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Systematics of the "Epiles" Group of *Poa* (Poaceae)

ROBERT J. SORENG

Biology Department, New Mexico State University,
Las Cruces, New Mexico 88003
Present address: L. H. Bailey Hortorium, Cornell University,
Ithaca, New York 14853

ABSTRACT. The taxonomy of the western North American "Epiles" group of *Poa* is revised in the light of new information on morphology, anatomy, breeding systems, and chloroplast DNA restriction sites. The artificial group, "Epiles" s.l., of A. S. Hitchcock is divided into three homogeneous parts: sect. **Madropoa** subsect. **Epiles**, sect. **Secundae** subsect. **Halophytae** (all formalized here), and sect. *Abbreviatae*. These three sections belong to three larger chloroplast groups in *Poa*. A new subspecies, **P. cusickii** subsp. **pallida**, is proposed, and hybrids between this and *P. fendleriana* are distinguished as *P.* × *nematophylla*. From the Sierra Nevada, **P. stebbinsii** is proposed as a new name for *P. hansenii* sensu auct., and a new species, **P. keckii**, is segregated from *P. suksdorfii*. A descriptive key to western North American "Epiles" group s.l., distributional maps, and illustrations of species of the subsect. *Epiles* s. str., and species newly referred to sect. *Abbreviatae* are provided. New and additional chromosome counts are reported for: *P. cusickii* subsp. *pallida*, $2n = 56+II$; *P. secunda* (*P. juncifolia* form, previous citation as *P. cusickii*), $2n = 42$; *P. napensis*, $2n = 42$; *P. strictiramea*, $2n = 28+I$; and *P. unilateralis*, $2n = 84$.

Much confusion has surrounded the species included within the "Epiles" group of *Poa* L. as proposed by A. S. Hitchcock (1935). The group, as originally defined, is clearly artificial, including all perennial species of North America with a cespitose habit and keeled glabrous lemmas. Loss of lemma pubescence has occurred in many diverse groups of *Poa* around the world, even within species. The fact that several "Epiles" taxa sometimes have pubescent lemmas has led to frequent misidentifications and confusion about relationships among the species. Difficulties have been compounded by interspecific hybridization and apomixis in some species, and by a lack of detailed circumscription and biological understanding of the taxa involved. Overly simplified keys have also hindered identifications in this very complex group. The objectives of the present paper are to redefine the limits of the "Epiles" group, formally describe subgeneric taxa and two new species, and present a biological interpretation of the species based on new knowledge of their chloroplast origins (Soreng, in press), anatomy, morphology, cytology, breeding systems, and geography of the apomicts (Soreng 1986). Populations from the Sierra Nevada previously referred to as *Poa hansenii* Scribner and *P. suksdorfii* (Beal) Vasey ex Piper represent new species. In recognition of two renowned Californian botanists, the names *P. keckii* and *P. stebbinsii* are proposed. The two species have been well collected by botanists in the high Sierra Nevada, but had not been examined in detail. Because good descriptions and illustrations are already available for the other taxa in the group (Marsh 1952; Hitchcock 1969), only a descriptive key is presented.

MATERIALS AND METHODS

Leaf epidermal peals were prepared by softening tissues with Pohl's softener, scraping away the opposing epidermis and mesophyll with a razor, mounting the exposed epidermis on a slide, staining it with safranin, and clearing the tissue with glycerol. Chromosome counts were made by fixing bud material in Carnoy's Fixative and staining pollen mother cells in acetocarmine. Breeding system phenotypes were determined by surveying herbarium collections and population samples for intraspecific patterns of deviation from hermaphroditism, indicating gynodioecism or dioecism, or, when all individuals are pistillate, apomixis (Soreng 1986). Chloroplast DNA methods, results, and phylogenetic analysis are reported by Soreng (in press).

Specimens examined in this study were borrowed from ARIZ, ASU, CAN, CAS, DS, GH, ID, MICH, MSC, MO, NMC, NY, ORE, OSC, TAES, TEX, UBC, UC, US, V, WIS, WSU, WTU,

WYAC, or collected in situ. Lists of exsiccatae will be deposited at MO.

Results and Discussion

Concepts of Taxa. The species concept I apply is similar to that used in *Antennaria* by Bayer and Stebbins (1983), but additionally incorporates elements of the phylogenetic species concept as modified by Nixon and Wheeler (in press): A species is defined as a population or smallest set of populations that are coherent in biology, and that share a unique combination of fixed morphological characteristics, which consistently distinguish the component populations from other sets of populations. I view such characteristics as an indication of the actual reproductive isolation of the species from other sets of biologically coherent populations. I have applied the rank of subspecies to sets of populations that are geographically distinctive, but distinguishable only by characteristics of a type that vary within populations across the whole species. A variety may occur sympatrically or form distinct populations within the range of a subspecies as is common among apomictic lineages. Two kinds of variation occur: 1) Intergradient characteristics indicating incomplete segregation of incipient species or broad secondary contact between former sister species; and 2) intergradient characteristics indicating contact between more distantly related species. The latter kind is more difficult to deal with. Populations with characteristics of this kind are treated as subspecific variants within the most similar parent species, nothotaxa, or species depending on their degree of distinctness, or stability of the new character combinations. Because occasional hybrids occur between many species where apomixis is involved, I have formally recognized only those that occur over a substantial geographic range and are, therefore, likely to be encountered. Local hybrid populations of note are discussed under the species to which they key. I have attempted to recognize taxa as sets of biologically and morphologically coherent sexual or asexual populations, but I separate the sexual populations from the apomicts only when they can be morphologically distinguished. Facultatively apomictic clones or lineages (microspecies of other authors) are considered to be individuals in an extended time frame (living 100s to 1000s of years), and are treated taxonomically as if they comprised subsets of populations, or races, within sexual species, but with interbreeding events occurring infrequently and when extended over long periods of time, resulting in groups of lineages with inheritance and variation patterns similar to those found within polymorphic sexual species.

Subgeneric Classification. Three groups are distinguished from what has been called the "Epiles" group by Hitchcock (1935). All three are considered to be members of subg. *Poa* in the broad sense (Soreng, in press). The sect. *Madropoa* and *Secundae* and subsect. *Epiles* and *Halophytae* are described below in the "Taxonomy" section. The following classification includes all the known species within each taxonomic rank.

I. Sect. nov. *Madropoa* R. J. Soreng subsect. nov. *Epiles*: *P. cusickii* Vasey (including *P. epilis* Scribner), *P. leibergii* Vasey (including *P. vaseyochloa* Scribner), *P.* × *nematophylla* Rydb. (pro sp.), *P. porsildii* Gjaerevoll, *P. pringlei* Scribner, *P. stebbinsii* R. J. Soreng, sp. nov. Western North America (figs. 1, 2).

II. Sect. *Abbreviatae* Nannf. ex Tzvelev: *P. abbreviata* R. Br., *P. hartzii* Gand., *P. keckii* R. J. Soreng, sp. nov., *P. kolymensis* Tzvelev, *P. lettermanii* Vasey (including *P. montevansii* Kelso), *P. pattersonii* Vasey, *P. pseudoabbreviata* Rosch. (including *P. brachyanthera* Hultén), *P. suksdorfii* (Beal) Vasey ex Piper, *P. vrangelica* Tzvelev. Circumpolar, especially Beringia.

III. Sect. nov. *Secundae* V. Marsh ex R. J. Soreng subsect. nov. *Halophytae* V. Marsh ex R. J. Soreng: *P. unilateralis* Scribner in Vasey, *P. napensis* Beetle. Western North America.

The above taxonomic arrangement treats the 10 species of "Epiles" group (sensu Hitchcock 1935, emend. Hitchcock and Chase 1951) except for *Poa strictiramea* A. Hitchc. (=*P. involuta* A. Hitchc.). That species, of arid mountains in and around the Chihuahuan Desert, shows only weak affinities to other "Epiles," and cannot be satisfactorily placed in any North American group at this time. The fact that a possible nearest relative of *P. strictiramea*, *P. ruprechtii* Peyr. of Mexico, has sheaths closed over more of their length, pubescent lemmas, is partially gyno-

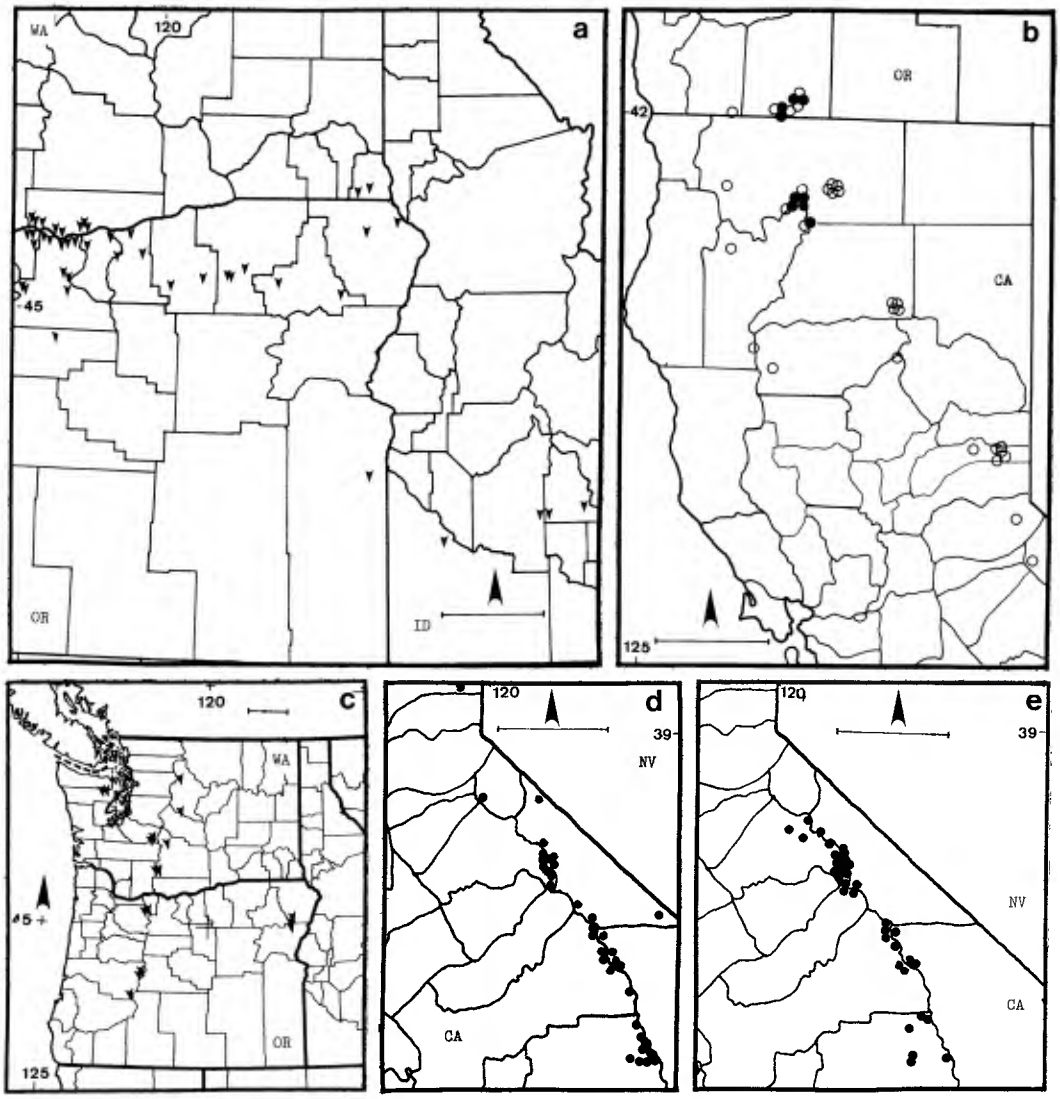

FIG. 1. Distribution of *Poa* species in western North America. a. *P. leibergii.* b. *P. pringlei* (open circles indicate pistillate collections, closed circles staminate collections). c. *P. suksdorfii.* d. *P. keckii.* e. *P. stebbinsii.* Bars equal 100 km.

dioecious and rhizomatous, and that *P. strictiramea* shares a derived chloroplast with other species with those characteristics, suggests that *P. strictiramea* is either highly modified or of hybrid origin.

Section *Abbreviatae* appears to be a natural group with the species sharing a common morphology and biology. Their sheaths are open to near the base, they all have perfect flowers with short anthers, and they are all low tufted plants of nearly barren, high alpine and tundra habitats. Although *P. hartzii* is apomictic (its anthers are consistently sterile), the other species are thought to be predominantly sexual. Section *Abbreviatae* contains two of the three diploid *Poa* in North America, and is morphologically allied to species of sect. *Stenopoa* Dumort. (*P. glauca-nemoralis-palustris* complex) with which the polyploids hybridize (Tzvelev 1983, p. 708). Moreover, chloroplast DNA analysis indicates that *P. keckii* and the diploid *P. pseudoabbreviata* share a derived and nearly identical chloroplast ge-

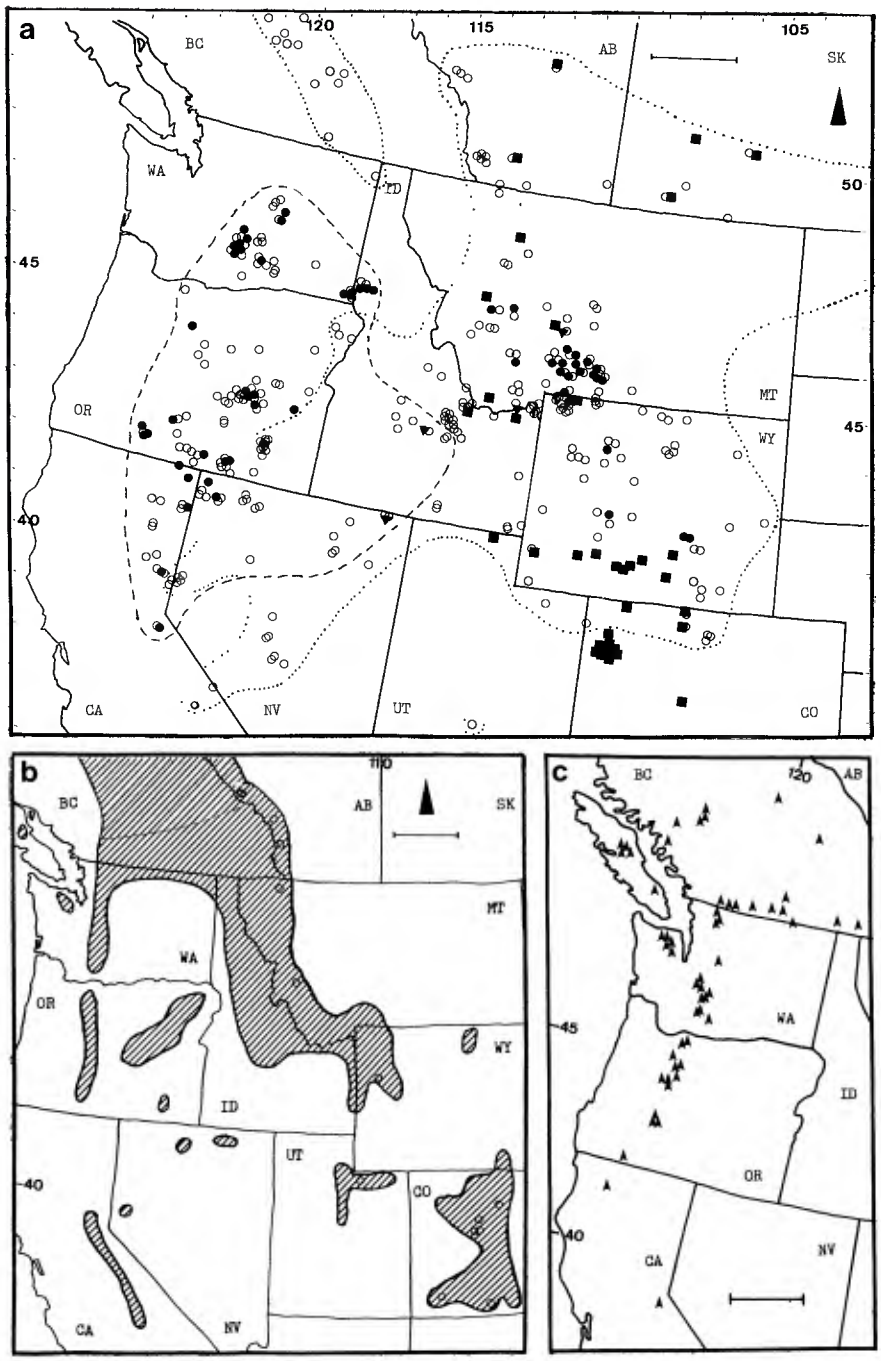

FIG. 2. Distribution of certain *Poa* species in western North America. a. *P. cusickii* subsp. *cusickii* inside dashed lines; subsp. *pallida* inside dotted lines, open circles = pistillate, closed circles = staminate; and *P.* × *nematophylla*, triangles = staminate, squares = pistillate. b. *P. cusickii* subsp. *epilis* var. *epilis* geographic range (hatched) and population samples (circles). c. var. *purpurascens*. Bars equal 200 km.

nome with polyploid species of sect. *Stenopoa* (Soreng, in press).

Subsection *Halophytae* shares characteristics with three other halophytic or partly halophytic groups: 1) *Poa* sect. *Secundae* (including *P. curtifolia* Scribner, *P. secunda* J. S. Presl s.l., *P. stenantha* Trin., and *P. tenerrima* Scribner); 2) *Poa* subg. *Arctopoa* (Griseb.) Prob. (represented in North America by only *P. eminens* J. S. Presl); and 3) the genus *Puccinellia* Parl. Subsection *Halophytae* exhibits the cespitose habit, open sheaths, and papillae on the leaves as in *Puccinellia*, but their longer and entire glumes, keeled and acute lemmas, and diffusely pubescent calluses are more similar to *Poa* sect. *Secundae*. Section *Secundae* has a similar lemma texture, pubescence patterns, and also exhibits the cespitose habit with open sheaths. The species of sect. *Secundae* lack papillae, but do have rounded lemmas as in *Puccinellia*. Species of subg. *Arctopoa*, as do the remainder of *Poa*, have keeled lemmas, but in this subgenus lemmas are almost membranous, and unlike the other halophytes the plants produce well developed rhizomes. Chloroplast DNA data from *P. napensis* place it together with *P. secunda* s.l. as a sister group to the derived group of sects. *Abbreviatae, Coenopoa, Oreinos, Stenopoa,* and *Tricopoa*. The coupling of ancestral and non-poa-like characteristics with an advanced *Poa* chloroplast type supports the hypothesis that sect. *Secundae*, including the subsect. *Halophytae*, was of hybrid origin (Stebbins 1950; Soreng, in press).

The presence or absence of papillae on the long-cells of mature leaf blades provided significant clues to relationships and species limits in *Poa* (Soreng, unpubl. data). Papillae are rare in *Poa*, yet occur nearly ubiquitously in the closely related genus *Puccinellia*. Among 80 other species of *Poa* surveyed, papillae were absent on leaves of *P. cusickii* s.l., *P. leibergii, P. lettermanii, P. pringlei, P. secunda* s.l., *P. stebbinsii*, and *P. suksdorfii*. *Poa keckii* and *P. napensis* have papillae on epidermal long-cells similar to those found in *Puccinellia*, as does *P. unilateralis* (and *P. pachypholis* Piper).

Subsection *Epiles* as defined here may be found to be of hybrid origin. They share some characteristics with sect. *Abbreviatae*, but exhibit much stronger affinities to subsect. *Madropoa*, which contains rhizomatous, folded-involute, and hairy-leaved, dioecious bluegrasses of western North America [including: *P. atropurpurea* Scribner, *P. confinis* Vasey, *P. douglasii* Nees, *P. fendleriana* (Steudel) Vasey, *P. macrantha* Vasey, *P. piperi* A. Hitchc.]. The above type of leaf, with its well developed adaxial costal and intercostal hairs, appears to be restricted in North and South American *Poa* to (with one exception) the diclinous group of species. It occurs in the Old World *Poa* only in the monotypic sect. *Leptophyllae* Edmondson (*P. stiriaca* Fritsch & Hayek ex Dorfler) and appears again in Australian tussock *Poa* (see Vickery 1970) including *P. labellardieri* Steudel (R. Ellis, pers. comm.). The exceptional North American species, *P. suksdorfii*, is in several respects intermediate between the dioecious *P. pringlei* and species of sect. *Abbreviatae* in which it is placed here. Chloroplast DNA data show that *P. cusickii* shares a derived chloroplast genome with subsect. *Madropoa* species; *P. confinis, P. fendleriana, P. piperi* (Soreng, in press).

Breeding Systems. Analysis of breeding systems has proven useful for understanding the "Epiles" group (table 1) and other taxa (Soreng 1985, 1986, and unpubl. data). *Poa pringlei* and *P. cusickii* are dioecious, but both have apomictic races in which only pistillate plants are represented. East of the Klamath-Siskiyou region *P. pringlei* is represented only by pistillate plants. All plants of *P. cusickii* subsp. *epilis* (Scribner) W. A. Weber are pistillate. As determined by the distribution of staminate plants over large geographic ranges, subsp. *cusickii* and subsp. *pallida* R. J. Soreng include regions of sexual and asexual reproduction that are correlated with predictable ecological differences (Soreng 1986). Although Keck (unpubl. manuscript) suggested that *P. leibergii* and *P. stebbinsii* are apomictic, I found evidence to the contrary. In herbarium samples hermaphroditic and pistillate plants are about equally represented, and geographically are sympatric, indicating these taxa are sexual and gynodioecious. Population samples and seed-set studies of the above species support these interpretations. *Poa suksdorfii* and *P. keckii*, which were included in *P. pringlei* by Hitchcock (1935), at the other extreme, are hermaphroditic. These differences are associated with long anthers (2–4.5 mm long) in dioecious and gynodioecious taxa and short anthers (0.7–1.8 mm long) in hermaphroditic taxa, and support their present placement in different groups. An alternative possibility is that the hermaphroditic *P. suksdorfii* and *P. keckii* arose from hy-

TABLE 1. Sex ratios in herbarium and population samples of *Poa* sect. *Madropoa* subsect. *Epiles*. Number examined in parentheses after taxon. Sex-ratios are given as females (f) to males (m), or females to "other" including hermaphrodites (h), part hermaphrodite/part females, and males. Collectors are Soreng (S), Bayer (B), Dunford (D), Spellenberg (Sp), and Stebbins (St).

Taxon	Herbarium sex-ratio	Population sex-ratios
P. cusickii		
subsp. *cusickii*	(190) 2.3:1	U.S.A. **CALIFORNIA.** Lassen Co.: *S 2994*, 25f:23m. Plumas Co.: *S 2995*, 30f:12m. **OREGON.** Crook Co.: *S 2976*, 40f:0. Harney Co.: *S 2977*, 1f:1m; *S 2980*, 50f:24m. Jefferson Co.: *S 2970*, 18f:14m; *S 2974*, 34f:0. Lake Co.: *S 823*, 3f:0; *S 885*, 6f:0; *S 2993*, 36f:13m.
subsp. *pallida*	(253) 5:1	U.S.A. **IDAHO.** Fremont Co.: *S 2433*, 6f:0. **MONTANA.** Dear Lodge Co.: *S & Sp 1207*, 9f:0. Park Co.: *S 2435*, 23f:23m; *S 2436*, 14f:5m; *S 2445*, 8f:7m; *S 2449*, 43f:18m; *S 2453*, 27f:34m; *S 2451*, 35f:23m. Sweetgrass Co.: *S 2450*, 2f:2m:18 viviparous. **WYOMING.** Park Co.: *S & Sp 1226*, 30f:0. Yellowstone Natl. Park: *S 2456*, 12f:11m.
subsp. *epilis*		
var. *epilis*	(384) 384:0	CANADA. **ALBERTA.** Banff: *S & Sp 1002*, 30f:0. Kananaskis: *S & Sp 1040*, 30f:0. Plateau Mt.: *S & Sp 1099*, 30f:0. U.S.A. **CALIFORNIA.** Mono Co.: *S 3369*. **COLORADO.** Clear Creek Co.; *S, B, D, & St 2562*. Gunnison Co.: *S & D 2506*, 36f:0; *S, B, D & St 2571*, 11f:0. Pitkin Co.: *S & Sp 1377*, 30f:0. Rio Grande Co.: *S, B, D, Sp & St 2504*, 15f:0. San Juan Co.: *S 1856*, 30f:0 (pubescent lemmas). **MONTANA.** Dear Lodge Co.: *S & Sp 1186*, 30f:0. Glacier Natl. Park: *S & Sp 1108*, 30f:0. **UTAH.** Duchesne Co.: *S & Sp 1341*, 30f:0. **WYOMING.** Sublette Co.: *S & Sp 1280*, 30f:0.
var. *purpurascens*	(85) 85:0	
P. leibergii	(87) 0.9f:1 other	U.S.A. **IDAHO.** Elmore Co.: *S 2407*, 23f:9h. **OREGON.** Wasco Co.: *S 2397*, 13f:8h. Jefferson Co.: *S 2971*. Umatilla Co.: *S 2399*, 8f:18h (also hybrids to *P. secunda*). Union Co.: *S 2402*, 3f:10h (toward *P. cusickii*).
P. × *nematophylla*	(39) 38:1	U.S.A. **COLORADO.** Jackson Co.: *S, B, D & St 2576*, 36f:1m. **IDAHO.** Fremont Co.: *S 2432*, 34f:0.
P. porsildii	(14) 1:1	
P. pringlei	(68) 2.2:1	U.S.A. **OREGON.** Jackson Co.: *S 3356*, 30f:30m.
P. stebbinsii	(58) 0.4f:1 other	U.S.A. **CALIFORNIA.** Inyo Co.: *S 3362*. Mono Co.: *S 3368*.

bridization between the diclinous subsect. *Epiles* and species of the hermaphroditic sect. *Abbreviatae*, subsequently repressing dicliny and expressing some intermediate characteristics.

The sequence of origin of breeding systems found within subsect. *Epiles* may be as follows. I suggest the species were derived from a common ancestor with the dioecious, rhizomatous *Poa* of North America, these in turn evolved from diclinous ancestors that gave rise to the partially gynodioecious *P. nervosa* complex [including *P. curta* sensu auct, *P. cuspidata* Nutt., *P. nervosa* (Hooker) Vasey s. str., *P. rhizomata* A. Hitchc., *P. ruprechtii*, *P. tracyi* Vasey]. Whether partial gynodioecy (Soreng and Hatch 1983) is distinct from gynomonoecy and arose directly from hermaphroditic species or is simply an exaggerated form of gynomonoecy is not clear (D. Lloyd, pers. comm.). Although the occurrence of gynomonoecy in a group of South American species that share a similar chloroplast type supports a gynomonoecious origin, neither interpretation is inconsistent with the chloroplast DNA cladogram of *Poa* (Soreng, in press).

TAXONOMY

1. Sect. **Madropoa** R. J. Soreng, sect. nov.—TYPE: *P. piperi* A. Hitchc.

Perennes dense caespitosae vel stoloniferae vel rhizomatae, innovationibus intravaginalibus, extravaginalibus, vel simul intravaginalibus et extravaginalibus. Foliorum laminae basalium firmae, plicatae, marginibus involutis, in superficie breviter ciliatae ad nervos et inter nervos. Paniculae 2.5–10(12) cm longae, ramis plerumque contractis vel interdum late expansis. Lemmata carinata, glabra vel villosa ad nervos. Calli abaxialiter aliquantum lateraliter compressi, glabri vel pubus brevibus diffusis vel raro elongatis praediti. Gramina dioica vel gynodioica, plantae sexus dissimilis vix dimorphicae. Antherae 1.5–4.5 mm longae.

Cespitose or tufted stoloniferous or rhizomatous perennials, branching intravaginal, extravaginal, or intra- and extravaginal; culms and sheaths round in cross-section; upper culm leaf sheaths closed 1/10–1/2(3/4) their length; innovation leaves more or less firm, folded, involute, filiform or broader, 0.2–1.5 mm wide when folded (rarely thin, weakly keeled, filiform, and soon withering), the adaxial surface usually bearing costal and intercostal hooks or prickle hairs; leaf-blade epidermis with sinuous walled, parallel-sided long-cells adaxially and abaxially, generally with short-cells, hooks, and cork-cell/silica-body pairs, long-cells lacking papillae; panicles contracted and lanceolate to ovate in outline, rarely open, the axes and branches densely scabrous to smooth; lemmas keeled, smooth or scabrous, glabrous or villous on the nerves; callus more or less laterally compressed, concave on the sides near the back, glabrous, or with a more or less diffuse tuft of hair from the dorsal side; paleas finely scabrous to nearly smooth, infrequently villous on the keels, frequently spinulose between the keels. The species dioecious or gynodioecious.

Ia. Subsect. *Madropoa*.

Plantae plerumque stoloniferae vel rhizomatae. Paniculae ramis plerumque contractis. Lemmata vel calli pubescentes vel infrequenter glabri.

Stoloniferous or rhizomatous plants; innovations intra- and extravaginal; upper culm leaf sheaths closed 1/3–1/2 their length; blades firm, rarely filiform; leaf-blade cross-section with well developed sclerenchyma girders adjoining the abaxial epidermis under the primary and sometimes the secondary vascular bundles; panicles contracted; lemma or callus pubescent, or infrequently glabrous. Including *P. atropurpurea* Scribner, *P. confinis* Vasey, *P. douglasii* Nees, *P. fendleriana* (Steudel) Vasey, *P. macrantha* Vasey, *P. piperi* A. Hitchc.

Ib. Subsect. **Epiles** A. Hitchc. ex R. J. Soreng, subsect. nov.—TYPE: *P. epilis* Scribner.

Plantae caespitosae. Paniculae ramis interdum late expansis. Lemmata et calli glabri.

Plants cespitose, branching intravaginal, extravaginal, or both; upper culm leaf sheaths closed 1/10–3/4 their length; innovation leaves firm [rarely (in *P. leibergii*) soft, weakly keeled, and soon withering], sometimes filiform; leaf-blade cross-section with large hemicircular sclerenchyma bands adjoining the abaxial epidermis under the primary and sometimes the secondary vascular bundles, the bands sometimes continuous with the primary vascular bundles (bands reduced in *P. leibergii*), short-cells sometimes infrequent; panicles contracted or infrequently open; lemmas smooth or scabrous, glabrous (or sometimes with sparse soft pubescence in hybrid taxa); callus glabrous (or rarely sparsely hairy in hybrid taxa, but not with a well developed single dorsal tuft of hairs); palea keels never villous.

1. **Poa stebbinsii** R. J. Soreng, sp. nov. (figs. 3, 4).—TYPE: California, Tulare Co., Sierra Nevada, Bubbs Creek Canyon, 10,300 ft, 26 Jul 1948, *J. T. Howell 25020* (holotype: US—2079027!; isotype: CAS!).

Poa hansenii sensu Keck in part, non Scribner, syn. *P. cusickii* subsp. *cusickii*.

A *P. cusickii* s.l. [cum *P. hansenii* Scribner (typo) et *P. epili* Scribner] et *P. leibergii* Vasey ligulis innovationum superiorum longissimis 3–6 mm longis plerumque pellucidis vel nonnihil lactaneis, laevibus (non 0.2–2.5 mm longis, plerumque lactaneis, scabris), laminis innovationum satis firmis plicatis involutis (non gracilibus et frequenter planis ut in *P. leibergii*), lemmatibus usque ad 5.5 ($\bar{x} = 4.4$) mm longis [non (5)5.5–7.5 mm longis ut in *P. pringlei*], plantis gynodioeciis (non dioeciis ut in *P. pringlei* et *P. cusickii*), differt.

Plants with a (5)6–15 cm tall tuft of moderately firm basal leaves, with culms (6)10–30(40) cm tall, branched only at the very base, branches extravaginal with short bladeless leaves near

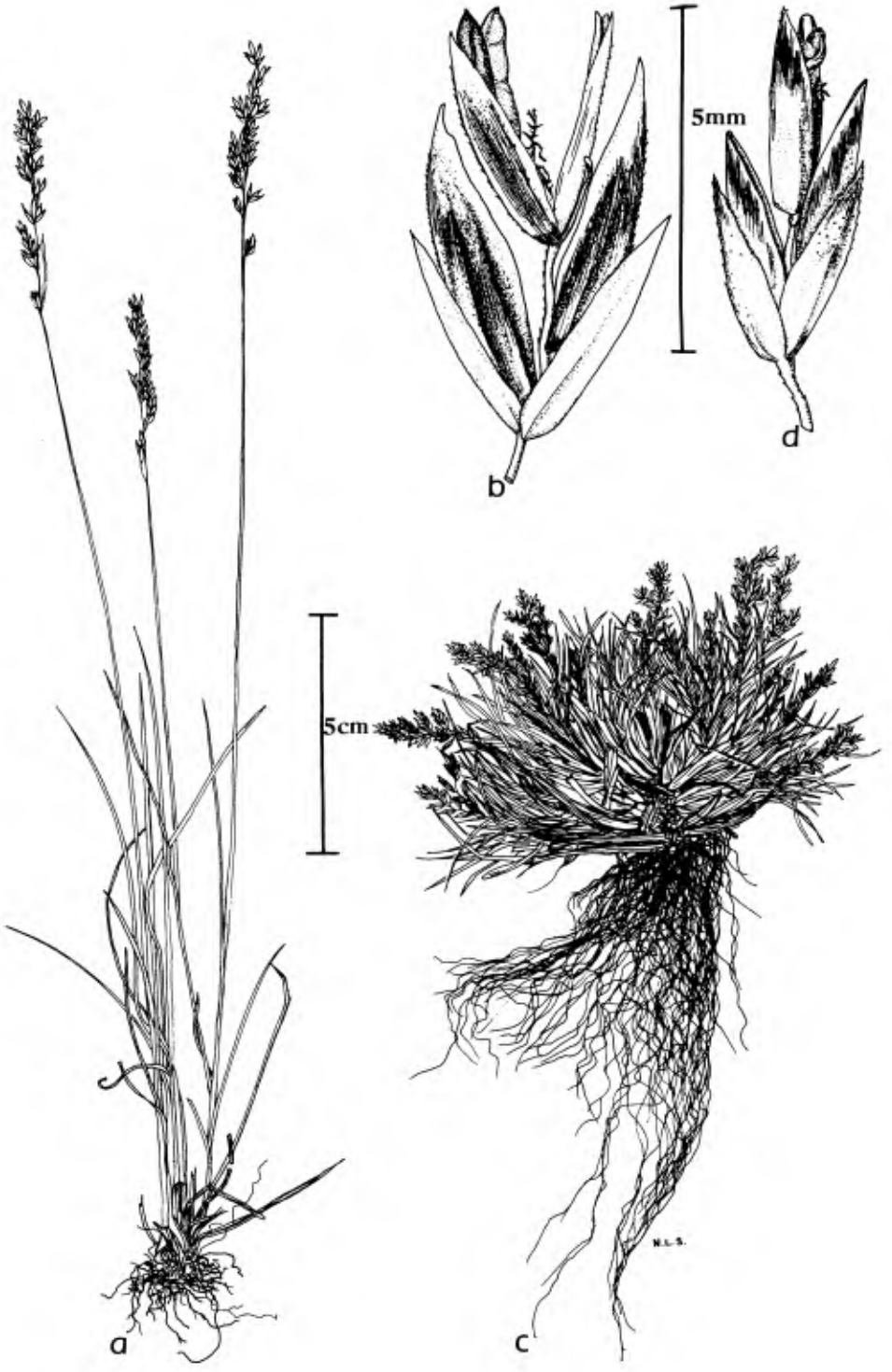

FIG. 3. *Poa stebbinsii*. a. habit (from holotype). b. spikelet. *Poa keckii*. c. habit (from holotype). d. spikelet.

FIG. 4. Ligules and lemmas of certain taxa of *Poa*. Ligules of upper innovation leaves. a. *P. cusickii* subsp. *epilis* var. *epilis*. b. *P. stebbinsii*. c. *P. cusickii* subsp. *cusickii*. d. *P. leibergii*. Lemmas (proximal). e. *P. suksdorfii* (perfect). f. *P. pringlei*. g. *P. stebbinsii*. h. *P. keckii* (perfect). i. *P. cusickii* subsp. *epilis* var. *epilis* (pistillate, apomict). j. *P. cusickii* subsp. *pallida* (pistillate). k & l. *P. cusickii* subsp. *cusickii*. k. pistillate, apomict. l. pistillate.

the base; leaves chiefly basal; culm sheaths with the margins fused ⅕–⅖ of the length; leaf-blades thick, moderately firm, folded and involute on the margins, those of the upper culm nodes with mostly 7–9 veins expressed, the ventral surface appearing smooth, scabrous, or puberulent (the collars smooth); ligules smooth (or rarely sparsely scabrous abaxially in hybrids?), clear to somewhat opaque, the longest ones of the upper innovation leaves mostly clear and (2.5)3–6 mm long, obtuse to acuminate, frequently deeply lacerate; anatomically the leaf blades without papillae on the long-cells, short-cells of adaxial and sometimes abaxial surfaces frequently with short or longer hooks both costally and intercostally, abaxial surfaces mostly with cork-cell/silica-body pairs; culm nodes buried in the basal tuft or rarely exposed; peduncle 3–20(29) cm long, the ratio of the peduncle length to panicle length 2:1 to rarely over 6:1; panicle loosely compact or open, ovate to lanceolate, (2.4)3.0–6.5(7.2) cm long, 9–38(60)-flowered, the slender branches sparsely to fairly densely scaberulous, round or angled, the pedicels mostly over 2 mm long; spikelets 2–4-flowered, anthocyanic (less so in pistillate plants); glumes smooth, thin, lustrous, acute, scabrous on the upper keel, both shorter or the second nearly equaling the first lemma in length, the first 2.5–4.0 mm long, the second 2.7–4.7 mm long; lower lemmas smooth to scaberulous, glabrous, keeled, 3.7–5.0(5.5) averaging 4.4 mm long, 5-nerved, the intermediate ones mostly obscure; callus glabrous; palea finely scabrous on the keels; rachillas smooth or hirsutulous, the internodes ca. 1 mm long; flowers perfect, pistillate, or sometimes appearing staminate; anthers 2.0–4.5 mm long; ovary glabrous.

Chromosome number. Hiesey and Nobs (1982) reported *P. leibergii* at $2n = 81$ (CI 4244) [*P. stebbinsii* from the Sierra Nevada was called *P. leibergii*], this probably equals *P. stebbinsii* but voucher not seen unless the CI number corresponds to *Keck 4366* (with same label data). Keck (1963) reported $2n = 42$ for "*P. hansenii*," but no specimen was cited.

Habitat. Subalpine to lower alpine, 2870–3660 m (1680 m an intermediate plant) in grassy meadows and along rocky shores, in granitic and metamorphic substrates.

Distribution and representative specimens examined. U.S.A. E California, Sierra Nevada (Placer Co., Emigrant, *Hoover 5519*, S to Tulare Co., Mineral King area, *Howell 17813*) (fig. 1e).

Comments. A new name is required for *P. hansenii* sensu auct. Hitchcock (1935) submerged *P. hansenii* Scribner, including plants here referred to as *P. stebbinsii*, under *P. leibergii*. Marsh (1952) and Keck (1963) considered *P. leibergii* and *P. hansenii* (sensu Keck in part) distinct. Keck applied the name *P. hansenii* to the alpine plants of the Sierra Nevada, whereas Marsh reduced *Poa hansenii* to synonymy under *P. cusickii* and suggested there was an unnamed species in the Sierra. My interpretation, based on a much larger series of collections, agrees with Marsh's, and alpine plants from the Sierra Nevada previously referred to as *P. hansenii*, are here called *P. stebbinsii*. *Poa leibergii*, *P. cusickii*, and *P. stebbinsii* are anatomically, morphologically, and ecologically distinct from one another.

The type of *P. hansenii* (*Hansen 605*, California, Amador Co., 2440 m) differs from *P. stebbinsii* in several respects. It is a rather slight plant (10–20 cm tall) of *P. cusickii* subsp. *cusickii*. Several specimens of *P. cusickii* subsp. *cusickii* are indistinguishable in detail from the type of *P. hansenii*: *Train 3279*, Ormsbey Co., Nevada; *Hutton 48*, Modoc Co., California; *Whitney 3264*, Lassen Co., California; and *Soreng 2994*, Lassen Co., California. The most similar collection to the type of *P. hansenii*, *Train 3279*, is unusual in having thin leaves with few short cells as in *P. leibergii*. All these collections including *Hansen 605* occur north of and at lower elevations than *P. stebbinsii*, and where *P. cusickii* subsp. *cusickii* is frequent. These plants flower in June to early July, vs. late July to mid-August for *P. stebbinsii*. The ligules of the upper innovation leaves of these plants are scabrous, truncate, and less than 1 mm long, the blades are filiform, and branching is strictly intravaginal (as in *P. cusickii* subsp. *cusickii* and subsp. *pallida*; subsp. *epilis* has a mixture of intra- and extravaginal branching). In *P. stebbinsii* the innovation ligules are smooth, acuminate and 3–6 mm long, the blades broader, and branching is exclusively (?) extravaginal. Only two plants, from Tuolumne Co., California, were found to be intermediate in the ligule character: *Yates 6158* (Sonora Pass, 2900 m) and *Springer 119* (Pinecrest, 1680 m). In these the ligules are long, as in *P. stebbinsii*, but scabrous. The type of *P. hansenii* also has denser panicles and more spikelets (36–39) than *P. stebbinsii* (with two exceptions out of 64 specimens). Besides occurring primarily at lower elevations (except for some apomictic lines), *P. cusickii* is primarily dioecious, vs. gynodioecious. Within *P. cusickii* s.l., only subsp. *epilis* is strictly pistillate and apomictic, and occurs in the high Sierra Nevada sympatrically with *P. stebbinsii*. *Poa stebbinsii* is only slightly morphologically removed from the polytypic *P. cusickii*, or from the larger-flowered and dioecious *P. pringlei*, but very few plants have been found that could be considered intermediate.

As treated here, *P. stebbinsii* forms a geographically, ecologically, and reproductively distinct set of populations. However, owing to hybridization, distinctions between this and *P. secunda* or *P. keckii* can be difficult. The presence of more or less rounded lemmas with at least a few short hairs near the base, dull-finished glumes, and milky colored ligules (leaves normally thin, and withering) indicates *P. secunda* parentage. Papillae on the long-cells of leaves, thickish lemmas, intravaginal branching, and anthers less than 2.0 mm long indicate genes of *P. keckii*.

2. POA PRINGLEI Scribner, Bull. Torrey Bot. Club 10:31. 1883.—*Atropis pringlei* (Scribner) Beal, Grasses N. Amer. 2:578. 1896.—*Puccinellia pringlei* (Scribner) Ponert, Feddes Repert. 84:740. 1974.—TYPE: California, Mts. about the headwaters of the Sacramento River [probably Trinity or Shasta Co.], "8,000'," 1 Sep 1882, *Pringle* (lectotype designated here: US—556759!; isolectotypes: GH—2 sheets!, MICH!, MO!, NY!, US—824899!, 748845 in part!) (fig. 4).

P. argentea Howell in Vasey, Bull. Torrey Bot. Club 15:11. 1888.—*Melica argentea* (Howell) Beal, Bull. Torrey Bot. Club 17:153. 1890.—*Melica nana* Beal, Grasses N. Amer. 2:504.

1896 [new name for *M. argentea* Beal because of *M. argentea* E. Desv. an error for *M. argentata* E. Desv.].—TYPE: Oregon, Siskiyou Mts., Ashland Butte, 1887, *T. Howell* (holotype: ORE—15428!; isotypes: JEP!, NY!, US—556756!, 924677!).

Chromosome number. Unknown.

Habitat. Subalpine to alpine, 1980–2900 m, on igneous to serpentine substrates, in talus gravels and sands, in dry to more often moist open ground particularly around snow beds.

Distribution and representative specimens examined. U.S.A. NW and E California, Klamath-Siskiyou region to Mt. Shasta, Mt. Lassen, and the N Sierra Nevada (S to Alpine Co., Ebbetts Pass, *McNeal 1988*) and SW Oregon (Josephine Co., Bolan Lake, *Hitchcock & Martin 5241*, and Jackson Co.) (fig. 1b).

Comments. Sexual populations of this species are restricted to the Klamath-Siskiyou region. From Mt. Shasta east, only pistillate and evidently apomictic plants are known. *Poa pringlei* may be distinguished from *P. cusickii* s.l. by its longer innovation ligules, and from *P. suksdorfii* by being dioecious and having long anthers. What appear to be apomictic hybrids between *P. pringlei* and *P. cusickii* occur on Mt. Lassen (*Swallen 11368, 13742, 13755, 13762*, among other collections). These have sheaths closed more than ⅔ the length and loose panicles. Another possible hybrid population between these species occurs on Mt. Rose, Washoe Co., Nevada, and was discussed by Marsh (1952) as the Mt. Rose form.

3. POA LEIBERGII Scribner, U.S.D.A., Div. Agrostol. Bull. 8:6, pl. 2. 1897.—TYPE: Oregon, Malheur Co. "summits of ridges which form the NW angle of the barren valley," Owyhee-Malheur Divide, 1250 m, 31 May 1896, *Leiberg 2171* (lectotype designated in Hitchcock 1935, fig. 250: US—276821!; isolectotypes: GH!, UC!, US—1869462!, 748849!) (fig. 4).

P. pulchella Vasey, Bot. Gaz. (Crawfordsville) 7: 32. 1882 [non Salisb. 1796].—*Atropis pulchella* (Vasey) Beal, Grasses N. Amer. 2:574. 1896.—*Poa vaseyochloa* Scribner, U.S.D.A. Div. Agrostol. Circ. 9:1. 1899.—*Poa gracillima* Vasey var. *vaseyochloa* (Vasey) M. E. Jones, Contr. W. Bot. 14:14. 1912.—*Puccinellia pulchella* (Vasey) Ponert, Feddes Repert. 84:740. 1974.—TYPE: Washington, Klickitat Co., Mountains, 28 Apr 1881, *Suksdorf s.n.* (holotype: US—556817! [Hitchcock 1935, fig. 245]; isotype: WSU [*291*, Klickitat Co., Columbia River, moist hillsides, 28 Apr 1881], taken as an isotype by Marsh).

Chromosome number. Unknown (see discussion under *P. stebbinsii*).

Habitat. Lower sagebrush zone to subalpine, 150–1650 m, moist mossy situations on steep north slopes, ledges and cliff bases, in seeps and snow pockets, to margins of swales, and moist meadows.

Distribution and representative specimens examined. U.S.A. E Oregon and SE Washington from the vicinity of the Columbia and Snake river gorges to W-Central and SW Idaho [Camas Co.: *Christ & Ward 7005*; Elmore Co.: *Soreng 2504*; Owyhee Co.: *Grimes* (NY!)] (fig. 1a).

Comments. This species is in most cases easily distinguished from *P. cusickii* subsp. *cusickii* by its delicate, few-spikeleted panicles and thin, soon withering leaf blades. It occurs in distinctly different microhabitats and flowers earlier. However, the two have been found growing together and some intermediacy is evident in plants from the region of overlap.

4. POA PORSILDII Gjaerevoll, Danske Kongel. Norske Vidensk. Selsk. Forh. 29(16):73–74. 1975.—TYPE: Canada, Yukon Terr., MacMillan Pass, "alpine treeless country," 4000–5000 ft, 31 Aug 1944, *Porsild & Breitung 11188* (holotype: TRH; isotype CAN!).

Chromosome number. Unknown.

Habitat. Moist alpine heath along creeks and near the edges of snow beds.

Distribution and representative specimens examined. Canada. Northwest Territory, Mackenzie District, Nahanni Natl. Park (*Talbot T5060-4*); Yukon Territory, Selwyn, and Ogilvie Mts. U.S.A. E-Central Alaska, White Mts.: *Hamet-Ahti 1201*.

Comments. *Poa porsildii* is a dioecious, sexual species of unglaciated tundras in east-central Alaska, Yukon Territory, and western District of Mackenzie. Although it has been included in *P. leibergii* (Hultén 1968; Scoggan 1972), I believe it is closer and directly related to *P. cusickii* subsp. *epilis*. It is distinguished from the latter taxon only by the presence of open, flexuous-

branched, fewer (10–30) flowered panicles, and in reproducing sexually.

5. POA CUSICKII Vasey subsp. CUSICKII, Contr. U.S. Natl. Herb. 1:271. 1893.—TYPE: Oregon, Baker Co., Powder River, May 1885, *Cusick 1219* (lectotype designated here: US—556821; isolectotypes: NY—3 sheets, "moist hillsides"!, ORE—"near the mouth of Magpie Cr., north hillsides of the Powder River, Baker Co."!, US—1869103!, 924906! 824863 [J. D. Smith Herb.]!, WSU!) (fig. 4).

Poa filifolia Vasey, Contr. U.S. Natl. Herb. 1:271. 1893 [non Shur. applied in syn. only].—*Poa idohoensis* Beal, Grasses N. Amer. 2:539. 1896.—*P. scabrifolia.* Heller, Bull Torrey Bot. Club 24:310. 1897.—TYPE: Idaho, Nez Perce Co., rocky banks of Hatwai Creek, in 1892, *Sandberg 138* (holotype: US—556823!; isotype: CAS!).

Poa spillmanii Piper, Erythea 7:102. 1899.—TYPE: Washington, Douglas Co., between Coulee City and Waterville, 27 May 1896, *Spillman* (holotype: US—1939412!; isotype: US—556824!).

Poa cottonii Piper, Proc. Biol. Soc. Wash. 18:146. 1905.—TYPE: Washington, Yakima Co., Rattlesnake Mt., 7 May 1902, *Cotton 557* (isotypes: GH!, US—556820!, WSU—2 sheets!, WTU!).

Poa capillarifolia Scribner and T. Williams, U.S.D.A. Div. Agrostol. Circ. 9:1. 1899.—TYPE: California, *Hansen 2614* (holotype: US—556822!).

Poa hansenii Scribner, U.S.D.A. Div. Agrostol. Bull. 11:53, pl. 9. 1898.—*P. pringlei* var. *hansenii* (Scribner) Smiley, Univ. Calif. Pub., Bot. 9:104. 1921.—TYPE: California, Amador Co., Silver Lake, 8000 ft, 27 Jun 1892, *Hansen 605* (holotype: US—556760!; isotype: UC!).

Chromosome number. $2n = 28$ [*Stebbins and Love 2921!, 2933!* (Stebbins and Love 1941)]. Report of $2n = 42$ (Hartung 1946) (*Keck 5408* CI!) appears to equal *P. juncifolia* Scribner.

Habitat. In densely vegetated moist meadows to open sparsely vegetated woods, from sagebrush zone to woodland parkland and mixed coniferous forests to lower alpine, 300–2500 m.

Distribution. U.S.A. E California, W and S Idaho, N Nevada, E Oregon, and E Washington (fig. 2a).

Comments. Studies on the morphology and geography of sexual and asexual reproduction in diclinous *Poa* indicate there are two geographically and ecologically, and possibly cytologically, distinct sexual populations within *P. cusickii* s.l. These are distinguished as subsp. *cusickii* and subsp. *pallida*. However, apomictic plants are more common than sexual ones in both subspecies. In addition, there are two groups of plants that are strictly pistillate: subsp. *epilis* and its var. *purpurascens* (Vasey) C. Hitchc. (Soreng 1986). Subspecies *cusickii* is comprised of a quite variable group of populations occurring east of the Cascade Mountains in the western Great Basin and Columbia Plateau. Panicle form is particularly variable. Panicles may be loosely contracted and long branched to compact and shorter branched, but the branches are slender and the longest more than 17 mm, except in depauperate individuals. This subspecies is dioecious throughout most of its range, but perfect-flowered individuals are not infrequent in the northern extent.

6. **Poa cusickii** subsp. **pallida** R. J. Soreng, nom. nov.—*Poa subaristata* Scribner in Beal, Grasses N. Amer. 2:533. 1896 [non R. Phil., also in 1896 (October), but earlier].—TYPE: Wyoming, Yellowstone Natl. Park, East Fork, "alpine," 10,000', Aug 1885, *Tweedy 633* (holotype: US—1939411!; isotype: GH!) (fig. 4).

Poa scaberrima Rydb., Bull. Torrey Bot. Club 36: 534. 1909.—TYPE: Idaho, Beaver Canyon, 27 Jun 1895, *Rydberg 2055* (holotype NY!; isotype: US—924854!).

Chromosome number. $2n = 56$ (*Dore 11760!*), 59 (*Dore 12195!*), $2n = 56+II$ (*Soreng 2456*, Montana, Park Co., above Jardine).

Habitat. Similar to that of subsp. *cusickii* but generally of higher, drier and more often alpine situations, 900–3300 m.

Distribution and representative specimens examined. Canada. E British Columbia, Alberta, Manitoba, Saskatchewan (Frenchmans River, *Macoun 13260*), S. Yukon Territory (*Raup 13050*). U.S.A. E California (White Mts., *DeDecker 1246*), N Colorado, Idaho, Montana, W North Dakota, N Nevada, E Oregon, (W South Dakota?), N Utah (to Sevier Co., Mt. Marvin, *Rydberg & Carlton 7557*) and Wyoming (fig. 2).

Comments. *Poa subaristata* is a later homonym (non R. Phil.), therefore, a new name was chosen for the new subspecies. Subspecies *pallida* differs from subsp. *cusickii* in having consistently short panicles [2–6(9.5) cm long, vs. mostly 5–10 cm long], and shorter panicle branches (less than 17 mm long) with stouter pedicels giving the panicle a stricter, more condensed appearance. Spikelets of subsp. *pallida* also have a soft shining appearance, vs. a dull or glossy finish in subsp. *cusickii*. The distinctions of the panicle axis and branch length are least sharp in eastern California, but appear to hold when considered by population means rather than individuals. Where known, plants are octoploid vs. tetraploid. Sexual populations of this subspecies are confined mostly to the east slope of the Rocky Mountains (Montana and Wyoming), but apomictic plants occur over a wide geographic range. Viviparous plants are known from Montana and southwestern Canada. A sexual population of plants from wet meadows in Park Co., Colorado (*Wittman & Wittmann 1187*) is unusual in having very slender, elongate rhizomes, but otherwise appears identical to more northern sexual populations of this subspecies.

7. POA CUSICKII subsp. EPILIS (Scribner) W. A. Weber var. EPILIS, Phytologia 51:375. 1982.—*Poa epilis* Scribner, U.S.D.A. Div. Agrostol. Circ. 9:5. 1899.—*Poa purpurascens* var. *epilis* (Scribner) M. E. Jones, Contr. W. Bot. 14: 14. 1912.—TYPE: Colorado, Routt Co., Buffalo Pass, open places in timber, 10,000 ft, 13 Aug 1898, *Shear & Bessey 1457* (holotype US—556768! [Hitchcock 1935, fig. 243]; isotypes: NY!, UC!).

Chromosome number. $2n = 56$ (*SES*), reported by Armstrong (1937). A report of $2n = 70$ (*CI 4241*) by Hiesey and Nobs (1982) (voucher not seen). Hartung (1946) reported $2n = 84$, but both *P. cusickii* subsp. *pallida* and *P. secunda* are on a single specimen collected from a pot with the corresponding collection information (*V. L. Marsh*, in 1948, WTU!) so it is not clear which species she examined.

Habitat. Subalpine to lower alpine, moderately moist meadows, heath, and forest openings especially around snow pockets.

Distribution. Canada. Alberta and British Columbia. U.S.A. E California, W Colorado, Idaho, W Montana, N Nevada, E Oregon, N Utah, Washington, and Wyoming (fig. 2b).

Comments. This subspecies is quite similar to subsp. *pallida*, but there is little intermediacy between them. Interbreeding is inhibited, at least in part, because where parapatric, both taxa are pistillate. Both occur over a wide geographic range, but subsp. *epilis* is limited to a vary narrow range of habitat and consistently occupies more mesic sites. Panicle branches of subsp. *epilis* are smooth to sparsely scabrous, vs. moderately to densely scabrous in subsp. *pallida*. Subspecies *epilis* has proportionally fewer vegetative shoots, usually some being extravaginal vs. strictly intravaginal, and more flowering shoots. Culm nodes are more elevated in mature plants of subsp. *epilis* and culm leaves are often flat and broadened. Lemmas are more deeply green (vs. pallid green in subsp. *pallida*) and exhibit an anthocyanic flush in the hyaline margin. These coloration and scabrosity differences were quite stable in transplant studies. Subspecies *epilis*, which is strictly pistillate, may have originated from hybridization between subsp. *pallida* and *P. porsildii* in the Pleistocene. Subspecies *epilis* is remarkably uniform throughout its range but putative hybrids between this and other related species are occasionally found. A viviparous form has been collected in Utah.

8. POA CUSICKII subsp. EPILIS var. PURPURASCENS (Vasey) C. Hitchc.—*Poa purpurascens* Vasey, Bot. Gaz. (Crawfordsville) 6:297. 1881 [non Sprengel 1819].—*Poa paddensis* Will., U.S.D.A. Div. Agrostol. Bull. 2nd ed. 17: 261, fig. 557. 1901.—*Poa subpurpurea* Rydb., Bull. Torrey Bot. Club 32:606. 1905.—*Poa alpina* var. *purpurascens* Vasey, Descr. Cat. Grasses U.S. 79. 1885.—*Poa alpina* L. var. *purpurascens* Beal, Grasses N. Amer. 2:543. 1896.—*Poa cusickii* var. *purpurascens* (Vasey) C. Hitchc., Vasc. Pl. Pacific Northwest 1: 659. 1969 [as (Beal) C. Hitchc. Emend. C. L. Hitchc., Fl. Pacific Northwest 659. 1973].—TYPE: Oregon, Mt. Hood, 4–6000 ft, Aug 1981, *T. Howell s.n.* (lectotype designated here: US—556826!; isolectotypes: GH!, ORE!, OSC!, US—133409!).

Chromosome number. A population voucher, *Pojar 249*, for a single report of $2n = 28+II$ by Pojar (1973) for *P. epilis*, represents this variety.

Habitat. Subalpine to alpine, on igneous substrates, moist meadows to open forests.

Distribution and representative specimens examined. Canada. S British Columbia (*Macoun*

63437). U.S.A. Cascade and Olympic mts., rare in the Sierra Nevada: NW and E California (Eldorado Co., Desolation Valley, *Stebbins 3313*; Syskiyou Co., English Peak, *Oettinger 1605*), Oregon, and Washington (fig. 2).

Comments. *Poa purpurascens* Vasey is illegitimate as a later homonym, and was replaced by a new name, *P. alpina* var. *purpurascens*, proposed by Vasey in 1885. This variety was transferred to *P. cusickii* as var. *purpurascens* (Vasey) C. Hitchc. The variety is quite variable and it may be trivial to recognize it as distinct from var. *epilis*. However, plants referable to it are numerous enough, occur over a definable ecological and geographical range, and are distinguishable from var. *epilis* in most cases. It is strictly pistillate and appears to have originated from hybridization between *P. cusickii* var. *epilis* and members of the *P. nervosa* group, most likely with plants similar to *P. rhizomata*. Panicles of var. *purpurascens* are generally more sparsely and laxly flowered than those of var. *epilis*, have larger spikelets, and at least the lower lemmas are sparsely puberulent on the keel, sometimes the marginal nerves, and frequently on the callus. This variety is sometimes difficult to distinguish from *P. wheeleri* Vasey [=*P. nervosa* var. *wheeleri* (Vasey) C. Hitchc.] in that culm bases are often decumbent and extravaginal in origin giving the appearance of being short rhizomatous, but the basal sheaths are smooth and never retrorsely pubescent. Misidentifications of specimens of var. *purpurascens* and *P. wheeleri* from Crater Lake, Oregon, are responsible for records of *P. stenantha* in southern Oregon.

9. POA × NEMATOPHYLLA Rydb. (pro. sp.), Bull. Torrey Bot. Club 32:606. 1905.—TYPE: Colorado, Meeker, *Osterhout 2601* (holotype: NY!).

Poa cusickii subsp. *pubens* Keck, in C. L. Porter, Flora Wyom., Part 3, Wyoming Agr. Exp. Sta. Bull. 418:22. 1964.—TYPE: Wyoming, Sweetwater Co., Orendo Butte, on the sandy plain of the Red Desert, 11 Jun 1900, *Nelson 7130* (holotype: US; isotypes: GH!, NY—2 sheets!, RM, US!).

Poa longiligula var. *wyomingensis* T. Williams, U.S.D.A. Div. Agrostol. Circ. 10:3 1899.—TYPE: Wyoming, Sweetwater Co., Tipton, 17 Jun 1898, *Nelson 4799a* (holotype: US—556787!; isotypes: [*4799* appears to be same plant] MICH!, NY!, US—556786!).

Chromosome number. Unknown.

Habitat. Similar to *P. cusickii* subsp. *pallida*, but mostly of more xeric conditions, low hills in plains to upper sagebrush zone.

Distribution. Canada. Alberta, Manitoba, and Saskatchewan. U.S.A. NW Colorado, E Idaho, Montana, NE Utah, and Wyoming (fig. 2a).

Comments. Evidence from population and herbarium studies, and principal components analysis, indicates this taxon may have originated via hybridization between *P. cusickii* subsp. *pallida* and *P. fendleriana* (Soreng 1985, and unpubl. data). Plants of this taxon are intermediate but highly variable in form. They are most abundant in the region of contact between the putative parental taxa, but are also occasionally collected on the northern Great Plains. These plants are apparently apomictic because very few male plants have been found, yet the females set seed.

II. Sect. *Abbreviatae*.

Low growing (less than 25 cm tall) cespitose perennials, with reproductive and short intravaginal vegetative shoots; sheaths of upper cauline leaves with margins fused $\frac{1}{10}$–$\frac{1}{4}(\frac{1}{3})$ the length; leaf blades folded and involute on the margins, not hairy adaxially (or densely scabrous to puberulent adaxially in *P. suksdorfii*); anatomically the leaf blades with or without small hooks confined to costal regions, or with both costal and intercostal hooks, without papillae on the long-cells (or, in *P. keckii*, with them); panicle branches scabrous to almost smooth; glumes frequently as long or longer than the first lemma; lemmas distinctly keeled, somewhat pilose on the lower part or glabrous, without or rarely with a small tuft of hairs on the dorsal side of the callus; palea nearly smooth or spinulose on the keels, vestiture of the lower half often modified into short hairs; flowers perfect or sometimes the upper ones within a spikelet pistillate, anthers 0.2–1.8 mm long.

10. **Poa keckii** R. J. Soreng, spec. nov. (fig. 3, 4).—TYPE: California, Tuolumne Co., Mt. Conness, 12,000 ft, 15 Aug 1944, *J. T. Howell 20566* (holotype: US—1895937!; isotypes: CAS!, DS!).

A *Poa suksdorfii* (Beal) Vasey ex Piper cellulis-longis unipapillatis (non nonpapillatis), uncis curtis plerumque non nisi in nervos (non uncis

pluries curtis plerumque longioribus, in nervos et inter nervos), ligulis abaxialiter laevibus vel ut maxime parce scabris (non scabris vel scabropuberulis), laminis nodorum superiorum nervis 7–15 expressis arcte dispositis (non 5–9 late dispersis), lemmatibus 3.0–4.8 ($\bar{x}$ = 3.8) mm longis [non 4.0–5.8 ($\bar{x}$ = 4.8) mm longis], glabris vel pluries sparsissime puberulis (non semper glabris), differt.

Basal tuft of leaves 3–6(12) cm tall, dense, firm; culms 3–7(22) cm tall, branched intravaginally at very base or just above in older plants; leaves chiefly basal, culm sheaths with the margins fused 1/10–1/6 of the length; leaf blades thick, firm, folded and involute on the margins, those of the upper culm nodes with 7–15 veins expressed (fewer in other leaves), the adaxial surface smooth in appearance or sparsely scabrous (the collars smooth); ligules smooth or sparsely scabrous abaxially, milky-colored and somewhat opaque, those of the upper innovation leaves less than 3 mm long, obtuse to acute; culm nodes buried in the basal tuft; anatomically at least the adaxial surface of the leaf blades frequently with one oblique papilla per long-cell (usually situated sub-terminally), the papillae sometimes slightly overarching stomata as in *Puccinellia*, cork-cell/silica-body pairs present or absent; peduncles 2.0–12.5 cm long, the ratio of the peduncle length to panicle length 1:1 to rarely over 3:1; panicle compact to slightly open, ovate to lanceolate, 1.5–6(10) cm long, barely exerted to well elevated above the basal tuft, with 8–30 spikelets, the branches sparsely to fairly densely scabrous, round or angled, the lateral pedicels (0.5)1.5–5 (mostly more than 2) mm long; spikelets 2–3-flowered, anthocyanic; glumes smooth, shining, acute, scabrous on the upper keel, the first shorter or equaling the first lemma in length, 3.0–4.7 mm long, the second frequently longer than the first lemma, 3.0–4.9 mm long; lower lemmas lanceolate in outline, smooth to scaberulous, glabrous or frequently very sparsely and finely puberulent on the keel and marginal nerves and sometimes between these on the sides above the base, keeled, 3.0–4.8 averaging 3.8 mm long, 5-nerved, the intermediate ones mostly obscure; callus glabrous; palea finely scabrous on the keels; rachillas smooth or hirsutulous, the internodes less than 1 mm long; flowers perfect or very rarely pistillate (hybrids?); anthers 0.6–1.7(2.0) mm long; ovary glabrous.

Chromosome number. Unknown.

Habitat. Primarily high alpine, (2350)3200–4360 m, in open places on lavas, granitics, and metamorphics, in crevices of rocks and walls, and loose gravels, screes and sand.

Distribution and representative specimens examined. U.S.A. E California, Sierra Nevada (Nevada Co., Basin Peak, *True & Howell 116343*; Alpine Co., Lake Alpine, *Howden 11380*; S to Tulare Co., Boreal Plateau, *Sharsmith 3428*) and adjacent ranges of the Great Basin (Mono Co., White Mts., *Duran M116a*, and Sweetwater Mts., Mt. Patterson, *Hoover 5555*) (fig. 1d).

Comments. A. S. Hitchcock (1935) submerged *Poa suksdorfii*, including plants referred to here as *P. keckii*, under *P. pringlei*. He included in the latter taxon a much wider range of variation and distribution than is generally recognized today by also including many Rocky Mountain specimens of *P. cusickii* subsp. *pallida* (the latter taxon illustrated as *P. pringlei* in his manual of grasses; 1935, fig. 246). Later authors (Marsh 1952; Keck 1963; C. L. Hitchcock 1969; Soreng 1986) clarified important morphological, ecological and reproductive differences between these taxa and treated them as distinct species. Differences between the northern and southern populations included in *P. suksdorfii* s.l. had not been noted by previous authors.

Although there is overlap in most morphological characteristics, *Poa keckii* differs from *P. suksdorfii* in so many characters (table 2), some of them exclusive, that a direct relationship between them is questionable. Thus I treat them as species rather than subspecies. *Poa suksdorfii* is restricted to the Cascade and Wallowa mountains of Oregon and Washington, and *P. keckii* to the Sierra Nevada and adjacent Great Basin ranges. Whereas *P. suksdorfii* is more similar to *P. pringlei* than *P. keckii* in several respects, *P. keckii* is more closely allied to *P. pattersonii*.

11. POA SUKSDORFII (Beal) Vasey ex Piper, Contr. U.S. Natl. Herb. 11:135. 1906.—*Atropis suksdorfii* Beal, Grasses N. Amer. 2:574. 1896.—TYPE: Washington, Mt. Paddo [Mt. Adams], gravelly places near glaciers, 7–8000 ft, 3 Sep 1891, *Suksdorf 1116* (holotype: US—556755!; isotypes: GH!, MICH!, MO!, OSC!, UC!, US—824830 [from J. D. Smith herbarium]!, WSU!) (fig. 3).

Plants with a short 6–15 cm tall dense tuft of rather firm basal leaves, with culms 7–25 cm

TABLE 2. Comparison of *Poa keckii* and *P. suksdorfii*.

Characteristic	*P. keckii*	*P. suksdorfii*
Basal tuft of leaves	3–6 (12) cm	6–15 cm
Plant height	3–7 (22) cm	7–25 cm
Culm sheath closed	10–20%	14–33%
Leaf of upper culm node	7–15 veins exposed	5–9 veins exposed
Ventral blade surface	smooth or sparsely scabrous with short hooks costally	scabrous or scabrid-puberulent with medium to longer hooks costally and intercostally
Leaf-blade papillae	present	absent
Ligules	smooth or sparsely scabrous	scabrous or scabrid-puberulent
Collars	smooth	scabrous
Peduncles	2–12.5 cm	7–16 cm
Lateral pedicels	(0.5)1.5–4+ mm	0.5–1.5(3+) mm
First glume length (mm)	3.0–4.7, $\bar{x}$ = 3.7	3.6–5.7, $\bar{x}$ = 4.4
Second glume length (mm)	3.0–4.9, $\bar{x}$ = 3.9	3.5–6.2, $\bar{x}$ = 4.8
First lemma length (mm)	3.0–4.8, $\bar{x}$ = 3.8	4.1–5.8, $\bar{x}$ = 4.8
Lemmas	glabrous or frequently sparsely puberulent	glabrous

tall, branched intravaginally at the very base or just above in older plants; leaves chiefly basal; culm sheaths with the margins fused ⅐–⅓ of the length; leaf blades thick, moderately firm, folded and involute on the margins, those of the upper culm nodes with 5–9 veins expressed (as in other leaves), at least those of the innovations frequently densely scabrous to puberulent ventrally (especially about the collars); ligules smooth to densely scabrous abaxially, milky-colored and somewhat opaque, those of the upper innovation leaves less than 3.5 mm long, obtuse to acute; anatomically the leaf blades without papillae on the long-cells, short-cells of the adaxial surface frequently developed into short or longer hooks both costally and intercostally, and of the abaxial surface with cork-cell/silica-body pairs; culm nodes buried in the basal tuft or rarely sightly elevated; peduncles 7–16 cm long, the ratio of the peduncle length to panicle length 2:1 to rarely over 4.5:1; panicle compact, lanceolate, 3–5(6) cm long, included to little exerted above the basal tuft, with 14–40 spikelets, the branches smooth to moderately scabrous, angled, the lateral pedicels 0.5–1.5(4) mm long; spikelets loosely 2–4-flowered, more or less anthocyanic; glumes smooth, shining, acute, sparsely scabrous on the upper keel, mostly 3–5-nerved, the first shorter or equaling the first lemma in length, 3.6–5.7 mm long, the second frequently longer than the first lemma, 3.5–6.2 mm long; lemmas narrowly lanceolate in outline, smooth to scaberulous, glabrous, keeled, the lower ones 4.1–5.8 averaging 4.8 mm long, 5-nerved, the intermediate ones mostly obscure; callus glabrous; palea finely scabrous on the keels; rachillas smooth or hirsutulous, the internodes 1–1.5 mm long; flowers perfect, rarely pistillate in part; anthers 0.8–1.7 mm long; ovary glabrous.

Chromosome number. Unknown.

Habitat. Alpine, 1830–2960 m, open places on igneous substrates, on moraines, ridges, and peaks, in gravels, screes, and sands.

Distribution and representative specimens examined. U.S.A. Washington, Olympic Mts. (Jefferson Co., *Thompson 7937*); Cascade Mts. from Mt. Ranier S; Oregon, Cascade Mts., Mt. Hood S to Diamond Peak (Lane Co., *Coville & Applegate 507*); Wallowa Mts. (fig. 1c).

12. POA LETTERMANII Vasey, Contr. U.S. Natl. Herb. 1:273. 1893.—*Atropis lettermanii* (Vasey) Beal, Grasses N. Amer. 2:579. 1896.—*Puccinellia lettermanii* (Vasey) Ponert, Feddes Repert. 84:740. 1974.—TYPE: Colorado, Grays Peak, *Letterman 7* (holotype: US—556753!).

Poa brandegei Scribner in Beal, Grasses N. Amer. 2:544. 1896.—TYPE: Colorado, Grays Peak, *Jones 714* (holotype: US—556754!).

Poa montevansii Kelso, Biol. Leafl. 29:2. 1945.—TYPE: Mt. Evans, Colorado, *Kelso & Kelso 427*

(holotype: US—1866386! [Hitchcock and Chase 1951, fig. 173]).

Chromosome number. $2n = 14$ (A. Löve, pers. comm.).

Habitat. High alpine in sandy to gravelly open ground often around boulders and on ledges.

Distribution. Canada. W Alberta, E British Columbia. U.S.A. E California, W Colorado, Idaho, W Montana, NE Nevada, Oregon, N Utah, Washington, and Wyoming.

Comment. The distinction between this species and *P. abbreviata* subsp. *jordalii* (A. Pors.) Hultén, with puberulent lemma keel and marginal nerves from Siberia, Alaska, and the Yukon, needs evaluation.

III. Sect. **Secundae** V. Marsh ex R. J. Soreng, sect. nov.—TYPE: *P. secunda* J. S. Presl.

Perennes dense caespitosae, innovationibus intravaginalibus et extravaginalibus, vel intravaginalibus. Vaginae margines non nisi prope basin connati. Foliorum laminae basalium tenuissimae vel firmae, 1–3 mm latae, planae vel plicatae vel involutae, in superficie breviter scabridae ad nervos (non inter nervos) vel laeves, interdum papillatae. Lemmata glabra vel plus minusve aequaliter ad basin pilosa, abaxialiter rotundata vel carinata. Calli abaxialiter rotundati, circum basin pubescentes vel glabri. Flores hermaphroditi. Antherae 1.5–3 mm longae. Chromosomatum numerus $n = 21$.

Cespitose perennials, branching intra- and extravaginal, or strictly intravaginal; sheath margins fused only near the base; blades of the basal tuft soft and narrow or firm, 1–3 mm wide, flat, folded, or involute, the adaxial surface short scabrous only on the nerves or smooth, long-cells sometimes with papillae; glumes ⅔ the length of the first lemma or more; lemmas smooth to scabrous, glabrous or more or less evenly puberulent toward the base; callus round across the back and smoothly transitional to the lemma (not swollen or laterally sulcate), with or without crisp short hairs around the base of the lemma; base chromosome number, $n = 21$.

IIIa. Subsect. *Secundae.*

Plantae interdum halophilae. Laminae sine papillis. Lemmata abaxialiter plus minusve rotundata vel carinata.

Plants sometimes halophilic; long-cells of leaves lacking papillae; spikelets narrowly lanceolate, little compressed; lemmas more or less rounded across the back; distal rachilla internodes elongated, more than 1.2 mm long. Including: *P. curtifolia* Scribner, *P. secunda* J. S. Presl s.l., *P. stenantha* Trin., and *P. tenerrima* Scribner.

IIIb. Subsect. **Halophytae** V. Marsh ex R. J. Soreng, subsect. nov.—TYPE: *P. unilateralis* Scribner.

Plantae halophilae, innovationibus intravaginalibus. Laminae firmae, cellis-longis unipapillatis. Lemmata carinata.

Halophytic plants; branching intravaginal; long-cells of firm leaves producing a single oblique papilla per cell, the papillae tending to overarch the stomata (as in *Puccinellia*); spikelets more or less compressed; lemmas keeled; rachilla internodes 1 mm or less in length.

13. POA UNILATERALIS Scribner in Vasey, U.S.D.A. Div. Bot. Bull. 13(2):pl. 85. 1893.—*Atropis unilateralis* (Scribner) Beal, Grasses N. Amer. 2:581. 1896.—*Puccinellia unilateralis* (Scribner) Ponert, Feddes Repert. 84:740. 1974.—TYPE: California, San Francisco, in 1882, *M. E. Jones 15* (holotype: US—556774!).

Poa pachypholis Piper, Proc. Biol. Soc. Wash. 18: 146. 1905.—TYPE: Washington, Pacific Co., Ilwaco, ocean cliffs, 22 Jun 1904, *Piper 4900* (holotype: US—556775!; isotypes: US—748809!, 923750!, 3151666!, US—sn. "Office of the Agrostologist, U.S.D.A. Herb."!, WSU!, WTU!).

Chromosome number. *P. unilateralis* form, $2n = 42$, and 84 (*Clausen 2151*!); *P. pachypholis* form, $2n = 42$ (*Spellenberg & Sutherland 1522A*!).

Habitat. Sea cliffs and bluffs, on weathered sandstones to heavy clays, in open ground and meadows in saltspray zone.

Distribution and representative specimens examined. U.S.A. Pacific Coast, Central to N California (Monterey Co., *Davy 7212*), N to Oregon (reaching Tillamook Co., *Peck 3163*) and S Washington.

Comments. Although *Poa unilateralis* is said by some authors to have glabrous lemmas and *P. pachypholis* pubescent ones, nearly all plants of *P. unilateralis* have at least some pubescence on at least the lower lemmas of any spikelet. The pubescence patterns are similar in each, with plants from the type locality of *P. pachy-*

pholis representing an extreme, which is also found farther south in plants otherwise indistinguishable from *P. unilateralis*. Chromosome numbers of $2n = 42$ are represented in both, and both have "puccinellioid" papillae on the leaf-blade epidermis. The leaves of *P. pachypholis* are narrow and firm and have frequent cork-cell/silica-body pairs, whereas those of *P. unilateralis* are narrow to broad, lax or firm, but not narrow and firm, and cork-cell/silica-body pairs were lacking in the four plants examined. Panicles are also somewhat less congested than typical of *P. unilateralis*. Further study might provide more evidence for recognition of *P. pachypholis* as a subspecies of *P. unilateralis*, but no formal recognition is given here.

14. POA NAPENSIS Beetle, Leafl. W. Bot. 4:289. 1946.—TYPE: California, Napa Co., Myrtledale Hot Springs, 7 May 1946, *Beetle 4256* (holotype: DAV; isotypes: CAS! US—1886553! [Hitchcock and Chase 1951, fig. 167]).

Chromosome number. $2n = 42$ (*Soreng 2926*, California, Napa Co., Calistoga Hot Springs, airport).

Habitat. Low stony ground in mineralized soils about hot-springs.

Distribution. U.S.A. California, Napa Co., vicinity of Calistoga.

Comments. The original description said this species is close to *P. cusickii*, but I have found no evidence to support that connection. This species is closely related to *P. unilateralis* as evidenced by general habit, sheaths open nearly to the base, the presence of puccinellioid papillae on epidermal long-cells, scabrous branches, and occurrence in saline soils. The rare occurrence of hairs around the callus on *P. napensis* lemmas also supports the relationship to *P. unilateralis*. Both species have $2n = 42$ chromosomes. Long terminally-flowered, loosely ascending, scabrous branched panicles, mostly glabrous lemmas, and long, firm, narrow, scabrous leaf blades, clearly distinguish *P. napensis* from *P. unilateralis*.

Incertae Sedis

15. POA STRICTIRAMEA A. Hitchc., Contr. U.S. Natl. Herb. 17(3):375. 1913.—TYPE: Mexico, Chihuahua, Cusihuiriachic, cool ledges of La Bufa Mt., 2 Sep 1887, *Pringle 1437* (holotype: US—820909!; isotypes: GH!, MICH!, NY—2 sheets!).

Poa involuta A. Hitchc., Proc. Biol. Soc. Wash. 41:159. 1928.—TYPE: Texas, Brewster Co., Chisos Mts., upper slopes of hills, first ridge SW of Juniper Canyon, 15–18 Jul 1921, *Ferris & Duncan 2811* (holotype: US—1125239!; isotypes: CAS!, US—1865159!).

Poa filiculmis Swallen, Contr. U.S. Natl. Herb. 19:400. 1950 [non Rosch., 1949].—*Poa coahuilensis* Beetle, Phytologia 52:17. 1982.—TYPE: Mexico, "15 km w. of Concepcion del Oro. just within the border of Coahuila" [M. Johnston belives this is in Zacatecas], valley floor sparsely covered by yuccas and Larrea, 2300 m, 24°52'N 101°45'W, 19 Jul 1941, *Stanford, Retherford & Northcraft 477* (holotype: US—1815803!; isotypes: ARIZ!, GH!, MO!, NY!).

Chromosome number. $2n = 28+I$ (*Soreng 2304*, Chihuahua, Babicora).

Habitat. Mountains in and around the Chihuahuan Desert. Steep north facing slopes and bases of cliffs, in igneous and limestone substrates, from upper creosotebush to middle elevations in pine-oak zones.

Distribution. Mexico. Chihuahua, Coahuila, Durango, Nuevo Leon, and Zacatecas. U.S.A. SW Texas.

Comments. Among 68 characters evaluated in *P. involuta* s. str. (Marsh 1952), *P. strictiramea* from western Chihuahua differs only in ligule length. As the latter character varies among specimens from around the Chihuahuan Desert and their habitat is similar across the region, I see no reason to recognize these as distinct species. Lemmas of this species may be finely puberulent or glabrous, and sparsely short webbed or not, branches are intra- and extravaginal, sheaths are open to near the base, but not scabrid-puberulent adaxially between the nerves, and are setaceously tipped, and upper culm blades are well developed and elongate. The flowers may be perfect or have aborted but little reduced anthers. In habit, plants of this species resemble *P. napensis* more than they do any other North American *Poa*, but have wide open panicles and upper culm leaves as long or longer than their sheaths, and leaves lacking papillae on the long-cells.

Poa filiculmis has been included within *P. stric-*

tiramea by M. Johnston, but *P. filiculmis* is barely distinguishable from *P. mulleri* Swallen, and its placement here needs further evaluation.

Artificial Key to the "Epiles" Group Sensu A. Hitchcock

Description of taxa included in the following key: Plants of western North America (N of Lat. 24°N); cespitose perennials; spikelets distinctly laterally compressed, ovate to narrowly ovate in outline; lemmas distinctly keeled, smooth or scabrous, glabrous to sparsely soft puberulent, or if distinctly pubescent, then the culm sheaths closed more than ⅓ the length and the flowers pistillate, or the plants of saline soils and with papillae on some long-cells; callus without a single well defined dorsal tuft of hair.

1. Panicles elongate, 10–30 cm long, wide open at maturity; upper culm blades as long or longer than their sheaths; long-cells of leaf blades without papillae (magnification × 100); plants from mts. in and around the Chihuahuan Desert ..... 14. *P. strictiramea*
1. Panicles mostly less than 10 cm long and contracted at maturity, if longer, then contracted at maturity, if open then less than 8 cm long; upper culm blades mostly much shorter than their sheaths; long-cells of leaf blades with or without papillae (×100); plants from N and W of the Chihuahuan Desert.
   2. Upper culm sheath margins fused only near the base; flowers perfect (tending to be protandrous), anthers more than 1.5 mm long; lower lemmas glabrous to scabrous or sparsely pubescent on the keel and marginal nerves and base, and sometimes with short hairs arranged around the base of the lemma on the callus; halophytic plants of low elevations of the Pacific seacoast and hot-spring areas in Napa Co., California. [*Poa secunda* Presl (*P. ampla* Merr., *P. juncifolia* Scribner, *P. nevadensis* Vasey forms) with slightly keeled lemmas, and elongate spikelets may key out here, but occurs farther inland.]
      3. Panicles tightly contracted, the branches short, sparsely to densely scabrous, flowered from the base; lower lemmas, at least, sparsely pubescent on the nerves near the base, frequently with short hairs around the base of the lemma on the callus; leaf blades dimorphic, the early ones firm and with papillae on the long-cells, the later ones often much finer and soon withering; seacoast plants ..... 12. *P. unilateralis*
      3. Panicles loosely contracted to somewhat open, the branches elongate, densely scabrous, closely-flowered in the distal half; lower lemmas glabrous or at most with very short hairs on the callus or keel near the base; leaf blades monomorphic, with papillae on the long-cells, all firm; plants from around hot-springs in Napa Co., California ..... 14. *P. napensis*
   2. Upper culm sheath margins fused $\frac{1}{10}$ their length or more; flowers perfect and anthers mostly less than 1.5 mm long, or the species gynodioecious or dioecious; lower lemmas glabrous to scabrous or sparsely pubescent but with calluses entirely glabrous (except in *P. cusickii* var. *purpurascens*); plants not of saline or strongly mineralized soils.
      4. Flowers perfect (rarely pistillate); longest anthers 0.2–1.8(2.0) mm; long-cells of the leaf blades with or without papillae (magnified ×100); plants high alpine, mostly less than 15(25) cm tall.
         5. Plants mostly less than 7 cm tall; leaf blades flat to folded and weakly involute, thin, soft; anthers 0.2–0.8 mm long; lemmas 2.5–3.5 mm long, the lowest frequently exceeded in length by both glumes, rarely with a few short hairs on the keel ..... 12. *P. lettermanii*
         5. Plants mostly 5–20 cm tall; leaf blades folded and involute on the margins, thick, firm; anthers 0.7–1.8(2.0) mm long; lemmas 3.2–5.5 mm long, the lowest frequently exceeded by the second glume but rarely by the first, occasionally with a few hairs on the keel.
            6. Adaxial surface of leaf blades with intercostal hooks, appearing densely hairy or scabrous or infrequently smooth (×25), without papillae (×100), the abaxial surface of the upper culm leaf with 5–7(9) well spaced ribs; lemmas smooth to scaberulous, glabrous; panicles very narrow, lateral pedicels mostly 1–1.5(2.0) mm long; plants of Oregon and Washington ..... 11. *P. suksdorfii*
            6. Adaxial surface of leaf blades without intercostal hooks, appearing smooth (×25), with papillae on the long-cells (×100), the abaxial surface of the upper culm leaf with (5)7–14 closely spaced ribs (seen with the naked eye); lemmas smooth to scaberulous, glabrous or with a few hairs on the keel and sometimes on the sides above the base; panicles contracted or more open, the lateral pedicels mostly over 1.5 mm long; plants of E-Central California ..... 10. *P. keckii*
      4. Flowers perfect or unisexual; most fertile anthers more than 2.0 mm long, sterile anthers rudi-

mentary or partially developed but appearing nonfunctional; long-cells of the leaf blades without papillae (×100); plants of steppe to alpine, often greater than 15 cm tall.

7. Leaf blades of flowering shoots and innovations filiform, thin, soft, and soon withering, flat or folded, smooth or sparsely and minutely scabrous adaxially; innovations intravaginal, lacking bladeless leaves below; short-cells sparse; panicles sparsely few-flowered, with (1)6–17(22) spikelets, the branches smooth to sparsely scabrous, the lowest ones rarely with more than two or three spikelets; culm sheaths closed ⅖–⅘ the length; lemmas glabrous, smooth to scabrous; delicate, gynodioecious, early spring flowering plants, of moist ground in SW Washington, E Oregon, and SW and W-Central Idaho. (Alpine plants of *P. secunda* with glabrous or very nearly glabrous lemmas may key here, but these have lemmas more rounded on back, culm sheaths closed less than ¼ the length, and more fusiform smooth-sided long-cells vs. rectangular and sinuous-sided long-cells.) ..... 3. *P. leibergii*

7. Leaf blades filiform or broader, but not thin, soft, and soon withering, those of the innovations, at least, moderately firm and persisting, adaxially scabrous to short pubescent or sometimes appearing nearly smooth; innovations sometimes extravaginal with bladeless leaves below; short cells common (very rarely sparse); panicles sometimes more densely flowered, the branches smooth to densely scabrous; culm sheaths closed 1/10–¾ the length; lemmas sometimes sparsely pubescent; habitat and distribution broader.

8. Longest ligules of uppermost innovation leaves more than 1.5 mm long, obtuse to acuminate, or lacerate, smooth or scabrous, clear or slightly milky-colored; innovation blades smooth abaxially; upper culm sheaths closed 1/17–⅓(⅖) the length (rarely more in hybrids); plants less than 30(40) cm tall; lemmas thin, completely glabrous; high montane to alpine plants from SW Oregon to the Sierra Nevada, California.

9. Lemmas less than or equal to 5(5.5) mm long; innovations extravaginal with bladeless leaves below; ligules of innovation leaves smooth, rarely sparsely scabrous, mostly clear, the longest uppermost ones 2.5–6 mm long; basal shoots mostly erect, not noticeably decumbent and branched at the lower nodes; delicate, gynodioecious, subalpine to alpine plants of the Sierra Nevada, California ..... 1. *P. stebbinsii*

9. Lemmas more than (5)5.5 mm long; innovations intravaginal, lacking bladeless leaves below; ligules of innovation leaves smooth to scabrous, the longest 1.5–6 mm long; basal shoots usually distinctly decumbent and frequently branched at the lower nodes; high montane to subalpine plants of the Klamath-Siskiyou region (pistillate and staminate) to the N Sierra Nevada (pistillate only). (Culm sheaths 1/7–⅓ closed, and panicles strict and narrow, or in hybrid combinations, at Mt. Shasta, Mt. Lassen and in the Sierra Nevada, frequently taller, with culm sheaths closed more than ⅖ and panicles loose.) ..... 2. *P. pringlei*

8. Longest ligules of uppermost innovation leaves less than 1.5(3) mm long, truncate to obtuse, more or less scabrous, milky-colored; innovation blades smooth or often scabrous abaxially; upper culm sheaths closed (⅛)¼–⅘ the length; plants frequently more than 30 cm tall; lemmas firmer, glabrous or pubescent; plants more widespread.

10. Basal tuft of leaves dense, innovations all intravaginal, lacking bladeless leaves below; all culm nodes enclosed in sheaths or the uppermost barely exposed; culm leaf blades similar to, or somewhat broader than, those of the innovations, rarely flat, innovation blades more or less filiform, mostly less than 1 mm wide when expanded; panicle axis, branches, and pedicels moderately to densely scabrous, more or less angled; plants growing at lower and in drier situations to alpine grasslands. (Plants that key out here but have puberulent lemmas are hybrids referred to as 9. *P.* × *nematophylla*.)

11. Longest lower branches of at least some panicles more than 17 mm long, the branches and pedicels slender; panicles to 9(12) cm long, loosely flowered, usually anthocyanic; spikelets relatively dull or sometimes glossy; plants of the Columbia Plateau and the W side of the Great Basin ..... 5. *P. cusickii* subsp. *cusickii*

11. Longest lower branches of the panicles less than 17 mm long, the branches and pedicels stout; panicles to 6 cm long, compact, usually pallid-green, sometimes anthocyanic; spikelets relatively softly shining; plants of the N Great Plains, Rocky Mts., and interior Great Basin, extending to high peaks of the W Great Basin .. .. 6. *P. cusickii* subsp. *pallida*

10. Basal tuft of leaves looser, innovations, in part, extravaginal (except in *P. porsildii*) with bladeless leaves below; at least one culm node well exerted and exposed at maturity;

culm leaf blades frequently broader than those of the innovations and flat or folded, innovation blades up to ca. 3 mm wide when expanded; panicle axis, branches, and pedicels smooth to sparsely (moderately) scabrous, round or angled; plants of mesic situations in high mountain meadows to high alpine tundra.

12. Panicles open, the branches divergent at right angles, flexuous, smooth; plants sexual, staminate and pistillate individuals ca. equal in number; plants occurring N of 60°N lat. ..... 4. *P. porsildii*

12. Panicles contracted, sometimes loosely so, the branches steeply ascending, more or less strict, smooth or moderately scabrous; plants pistillate (anthers rarely if ever fully developed, mostly rudimentary); plants occurring S of 60°N lat.

13. Lemmas of all florets smooth to scabrous (×25; rarely, in hybrid combinations in the Rocky Mts., puberulent on the keel and marginal nerves, but the callus glabrous), 4–5.5 mm long; panicles tending to be compact, strict, and with more than 20-spikelets; plants widespread in alpine areas of W North America, but less frequent in the Cascade Mts. and westward than var. *purpurascens* ..... 7. *P. cusickii* subsp. *epilis* var. *epilis*

13. Lemmas of at least some lower florets of some spikelets very sparsely to moderately pubescent on the base of the keel and frequently with a few short hairs on the callus [×25; infrequently all glabrous but then lemmas large, (4.5)5–7.5 mm long, and culm sheaths closed ⅗ or more]; panicles loosely contracted, and fewer-flowered; plants of SW British Columbia, Cascade and Olympic mts., S to Crater Lake, Oregon, with outlying populations in the Klamath-Siskiyou region and Sierra Nevada ..... 8. *P. cusickii* subsp. *epilis* var. *purpurascens*

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