

1. TAKAKIACEAE S. Hattori & Inoue

John R. Spence
Wilfred B. Schofield

Stems erect, arising sympodially from creeping pale or white stolons bearing clusters of beaked slime cells, rhizoids absent, stem in cross section differentiated into outer layer of smaller, thick-walled cells and cortex of larger thin-walled cells, sometimes with small central cells, these often with trigones, outer cells with simple oil droplets. **Leaves** typically 3-ranked, terete, forked, of (1-)2-4 terete segments, segments sometimes connate at base, in cross section of 3-5 cells, one or more larger central cells surrounded by smaller cells, oil droplets present in all cells, 2-celled slime hairs with enlarged apical cell present in axils of leaves. **Specialized asexual reproduction** by caducous leaves or stems. **Sexual condition** dioicous, gametangia naked. **Seta** with foot, persistent, elongating prior to capsule maturation. **Capsule** erect, symmetric, well-defined neck region absent, stomates absent, dextrorsely spiralled at maturity, columella ephemeral, basifixed, not penetrating the archesporial tissue, peristome absent, dehiscence by longitudinal helical slit. **Calyptra** fugacious to rarely persistent, typically mitrate. **Spores** 3-radiate, slightly roughened to papillose.

Genus 1, species 2 (2 in the flora): North America, se Asia (including Borneo).

Takakiaceae are plants of cool, cold-temperate to arctic-alpine oceanic climates. They were first collected in the Himalayas by J. D. Hooker and placed in the hepatic genus *Lepidozia* as *L. ceratophylla* by W. Mitten. The consensus has been that it was a highly unusual liverwort with affinity to the Calobryales. Distinctive features include erect shoots arising from a stolon, terete leaves, sometimes fused at or near the base and thus of 2-4 segments, naked lateral gametangia, slime cells, oil droplets, and chromosome numbers of $n = 4$ or 5 . In 1993 sporophytes and antheridia were discovered in a population from Atka Island of the Aleutian Islands (D. K. Smith and P. G. Davison 1993). The sporophyte exhibits its affinity with the mosses, and is similar in some respects to sporophytes of the Andreaeopsida, by the columella, persistent seta, capsule that matures after seta elongation, dehiscence by a diagonal slit, and absence of elaters. R. M. Schuster (1997) suggested that gametophytically *Takakia* is more like a liverwort, and sporophytically more like a moss. The Japanese common name is perhaps most telling, literally translated as "puzzling moss."

SELECTED REFERENCES Hattori, S. 1963. *Takakia* of North Borneo (1). J. Jap. Bot. 38: 215–217. Hattori, S. and H. Inoue. 1958. Preliminary report on *Takakia lepidozoioides*. J. Hattori Bot. Lab. 19: 133–137. Hattori, S., Z. Iwatsuki, M. Mizutani, and S. Inoue. 1974. Speciation of *Takakia*. J. Hattori Bot. Lab. 38: 115–121. Hattori, S., A. J. Sharp, M. Mizutani, and Z. Iwatsuki. 1968. *Takakia ceratophylla* and *T. lepidozoioides* of Pacific North America and a short history of the genus. Misc. Bryol. Lichenol. 4: 137–149. Higuchi, M. and Zhang D. C. 1998. Sporophytes of *Takakia ceratophylla* found in China. J. Hattori Bot. Lab. 84: 57–69. Renzaglia, K. S., K. D. McFarland, and D. K. Smith. 1997. Anatomy and ultrastructure of the sporophyte of *Takakia ceratophylla* (Bryophyta). Amer. J. Bot. 84: 1337–1350. Schuster, R. M. 1997. On *Takakia* and the phylogenetic relationships of the Takakiales. Nova Hedwigia 64: 281–310. Smith, D. K. and P. G. Davison. 1993. Antheridia and sporophytes in *Takakia ceratophylla* (Mitt.) Grolle: Evidence for reclassification among the mosses. J. Hattori Bot. Lab. 73: 263–271.

1. TAKAKIA S. Hattori & Inoue, J. Hattori Bot. Lab. 19: 133. 1958 • [For N. Takaki, 1915–2005, who first collected the genus in Japan]

Plants small, bright green, in dense turfs. Stems short, 0.5–2 cm, erect, mostly unbranched or weakly sympodially branching with colorless branches arising at acute or right angles from the erect leafy stems. Leaves reduced proximally and widely spaced, distally more densely arranged and roughly 3-ranked or irregularly arranged, of 1–4 segments, erect or spreading. Sexual condition with antheridia lateral, elongate, orange-brown when mature, archegonia lateral and often orange-tinged, not halting subsequent stem growth. Seta 0.5–2.6 mm, straight and erect. Capsule elongate-elliptic, 0.6–2.3 × 0.3–0.5 mm, green becoming brown. Spores 25–36 μm.

Species 2 (2 in the flora): nw North America, Asia (Borneo, China, India, Japan, Nepal).

1. Leaves essentially 3-ranked, mostly of 4 segments, connate at base, not caducous, in median cross-sectional segments with 2–5 inner large cells and 10–15 smaller thick-walled epidermal cells, distal portion of leafy shoots rigid, brittle and caducous, sporophytes infrequent; plants without a distinctive odor when dry 1. *Takakia ceratophylla*
1. Leaves irregularly ranked, of (1–)2(3–4) segments, not or only occasionally connate at base, somewhat caducous, in median cross-sectional segments with 1–2 inner thin-walled cells and ca. 8 smaller thin-walled outer epidermal cells, distal portion of leafy shoots often lax, not caducous; sporophytes unknown; plants cinnamon-scented when dry 2. *Takakia lepidozoioides*

1. *Takakia ceratophylla* (Mitten) Grolle, Oesterr. Bot. Z. 110: 444, fig. 1. 1963 [F]



Lepidozia ceratophylla Mitten, J. Proc. Linn. Soc., Bot. 5: 128. 1861

Plants absent distinctive odor when dry, distal portion of leafy shoot readily caducous. Stems in cross section with 2 layers of thicker walled epidermal cells, stoloniferous stems mainly subterranean. Leaves typically of

thick-walled cells, in 4 segments, connate at base, cross section of each segment with 3–5 inner cells and 10–15 smaller outer epidermal cells, outer cells small, 25 × 10 μm, regularly arranged. Slime hairs thick-walled. Sporophytes infrequent. Capsule terminal, usually single.

Capsules mature late summer–early fall (Jul–Sep). Uncommon to rare on moist soils and shaded banks, slopes and over rocks in tundra; low to moderate elevations (70–700 m); Alaska; Asia (China in Yunnan, India in Sikkim, Nepal).

Takakia ceratophylla appears to be somewhat tolerant

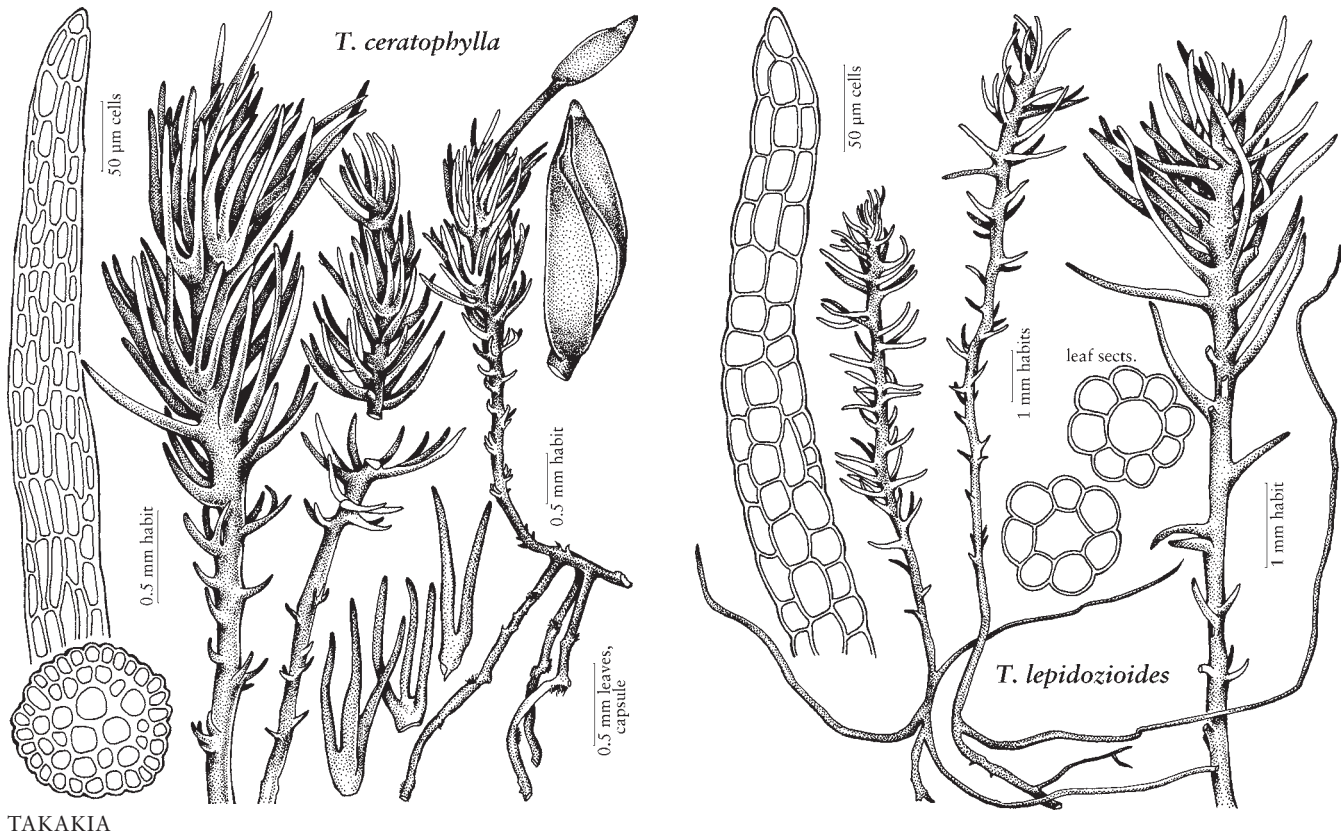
of desiccation. Frequently it grows with other drought-tolerant bryophytes such as *Andreaea* and *Gymnomitrium*. The shoots are more rigid than those of *T. lepidozoioides*, and leaf arrangement is more regular. Rhizomatous shoots are predominantly subterranean.

2. *Takakia lepidozoioides* S. Hattori & Inoue, J. Hattori Bot. Lab. 19: 137, figs. 1–24. 1958 [F]



Plants with cinnamon-like odor when dry; distal part of leafy shoots not caducous. Stems in cross section usually with 1 layer of thicker walled epidermal cells; stoloniferous stems well developed and extensive above surface of substrate. Leaves typically of 2 segments, not or only occasionally

connate at base, some solitary, occasionally of 3–4 segments, sometimes caducous, in cross section of thin-walled cells, in distal part of segment with single large central cell and 7–10 smaller outer cells, these 30–45 × 20–25 μm, irregularly arranged. Slime hairs thin-walled. Sporophytes unknown.



Uncommon on moist humus, in usually somewhat shaded habitats, over rocks or on banks, rock crevices, especially near waterfalls, but also on peaty banks in wetland slopes, humid coastal to subalpine and alpine; low to moderate elevations (0–1000 m); B.C.; Alaska; Asia (Borneo, Japan, Nepal, Taiwan).

Takakia lepidozoioides grows most frequently in highly humid or misty sites, often deeply shaded. Algae and cyanobacteria are frequent associates. The shoots are often lax, and extensive rhizomatous shoots are conspicuous.