An unusual form of Huperzia selago (Lycopodiaceae) and its implications for gemma homology in the genus

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Shorter Notes

An unusual form of *Huperzia selago* (Lycopodiaceae) and its implications for gemma homology in the genus.—Uniquely among lycophytes, members of the genus *Huperzia* (Lycopodiaceae) are characterized by the presence of asexual propagules borne along the shoot axis. These are highly organized structures consisting of a base, known as the gemmiphore, that is six-leaved and persistent, and an apical portion known as the gemma. This latter portion comprises six decussately arranged, food-storing leaves enclosing a minute terminal shoot. This apical portion disperses by abscission from the gemmiphore. These gemmiphore-gemmae structures (hereafter referred to simply as ''gemmae'') are distributed along the plant's main shoots and are thought to be dispersed by rain or wind. Gemmae are important in forming and maintaining *Huperzia* populations and contribute to the commonness of interspecific hybrids, which lack viable spores (Wagner and Beitel, *in* Flora of North America. Editorial Committee, eds. 1993+ *Flora of North America North of Mexico*. New York and Oxford. 2:20–21. 1993; Reutter, Amer. Fern J. 77:50–57. 1987).

Although the morphology and function of gemmae have been featured in studies of *Huperzia* taxonomy, systematics, and ecology, researchers have not reached a consensus about their homology. Citing their single vascular bundle and position in the plant's normal phyllotaxy, several authors (Hegelmaier, Bot. Zeit. 30:775–851. 1872; Smith, Bot. Gaz. 69:426–437. 1920) have suggested that they are homologues of leaves. In contrast, other authors have suggested that they are homologues of shoots because of their meristem organization and ability to produce lateral microphyll-like structures (Campbell, The Structure and Development of Mosses and Ferns (Archegoniatae):499–500. 1905; Stevenson, Bot J. Linn. Soc. 72:81–100. 1976). This lack of consensus is reflected in the terms used to refer to the structures in literature, including ''gemmiferous branchlets'' (Wagner and Beitel, 1993), ''a bud…and a stipe'' (Wang *et al.*, Acta Bot. Yunnanica 29:521–526. 2007) and ''bulbils'' (Zhang and Iwatsuki, *in Flora* of China. Wu, Z., Raven, P.H. & Hong, D. (eds.) vol. 2–3, Lycopodiaceae through Polypodiaceae. 2013. Beijing and St. Louis).

While conducting botanical surveys for the Minnesota Department of Natural Resources, near Steep Lake in the Superior National Forest, Minnesota (48°18′32″N, 92°13′44″W), one of us (LBG) discovered an unusual *Huperzia selago* (L.) Bernh. ex Schrank & Mart. growing in a wet area adjacent to the lake's outlet. This plant lacked normal gemmae but possessed short (7–13 mm long) shoot-like structures (hereafter, ''short shoots'') along the main stems (Fig. 1). These short shoots were of unequal lengths relative to the main shoots or branches, thereby deviating from the strictly isodichotomous branching that characterizes *Huperzia*. All other *Huperzia* plants in the vicinity appeared normal, suggesting that this unusual growth form was the result of abnormal development rather than ecotypic variation.

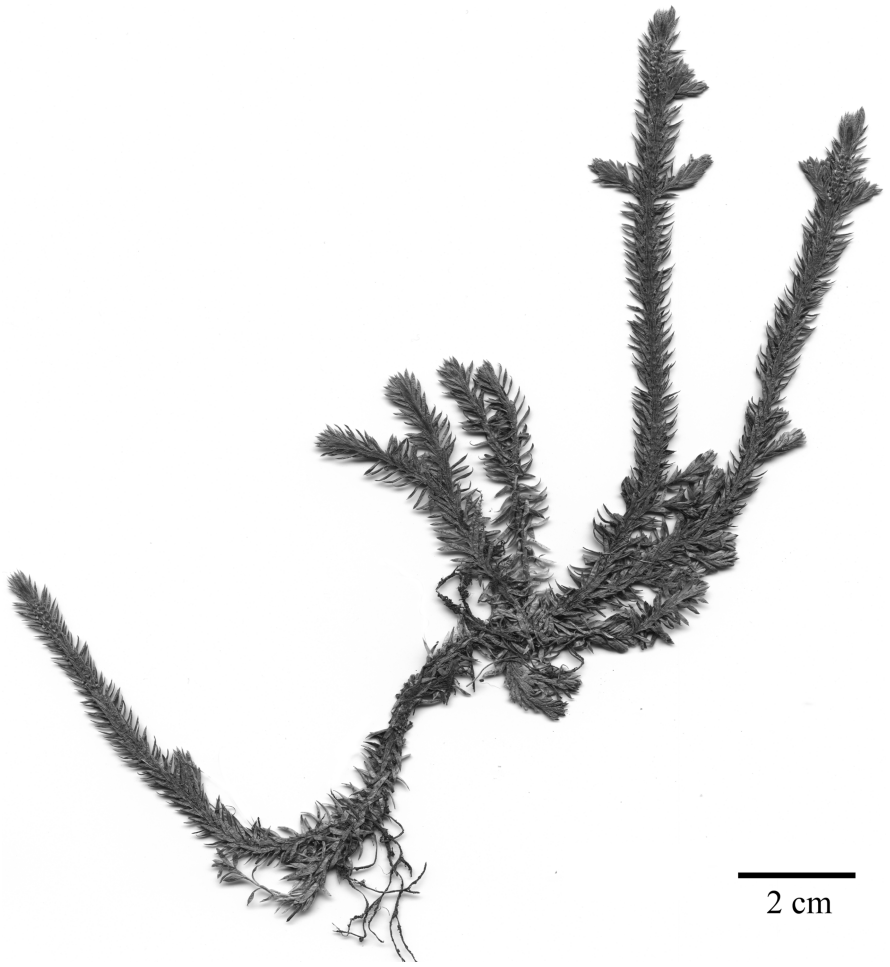

FIG. 1. Unusual form of *Huperzia selago* (*Gerdes 6938*, MIN) with short shoots in place of normal gemmae. Note proliferation from short shoot at bottom left.

Further examination of the Steep Lake specimen (*Gerdes 6938*, MIN) revealed aspects of the positioning and morphology of the short shoots that suggest that they were essentially gemmae that had failed to differentiate during development. Like gemmae, many of the short shoots were arranged in distinct pseudowhorls along the main shoot axis and were positioned in a ''phyllotactic'' series consistent with that previously described for gemmae (Smith, 1920; Stevenson, 1976). The specimen had 17 such short shoots, generally arranged in groups of 2 or 3 in distinct zones along the main shoot axis, although some single short shoots were observed (Fig. 1). The shoot-bearing zones occur at the end (summit) of each year's growth, as evidenced by the presence of sporangia of different age classes above and below each pseudowhorl. The short shoots were arranged within the plant's regular

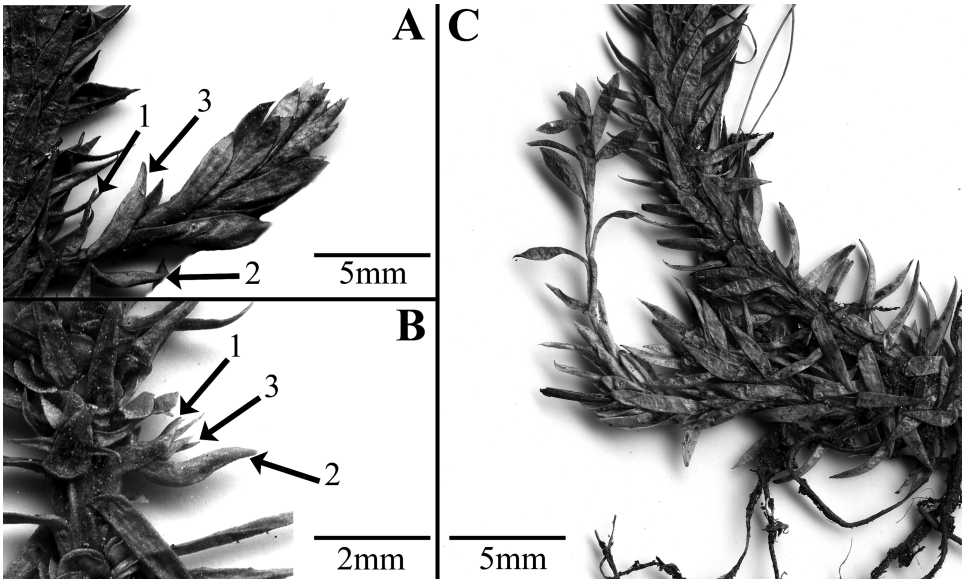

FIG. 2. A) A short shoot (from *Gerdes 6938*, MIN) showing its position on the main stem, variable phyllotaxy, and slight modification of the proximal leaves. B) A normally formed gemmiphore (from *Gerdes 6431*, MIN) comprising three pairs of highly modified leaves, following gemma dispersal. C) Juvenile growth proliferating from apex of a short shoot. In A and B, numbered arrows refer to each of three pairs of decussately arranged leaves.

phyllotaxy (i.e., in the place of leaves) and were positioned at an acute (~45–65°) angle relative to the main shoot axis.

Also, the homology of the short shoots with gemmae was suggested by slight differentiation of leaf shape of the proximal leaves and by a reduction in the number of orthostichies in which the proximal leaves are inserted (Fig. 2A). The three pairs of proximal leaves were twisted toward the apex of the main shoot (Fig. 2A), similar to the leaves of a normal gemmiphore (Fig. 2B; image from *Gerdes 6431,* MIN), whereas the distal leaves were oriented normally; i.e., ascending to weakly appressed to the short-shoot axis. The proximal leaves were generally shorter and narrower than those closer to the shoot apex. Compared to the leaves of a normal gemmiphore, the proximal leaves of the short shoots were relatively large.

The short shoots were firmly attached to the main shoot and, unlike normal gemmae, showed no evidence of an abscission layer above the proximal leaves. The number of orthostichies generally increased from a decussate arrangement among the proximal leaves to at least 5 or 6 ranks in the distal portion of the shoots. A juvenile shoot had ''germinated'' from the apex of one short shoot (Fig. 2C). The juvenile shoot appeared similar (e.g., with distant, oblanceolate leaves) to young plants growing from dispersed gemmae. The presence of the juvenile shoot indicates that the short shoots are capable of gemma-like proliferation.

The positional argument has been used by some authors (Hegelmaier, 1872; Smith, 1920) to support the hypothesis that the structure is a modified leaf, but we find the capacity to transform into an otherwise typical shoot, with indeterminate growth, normal phyllotaxy, and normally formed leaves inconsistent with that interpretation. It appears that these short shoots failed to differentiate into normal, highly organized gemmae with arrested growth and continued to elongate for some time, resulting in their unspecialized appearance, variable orthostichies and largely unmodified leaves. Thus, if this unusual form of *Huperzia selago* represents a reversal to a more ancestral structural form, the discovery of this specimen lends support to the conclusions drawn by Stevenson (1976), who surmised that *Huperzia* gemmae are ''diminutive stem dichotomies.''

If *Huperzia* gemmae represent evolutionarily modified shoots, it is apparent that two types of branching occur in members of the genus: a pattern of isodichotomous branching that underlies the general growth form, and a secondary, tightly controlled pattern that gives rise to gemmae. At a basic level, three major developmental shifts must occur to establish a normal, functional gemma: 1) a shoot meristem must be formed in a position that would normally bear a leaf, 2) the extension of the shoot must be slowed and then arrested at an early stage of development and 3) an abscission layer must form to allow the gemma to be dispersed. Currently, fundamental questions about these processes remain unanswered, including: what mechanisms cause the differentiation of a shoot meristem in a leaf-like position? What cues constrain gemma formation to confined regions of growth in some, but not all species? Did gemmiferous shoots evolve *de novo* in the huperzioid lineage, or were they modified from shoots of an anisodichotomously branching ancestor? With these and other questions in mind, it is evident that study of the anatomy and especially the development of *Huperzia* gemmae has significant implications for understanding not only the morphology and ecology of the genus, but also the evolution of the lycopod body plan.

Voucher: USA, Minnesota, St. Louis County: Superior National Forest, Boundary Waters Canoe Area Wilderness, Steep Lake, approximately 12.36 miles ENE of Crane Lake, MN. Drainage at the northeast end of lake. Below well established beaver dam along edge of drainage with *Lycopus uniflora*, *Trientalis borealis*, *Dulichium arundinaceum*, *Carex cryptolepis*, etc. 48° 18′ 32″N, 92° 13′ 44″W, 18 August 2013, *Gerdes 6938* (MIN).

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