# A synopsis of the *Juncus hesperius* group (Juncaceae, Juncotypus) and their hybrids in western North America

PETER F. ZIKA

WTU Herbarium, Box 355325, University of Washington, Seattle, WA 98195-5325, USA; e-mail: Zikap@comcast.net

**Abstract**. A synopsis of North American species in the *Juncus hesperius* group is presented. *Juncus exiguus, J. hesperius,* and *J. laccatus* form a trio of closely related species in the section *Juncotypus*, restricted to western North America. They are illustrated and mapped based on extensive field and herbarium studies. A key to North American members of *Juncus* section *Juncotypus*, north of Mexico, is presented. Putative hybrids in the group are morphologically intermediate and rare in mixed populations. The following putative hybrid combinations are documented: *J. exiguus* × *J. effusus* subspecies *pacificus* from California; *J. exiguus* × *J. laccatus* from California; *J. hesperius* × *J. effusus* subspecies *pacificus* from British Columbia, California, and Washington; *J. hesperius* × *J. laccatus* from Washington, and *J. hesperius* × *J. patens* from California. Three putative hybrids are illustrated.

**Key Words:** Hybrids, Juncaceae, *Juncotypus*, *Juncus*, rush.

*Juncus* L. section *Juncotypus* Dumort. includes 67 species world-wide, with representatives from all continents except Antarctica. There are 22 native taxa in North America, north of Mexico, as well as four introductions from Eurasia and Australia (Kirschner et al., 2002). Many of the species are variable and controversial, and the species boundaries in several groups were elucidated only recently (Kirschner et al., 2002; Snogerup et al., 2002). North American members of the *J. balticus* Willd. group were included as part of *J. arcticus* Willd. by Balslev (1996) and Brooks (2000). A more satisfactory global treatment segregated *J. balticus* and the related *J. mexicanus* Willd. in our region (Snogerup et al., 2002), with *J. balticus* subsp. *littoralis* (Engelm.) Snogerup in eastern North America, and *J. balticus* subsp. *ater* (Rydb.) Snogerup in western North America. Within the latter there is a great deal of morphological variation in stem diameter and sheath characters, which may represent unrecognized taxa (Lint, 1977), or possibly phenotypic responses to local environments (Zika, 2006). *Juncus balticus* still needs study to clarify morphological boundaries. The *J. effusus* L. group was not probed in detail in the Flora of North America (Brooks, 2000), but recent works have clarified North American representatives of *J. effusus* s. str. (Hämet-Ahti, 1980; Snogerup et al., 2002; Zika, 2003). There are two native subspecies in western North America, *J. effusus* subsp. *austrocalifornicus* Lint ex Zika in the southwestern United States and northern Mexico, and *J. effusus* subsp. *pacificus* (Fernald & Wiegand) Piper & Beattie ranging along the coast from California to British Columbia (Zika, 2003).

*Juncus effusus* can be defined as stout-stemmed, cespitose, and bladeless plants with smooth shiny stems (culms). Related to it are three dark-flowered native species in western North America. These are *J. hesperius* (Piper) Lint, *J. exiguus* (Fernald & Wiegand) Lint ex Snogerup & Zika, and *J. laccatus* Zika. In the past, if they were recognized at all, it was usually at the rank of variety, under *J. effusus* s. l. (Fernald & Wiegand, 1910). Regional floras have overlooked them, or tried to distinguish them based on inadequate floral

characters (Hitchcock & Cronquist, 1973; Swab, 1993; Brooks, 2000; Češka, 2001). Their distribution and ecology were also confused. Members of the *J. hesperius* group are best segregated from *J. effusus* by their more slender and prominently ridged stems and characters of the distal leaf sheaths, also called cataphylls (Kirschner et al., 2002; Snogerup et al., 2002). These segregates from *J. effusus* are treated at the rank of species here, as they retain their morphological differences when sympatric with *J. effusus* subsp. *pacificus* at many sites, and intermediate morphology is quite scarce in the field and herbarium. Previously undocumented intermediates suspected to be interspecific hybrids are discussed at the conclusion of this paper. Several of the putative hybrids and their parents are illustrated to emphasize the differences between the taxa. A key is presented to all North American members of section *Juncotypus,* native or naturalized north of Mexico. Distribution maps for the *J. hesperius* complex (Figs. 1 and 2) were based on herbarium specimens examined at the institutions listed in the acknowledgements. Literature reports were not mapped because they were unreliable (Zika, 2003).

## Key to *Juncus* section *Juncotypus* species native and naturalized in North America, north of Mexico

Several notes are useful in interpreting the key, which follows the taxonomy of Kirschner et al. (2002). Although anther and filament characters are used, flowering material is difficult to identify and does not make an acceptable herbarium voucher. In Juncaceae the stamens persist under the tepals into fruit; only specimens with ripe fruits and mature seeds should be used in the keys. Among the cespitose species, the stem provides different characters useful for determination when fresh or dry. Living upper stems of some species, such as *Juncus effusus* or *J. laccatus*, are completely smooth and shiny. Other taxa are dull and ridged when fresh. Striations on the stem are easily detected in the field by rolling several stems together to feel if the ridges catch like gears (e.g., *J. patens* E. Mey. or *J. inflexus* L.), and should be noted on specimen labels. Upon drying, the stem's vascular system is revealed as a series of fine ridges, visible at 10× magnification. The number of ridges visible on one side is a useful comparative character, as is the fertile stem diameter, measured 1 cm above the distal sheath apex (Table I). The ridges can be obscure and difficult to detect even when dry (*J. balticus*), quite numerous but subtle (*J. effusus* and *J. textilis* Buchenau), or few and with strong vertical relief, the ridges are more or less visible at arm's length, and (at 10×) the ridges are capped by swollen shiny cells (*J. conglomeratus* L.). In the *J. hesperius* group the stem ridges are lower, and become much more evident after pressing.

The key relies on delicate sheaths; these are easily damaged unless specimens are carefully dug, never pull them from the ground. For bladeless taxa like members of the *Juncus hesperius* and *J. effusus* groups, the distal leaf sheaths have taxonomically important characters (Table II), including venation, apex symmetry, thickness, gloss, color, where the margins overlap, and the presence or absence of granular papillae (at 10×). Sparse samples may poorly document sheath characters, thus some museum specimens can not be determined with certainty. Finally, the strongly asymmetrical sheath apex of several taxa (e.g., *J. hesperius*) is not evident on every sheath, and is often lacking on young shoots, so several sheaths on fruiting stems should be inspected. While native western North American subspecies of *J. effusus* (subsp. *austrocalifornicus,* subsp. *pacificus*) have pronounced asymmetrical sheath apices, their counterparts in eastern North America [subsp. *solutus* (Fernald & Wiegand) Hämet-Ahti] and Eurasia (subsp. *effusus*) are essentially symmetrical, and both are introduced and weedy in western North America.

1. Rhizomes long and creeping, stems solitary, scattered or in loose colonies.
   2. Leaf blades well developed on the distal sheaths of some stems, blades stem-like . . . . . *J. mexicanus*

2. Leaf blades absent, or reduced to vestigial bristles.
3. Fruiting tepals usually 6–8 mm long; infructescences diffuse or dense heads.
4. Infructescences dense, capitate, branches obscured; older sheaths shiny; stems usually flattened, often arching, twisted . . . . . *J. breweri*
4. Infructescences somewhat loose or sparse, branches obvious; older sheaths shiny or dull; stems usually round and erect.
5. Anthers 3–5× as long as the 0.4–0.6 mm long filaments; tepals broad, ascending or incurved, obscuring most of the elliptic to oblong fruits; coastal, San Francisco Bay region north to southern Oregon. . . . . *J. lescurii*
5. Anthers 1–1.5× as long as the 0.5–1.1 mm filaments; tepals narrow, spreading, revealing much of obovate to oblanceolate fruits; Queen Charlotte Islands north to coastal Alaska and northeast Asia . . *J. haenkei*
3. Fruiting tepals 3–5.5(–6) mm long; infructescences ± diffuse or open, never in dense heads.
6. Tepals green, pale brown, or pale reddish.
7. Tepals 1.8–2.5 mm long; fruits longer than tepals; southeastern U.S.A. . . . . *J. gymnocarpus*
7. Tepals 2.5–5 mm long; fruits shorter than tepals; boreal and western U.S.A.
8. Anthers shorter than or equaling 0.5–0.9 mm long filaments; fruits pale; inflorescence bract usually 1–1.5× the length of the stem, stems 0.2–0.6 m tall; circumboreal, south to Oregon, New Mexico, and West Virginia . . . . . *J. filiformis*
8. Anthers longer than 0.3–0.9 mm filaments; fruits dark; inflorescence bract much shorter than stem, stems 1–3 m tall; endemic to southwestern California . . . . . *J. textilis*
6. Tepals with dark brown to blackish stripes.
9. Anthers 1.2–2.2 mm long, 2–6× as long as 0.3–0.7 mm long filaments; infructescences usually diffuse; mature fruits shorter than to longer than tepals.
10. Pedicels and infructescence branches usually flexuous; bractlets subtending flowers usually 1.5–2.5 mm long; western North America, east to the Dakotas . . . . . *J. balticus* subsp. *ater*
10. Some pedicels and infructescence branches usually straight; bractlets subtending flowers usually 1–1.5 mm long; eastern North America, west to eastern Manitoba . . . . . *J. balticus* subsp. *littoralis*
9. Anthers 0.6–1.2 mm long, slightly longer than 0.5–1 mm long filaments; infructescences usually compact; mature fruits usually longer than tepals.
11. Fruits blunt or truncate, abruptly tapered to very short persistent stylar beaks 0–0.3 mm long; petals (inner tepals) blunt, margins broadly scarious; infructescence bracts less than 6 cm long. . . . . *J. arcticus* subsp. *alaskanus*
11. Fruits acute or acuminate, sometimes more gradually tapered to prominent beaks, beaks and persisting styles 0.3–1 mm long; petals acuminate, margins narrowly scarious; infructescence bracts usually 10–20 cm . . . . . *J. haenkei*

1. Rhizomes short, stems cespitose, usually in dense tufts like a bunchgrass.
12. Stamens 6 per flower.
13. Seeds with long tails; infructescences sparse, 1–7 flowers; fresh stems green to dark green, ridges inconspicuous.
14. Leaf blades absent, reduced to vestigial bristles; fruit apices notched . . . . . *J. drummondii*
14. Leaf blades well developed on distal sheaths, resembling stems; fruit apices acute or notched.
15. Fruit apices notched; tepals 4–5 mm long. . . . . *J. hallii*
15. Fruit apices acute; tepals 6–9 mm long . . . . . *J. parryi*
13. Seeds blunt or apiculate; infructescences usually well developed, 10–100+ flowers; fresh stems blue-green, ridges prominent (roll fresh stems between fingers to feel the ridges).
16. Fruits ovoid to ellipsoid, often dark or blackish distally, apex pointed, styles forming a prominent beak; petals usually shorter than fruits; pith chambered; Eurasian introduction in eastern North America, Oregon and Hawaii . . . . . *J. inflexus* subsp. *inflexus*
16. Fruits subglobose, pale or reddish, apex rounded to subacute, styles deciduous or inconspicuous; petals usually longer than fruits; pith solid; native in Pacific States and western Mexico . . . . . *J. patens*
12. Stamens 3 per flower.
17. Petals blunt; tepals shorter than fruits; pith chambered; Australian introduction in cismontane California . . . . . *J. usitatus*
17. Petals acuminate; tepals usually equaling or longer than fruits; pith solid (chambered only in some aquatic *J. effusus* subsp. *solutus*); widespread in North America
18. Stems with prominent ridges; fresh upper stems dull or matt; dried stems coarsely ridged, ridges visible in high relief at 10×, dried ridges capped with shiny bulging cells.
19. Inflorescence bracts swollen at the base of the inflorescence; bracts often somewhat reflexed in fruit; proximal sheath bases warm reddish-brown to brown; infructescences capitate, occasionally lobed; widespread but uncommon Eurasian introduction. . . . . *J. conglomeratus*
19. Inflorescence bracts not swollen; bracts erect in fruit; proximal sheath bases usually purplish-black, occasionally dark red-brown; infructescences usually open, diffuse; native in eastern North America, west to Minnesota, rare introduction in western North America . . . . . *J. pylaei*

18. Stems with relatively inconspicuous ridges; fresh upper stems shiny; dried stems with lower ridges, fine or coarse, ridges visible in low relief at 10×, dried ridges capped with low dull cells.
    20. Upper sheath apices usually strongly asymmetrical on fruiting stems.
        21. Sheath apices thickened, with raised (convex) rims; sheaths usually dark brown to black . . . . . *J. effusus* subsp. *pacificus*
        21. Sheath apices thin with broad membranous wings, flattened and lacking raised rims; sheaths green (fresh) to pale or mid brown (dried).
            22. Tepals with dark brown to black stripes; fruiting stems slender, usually 0.8–1.9 mm diam. . . . . *J. hesperius*
            22. Tepals light brown; fruiting stems stout, usually 2–3.5 mm diam. . . . . *J. effusus* subsp. *austrocalifornicus*
    20. Upper sheath apices usually symmetrical on fruiting stems.
        23. Visible stem ridges 6–16 per side (10×), low and relatively coarse or wide when dried; proximal sheaths smooth (10×); fruiting stems slender, 0.6–2.6 mm diam. above sheath; tepals usually with mid to dark brown stripes; western montane natives.
            24. Distal half of distal sheaths green to pale brown, thin, dull, nerves prominent, apices thin, slightly inrolled towards the stem . . . . . *J. exiguus*
            24. Distal half of distal sheaths mid-brown, dark brown or black, thick and glossy, nerves obscure, apices thickened, not inrolled . . . . . *J. laccatus*
        23. Visible stem ridges 18–26 per side (10×), slender and relatively inconspicuous when dried; proximal sheaths papillose (10×); fruiting stems stout, 2.2–4.9 mm diam. above sheath; tepals usually pale brown; eastern North American or introduced.
            25. Tepals spreading or curving away from fruits; upper sheaths 6–14 cm long, margins dark-banded; sheaths clasping the stems, sheath margins overlapping 2–4 cm from apex; widespread Eurasian introduction. . . . . *J. effusus* subsp. *effusus*
            25. Tepals erect, pressed to fruits; upper sheaths usually 15–27 cm, margins pale; sheath margins often not clasping stems, margins often not overlapping and split to the base, loose, flattened or unrolled; native in eastern North America, rare introduction in western North America . . . . . *J. effusus* subsp. *solutus*

## Taxonomic Treatment

**Juncus exiguus** (Fernald & Wiegand) Lint ex Snogerup & Zika, Preslia 74: 260. 2002. *Juncus effusus* L. var. *exiguus* Fernald & Wiegand, Rhodora 12: 87. 1910. Type. U.S.A. California: [Mariposa Co.], Yosemite Valley, Jul 1866; *H. N. Bolander 4949* [also distributed by Englemann as Herbarium Juncorum Boreali-Americanorum *Normale 9*] (holotype: GH; isotypes: CAN; CAS; DAO; DS [54102]; DS [78159]; GH; ISC; JEPS; MICH; MO; NY

TABLE I
CRITICAL STEM AND ANTHER CHARACTERS TO DISTINGUISH SELECTED *Juncus* SECT. *Juncotypus* IN NORTH AMERICA.

| *Juncus* sp. | Stem ridges[a] | Stem diam. (mm)[b] | Anther length (mm) | Anther # |
|---|---|---|---|---|
| *J. aemulans* | 6–13 | 0.9–1.9 | 0.4–0.8 | 3 |
| *J. conglomeratus* | (10–)14–20 | 2.2–3.3 | 0.5–0.8 | 3 |
| *J. effusus* subsp. *pacificus* | (12–)15–24(–28) | (1.5–)2–4(–6.2) | 0.5–0.9(–1.1) | 3 |
| *J. effusus* subsp. *pacificus* × *J. exiguus* | 12–18 | 1.4–1.8 | 0.5–0.7 | 3 |
| *J. effusus* subsp. *pacificus* × *J. hesperius* | 9–23 | 1.3–3.6 | 0.5–0.7 | 3 |
| *J. exiguus* | 6–11(–13) | 0.7–1.5(–1.9) | (0.3–)0.4–0.8(–0.9) | 3 |
| *J. hesperius* | 5–14(–18) | 0.8–1.9(–2.7) | 0.5–0.8 | 3 |
| *J. hesperius* × *J. laccatus* | 7–10 | 0.9–1.7 | 0.4–0.5 | 3 |
| *J. inflexus* subsp. *inflexus* | 5–11 | 1.7–3.2 | 0.6–0.8 | 6 |
| *J. laccatus* | 6–16 | 0.6–2.6 | 0.4–0.9 | 3 |
| *J. patens* | (8–)10–15 | (0.8–)1.1–2.3 | 0.4–0.9 | 6 |
| *J. patens* × *J. hesperius* | 10–14 | 1.3–1.9 | 0.6–0.8 | 6 |
| *J. pylaei* | 9–26 | 1.2–4.4 | 0.5–0.7 | 3 |
| *J. usitatus* | 9–28 | 1.1–4.7 | 0.3–0.6 | 3 |

[a] Data from dried material. Stem ridges = number of stem ridges visible on one side of stem, 1 cm above distal sheath apex

[b] Stem diam. = diameter of fruiting stem, 1 cm above distal sheath apex

[1365200]; NY [1365201]; NY [1365202]; NY [1365203]; NY [1365204]; NY [1365205]; POM; RM; RSA; UC [2527]; UC [311708]) (Figs. 1 and 3A–D).

**Selected specimens examined. U.S.A. Arizona:** Pima Co., Soldiers Camp, Mt. Bigelow, 2286 m, Santa Catalina Mtn. Range, 2 Sep 1938, *Benson 9067* (RSA). **California:** Del Norte Co., near Smith River, S Fork, near Gasquet, 122 m, 26 Jul 1979, *Muth 10511* (HSC); [Fresno Co.], Kearsarge Lakes, 3353 m, 23 Jul 1912, *Hopping 18* (CAS-2 sheets); Glenn Co., Plaskett Meadows, 1829 m, 3 Aug 1943, *J. T. Howell 18965* (RSA, WTU); Humboldt Co., near North Trinity Mtn., 1799 m, 1 Aug 1979, *Clifton & Griswold 12005* (HSC); Kern Co., Greenhorn Range, Cow Cr. below Tiger Flat, 1920 m, 27 Jul 1961, *Twisselmann 6414* (ARIZ, RSA); Mariposa Co., Mariposa Grove, Yosemite National Park, 1950 m, 18 Jul 1934, *Bartholomew s.n.* (UC); Placer Co., Forest Hill Rd., 20.5 mi NE of city of Foresthill, 1662 m, 12 Aug 2009, *Helmkamp & Helmkamp 15431* (UCR, WTU); Plumas Co., Linnea Fen, 1771 m, 12 Aug 2007, *Janeway 9171* (WTU); Shasta Co., Rte. 25, at 1.5 road mi NE of junction with Rte. 26, 1740 m, 26 Aug 2009, *Zika 24636* (CHSC, CAS, JEPS, OSC, PRA, WS, WTU); Sierra Co., pond SE of Gold Lake, 1951 m, 6 Sep 1969, *Thorne & Tilforth* 39190 (OSC, RSA); Siskiyou Co., Widow Cr., Mt. Shasta, 1341 m, 10 Oct 1916, *Goldsmith 36* (JEPS); Tehama Co., springs at head of Burnt Cr., E side of Anthony Peak, 1890 m, 2 Sep 1991, *Ertter 10761* (UC); Trinity Co., S slope of N Yolla Bolly Peak, 2271 m, 21 Jul 1951, *Munz 16810* (NY, RSA); Tulare Co., small streamlet, 1920 m, 19 Sep 1957, *Twisselmann 4065* (GH, SD). **Oregon:** Coos Co., Rock Cr., E slope Iron Mtn., 26 Aug 1948, *Baker 5668* (ID, NY, OSC); Jackson Co., 0.3 mi S of summit of Table Mtn., 1795 m, 22 Jul 2008; *Zika & Lang 23935A*

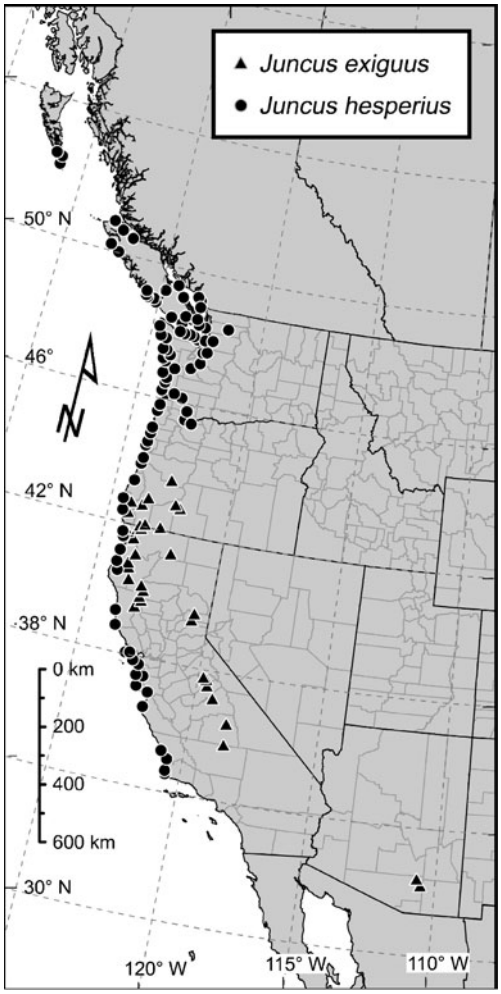



**Fig. 1.** Distribution of *Juncus exiguus* and *J. hesperius*, based on herbarium specimens.

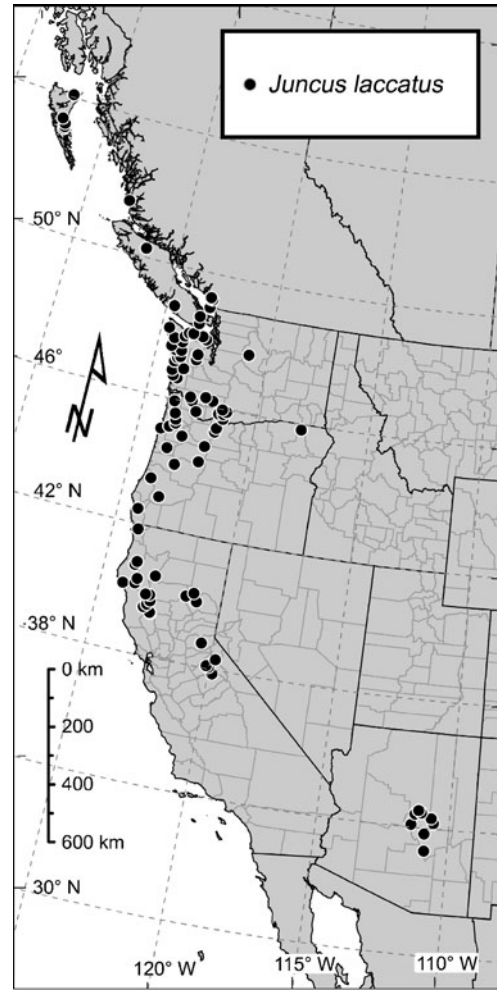



**Fig. 2.** Distribution of *Juncus laccatus*, based on herbarium specimens.

(CHSC, OSC, PRA, WTU); Josephine Co., Lower Bigelow Lake, 16 Aug 1949, *Baker & Ruhle 593* (ID, NY, WTU); Klamath Co., lower Annie Cr., Crater Lake National Park, 1332 m, 11 Sep 2001, *Zika 16531* (CRLA, WTU); Lane Co., Calapooya Range, Fairview Mtn., 28 Sep 1947, *Baker 5135* (ID).

*Diagnostic characters*.—The apex of the distal sheaths are symmetrical and green, except at the very tip, where they are often black and slightly incurved towards the stem. The lower sheaths are never granular papillose, but occasionally the cell wall boundaries are faintly raised on dried material, resembling brickwork at 40×. The sheath veins are prominent, and usually gradually taper to the tip; with age the sheaths fade to light brown. The fresh stems are green and scarcely ridged; but upon drying become slightly blue-green with prominent ridges, thus herbarium specimens appear different.

*Typification*.—There are some difficulties with the type of *Juncus effusus* var. *exiguus*. Fernald and Wiegand (1910) chose a GH specimen as the type, *H. N. Bolander 4949*, part of an 1866 gathering. The holotype at GH matches the protolog and was collected from Yosemite Valley in 1866, and is numbered 4949. Isotypes numbered 4949 exist at DS and UC. Tony Reznicek and Rich Rabeler at MICH (pers. comm.) have pointed out an isotype at MO (type image; Tropicos, 2011) is hand-labeled in two places as number 4949. It also bears a printed label, with the data: "Yosemite Valley, 1866, coll. *Bolander s.n.*, Herbarium Juncorum Boreali-Americanorum *Normale 9* [Ed. G. Englemann, St. Louis, Missouri 1868]." Most authors have treated *Normale 9* as a paratype (Lint, 1977; Kirschner et al., 2002; Snogerup et al., 2002). The punctuation and wording of the protolog suggests that Fernald and Wiegand (1910) were treating *Normale 9* as duplicates of the type. This is confirmed by the annotations on Englemann's MO sheet. He distributed a number of sheets labeled *Normale 9* that do not bear Bolander's number 4949 on the printed labels, but should be considered isotypes, not paratypes.

*Distribution and ecology*.—*Juncus exiguus* does not occur north of the central Oregon Cascades (Fig. 1). It is a montane species, usually found from 1220 to 2440 m elevation, although the species occurs on riverbanks as low as 122 m in the Klamath Mountains. Non-fruiting plants were collected as high as 3353 m in the southern Sierra Nevada Highlands (Fig. 1). It favors seeps, shores, riparian zones, wet meadows, and occasionally is found in peatlands or ditches. Some collections are from recently burned pine forests. It is tolerant of varied substrates. Herbarium labels and maps (Consortium of California Herbaria, 2011) mention sedimentary argillite and sandstone, igneous granitic rocks (diorite, granodiorite), volcanics including andesite, ultramafics (peridotite) and metamorphic schist (blueschist) as substrates.

**Juncus hesperius** (Piper) Lint, Preslia 74: 262. 2002. *Juncus effusus* L. subsp. *hesperius* Piper, Contr. U.S. Natl. Herb. 11: 180. 1906. *Juncus effusus* L. var. *brunneus* Engelm., Trans. Acad. Sci. St. Louis 2: 491. 1868. Type. U.S.A. California: [Marin Co.], shaded shores of Bolinas Bay, near San Francisco, 12 Aug 1866, *A. Kellogg s.n.* [distributed by Engelmann as Herbarium Juncorum Boreali-Americanorum *Normale 10*] (lectotype: MO, designated by Snogerup et al., 2002; isolectotypes: CAS; DS; GH; ISC; LD-n.v.; MICH; NY [247622]; NY [247623]; NY [247624]; NY [247625]; NY [621898]; POM; RSA) (Figs. 1 and 3E–I).

**Selected specimens examined. CANADA. British Columbia:** Cape Fanny, Moresby Is., Queen Charlotte Is., 8 Aug 1957, *Mills 1* (DAO); Bull Harbor, Hope Is., 6 Jul 1961, *Calder & MacKay 31319* (DAO); Lasqueti Is., Woolen Rd., 15 m, 1985, *Wallis & Češka 25605* (UBC); Vancouver, near Acadia Camp, 22 Jun 1949, *Beamish 150* (UBC); Vancouver Is., Port Hardy, near airport, 13 Jul 1961, *Calder & MacKay 31454* (DAO); Alberni, 0 m, 2 Aug 1887, *Macoun 27850* (CAN); Florencia Bay between Tofino & Ucluelet, 27 Jul 1961, *Calder & MacKay 31943* (DAO); Pacific Rim National Park, Nettle Is., bog, 9 Aug 1972, *Harcombe & Mitchell 8097* (UVIC).

**U.S.A. California:** Del Norte Co., 4 air mi ESE of Oregon Mtn., 530 m, 21 Jun 2010, *Zika 24941* (CHSC, JEPS, WTU); Humboldt Co., 2 mi E of Carlotta, 15 Jun 1938, 30 m, *Tracy 15938* (DAO, ISC, RSA, UC); Marin Co., ca. 1.5 mi N of Inverness, 28 Jun 1949, *Nobs & Smith 887* (ARIZ, DAO, UC); Mendocino Co., Fort Bragg, 65 m, 4 Nov 2008, *Zika 24285* (CHSC, RSA, UC, WS, WTU); Monterey Co., Carmel Bay, 22 Jun 1919, *Ferguson & Ferguson 301* (JEPS); San Luis Obispo Co., near Callender, 20 Oct 1946, *Hoover 6523* (LL, UC); San Mateo Co., ca. 1 mi S of Half Moon Bay, 26 Aug 1949, *Nobs & Smith 1588* (UC); Santa Barbara

TABLE II
CRITICAL SHEATH CHARACTERS TO DISTINGUISH SELECTED *Juncus* SECT. *Juncotypus* IN NORTH AMERICA.

| *Juncus* sp. | Sheath gloss; texture[a] | Sheath tip; outer vein convergence; overlap[b] |
|---|---|---|
| *J. aemulans* | Shiny or dull proximally; smooth or ± granular | Strongly asymmetrical, occasionally symmetrical, wings thin; ± gradual; split 3–21 mm from apex |
| *J. conglomeratus* | Dull to slightly shiny; granular | Symmetric, blunt; gradual, ± abrupt, or not converging; split 35–65 mm from apex |
| *J. effusus* subsp. *pacificus* | Dull or shiny proximally; granular | Wings asymmetric, wide, thick rim; abrupt; split 1–3 mm from apex |
| *J. effusus* subsp. *pacificus* × *J. exiguus* | Shiny proximally; smooth or granular proximally | ± Symmetrical, narrow wings, thin rim; gradual or abrupt; split 2–3 mm from apex |
| *J. effusus* subsp. *pacificus* × *J. hesperius* | Dull or shiny proximally; granular | Asymmetric wings, thin or thick rim; abrupt; split 1–85 mm from apex |
| *J. exiguus* | Dull or shiny proximally; smooth (occasionally minutely reticulate-cellular at 20× but not granular) | Symmetric narrow thin wings, often dark and inrolled; mostly gradual, some abrupt or not converging; split 8–43(–75) mm from apex |
| *J. hesperius* | Slightly shiny or dull proximally; granular | Asymmetric wide thin wings usually; gradual or some not converging; split 4–49(–65) mm from apex |
| *J. hesperius* × *J. laccatus* | Dull to ± shiny distally; ± granular or smooth | Symmetric, truncate, wingless; gradual; split 6–61 mm from apex |
| *J. inflexus* subsp. *inflexus* | Shiny proximally; smooth | Symmetric, acute or acuminate, wings thin, narrow; gradual; split 5–120 mm from apex |
| *J. laccatus* | Shiny, smooth; veins absent or usually not prominent | Symmetric, blunt or notched, thick, wingless; abrupt or not converging; split 12–72 mm from apex |
| *J. patens* | Shiny proximally; strong raised veins, not granular | Symmetric, acute (blunt), narrow wing thin; gradual; split 10–70 mm from apex |
| *J. patens* × *J. hesperius* | Shiny proximally; smooth or granular | Symmetric, blunt to acute, narrow thin wing; gradual; split 22–58 mm from apex |
| *J. pylaei* | Dull or shiny; granular | Symmetric, blunt or acute; moderate to abrupt; some not converging; split 4–120 mm from apex |
| *J. usitatus* | Shiny proximally; smooth (papillose) | Symmetric, wing thin, narrow, blunt; abrupt or gradual; split 10–150 mm from apex |

[a] Data from dried material. Sheath gloss = shininess of sheath, if any; texture = surface texture, papillose-granular or not at 10×.

[b] Sheath tip = distal sheath summit symmetry and shape; outer vein convergence = distal sheath vein convergence at sheath apex; overlap = length above overlapping distal sheath margins, the split measured from sheath apex to distal-most point of overlap of lateral sheath margins.

Co., near summit of Mt. Tranquillon, SW of Lompoc, 5 Oct 1952, *C. F. Smith 3825* (RSA); Santa Cruz Co., Aptos Cr. drainage, 198 m, 9 Jul 1989, *D. W. Taylor 10408* (UC); Sonoma Co., Ridge Crest Rd., Sea Ranch S of Gualala River, 30 m, 20 Jun 1977, *C. Davidson 6035* (RSA, SD). **Oregon:** Clatsop Co., hills NE of town of Seaside, 115 m, 27 Jul 2007, *Zika 23290* (CIC, NY, OSC, UBC, UC, WTU); Columbia Co., McNulty, 10 m, 2 Jul 2007, *Zika 23117* (CHSC, OSC, WS, WTU); Coos Co., confluence of Fourmile Cr. and New River, 19 Jul 2006, *B. L. Wilson & Coberly 11837* (WTU); Curry Co., Port Orford, 30 Jun 1919, *Peck 8612* (GH, NY, WILLU); Lincoln Co., near Siletz Bay, 1.5 mi SE from Taft, 30 Jul 1959, *Bennett 1604* (NY); Marion Co., NW of Stayton, 140 m, 7 Jun 2007, *Zika 23053* (OSC, WS, WTU); Multnomah Co., Rte. 30, 7 air km S of Scappoose, 15 m, 2 Jul 2007, *Zika 23118* (PRA, WS, WTU). **Washington:** Clallam Co., Sequim; 80 m, 26 Aug 2002, *Zika 17663* (WTU); Clark Co., 1.5 air km NW of Lacamas Lake, 55 m, 2 Jul 2007, *Zika 23123* (CHSC, RSA, WTU); Cowlitz Co., 1.5 air km N of Crims Is., 35 m, 27 Jun 2007, *Zika 23091* (CAS, OSC, RSA, UBC, UC, WS, WTU); Grays Harbor Co., Moclips, 31 Jul 1918, *Piper s.n.* (WS); Island Co., Deception Pass, Whidbey Is., 14 Jun 1936, *H. W. Smith 833* (UC, WTU); Jefferson Co., 10 mi E of Queets, 7 Sep 1957, *Thorne 19143* (RSA); King Co., Fauntleroy Cove, Seattle, 5 m, 19 Jun 2001; *Zika & Jacobson 16292* (PRA, WTU); Lewis Co., Drews Prairie, 95 m, 27 Jul 2007, *Zika 23305* (UC, WTU); Pacific Co., 1.5 mi S of Grayland, 5 m, 27 Aug 2002; *Zika 17703* (WTU); Pierce Co., Point Defiance Park, Tacoma, 46 m, *Keil 2088* (ASU, USFS); San Juan Co., near S shore of False Bay, San Juan Is., 20 m, 8 Sep 2001, *Zika 16512* (PRA, WTU); Skagit Co., Shannon

Point, Fidalgo Is., 14 Aug 1974, *Sundquist 2510* (WWB); Thurston Co., Chambers Lake, 23 Aug 1892, *Henderson s.n.* (WS); Wahkiakum Co., Cathlamet, 65 m, 27 Jun 2007, *Zika 23096* (WTU).

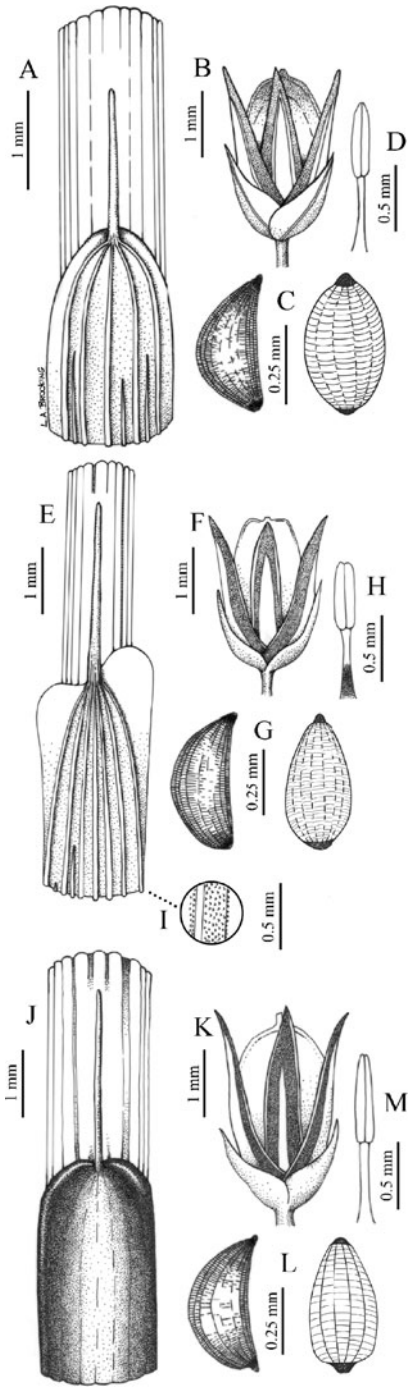
*Diagnostic characters.—Juncus hesperius* is characteristically a narrow-stemmed species. On the central California coast some specimens have slightly thicker stems, but the trend is irregular and sporadic. The well-developed distal sheath apices on fruiting stems have distinctive asymmetrical thin wings, lacking in *J. exiguus* and *J. laccatus*. The distal halves of the distal sheaths are green, aging to light brown, and occasionally have dark margins. The proximal halves of the sheaths are granular papillose, a diagnostic feature absent in both *J. exiguus* and *J. laccatus*. The fresh stems are slightly dull and slightly ridged, but upon drying the stem ridges become pronounced.

A Mexican species, *Juncus aemulans* Liebm., is closely related to *J. hesperius*, and is sometimes confused with it. The type of *J. aemulans*, from "Cerro Leon, Mexico" was cited by Piper (1906) along with specimens of *J. hesperius* from Washington, which Piper called *J. effusus* subsp. *hesperius*. Following Balslev (1996) I consider *J. aemulans* distinct from *J. hesperius*. *Juncus aemulans* sheaths usually lack papillae, and it often has symmetrical sheath summits. However, Mexican specimens are few, and the distinctions between the two need more study from a larger series of collections.

*Distribution and ecology.—Juncus hesperius* is primarily coastal, but penetrates inland along the Columbia River, as well as ascending some hills in the Coast Ranges of Oregon and California (Fig. 1). The species ranges from sea level to 735 m elevation, on damp to wet sandy, peaty, or gravelly substrates, in full sun or partial shade. Natural habitats include marshes, peatlands, shores, riparian zones, swamps, wet meadows, wet prairies, old growth forest, and freshwater springs in coastal dunes or salt marshes. It is a successful colonist of exposed damp or wet soil in pastures, ditches, trails, logging clearings, disturbed ground, and cranberry farms. Collections are labeled or mapped from a variety of bedrock types, including sedimentary limestone, mudstone, sandstone, and slate, igneous volcanics (basalt and rhyolite), and metamorphic serpentinite (Consortium of California Herbaria, 2011).

Disjunct Queen Charlotte Island (Haida Gwaii) localities, at the northern limit of its range (Fig. 1), suggest that some *Juncus hesperius* populations survived the last continental glaciation as relict populations in glacial refugia off the coast of British Columbia (Warner et al., 1982; Hetherington et al., 2003; Burg et al., 2005; Topp & Winker, 2008). If widely distributed, the mainland populations at similar latitudes did not survive glaciation. As the ice sheets melted, *J. hesperius* could not easily recolonize from the south over the many deep fjords along the highly dissected shoreline of southeastern Alaska and northern British Columbia (Calder & Taylor, 1968). A similar distribution (and suggested explanation) is found for *J. laccatus* (Fig. 2) and *J. effusus* subsp. *pacificus* (Zika, 2003). All three taxa are at the extreme northern limit of their natural ranges in the Queen Charlotte Islands, and have never been documented in Alaska or the northern coastal mainland of British Columbia. The three are unlikely to have been recently introduced to the Queen Charlotte Islands (by migratory birds or logging equipment, for example), for they are not found in similar disturbances or habitats on the adjacent mainland of Alaska or British Columbia. Their distribution is a striking contrast to nonnative *J. effusus* subsp. *effusus*, which is a recent and weedy introduction throughout settled areas in southeastern Alaska, and is found in the same habitats as *J. hesperius, J. effusus* subsp. *pacificus*, and *J. laccatus* in the Queen Charlotte Islands, and along the coastlines of southern British Columbia, Washington, and Oregon (Zika, 2003).

**Juncus laccatus** Zika, Preslia 74: 261. 2002. Type: U.S.A. Washington: Clallam Co., Olympic Peninsula, Rte. 101 near Dry Cr., 6 air km SSE of Angeles Point, 140 m, 27 Sep 2001, *P. F. Zika 16611* (holotype: WTU; isotypes: CAN, GH, MICH, MO, NY, OSC, PRA, UBC, UC, US, WTU) (Figs. 2 and 3J–M).




◀ **Fig. 3. A–D.** *Juncus exiguus*. **A.** Apex of distal sheath. **B.** Fruit and tepals. **C.** Seeds. **D.** Stamen. **E–I.** *Juncus hesperius*. **E.** Apex of distal sheath. **F.** Fruit and tepals. **G.** Seeds. **H.** Stamen. **I.** Detail of granular-papillose sheath. **J–M.** *Juncus laccatus*. **J.** Apex of distal sheath. **K.** Fruit and tepals. **L.** Seeds. **M.** Stamen. (A–D drawn from *Zika 16484*, WTU; E–I from *Zika 16512*, WTU; J, K, M from *Zika 17664*, WTU; L from the holotype).

*Juncus effusus* L. var. *gracilis* Hook., Fl. Bor.-Amer. 2: 190. 1838. *Juncus effusus* L. subsp. *gracilis* (Hook.) Piper & Beattie, Fl. N.W. Coast 88. 1915. Type. U.S.A. [Oregon or Washington]: Northwest coast of America, Columbia [River], 1825, *D. Douglas s.n.* (lectotype: K, designated by Snogerup et al., 2002).

**Selected specimens examined. CANADA. British Columbia:** Queen Charlotte Is., Moresby Is., Alliford Bay, 5 Aug 1957, *Calder et al. 23234* (DAO, UBC, UC); Graham Is., 16 km NW of Queen Charlotte City, 100 m, *Zika 13567* (WTU); Vancouver Is., Sidney, 7 Jul 1913, *Malte s.n.* (CAN); Vancouver, 20 Aug 1911, *Malte s.n.* (CAN).

**U.S.A. Arizona:** Coconino Co., Kehl Springs Campground, 6.8 mi NE of Rte. 87, 2438 m, 18 Sep 1977, *Parfitt 2336* ASU; Gila Co., Garden Spring, Barnhardt Canyon, Mazatzal Mtns., 1323 m, 1 Jun 1983, *Morefield & Windham 1456* (ASC); Navajo Co., tributary of Black Canyon Lake, Sitgreaves National Forest, 18 Aug 1967, *Correll & Correll 34866* (LL, NY). **California:** Butte Co., Concow Rd., 10 road mi above and N of Rte. 70, 1100 m, 17 Jun 2009, *Zika 24514* (CHSC, JEPS, UBC, WTU); Colusa Co., Fouts Camp, Snow Mtn., 1890 m, 9 Sep 1974, *Heckard 3852* (JEPS); Del Norte Co., near Hurdygurdy Cr., close to Gasquet, 640 m, 15 Jun 1979, *Overton & Butler 4918* (HSC); El Dorado Co., near Bridal Veil Falls, 3 mi W of Riverton, 12 Sep 1969, *J. T. Howell 46093* (ASU); Glenn Co., Plaskett Meadows, 1829 m, 3 Aug 1943, *J. T. Howell 18965* (WTU); Humboldt Co., Rte. 101 between Stone and Big Lagoons, 80 m, 30 Jul 2007, *Zika 23330* (CHSC, CIC, RSA, UC, WS, WTU); Lake Co., near W ridge of West Peak, Snow Mtn., 2012 m, 17 Sep 1980, *Heckard & Hickman 5471* (JEPS); Mendocino Co., Leech Lake Mtn., ca. 2 mi N of Ham Pass Rd., 1889 m, 10 Jul 1984, *Wheeler 3694* (HSC); Plumas Co., ca. 5 air mi NW of La Porte, 1725 m, 14 Aug 2008, *Ahart 15217* (WS, WTU); Shasta Co., near North Fork Battle Cr. on Rte. 44, 1220 m, 14 Jul 2008, *Zika 23887* (JEPS, WTU); Tehama Co., Childs Meadows, 1494 m, 27 Aug 2009, *Ahart et al. 16339* (WTU); Tuolumne Co., Mather, Yosemite National Park, 1400 m, 2 Jun 1931, *Keck 1189* (GH, POM); Trinity Co., near Panther Rock Cr., near Alderpoint, 1045 m, 16 Jul 1979, *Butler 7403* (HSC); Yuba Co., small pond, ca. 1 air mi E of Clipper Mills, 1021 m, 7 Aug 2007, *Ahart 14414* (WS, WTU). **Oregon:** Clatsop Co., hills NE of Seaside, 115 m, 27 Jul 2007, *Zika 23289* (CHSC, NY, OSC, PRA, RSA, UBC, UC, WS, WTU); Curry Co., Winchuck area, 664 m, 2 Jul 1973, *Denton 2983* (ID, NY, WTU); Hood River Co., Rte. 35, Parkdale, 460 m, 28 Aug 2008, *Zika 24158* (OSC, WTU); Lane Co., river shore, Eugene, 131 m, 4 Sep 1920, *J. C. Nelson 3370* (GH); Linn Co., H. J. Andrews Experimental Forest, Unit 31, 1067 m, 15 Jun 1960, *Franklin 108* (USFS, WS); Multnomah Co., Bull Run watershed, 10 Rd., 305 m, 16 Aug 2006, *Wilson &*

*Newhouse 12042* (WTU); Union Co., NW corner of Jubilee Lake, Blue Mtns., Umatilla National Forest, 1425 m, 20 Jul 2000, *Markow 12039* (RM); Wasco Co., Dufer Valley Rd., 745 m, 27 Aug 2008, *Zika 24148* (CHSC, NY, OSC, WTU). **Washington:** Chelan Co., Rte. 2, 4 air km SE of Merritt Lake; 725 m, 22 Sep 2003, *Zika 19097* (WTU); Clallam Co., E end of Lake Sutherland, 175 m, 27 Sep 2001, *Zika 16608* (UC, PRA, WTU); Clark Co., NE 219th Street, near NE 10th Avenue, 90 m, 10 Sep 2002, *Zika 17792* (PRA, NY, WTU); Cowlitz Co., 1.5 air km S of Rocky Point, E of Cowlitz River; 15 m, 27 Jun 2007, *Zika 23084* (WTU); Grays Harbor Co., near Montesano, 61 m, 27 Jun 1898, *Heller & Heller 3970* (GH, ISC, NY-2 sheets, RM, UC); Jefferson Co., Maynard, Port Discovery, 10 m, 26 Aug 2002, *Zika 17659* (WTU); Klickitat Co., Trout Lake, 570 m, 28 Aug 2008, *Zika 24171* (CHSC, WS); Skamania Co., South Prairie, Forest Service Rd. 66, 910 m, 28 Aug 2008, *Zika 24166* (CHSC, WTU).

*Diagnostic characters.*—Among North American rushes, *Juncus laccatus* has unusual sheaths that are shiny, smooth, and thickened, with obsolete or inconspicuous veins, somewhat like *J. breweri* Engelm. Fresh stems of *J. laccatus* are smooth to slightly ridged and slightly dull, but upon drying the broad low stem ridges become prominent.

*Cytology.*—Two chromosome levels are recorded on verified herbarium vouchers. *Parfitt 2336* is labeled as a voucher for $2n=40$, *Calder et al. 23234* is labeled as a voucher for $2n=80$ (Taylor & Mulligan, 1968).

*Distribution and ecology.*—*Juncus laccatus* ranges from the Queen Charlotte Islands to the mountains of northeastern Oregon (where it is disjunct, rare, and local), the Sierra Nevada of California, and the high peaks of central Arizona (Fig. 2). It is curiously absent from much of Washington's Puget Sound, yet relatively common in the cooler and wetter climate of the outer coast of Washington. *Juncus laccatus* is found at sea level along the coast and in the north. To the south, montane populations are found at increasingly higher altitudes, up to 2438 m in Arizona. Habitats include shores, riparian zones, wet meadows, springs, washes, peatlands, freshwater fringes of coastal salt marshes, and canyon bottoms. It occasionally colonizes ditches, mudflows, lahars, and logging clearings. The underlying bedrock is varied, including sedimentary rocks such as argillite, shale and sandstone; igneous rocks such as granodiorite and andesite; as well as metamorphic rocks, including ultramafics, schist, phyllite, and greenstone (Consortium of California Herbaria, 2011).

## Putative Hybrids

These specimens are believed to be hybrids for several reasons. When seen in the field, both parents are present, share the same habitat, are easily recognized and outnumber the putative hybrids, which are morphologically intermediate. In the herbarium only a few specimens were found that were not easily assigned to one of the parental taxa.

Partial pollen sterility has been used to confirm some *Juncus* hybrids (Stace, 1975), but was not examined here. Reduced seed set or poor capsule formation is frequent in many species of *Juncus*, and may be induced by galls, fungal attack, limited pollination, vernal frost, excessive shade, desiccation, or other factors (Wilcox, 2010). Hybridity can also result in poor seed set (Stace, 1975); specimens with poor seed set or aborted capsules are noted below.

No genetic or molecular work is available to support hybrid status for the plants listed below. The evidence supporting hybridizaton is morphological and ecological. Surface characters of the stem and sheath were emphasized (Edgar, 1964; Nilsson & Snogerup, 1971; Wilcox, 2010). *Juncus* section *Juncotypus* is reported to produce many hybrids, even between species not very closely related, especially in Australia. Kirschner et al. (2002) list 25 crosses in the section, with varying levels of confirmation of hybrid status, but does not list any of the hybrid combinations below. Based on morphological intermediacy, Lint (1977) mapped some hybrids between *J. exiguus* and *J. laccatus*, and between *J. effusus* subsp. *pacificus* and *J. hesperius*, but did not provide any documentation, cited no specimens, and did not perform crossing experiments or chromosome analysis. The other putative hybrids listed below are new reports. Three hybrids are illustrated (Fig. 4) to facilitate their identification.

### Juncus exiguus × J. effusus subsp. pacificus

*Diagnostic characters.*— The Ahart gathering resembles *Juncus exiguus*, with a split sheath and nearly symmetrical sheath apices. However, the influence of *J. effusus* subsp. *pacificus* is suggested by the granular basal

sheaths, the slightly wider than usual stems, 1.4 to 1.8 mm in diameter above the sheath apex, and the 12 to 18 stem ridges visible on one side. *Juncus exiguus* usually has smooth sheaths and stems 0.7 to 1.5(–1.9) mm wide, with 6 to 11(–13) visible ridges on one side (Table I).

**Representative specimens examined. U.S.A. California:** Plumas Co., damp roadside 1 mi NE of La Porte, 1615 m, 13 Aug 2008, *Ahart 15159* (OSC).

### Juncus exiguus × J. laccatus

*Diagnostic characters.*—This specimen has slightly shiny thickened sheaths, as in *Juncus laccatus*. Most of the distal sheath length is green to pale brown, and some sheaths are not shiny or not thickened, as in *J. exiguus*. Both putative parents are known from the mountains of Humboldt Co.

**Representative specimens examined. U.S.A. California:** Humboldt Co., wet seep between Alder Springs and road to Pine Mtn., 1525 m, 28 Jul 1976, *Nelson & Nelson s.n.* (HSC).

### Juncus hesperius × J. patens

(Fig. 4; sheath: A × B, tepals: D × E).

*Diagnostic characters.*—In both collections some of the proximal sheaths are granular-papillose, and the tepals are dark-striped, suggesting *Juncus hesperius* parentage. Flowers with six stamens, and narrow, usually symmetrical apices on the distal sheaths show the influence of *J. patens*. The capsules do not seem to have any well-formed seed, even on specimens collected late in the season. Label data for Buck's gathering notes three hybrid individuals were seen with: "culm color ± intermediate between grass-green of *J.* [*hesperius*] & blue-green of *J. patens*." Jim West of Swanton (pers. comm.) discovered this hybrid, and notes he has transplanted a dozen hybrid individuals to the University of California Santa Cruz Arboretum, where it is now in cultivation. If it transplants easily, with its sterility it (or its parents) might be a good horticultural replacement for the invasive *J. usitatus* which is spreading over the Sacramento Valley and is still sold commercially as a native rush in nurseries of northern California.

**Representative specimens examined. U.S.A. California:** Santa Cruz Co., Swanton, 137 m, 3 Jul 1983, *Buck 407 & West* (JEPS); 1 air mi NE of Greyhound Rock, Last Chance Rd., 180 m, 29 Aug 2010, *Neubauer 25402* (CAS, CHSC, JEPS, MO, NY, WS, WTU).

### Juncus hesperius × J. effusus subsp. pacificus

(Fig. 4; sheath: B × C, tepals: E × F).

*Diagnostic characters.*—The Taylor collection has narrow ridges on the dried stems, and thick dark rims on the distal sheath apices, implying that *Juncus effusus* subsp. *pacificus* is involved in the parentage. However, the stems are thin and the sheaths are mostly green, as in *J. hesperius*. The tepals are dark, which also suggests *J. hesperius* influence, although rare specimens of *J. effusus* can have darker tepals. Both putative parents are common in the area. This collection is cited with some hesitation; *J. effusus* subsp. *pacificus* is variable, and depauperate plants can approach the hybrid.

Jepson's gathering displays pale brown tepals and thick dark rims on the sheath apices, features of *Juncus effusus* subsp. *pacificus*. The spreading tepals are more like *J. hesperius*. The slender stems with only 10 ridges visible on one side, and the low broad shape of the ridges also suggest the influence of *J. hesperius.* Most of the capsules appear aborted or sterile. Both putative parents are common in the area.

The Nobs and Smith collection has wide stems, 3.1 to 3.5 mm in diameter above the sheaths, and 20 to 23 visible stem ridges, typical for *Juncus effusus* subsp. *pacificus*, which usually has the upper sheath margins overlapping within 1 to 3 mm of the apex. This "high overlap" is not present in the putative hybrid. In addition to the more deeply split sheaths, the tepals are dark and the sheaths are pale, presumably an influence of *J. hesperius*. Some normal seeds were produced, but viability was not tested.

Johnson's material has thick-rimmed and dark distal sheath apices, like *Juncus effusus* subsp. *pacificus*. The dark tepals, stems with only 12 to 15 ridges visible on one side, slim stems, and narrow sheaths all suggest the influence of *J. hesperius*. Seeds are common, but are poorly formed, and might be infertile or merely immature. Both putative parents are common in the area.

**Representative specimens examined. CANADA. British Columbia:** Vancouver, Saanichton, Mt. Newton, 30 Jul 1941, *T. M. C. Taylor 1133* (DAO).

**U.S.A. California:** Humboldt Co., redwoods, Weatt, 29 Jul 1932, *Jepson 16440* (JEPS); San Luis Obispo Co., 4 mi S of Pismo Beach, 9 Sep 1948, *Nobs & Smith 669* (UC). **Washington:** King Co., Seattle, 20 Jun 1988, *Johnson 241* (WTU).

### Juncus laccatus × J. hesperius

(Fig. 4, sheath: G × H).

This is the most frequently observed and collected of the reported hybrids. Its putative parents are often found growing together in coastal areas, but very few sites yield intermediate plants.

*Diagnostic characters.* —The specimens collected from Elwha have some slightly asymmetrical sheath apices, and the sheaths are papillose with prominent veins, all features of *Juncus hesperius*. However, some sheaths, on the same plant, are slightly shiny and dark, the distal sheath tips are slightly thickened and darkened, some are symmetrical, and the fresh stems were shiny and smooth, all characters of *J. laccatus.* Some normal seed was produced, but a number of capsules were apparently aborted.

The Clark County gathering displays proximal sheaths that are slightly glossy and lack papillae, suggesting the influence of *Juncus laccatus.* The apices of the distal sheaths are mostly green, thin and veiny like *J. hesperius,* but symmetrical as in *J. laccatus*. Seed set is poor and much of the seed is malformed. The putative parents are both common at the site, bear abundant and normal seed, and greatly outnumber the putative hybrids.

The collection *Zika 23085* shows papillose and veiny proximal sheaths, like *Juncus hesperius*. The apices of the distal sheaths are symmetrical and darkened, and a few are slightly thickened, suggesting the influence of *J. laccatus*. Well-formed seed is abundant, but its viability was not tested. The disturbed sunny roadbank seep has both parents common and outnumbering the putative hybrid.

Finally, *Legler 454* has granular-papillose proximal sheaths, and the sheath veins are prominent, as in *Juncus hesperius*. The distal sheath apices are darkened, symmetrical, and sometimes glossy and thickened, apparently the influence of *J. laccatus*. Both putative parents are present at the site. The plant was collected too early in the growing season to assess seed formation.

**Representative specimens examined. U.S.A. Washington:** Clallam Co., Aldwell Reservoir, Elwha River, 80 m, 27 Sep 2001, *Zika 16606* (PRA, WTU); Clark Co., pasture near NE 10th Avenue, 90 m, 10 Sep 2002, *Zika 17794* (NY, PRA, UC, WTU); Cowlitz Co., Interstate Rte. 5, exit 39, 1.5 air km S of Rocky Point, 15 m, 27 Jun 2007, *Zika 23085* (DAO, OSC, PRA, RSA, UBC, UC, WS, WTU); Pacific Co., Ellsworth Cr., 31 May 2003, *Legler 454* (WTU).

### Acknowledgments

I am grateful to the curators and staff at the following herbaria for loans or access to collections: ALTA, ASU, BISH, BM, BOIS, C, CAN, CAS, CHSC, COCO, COLO, CRLA, DAO, DBG, DS, ELRG, F, FHL, FTU, FVCC, GFND, GH, HSC, ID, ISC, JEPS, K, KHD, LINN, LL, MALA, MICH, MO, MONT, MONTU, NEBC, NMC, NMRC, NY, ORE, OSC, P, PMAE, POM, RM, RSA, SD, SOC, SJNM, SRP, TEX, TNFS, UBC, UC, UNM, US, USFS, UTEP, UVIC, V, WILLU, WS, WTU, WTUH, and WWB. In addition I would like to thank the directors and staff of institutions not listed in Index Herbariorum: the Arboretum of the University of California Santa Cruz; Reed College, Portland, Oregon; Olympic National Forest, Olympia, Washington; The Evergreen State College, Olympia; North Cascades National Park, Marblemount, Washington; Olympic National Park, Port Angeles, Washington; and the Slater Museum of Natural History at the University of Puget Sound, Tacoma, Washington. Partial funding was received from the Lawrence R. Heckard Fund of the Jepson Herbarium and the Washington Native Plant Society. The line drawings are by Linda Brooking; the maps were prepared by Ben Legler. I extend my appreciation to my reviewers, as well as to Adolf Češka, Ken Chambers, the late Steve Clements, Alison Colwell, Barbara Ertter, Leena Hämet-Ahti, Jan Kirschner, the late Harold Lint, Frank Lomer, Julie Nelson, Dylan Neubauer, Sven

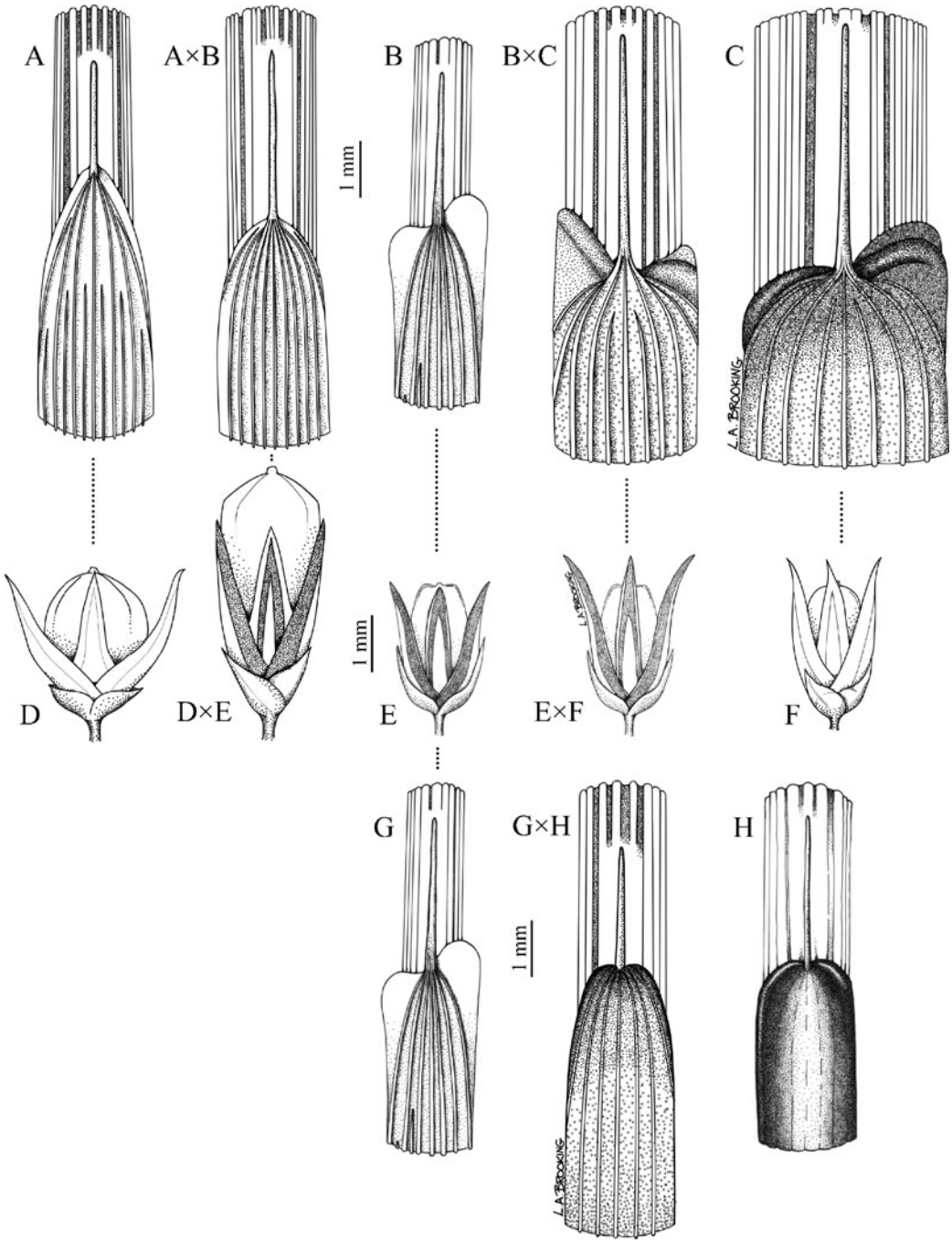



**Fig. 4.** Comparison of four parents and three hybrids of the *Juncus hesperius* complex. **A–C.** *Juncus* distal sheath apices. **A.** *Juncus patens*. **A × B.** *Juncus hesperius* × *J. patens*. **B.** *Juncus hesperius*. **B × C.** *Juncus effusus* subsp. *pacificus* × *J. hesperius*. **C.** *Juncus effusus* subsp. *pacificus*. **D–F.** *Juncus* tepals and mature capsules. **D.** *Juncus patens*. **D × E.** *Juncus hesperius* × *J. patens*. **E.** *Juncus hesperius*. **E × F.** *Juncus effusus* subsp. *pacificus* × *J. hesperius*. **F.** *Juncus effusus* subsp. *pacificus*. **G–H.** *Juncus* distal sheath apices. **G.** *Juncus hesperius*. **G × H.** *Juncus hesperius* × *J. laccatus.* **H.** *Juncus laccatus.* (A, D drawn from *Zika & Witham 23022*, WTU; A × B and D × E from *Buck & West 407*, JEPS; B, E, G from *Zika 16512*, WTU; B × C, E × F from *Johnson 241*, WTU; C, F from *Zika 16520*, WTU; G × H from *Zika 17794*, WTU; H from *Zika 17664*, WTU).

Snogerup, Michael Wilcox, Barbara Wilson, and Thomas Zanoni for their assistance. I am delighted that Rich Rabeler and Tony Reznicek at MICH directed me to the previously unrecognized isotypes of *Juncus exiguus*. I am especially grateful to Kanchi Gandhi at GH for pointing out the earliest authorship for the combination *J. effusus* subsp. *pacificus*.

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