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Huperzia continentalis (Lycopodiaceae), a New Species of Gemmiferous Firmoss Separated from *Huperzia haleakalae*

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Abstract—A new species of gemmiferous clubmoss, ***Huperzia continentalis***, is described. This species is most abundant in northwestern North America, but also occurs in Greenland, northern Europe, and northeastern Siberia. Material of this species was previously treated as *Huperzia haleakalae*, but detailed morphological study shows that the species differ by color, leaf size and shape, and gemma distribution. With the recognition of ***Huperzia continentalis***, *H. haleakalae* is only known from the type, collected on Maui in 1840, and is likely extinct. *Huperzia continentalis* is also compared to similar species of *Huperzia* with which it co-occurs; it is readily distinguished from these taxa by plant size, leaf dimensions, and the size and distribution of gemmae. Hybrids between *H. continentalis* and four other *Huperzia* species are discussed.

Keywords—Circumboreal, cryptic species, Hawaii, lycophyte.

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Though they have been the subject of considerable taxonomic study, the gemmiferous firmosses (*Huperzia* Bernh., Lycopodiaceae [Huperziaceae sensu Ching 1981; Haines 2003]) of North America remain poorly understood because of subtle differences between species, confusion about the geographic distribution of some taxa, and the prevalence of hybrids that are morphologically intermediate to their progenitors. As a result, most taxa have, at some point, been confused with the widespread *Huperzia selago* (L.) Bernh. ex Schrank & Mart., the type species of the genus. The misapplication of this name among North American *Huperzia* was partially resolved by the efforts of Joseph Beitel, who recognized several distinct species and abortive-spored, morphologically intermediate hybrids (Beitel 1979; Beitel and Mickel 1992). In their treatment of the genus for the *Flora of North America*, Wagner and Beitel (1993) increased the number of recognized *Huperzia* species in North America from three (e.g. Fernald 1950; Lellinger 1985; Cody and Britton 1989) to seven. Three of the four newly recognized species had previously been treated as poorly defined and partially overlapping intraspecific taxa within *H. selago*. The fourth species added to the flora of continental North America by Wagner and Beitel was *H. haleakalae* (Brack.) Holub, a species that had been described more than a century earlier from a single collection gathered on Mt. Haleakalā on the Hawai'ian island of Maui. Wagner and Beitel (1993) newly reported it from "alpine and subalpine mossy meadows" from Colorado to Yukon and Alaska. Along with this rather distinct habitat preference, they distinguished *H. haleakalae* from other continental members of the *H. selago* complex by its lustrous, often yellowish leaves, gradual leaf dimorphy, and gemma size, shape, and distribution (Wagner and Beitel 1993). However, following Wagner and Beitel's treatment, *Huperzia* of western North America has received little attention from taxonomists, and large numbers of specimens in herbaria remain misidentified as *H. selago*.

Concerned that the name *Huperzia haleakalae* might also have been misapplied to North American plants, we examined the type material of *Lycopodium haleakalae* Brack., deposited at BISH, K, P, and US. Detailed study of this material indicated that the type collection differs from the plants of continental North America by a number of characters, including leaf morphology, plant color, and gemmiphore distribution. Based on morphological analysis of these and other characters from over 600 herbarium specimens, we recognize the continental plants as a species distinct from *H. haleakalae* and describe it here.

Taxonomic Treatment

Huperzia continentalis Testo, A. Haines & A. V. Gilman, sp. nov.—TYPE: U.S.A. Washington, Skagit County, North Cascades National Park. 1 air kilometer south of Easy Pass. Fisher Creek. Wet meadow complex. Full sun. Erect from bent base. Mid-green. In sphagnum and moist soil by channel. Locally common. 48°33.7′N, 120°50.5′W, 23 Aug 2003, *P. F. Zika, J. Duemmel, and W. Lockwood 18862* (holotype: WTU!; isotype: VT!).

Plants terrestrial. Shoots erect, dichotomously branched, 8–15(–24) cm tall, 0.8–1.0 cm wide (including leaves). Leaves ascending to tightly appressed, yellowish-green to orange-brown, lustrous; gradually dimorphic; leaves of proximal portion of shoot lanceolate, 5–7(–10) mm long and 0.7–1.5 mm wide; leaves of distal portion of shoot broadly lanceolate, widest at or near base, 2.5–5 mm long and 0.7–1.5 mm wide, margins smooth or essentially so. Gemmiphores and gemmae distributed throughout mature portion of shoot (i.e. not confined to one or more pseudowhorls at the summit of annual growth); gemmae 3.0–3.5 mm long, (2.6–)2.9–3.4 mm wide, broadly obovate to circular; lateral leaves of gemmae (1.3–)1.5–1.7 mm wide, unequally arched and subdimidiate, apices acute to obtuse. Sporangia reniform, yellow, borne on adaxial surface of leaf at base, 0.7–1.1 mm wide. Spores 33–40 μm, tetrahedral. Figures 1, 2, 3.

Diagnostic Characters—*Huperzia continentalis* is rather variable morphologically (Fig. 1), but can be distinguished from other North American species of *Huperzia* by its gradually dimorphic leaves, lustrous appearance, unconfined gemmiphore distribution, and medium-sized gemmae with unequally

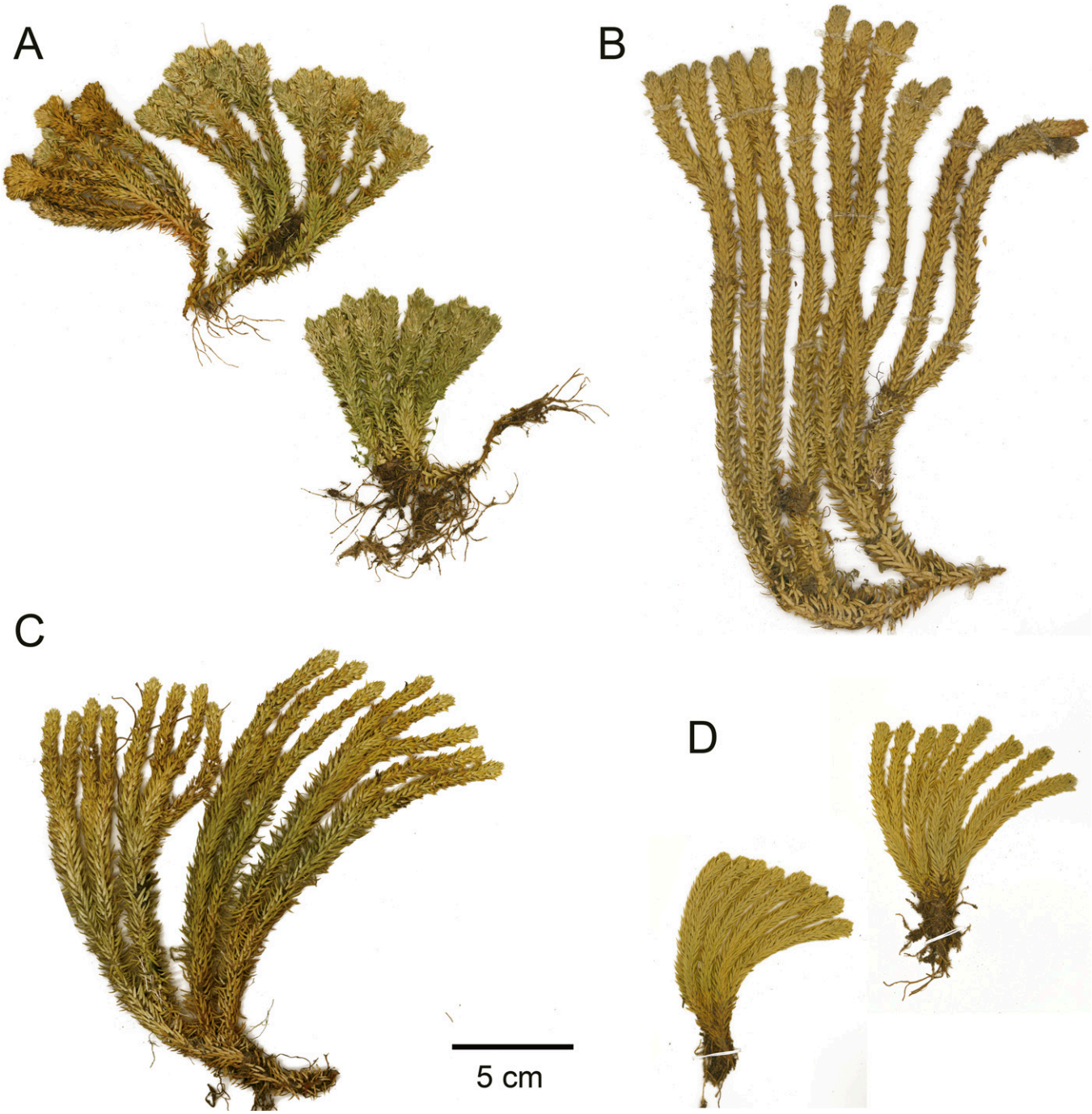

FIG. 1. Gross morphology and variation in *Huperzia continentalis*. A. *Murray et al. 12531* (ALA), St. Matthew Island, Alaska, U. S. A. B. *Abbe & Abbe 3171* (GH), Richmond Gulf, Quebec, Canada. C. *Zika 16970* (WTU, VT), Kagalaska Island, Alaska, U. S. A. D. *Spellenberg & Soreng 5645* (NY), Lake Louise, Alberta, Canada.

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arched lateral leaves. It can be differentiated from both *H. haleakalae* and *H. selago* by its typically lustrous yellowish green to orange brown leaves (vs. non-lustrous, pale green leaves in *H. haleakalae* and non-lustrous dark green leaves in *H. selago*) and its unconfined gemmiphores and gemmae (those of *H. haleakalae* and *H. selago* are confined to a single pseudowhorl at the summit of each zone of annual growth). *Huperzia continentalis* also differs from *H. haleakalae* by having relatively narrower leaves. The new species is closely allied to *H. arctica* (Grossh. ex Tolm.) Sipliv., from which it differs by its larger overall size, less-highly branched appearance, longer and relatively narrower leaves, and larger gemmae.

Etymology—The epithet refers to this species' primarily continental distribution, and serves to distinguish it from *Huperzia haleakalae*, the Hawaiian endemic with which it was previously confused.

Distribution and Habitat—*Huperzia continentalis* is distributed throughout northwestern and northern North America including Greenland, and in northeastern Asia and northwestern Europe. It is much more widely distributed than

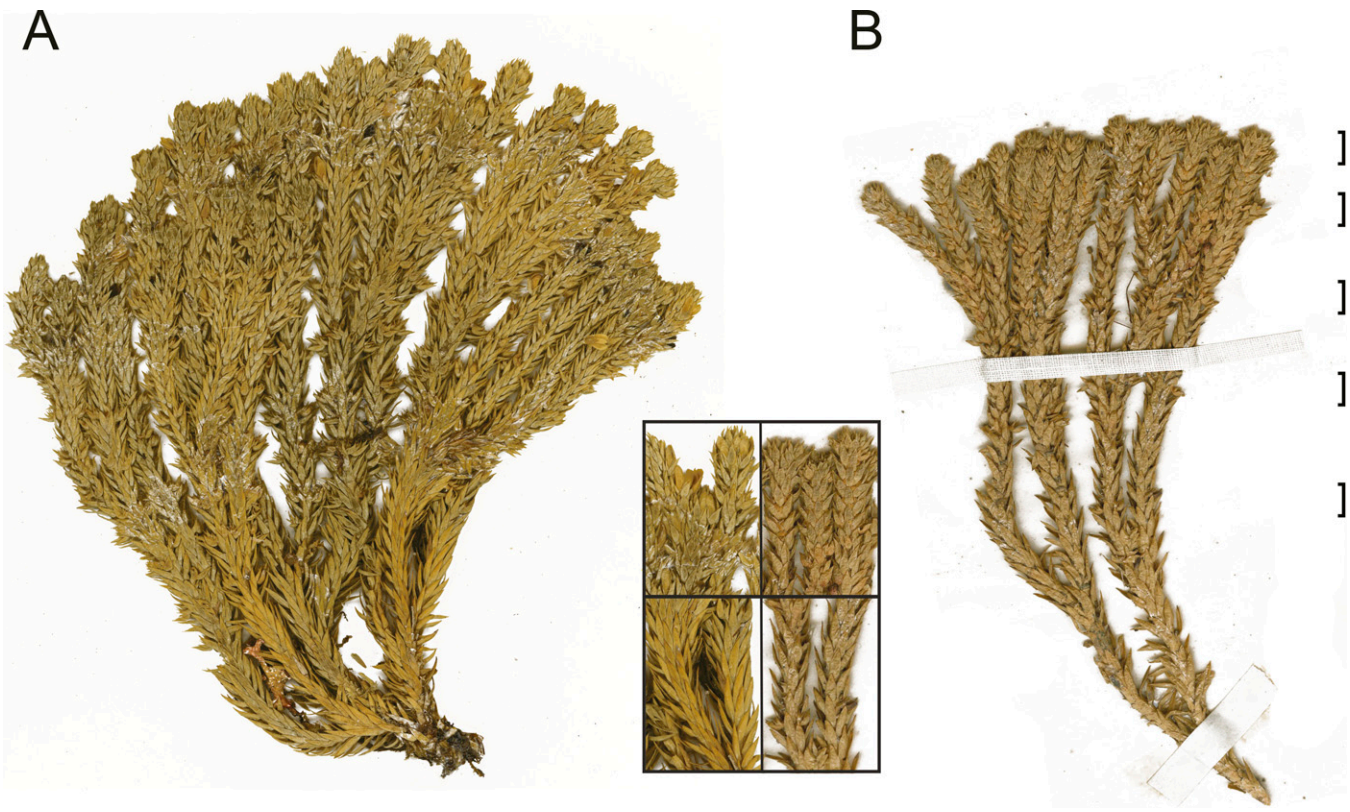

Fig. 2. Morphological comparison of *Huperzia continentalis* (A, *Calder & Gillett 26592* [DAO, WTU]) and *Huperzia haleakalae* (B, *Brackenridge s.n.* [US]). Top pair of insets show gemmiphore distribution and leaf size/morphology at shoot apices, bottom pair of insets show leaf size/morphology in middle portion of shoots. Brackets show the position of pseudowhorls of gemmae on *Huperzia haleakalae*.

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previously recognized (as *H. haleakalae* in Wagner & Beitel 1993; Fig. 4). It is most common in the Rocky Mountains and associated mountain ranges from northern Washington to central Alaska, the Aleutian Island chain, and to the east and south in Montana, Wyoming, and Colorado. In addition, *H. continentalis* occurs across northern Canada, from Yukon to Quebec, and is also known from Greenland, northern Europe, and northeastern Russia. Though we have examined several hundred herbarium specimens representing the *H. selago* complex from Europe and Asia and have only found a few representatives, further examination of material from those regions may extend its range.

The species is typically associated with subalpine and alpine meadows and rocky slopes, but also occurs in mesic tundra in the northern portion of its range. Throughout much of its main range, *Huperzia continentalis* is restricted to moderate to high elevations (1,200–2,400 m) but it also occurs at low elevations, particularly at the northern edge of its distribution.

Representative Specimens Examined—CANADA. Alberta: Banff National Park, ca. 1 km west of Highway 93 ca. 60 mi north of Banff, northeast-facing slopes southeast of Peyto Lake, 2,300 m, 28 Jul 1980, *Spellenberg & Soreng 5645* (NY); Lake Louise, 9 Jul 1925, *Malte & Watson 1056* (GH). British Columbia: Columbia Shuswap, upper Spillimacheen, near 51°30′N, 6,300 ft, 1 Aug 1904, *Heacock 423* (GH); Columbia Shuswap, Seymour Lake, North Monashee, 51°24′N, 118°35′W, 5,100 ft, 31 Jul 1960, *Dodson E32* (UBC); Glacier, Asulkan Valley, 4,100–6,000 ft, 19 Jul 1906, *Brown 5850* (GH); Northern Rockies, foot of Mount St. George at mile 392, Summit Pass, 59°N, 124°W, 5,250 ft, 10 Aug 1962, *Taylor 108/62* (WTU); Northern Rockies, below Mount St. George at mile 393 Alaska Highway, 58°38′′N, 124°42′W, 5,000 + ft, 6 Jul 1960, *Calder & Gillett 26592* (DAO, WTU); Northern Rockies, vicinity of Summit Pass, summit of high alpine moraine, 58°31′N, 124°34′W, 26 Jul 1943, *Raup & Correll 10835* (GH, MICH); Northern Rockies, vicinity of Summit Pass, summit, above timberline, 58°31′N, 124°34′W, 11 Jul 1943, *Raup & Correll 10478* (MICH); Squamish-Lilooet, Garibaldi, near Mimulus Creek, mountain slope, 49°58′N, 123°09′W, 5,500 ft, 28 Jul 1914, *Davidson s.n.* (UBC); Squamish-Lilooet, Garibaldi Park, moist open alpine meadows, 49°48′N, 123°00′W, 4,735 ft, 6 Sep 1960, *Peterson s.n.* (UBC); Squamish-Lilooet, Tenquille Lake area, Crown Mountain, 6,000–6,500 ft, 27 Jul 1960, *Beamish & Vrugtman 60949* (GH; WTU); Strathcona, Castlecrag Mountain, 49°40′N, 125°22′W, 4,000 ft, 26 Jul 1957, *Underhill 484* (WTU); Stikine, Ruby Mountain, west of Ruby Creek, above Surprise Lake, Atlin area, 59°42′N, 133°21′W, 6 Jul 2004, *Lee 1381* (UBC); Stikine, Haines Rd., mile 60, damp valley bottom, 59°30′N, 136°30′W, 800 m, 8 Jul 1956, *Taylor et al. 1191* (UBC); Stikine, Atlin Provincial Park, Teresa Island, 59°26′N, 133°49′W, 5,100 ft, 30 Jul 2001, *Latimer 32* (UBC). Newfoundland: Button Islands, Lacie Island, granitic slopes, 31 Jul 1934, *Potter & Brierly 2013* (GH); Ekontiasuk, Cape Chudleigh, 20–30 Aug 1894, *Schmitt 315* (GH); Northern Peninsula, Little Quirpon, 515 m southwest of seashore road, 51.5765°N, 55.4477°W, 62 m, 6 Aug 2014, *Britton & McIntosh 18729* (VT). Northwest Territories: Mackenzie District, Mackenzie Mountains, 6 miles NE O'Grady Lake, black shale, 63°03′N, 128°55′W, 5,000–5,500 ft, 28 Jul 1967 *Cody 16794* (DAO); Mackenzie District, Mackenzie Mountains, 17 miles W of Little Divide Lake, turfy limestone, stoney tundra slope, 63°17′N, 128°17′W, 5,000 ft, 26 Jul 1967 *Cody 16655* (DAO); Mackenzie District, Mackenzie Mountains, mountains on north side of June Lake, rocky tundra turf, limestone formation, 63°31′N, 128°40′W, 5,500 ft, 1 Aug 1967, *Cody 17185* (DAO); Mackenzie District, Ragged Range, NE side of Glacier Lake, 62°07′N, 127°33′W, 6,500 ft, 12 Jul 1972 *Cody & Brigham 20841* (DAO); Mackenzie District, Mackenzie Mountains, Cirque Lake, high alpine tundra, 63°17.5′N, 130°08′W, 5,000–6,000 ft, 8 Jul 1972 *Cody & Brigham 20569* (DAO); Mackenzie District, Hornaday River, damp loam soil, 16 Jun 1974, *Owen & Larsen 74–4011* (DAO); Mackenzie District, Coppermine, dry rocky areas of tundra, 67°50′N, 115°10′W, 6 Aug 1951, *Findlay 258* (DAO); Mackenzie District, Coppermine, Coronation Gulf, at mouth of Coppermine River, 67°47′N, 115°30′W, 4 Aug 1948, *Shacklette 3281* (MICH); Mackenzie District, Canoe Lake, 31 Jul 1972, *Peterson 21758* (DAO). Nunavut: Baffin Island, southeast Cape Hooper, Tanner Bay, 68°26′N, 66°49′W, 30 Aug 1999, *Elven 3503/99* (ALA); Baffin Island,

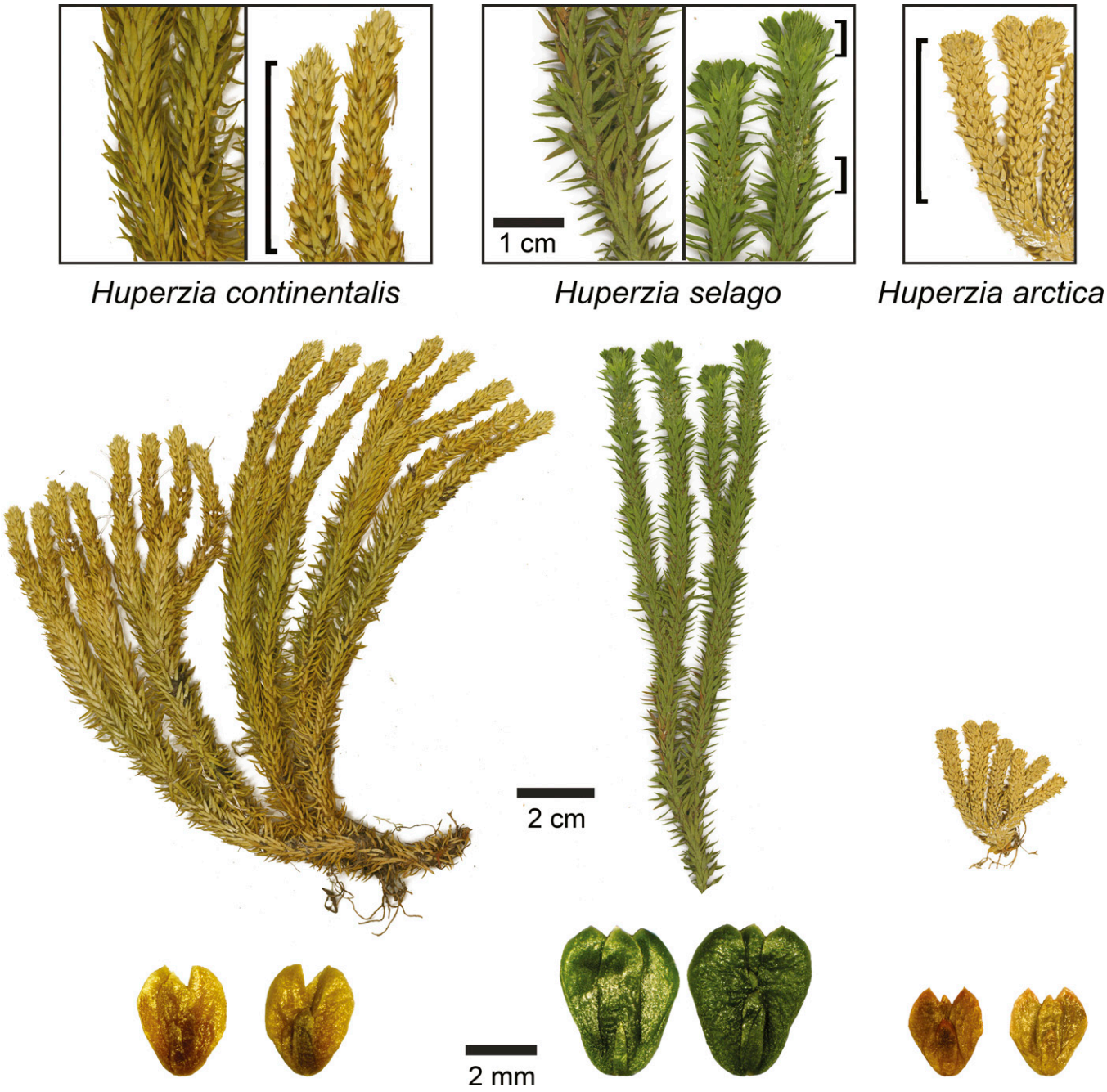

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FIG. 3. Morphological comparison of *Huperzia continentalis* (left; *Zika 16970* [WTU, VT]), *Huperzia selago* (center; *Lee 6715* [MIN]), and *Huperzia arctica* (right; *Bruggemann 60* [DAO]). Top: Leaf morphology and gemmae distribution in middle (left) and distal (right) portions of shoots. Middle: Comparison of plant size, color, and gross morphology. Bottom: Comparison of gemma size and morphology (gemma images reproduced from Gilman and Testo, 2015).

Pangnirtung, Cumberland Gulf, 66°8′N, 65°41′W, 21 Aug 1927, *Malte 118357* (GH); East coast of Coats Island, 62°49′N, 81°50′W, 19 Sep 1930, *Porsild 5865* (GH); Whale Point, N.W. coast, Hudson Bay, Jul 1894, *Comer s.n.* (GH); mainland near Depot Island, N.W. coast, Hudson Bay, 63°55′N, 90°20′W, Jun 1894, *Comer s.n.* (GH); Ukkusiksalik National Park, Wager Bay area, 65°17′N, 89°13′W, 265m, 6 Aug 1984, *Scotter & Zoltai 76140* (DAO); Ukkusiksalik National Park, inland north of Wager Bay, gneiss rock outcrop, xeric mossy heath tundra, 65°52′43″N, 89°26′42″W, 20 Jul 2005, *Tremblay 085–2005* (DAO). Ontario: Kenora, ca. 19 km inland from Hudson Bay coast, ca. 31 km SW of Cape Henrietta Maria, Polar Bear Provincial Park, rocky ridge and adjacent wet tundra, 54°58′N, 82°40′W, 5 Jul 2001, *Oldham & Sutherland 25960* (MICH, NHIC, VT); Kenora, ca. 14 km inland from Hudson Bay coast, ca. 30 km SW of Cape Henrietta Maria, Polar Bear Provincial Park, moist tundra, 55°09′N, 82°40′W, 5 Jul 2001 *Oldham & Sutherland 26034d* (MICH, NHIC, VT); Kenora, ca. 47 km inland from Hudson Bay coast, ca. 69 km SW of Cape Henrietta Maria, Polar Bear Provincial Park, boggy tundra, 54°46′N, 83°10′W, 8 Jul 2001, *Oldham & Sutherland 26154* (MICH, NHIC, OAC); Kenora, ca. 12 km inland from Hudson Bay coast, ca. 30 km SW of Cape Henrietta Maria, Polar Bear Provincial Park, beach ridge and adjacent tundra, 54°57′N, 82°40′W, 6 Jul 2001 *Oldham & Sutherland 26041* (MICH, NHIC). Quebec: Nord-du-Québec, Richmond Gulf, mainland south of Cairn Island, moist pockets and cracks in granite hills, 5 Jul 1939, *Abbe & Abbe 3171* (GH); Nord-du-Québec, Monts de Puvirnituq, cours supérieur de la rivière Déception, près de celle-ci du côte oust, à environ 17.4 km au nord de Kattiniq et 12 km à l'est de Purtuniq, 61°49′41″N, 73°44′55″W, 400 m, 6 Aug 2011, *Tremblay 332–11* (DAO). Saskatchewan: Lake Athabaska, vicinity of Charlot Point, 59°36′N, 109°13′W, 28 June 1935, *Raup 6367* (GH). Yukon: Ogilvie

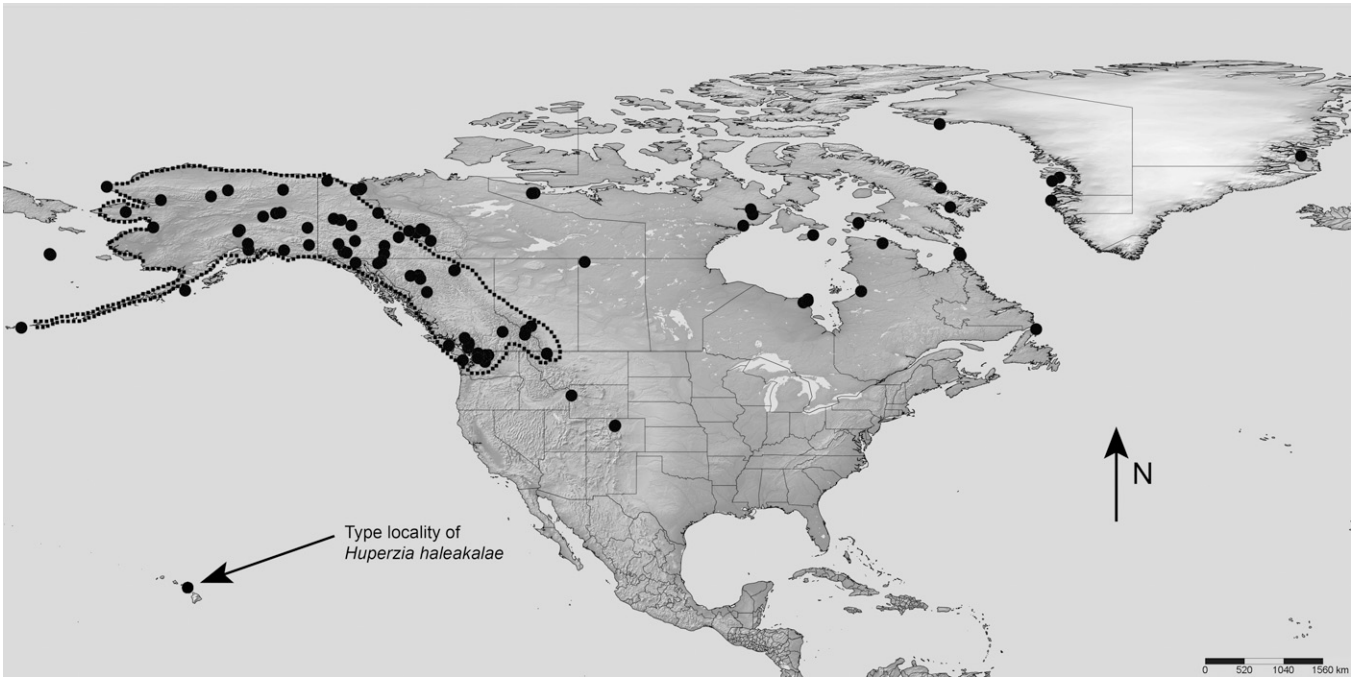

FIG. 4. Distribution of *Huperzia continentalis* in North America. Dots represent collection localities, dashed line represents approximate range of *Huperzia haleakalae* in continental North America according to Wagner and Beitel (1993).

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Mountains, mountain east of mile 50–54, 10 July 1966, *Porsild 175* (GH, WTU); Dawson Quad., Ogilvie Mountains, North Fork Pass, herbaceous-heath slope, 64°36′N, 138°20′W, 1,500 m, 8 Jul 1984, *Parker 1199* (ALA); Ogilvie Mountains, Tombstone Range, Yakamaw Creek watershed east of Angelcomb Peak, 64°36′N, 138°14′W, 5,200 ft, 20–22 Jul 1999, *Cody 36814* (DAO); Ogilvie Mountains, Patrol Range, headwaters of Chandindu River, 64°45′N, 139°06′W, 4,700 ft, 20–22 Jul 1999, *Cody 36576* (DAO); Richardson Mountains, turf by mountain stream, 68°11′N, 136°28′W, 3,500 ft, 13 Jul 1982, *Cody & Ginns 31738* (DAO); Richardson Mountains, moist hummocky turf, 68°22′N, 135°49′W, 3,500 ft, *Cody & Ginns 30497* (DAO); Miller's Ridge, west of Carmacks, hummocky tundra, 62°06′N, 136°34′W, 28 Jun 1980, *Cody 26425* (DAO); Kluane Range, Mt. Desolei east of Kimberley Creek, 60°50′N, 137°57′W, 4,000–5,000 ft, 30 Jul 1980, *Cody & Ginns 28672* (DAO); British Mountains, west of Firth River, broken rocky saddle between mountains, 69°17′N, 139°50′W, 12 Jul 1980, *Cody 27812* (DAO); Mallik Island, south shore, south of Baffin Island, dry *Cassiope* heath, 6 Aug 1970, *Hainault & Norman 5824* (DAO); Snake River Drainage, Popcornfish Lake, moist *Dryas* tundra, 65.4435°N, 133.8083°W, 3255 ft, 6 Jul 2005, *Bennett et al. 05–0234* (UBC); Rose-Lapie River Pass, mile 105 Canol Road, schist mountain east of lake, alpine slopes above timberline, 4,000–6,000 ft, 11 Jun 1944, *Porsild & Breitung 9383* (WTU); Lower Lapie River crossing, mile 132 Canol Road, grassy summit and upper slopes of mountain south of road, 5,600 ft, 26 Jun 1944, *Porsild & Breitung 9898* (WTU); Canol Dome, about 2 km south of Canol Road and 13 km northeast of Johnson's Crossing, vicinity of Alaska Highway, Mile 837, 60°33′N, 133°06′W, 1,400–1,715 m, 30 Jun 1959, *Shetler & Stone 3098* (MICH); Mountain slope south of Haines Road junction, 60°42′N, 137°34′W, 27 Jun 1944, *Harris 12022* (GH); Mountain slopes and summits 4 miles southeast of Ptarmigan Heart, alpine tundra, 61°44′N, 138°32′W, 13 Jul 1948, *Raup et al. 13625* (GH); Sam Lake, moist tundra along east shore, 21 Jun 1974, *Goski & Nagy 74–129* (DAO); Red Mountain, south-facing slopes of shale and chert, 63°96404′N, 136°63612′W, 1,510 m, 27 Jun 2012, *Bennett et al. 12–0080* (BABY, DAO).

GREENLAND. Kujalleq: Northeast Greenland National Park: Kong Oscar's Fjord, delta remnants, 72°14′N, 23°55′W, 1 Aug 1957, *Raup et al. 573* (GH). Qaasuitsup: Disco, Lyngmarken, 29 Jun 1898, *Pedersen s.n.* (GH); Godhavn, Disco Island, 17 Aug 1924, *Robinson 52* (GH); Cape York, 23 Jul 1894, *Wetherill 50* (GH); Egedesminde, *Rink s.n.* (GH). Qeqqata: Holsteinsborg, 3 Jun 1889, *Hartz s.n.* (GH).

NORWAY: Svalbard: Spitzbergen, Green Harbor, Aug 1933, *Rugg s.n.* (GH).

RUSSIA: Chukotka: Anadyr, slopes and coastline west of town, 64°44′N, 177°30′W, 50 m, 4 Jul 1993, *Parker 4215* (ALA); Chukotsk Peninsula, Cape Chaplino, vicinity of Chaplino Hot Springs and Lake Naybak, moist low heath tundra, 64°25′N, 172°30′W, 15 m, 30 Jul 1995, *Parker & Zagrebin 6161* (ALA).

U.S.A. Alaska: Anchorage, Chugach State Park, Eklutna Valley, alpine tundra on north slope, 3,000–3,500 ft, 23 Jun 1984, *Marvin 1541* (NY); Aleutians West, central Aleutian Islands, Kagalaska Island, southeast side of island, steep open slope, near and above pond shore, 51°47.7′N, 176°20.0′W, 40 m, 15 Jun 2002, *Zika 16970* (WTU, VT); Bethel, St. Matthew Island, north end between Seal Point and Glory of Russia Cape, 60°33′N, 172°55′W, 19 Jul 1997, *Murray et al. 12531* (ALA); Denali, McKinley National Park, Sable Pass, 3,400 ft, 29 Jul 1956, *Langenheim 4227* (WTU); Denali, Mount McKinley National Park, northwest slope to summit of Mount Eielson, dry slope in moist tundra, 63°25′N, 150°20′W, 3,500 ft, 23 Jul 1956, *Viereck 1452* (GH); Denali, McKinley National Park, slopes between Copper Mt. & Muldrow, 1,000m, 18 Jul 1928, *Mexia 2115* (MICH); Fairbanks North Star, Steese Highway northeast of Fairbanks, just northeast of Cripple Creek, 24 June 1999, *Gilman 99220* (VT); Kodiak Island, Aghiyuk Island, northeast shore, 56°11.5′N, 156°47.5′W, 410 ft, 1 Jul 2002, *Zika 16995* (WTU); Matanuska-Susitna, Rish Hook Willow Road about 28.0 mi east of the intersections with Rt. 3 north of Willow, alpine tundra, 61°46′07.2″N, 149°19′21.5″W, 3650 ft, 4 Jul 2005, *Goldman 3465* (GH, WTU); Nome, Bendeleben Quad., Seward Peninsula, Lost Jim Lava Flow, 65°33′N, 163°52′W, *Murray et al. 10731A* (ALA); Nome, Seward Peninsula, tundra, Jul 1936, *Jones 8967* (WTU); Nome, Unalakleet Quad., Nulato Hills, South River drainage, 25km southeast of Unalakleet, 63°43′N, 160°35′W, 310 m, 9 Jul 1997, *Parker et al. 7003* (ALA); Nome, St. Lawrence Island, Boxer Bay, alpine rock desert on top of Womyee Mtn., 500 m, 29 Jul 1966, *Young 614* (GH); North Slope, Bering Strait District, Cape Dyer, Drainage of Kipaloq and Angowlik Creeks, snow-bed community, 68°36–40′N, 166°8–15′W, 0–1,000 ft, 16 Jul 1960, *Viereck and Bucknell 4100* (ALA); North Slope, Anaktuvuk Pass, arctic north slope, 2,000 ft, 2 Jul 1949, *Spetzman 1597* (DAO); Northwest Arctic, Selawik Quad., Waring Mountains, vicinity 3 km west of VABM Slam, cobbley ridgetops and heath slopes, 66°58′N, 159°41′W, 300–400 m, 25 Jun 2000, *Parker et al. 9340* (ALA); Southeast Fairbanks, Mount Fairplay, near the road between Chicken and Tok, 5545 ft, 7 Aug 1951, *Scamman 6251* (GH); Valdez-Cordova, Cordova Quad., vicinity of Schwan Glacier terminus, 60°59′N, 145°01′W, 900 m, 15 Aug 1986, *Parker 1931* (ALA); Valdez-Cordova, southeastern Wrangell Mountains, east-facing slopes of Chitistone Pass, 5,900 ft, 8 Jul 1967, *Scott 1684* (MICH); Yukon-Koyukuk, Titus Mountain, northwest of Old John Lake, 2 Aug 1950, *Jordal 3821* (MICH); Yukon-Koyukuk, Twelve Mile Summit, 85.6 miles northeast of Fairbanks, 2982 ft,

10 Jul 1975, *Taylor et al. 19440* (NY); Yukon-Koyukuk, Survey Pass Quad., vicinity of confluence of Alatna and Nahtuk Rivers, alpine mountain slopes, 67°25′N, 153°43′W, 450–600 m, 30 Jun 1973, *Murray 3852* (ALA); Yukon-Koyukuk, Eagle Summit, near Steese Highway, 109 miles north of Fairbanks, 3,880 ft, 23 Jun 1945, *Scamman 3455* (GH); Yukon-Koyukuk, Eagle Summit, near Steese Highway, 109 miles north of Fairbanks, 3,880 ft, Jul 1951, *Scamman 6188* (GH). Colorado: Grand County, Arapaho National Forest, Front Range, Indian Peaks Wilderness, Pawnee Pass/Pawne Lake, 40.0761°N, 105.6354°W, 10,920–12,560 ft, 24 Jul 2003, *Foley 3386* (RM); Larimer County, Estes Park, 11,000 ft, 18 Aug 1906, *Cooper 169* (RM); Larimer County, Estes Park, St. Vrain Mountain, 11,000 ft, 22 Jun 1908, *Cooper 91* (RM). Montana: Glacier County, Glacier National Park, Logan Pass, meadow, 18 Sep 1937, *Barkley 1735* (WTU). Washington: Chelan County, North `Cascades National Park, 1 km west of Heather Pass, subalpine meadow, 1,941 m, 16 Aug 2008, *Bivin 08–35* (WTU); Chelan County, Above Route 20 near milepost 161, between Rainy Pass and Washington Pass, 3 air kilometers north of Blue Lake, 48°31′N, 120°40.9′W, 1,610 m, 3 Sep 2009, *Zika 24646* (WTU); Clallam County, Mt. Olympus National Monument, near Mt. Appleton, arctic-alpine zone, 6,000 ft, 6 Sep 1935, *Jones 8459* (WTU); King County, Cascade Mountains, Stevens Pass, 4,500 ft, 20 Aug 1893, *Sandberg & Leiberg 790* (WTU); Skagit County, North Cascades National Park, Boston Basin, rocky basin below glacier, 48°29′ 48.01041″N, 121°3′47.35594″W, 5,700 ft, 10 Aug 2002, *Legler 48* (WTU); Snohomish County, East side of Devil's Thumb, in rocky bowl below southern point on ridge, above Windom Lake, 48°7′29″N, 121°32′34″W, 1,399 m, 26 Sep 2004, *Legler 2367* (WTU); Whatcom County, Mount Baker National Forest, Twin Sister Range, on rocky slope above Hildebrand Lake, 5,000 ft, 14 Aug 1939, *Muenscher 10231* (WTU); Mount Baker region, Chain Lakes, wet bank, 5,000 ft, 12 Aug 1930, *Thompson 5747* (WTU); Olympic Mountains, meadows, 5,000 ft, Aug 1895, *Piper 2232* (GH). Wyoming: Teton County, Grand Teton National Park and vicinity, Teton Range, in Glacier Gulch, ca. 16 air mi SW of Moran, ca. 6.5 air mi NW of Moose, moist north-facing ledge with alpine tundra, 43.7337°N, 110.7829°W, 9,520 ft, 2 Aug 2006, *Scott 2666* (RM).

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Discussion

As it has previously been recognized, *Huperzia haleakalae* was the most widely distributed *Huperzia* species in North America outside of *H. selago*, and the only member of the genus with a temperate North American-Hawaiian disjunction. Among homosporous lycophytes, the only other species with such a distribution is the pantropical weed *Palhinhaea cernua* (L.) Vasc. & Franco, which has a scattered distribution in the southern United States. The recognition of *H. continentalis* restricts *H. haleakalae* to Hawaii, where it is only known from the type collection. As extensive searches of the type locality have failed to relocate the taxon (Palmer 2003, Vernon and Ranker 2013), it is likely that this species is extinct. The two abortive-spored hybrids from Hawaii that are thought to have *H. haleakalae* as a progenitor (*H.* ×*erubescens* W. H. Wagner non (Brack.) Holub and *H.* ×*medeirosii* Beitel & W. H. Wagner) are rare and appear to persist due to vegetative reproduction via gemmae (Wagner et al. 1999).

If *Huperzia haleakalae* is rediscovered in Hawaii or elsewhere, a number of characters can be used to distinguish it from *H. continentalis* (Fig. 2). *Huperzia haleakalae* was reported as pale green in color in life, whereas most plants of *H. continentalis* are, at least in part, yellowed or golden-brown, both in life and in herbarium specimens (some plants are dark green). Gemmiphore distribution also differs between the two taxa: those of *H. haleakalae* are confined to a single pseudowhorl at the summit of each year's growth, whereas those of *H. continentalis* are distributed continuously. As no gemmae were present on the type collections of *H. haleakalae*, it is unknown how they may differ from those of *H. continentalis*. The leaves of *H. haleakalae* are wider than those of *H. continentalis* in both the proximal (2.2–3.0 vs. 0.7–1.5 mm) and distal (1.8–2.5 vs. 0.7–1.5 mm) regions of the shoots; those of the former are ovate-lanceolate whereas those of the latter species are lanceolate to broadly lanceolate.

From *Huperzia selago*, with which it co-occurs across much of its range and is often confused, *H. continentalis* differs in plant color (typically dark-green in *H. selago*, typically yellowish green or golden-brown in *H. continentalis*), gemmiphore distribution (confined to annual pseudowhorls in *H. selago*, distributed continuously along the shoot axis in *H. continentalis*) as well as the size and shape of their gemmae (Fig. 3). Gemmae of *H. selago* are typically 4.0–4.4 mm long and narrowly obtuse to broadly acute in outline with acute leaf apices, whereas those of *H. continentalis* are 3.0–3.4 mm long and broadly obovate with generally obtuse leaf apices. Identification of specimens that lack gemmae can be difficult in some cases, particularly in plants from northern Canada and Alaska. Many specimens of *H. selago* from these regions are small, yellowed, and have short zones of annual growth, which can make the distribution of gemmiphores appear nearly continuous. This morphology appears to be in response to growth conditions and is part of the considerable variation of *H. selago*, which is badly in need of worldwide study.

The species most similar to *Huperzia continentalis* in North America is *H. arctica*, with which it co-occurs at the northern boundary of its known range, ca. 65–70°N latitude. This taxon was not recognized in Wagner and Beitel's (1993) treatment of North American *Huperzia*, but this name has been used in more recent studies (Elven et al. 2011, Gilman and Testo 2015). We use the name *H. arctica* provisionally here following these recent studies, as study of an image of the type (from Russia) suggests that this name may be misapplied to North American plants and further study is needed. Small plants of *H. continentalis* can be confused with *H. arctica*, though the species consistently differ in a number of characters (Fig. 3). Most plants of *H. continentalis*, including those from far northern localities, are larger than *H. arctica*. Plants of *H. continentalis* from northern Alaska and Yukon are generally 6–9 cm tall, whereas those of *H. arctica* are usually 2–4 cm. *Huperzia continentalis* also differs from *H. arctica* by the size, presentation, and color of its leaves and the size and shape of its gemmae. In *H. continentalis*, leaves in the proximal portion of the shoots are typically 5–7 mm long and 0.7–1.5 mm wide, and those in the distal portion of the shoots are 2.5–5 mm long and 0.7–1.5 mm wide. In *H. arctica*, leaves in the proximal portion of the shoots are typically 2.5–3.5 mm long and 0.7–1.0 mm wide, and those in the distal portion of the shoots are 2.0–2.5 mm long and 0.5–1 mm wide. The leaves of *H. continentalis* are generally straight-ascending to appressed, whereas those of *H. arctica* are arched-ascending. In the northern portion of its range, *H. continentalis* tends to have older shoots that are orange-yellow, whereas those of *H. arctica* are mostly stramineous. As discussed by Gilman and Testo (2015) the gemmae of *H. continentalis* (treated therein as *H. haleakalae*) are consistently larger (3.0–3.5 × 2.9–3.4 mm) than those of *H. arctica* (2.4–2.7 × 2.1–2.3 mm) and typically have unequally arched lateral leaves with obtuse apices, whereas those of *H. arctica* are typically symmetrically arched and have acute apices. The distinction of these taxa is further supported by the fact that these morphological differences are evident on sheets of mixed collections (e.g. *Taylor et al. 19440*, NY).

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The range of *Huperzia continentalis* overlaps with two other species in North America, *H. miyoshiana* (Makino) Ching, and *H. occidentalis* (Clute) Kartesz & Gandhi. These are morphologically distinct species that are generally confined to conifer forests in the Pacific Northwest. In the rare situations where these taxa do co-occur with *H. continentalis*, both can be distinguished by the distribution of their gemmiphores, which are confined to a single pseudowhorl at the summit (*H. occidentalis*) or at most, distal half (*H. miyoshiana*), of each zone of annual growth. They also differ from *H. continentalis* conspicuously in leaf shape (leaves linear to narrowly lanceolate in *H. miyoshiana*, oblanceolate and serrate in *H. occidentalis*, and lanceolate to broadly lanceolate in *H. continentalis*) as well as the size and morphology of their gemmae (Gilman and Testo 2015).

Prior to the recognition of eastern North American *Huperzia appalachiana* Beitel & Mickel (=*H. appressa* (Desv.) Á. Löve & D. Löve) and western North American *Huperzia haleakalae* (= *H. continentalis*), all plants with unconfined gemmiphore distributions and appressed leaves were treated as *Lycopodium selago* L. var. *appressum* Desv. (Beitel 1979; Cody and Britton 1989). This practice caused considerable taxonomic confusion, which was mostly resolved by the aforementioned revisions to the group. *Huperzia continentalis* and *H. appressa* should not be mistaken for each other as they are not known to occur in the same regions, and differ in characters of branch width, leaf dimorphism, and gemmae shape. However, both Beitel and Mickel (1992) and Wagner and Beitel (1993) may have caused confusion by incorrectly attributing *H. appressa* (as *H. appalachiana*) to Greenland and stating that it was the only *Huperzia* species present there. In fact, *H. appressa* appears to be absent from Greenland, but *H. arctica*, *H. continentalis*, and *H. selago* all occur there (Elven et al. 2011; Gilman and Testo 2015). *Huperzia appressa* is restricted to non-calcareous cliffs, outcrops, and talus slopes from southeastern Newfoundland and Quebec to Georgia and its range does not overlap with that of *H. continentalis*.

A critical advancement in the study of *Huperzia* systematics was the identification of abortive-spored hybrids among members of the *Huperzia selago* complex (Beitel and Mickel 1992), as their presence is strong evidence that these morphologically similar taxa are divergent at the species level. Recognition of *H. continentalis* at the species level, in turn, is supported by its formation of hybrids with other taxa. Wagner and Beitel (1993) reported hybrids between it (as *H. haleakalae*) with *H. miyoshiana* and *H. occidentalis*, but did not cite any hybrid specimens in their treatment. We have identified hybrids between *H. continentalis* and those two taxa, as well as with *H. selago* and *H. arctica*. Like all *Huperzia* hybrids, these plants are morphologically intermediate to their progenitors and possess polymorphic spores.

Huperzia continentalis × *H. miyoshiana* is known from maritime habitats in southern Alaska (*DeLapp and Duffy 93–10*, ALA), the Aleutian Islands (*Dick 63*, ALA; *Mason 6009*, ALA; *Harms 5277*, GH; *Soule 502*, WTU), and western Washington (*Suksdorf 2809*, GH; *Thompson 9983*, GH), where the parental species grow in close proximity to each other. This hybrid resembles *H. miyoshiana* but is a coarser plant with unconfined gemmiphores and narrowly lanceolate (instead of linear) leaves.

We have encountered specimens of *H. continentalis* × *H. occidentalis* from British Columbia (*Butters & Holway 484*, GH), southeastern Alaska (*Looff X16*, GH), and Montana (*MaGuire 453*, GH, *Williams s.n.*, GH); these plants have confined gemmiphores and (mostly) oblanceolate leaves like *H. occidentalis* but lack the patent leaves and annual growth constrictions characteristic of that species.

Huperzia continentalis × *H. selago* is currently known from Alaska (*Eyerdam 765*, NY; *Wiggins 13850*, GH; *Scamman 35*, GH; *Scamman 5172*, GH), Alberta (*Malte and Watson 1055*, GH), British Columbia (*Raup & Correll* 10478, GH; Thompson *14433*, GH), northern Northwest Territories, (*Oldenburg 43–617*, GH) and western Greenland (*Porsild & Porsild s.n.*, GH). These specimens are rather robust, with loosely appressed, gradually dimorphic leaves and gemmiphores that are mostly but not completely confined to pseudowhorls at the summit of annual growth zones.

Huperzia continentalis × *H. arctica* is known to us by a single specimen from eastern Russia (*Solstad & Elven 05/0539*, ALA); this specimen resembles a robust *H. arctica* but has longer leaves and larger gemmae than are found in that species. This hybrid is likely to be prevalent in regions where *H. continentalis* and *H. arctica* co-occur, given their similar habitat preferences in those areas.

This study contributes to the efforts of earlier researchers who sought to resolve taxonomic confusion among North American *Huperzia* (e.g. Wilson 1932, Waterway 1986, Beitel and Mickel 1992, Wagner and Beitel 1993, Haines 2003). Examination of *H. continentalis* across its range largely resolves the question posed by Wagner and Beitel (1993) about the identity of collections from central and northwestern Canada and further informs the circumscription of the widespread and poorly understood *H. selago* complex. Additional study, particularly with the inclusion of molecular data, should provide insight into remaining problems in the group, including the status of diminutive plants from the American arctic that are currently treated as *Huperzia arctica*.

Lectotypification of Lycopodium haleakalae—During examination of material for this study, we encountered three sheets of the type collection (*Brackenridge s.n.*, BISH, K, P, US). These sheets had been annotated as *Huperzia haleakalae* and verified as type specimens of *Lycopodium haleakalae* Brack. by Beitel in 1983, at which time he annotated the sheet at US as the holotype and those at BISH and P as isotypes (he apparently did not see the specimen at K). However, no type designation was ever published, and the sheets have remained syntypes. We lectotypify the species here:

Huperzia haleakalae (Brack.) Holub, Folia Geobot. Phytotax. 20: 73. 1985. *Urostachys haleakalae* (Brack.) Herter ex Nessel; *Lycopodium selago* L. var. *haleakalae* (Brack.) Warb.; *Lycopodium haleakalae* Brack. in Wilkes, U.S. Expl. Exped. 16: 321. 1854.—LECTOTYPE designated here: U. S. A. Hawaii, E. Maui, banks of crater, [20°42′N, 156°15′W], Mar 1840, *Brackenridge s.n.* (US!; isolectotypes: BISH, image!, K, image!, P, image!).

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