

SEQUENTIALLY ADJUSTED SEX-RATIOS IN GYNOMONOECISM, AND
POA DIABOLI (POACEAE), A NEW SPECIES FROM CALIFORNIA

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ABSTRACT

Poa diaboli is described as a new and rare species of *P.* subsect. *Madropoa* from the coastal mountains of southern California. Its breeding system is like that in species of *Poa* previously said to be partially gynodioecious. However, in species of *Poa* with the corresponding breeding system syndrome, plants that are totally pistillate-flowered are rare and possibly only late-flowering individuals. We conclude that the breeding system of these species of *Poa* is better classified as a new subset of gynomonoeicism, here termed sequentially adjusted gynomonoeicism. Subtypes of gynomonoeicism in the grasses, and in *Poa*, are outlined.

Key Words: breeding systems, Gramineae, grass, gynomonoeicism, *Poa*, Taxonomy.

The new species of *Poa* L. was possibly first collected by David Keil in 1998. Because of its uncertain identity, and isolated geographical occurrence from similar species, it was brought to the attention of first author. It was initially thought to be dioecious, but further investigation of new collections with longer series of specimens, revealed that it is either weakly gynodioecious or exhibits an unusual form of gynomonoeicism.

***Poa* (subsect. *Madropoa*) *diaboli* Soreng & Keil, sp. nov. (Fig. 1)—TYPE:** USA, California, San Luis Obispo Co., W end of San Luis Range, Montana de Oro State Park, slopes W of Valencia Peak, very local on steep N facing slope in coastal scrub, 164–245 m, 27 March 1998, D. Keil 26474 (holotype: US, isotypes: OBI-55333, [CAS, K, RSA; to be distributed])

A *Poa* confine *robustiore*, *altiore* (26–50 cm versus 7–30 cm), *paniculis longioribus* (4–8.5 [10.5] versus 1–5 cm), *diffusioribus*, *laminis planis vel plicatis*, *lemmatis longioribus* ([3.2–] 4.25–5 versus 2.4–4 mm), *venis sine pilis*, *rachillis visibilibus longioribus plerumque asperate sine pilis*, *plantis gynomonoeiciis*, *antheris plerumque longioribus* ([1.4] 1.75–2.6 versus 1.5–2 mm), *dif-fert*.

Sequentially adjusted gynomonoeicious, perennial grass, rhizomatous and stoloniferous, forming loose, leafy, tufts up to 25 cm tall and 30 cm across. Vegetative shoots numerous, shoot emergence extravaginal with rudimentary prophylls, and pseudo-intravaginal with tubular prophylls, and intravaginal with well developed prophylls. Culms 26–50 cm long, 0.5–0.9 mm diam., numerous, widely

spreading to sortly decumbent and erect, leafy, one or more nodes exposed, uppermost node in lower third to middle of culm, frequently branching above the base with several shoots developing in from adjacent nodes with contracted internodes. Leaves; cataphylls present on extravaginal shoots; sheaths keeled, lightly scabrous, uppermost 4.5–9 cm long, margins fused $\frac{3}{5}$ – $\frac{7}{10}$ the length; collars scabrous to pubescent on margins; ligules of middle and upper culm leaves 1.0–3.0 mm long (of lateral shoots and basal culm leaves less than 1 mm long), apex truncate and lacerate to (mostly) obtuse or acute, apically scabrous, abaxial surface moderately to densely scabrous; blades flat (especially upper culm ones) or more often folded, thin, slender, 0.8–2.0 (–2.5) mm wide, narrowly prow-tipped, abaxial surface smooth, veins prominent, keel and margins scabrous, adaxial surface of innovation blades sparsely to moderately densely scabrous or short-hairy on and between the veins (infrequently glabrous between veins), culm blades generally gradually decreasing in length upwards, uppermost blades 2.9–6 (–7) (pistillate specimens), or (3–) 4–8.6 (–11) (perfect specimens) cm long; upper-sheath to blade-length ratio 1.4–2.4: 1, averaging 1.8 (pistillate specimens), 0.6–2.1: 1, averaging 1.4 (perfect specimens). Panicle synflorescences exerted above the vegetative mounds, erect to nodding, pyramidal to ovate, open, or eventually loosely contracted, sparse, 4.0–8.5 (–10.5) cm long; branches 1–2 per node, spreading to ascending, slender, moderately strict, angled, moderately to densely scabrous mainly along angles, with spikelets in the distal $\frac{1}{2}$, longest branches 2.1–4.5 (–7) cm. Spikelets lanceolate, 5.3–9 mm long; glumes

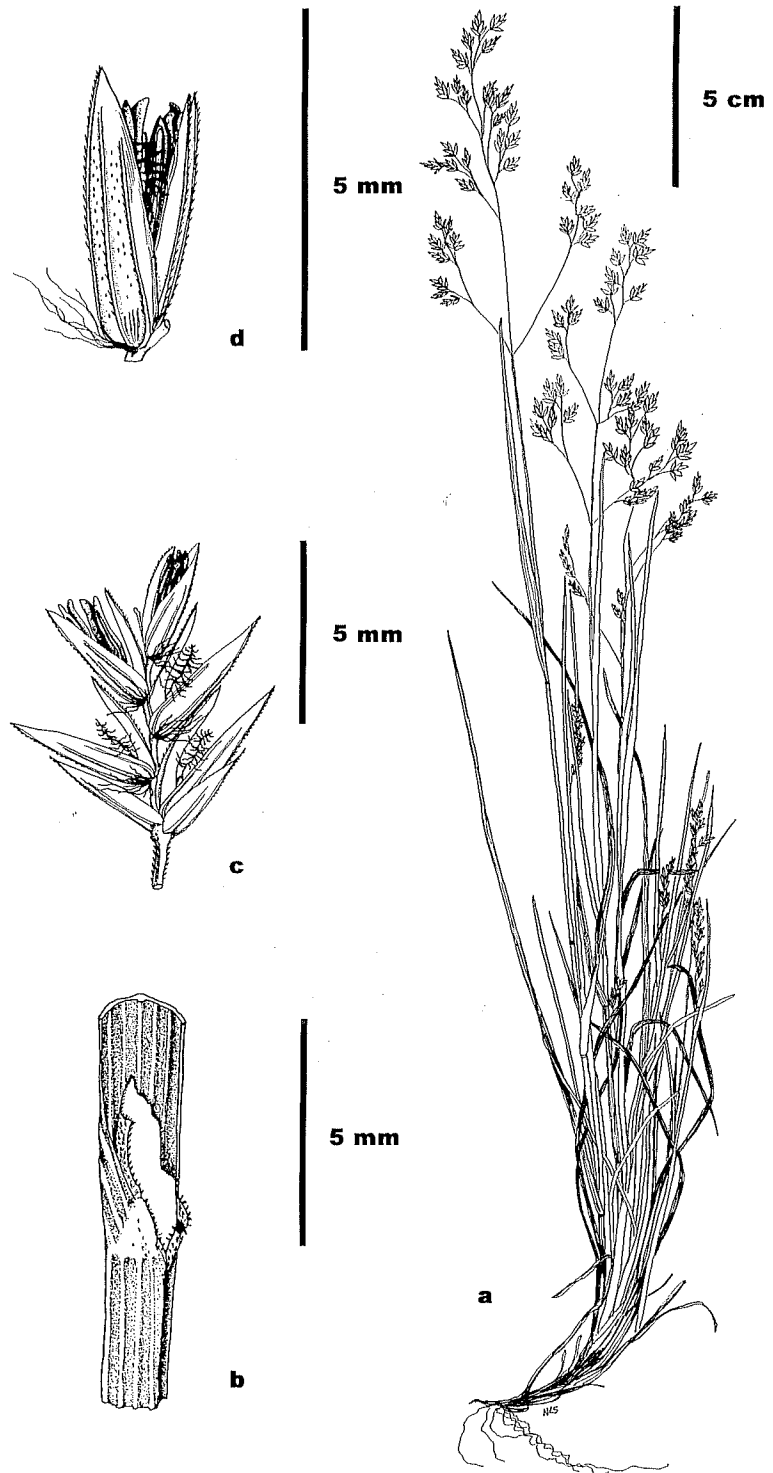


FIG. 1. *Poa diabolii*. Illustration of Keil 26474, holotype US; a) habit; b) ligule; c) spikelet (perfect-flowered); d) floret.

narrowly lanceolate, 3-veined, lower (2.0–) 2.7–3.8 mm long, upper, (2.3–) 2.9–3.9 mm long; rachilla internodes 1.0–1.3 mm long, laterally visible, sparsely to densely, coarsely scabrous or infrequently entirely smooth; florets (2–) 3–6 (–7); caluses webbed, webs diffuse, arising around the lemma base, hairs thin, sinuous reaching as far as midlemma, sparser and shorter laterally, or loosely concentrated dorsally and absent laterally; lemmas pale green throughout, to anthocyanic along the margins to apex or throughout, lanceolate to narrowly lanceolate, (3.2–) 4.25–5.0 mm long, fairly thin, strongly keeled, apex acute to narrowly acute (infrequently the keel vein excurrent as a tiny mucro), margins very narrowly hyaline, surface sparsely to moderately-densely scabrous throughout, glabrous, veins 5, prominent, moderately to densely scabrous, lateral veins extending to within 1 mm of upper margins; paleas $\frac{5}{6}$ to = lemmas in length, keels coarsely and closely scabrous, surface between keels narrow, scabrous. Flowers bisexual or pistillate; anthers (1.4–) 1.75–2.6 mm long, or rudimentary and sterile; ovary glabrous, fully matured caryopses unknown; lodicules 1.0 mm long, broadly lanceolate, long lobed. Chromosome number unknown.

Flowering. March to April.

Habitat. North facing slopes and ridgetops within 2–3 km of the Pacific coast, fire successional area of mesic chaparral, grassy coastal-scrub, coastal live oak woodland, and mesic Bishop pine forest, thin soils over an Edna Shale substrate, 120–400 m elev.

Distribution. United States, California, San Luis Obispo Co., San Luis Range (also known as the Irish Hills).

Paratypes. USA. California, San Luis Obispo Co., NW end of San Luis Range: Montana de Oro State Park, slopes W of Valencia Pk., ca. 230 m, 27 Apr 1998, *D. Keil 26941* (OBI); N slopes of Valencia Pk., 35°15'50–54"N × 120°52'19–24"W, 240 m to 383 m, 7 Apr 2003, *R. Soreng, E. Frenzel, S. Krenn & J. Blecha 7401* (US); Pacific Gas & Electric, Diablo Canyon power plant lands, North Ranch, 0.4 km E from coast road on Crowbar Canyon Rd., 35.228°N × 120.864°W, ca. 120 m, 19 Apr 2001, *D. Keil & E. Frenzel 29331* (OBI); same loc., 120 m, 6 May 2001, *E. Frenzel & D. Haines s.n.* (OBI; DNA voucher); North Ranch, ridge above Coon Cr. Canyon, 35.243°N × 120.876°W, ca. 365 m, 19 Apr 2001, *D. Keil & E. Frenzel 29336* (OBI); 0.3 km inland from coastal road along Crowbar Canyon Rd. at mouth of Crowbar Canyon, ca. 120 m, 14 Apr 2001, *E. Frenzel DC-19* (OBI); Ridge top S of Coon Cr., ca. 0.5 km E of "Last" benchmark and above road cut, ca. 400 m, 27 Mar 2001, *E. Frenzel & D. Haines 81* (OBI).

Conservation status. Narrowly endemic, locally frequent. The geographic range known from collec-

tions may be less than 15 sq km. However, it occurs in very rugged country, and estimates of potential habitat suggest the range is somewhat larger. It was reportedly collected from the San Luis Range in Ruda Canyon (*Glenn Clifton* in 1993), but we have not been successful in locating the voucher.

Presumably the species was overlooked because until recently the surrounding lands were mostly in large private holdings and extensively grazed. Light grazing of continues on some of the Diablo Canyon Power Plant land. Montana de Oro State Park (MOSP) land was privately owned until the late 1960's and was grazed until the early 1970's. The coastal bench lands were used for military exercises for a short period prior to the establishment of the state park (Sally Krenn, Jim Blecha personal communication). Attempts to revegetate MOSP lands, and eradicate the invasive *Ehrharta calycina* (Velt Grass), included a controlled burn covering the area from the coastal bench to the top of Valencia Peak in 1997 (Vince Cicero personal communication). David Keil first noticed the new species in an area of recently burned chaparral vegetation in the following year. The largest population of the new *Poa* yet discovered occurs on the peak area, and it seems the fire did not adversely impact this population, and may have benefited it.

The new species epithet, *diaboli* (spelling verified in Kunkel 1990), commemorates both its occurrence on grounds of the Diablo Canyon Nuclear Power Plant, and secondly the difficulties it has caused the authors in determining its affinities and its breeding system.

BREEDING SYSTEM DETERMINATION

Dicliny is widespread in the Poaceae (R.Br.) Barnh. (Connor 1979). However, gynomonocism is considered uncommon, occurring in only eight genera and not in all species of those (Connor 1979). Connor characterized several variations in the pattern of sex expression among genera of gynomonocious grasses, and all cases seem to be more or less spatially fixed in expression, and sequentially regular. Pistillate flowers consistently occur in a specific orientation, either within spikelets, or within pairs or sets of spikelets (Connor 1979), and, although there may be differences in timing of flowering, there are no reported changes in the ratio of one type of flower to another through the growing season in gynomonocious species. The variations may be categorized as follows:

- I. Spikelets all alike, certain florets consistently pistillate.
 - a) proximal floret pistillate, distal floret(s) perfect.
 - b) proximal floret(s) perfect, distal floret(s) pistillate.
- II. Spikelets pistillate or perfect, these arranged in pairs or sets.

15 sq km. However, it occurs rarely, and estimates of potential range is somewhat larger. It was first reported from the San Luis Range in Clifton in 1993), but we have not located the voucher.

This species was overlooked because surrounding lands were mostly in private and extensively grazed. Light was not used until the early 1970's. The area was used for military exercises and to the establishment of the area in, Jim Blecha personal communication) to revegetate MOSP lands, as well as *Ehrharta calycina* (Veltman) controlled burn covering the area from the top of Valencia Peak (Soreng personal communication). We added the new species in an area of sparse vegetation in the forest population of the new *Poa* species on the peak area, and it did not adversely impact this population.

The name *diaboli* (spelling verified), commemorates both its occurrence in the Diablo Canyon Nuclear Plant and the difficulties it has had in determining its affinities and

STEM DETERMINATION

read in the Poaceae (R.Br.) (1815). However, gynomonoeism is common, occurring in only eight species of those (Connor 1979) characterized several variations in expression among genera of grasses, and all cases seem to be fixed in expression, and sessile flowers consistently occur, either within spikelets, or at the base of spikelets (Connor 1979), may be differences in timing of reported changes in the ratio of perfect to another through the gynomonoeic species. The variations are as follows:

1) Proximal floret(s) consistently pistillate, distal floret(s) consistently perfect, distal floret(s) consistently perfect, these arranged

- a) sessile spikelet perfect, pedicellate spikelet pistillate.
- b) sessile spikelet pistillate, pedicellate spikelet perfect.
- c) lateral spikelets pistillate, terminal spikelet perfect.

Most of Connor's reports of gynomonoeism come from species or genera belonging to grass tribes or subfamilies in which the number of florets per spikelet is fixed at either one or two (subfam. Ehrhartoideae Link trib. Olyreae Kunth ex Spenn., subfam. Panicoideae Link, respectively), and where paired spikelets are common. Connor (1979) reports gynomonoeism in species with spikelets with indeterminate numbers of florets only from *Centotheca* Desv. (subfam. Panicoideae trib. Centothecae Ridl.), *Munroa* Torrey (subfam. Chloridoideae Kunth. ex Beilschm.), and *Poa* (subfam. Pooideae Benth.). In each of these genera the syndrome is different. *Munroa* fits categories Ia and IIc (above), and *Centotheca* and *Poa* fit category Ib. In *Centotheca* only the proximal floret is perfect and those distal to it are pistillate. In *Poa*, generally only the distal most floret is pistillate, and all more proximal florets are perfect. We are not aware of any reports of changes in the frequency of pistillate flowers through time in gynomonoeic grasses.

The breeding system of *Poa diaboli* falls on the borderline between gynomonoeism and gynodioecism. To characterize the breeding system of the new species, individual specimens (pre-2003) were checked for presence or absence of perfect or pistillate flowers (i.e., those with developed pistils and rudimentary anthers; there seem to be no staminate flowers). For this analysis individual specimens were considered to be samples with one or more synflorescences attached to a shared base, or single flowering shoots that were pressed or mounted on the same sheet and appear to be from the same individual: The individual specimens do not necessarily represent different plants, and more precise study of individuals through a season and through successive years is needed in the future. We assume that male sterility, as indicated by the occurrence of rudimentary anthers, is under genetic control, that anthers are not simply aborted due to environmental factors (i.e., disease, moisture or nutrient stress, temperature shock, etc.; though possibly triggered by these), nor due to genetic abnormalities. The occurrence of rudimentary anthers is regular enough within and among specimens that this seems to be a warranted assumption. Moreover, the pattern is consistent with that found in other species of diclinous *Poa* (Soreng 1991, 2000). In genetically imbalanced plants of *Poa*, if anther abortion occurs, it usually occurs in a late stage of development, and some pollen is formed, although usually malformed to some degree (RJS personal observation). However, in diclinous species, as in the

present case, anther development is halted at a much earlier, presumably pre-tapetal, stage.

There are three completely pistillate specimens among an estimated 20 specimens with at least some perfect-flowers. These three specimens may represent truly pistillate plants, or late flowering plants that, had they developed earlier, would also have produced shoots with perfect-flowers, or plants in which pistillate shoots have become separated from shoots with perfect-flowers in the process of collecting the plant. In seven of the specimens with perfect-flowers there are some panicles with a few pistillate spikelets among the lower spikelets of their synflorescences, and three specimens with early maturing mainly or wholly perfect-flowered panicles and late maturing, smaller, completely pistillate-flowered panicles.

In a survey of the Valencia Peak population in 2003 (Soreng et al. 7401) one synflorescence was taken off of 42 plants at least 2 m apart. The synflorescence count was; three pistillate-flowered, five partly perfect-flowered/partly pistillate-flowered, and 34 perfect-flowered. Both the pre-2003 specimen count and the 2003 population census results suggest that the new species is either intermediate between being gynomonoeic and gynodioecious, or, more likely, as no completely pistillate plants were found, the ratio of pistillate and perfect flowers is sequentially adjusted.

A corresponding syndrome is present in a several other species of *Poa*. This includes co-occurrence within populations of: 1) many individuals that are perfect-flowered only, along with a high percentage of individuals (but averaging less than half) that have mixtures of perfect and pistillate flowers; 2) within mixed-flowered individuals, pistillate flowers occur in terminal florets within some spikelets, and often in all flowers of spikelets below the mixed-flowered spikelets, both arrangements increasing in frequency in late developing (lower) parts of synflorescences, and in later developing synflorescences; 3) some late developing, completely pistillate synflorescences, in individuals with earlier developing perfect-flowered, or partly perfect-flowered synflorescences; and, 4) few (or no) individuals having only pistillate flowers, but then all synflorescences developing late in the breeding season. This syndrome is characteristic of the *Poa* sect. *Homalopoa* Dumort. "*P. nervosa* complex" of North America (i.e., *P. arnowiae* Soreng, *P. cuspidata* Nutt., *P. nervosa* (Hook.) Vasey s.str., and *P. tracyi* Vasey; three other species in this complex are dioecious (*P. sierrae* T.J. Howell), subdioecious (*P. rhizomata* Hitchc.), or dioecious and gynodioecious (*P. chambersii* Soreng); see Soreng and Hatch 1983; Soreng 1991, 1998, 2000). The same syndrome has also been diagnosed in populations studied in the field and lab in a few South American species (e.g., *P. fibrifera* Pilg., an undescribed species from southern Peru and northern Chile, Peterson & Soreng 15615 [CONC, US]),

and a few southeast Asian species (e.g., *P. grandis* Hand.-Maz., Soreng, Peterson & Sun 5628; [KUN, PE, US] RJS personal observation).

This breeding system, which seems more like gynomonoeicm, differs from true gynodioecism wherein pistillate individuals are clearly distinct, occur in a more regular and higher proportion to perfect-flowered individuals (but not much more than half), and also mature more or less simultaneously with those (at least in *Poa*; RJS personal observation). Soreng and Hatch (1983), and Soreng (1991, 2000), previously identified this syndrome as "partial gynodioecy". However, because, in the several species with this syndrome, individual plants that are totally pistillate throughout a season are rare or uncommon, RJS is inclined to agree with David G. Lloyd (personal communication 1992) that the syndrome is more like an extreme, and previously unrecorded, form of gynomonoeicm, than like weak gynodioecism. This form of gynomonoeicm is not easily distinguished from gynodioecism without careful examination of the distribution of different-sexed flowers in multiple populations in the field and common-garden studies, however, few totally pistillate plants are expected, along with a shift to pistillate flowers as the season progresses (Lloyd 1974, 1980).

There seems to be a need to differentiate subtypes of gynomonoeicm in *Poa*, so we shall call this system "sequentially adjusted gynomonoeicm" to distinguish it from the common form of gynomonoeicm in other *Poa*, and seemingly in other grasses, in which sex expression is fixed in spatial orientation, and is not known to change in frequency through time. Outside Poaceae, Acevado-Rodríguez [2003] identified a syndrome in *Talisia* (Sapindaceae) in which individuals are "sequentially monoecious", shifting from staminate to pistillate flower production and back to staminate flowers within a season. We are unaware of any reports of sequentially adjusted sex expression in gynomonoeicm plants. Here we take up the terms "sequentially adjusted" to denote the temporal shift in sex expression through the growing season. In other gynomonoeicm *Poa*, sex expression is fixed in frequency and time. In *P. annua* L. and other species of *P. sect. Ochlopoa* Asch. & Graebn., and many South and Central American species, and some Himalayan species, pistillate flowers are consistently and only produced in the terminal floret, or less often also in the subterminal floret, within spikelets (Hackel 1904; Nannfeldt 1938; Chrték and Jirásek 1962; Connor 1979; Anton and Connor 1995). The latter syndrome is common, and may be distinguished as fixed-sex-expression gynomonoeicm. These species are not known to produce any pistillate spikelets, mostly pistillate synflorescences, or any totally, perfect-flowered individuals. Moreover, there is no known change in frequency of pistillate florets through time, within or between plants.

In their paper on "Floral biology and reproduction in *Poa*" Anton and Connor (1995) described the many variations in *Poa* breeding systems known to them. They noted Soreng's application of the term "partially gynodioecious" to several North American species, but indicated their unfamiliarity with this variation, also suggesting that it might represent an exaggerated form of gynomonoeicm. They comment on the uniformity of the syndrome of gynomonoeicm in many South and Central American species of *Poa*, and in species of the European (now cosmopolitan) *P. sect. Ochlopoa*. In these species, the lowermost 1 or 2 florets of 2 or 3 (-4) flowered spikelets are perfect, and the upper floret is pistillate. This also occurs in several Himalayan species of *Poa* (e.g., *P. sikkimensis* (Stapf) Bor; RJS personal observation from herbarium specimens and Soreng, Peterson, & Sun 5676 [KUN, PE, US]). Seed is normally set in both types of flowers. They report no evidence of variation in flowering among most gynomonoeicm *Poa* (except for *P. supina* Schrad. of Europe, in which the pistillate florets open one day before the perfect ones within the same spikelets). They indicate that in a few gynomonoeicm species all flowers may be pistillate or perfect in some plants or synflorescences (e.g., *P. glomerifera* Hack., *P. horridula* Pilg.). The latter two species, like *P. fiberifera*, *P. grandis*, and others mentioned above, may also exhibit sequentially adjusted gynomonoeicm (RJS personal observation from study of herbarium specimens; also observed by Maria Negritto personal communication).

RELATIONSHIPS AND IDENTIFICATION OF THE NEW SPECIES

Although *P. diaboli* seems to share sequentially adjusted gynomonoeicm with species of *P. sect. Homalopoa* s.lat., the North American species of that group occur in forested habitats, and have much broader leaves and more loosely-tufted, erect habits, and lack hairs on the adaxial surface of innovation blades. Also, if those have a web on the callus, as most species of *P. sect. Homalopoa* and other *Poa* do, they have a single, tight, dorsal tuft of hairs. If the new species were gynodioecious, this would support a close relationship to species of *Poa* sect. *Madropoa* Soreng, especially those of the rhizomatous subsection *Madropoa* Soreng. If it exhibits sequentially adjusted gynomonoeicm, as we think, this species might represent an early transitional element between the *P. nervosa* complex and *P. sect. Madropoa*.

In comparison with species of *P. sect. Madropoa*, *P. diaboli* is unusual in the possession, in some specimens, of thin, flat culm leaves, and folded leaves that lack long, hooked or sinuous prickly hairs on and between the veins of upper leaf-blade surfaces, even on innovation shoots. In these features, it approaches *P. leibergii* Scribn. (of mossy,

Floral biology and reproduction and Connor (1995) described in *Poa* breeding systems noted Soreng's application of "gynodioecious" to several species, but indicated their unfamiliarity, also suggesting that it is a exaggerated form of gynomonoeism on the uniformity of the monoecism in many South American species of *Poa*, and in species of (cosmopolitan) *P.* sect. *Ochloa*. The lowermost 1 or 2 florets of the red spikelets are perfect, and the upper ones are staminate. This also occurs in several species of *Poa* (e.g., *P. sikkimensis* Soreng, personal observation from herbarium, Peterson, & Sun 5676). The lowermost 1 or 2 florets are normally set in both types but there is no evidence of variation in the staminate-gynodioecious *Poa* (excl. *P. sikkimensis* Soreng, personal observation from herbarium, Peterson, & Sun 5676). They indicate that in some species all flowers may be staminate in some plants or synflorescence (e.g., *P. horridula* Hack., *P. fiberifera*, *P. mentioned above*, may also exhibit gynomonoeism (RJS personal observation from herbarium specimen) by Maria Negritto personal

NEW IDENTIFICATION OF THE NEW SPECIES

P. diabolica seems to share sequentially with species of *P.* sect. *Homalopoa* in the North American species of forested habitats, and have more loosely-tufted, erect spikelets on the adaxial surface of innovation, if those have a web on the surface of *P.* sect. *Homalopoa* and have a single, tight, dorsal tuft of hairs. Species were gynodioecious, in close relationship to species of *Poa* Soreng, especially those of section *Madropoa* Soreng. If it is an adjusted gynomonoeism, as it might represent an early transverse the *P. nervosa* complex *poa*. The species of *P.* sect. *Madropoa* unusual in the possession, in addition, flat culm leaves, and folding, hooked or sinuous prickles on the veins of upper leaf-blade innovation shoots. In these features *P. leibergii* Scribn. (of mossy,

shaded cliffs and open slopes where snow pockets remain into early spring, of the Columbia Plateaus; gynodioecious) and *P. stebbinsii* Soreng (of subalpine wet meadows, of the high Sierra Nevada; gynodioecious), both of *P.* sect. *Madropoa* subsect. *Epiles* Soreng. However, *P. diabolica* more often does have hairs on and between the veins of adaxial blades surfaces of its innovation shoots, like most other *Madropoa* species. Moreover, it has the additional features of a rhizomatous and/or stoloniferous habit, and a diffusely cobwebby callus, typical of species *P.* sect. *Madropoa* subsect. *Madropoa* Soreng

The hairs of the callus in *Poa diabolica* are long, soft, and sinuous, as in most *Poa*, but are more or less, diffusely distributed around the sides and back of the callus in many florets. The form and insertion of the callus hairs most closely resemble those found in *P. confinis* Vasey (of coastal dunes and adjacent sandy forests, from southernmost Alaska south to Pt. Reyes in Marin Co., California; gynodioecious to dioecious), *P. douglasii* Nees (coastal dunes, from Mendocino Co. south to Pt. Sur, Monterey Co., with isolated populations at Vandenberg Air Force Base, south base [a new record, *D. Keil* 24742], and on San Miguel and Santa Rosa Islands of Santa Barbara Co.; dioecious), and *P. piperi* Hitchc. (of forest openings on serpentine, endemic to the Klamath-Siskiyou region of southwest Oregon and northwest California; dioecious), all of *P.* subsect. *Madropoa*. *Poa confinis* is gynodioecious to dioecious ($n = 90$, sex ratio 1.4:1, pistillate-flowered individuals to staminate-flowered, perfect-flowered, and mixed perfect and pistillate-flowered individuals).

In our estimation, despite some differences in morphology and breeding system, *Poa diabolica* belongs to *P.* subsect. *Madropoa* where it approaches *P. piperi*, but is most similar to *P. confinis*. In most characteristics examined the new species is larger than *P. confinis*, but range of variation measurements often overlap. However, among other differences noted above, the lemmas of *P. confinis* are usually at least sparsely short hairy on the keel, whereas the new species is devoid of hairs (other than fine hooks or prickle hairs) on the lemma. In the treatment of *Poa* (Soreng 1994) in *The Jepson Manual: Higher Plants of California* the new species keys out to a choice between *P. kelloggii* and *P. piperi*. Different specimens key to one or the other but fit neither species description. Lead number nine may be modified as follows:

- 9a. Sheaths of upper culm leaves open most of their length; innovation blades smooth or mainly scabrous over the veins adaxially; synflorescences 10–20 cm long; flowers all perfect . . . *Poa kelloggii*
- 9a'. Sheaths of upper culm leaves closed over 1/2 of their length or more; innovation blades often hairy adaxially; synflorescences 4–10 cm long; flowers all perfect or some unisexual.
- 9b. Leaves thin, soft, mostly 0.8–1.5 mm wide and

folded, or up to 2.5 mm wide and flat, those of the culm gradually reduced in length upward, frequently flat; lemmas up to 5 mm long; plants perfect-flowered or some (rarely all) flowers pistillate *Poa diabolica*

9b'. Leaves thicker, somewhat firmer, mostly 1.5–3 mm wide, those of the culm sharply reduced in length upward, never flat; lemmas mostly 5–7 mm long; plants nearly all pistillate or staminate-flowered *Poa piperi*

The morphology and transitional breeding system suggest *Poa diabolica* is either a geologically old element in *P.* subsect. *Madropoa*, or that it is an isolated population, likely derived from *P. confinis*, or its progenitor, which has reverted to a more perfect-flowered breeding system in the face of density dependent pollination factors.

Few native species of *Poa* are known from the San Luis Range or the adjacent and more inland Santa Lucia Range (*P. howellii* Vasey & Scribn., *P. secunda* J. Presl subsp. *secunda* [*P. scabrella* (Thurb.) Vasey form]). The new species is readily distinguished from *P. howellii*, which occurs in the Santa Lucia Range, and in Price Canyon in the San Luis Range, by its strongly perennial habit, absence of soft hairs on the body of the lemma, diffuse callus web, and its longer anthers. From *P. secunda s.lat.*, common and widespread western North America, and sympatric with the new species (DJK personal observation; also recorded from the south end of the San Luis Range, *Dudley s.n.*, SU), it is distinguished by the rhizomatous habit, presence of strongly keeled lemmas with a narrowly hyaline margin, more closed culm sheaths, and presence of a well developed web on the callus, and from *P. secunda* subsp. *secunda* (the only subspecies in the region) by the lack of any soft or crisp hairs on the lemma surface.

Chloroplast DNA (cpDNA) restriction site data (Lynn Gillespie personal communication) has confirmed the postulated relationship of *P. diabolica* with members of a clade including species of *P.* sects. *Homalopoa* and *Madropoa*, and refuted membership in many other sections including *P.* sect. *Sylvestres* Soreng (including *P. kelloggii*, and *P. maricida* Hitchc., also new cpDNA data) and *P.* sect. *Secundae* Soreng (including *P. secunda*) (see Soreng 1990, for a general cpDNA phylogenetic hypothesis for *Poa*).

Of introduced species reported from San Luis Obispo Co., only the annuals *Poa annua* L., and *P. infirma* Kunth (RJS personal observation 2003), are known to occur in the area, but these have little in common with the new species.

It is reasonable to postulate that the isolated geographic occurrence of *Poa diabolica* in the south central California coastal hills represents a relictual Pleistocene distribution for species of *P.* sect. *Madropoa*, as the nearest station for its closest relative, *P. confinis*, is over 325 km to the north. Other sec-

tional members (other than *P. douglasii*) are distributed much further north or well inland.

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