

Reassessing the taxonomic diversity of *Plagiothecium* section *Orthophyllum* in the North American bryoflora

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Abstract. At the beginning of the twentieth century, *Plagiothecium nemorale* s.l. and *P. succulentum*, both belonging to *P.* sect. *Orthophyllum*, were considered to be distributed across almost the entire Northern Hemisphere. However, in the mid-twentieth century these taxa were recircumscribed resulting in their exclusion from the North American bryoflora and restricting their distributions to Asia and Europe, and in the case of *Plagiothecium nemorale* s.l., also North Africa. More recently, it was found that *P. nemorale* s.l. is a taxonomic complex comprising three distinct species: *P. nemorale* s.s., *P. longisetum*, and *P. angusticellum*. I revised the North American material of *P.* section *Orthophyllum* deposited in three herbaria (NY, FH, F) and found that five examined taxa of the section are present in the North America. Two of the species *P. angusticellum* and *P. longisetum*, have not been recorded from North America previously, while two others, *P. nemorale* and *P. succulentum*, had not been listed in the North American bryoflora for 50 years. One taxon is new for the U.S.A. – *P. succulentum* f. *propaguliferum*. Here I provide detailed descriptions of the anatomical and morphological features of the recorded taxa along with photographic documentation of their most important characteristics. I also summarize their known distributions in North America and ecological preferences and provide a key for their identification.

Keywords: Taxonomic revision, *P. nemorale*, *P. longisetum*, *P. angusticellum*, *P. succulentum*.

As science has developed, so has the range of the family Plagiotheciaceae M.Fleisch, as earlier morphological and anatomical studies (Brotherus, 1909; Fleischer, 1912; Jedlička, 1948; Iwatsuki, 1970; Lewinsky, 1974; Buck & Ireland, 1989) have been supplemented by more modern ones based on molecular research (Pedersen & Hedenäs, 2001, 2002; Wynns & Lange, 2014; Wynns et al., 2017; Wynns & Schröck, 2018; Ignatova et al., 2019; Wolski, Nowicka-Krawczyk, 2020). One of the genera belonging to this family is *Plagiothecium* Schimp., globally distributed pleurocarpous mosses which are especially widespread in the temperate zone and the tropics (Dierßen, 2001; Ochyra et al., 2008; Wynns, 2015).

Jedlička (1948) erected *P.* sect. *Orthophyllum* Jedl. in his *Monographia Specierum Europaearu*, gen. *Plagiothecium* s. s., within which he included three species: *P. Roeseanum* (Hampe) Bryol. Eur. [synonym of *P. cavifolium* (Brid.) Z.Iwats.],

P. succulentum (Wilson) Lindb., and *P. neglectum* Mönk. [synonym of *P. nemorale* (Mitt.) A.Jaeger]. More recently, Wynns (2015) recognized six species in section *Orthophyllum*: *P. cavifolium*, *P. cochleatum* Dixon, *P. japonicum* Sakurai, *P. nemorale*, *P. rhizophyllum* Sakurai, and *P. succulentum*. New research on *P. nemorale* s.l. (Wolski, Nowicka-Krawczyk, 2020) resulted in the restoration of one of its synonyms – *P. longisetum* Lindb., and the description of a new species, *P. angusticellum* G. J. Wolski & P. Nowicka-Krawczyk; both are properly placed in section *Orthophyllum*.

In the nineteenth century, *Plagiothecium sylvaticum* (Brid.) Bruch & Schimp. was included in the North American bryoflora, it being the only species recorded from North America at the time that is now considered to be a synonym of *P. nemorale* (Sullivant & Lesquerux, 1865; Macoun & Kindberg, 1892; Renauld & Cardot, 1892; Macoun, 1889). Although studies of the

North American bryoflora increased in the twentieth century (e.g., Andrews, 1921; Thomas, 1952; Ireland et al., 1987; Anderson et al., 1997), records of *Plagiothecium* were relatively rare and few additional taxa of the genus were recorded from the area. Species which are now considered to be synonyms of *P. nemorale* and *P. succulentum* were recorded only extremely rarely and mainly in studies from the first half of the twentieth century (Grout, 1939; Sharp, 1939; Gier, 1949; Clebsch, 1954; Githens, 1957; Norris, 1967).

Trends in the taxonomic history of *Plagiothecium* in North America are well illustrated by analysis of the bryophyte lists for the continent. Grout (1932, 1940) recognized 31–32 taxa of *Plagiothecium* in North America, including *P. sylvaticum* and *P. sylvaticum* var. *succulentum* (Wilson) Husnot. Over time, many of these taxa were transferred to other genera, leaving only 13 taxa of *Plagiothecium* (including *P. sylvaticum* and *P. succulentum*) in North America in the list of Crum et al. (1965) and subsequently supported by the research of Worley and Iwatsuki (1970).

Undoubtedly the most influential works on North American *Plagiothecium* were Ireland's (1969, 1985, 1986) taxonomic revisions, in which he recognized only six to eight species of *Plagiothecium* in the North American bryoflora. In those works, he synonymized several taxa, mainly within *P. cavifolium*, and excluded from North America others, including *P. sylvaticum*, *P. neglectum*, *P. nemorale*, and *P. succulentum*. The distributions of these last two taxa, previously considered to range across the whole Northern Hemisphere, were thus restricted to Asia and Europe, and in the case of *P. nemorale* s.l. also northern Africa (Hill et al., 2006; Ignatov et al., 2006; Ros et al., 2013; Suzuki, 2016).

Ireland's taxonomic concepts were largely followed in subsequent bryological lists for this part of the world. For example, Crum et al. (1973) listed only seven taxa of *Plagiothecium* in their next list for North America, which was then followed by Anderson et al. (1990). In a worldwide revision of the *Plagiothecium*, Wynns (2015) added a number of taxa of the genus to the North American bryoflora, but continued to exclude *P. nemorale* and *P. succulentum*.

My revision of North American material of *Plagiothecium* sect. *Orthophyllum* suggests that recent treatments underestimated the taxonomic

diversity of the group in North America and brings into question the widespread adoption of Ireland's taxonomic concepts. This article presents the results of this research.

Materials and methods

Nine-hundred specimens of *Plagiothecium* sect. *Orthophyllum* from three North American herbaria (NY, FH, F) were reviewed. All of them from these collections were studied more closely and qualitative and quantitative characteristics of their gametophytes were measured. Characters examined included – qualitative features related to the stem leaves: such as leaf shrinkage, symmetry, shape and concavity, the curvature and serrations of the leaf apex, the shape of leaf cells, the shape of decurrent cells, and the formation, or not, of distinct auricles by these cells, and quantitative features (length and width) of the above-mentioned structures. The resulting data were used to make species descriptions and to direct photographic imaging. Taxon distributions and ecological preferences were summarized from specimen label data. The taxon descriptions are based exclusively on specimens originating in North America. All examined specimens are listed in Appendix 1. The names of individual taxa were adopted from Wynns (2015), with the exception of the *P. nemorale* complex (Wolski, Nowicka-Krawczyk, 2020).

Results

The revision indicated that in North America there are two species that have been excluded since the widespread adoption of Ireland's (1969) classification and have not subsequently been recorded for the continent: *P. nemorale* and *P. succulentum*. In addition, a form of the second species has been found – *P. succulentum* f. *propaguliferum* E. Bauer, and this taxon is listed for the first time in the U.S.A. area. Also, the revision indicates one species that until now was considered a synonym but now is treated as separate – *P. longisetum*, and one new for North America – *P. angusticellum*. The analysis of herbarium materials indicates that those species in the past years were most often wrongly determined as *P. cavifolium* and *P. denticulatum* (Hedw.) Schimp.

TAXONOMIC TREATMENT

Plagiothecium nemorale (Mitt.) A. Jaeger, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1876–1877: 451. 1878. *Stereodon nemoralis* Mitt., Journal of the Proceedings of the Linnean Society, Botany, Supplement 1: 104. 1859. *Plagiothecium silvaticum* var. *nemorale* (Mitt.) Par., Index Bryologicus 967. 1898. Type: [India] In Himalayae orient. reg. temp., Sikkim, in monte Tonglo (ad radicem filicis cujusdam), *s.d.*, *J. D. Hooker s.n.* (NY 913349!).

Plagiothecium silvaticum sensu Schimp., non Brid., Bryologia Europaea 5: 192. 503, fasc. 48 Monogr. 14. 11. 1851.

Plagiothecium neglectum Mönkm. Die Laubmoose Europas. 866. 1927. Type: sine loco, sine dato, *sine coll. s.n.*

Plagiothecium saxicola Sak., Botanical Magazine, Tokyo 48: 395. 1934. Type: [Japan], Hondo, Prov. Aki, Mt. Fukuji, ad saxas, 4 Jan 1933, *Y. Doi Typus in Herb. K. Sakurai 3282* (MAK3282, PC 132573!).

Plagiothecium silvaticum var. *latifolium* Cardot, Bulletin de la Société Botanique de Genève sér. 2, 4: 385. 1912. Type: [Japan], Iyo (Gono) *s.d.* (original material: *n.v.*); Corée: île Quelpaert, sine dato, *Faurie 507* (treated as an isosytype by Iwatsuki (1970): KYO507).

Plagiothecium silvaticum var. *rhynchostegioides* Cardot, Bulletin de la Société Botanique de Genève sér. 2, 4: 385. 1912. Type: [Japan]: Mororan, bas-fonds, sur pierres, *Cardot 2965* (treated as an isotype by Iwatsuki (1970): KYO2965).

Plants medium-sized, dark green, dull, without metallic luster. Stems to 1.5 cm long, complanate-foliolate, in cross-section rounded, with a diameter of 350–450 μm , central strand developed, epidermal cells 7.5–17.5 \times 12.5–25 μm , parenchyma thin-walled, 20–50 \times 30–50 μm ; leaves spreading, in dry condition shrunken, concave, symmetrical, ovate (Fig. 1), those from the middle of the stem 0.1–1.5 mm long, 0.9–1 mm wide measured at the widest point; those near the top of the stem much smaller; the apex straight, acuminate, apiculate and denticulate; costae 2, very rarely 1 or 3, extending to half of leaf length, reaching 0.40–0.60 mm; laminal cells in transverse rows, narrowly hexagonal toward the apex and mid-leaf, and elongate-hexagonal toward the insertion, the length and width variable depending on location: 40–70 \times 15–20 μm at apex, 50–90 \times 17–20 μm at mid-leaf, and 100–140 \times 17–20 μm at lower part of leaf (Fig. 1);

decurrencies of three rows of rectangular cells, 37.5–87.5 \times 15–20 μm . Sporophytes unknown in North America.

Distribution and habitat.—Specimens of *Plagiothecium nemorale* in North America have been seen only in eastern North America. This species is recorded from Canada (Nova Scotia) and the U.S.A. (Maine, New York, and North Carolina) (Fig. 6). In these localities, it grows in epigeic (along the trail), epilithic (in deciduous forests on shady rocks), and epiphytic habitats (on the moist base of a tree in a *Fagus* forest; see Appendix 1).

Plagiothecium longisetum Lindb., Acta Societatis Scientiarum Fennicae 10: 232. 1875. Type: [Japan]. ad Nikosan ins. Kiusiu, fertile, 16 Junii 1863, *S. O. Lindberg* (PC0132572!, H-SOL 1563 011!). *Plagiothecium longisetum* var. *brevinerve* Ihsiba, Transactions of the Sapporo Natural History Society 13: 396. 1934. Type: [Japan]. Mt. Hakk da, Mutsu, 1933, *S. Murai s.n.*

Large plants, yellowish green, without metallic luster. Stems to 2.5–3 cm long, complanate-foliolate, in cross-section rounded, with a diameter of 230–300 μm , central strand developed, epidermal cells 20–25 \times 17.5–25 μm , parenchyma thin-walled, 20–27.5 \times 15–30 μm ; leaves concave, strongly asymmetrical, ovate (Fig. 2), spreading, in dry condition shrunken, those from the middle of the stem 1.8–2.6 mm long, 1.4–1.5 mm wide measured at the widest point; those near the top of the stem much smaller; the apex straight, not denticulate, acute to apiculate; costae 2, extending to half of leaf length or more, reaching 0.80–1 mm; elongate-hexagonal cells in irregular transverse rows, areolation very lax; the length and width variable depending on location: 62–112 \times 17–20 μm at apex, 100–130 \times 17–20 μm at mid-leaf, and 100–150 \times 20–23 μm at lower part of leaf (Fig. 2); decurrencies of 3 rows of rectangular cells, 45–62.5 \times 15–25 μm . Sporophytes unknown in North America.

Distribution and habitat.—Specimens of *Plagiothecium longisetum* in North America have been seen in eastern North America and the Pacific Northwest. This species is recorded from Canada (British Columbia) and the U.S.A. (Pennsylvania, Virginia) (Fig. 6). In these localities, it grows mainly in epigeic (seepy humus, on the floor of *Rubus spectabilis* thicket) and epilithic

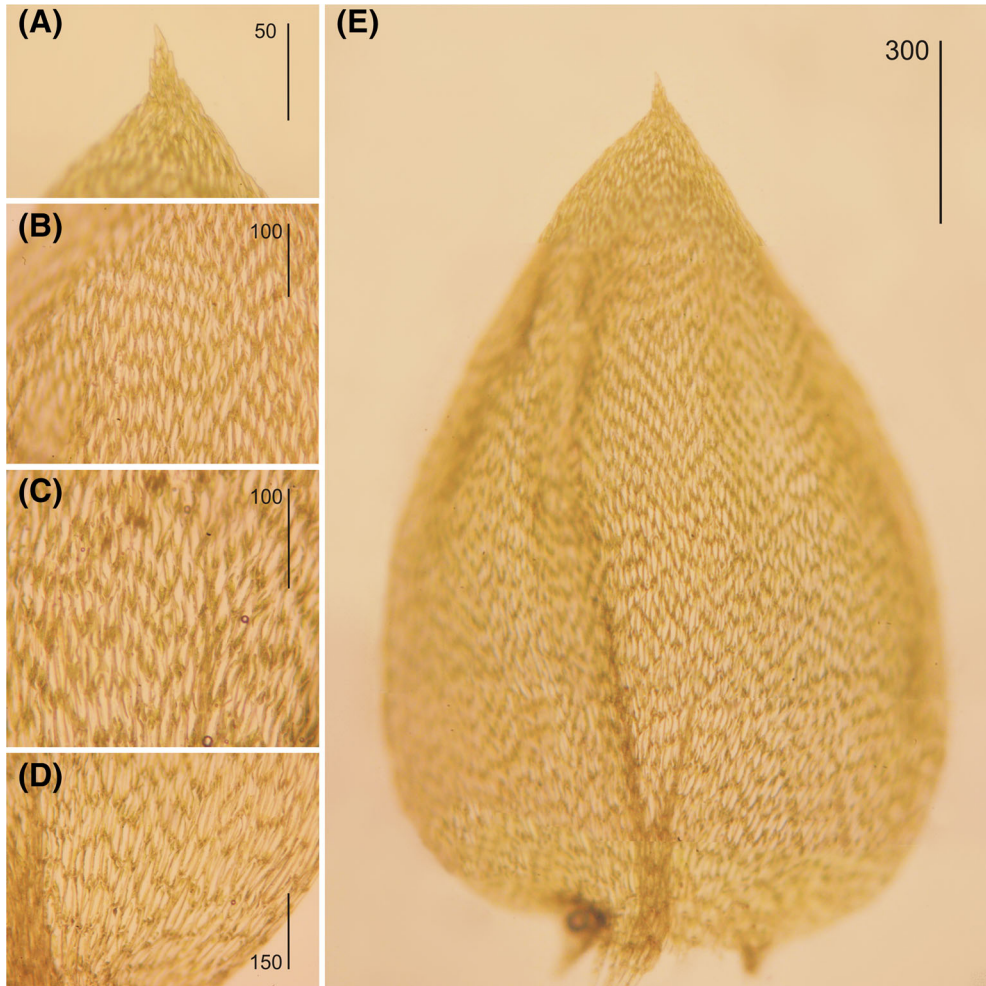


FIG. 1. *Plagiothecium nemorale* specimens from North America (from *R. Düll* 855, NY 00506577). A. Leaf apex. B–D. Cells exhibiting shape and dimensions from three different leaf zones. B. Distal zone, C. Mid zone, D. Basal zone. E. Stem leaf of the examined species. (Scales in μm .)

habitats (on shady rocks, on moist shaded sandstone, on boulders in shade; see Appendix 1).

Plagiothecium angusticellum G. J. Wolski & P. Nowicka-Krawczyk, PLOS ONE 15(3): e0230237. 2020. Type: Poland. Łódzkie Voivodeship, Grały nad Moszczenicą reserve, 51°55'N, 19°29'E, at the base of *Carpinus betulus* in *Fraxino-Alnetum* forest, 11 Dec 2017, G. J. Wolski (holotype: LOD 14927!; isotype: LOD 14937!).

Plants medium-sized, light green, without metallic luster. Stems to 1.5 cm long, complanate-foliate, in cross-section rounded, with a diameter

of 250–300 μm , central strand developed, epidermal cells $7.5\text{--}12 \times 15\text{--}25.5 \mu\text{m}$, parenchyma thin-walled, $15\text{--}37.5 \times 17.5\text{--}26 \mu\text{m}$; leaves spreading, in dry condition not shrunken, ovate, concave, asymmetrical (Fig. 3), those from the middle of the stem 1–1.7 mm long, 0.6–1 mm wide measured at the widest point; those near the top of the stem much smaller; the apex acuminate, slightly curved, not denticulate; costae 2, short, not extending to half of leaf length, reaching 0.4–0.75 mm; laminal cells narrowly elongate-hexagonal, gently asymmetric, in irregular transverse rows, the length and width variable depending on location: $75\text{--}100 \times 12.5\text{--}17.5 \mu\text{m}$ at apex, $110\text{--}120 \times 12.5\text{--}17.5 \mu\text{m}$ at mid-leaf, and 90–

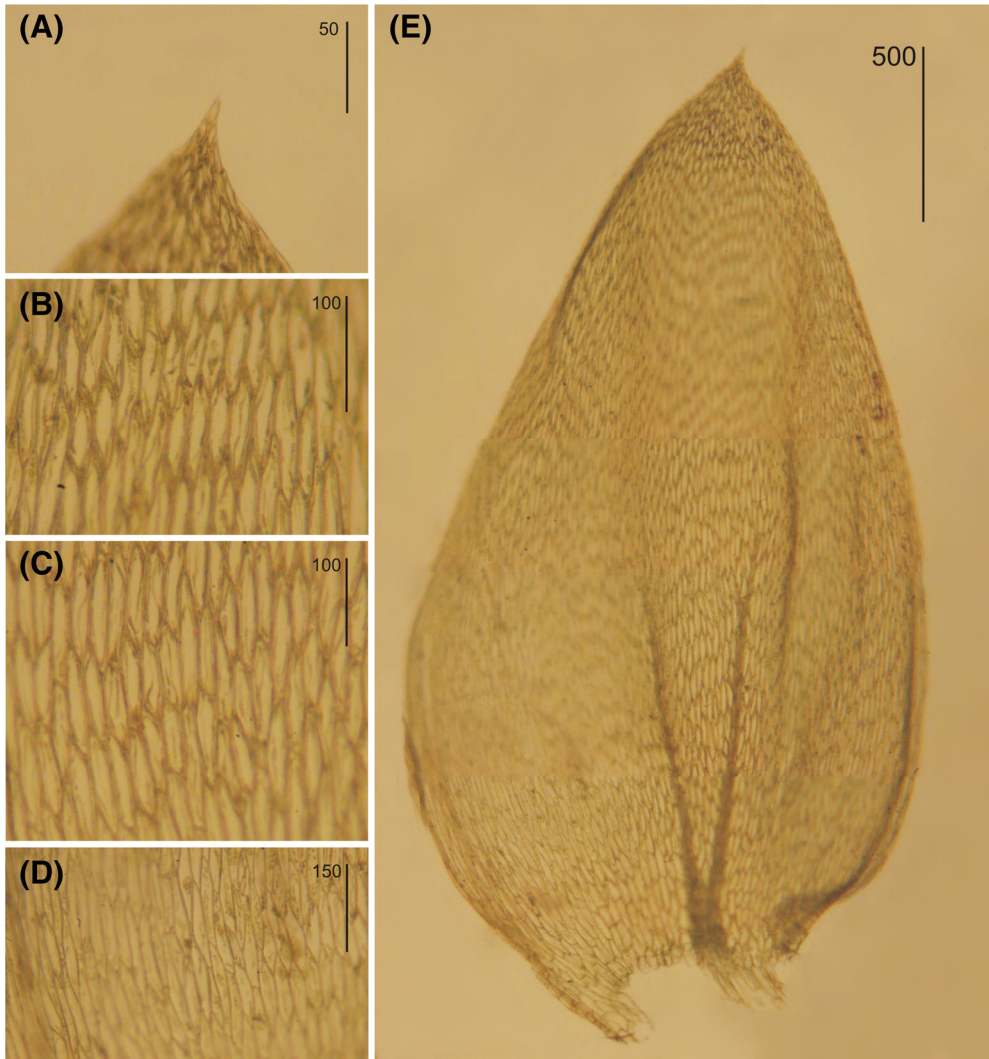


FIG. 2. *Plagiothecium longisetum* specimens from North America (from W. B. Schofield 31,629, NY 00163472). A. Leaf apex. B–D. Cells exhibiting shape and dimensions from three different leaf zones. B. Distal zone. C. Mid zone. D. Basal zone. E. Stem leaf of the examined species. (Scale in μm .)

$137.5 \times 17.5\text{--}20 \mu\text{m}$ at lower part of leaf (Fig. 3); decurrencies of 2 rows of rectangular to quadrate cells, $45\text{--}87.5 \times 10\text{--}17.5 \mu\text{m}$. Sporophytes unknown in North America.

Distribution and habitat.—Specimens of *Plagiothecium angusticella* in North America have been seen only in eastern North America. This species is recorded so far only from the U.S.A. (Connecticut, and West Virginia) (Fig. 6). In these localities, it grows mainly in epigeic (in mixed conifer-hardwood forests, on extensive rock outcrops, in humid mixed hardwood-hemlock forests with acidic rock outcrops along

rivers) and epilithic habitats (in calcareous seepage in vertical rock face; see Appendix 1).

Plagiothecium succulentum (Wilson) Lindb., Botaniska Notiser 43: 143. 1865. 1865. *Hypnum denticulatum* var. *succulentum* Wilson, Bryologia Britannica 407. 1855. Type: Wilson Winwck Stone Quarry, near Warrington; J. Nowell near Todmorden.

Plagiothecium sylvaticum var. *succulentum* (Wilson) Spruce, Journal of Botany, British and Foreign 18: 357. 1880.

Plagiothecium denticulatum var. *succulentum* (Wilson) Dixon, The Student's Handbook of British Mosses. 437. 1896.

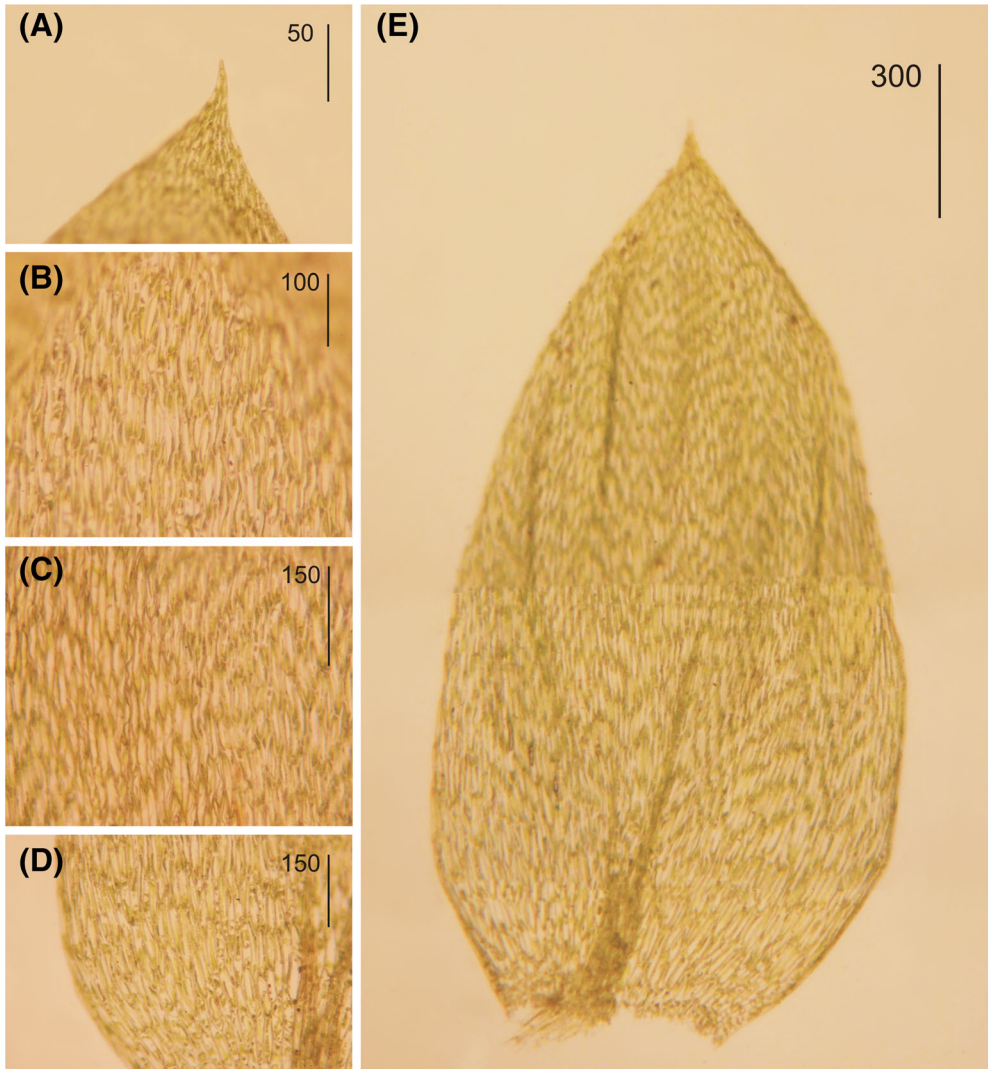


FIG. 3. *Plagiothecium angusticellum* specimens from North America (from B. Goffinet, 11,795, NY 02331429). A. Leaf apex. B–D. Cells exhibiting shape and dimensions from three different leaf zones. B. Distal zone. C. Mid zone. D. Basal zone. E. Stem leaf of the examined species. (Scale in μm .)

Plagiothecium sylvaticum ssp. *succulentum* (Wilson) Amann & Meyl., Flore des Mousses de la Suisse 1: 174. 1919.

Plants medium-sized to large, usually yellowish to yellowish-green or golden green, very glossy. Stems to 3 cm long, complanate-foliate, in cross-section rounded, with a diameter of 220–351 μm , central strand developed, epidermal cells $4.7\text{--}8.7 \times 5.2\text{--}14.9$ μm , parenchyma thin-walled, $12.6\text{--}31.4 \times 7.4\text{--}36.5$ μm ; leaves spreading, in dry condition not shrunken, complanate,

symmetrical, ovate-lanceolate (Fig. 4), at the middle of the stem $2.46\text{--}3.08 \times 0.82\text{--}1.38$ mm, those near the stem apex much smaller, tapering to a narrow acuminate, entire apex; costae 2, extending to half of leaf length, reaching 0.70–1.36 mm; laminal cells linear-rhomboidal, linear-hexagonal, overlapping, not in transverse rows, their size depends on the location on the leaf, the longest in the middle part of leaf, the widest at the base, apical cells $68.3\text{--}197 \times 7.8\text{--}17.5$ μm , those at mid-leaf $132.5\text{--}245.5 \times 10.2\text{--}17.9$ μm , those

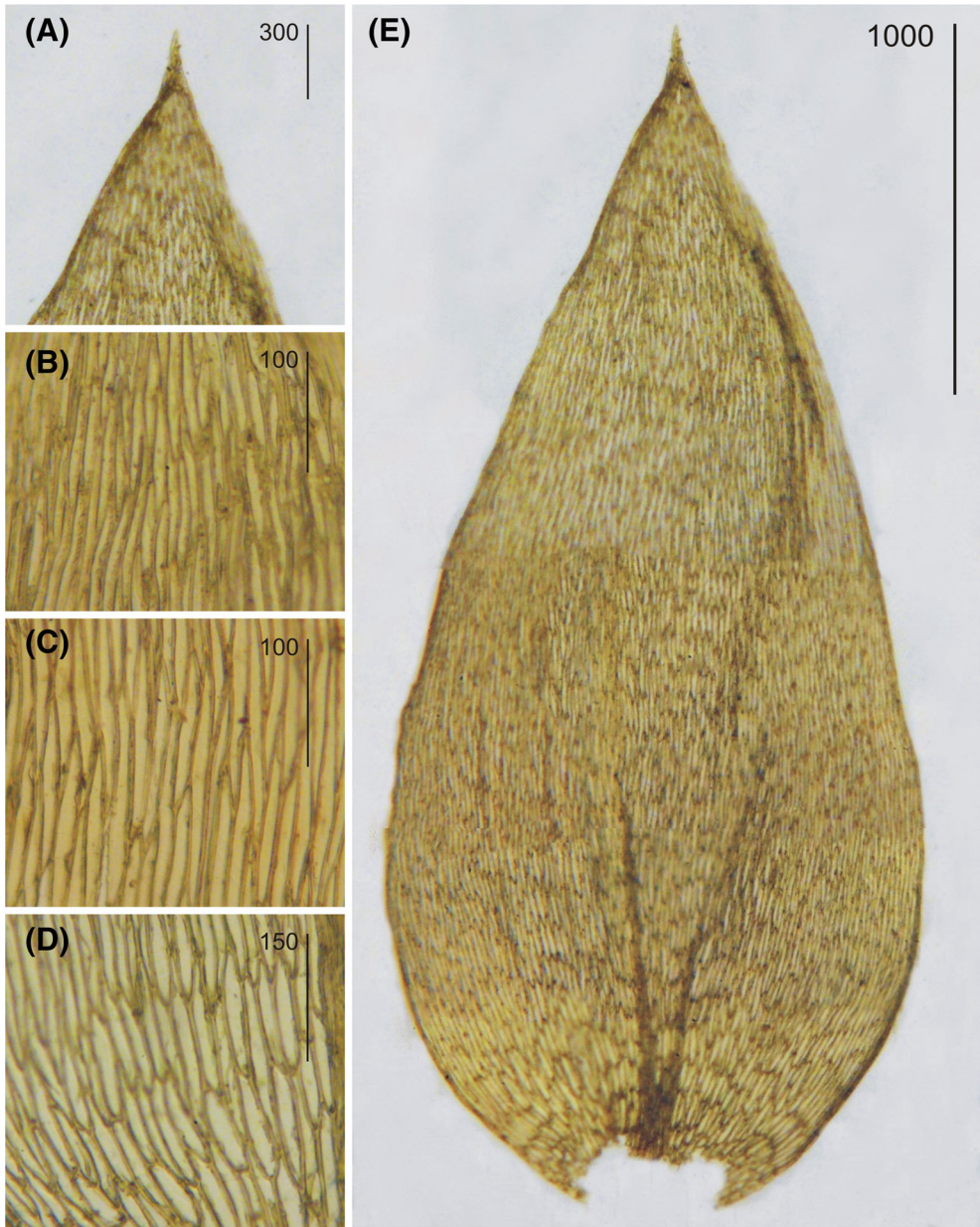


FIG. 4. *Plagiothecium succulentum* specimens from North America (from *W. R. Buck*, 32,700, NY 00481218). A. Leaf apex. B–D. Cells exhibiting shape and dimensions from three different leaf zones. B. Distal zone. C. Mid zone. D. Basal zone. E. Stem leaf of the examined species. (Scale in μm .)

toward the insertion $82.9\text{--}194.4 \times 10.9\text{--}28 \mu\text{m}$ (Fig. 4); cells of decurrencies in 2–3 rows, rectangular to quadrate, $22.3\text{--}58.9 \times 10.4\text{--}20.1 \mu\text{m}$. Sporophytes unknown in North America.

Distribution and habitat.—*Plagiothecium succulentum* in North America is distributed only

in eastern North America. This species is noted from Canada (Labrador, Ontario, Quebec) and the U.S.A. (Connecticut, Georgia, Maryland, Massachusetts, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Vermont, Virginia, West Virginia, Wisconsin) (Fig. 6). In

these localities, it grows mainly in epilithic habitats (on wet rocks, dripping sandstone ledges in the deep shade under hemlocks, moist shady rocks, vertical rocks near falls, moist ledges, and in cool, damp and shaded lower parts of cliffs), less often in epiphytic (on tree roots), epigeic (on wet, springy humus) and epixylic habitats (decayed wood). In these habitats, this species was listed in dense woods; mixed hardwoods, wet cliffs (cool damp shaded lower parts of cliffs), next to falls; in spruce-fir forests with *Rhododendron* and *Sorbus*, deep wooded ravines, and on mountainsides; see Appendix 1.

Plagiothecium succulentum* f. *propaguliferum

E. Bauer, Deutsche Botanische Monatschrift 20: 2. 1902. Type. Bryotheca Bohemica, No. 259, an Erlenstöcken in Erlbruche am Schiessniger Teiche bei B. Leipa, Bohemia, Czech Republic V. *Schiffner*, (Isotype: C 9395!).

Plants small to medium-sized, dark golden to brown, very glossy. Stems to 2–2.5 cm long, complanate-foliate, in cross-section rounded, with a diameter of 367–534 μm , central strand developed, epidermal cells 10.4–25.4 \times 18.8–35.2 μm , parenchyma thin-walled, 24.2–52.8 \times 23.4–58 μm ; leaves spreading, in dry condition shrunken, complanate, symmetrical, ovate-lanceolate (Fig. 5); at the middle of the stem 3.20–3.60 \times 1.40–1.53 mm, those near the stem apex much smaller, tapering to a narrow acuminate, entire apex; costae 2, extending to half of leaf length, reaching 0.76–1 mm; laminal cells linear-rhomboidal, linear-hexagonal, overlapping, not in transverse rows, their size depends on the location on the leaf, the longest in the middle part of the leaf, the widest at the base, apical cells 162.2–252.1 \times 17–21.7 μm , those at mid-leaf 176.6–264.5 \times 17.7–19.6 μm , those toward the insertion 168–273.5 \times 27.6–35.8 μm (Fig. 5); decurrencies of 2–3 rows of rectangular cells, 25–63.9 \times 14.5–25.6 μm . Sporophytes unknown in North America.

Distribution and habitat.—During this research, specimens of *Plagiothecium succulentum* f. *propaguliferum* were noted only from one locality in eastern North America (U.S.A., Vermont) (Fig. 6), where it occurs in epilithic habitats (in damp crevices in the shade of cliffs; see Appendix 1).

Discussion

Species of *Plagiothecium* sect. *Orthophyllum* are frequently misidentified in herbaria and the literature, and representatives of the section are often considered to be taxonomically problematic (Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001; Wolski, 2017, 2018). However, many of these challenges are the result of a lack of basic taxonomic research to document intraspecific variability in problematic taxa (Wynns et al., 2017; Ignatova et al., 2019; Wolski, Nowicka-Krawczyk, 2020). Moreover, many of the taxa of the section can be distinguished in both Eurasia and North America on the basis of easily recognizable features (Grout, 1932; Sharp, 1939; Greene, 1957; Nyholm, 1965).

Plagiothecium sylvaticum (at present a synonym of *P. nemorale*) among representatives of the genus *Plagiothecium* was described as a species with leaves more or less shrunken in dry condition (Grout, 1932; Sharp, 1939). This is a very important taxonomic feature that helps distinguish, among others, *P. nemorale* from other species of the genus (Green, 1957; Nyholm, 1965; Iwatsuki, 1970; Smith, 2001, Wolski & Nowicka-Krawczyk, 2020).

Within North America, all five of the documented taxa of section *Orthophyllum* occur in eastern North America, with a distinct dominance of *P. succulentum*, but in the Pacific Northwest only *P. longisetum* occurs. In comparison with the Eurasian material of *P. nemorale*, *P. longisetum* and *P. angusticellum* (Wolski, Nowicka-Krawczyk, 2020), the North American material of these species tends to have lower values for the analyzed quantitative features. Despite this, values of the most taxonomically significant features – the length and width of leaf cells – are relatively similar to the average values in the Eurasian populations.

The specimens cited in this study were previously identified as either *P. denticulatum* or *P. cavifolium*. The easiest way to distinguish the species treated here from *P. denticulatum* is by the symmetry of the leaves and form of decurrent cells. *Plagiothecium denticulatum* is characterized by very clearly asymmetric leaves (most leaves rounded asymmetric) and decurrent cells that are rounded, inflated and

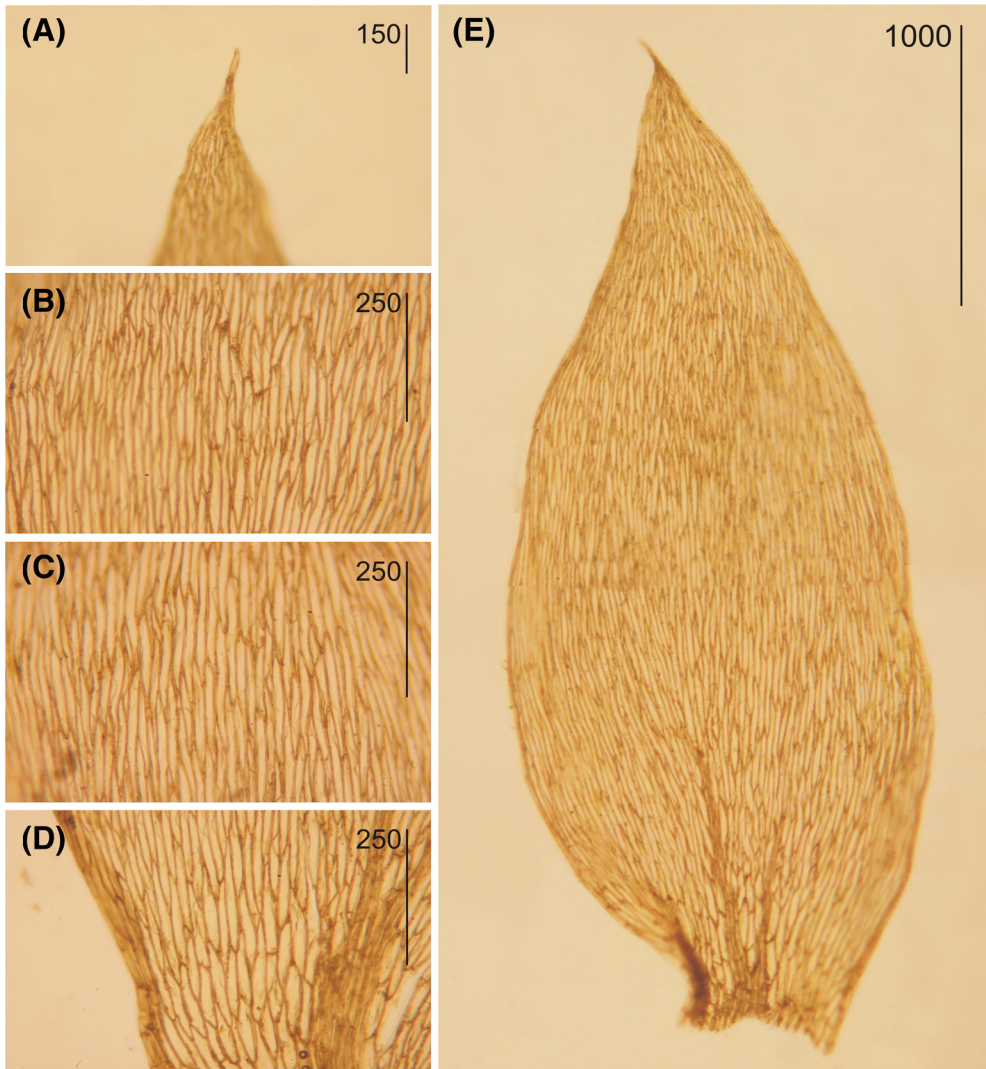


FIG. 5. *Plagiothecium succulentum* f. *propaguliferum* specimens from North America (from A. J. Grout, NY 00506521). A. Leaf apex. B–D. Cells exhibiting shape and dimensions from three different leaf zones. B. Distal zone. C. Mid zone. D. Basal zone. E. Stem leaf of the examined species. (Scale in μm .)

form distinct auricles (best viewed in situ on the stem). *Plagiothecium nemorale* and *P. succulentum* (including *P. succulentum* f. *propaguliferum*) have symmetric leaves, while *P. longisetum* and *P. angusticellum* have asymmetric or slightly asymmetric leaves. However, in all four of these species, the shape of decurrent cells is rectangular or quadrate, not inflated, and they do not form distinct auricles (Green, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001; Wolski, 2017, 2018; Wolski, Nowicka-Krawczyk, 2020).

The best features to distinguish the species treated here from *P. cavifolium* are the arrangement of leaves on the stem, leaf symmetry, and cell shape dimensions (Fig. 7). *Plagiothecium cavifolium* has julaceous, imbricate, symmetric leaves and long and narrow ($76\text{--}144 \times 10\text{--}16 \mu\text{m}$), slightly asymmetric cells. In contrast, the species treated here have complanately arranged, symmetric and asymmetric leaves. Cells at mid-leaf are short and wide ($50\text{--}90 \times 17\text{--}20 \mu\text{m}$) and symmetric in *P. nemorale*; long and wide ($100\text{--}130 \times 17\text{--}20 \mu\text{m}$) in



FIG. 6. Distribution of the examined taxa of *Plagiothecium* sect. *Orthophyllum* in North America.

P. longisetum; long and narrow ($90\text{--}120 \times 12.5\text{--}17.5 \mu\text{m}$) and slightly asymmetric in *P. angusticellum*; very long and narrow ($132.5\text{--}245.5 \times 10.2\text{--}17.9 \mu\text{m}$) and slightly asymmetric in *P. succulentum*; and very long and wide ($176.6\text{--}264.5 \times 17.7\text{--}19.6 \mu\text{m}$) and slightly asymmetric in *P. succulentum* f. *propaguliferum* (Green, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001; Wolski, 2017, 2018; Wolski, Nowicka-Krawczyk, 2020).

Other species that could be confused with those treated here are *P. japonicum* and *P. fallax* Cardot & Thér. The first is known from North America only from Alaska and was treated by Iwatsuki (1970) as a form of

P. nemorale – *P. nemorale* f. *japonicum* (Sak.) Iwats., but is now considered a separate species (Wynns 2015). *Plagiothecium japonicum* is quite similar to *P. nemorale*, but has larger, broadly ovate, concave leaves, with an acuminate apex, larger costae, and rigid, dilated cells; it is quite easy to distinguish from other species. Genetic analysis indicates that *P. japonicum* may be a hybrid or an allopolyploid of *P. cavifolium* and *P. nemorale* (Wynns 2015), although this requires further research. *Plagiothecium fallax* is also known in North America from Alaska, but has a broad distribution in Japan. It is similar to some of the treated species due to

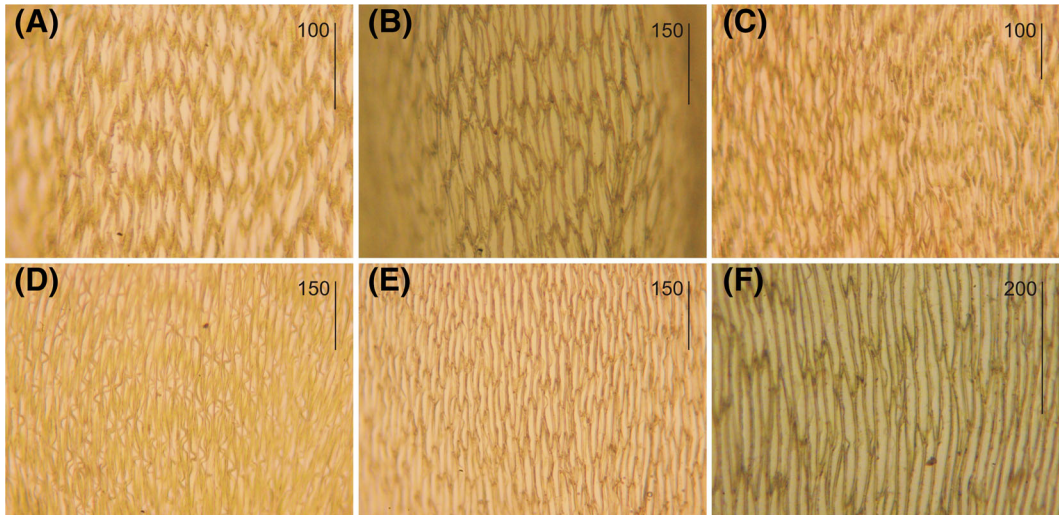


FIG. 7. Comparison of cells from the central part of the leaf in six species of *Plagiothecium*, exhibiting interspecific differences in cell dimensions and shape. **A.** *P. nemorale* (R. Düll, 855, NY 00506577). **B.** *P. longisetum* (W. B. Schofield, 31,629, NY 00163472). **C.** *P. angusticellum* (B. Goffinet, 11,795, NY 02331429). **D.** *P. denticulatum* (F. J. Herman, 18,234, NY 00506531). **E.** *P. cavifolium* (P. M. Patterson, 2914, NY 506587). **F.** *P. succulentum* (W. R. Buck, 32,700, NY 00481218).

its broadly ovate-lanceolate, asymmetric leaves, and rather open areolation of the cells. It resembles a smaller, less undulate version of *P. undulatum* (Hedw.) Schimp. with very

small alar decurrencies, and as indicated by Wynns (2015), is relatively easy to distinguish from other representatives of *Plagiothecium*.

Key to the taxa of *Plagiothecium* sect. *Orthophyllum* from North America and other taxa commonly confused with them

1. Leaves asymmetric (mostly rounded asymmetric); decurrent cells rounded; inflated; forming distinct auricles; the apex of the leaf usually denticulate *P. denticulatum*
1. Leaves symmetric or asymmetric; decurrent cells usually rectangular; not forming distinct auricles; the apex denticulate or not.
 2. Leaves symmetric; cells at mid-leaf short (50–90 × 17–20 µm); narrowly hexagonal or elongate hexagonal; in transverse rows; the apex denticulate *P. nemorale*
 2. Leaves symmetric or asymmetric; cells longer than 100 µm; linear-rhomboidal, linear-hexagonal; straight to slightly flexuose; in transverse rows or not; the apex not denticulate.
 3. Leaves asymmetric.
 4. Plant yellowish-green; without metallic luster; leaves in dry condition shrunken; concave; asymmetric; ovate; the apex straight, not denticulate; cells long and wide; elongate hexagonal; 100–125 × 17–20 µm at mid-leaf; in transverse rows. *P. longisetum*
 4. Plant green; without metallic luster; most leaves complanate; concave; asymmetric; not shrunken in dry condition; the apex slightly curved; acuminate; not denticulate; cells along and wide (90–137.5 × 17.5–20); slightly asymmetric. *P. angusticellum*
 3. Leaves symmetric.
 5. In dry condition leaves shrunken *P. succulentum* f. *propaguliferum*
 5. In dry condition leaves not shrunken.
 6. Plants light green to yellowish; leaves on the stem julaceous; imbricate and concave; symmetric; cells long and narrow (76–144 × 10–16 µm); forming transverse rows; slightly flexuose. *P. cavifolium*
 6. Plants yellowish to golden green; very glossy; leaves symmetric; ovate-lanceolate; cells linear-rhomboidal or linear-hexagonal; long and wide (132.5–245.5 × 10.2–18 µm); not forming transverse rows *P. succulentum*

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- APPENDIX I.** Additional specimens examined.
- Plagiothecium nemorale*. CANADA. Nova Scotia:** Inverness County, Cape Breton Highlands National Park, along the Acadian Trail, near Cheticamp Campground, northeast of Inverness, 46°38'N, 61°01'W, 22 Jul 1968, *R. R. Ireland 12085* (NY 00163469).
- U.S.A. Maine:** Canton, 23 Aug 1934, *J. C. Parlin* s.n. (NY 00481248). **New York:** Cattaraugus County, Allegany State Park, around “Thunder Rock” in deciduous forest primitive rock, on rocks (shady), elev. 720 m., 22 May 1981, *R. Dill 855* (NY 00506577); Ulster County, town of Shandaken, Catskill Forest Preserve, Slide Mountain Wilderness Area, W slope of Slide Mountain, along the trail from the parking area W of NY 47, 42°00'28"N, 74°25'13"W, elev. 300 m., northern hardwoods, 13 Sep 2008, *W. R. Buck 54032* (NY 01077084). **North Carolina:** McDowell County, on the moist, diffusely lit base of a tree in the *Fagus* forest on the crest of the mountain at Craggy Gardens north of Marion, elev. 1600 m., 1 Jul 1983, *D. H. Norris 68,967* (NY 00588089).
- Plagiothecium longisetum*. CANADA. British Columbia:** Queen Charlotte Is., W. Moresby Id., N side of Gowgaia Bay, seepy humus of bank, 13 Jul 1966, *W. B. Schofield 31629* (NY 00163472); Vancouver, Lynn Creek Canyon, on the floor of *Rubus spectabilis* thicket, 20 Feb 1978, *W. B. Schofield & G. Godfrey 67662* (NY 00159540).
- U.S.A. Pennsylvania:** Pocono Mts., Buck Hill Falls, near the Inn, 9 May 1947, *H. S. Blair* s.n. (NY 00481490); McKean County, rocks on moist shaded sandstone, 12 Mar 1897, *Burnett 601* (NY 00481207). **Virginia:** Botetourt County, on boulder in shade, 22 Jun 1959, *P. M. Patterson 2914* (NY 00506587).
- Plagiothecium angusticellum*. U.S.A. Connecticut:** Windham County, town of Westford, Yale Myers Forest, Boston Hollow, along Boston Hollow Road, between Eastford Road and Barlow Road, mixed conifer-hardwood forest with extensive rock outcrops, 19 Sep 2009, *W. R. Buck 55530* (NY 01136516). **West Virginia:** Tucker County, Monongahela National Forest, Dolly Sods Wilderness, Red Creek trail, humid mixed hardwood-hemlock forest with acidic rock outcrops along the river, in calcareous seeping in a vertical rockface, 38°58'22"N, 79°23'51"W, elev. 800 m., 04 Jul 2014, *B. Goffinet 11795* (NY 02331429).
- Plagiothecium succulentum*. CANADA. Labrador:** *A. C. Waghorne* s.n. (NY 00163504). **Ontario:** Agloma District, 1.3 miles north of Agawa River on Rt. 17 on east side of road in rocky cliffs and valleys, conifers in lower part and maples in area on top of hill, 31 May 1958, *C. M. Wetmore 1148* (NY 00164186); 01 Jul 1935 (NY 00164187); Owen Sound, West Hill, on tree roots in woods, 1 Jul 1935, *E. A. Moxley* s.n. (NY 00163508, FH 848924). **Quebec:** Luskville Falls, northeast of Luskville, 45°38'N, 76°00'W, 6 Jul 1969, *R. R. Ireland & L. Ley 10022* (NY 00163481).
- U.S.A.** Deep wooded ravines, on the mountains of New Jersey, New York, and New England (NY 00506571). **Connecticut:** East Haven County, 22 Jun 1879, *J. A. Allen 473483* (NY 00481062). **Georgia:** Rabun County, Chattahoochee National Forest, Rabun Bald, 34°58'N, 83°18'W, elev. 1115–1420 m., mixed hardwoods with gneissic cliffs, 04 Oct 1997, *W. R. Buck 32700* (NY 00481218, NY 00506524). **Maryland:** Garrett County, dripping sandstone ledge in the deep shade under hemlocks, the bank of the Youghiogheny River below Swallow Falls, 8 miles NNW, elev. 2400, 30 Aug 1958, *F. J. Hermann 14,889* (NY 004734911). **Massachusetts:** Barre, *J. W. Grosvenor* s.n. (F C1058822F). **New Hampshire:** White Mts., *Oakes* s.n. (NY 00506573). **New York:** Dec 1867, *C. F. Austin* s.n. (NY 00506565, NY 00505535); Sand Lake (NY 00481214); 17 Jun 1874, *Watkins* s.n. (NY 00481215). **North Carolina:** Macon County, Falls, on Cullasaja River NW of Highlands, in moist shady rocks next to falls, elev. 3500 ft., 12 Aug 1977, *M. L. Hicks 6823* (NY 02682709); Jackson County, vicinity of Woodfin Cascades, Woodfin Mountain, 3 km NW of Balsam Gap, vertical rocks near falls, elev. 1280–1310 m., 35°26'N, 83°06'W, 06 May 1990, *P. L. Redfearn & A. Redfearn 36273* (NY

- 1596884); Mitchell County, Pisgah National Forest, Roan Mt. Gardens, spruce-fir forest with *Rhododendron* and *Sorbus*, elev. ca. 1920 m., 36°06'N, 82°08'W, 24 Sep 1993, *W. R. Buck 24062* (NY 00481196). **Ohio**: Jackson County, on a wet rock, 03 May 1936, *Bartley & Pontius 153* (NY 00506545). **Pennsylvania**: McKean County, Bradford, 04 Aug 1894, *D. A. Burnett* s.n. (FH 00848908). **Tennessee**: Sevier County, above Rocky Spur, Rainbow Falls trail to Mt. Le Conte, Great Smoky Mountains National Park, 28 Jul 1959, *W. B. Schofield 10698* (NY 00506604, F C1058792F). **Vermont**: Newfane, downers Glen, Monchester, 03 Aug 1939, *I. M. Haring* s.n. (NY 00481051); decayed wood and humus, moist ledges, Baker Brook ravine, elev. 1600 m., 16 Aug 1903, 23 Jul 1921, *A. J. Grout* s.n. (NY 00481053, NY 00506594), elev. 1600 m., *A. J. Grout* s.n. (F C1058849F), decayed wood and humus, elev. 1600 ft., 23 Jul 1921 (NY 00506522), moist ledges, 18 Jul 1921 (NY 00481055), 16 Aug 1903 (NY 00481056). **Virginia**: Smyth County, on wet, springy humus at the base of a small cliff, 09 Jul 1956, *P. M. Patterson & R. M. Schuster 2755* (NY 00506584); May–Jun 1892, *A. M. Vail & E. G. Britton* s.n. (NY 00481173, NY 00481174). **West Virginia**: Pocahontas County, Monongahela National Forest, vicinity of Island Camp along Greenbriar River 38°34'46"N, 79°42'17"W, on moist rock, 6 May 1976, *W. R. Buck B940* (NY 01105252); 08 Jun 1934, *C. M. Roberts* s.n. (NY 00481180). **Wisconsin**: Richland County, 0.5 mi. N of Lloyd, NE-facing Cambrian sandstone cliffs along Willow Creek, cool damp shaded lower parts of cliffs, 30 Jun 1974, *M. Nee 12,478* (NY 00481231); 1869, *C. F. Austin* s.n. (NY 00481076, FH 848917).
- Plagiothecium succulentum* f. *propaguliferum*. **U.S.A.** **Vermont**: Mansfield Mt., 8 Aug 1906, *A. J. Grout* s.n. (NY 00506521).