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Use of Gemma Characters to Identify North American *Huperzia* (Lycopodiaceae)

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Abstract.—All North American firmosses (*Huperzia*: Lycopodiaceae) produce highly specialized vegetative propagules known as gemmae. Though gemmae are of interest to morphologists, they have been used only rarely as aids in identification. To improve understanding of their variation among North American species and to explore their systematic utility we surveyed gemmae of all species in North America north of Mexico and provide measurements, comparative descriptions, and images. Several characters of the gemmae, including their size, shape, and morphology of the leaves that comprise them vary considerably across the species studied and can be used to distinguish species. A dichotomous key based on gemma characters is provided, and several notable range expansions are reported. We anticipate this study will help resolve confusion regarding the identity of North American *Huperzia* species, particularly among the taxa in the northern and western regions of the continent, which remain poorly understood.

Key Words.—Firmosses, morphology, gemmae, bulbils, lycophytes

The temperate firmoss genus *Huperzia* Bernh. is characterized in part by their terrestrial growth and production of gemmae and is sister to the tropical, non-gemmiferous firmosses, *Phlegmariurus* Holub (Wikström and Kenrick, 1997, 2000). Identification of North American species continues to pose a significant challenge (Wagner and Beitel, 1993; Haines 2003), which is based on their simple body plan and paucity of morphological structures, and intraspecific variation. This, in turn, results in an incomplete understanding of species' ranges. There has been considerable difficulty in identification of specimens, especially those from northern and western parts of the continent since the most recent revision of the North American species in the Flora of North America (Wagner and Beitel, 1993). That revision was, essentially, an unfinished work because its primary author, Beitel, passed away before he had completed field work and other studies in his doctoral program. Although the most comprehensive treatment of North American firmosses to date, it failed to resolve some uncertainties. As a result, more recent North American authors (Tzvelev, 2003; Aiken *et al.*, 2007; Dignard, 2014) have subsequently recognized taxa and distributions in North America inconsistent with those

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of Wagner and Beitel (1993), relying instead on European and Asian authorities (e.g. Rothmaler, 1993; Zhang and Iwatsuki, 2013).

Although it was stated by Wagner and Beitel (1993) that characters of the gemma, including "size, overall outlines, and gemma leaf shapes" were diagnostic, they published only limited data, and did not discuss or illustrate gemma outlines or leaf shapes. Various authors have used the size and general shape of lateral leaves, along with the shape of their apices, to discriminate species pairs on a case-by-case basis (Butters & Abbe, 1953; Waterway, 1986; Beitel and Mickel, 1992; Brunton *et al.*, 1992) or in regional treatments (Wagner *et al.*, 1999; Palmer, 2003; Haines, 2003). However, to date, no comprehensive treatment has been available. Our goals in this paper are to survey the morphology of gemmae of all North American species and to demonstrate their utility for identification. We provide images, morphometrics, and written descriptions.

Groundplan description.—Firmoss gemmae are vegetative reproductive structures distributed along or near the summit of the annual shoot growth increments. Smith (1920) provided a general description which, for clarity in our descriptions of individual taxa, we enlarge here.

Development of an individual gemma begins with the formation of a specialized shoot known as a gemmiphore. This shoot comprises six leaves, decussately arrayed in three pairs that, together, form a cupule in the center of which forms the gemma. The proximal gemmiphore leaf is enlarged and forms a rigid platform on which the mature gemma is horizontally positioned, its broadest surface presented upward. When fully grown, an abscission layer is formed between the gemmiphore and gemma. The gemma is readily detached and falls or is projected from the gemmiphore, sometimes by the force of raindrops (Victorin, 1925).

The basic structure of the gemma is relatively simple (Fig. 1). Like the gemmiphore, the gemma is a modified branch that comprises six leaves inserted on a very short axis and, distal to these, a minute terminal shoot with spirally inserted leaves (Bierhorst, 1971; Testo and Gerdes, 2015). Stevenson (1976) found that the six outer leaves are in a low parastichous spiral but, for our purposes, it is sufficient and preferable to describe them as three opposite pairs, each perpendicular to the next pair. From the outside, only five are normally visible although, rarely, the distal tip of the sixth leaf may also be visible. The terminal shoot is enclosed by the six outer leaves and is always hidden from view. When a detached gemma falls to the ground, the terminal shoot begins to grow to form the main axis of a new, independent plant.

A mature gemma is normally positioned horizontally relative to the axis of the main shoot on which it occurs. Thus the gemmae leaves are here described as if viewed from above or below and the terms "abaxial" and "adaxial" are used in relation to the axis of the gemma.

The leaves of the proximal pair, hereafter referred to as the "upper" and "lower" leaves (Fig. 1) are appressed to the other leaves so only their abaxial surfaces are visible. They are conspicuously shorter than those of the middle

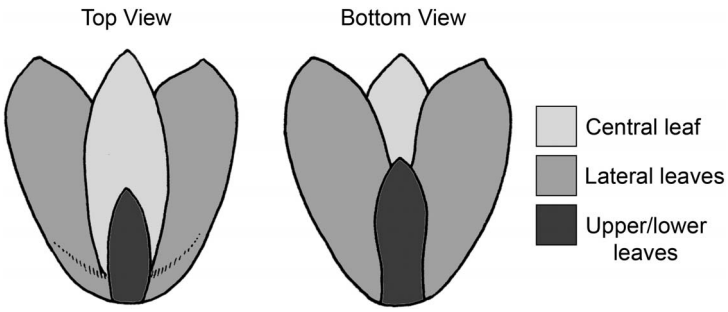

FIG. 1. Generalized diagram of the structure of a *Huperzia* gemma. Hatched lines indicate the twisted base of the lateral leaves. The lower leaf of the distal pair is not shown.

and distal pairs. They are of different size and shape relative to each other and vary from oblong to narrowly elongate-triangulate or lanceolate.

The middle pair, hereafter referred to as the "lateral" leaves (Fig. 1) are the largest and most conspicuous of the gemma leaves. They are presented in a different rank than the other gemma leaf pairs and twisted 90° into the plane of the other two pairs and are arrayed so that their adaxial surfaces are visible when viewed from above. The lateral leaves are asymmetrically elliptical to obovate with their outer margins typically more strongly curved than their inner margins. Their apices vary from obtuse to acute, and in some species they possess a mucronulate tip.

The distal pair is aligned in the same rank as the proximal leaf pair. Typically, only the upper leaf of this pair is visible. It is referred to hereafter as the "central" leaf (Fig. 1) because it is presented in the center of the gemma above and between the two lateral leaves. Its shape varies from broadly oblong to broadly pandurate, with an acute or obtuse apex. Because the lower leaf of the distal pair is usually hidden, it is not readily available for observation and will not be discussed further.

MATERIALS AND METHODS

In their Flora of North America treatment, Wagner and Beitel (1993) recognized seven species of *Huperzia* in continental North America north of Mexico. We also recognize *Huperzia arctica* (Gross. ex Tolm.) Sipl., a circumarctic species not mentioned in their treatment; and following Haines (2003) we use the older name *Huperzia appressa* (Desv.) Á. Löve & D. Löve for the taxon treated by Wagner and Beitel (1993) as *Huperzia appalachiana* Mickel & Beitel. For our study, species determinations were based on comparison to type material and to descriptions by Tolmachev (1960), Wagner and Beitel (1993), and Haines (2003).

We examined 1103 gemmae from 150 specimens (Appendix 1) from the following herbaria: ALA, GH, NY, VT and WTU. Our sampling approach incorporated specimens from across each species' range in North America and included approximately equivalent representations of both gemmae and speci-

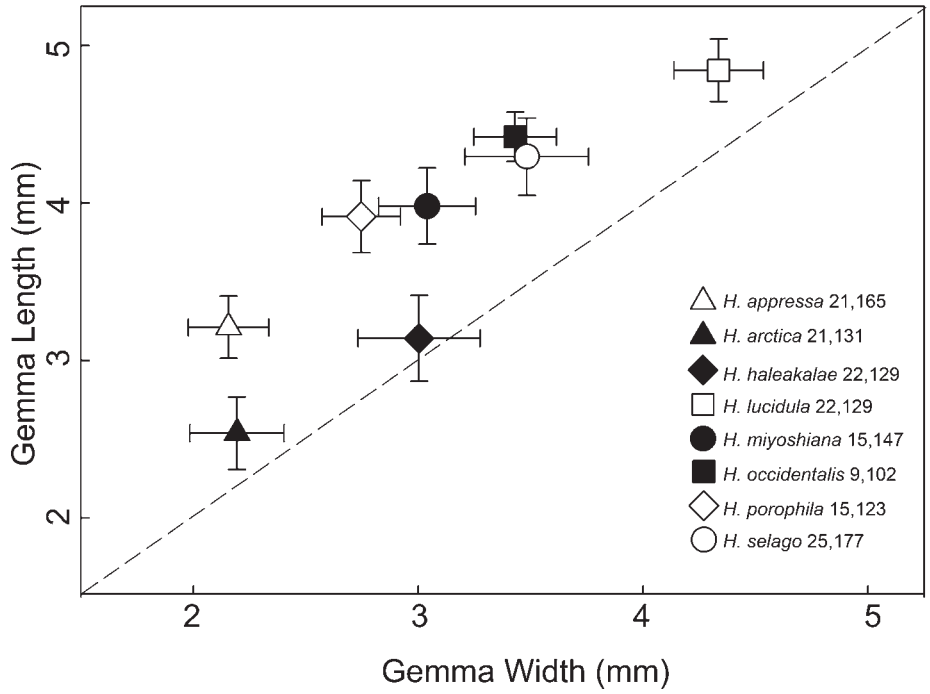

FIG. 2. Scatter plot showing overall length and width of North American *Huperzia* gemmae. Error bars represent ± 1 standard deviation. The dashed line marks a 1:1 length:width ratio.

mens across the species studied. The number of specimens examined per species ranged from 9 for *H. occidentalis* to 25 for *H. selago*; the number of gemmae examined per species ranged from 102 for *H. occidentalis* to 177 for *H. selago*. In general, 6–12 gemmae from each specimen were obtained from the specimen's damage packet or removed from the plant using a dissecting probe; for some specimens, fewer gemmae were available for measurement. Care was taken to use fully formed gemmae, but to exclude over-mature gemmae, which sometimes possess widely flared lateral leaves. For each gemma, we measured the following: 1) the length of the gemma along its longest axis; 2) the width of the gemma at its widest point; 3) the length of the upper leaf and 4) the length of the lower leaf.

To evaluate the effects of drying on gemma shape and size, the length and width of 12–20 gemmae from representative collections of from two individuals belonging to three species that span most of the range of observed gemma sizes were measured prior to and after pressing and drying. These were: *H. appressa* (*Testo 345*, VT, 20 gemmae; *Corwin s.n.*, VT, 13 gemmae), *H. lucidula* (*Testo 346*, VT, 18 gemmae; *Testo 403*, VT, 14 gemmae) and *H. selago* (*Testo 330*, VT, 15 gemmae; *Testo 330A*, VT, 13 gemmae).

All measurements were obtained at 40× magnification under a Leica MZ8 stereoscope fitted with a SPOT Insight Firewire 2.0 camera (Spot Imaging Solutions, Sterling Heights, MI, USA). Angles of leaf apices were measured on

composite drawings made by stacking 8–10 images of individual gemmae from each species using Adobe Photoshop CS2 software and tracing averaged leaf outlines. Composite images of whole gemmae were obtained by stacking 15–20 images taken at 20× magnification.

Results and Discussion

Sizes.—Overall gemma size differed across species (Fig. 2). Gemma lengths (±SD) ranged from 2.54 ± 0.26mm for *H. arctica* to 4.84 ± 0.24mm for *H. lucidula*; gemma widths ranged from 2.16 ± 0.18mm for *H. appressa* to 4.34 ± 0.20mm for *H. lucidula*.

Upper and lower leaf lengths are given in the individual species description. In general, upper leaves range from 0.3× to 0.5× the length of the entire gemma, with the relatively shortest belonging to *H. lucidula* and *H. miyoshiana* and the relatively longest to *H. arctica* and *H. selago*. The lower leaf is always longer than the upper leaf, ranging from 0.4× to 0.6× as long as the gemmae, with the relatively shortest belonging to *H. lucidula*, *H. miyoshiana* and *H. occidentalis* and the relatively longest belonging to *H. selago*.

Shapes.—Gemma shapes range from narrowly elliptic (*H. appressa* and *H. porophila*) to broadly obovate and nearly circular (*H. haleakalae*, *H. arctica*). Other shapes include oblong (*H. miyoshiana*) to broadly obpyriform (*H. occidentalis*) and obcampanulate (*H. lucidula, H. selago*).

Upper leaf shapes range from narrowly lanceolate (*H. lucidula*, *H. selago*), to oblong (*H. haleakalae*) and narrowly elliptic (*H. arctica*).

Lateral leaves are distinctively shaped for some species, particularly the very broad, somewhat squarish ones of *H. lucidula* (Fig. 3). Those of *H. haleakalae* and *H. arctica* are strongly and evenly curved along their outer margins, while their inner margins are nearly straight, resulting in a nearly circular appearance of the gemma as a whole. Angles of the lateral leaf apices range from narrowly acute to slightly obtuse, with mucronulate tips being found in several species, most notably *H. lucidula* and *H. selago*.

Shapes of the central leaf vary from oblong to narrowly elliptic, with an obtuse to acute apex.

The lower leaves are mostly uniform in their relative length, but vary in shape similarly to the upper leaf, ranging from narrowly lanceolate (*H. porophila*) to oblong (*H. appressa*, *H. selago*) to slightly pandurate (*H. haleakalae*, *H. miyoshiana*).

Descriptions of gemmae of North American Huperzia.—

Huperzia appressa.—(Fig. 3A, I) **Outline** biconvex to narrowly obovate, broadest above middle at 0.75–0.85× of overall length; length [2.7] 3.0–3.4 [3.7] mm; width [1.7] 2.0–2.3 [2.5] mm. **Upper leaf** ca. 0.4×–0.45× as long as gemma, slightly pandurate, narrowing distally to an elongate, acute apex, margins meeting at ca. 50°. **Central leaf** lanceolate to oblong, with an acute apex at ca. 75°. **Lateral leaves** relatively narrow, outer margins straight from base to near middle, then curving to acute apices, margins meeting at ca. 60°.

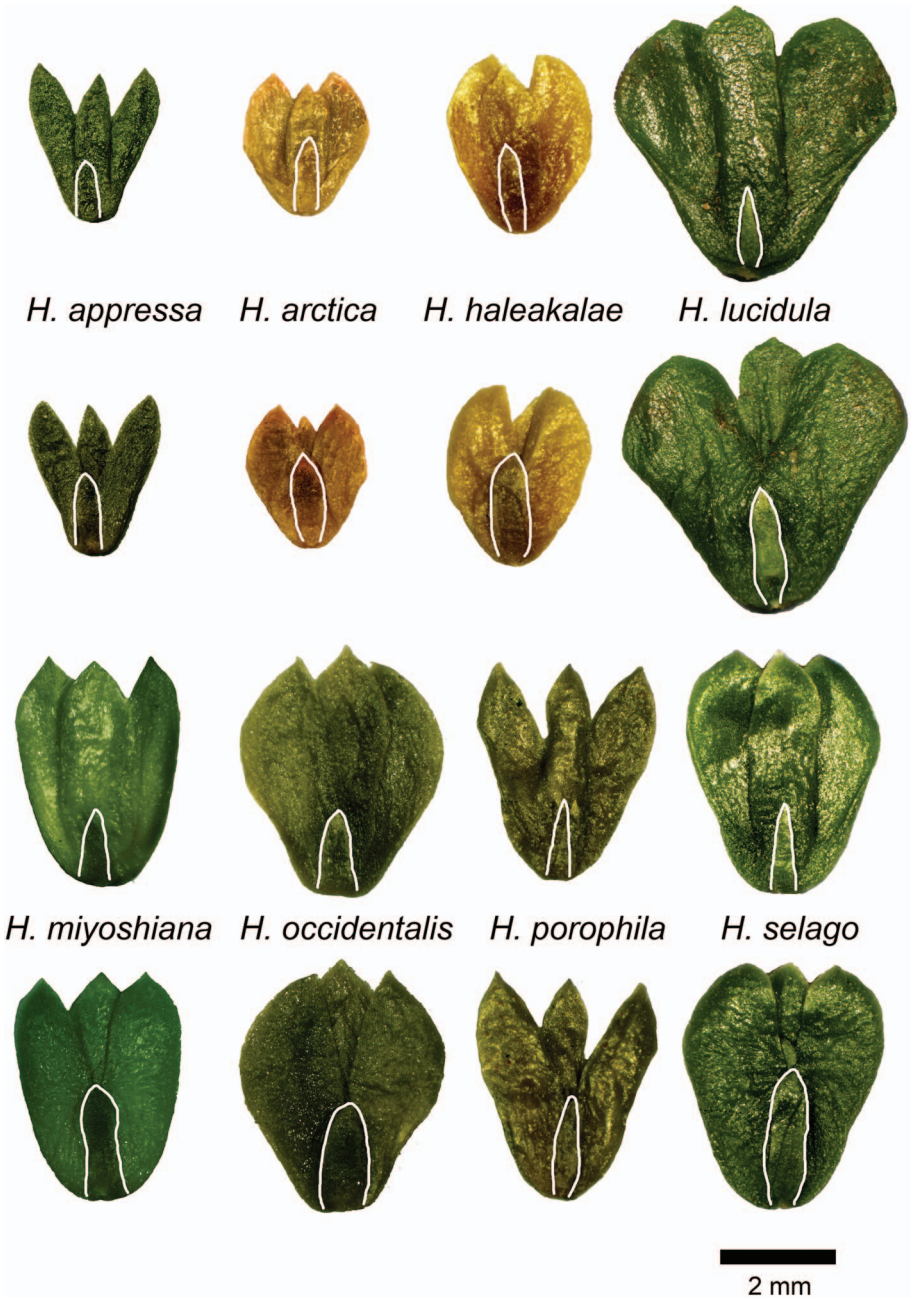

FIG. 3. Gemmae of North American *Huperzia*. Images above species names are adaxial surface views, corresponding images below species names are abaxial surface views. White lines outline the shape of the upper and lower leaves.

Lower leaf ca. 0.5× as long as gemma, oblong with a broadly acute apex with an angle of ca. 80°–85°.

Huperzia appressa has the narrowest gemmae of all North American species, often appearing lens-shaped. The lateral leaves are relatively thin compared to those of other eastern North American species. Gemmae of this species are produced continuously during the growing season, unlike those of other species in its range, which are clustered near the tip of each year's growth.

Huperzia arctica.—(Fig. 3B, J) **Outline** broadly obovate to nearly circular, broadest above middle at 0.65–0.75× of overall length; length [2.1] 2.4–2.7 [3.0] mm; width [1.9] 2.1–2.3 [2.5] mm. **Upper leaf** ca. 0.5× as long as gemma, narrowly elliptic, apex acute, margins meeting at ca. 35°. **Central** leaf narrowly biconvex, apex acute, margins meeting at ca. 75°. **Lateral leaves** very broadly obovate, rounded towards obtuse apices, margins meeting at ca. 95°. **Lower leaf** ca. 0.6× as long as gemma, oblong to broadly spatulate with a broadly acute apex, margins meeting at ca. 85°

As in *H. appressa* and *H. haleakalae*, gemmae of *H. arctica* are often distributed along the length of the short annual shoot increments. Some authors (Tolmachev, 1960; Dignard, 2014) have noted that gemmae are particularly abundant in this taxon. The outside edges of the lateral gemmae leaves often curve toward the adaxial surface, producing a cupped appearance. Like the entire plant, the gemmae are yellow in color and lustrous.

Huperzia haleakalae.—(Fig. 3C, K) **Outline** very broadly obovate to nearly circular, broadest above the middle at 0.55–0.60× of overall length; length [2.7] 3.0–3.2 [3.4] mm; width [2.6] 2.9–3.1 [3.2] mm. **Upper leaf** ca. 0.45× as long as gemma, oblong, narrowing abruptly to apex, margins meeting at ca. 90°. **Central leaf** biconvex, narrowing to an acute tip, margins meeting at ca. 65°. **Lateral leaves** nearly semi-circular; outer margins evenly curved to apices, margins meeting at ca 90°. **Lower leaf** ca 0.50–0.60× as long as gemma, biconvex or slightly pandurate with a ± broadly spathulate tip; apex acute, margins meeting at ca. 75°.

Gemmae of *H. haleakalae* are notably rounded due to strong curvature of the lateral leaf margins; this shape and their relatively small size easily distinguish this species from *H. miyoshiana*, and *H. selago,* with which it overlaps in much of its range. They are yellow in color and lustrous in appearance, similar to those of *H. arctica*. This shared color, along with the similarity in gemma shape and their distribution all along the shoot, may imply a close relationship between these species.

Huperzia lucidula.—(Fig. 3D, L) **Outline** broadly obcampanulate, flaring to a broad distal portion, broadest above the middle at ca. 0.75–0.8× of overall length; length [4.4] 4.7–4.9 [5.4] mm; width [3.8] 4.2–4.5 [4.6]. **Upper leaf** ca. 0.25×–0.3× as long as gemma, narrowly lanceolate, narrowing to an elongate, acuminate apex, margins meeting at ca. 15°–20°. **Central leaf** broadly oblong, margins nearly parallel to near tip, then curving abruptly to a mucronulate, broadly obtuse apex, margins meeting at ca. 140°–150°. **Lateral leaves** broadly widening from bases to near distal end, apices mucronulate,

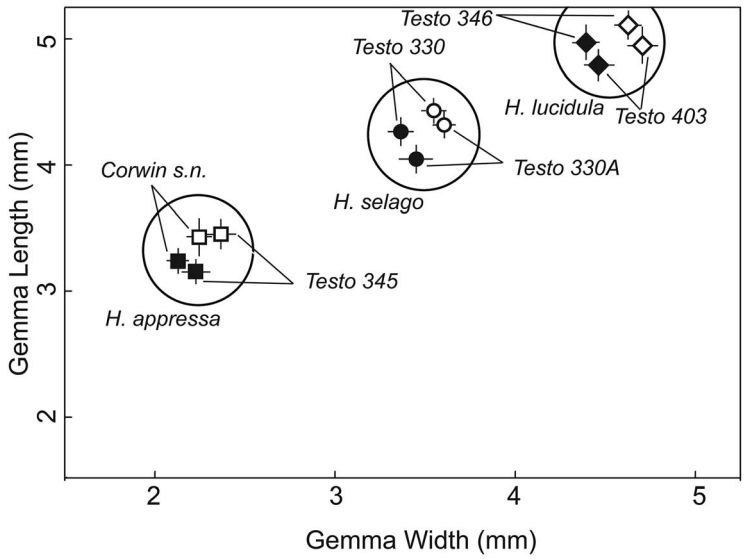

FIG. 4. Measurements of fresh and dried gemmae from *Huperzia appressa* (squares), *Huperzia lucidula* (diamonds), and *Huperzia selago* (circles). Open symbols represent fresh gemma measurements, closed symbols represent dried gemma measurements. Error bars represent ± 1 standard deviation.

very broadly obtuse, margins meeting at ca. 165°–180°. **Lower leaf** ca. 0.45× as long as gemma, narrowly oblong, slightly pandurate, apex rounded to acute.

Huperzia lucidula possesses the largest gemmae of any North American *Huperzia*. The very broad outline, mucronulate lateral leaf apices, and small, narrow upper leaf is distinctive. Its gemmae are dark green, a color shared by *H. porophila*, which is an allopolyploid thought to be derived in part from this species (Waterway, 1986; Wagner and Beitel, 1993).

Huperzia miyoshiana.—(Fig. 3E, M) **Outline** broadly oblong-elliptical, broadest above middle at 0.65–0.75× of overall length; length [3.5] 3.8–4.1 [4.3] mm; width [2.7] 2.9–3.1 [3.4] mm. **Upper leaf** ca. 0.3× as long as gemma, narrowly lenticular with an acute apex, margins meeting at ca. 60°. **Central leaf** biconvex, with an acute apex; margins meeting at ca. 70°. **Lateral leaves** broadly elliptic with acute apices, forming an angle of ca. 70°. **Lower leaf** ca. 0.45× as long as gemma, often slightly pandurate; apex broadly acute, margins meeting at ca. 80°.

Huperzia miyoshiana is easily distinguished from other species in its range by the sea-green color of its gemmae, which are produced in a series of 2–3 (rarely to 10) pseudowhorls at the summit of the year's growth and frequently give the shoot apex a 'bulbous' appearance. The lateral leaves of its gemmae are relatively thin, giving them a less fleshy appearance than those of other western North American species.

Huperzia occidentalis.—(Fig. 3F, N) **Outline** broadly obovate to obpyriform, broadest at 0.60–0.70× of overall length; length [4.0] 4.2–4.5 [4.6] mm; width

[3.1] 3.3–3.5 [3.6] mm. **Upper leaf** ca. 0.4× as long as gemma, broadly lanceolate, narrowed to an acute apex, margins meeting at ca. 65°. **Central leaf** spathulate with an acute to acuminate tip, margins meeting at ca. 80°. **Lateral leaves** with outer margins widely bowed out distally and evenly rounded to acute apices; margins meeting at ca. 85°. **Lower leaf** ca. 0.45× as long as gemma, broadly elliptic, narrowing to an acute tip, margins meeting at ca. 75°.

The narrowly elliptic lower leaf, large size, and broadly obovate to obpyriform shape of the gemma distinguish *H. occidentalis* from other species in its range. In growth habit and overall aspect this species resembles *H. lucidula* from eastern North America and has historically been treated as both a form and variety of this species. Differences in gemma size and shape and especially the shape of the upper leaf (lenticular in *H. occidentalis*, narrowly lanceolate in *H. lucidula*) support the distinctiveness of this Pacific Northwest and Rocky Mountain native.

Huperzia porophila.—(Fig. 3G, O) **Outline** narrowly elliptic to narrowly obovate, broadest above middle at 0.65–0.75× of overall length; length [3.5] 3.8–4.1 [4.2] mm; width [2.4] 2.6–2.9 [3.1] mm. **Upper leaf** ca. 0.35× as long as gemma, narrowly lanceolate, narrowly acute, margins meeting at ca. 25°. **Central** leaf narrowly oblong, acute, margins meeting at ca. 30°. **Lateral leaves** oblong-elliptic; tips acute, margins meeting at ca. 30°; inner margins (exposed above the central leaf) nearly straight. **Lower leaf** ca. 0.4× as long as gemmae, lanceolate, narrowly acute.

Gemmae of this species are intermediate in shape between those of its progenitors, *H. lucidula* and *H. appressa* (Wagner and Beitel, 1993). The oblong-elliptic lateral leaves and relatively narrow overall shape support the hypothesis of *H. appressa* parentage and the narrow lower and upper leaves and the gemma's dark green color are consistent with *H. lucidula* parentage for this species.

Huperzia selago.—(Fig. 3H, P) **Outline** narrowly obcampanulate, broadest towards the apex at 0.8× of overall length; length [3.6] 4.0–4.4 [4.6] mm; width [3.0] 3.3–3.6 [3.8] mm. **Upper leaf** ca. 0.45× as long as gemma, lanceolate; apex slightly obtuse, margins meeting at ca. 105°. **Central leaf** broadly oblong, with an obtuse, mucronulate apex; margins meeting at ca. 140°–150°. **Lateral leaves** narrowly obovate; margins slightly convex; tips obtuse to broadly acute, margins meeting at ca. 120°. **Lower leaf** ca. 0.6× as long as gemma, oblong; apex obtuse, margins meeting at ca. 95°.

Numerous infraspecific taxa and segregates of *H. selago* have been described by various authors over the years (e.g., Nessel, 1939) as taxonomists have struggled with its wide distribution and variability. Though several lines of evidence suggest that this taxon is still poorly known in North America, gemmae from specimens that we have examined — which span the known range of the species in North America and include new regional records — display a consistent and distinct morphology. The relatively long, oblong outer leaves, distally broadened lateral leaves, and bright green color are distinctive. Overall, the shape of *H. selago* gemmae is quite different from other species with which it is confused in North America, notably *H. appressa*

and *H. haleakalae*. Additionally, production of gemmae in this species is confined to one or two pseudowhorls at the summit of the year's growth, not all along the shoot as in those species.

Comparison of fresh and dried Huperzia *gemmae*.—For the three *Huperzia* species for which we compared fresh and dried gemmae, we found a consistent pattern of 5–15% reduction in both length and width (Fig. 4). Relative proportions and shapes of gemma leaves were indistinguishable between fresh and dried material for all species examined. Although we did not attempt to quantify color of fresh vs. dried gemmae, it was evident that no discoloration occurred during the drying process. Though the descriptions and key provided here are based on dried material, they can be used on fresh material if the size differences are accounted for. It should be noted that some gemmae on a plant can be disfigured during the process of pressing and drying; this is readily evident upon inspection. Like any herbarium material, gemma color can fade with age and exposure to light; such color changes are usually similar across all parts of the plant. Caution should be used when evaluating gemma color on old or otherwise discolored material.

Key to North American *Huperzia* Emphasizing Gemma Characters

Note: measurements are taken from dried specimens. Gemmae of herbarium specimens are 5–15% smaller in all dimensions than those of living plants.

1. Gemmae distributed throughout the length of the annual shoot increment (if gemmae are not present throughout, inspect for gemmiphores . . . . . 2.
   2. Gemma 3.0–3.4 × 2.0–2.3mm; shape biconvex to obovate; color medium to dark green; plants of eastern North America . . . . . *H. appressa*
   2. Gemma 2.0–3.2 × 2.1–3.1mm; shape rounded; color yellowish and glossy; plants of northern and western North America . . . . . 3.
      3. Gemmae mostly <3.0mm long; plants mostly of alpine meadows and talus slopes. . . . . *H. haleakalae*
      3. Gemmae mostly >3.0mm long; plants of tundra . . . . . *H. arctica*
1. Gemmae distributed near the tip of the annual shoot increment in 1–3 [–4] pseudowhorls; not throughout the length of the annual shoot increment . . . . . 4.
   4. Plants of forests and shaded rock outcrops or overhangs in eastern North America; gemmae broadly obcampanulate or narrowly elliptic. . . . . 5.
      5. Gemmae 4.7–4.9 × 4.2–4.5mm; broadly obcampanulate, nearly as wide as long; upper leaf narrowly lanceolate; lateral and central leaves broadly obtuse with mucronulate tips; plants of forests . . . . . *H. lucidula*
      5. Gemmae 3.8–4.1 × 2.6–2.9mm; obovate, 1.5× long as wide; upper leaf narrowly lanceolate; lateral and central leaves acute; plants of rock outcrops and overhangs . . . . . *H. porophila*
   4. Plants of forests, wetlands, and alpine meadows in western North America or widely distributed but generally not of eastern forests or shaded rock outcrops or overhangs (except some *H. selago*); gemmae not broadly obcampanulate nor narrowly elliptic. . . . . 6.

6. Gemmae broadly obovate to rounded; lower outer leaf broadly convex; plants of shaded forests in the Pacific Northwest . . . . . *H. occidentalis*
6. Gemmae oblong or obovate; lower outer leaf not broadly convex; plants of cliffs, wet areas and alpine meadows . . . . . 7.
   7. Gemma color deep green to bright green; shape obovate; upper leaf ca. 0.45× as long as gemma; central leaf broadly strap-shaped; lower leaf oblong . . . . *H. selago*
   7. Gemma color sea-green; shape oblong to slightly oblong-obovate; upper leaf ca. 0.3× as long as gemma; central leaf broadly biconvex; lower leaf pandurate . . . . . *H. miyoshiana*

Conclusions.—The simple body plan of *Huperzia* presents fewer systematically useful morphological characters than most plant groups, a challenge that has been manifested in long-standing and largely unresolved debate regarding both species and generic boundaries (Nessel, 1939; Ollgaard, 1987, 1992; Wagner and Beitel, 1992; Haines, 2003). To distinguish species and generate phylogenetic hypotheses, taxonomists working on the group have incorporated evidence from diverse datasets, including spore morphology (Wilce, 1972; Tryon and Lugardon, 1991), spore abortion (Beitel and Mickel 1992; Wagner and Beitel 1993), gametophyte morphology (Bruce, 1976), secondary metabolite production (Pedersen and Øllgaard, 1982), and sporangium anatomy (Wilce, 1965; Øllgaard, 1975). Here, we demonstrate that the gemmae of North American *Huperzia* provide ample characters for differentiating species and suggest that the same characters will prove useful elsewhere. Phylogenetic relationships among *Huperzia* species remain too poorly understood to explore the utility of gemma characters beyond identifying species and supporting hypotheses of hybrid origin, but affinities between some species (e.g. *H. arctica* and *H. haleakalae*) are indicated by gemma morphology.

Another factor that has confounded taxonomic resolution among North American *Huperzia* is the prevalence of interspecific hybrids, which can become locally abundant as a result of asexual reproduction. Wagner and Beitel (1993) commented extensively on the challenges presented by hybrids, which they described as "extremely common" and indicated were the source of considerable confusion experienced by North American students of the genus. Though describing gemma morphology of hybrids was not the goal of our study, we did encounter a number of sterile hybrids among the specimens we examined; these plants exhibited gemma characters intermediate to those of their putative parents. Similarly, the gemmae of the allopolyploid *H. porophila* are intermediate in size and shape to *H. lucidula* and *H. appressa* (Fig. 3), supporting the hybrid origin proposed for this species by Wagner and Beitel (1993) and opposing that of Waterway (1986), who suggested involvement of *H. selago* instead of *H. appressa*. With this pattern of intermediacy in mind, we suggest that plants possessing gemmae intermediate in size and shape to the descriptions provided here should be examined for abortive spores and other signs of hybridity, such as intermediate leaf shape and stomate distribution.

Though it is not the goal of this paper to report on ranges or reach broad taxonomic conclusions for North American *Huperzia* species, and although our sample size was limited in scope, nevertheless we encountered several noteworthy specimens. First, we identified a specimen of *H. miyoshiana* (*Calder and Taylor 23305,* GH) collected at Tilt Cove, in eastern Newfoundland. This is just the second known locality for *H. miyoshiana* in eastern North America (Brunton *et al*., 1992) and extends the species' range eastward approximately 170 km. Second, although Wagner and Beitel (1993) reported that, "Plants from Greenland formerly identified as *Huperzia selago* are *H. appalachiana*," and all *Huperzia* specimens from Greenland should be referred to *H. appalachiana* (= *H. appressa)*, we have encountered multiple specimens from southern Greenland that are clearly *H. selago*. During our studies we identified several specimens of *H. arctica*, a species not mentioned by Wagner and Beitel (1993) from northern Greenland. We also encountered specimens of *H. selago* from British Columbia, northern Labrador, and the western United States, all of which are beyond the range reported for this species by Wagner and Beitel (1993). In addition, we report two significant expansions of the known range of *H. haleakalae*, which in continental North America is known from the Pacific Northwest with several disjunct populations in central Rocky Mountain states. One specimen (*Raup 6367*, GH) was from the northern shore of Lake Athabaska in Saskatchewan; the other (*Abbe and Abbe 3171*, GH), from Richmond Gulf in northern Quebec, extends the range of *H. haleakalae* eastward by approximately 3000km. Other specimens not studied here suggest that the range of *H. haleakalae* may extend even further than our study indicates (A. Haines, personal communication) and the taxonomic status of this species (type from Hawaii) is being revisited. These new records highlight the need for further studies of gemma morphology and other characters in an effort to improve our understanding of species boundaries and distributions among North American *Huperzia*. To address these needs, we are currently working toward a revision of the genus in North America.

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APPENDIX 1. Material Examined

Huperzia appressa (Desv.) Á. Löve & D. Löve

CANADA. Ontario: Thunder Bay Dist., Near SW end of Thompson Island, *Abbe and Bierhorst 5204* (VT). S of Highway 61, 15 mi. E of Pigeon River, *Abbe and Bierhorst 5121* (VT).

U.S.A. Maine: Piscataquis Co., Mt. Katahdin, "shaded cliffs," *Fernald s.n.* (VT). Baxter State Park, Mt. Katahdin, "at timberline in moist spots," *Milstead 1094* (VT). Minnesota: Lake Co., Superior National Forest, 9.2 miles NNW of Isabella, prominent rock outcrop *Gerdes 5397* (MN). Superior National Forest, 9.2 miles NNW of Isabella, *Gerdes 5489* (MN). Superior National Forest, 9.2 miles NNW of Isabella, *Gerdes 5505* (MN). Superior National Forest, 9.2 miles NNW of Isabella, *Gerdes 5506* (MN). New Hampshire: Coos Co., Mt. Washington, *Flynn s.n.* (VT). Lion's Head Trail, Mt. Washington, *Hill 624* (VT). Grafton Co., Franconia, summit of Mt. Lafayette, *Anon. s.n.* (VT). New York: Essex Co., Northern sector of plateau of Mt. Skylight, *Pruski 3550* (NY). Franklin Co., Algonquin Mountain, *Cook 738* (VT). North Carolina: Mitchell Co., Roan Mountain, *Vasey s.n.* (VT). Yancey Co., summit of Mt. Mitchell, *Hill 38364* (VT). Vermont: Chittenden Co., Underhill, Mt. Mansfield, *Zika 4722* (VT). Underhill, summit of Mt. Mansfield, *Testo 345* (VT). Mt. Mansfield, *Pringle s.n.* (VT). Lamoille Co., Cambridge, Smuggler's Notch, *Zika 4749* (VT). Orleans Co., Lowell, Haystack Mountain, *Charette 2233* (VT). Washington Co., Duxbury, summit of Camel's Hump, *Blanchard s.n.* (VT).

Huperzia arctica (Gross. *ex* Tolm.) Sipliv.

CANADA. Ontario: Kenora Dist., Winisk, Hudson Bay Lowlands, west of James Bay, *Lundsden s.n.* (NY). Nunavut: Baffin Reg., Frobisher Bay, Baffin Island, *Senn and Calder 4032* (GH, VT). Baffin Island, Southeast Cape Hooper, Tanner Bay, *Elven 3503/99* (ALA). Keewatin Reg., Cape Fullerton, Hudson's Bay, *Macoun s.n.* (GH). Kitikmeot Reg., Ukkusiksalit Nat'l. Park, Walker Bay, *Tremblay 85-2005* (GH).

GREENLAND. Qaasuitsup, Disko Island, Lyngmarken, *Pedersen s.n.* (GH). Cape York, *Wetherill 50* (GH). Disko Island, Godhavn, *Krumlein s.n.* (GH). Disko Island, *Porsild s.n.* (GH). Harvard Island, Inglefield Gulf, *Angel 36*, (NY). Egedesminde, *Rink s.n.* (GH). Grenville Bay, Region of North Star Bay, *Ekblaw 29* (GH). Northeast Greenland Nat'l. Park, W coast of Cape Hedlund, Kempe Fjord, *Seidenfaden 472* (GH). Near Mestersvig, Kong Oscar's Fjord, *Raup 222* (GH). Sermersoog, Liverpool Land, S side of Hurry Island, Kalkdel Inlet, *Sørensen s.n.* (GH).

U.S.A. Alaska: Arctic Reg., Kotzebue, Kotzebue Sound, *Scamman 3950* (GH). Far North Reg., Flaxman Island, near Bullen Point, *Keller* 1232 (ALA). West side of Jago River, *Cantlon and Gillis 57-626* (ALA). Bering Strait District, Cape Dyer, drainage of Kipaloq and Angowlik creeks, *Viereck 4100* (ALA). Philip Smith Mountains, Uyamitquaq Creek and vicinity, *Batten 85-337* (ALA). Southcentral Reg., 13 mi. west of Paxson on Denali Road, *Harms 4192* (ALA).

Huperzia haleakalae (Brack.) Holub

CANADA. British Columbia: Columbia-Shuswap Dist., Glacier Nat'l. Park, Asulkan Valley, *Brown 585a* (GH; mixed sheet with *H. occidentalis, Brown 585b*). Northern Rockies Dist., Below Mt. St. George, Mile 393 Alaska Hwy., *Calder and Gillett 26592* (WTU). Quebec: Nunavik, Richmond Gulf, S of Cairn Island, "moist pockets and crack in granite hills," *Abbe and Abbe 3171* (GH). Saskatchewan: Northern Reg., Vicinity of Charlot Pt., Lake Athabaska, *Raup 6367* (GH; mixed sheet with *H. selago, Raup and Abbe 4591*). Yukon: North Yukon, Tombstone Nat'l. Park, Ogilvie Mountains, mountain E of mi. 50-54, *Porsild 175* (WTU). Ogilvie Mountains, North Fork Pass, *Parker 1199* (ALA).

U.S.A. Alaska: Arctic Reg., Seward Peninsula, Nome, *Neville Jones 8967* (WTU; mixed sheet with *H. selago, Thompson 14443*). Far North Reg., Waring Mountains, vicinity 3km west of VABM Slam, *Parker 9340* (ALA). Survey Pass, vicinity of Altna and Nahtuk rivers, *Murray 3852* (ALA). Interior Reg., Along Porcupine River, *Turner s.n.* (VT). NE of Cripple Creek, Steese Hwy. NE of Fairbanks, *Gilman 99220* (VT). Denali National Park and Preserve, NW slope to summit of Mt. Eielson, *Viereck 1452* (GH). Southcentral Reg., Matanuska-Susitna Borough, Hatcher Pass Rd., *Goldman 3465* (VT). Vicinity of Schwan Glacier terminus, *Parker 1931* (ALA). Wrangell-St. Elias Park & Preserve, Euchre Mountain, *Bennett and Loomis 03-806* (ALA). Southwestern Reg., Southeastern Kagalaska Island, "steep open slope, near and above pond shore," *Zika 16970* (VT, WTU). Saint Matthew Island, *Ward and Ward 26* (ALA). Bering Sea Region, Saint Matthew Island, *Murray 12531* (ALA). Nulato Hills, 25km southeast of Unalakleet, *Parker 7003* (ALA). Washington: Chelan Co., North Cascades, 3 air km N of Blue Lake, between Rainy Pass and Washington Pass, *Zika 24646* (VT, WTU). Clallam Co., Olympic Mountains, "meadows," *Piper 2232* (GH). Skagit Co., North Cascades Nat'l. Park, 1 air km S of Easy Pass, *Zika 18862* (WTU).

Huperzia lucidula (Michx.) Trev.

CANADA. Quebec: L'Estrie Reg., Comté de Compton, tourbiere de Johnville, *Guevremont 236* (VT).

U.S.A. Connecticut: Hartford Co., Farmington, Rattlesnake Mountain, *Hill 19779* (VT). Tolland Co., Mansfield, W of Mansfield City and Crane Hill Rds., *Pfeiffer 1285* (VT). Illinois: Winnebago Co., Near Fountaindale, *Bebb s.n.* (VT). Maine: Aroostook Co., Perham, Hanford Siding, *Seymour 23220* (VT). Maryland: Garrett Co., Grantsville, Crab Run Road, NW of intersection with River Road, *Hill 9539* (VT). Michigan: Houghton Co., T54N, R33W, Sec. 6, *Parmelee 2028* (VT). Minnesota: Cook Co., NE of Lutsen, "base of steep igneous rock cliff," *Brooks 2963* (VT). Superior National Forest, south of the Royal River and 0.32 miles SE of John Lake, *Gerdes 5944* (MN). Lake Co., Superior National Forest, approximately 5.74 miles NNW of Ely, *Gerdes 5707* (MN). Superior National Forest, approximately 9.6 miles north of Isabella, *Gerdes 6460* (MN). Superior National Forest, approximately 20.73 miles NW of Isabella, *Gerdes 6381* (MN). New York: Tompkins Co., Danby, Lake Cayuga, Michigan Hollow

Swamp, *Schuster s.n.* (VT). Pennsylvania: Indiana Co., White's Woods, 1 mi. NW of Indiana, *Chiesa s.n.* (VT). Vermont: Caledonia Co., Peacham, *Gilman 93001* (VT). Chittenden Co., Underhill, Mt. Mansfield, Sunset Ridge Trail, *Testo 346* (VT). Franklin Co., Fletcher, woods near Metcalf Pond, *Countryman 1133* (VT). Lamoille Co., Cambridge, E side of Smuggler's Notch, Mt. Mansfield, *Zika 4149* (VT). Cambridge, E of VT State Rt. 108, *Charette 2837* (VT). Rutland Co., Mount Tabor, Long Trail, *Seymour 24418* (VT). Tinmouth, *Carpenter s.n.* (VT). Washington Co., Worcester, moist woods, Worcester Pond, *Seymour 27729* (VT).

Huperzia miyoshiana (Makino) Ching

CANADA. British Columbia: Columbia-Shuswap Dist., Victor Lake Provincial Park, ca. 11 mi. W of Revelstoke, *Hitchcock and Martin 7574* (WTU). Queen Charlotte Islands, W coast of Graham Island, mountain near head of Shields Bay, *Calder and Taylor 23305* (GH). Newfoundland and Labrador: East Reg., North shores of Notre Dame Bay, Tilt Cove, "turfy, gravelly and ledgy crests, Castle Rock," *Fernald and Wiegand 4350* (GH).

U.S.A. Alaska: Southcentral Reg., Eleanor Island, Prince William Sound, east side of Northwest Bay, *Lewis s.n.* (ALA). Southeastern Reg., Juneau, *Scamman 1089* (GH). Near Juneau, Windfall Lake, *Anderson 6157* (GH). Prince of Wales Island, Hollis vicinity, Harris River, *Little 306* (VT). Tongass Nat'l. Forest, NE side of Port Armstrong, Baranoff Island, *Muller 4624* (WTU). Dall Island, Thunder Mountain, *Muller 5517* (ALA). Coronation Island, Egg Harbor, *Neiland 1133* (ALA). Wrangell-St. Elias National Park & Preserve, Black Glacier Creek, *Loomis 1558* (ALA). Southwestern Reg., SE Kagalaska Island, "steep open slope, near and above pond shore," *Zika 16970* (VT, WTU). Washington: Snohomish Co., Cascade Mountains, Martin Creek Trail, *Legler 68* (WTU). Mount Dickerman, *Thompson s.n.* (GH). Perry Creek trail, near Big Four Inn, *Thompson 14529* (NY).

Huperzia occidentalis (Clute) Kartesz & Gandhi

CANADA. British Columbia: Columbia-Shuswap Dist.: Glacier Nat'l. Park, Asulkan Valley, *Brown 585b* (GH; mixed sheet with *H. haleakalae, Brown 585a*).

U.S.A. Alaska: Southeastern Reg., Baranof Island, southeast end near Port Alexander, *Muller 5386* (ALA). Washington: Jefferson Co., Olympic Nat'l. Forest, 2km from trailhead to Lena Lake, *Testo s.n.* (VT). King Co., Near Snoqualmie Pass, "open rocky talus slopes," *Thompson 8918* (WTU). Pend Oreille Co., Near Roosevelt Grove of Ancient Cedars, above Granite Falls, *Zika 25077* (WTU). Snohomish Co., Cascade Mountains, Martin Creek Trail, *Legler 69* (WTU). Stevens Co.: Deer Creek, E of Kettle River, *Gilman 96189* (VT). Whatcom Co., 2 air mi. E of Beebe Mountain, Route 20 at East Creek trailhead, *Zika 25739* (WTU). Mt. Baker – Snoqualmie Nat'l. Forest, 1 air mi. NNE of Lake Wiseman, Elbow Lake Trail, *Zika 18978* (VT, WTU).

Huperzia porophila (F. E. Lloyd & Underw.) Holub

U.S.A. Iowa: Allamakee Co. Franklin, 96N 5W, Sect. 15, *Hartley s.n.* (GH). Indiana: Crawford Co., 1 mi. East of Taswell, *Deam 22376* (GH). 3 mi. W of

Fredonia, S of State Hwy., *Deam 44615* (GH). Minnesota: Cook Co., Superior National Forest, Royal River Corridor, approximately 0.07 miles south of the Boundary Waters Canoe Area Wilderness, *Gerdes 5924* (MN). Superior National Forest, Royal River Corridor, approximately 0.07 miles south of the Boundary Waters Canoe Area Wilderness, *Gerdes 5925* (MN). Boundary Waters Canoe Area Wilderness, rugged forested terrain northeast of Brule Lake, *Lee 5141* (MN). Lake Co., Superior National Forest, 9.27 miles NNW of Isabella, *Gerdes 5395* (MN). Superior National Forest, 9.27 miles NNW of Isabella, *Gerdes 5396* (MN). Missouri: Madison Co., Mine La Motte, *Palmer 31591* (GH). Ohio: Fairfield Co., Near Sugar Grove, *Jennings and Kellerman s.n.* (GH). Hocking Co., Near Logan, Hocking Hills State Park, sandstone cliff, *Testo s.n.* (VT). Unknown locality: *Dutton s.n.* (VT). Tennessee: Morgan Co., Rugby, *Svenson s.n.* (GH). Virginia: Lee Co., Vicinity of Rose Hill, sandstone cliffs, *Carr 890* (GH).West Virginia: Upshur Co., Near Carter, Natural Bridge of Laurel Fork, *Goodwin s.n.* (GH).

Huperzia selago (L.) Bernh. ex Schrank & Mart.

CANADA. Alberta: Peace River Dist., North shore of Lake Athabaska, Sand Point, *Raup and Abbe 4591* (GH; mixed sheet with *H. haleakalae, Raup 6367*). British Columbia: Kootenay Dist., Kokanee Glacier Provincial Park, "moist slopes," *Thompson 14443* (WTU; mixed sheet with *H. haleakalae, Neville Jones 8967)*. Newfoundland and Labrador: Labrador, N. Labrador, Ungava Bay, *Turner 663* (GH). E. Labrador, Battle Island, Battle Harbour, *Potter and Brierly s.n.* (GH). W. Labrador, "Betechewan," *Abbe s.n.*(GH). Nova Scotia: Victoria Co., 3 mi. W of Little River, shaded ledge, *Smith 22105* (VT). Nunavut: Kitikmeot Reg., Coppermine, "on rock ledges," *Oldenburg 43-617* (GH). Quebec: Gaspé Co., River St. Anne Des Monts, calcareous cliffs, *Fernald and Collins 152* (NY, VT).

GREENLAND. Qaasuitsup: Disko Island, ca. Neria, *Eugenius s.n.* (GH). Egedesminde, *Simmons 108* (GH).

U.S.A Alaska: Far North Reg., Schwatka Mountains, Reed Hot Springs, Reed River Vally, *Parker 13820* (ALA). Southeastern Reg., Ketchikan area, above town on Deer Mountain, *Neiland 791* (ALA). Annette Island, near top of Yellow Hill, *Stensvold 7918* (ALA). Minnesota: Cook Co., Boundary Waters Canoe Area Wilderness, 24 miles northwest of Grand Marais, *Lee 5310* (MN). Lake Co., Superior National Forest, 9.2 miles NNW of Isabella, *Gerdes 5508* (MN). Spuerior National Forest, approximately 10 miles east of Babbitt, *Gerdes 5359* (MN). St. Louis Co., Superior National Forest, Steep Lake, approximately 12.36 miles ENE of Crane Lake, *Gerdes 6939* (MN). Montana: Flathead Co., Glacier Nat'l. Park, 1 mi. S of Akokala Lake, Numa Ridge Fen, *Lesica 11044* (WTU). Ravalli Co., Along streamlet in deep cut, between Sheafman Pass and Fred Burr Creek, *Lackschewitz 2404* (NY). New Hampshire: Grafton Co., Beaver Brook, Mt. Moosilauke, *Copeland s.n.* (NY). New York: Essex Co., On rock in partial shade, Avalanche Lake, *Copeland 1412* (NY). Vermont: Caledonia Co., Peacham, S side of Peacham Pond, *Gilman s.n.* (VT). Lamoille Co., Cambridge, Smuggler's Notch, *Jones s.n.* (VT). Eden, Belvidere Mountain, old asbestos mine pit, *Testo 330* (VT). Johnson, *Grout s.n.* (VT).