NEW GENERIC CONCEPTS IN THE TRITICEAE OF THE INTERMOUNTAIN REGION: KEY AND COMMENTS

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Abstract.— Revision of the perennial genera of North American Triticeae requires recognition of seven new genera in the Intermountain Region: *Elytrigia, Leymus, Psathyrostachys, Pseudoroegneria, Thinopyrum,* and the hybrid genera × *Elyleymus* and × *Pseudelymus*. One previously recognized genus, *Sitanion,* is included in *Elymus*. Several new combinations are presented to accommodate the taxonomic changes. *Elymus trachycaulus* is treated as a widespread, polymorphic species with three subspecies in the region: subsp. *trachycaulus, subsecundus,* and *latiglumis*. *Agropyron dasystachyum* and *A. albicans* are treated as conspecific subspecies of *Elymus lanceolatus*. A key to the genera of the Triticeae occurring in the Intermountain Region is presented as well as keys and brief descriptions for those genera not included in, or substantially modified from, other regional treatments.

Agrostologists have been aware for a long time that traditional North American treatments of the Triticeae (e.g., A. Hitchcock 1951, Gould 1968, C. Hitchcock 1969, Holmgren and Holmgren 1977) do not reflect the evolutionary relationships within the tribe. Nevertheless, in the absence of any well-documented revision that included a high proportion of the North American species, most North American taxonomists have adopted A. Hitchcock's (1951) treatment, with relatively minor modifications, as the best available. Recently, however, Dewey (1982, 1983a, 1983b) has published a revision of the perennial genera that better reflects the genomic and ecological data available and is consistent with the morphological data. Although written in terms of North American taxa, Dewey's treatment is based on data from the full geographic and taxonomic range of the tribe.

This paper is designed to assist those who wish to use Dewey's generic concepts for plants from the Intermountain Region. It includes a key to the genera of the tribe in the region and, for those genera not included in, or substantially modified from Holmgren and Holmgren (1977), brief generic descriptions and keys to the infrageneric taxa that we recognize. Readers are referred to the Holmgrens' article for illustrations, detailed descriptions of the species, and the complete synonymy. Table 1 summarizes the differences between the treatment presented here and that found in their article.

Taxonomic Treatment

The genera that are most affected by the revised generic boundaries are *Agropyron* Gaertn., *Elymus* L., and *Sitanion* Raf. *Agropyron* has been restricted to the crested wheatgrasses, the remaining species being assigned to *Elymus, Elytrigia, Pseudoroegneria,* or *Thinopyrum*. Several species of *Elymus* have been placed in the segregate genus *Leymus* Hochst., but all species of *Sitanion* are now included in *Elymus*. The reasons for these and other changes are given in the discussion of individual genera. To assist those not familiar with the subtribal classification of the Triticeae, the genera and species within genera are treated alphabetically after the generic key.

The intergeneric hybrids are treated after the nonhybrid genera. Readers are advised that such hybrids are relatively rare in nature. We include them because they do exist but, in our experience, most plants thought to be hybrids are aberrant forms of good species. Interspecific hybrids are more common, particularly in disturbed areas. Part of the problem in identifying hybrids in the Triticeae, particularly interspecific hybrids, is that most can backcross to their parents,

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TABLE 1. Synopsis of our revised treatment of the Triticeae occurring in the Intermountain Region compared with that presented in the *Intermountain Flora* (Holmgren and Holmgren 1977).

REVISED TREATMENT	INTERMOUNTAIN FLORA
Aegilops cylindrica L.	*Aegilops cylindrica* L.
Agropyron cristatum L.	*Agropyron cristatum* L.
Agropyron desertorum J. A. Shultes	included in *A. cristatum* L.
Agrpyron fragile Roth	included in *A. cristatum* L.
× *Elyhordeum macounii* (Vasey) Barkworth & D. R. Dewey	× *Agrohordeum macounii* (Vasey) Lepage
× *Elyleymus aristatus* (Merrill) Barkworth & D. R. Dewey	× *Elysitanion aristatum* (Merril) Bowden
Elymus canadensis L.	*Elymus canadensis* L.
Elymus elymoides (Raf.) Sweezy	*Sitanion hystrix* (Nutt.) J. G. Smith
Elymus glaucus Buckley	*Elymus glaucus* Buckley
Elymus × *hansenii* Scribner, pro sp.	× *Elysitanion hansenii* (Scribner) Bowden
Elymus lanceolatus (Scribner & J. G. Smith) Gould	
subsp. *lanceolatus*	*Agropyron dasystachyum* (Hooker) Scribner
	var. *dasystachyum*
	Var. *riparium* (Scribner & J. G. Smith) Bowden
subsp. *albicans* (Scribner & J. G. Smith) Barkworth & D. R. Dewey	*Agropyron albicans* Scribner & J. G. Smith
	var. *albicans*
	var. *griffithsii* (Scribner & J. G. Smith) A. A. Beetle
Elymus multisetus (J. G. Smith) M. E. Jones	*Sitanion jubatum* J. G. Smith
Elymus × *pseudorepens* (Scribner & J. G. Smith) Barkworth & D. R. Dewey	*Agropyron* × *pseudorepens* Scribner & J. G. Smith
Elymus × *saundersii* Vasey	× *Agrositanion saundersii* (Vasey) Bowden
Elymus trachycaulus (Link) Gould ex Shinners	*Agropyron trachycaulum* (Link) Malte
subsp. *trachycaulus*	var. *trachycaulum*
subsp. *subsecundus* (Link) Barkworth & D. R. Dewey, pro parte	var. *glaucum* (Pease & Moore) Malte
subsp. *latiglumis* (Scribner & J. G. Smith) Barkworth & D. R. Dewey	var. *latiglumis* (Scribner & J. G. Smith) A. A. Beetle
subsp. *subsecundus* (Link) Barkworth & D. R. Dewey, pro parte	var. *unilaterale* (Cassidy) Malte
Elymus virginicus var. *submuticus* Hooker	*Elymus virginicus* var. *submuticus* Hooker
Elytrigia intermedia (Host) Nevski	*Agropyron intermedium* (Host) Beauv.
subsp. *intermedia*	var. *intermedium*
subsp. *barbulata* (Schur) A. Löve	var. *trichophora* (Link) Halac
Elytrigia repens (L.) Nevski	*Agropyron repens* (L.) Beauv.
Elytrigia spicata (Pursh) D. R. Dewey	*Agropyron spicatum* Pursh
Eremopyrum triticeum (Gaertner) Nevski	*Eremopyrum triticeum* (Gaertner) Nevski
Hordeum brachyantherum Nevski	*Hordeum brachyantherum* Nevski
Hordeum depressum (Scribner & Smith) Rydb.	*Hordeum depressum* (Scribner & Smith) Rydb.
Hordeum marinum Hudson	
subsp. *gussonianum* (Parl.) Thell.	*Hordeum geniculatum* All.
Hordeum murinum L.	
subsp. *murinum*	*Hordeum murinum* L.
subsp. *glaucum* (Steudel) Tsvelev	*Hordeum glaucum* Steudel
subsp. *leporinum* (Link) Arcang.	*Hordeum leporinum* Link
Hordeum pusillum Nutt.	*Hordeum pusillum* Nutt.
Hordeum vulgare L.	*Hordeum vulgare* L.
Leymus cinereus (Scribner & Merrill) A. Löve	*Elymus cinereus* (Scribner & Merrill)
Leymus flavescens (Scribner & Smith) Pilge	*Elymus flavescens* Scribner & Smith
Leymus salinus (M. E. Jones) A. Löve	
subsp. *salinus*	*Elymus salina* M. E. Jones
subsp. *salmonis* (C. L. Hitchc.) R. J. Atkins	*Elymus ambiguus* var. *salmonis* C. L. Hitchc.
Leymus simplex (Scribner & Williams) D. R. Dewey	*Elymus simplex* Scribner & Williams
Leymus triticoides (Buckley) Pilger	*Elymus triticoides* Buckley
Pascopyrum smithii (Rydb.) A. Löve	*Agropyron smithii* Rydb.

Table 1 continued.

Revised treatment	Intermountain Flora
Pseudoroegneria spicata (Pursh) A. Löve	*Agropyron spicatum* Pursh
× *Pseudelymus saxicolus* (Scribner & J. G. Smith) Barkworth & D. R. Dewey	× *Agrositanion saxicola* (Scribner & J. G. Smith) Bowden
Psathyrostachys juncea (Fischer) Nevski	*Elymus junceus* Fischer
Secale cereale L.	*Secale cereale* L.
Taeniatherum caput-medusae (L.) Nevski	*Taeniatherum caput-medusae* (L.) Nevski
Thinopyrum ponticum (Podp.) Barkworth & D. R. Dewey	*Agropyron elongatum* (Host) Beauv.
Triticum aestivum L.	*Triticum aestivum* L.

resulting in a morphological continuum as well as partial restoration of fertility. This problem is not unique to the Triticeae but it is exacerbated by the relatively small number of diagnostic characters available for these grasses.

Key to the Genera

1. Spikelets three at a node, each with only one floret; only the central floret fertile (exc. in *Hordeum vulgare* in which all three florets are fertile) .... *Hordeum*

— Spikelets not three at a node OR with more than one floret per spikelet (n.b watch out for some forms of *Elymus elymoides* [= *Sitanion hystrix*] in which the second floret of the central spikelet is reduced and the lateral spikelets have only a single, sterile, floret) 2

2(1). Annual or biennial, introduced cereals or weeds 3

— Perennial; native or introduced 7

3(2). Glumes ovate, with three or more (often many) nerves at midlength 4

— Glumes subulate to lanceolate, only one vein evident at midlength 5

4(3). Spikelets sunk in the rachis, the spike therefore very slender, less than 5 mm in diameter; rachis disarticulating at maturity .... *Aegilops*

— Spikelets not sunk in the rachis, the spike therefore with a larger diameter; rachis not disarticulating at maturity .... *Triticum*

5(4). Spikes less than 2.5 cm long; lemmas 5–7.5 mm long .... *Eremopyrum*

— Spikes more than 4 cm long; lemmas more than 8 mm long 6

6(5). Glumes more than 15 mm long, subulate, united at the base and tapering into a long slender awn; spikelets with only one fertile floret; lemmas glabrous .... *Taeniatherum*

— Glumes 6–15 mm long, narrowly lanceolate to linear, free to the base, gradually acuminate but not awned; spikelets with two fertile florets; lemmas conspicuously scabrous on the keel .... *Secale*

7(2). Spikelets solitary at each node, closely imbricate, often pectinate; internodes short, less than one third the length of the spikelets .... *Agropyron*

— Spikelets two or more at some nodes OR, if single at all nodes, neither closely imbricate nor pectinate and with internodes about half as long as the spikelets or longer 8

8(7). Glumes 3–10 mm long, very narrow, 1-nerved at midbody length, their keels lying over the sides of the lowest lemmas rather than the midvein; lemmas awnless or with awns up to 7 mm long 9

— Glumes 5–90 mm long, with 2–5 nerves evident at midbody length; keels of the glumes lying opposite the midveins of the lowest lemmas; lemmas often truncate or with awns more than 10 mm long 10

9(8). Rachis disarticulating at maturity; truly cespitose, branching intravaginal, rhizomes never present; old leaf sheaths becoming fibrous .... *Psathyrostachys*

— Rachis not disarticulating at maturity; often rhizomatous, sometimes shortly so, branching extravaginal; old leaf sheaths not fibrous .... *Leymus*

10(8). Plants fertile; anthers well-filled prior to anthesis, dehiscent, usually bleached and falling off after anthesis 11

— Plants sterile; anthers poorly filled prior to anthesis, nondehiscent, retaining their color and usually retained on the plant 13

11(10). Glumes 6–12 mm long; linear-lanceolate to lanceolate, tapering from below midlength into an awn-tip; only one spikelet at most nodes .... *Pascopyrum*

— Glumes varied but if 6–12 mm long either obtuse or tapering only in the distal third; number of spikelets per node 1–4, varying between species 12

12(11). Glumes acute to long awned, never truncate or obtuse; anthers 2–3.5 mm long and plants cespitose *or* anthers more than 3.5 mm long, plants rhizomatous, *and* leaf blades with subequal ribs .... *Elymus*

— Glumes varied, often truncate or obtuse; anthers 4–7 mm long, plants rhizomatous or cespitose, if both long anthered and rhizomatous [*E. repens*], leaf blades with 2–3 minor ribs alternating with the major ribs 13

13(12). Plants cespitose; glumes acute-tipped; spikelets only slightly longer than the internodes .... *Pseudoroegneria*

— Plants rhizomatous or cespitose, if cespitose the glumes truncate to obtuse; spikelets almost twice as long as the internodes 14

14(13). Plants cespitose .... *Thinopyrum*

— Plants rhizomatous .... *Elytrigia*

15(10). Lemmas with divergent awns more than 15 mm long; nodes with only one spikelet .... × *Pseudelymus*

— Lemmas awnless or with nondiverging awns; nodes with one or two spikelets 15

16(15). Internodes less than 3 mm long; lowest lemmas usually less than 8.5 mm long ... . × *Elyhordeum*

— Internodes more than 3 mm long; lowest lemmas usually 9 mm or longer 16

17(16). Glumes 12–24 mm long .... × *Elyleymus*

— Glumes awnless or 25–85 mm long .... *Elymus* hybrids

Aegilops L.

Bowden (1959) argued that *Aegilops* should be included in *Triticum*, primarily because species of both genera have been involved in the evolution of many of such polyploid wheat species at *T. durum* Desf. and *T. aestivum* L. He noted also that the International Code of Botanical Nomenclature requires that intergeneric hybrids must have a different generic name from their parents. By including *Aegilops* in *Triticum* he obviated the need for a new generic name for the polyploid wheats. His treatment has since been adopted by Morris and Sears (1967) and Gould (1968).

The difficulty with this approach is that, if applied consistently, the tribe has to be reduced to a single genus because its members are connected by a network of introgressants and hybrids. Krause (1898) advocated recognition of a single genus, but most taxonomists have rejected his position because it ignores the differentiation, both morphological and physiological, that has occurred within the tribe. MacKey (1975) pointed out that the combination of annual growth habit and self-fertilization, such as occurs in *Aegilops* and *Triticum*, "stimulates morphological and physiological discontinuity in connection with ecological specialization without the necessity for a simultaneous construction of sterility barriers based on karyological differentiation." Of the two genera in question, *Aegilops* has remained a weedy genus with a relatively narrow ecological amplitude and is generally restricted to poor soils. *Triticum*, on the other hand, has a much wider ecological amplitude and greater ability to occupy fertile land. This, combined with its tendency to produce a larger grain, has led to rapid evolution in response to selection pressures exerted in part by human cultivation. Thus, we prefer to treat the two as separate genera both because of their morphological discontinuity and their different evolutionary potentials.

The nomenclatural code requires that a hybrid genus be given a different name from any of its parents, but it does not state what groups of species are to be treated as hybrid genera. A group that has become sufficiently well established that its origins are "ancient history" can be treated as a "normal" genus even if it is known to have originated through hybridization. The species of *Triticum* are such a group.

Agropyron Gaertner

This genus is now restricted to members of the crested wheatgrass group. Its members can be recognized by the very short internodes of the inflorescence and, in most instances, the pectinate arrangement of the spikelets. All our species are more or less cespitose, although forms that produce short rhizomes exist. Only one genome, the C genome, has been found in *Agropyron* s.str. Both diploids and polyploids are known.

Agropyron s.str. includes about 10 species, all of which are native to Eurasia. Considerable controversy exists concerning the appropriate taxonomic treatment for the plants found in North America (cf, e.g., Hitchcock 1951, Sarkar 1956, Schulz-Schaeffer et al. 1963, Dewey 1969a, Taylor and McCoy 1973). The species exhibit considerable morphological intergradation (cf. Tsvelev 1976), and the problems of identification are exacerbated by their ability to hybridize when brought into contact (Knowles 1955, Dewey 1969a), as has happened in North America. The genus needs detailed biosystematic study, based on wild populations, a project beyond the scope of this paper. The treatment presented here is based in part on Dewey's examination of specimens in the Komarov Institute (the National Herbarium of the Soviet Union) and discussions with Tsvelev.

Key to the Species of *Agropyron*

1. Spikelets diverging from the rachis at an angle of more than 40 degrees; glumes widespread, forming an angle of more than 120 degrees, giving the spike a bristly appearance; spikes at least 8 mm wide .... *A. cristatum*

— Spikelets diverging from the rachis at an angle of less than 350 degrees; glumes appressed; spikes 5–10 mm wide 2

2(1). Lemma with an awn 1–2(4) mm long; glumes forming an angle of approximately 60 degrees .... *A. desertorum*

— Lemma without an awn, sometimes mucronate; glumes forming an angle of approximately 45 degrees (not common) .... *A. fragile* (= *A. sibiricum*)

Elymus L.

Elymus is the largest genus in the Triticeae, but genomically it is very uniform. All of its members are allopolyploids in which two genomes are present, one derived from *Pseudoroegneria spicata* or a relative thereof, and the other from *Hordeum*. Almost all plants examined, including all those from the Intermountain Region, are tetraploids ($2n$ = 28).

Despite their genomic similarity, species of *Elymus* fall into two distinct morphological groups. The largest group consists of selffertilizing, cespitose species with small anthers; the other of rhizomatous, outcrossing species, with long anthers. Dewey (1983a) earlier included the latter group in *Elytrigia* with other rhizomatous, long-anthered, but genomically distinct species; but he now (1983b) includes them in *Elymus*, a treatment that better reflects their phylogenetic affinities. These rhizomatous species of *Elymus* differ from those of *Elytrigia* in having glumes that are acute or shortly awned, rather than truncate or long-awned, and leaf blades with no evident alteration of major and minor ribs on the adaxial surface. As interpreted here, there is only one such species in the Intermountain Region, *Elymus lanceolatus* [= *Agropyron dasystachyum* and *Agropyron albicans*, cf. Table 1.]. The change in epithet is necessary because the combination *Elymus dasystachys* has been used for a European species.

Elymus includes two other species that used to be included in *Agropyron* (*E. scribneri* and *E. trachycaulus*), because they have only one spikelet per node. We maintain that the morphological, reproductive, and genomic similarity of these two species to others with a similar genomic composition is more significant than the number of spikelets per node.

Elymus elymoides [= *Sitanion hystrix*] and *E. multisetus* [= *S. jubatum*] have previously been included in *Sitanion* (A. Hitchcock 1951, C. Hitchcock 1969, Holmgren and Holmgren 1977), a genus characterized by a readily disarticulating rachis and subulate, long-awned glumes. Genomic studies have shown, however, that the species included in *Sitanion* are just as closely related to the SH species previously included in *Elymus* or *Agropyron* as these species are to each other (Stebbins and Snyder 1956, Stebbins et al. 1946, Stebbins and Vaarama 1954, Brown and Pratt 1960, Dewey 1967, 1969b, Church 1967a, b).

The disarticulating rachis, long subulate glumes, and reduced sterile florets constitute a set of adaptations for dispersal in open environments because the segments of the spike are easily blown over the ground. Similar features are found in one of the forms of the dimorphic species *Aegilops speltoides*. The other form consists of plants with a non-disarticulating rachis, short glumes, and more fertile florets. Zohary and Imber (1963) showed that the differences between the two forms are determined by a group of closely linked genes that are normally inherited as a block. No studies have been conducted to determine whether the same is true of the characteristics used to delimit *Sitanion*, but Zohary and Imber's study lends credence to our conviction that *Sitanion* does not merit recognition at the generic level.

Three hybrid species are included in our interpretation of *Elymus*, *E.* × *hansenii*, *E.* × *pseudorepens*, and *E.* × *saundersii*. These were previously referred to × *Elysitanion*, *Agropyron*, and *Agrositanion*, respectively. The change in their generic position results from changes in the treatment of their parental taxa.

Our treatment of *Elymus trachycaulus* differs somewhat from that endorsed by Holmgren and Holmgren (1977). The taxonomy of the slender wheatgrass complex, of which *Elymus trachycaulus* is a part, is extremely difficult to elucidate. Jozwik (1966) recognized four groups in North America, primarily on the basis of field, hybridization, and herbarium studies. He suggested that many of the members of two of his groups may have been derived by hybridization, one of them comprising plants derived from a variety of different hybrid combinations. He described the largest of the other two groups (which corresponds to subsp. *trachycaulus* in our treatment) as morphologically diverse, probably as a result both of innate genetic plasticity and introgression from other taxa. It has a wide ecological amplitude, growing along stream banks and in forests, meadows, and moist prairies. Geographically it is extremely widespread, extending from Mexico to Alaska and to both the west and east coasts of North America.

Subspecies *latiglumis* corresponds to Jozwik's other, primarily nonhybrid, group. Its members are more or less restricted to subalpine, alpine, and far northern locations, but at lower elevations they tend to intergrade with subsp. *trachycaulus*, probably in part because of hybridization.

Our third subspecies, subsp. *subsecundus*, corresponds to Jozwik's second group. This is the group that he believed consisted almost entirely of hybrids. His data indicated that the second parent could be one of several taxa, e.g. *E. elymoides, E. multisetus, E. glaucus,* and *H. jubatum.* Intermediates between the members of this subspecies and subsp. *trachycaulus* were numerous. He also found intermediates with subsp. *latiglumis,* but these were much less frequent.

We admit that our treatment of this complex is not altogether satisfying, but it seems the most appropriate treatment considering the data available. Even if more data were available, it would be impossible to design a completely satisfying treatment for such a group because the formal requirements of the nomenclatural code cannot perfectly reflect the dynamic interactions occurring in a group such as the slender wheatgrass complex.

Our treatment of *E. elymoides* also differs from that in Holmgren and Holmgren (1977) in that we are not recognizing any infraspecific taxa.

Key to Species and Hybrids of Elymus

1. Spikelets 2–7 at a node 2
— Spikelets solitary at each node 7

2(1). Glumes subulate, 1–2-nerved at midlength and with awns more than 20 mm long; rachis disarticulating at maturity 3
— Glumes lanceolate, 2–5-nerved at midlength, if 2-nerved the awns less than 5 mm long; rachis not disarticulating at maturity 5

3(2). Awns not diverging, even at maturity .... *E.* × *hansenii*
— Awns widely divergent at maturity 4

4(3). Glumes longitudinally divided into 3 or more narrow sections .... *E. multisetus*
— Glumes entire or bifid .... *E. elymoides*

5(2). Rachis flexible, spike nodding; glumes with an awn 10–30 mm long ..... *E. canadensis*
— Rachis stiff, spike erect; glumes unawned or short awned 6

6(5). Glumes bowed outward and indurate at the base, the nerves not evident in the indurate portion .... *E. virginicus* var. *submuticus*
— Glumes not bowed out, membranous at the base, nerves evident throughout .... *E. glaucus*

7(1). Plants rhizomatous; anthers 3–5 mm long 8
— Plants cespitose; anthers 1–3 mm long 10

8(7). Plants sterile, anthers not well filled at anthesis, not dehiscent ..... *E.* × *pseudorepens*
— Plants fertile, anthers well filled at anthesis, dehiscent (*E. lanceolatus*) 9

9(8). Lemmas awnless or with an awn-tip less than 5 mm long .... *E. lanceolatus* subsp. *lanceolatus*
— Lemmas with a divergent awn 5–12 mm long .... *E. lanceolatus* subsp. *albicans*

10(7). Lemmas awned, the awns widely divergent; culms decumbent, usually less than 35 cm tall .... *E. scribneri*
— Lemmas unawned or, if awned, then erect or only slightly divergent; culms erect, usually more than 50 cm tall 11

11(10). Glumes 1–2(3)-nerved; rachis tending to disarticulate at maturity; plants sterile .... *E.* × *saundersii*
— Glumes (3) 5-nerved; rachis not disarticulating at maturity; plants fertile (*E. trachycaulus*) 12

12(11). Lemma awns 8–24 mm long, erect to divergent . *E. trachycaulus* subsp. *subsecundus*
— Lemmas awnless or with short, erect, awns less than 5 mm long 13

13(12). Culms erect, 30–130 cm tall; glumes with a narrow hyaline margin .... *E. trachycaulus* subsp. *trachycaulus*

— Culms often geniculate or decumbent, less than 55 cm tall; glumes with a broad hyaline margin .... *E. trachycaulus* subsp. *latiglumis*

Elymus lanceolatus* subsp. *albicans (Scribner & J. G. Smith) Barkworth & D. R. Dewey, *comb. nov.*— Basionym: *Agropyron albicans* Scribner & J. G. Smith, USDA Div. Agrost. Bull. 4:32, 1897.

Elymus* × *pseudorepens (Scribner & J. G. Smith) Barkworth & D. R. Dewey, *comb. nov.*— Basionym: *Agropyron pseudorepens* Scribner & J. G. Smith, USDA Div. Agrost. Bull. 4:34, 1897, pro sp.

Elytrigia Desv.

All species of *Elytrigia* are outcrossing, but in their other characteristics, including their genomic composition, they are very diverse. It is undoubtedly the least satisfactory genus as presently constituted and the one that most needs further study. There are only two species in the Intermountain Region, both of which are introduced.

Key to the Species of *Elytrigia*

1. Glumes acute to awn tipped, membranous; rachis only slightly concave adjacent to spikelet .... *E. repens*

— Glumes truncate or mucronate, thick; rachis markedly concave adjacent to the spikelet (*E. intermedia*) 2

2(1). Lemmas glabrous; spikelets 3–8-flowered .... *E. intermedia* subsp. *intermedia*

— Lemmas hirsute; spikelets 2–3(-6)-flowered .... *E. intermedia* subsp. *barbulata*

Hordeum L.

The limits of this genus have not been changed but we have adopted the infrageneric treatment recommended by von Bothmer (pers. comm.), since he has studied the genus in both North and South America as well as Europe. This seems particularly appropriate since the taxa for which von Bothmer's treatment differs from that in Holmgren and Holmgren (1977) are all introduced Mediterranean weeds. Moreover, although Holmgren and Holmgren treated the subspecies of *H. murinum* at the specific level, they noted that the taxa were very closely related and often difficult to distinguish. Thus, the differences between the two treatments are not as great as it may appear. No key is presented since the Holmgren's key can be used, the only changes needed being nomenclatural. These are indicated in Table 1.

Leymus Hochst.

In our region, the species of this genus can be recognized by their short, subulate glumes that lie over the sides rather than the midveins of the lemmas, and by the absence of long awns. The genus includes both rhizomatous and cespitose, but extravaginally branching, species.

Species of *Leymus*, both here and elsewhere, tend to grow in alkaline or saline soils. Some are coastal in distribution; others are inland species. The two groups are morphologically distinct. Our species, not surprisingly, belong to the inland group.

Despite the morphological discontinuity between its coastal and inland members, species of *Leymus* are genomically similar. They are all allopolyploids based on the J genome, from *Psathyrostachys*, and the X genome whose origin is unknown. Tetraploids ($2n = 28$), hexaploids ($2n = 42$), and octoploids ($2n = 56$) are known. Thus species of *Leymus* differ from species of *Elymus* both in their genomic composition and their tendency to form higher polyploids.

In traditional treatments of the tribe, *Leymus* is included in *Elymus* since most of its members have more than one spikelet at a node. As indicated above, however, the two genera differ from each other in a number of other morphological characteristics. Moreover, *L. salinus* and *L. simplex* usually have only one spikelet at most, if not all, nodes. The treatment of *L. salinus* presented here is based on work by Atkins (1983; Atkins et al., in press).

Key to Species of *Leymus*

1. Plants strongly rhizomatous, the rhizomes long and slender 2
— Plants cespitose, sometimes with short rhizomes 5

2(1). Lemmas conspicuously hirsute, the hairs 1–2 mm long, not closely appressed to the lemma .... *L. flavescens*
— Lemmas glabrous to, at most, inconspicuously hirsute with hairs less than 1 mm long 3

3(2). Leaf blades with more than 7 veins, not densely hirsute above the ligule; most nodes with two or more spikelets .... *L. triticoides*
— Leaf blades with 5–7 prominent veins, densely short-hirsute above the ligule; most nodes with only one spikelet .... *L. simplex*

5(1). Leaf blades 4–15 mm wide, flat, many nerved; ligules 2–5 mm long; culms more than 1 m tall .... *L. cinereus*
— Leaf blades 2–4 mm wide when flat, strongly involute, 5–7-nerved; ligules less than 2 mm long; culms less than 1 m tall (*L. salinus*) 6

6(5). Basal leaf sheaths glabrous; most nodes with only one spikelet .... *L. salinus* subsp. *salinus*
— Basal leaf sheaths conspicuously hirsute; most nodes with two or more spikelets .... *L. salinus* subsp. *salmonis*

Leymus salinus* subsp. *salmonis (C. Hitchc.) Atkins, *comb. nov.*— Basionym: *Elymus ambiguus* var. *salmonis* C. Hitchc. Univ. Wash. Publ. Biol. 17(1):558, 1969. Holotype: WTU!

Pascopyrum A. Löve

Pascopyrum is a monotypic genus comprising only *P. smithii*. This species is an octoploid, its probable parents being *Elymus lanceolatus* and *Leymus triticoides* (Dewey 1975). Morphologically it is intermediate between its parents. This is particularly evident in the glumes, which are membranous and flat at the base, as it typical for *Elymus*, but then taper gradually into an acuminate tip resembling the linear lanceolate glumes characteristic of *Leymus*. Holmgren and Holmgren (1977) recognized two varieties within the species, but we do not consider either merits formal recognition.

Psathyrostachys Nevski

This genus is comprised of eight species that are native to the steppes and arid regions of southeastern Europe. They are all strictly cespitose and have disarticulating rachises and two spikelets at a node. All the species studied so far are diploids based on the J genome. *Psathrostachys juncea* (Russian wild rye) is the only species to have become established in North America.

Pseudoreogneria A. Löve

All species of *Pseudoroegneria* are based on a single genome, the S genome. The genus consists of several Eurasian species but only one North American species, *P. spicata*. Most of its members can be recognized by their rather slender habit and the single spikelets that are only slightly longer than the internodes.

In previous discussions of the tribe, Dewey (1982, 1983a, b) has included these species in *Elytrigia* in conformity with Tsvelev's (1976) treatment. It is clear, however, that they are genomically distinct and consequently, in keeping with the philosophy guiding this revised treatment, should be recognized at the generic level. No new combinations are necessary for the Intermountain Region.

Thinopyrum A. Löve

This is a Eurasian genus but one of its members, *T. ponticum*, has been introduced into North America and occurs along highways in the Intermountain Region. We have followed Holub (1973) and Melderis (1980) in adopting the epithet *pontica* for the plants that Holmgren and Holmgren (1977) referred to *Agropyron elongatum*. The epithet *elongata* is now interpreted as referring to a western Mediterranean species of relatively small, slender plants, all of which are diploids. *Thinopyrum ponticum* (Tall Wheatgrass) consists of robust decaploid plants that are widespread in Eurasia. It has been seeded at scattered locations in the Intermountain Region. The new combination is presented here:

Thinopyrum ponticum (Podp.) Barkworth & D. R. Dewey, *comb. nov.*— Basionym: *Triticum elongatum* (Host), Gram. Austr. 2:18, 1802).

× *Elyhordeum* Mansf. ex Zizin & Petr.

One hybrid between *Elymus* and *Hordeum* is established in the Intermountain Region, × *E. macounii*. Its parents are *Elymus trachycaulus* and *Hordeum jubatum* (Boyle and Holmgren 1955). In previous treatments it was included in × *Agrohordeum macounii*. The transfer to × *Elyhordeum* is made necessary by the transfer of *Agropyron trachycaulum* to *Elymus*.

× ***Elyhordeum macounii*** (Vasey) Barkworth & D. R. Dewey, *comb. nov.*— *Elymus trachycaulus* (Link) Gould ex Shinners × *Hordeum jubatum* L.— Basionym: *Elymus macounii* Vasey, Grasses U.S. 46, 1883. *Macoun*, Great Plains of B.C.

× *Elyleymus* Baum

One hybrid between *Elymus* and *Leymus* occurs in the Intermountain Region, × *Elyleymus aristatus*. Dewey and Holmgren (1962) have shown that its parents are probably *Elymus elymoides* and *L. triticoides*. Holmgren and Holmgren (1977) referred it to × *Elysitanion aristatum*.

× ***Elyleymus aristatus*** (Merrill) Barkworth & D. R. Dewey, *comb. nov.*— *Elymus elymoides* (Raf.) Barkworth & Dewey × *Leymus triticoides* (Buckley) Pilger.— Basionym: *Elymus aristatus* Merrill, Rhodora 4:147, 1902. *Cusick 2712*, "in large clumps, Silver Creek, Harney Co., Oregon."

× *Pseudelymus* Barkworth & D. R. Dewey, gen. hybr. nov.

× ***Pseudelymus*** Barkworth & D. R. Dewey, *gen. hybr. nov.*— *Pseudoroegneria* A. Löve × *Elymus* L.

One hybrid between *Pseudoroegneria* and *Elymus* has become established in western North America, × *P. saxicola*. The generic name × *Pseudelymus* is presented here to accommodate it and other such hybrids that may occur elsewhere.

The parents of × *P. saxicola* are *Pseudoroegneria spicata* and *Elymus elymoides* (Dewey 1964). The plants are usually completely sterile but, being perennial, once they are established at a location, they will persist there. The change in generic name is made necessary by changes in generic boundaries affecting its parents.

× ***Pseudelymus saxicola*** (Scribner & J. G. Smith) Barkworth & D. R. Dewey, *comb. nov.*— *Pseudoroegneria spicata* (Pursh) A. Löve × *Elymus elymoides* (Raf.) Sweezy.— Basionym: *Elymus saxicolus* Scribner & J. G. Smith, USDA Div. Agrostol. Bull. 18:20, 1899, pro. sp.

Discussion

Selection of the most appropriate taxonomic treatment of a polyploid complex is always difficult. This is particularly true when the members of the complex hybridize as readily as do members of the Triticeae. The problem is compounded by the great morphological reduction that characterizes all grasses and the prevalence of convergent evolution. The treatment presented here seeks to reflect as completely as possible all available data. It is therefore a compromise between a strictly genomic interpretation and one based entirely on morphological data.

The main advantage of this treatment is that it reflects a higher proportion of the genomic and morphological information available than does the traditional treatment. It is also in closer accord with the systems adopted by Tsvelev (1976) and Tutin et al. (1980). Since both the Soviet Union and Europe have more species of Triticeae than the United States and Canada combined, it is appropriate to consider seriously the treatments advocated by taxonomists in those regions.

Some of the new genera are not, perhaps, as easy to recognize as the old interpretation of *Agropyron* and *Elymus*. On the other hand, numerous herbarium specimens indicate that *Leymus salinus* and *Leymus simplex*, which have only one spikelet at most of their nodes, have often been misidentified as species of *Agropyron* rather than *Elymus*. Thus, even the traditional treatment was sometimes difficult to apply. The revised genera can be recognized on the basis of their gross morphological characters, although not the same characters as before. We hope that this treatment will assist those wishing to become familiar with the new generic concepts.

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