl. Glum. 328, 1854).

(d) Names for Group IV

The correct generic name is *Boissiera* Hochst. ex Steud. It has not been recognised as an independent subgenus or section of *Bromus*, so that combinations appropriate to these rankings do not exist. If included in the genus *Boissiera*, the type is the sole species *Boissiera squarrosa* (Soland.) Nevski. Smith (1969a) includes this species as a member of what is here described as Group I, under the name *Bromus pumilio* (Trin.) P. Smith.

(e) Names for Group V

For this Group the correct generic name is *Anisantha* C. Koch. As a subgenus of *Bromus* it should be named *Stenobromus* (Griseb.) Hackel, while as a section of *Bromus* it must be named *Genea* Dumortier. The lectotype of *Anisantha* C. Koch is *A. tectorum* (L.) Nevski (syn. *A. pontica* C. Koch). The lectotype of *Stenobromus* (Griseb.) Hackel is *Bromus rigidus* Roth in Roem. & Usteri, Mag. Bot. 4, 10: 21 (1790). The lectotype of *Genea* Dum. is *B. sterilis* L.

(f) Names of Group VI

If Group VI is treated as a genus, the best name for it is *Zerna* Panzer. The lectotype is *Z. ramosa* (Huds.) Lindm. Although Panzer's treatment of *Zerna* contained several disparate elements (including bromes in other Groups, and species in genera outwith *Bromus* s.l.) he refers first to *B. ramosus* Huds. and his figure may also be of that species. This name is the earliest (1813) generic name including members of Group VI, with the exception of *Schedonorus* Beauv. (1812) which consisted largely of *Festuca* species, and *Lasiopoa* Ehrhart (1789) which is not validly published. If Group VI is thought to be a subgenus of *Bromus* L., the correct name is *Festucoides* (Coss. & Dur.) Hackel. The lectotype is *B. erectus* Huds., Fl. Angl. 39 (1762). At sectional level within *Bromus*, Group VI is correctly named section *Pnigma* Dumortier, for which Soderstrom & Beaman (1968) have chosen *B. inermis* Leyss. (Fl. Hal. ed. 1: 16, 1761) as lectotype.

(g) Names for Group VII

As a genus this Group should be named *Ceratochloa* Beauv. As a subgenus of *Bromus* the correct name is *Ceratochloa* (Beauv.) Hackel, and as a section of *Bromus*, the correct name is *Ceratochloa* (Beauv.) Griseb. In each case the type is *Bromus willdenowii* Kunth, Rev. Gram. I: 134 (1829) (= B. *unioloides* auct.). (*Ceratochloa unioloides* (Willd.) Beauv., non *Bromus unioloides* H.B.K.).

(h) Names for Group VIII

The correct generic name for this Group is *Nevskiella* Kreczetovich & Vvedensky. It was subsequently treated as a subgenus of *Bromus*, by the same authors, bearing the same name. If recognised as a section, it should be named section *Nevskiella* (Krecz. & Vved.) Tournay. The type is *Bromus gracillimus* Bunge in Mém. Acad. Pétersb. sav. étrang. VII, 527, (1851); (*Nevskiella gracillima* (Bunge) Krecz. & Vved.)

(i) Names for Group IX

This Group must be named *Trisetobromus* Nevski if regarded as a discrete genus. As a subgenus of *Bromus* it should be named *Neobromus* Shear, and as a section it should be named *Neobromus* (Shear) Hitchc. The type is *Bromus trinii* Desv. in Gay, Hist. de Chil. Bot. 6: 441 (1853); (*Trisetobromus hirtus* (Trin.) Nevski).

5. Attribution of rank to groups I–IX

The attribution of suitable rank to taxa at the generic and infrageneric levels of the hierarchy is sometimes a difficult task. In the case of the brome grasses, the existence of so many names and different treatments attests the fact that this is such a problem group.

The first question to answer concerns the degree of relationship between the nine groups considered, taking all available evidence into account. All fall into the general description of *Bromus s.l.* given previously. This indication of homogeneity can be supplemented by data from genetics and serology. Between most of the nine groups some degree of gene exchange can occur, at least permitting the establishment of F_1 hybrids (see e.g.

Cugnac 1935; Cugnac & Camus 1944). Intergroup F_1 hybrids, where known, are infertile. F_1 hybrids within groups are more commonly fertile (Wilson, 1956; Smith, 1968 and in press). Rarely, such hybrids are as fertile as the parent species. Genetic information is not yet available for some of the groups.

Serological evidence (Fairbrothers & Johnson 1961; Smith 1965; 1969a, b) indicates a high level of similarity between the seed proteins of species in many of the groups of brome-grasses defined above. Species in other genera show significantly weaker serological relationships.

The differences between the groups are largely of morphological complexity in the reproductive parts. The size and shape of spikelets, lemma and awns, and the differences in nervature are associated with variation in dispersal methods and ecology. Though often striking at first sight, on closer study these differences are seen to be relatively trivial modifications of fundamentally similar structures. They are a good deal more trivial than the characters which define *Bromus s.l.* as a whole.

Recognition of some or all the separate groups as independent genera obscures the homogeneity of the group as one entity. In the north west Eurasian area, where most of the taxonomic conclusions on these grasses have originated, groups I, V, VI and VII appear quite distinct. In terms of morphology, however, groups I, V and VI are much less distinct in other parts of their range. Their distinguishing characters are less reliable. If these larger groups are regarded as genera, they are further reduced in discreteness by the incidence of amphidiploid hybrids known or suspected to occur between them. If all these grasses are included in a single large genus the result is a highly natural unit. With some subdivision, this taxon is a practical, convenient unit. It is an evolutionary entity which has the added merit of corresponding to the traditional or folk concept of the genus including brome-grasses.

The single genus, *Bromus s.l.*, would be a member of the tribe Bromeae, with the genus *Littledalea* as the only other occupant at present. Of the groups within *Bromus s.l.*, defined above, I consider that I, II, III and IV should all be included in one single infrageneric taxon. They are similar morphologically except in the minor diagnostic characters noted. They have a related distribution pattern, are closely related serologically and some at least are known to form completely fertile hybrids. *Bromus bromoideus* may not even be specifically distinct from *B. secalinus*. The relationships of *Boissiera* Hochst. ex Steud. (Group IV) and *Bromus danthoniae* (Group III) have been dealt with elsewhere (Smith 1969a). In these cases, the apparent differences are more peculiar than they are significant. Groups I to IV would therefore be best treated as a single infrageneric taxon of *Bromus* L., named *Bromus*.

Not much is yet known of the actual genetic and evolutionary affinities of the six infrageneric taxa it is proposed to recognise in *Bromus s.l.* Such information as there is supports the idea of their essential consanguinity. It seems expedient to recognise this, pending the accumulation of more data, by regarding them as sections of *Bromus s.l.* If subsequent research reveals that the differences between them are more fundamental than is at present supposed, attention can be drawn to this by raising the rank to subgenus. Where there is a reasonable choice in the attribution of rank,

it seems a good principle to confine possible errors based on inadequate knowledge to the lowest levels of the hierarchy consistent with convenience of use.

The names for the six sections here recognised within the genus *Bromus* L. are therefore:

Groups I–IV:	Section *Bromus*
Group V:	Section *Genea* Dumortier, Obs. Gram. Belg. 116 (1823).
Group VI:	Section *Pnigma* Dumortier, *l.c.* 117 (1823).
Group VII:	Section *Ceratochloa* (Beauv.) Griseb. in Ledeb., Fl. Ross. 4: 360 (1853).
Group VIII:	Section *Nevskiella* (Krecz. & Vved.) Tournay in Bull. Jard. bot. État. Brux. 31: 289–299 (1961).
Group IX:	Section *Neobromus* (Shear) Hitchcock, Manual of the Grasses of the United States 55 (1935).

Acknowledgments

I thank Professor G. L. Stebbins for supplying me with viable seed of *Megalachne* and Mr Peter Jura M.S. for kindly producing embryo sections. I am grateful to Messrs. B. L. Burtt, W. D. Clayton and J. E. Dandy for nomenclatural information and advice.

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