Plagiothecium talbotii, a new species from the Aleutian Islands (Alaska, U.S.A.)

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Abstract

Plagiothecium talbotii sp. nov. is described from Attu Island, Alaska, U.S.A. The newly-described species is not similar in appearance to any Northern Hemisphere species; only the habit is similar to P. platyphyllum. However, it not only occupies a different habitat than that species, but genetically and morphologically, it is clearly distinct from it. The results of DNA sequencing, a detailed description of the morphological features, illustrations, ecological preferences and currently known geographical distribution of P. talbotii are presented. The most important distinguishing morphological features of this species are: the size of the plant; dimensions and symmetry of the leaves; dimensions of cells and their areolation; entire leaf apex; and long decurrencies with some inflated cells. Additionally, we propose to place P. talbotii in section Plagiothecium, which is confirmed by genetic analysis and morphological features.

Keywords

Attu Island, Bryophyta, Plagiotheciaceae, S. S. Talbot, taxonomy

Introduction

Herbarium collections are unquestionably a rich and very important source of data on the ecology and distribution of plants. Revisions based on herbarium material are the primary source for taxonomic research. Now, having a number of methods at our
disposal (e.g. genetic analyses, mathematical modelling, SEM), integrative taxonomy sheds new light not only on the status or distribution of the taxa studied, but also on the relationships between them and not only at the species level (e.g. Huttunen et al. 2018; Guerra et al. 2019; Ignatov et al. 2020; Plášek and Ochyra 2020; Vigalondo et al. 2020; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2020; Melamed et al. 2021).

Despite the fact that the Northern Hemisphere is relatively well studied botanically, there are still many areas that are blank spots for this part of the world. The same is true for bryophytes as for vascular plants, but even more so. Many species, genera and even families require basic research related to their variability, distribution, ecology or taxonomic status (Anderson et al. 1990; Ignatov et al. 2006; Hodgetts 2015; Suzuki 2016; Hodgetts and Lockhart 2020; Wolski et al. 2021a, b).

The genus *Plagiothecium* Schimp. which currently has been divided by Wynns et al. (2018) into nine sections (*Leptophyllum* Jedl.; *Lycambium* Jedl.; *Ortholimnobium* (Dixon) J.T. Wynns; *Orthophyllum* Jedl.; *Plagiothecium*; *Pseudo-Neckera* (Kindb.) J.T. Wynns; *Rectithecium* (Hedenäs & Huttunen) J.T. Wynns; *Saviczia* (Abramova & I.I. Abramov) Z. Iwats.; *Struckia* (Müll. Hal.) J.T. Wynns) over the past decades may give the impression of being well-researched. However, the genus was described as fairly species-poor and represented in the Northern Hemisphere by only a dozen taxa (e.g. Ireland 1969, 1986; Iwatsuki 1970; Lewinsky 1974; Smith 2001). The understanding of *Plagiothecium* has changed relatively recently, when DNA-based research proved that many of the taxa have been too broadly circumscribed (Zuo et al. 2011; Wynns et al. 2018; Ignatova et al. 2019; Wolski and Nowicka-Krawczyk 2020) and that the bryoflora of North America, Europe and Asia is much richer in *Plagiothecium* than previously assumed (e.g. Wynns et al. 2018; Ignatova et al. 2019; Wolski, Jukoniné 2019; Wolski 2020a, b; Müller and Wynns 2020; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2021b).

However, despite extensive research now being carried out, the number of Northern Hemisphere species still seems to be underestimated. Alaska, including the Aleutian Islands, are a “blank spot” in our knowledge of mosses, including the genus *Plagiothecium*. As a result of the taxonomic revision of *Plagiothecium* from the Aleutians, we recently described a new species, *Plagiothecium schofieldii* (Wolski et al. 2021a). Examination of additional material resulted in yet another undescribed species being discovered.

**Materials and methods**

**Taxonomic analyses**

Specimens from the Missouri Botanical Garden (MO), the University of British Columbia (UBC) and The New York Botanical Garden (NY) were analysed during the revision of *Plagiothecium* from the Aleutian Islands. A single specimen (MO 5925637) was selected for DNA analysis, with the appropriate consent from the herbarium curator.
DNA isolation, amplification and sequencing

Total DNA was extracted using the GeneMATRIX Plant & Fungi DNA Purification Kit (Eurx, Gdansk, Poland) following the manufacturer’s protocol. Three equal samples of 20 mg of dry tissue from the leafy stems of bryophytes were homogenised in the lysis buffer, delivered by the purification kit, using a hand-held stainless steel homogeniser (Schlüter Biologie, Eutin, Germany). DNA extracts were quantified with a BioDrop DUO Spectrophotometer (BioDrop Ltd, Cambridge, U.K.) and the sample with high quality DNA (1.7–1.9 OD\text{260} /OD\text{280}) was selected for further analysis.

The molecular research was based on nuclear and chloroplast DNA markers: ITS (from the 3' end of the nuclear spacer ITS1, through the 5.8S rDNA, to the 5' end of the ITS2 spacer); and \textit{rpl16} cpDNA gene encoding ribosomal protein L16. Markers were selected, based on Wynns et al. (2018), Wolski and Nowicka-Krawczyk (2020) and Wolski et al. (2021) from \textit{Plagiothecium}-focused studies.

All markers were amplified by PCR in a few replicates to obtain high quality amplicons for sequencing. PCR was performed using primers and reaction conditions as described in Wolski et al. (2021).

PCR products were visualised on an agarose gel (1.5%, 90V, 40 minutes) stained with GelRED fluorescent dye (Biotum, Fremont, CA, U.S.A.) and two replicates of each marker per sample were chosen for sequencing. Amplicons from the PCR reaction were cleaned using Syngen Gel/PCR Mini Kit (Syngen Biotech, Wroclaw, Poland) according to the manufacturer’s protocol. Samples were sequenced with Sanger sequencing, using primers from amplification by SEQme s.r.o. company (Dobris, Czech Republic). The obtained sequences were assembled in Geneious 11.1.5 (Biomatters Aps, Aarhus, Denmark) (http://www.geneious.com). The sequences were submitted to the NCBI GenBank database (www.ncbi.nlm.nih.gov) under the accession numbers OM337522 for ITS and OM311940 for \textit{rpl16}.

Phylogenetic analyses

Phylogenetic analyses of the studied specimen and other species in the \textit{Plagiothecium} group (Table 1) were performed, based on a concatenated ITS-\textit{rpl16} sequence matrix. Sequences were aligned using the MAFFT v. 7 web server (Katoh et al. 2017) (http://mafft.cbrc.jp/alignment/server/) where the auto strategy was applied, the scoring matrix of 200PAM with Gap opening penalty of 1.53, UniREF50 for Maft-homologs and Plot and alignment with threshold of 39 score were set. The obtained alignments were checked for poorly and ambiguously aligned regions and small corrections were made by eye. The evolutionary models were calculated using PartitionFinder 2 software (Lanfear et al. 2016), chosen according to the Akaike Information Criterion (Table 2).

Phylogenetic calculations were performed using Maximum Likelihood analysis (ML) in the IQ-TREE web server (Trifinopoulos et al. 2016) (http://iqtree.cibiv.univie.ac.at/) with the ultrafast bootstrap (UFBoot) pseudolikelihood algorithm (Hoang et al. 2018) and 10000 replicates; and Bayesian Inference (BI) in MrBayes 3.2.2 (Ronquist et al. 2012)
Table 1. Voucher information and accession numbers for the specimens included in the phylogenetic analyses.

| Taxon                                      | Collection             | Locality                        | ITS       | rpl16      |
|--------------------------------------------|------------------------|---------------------------------|-----------|------------|
| Isopterygiopsis pulchella                  | UC barcode 1947397     | USA: CA                         | KY550336  | KY514042   |
| P. angusticellum                           | Wolski 5               | Poland                          | MN077501  | MN311136   |
| P. angusticellum                           | Wolski 22              | Poland                          | MN077507  | MN311142   |
| P. angusticellum                           | Wolski 23              | Poland                          | MN077508  | MN311143   |
| P. angusticellum                           | Wolski 25              | Poland                          | MN077510  | MN311145   |
| P. angusticellum                           | Wolski 26              | Poland                          | MN077511  | MN311146   |
| P. angusticellum                           | Wolski 29              | Poland                          | MN077513  | MN311148   |
| P. brasiliense                              | E barcode 00387968     | Brazil                          | KY550266  | KY513971   |
| P. cavifolium                              | CP; J.T. Wynns 1885    | Denmark: Sjaelland              | KF882225  | KF882325   |
| P. cavifolium                              | CP; J.T. Wynns 2960    | Germany: Schauinsland, Hochschwarzwald | KF882226 | KF882326 |
| P. conostegium                             | NY:S.P. Churchill et al. 19839 | Bolivia                      | KY550271  | KY513976   |
| P. conostegium                             | NY barcode 00845279    | Guatemala                       | KY550318  | KY514024   |
| P. conostegium                             | S-B53327               | Mexico                          | KY550272  | KY513977   |
| P. denticulatum                            | CP; J.T. Wynns 2081    | Denmark: Sjælland, Soro Kommune | KF882229  | KF882329   |
| P. denticulatum                            | BONN: O.M. Aphonina s.n. | Russia: Far East, Chukotka     | KF882275  | KY513980   |
| P. denticulatum var. bulbulae              | UC barcode 1798690     | USA: NV                         | KY550278  | KY513983   |
| P. denticulatum var. bulbulae              | UC barcode 1947417     | USA: CA                         | KY550277  | KY513982   |
| P. denticulatum var. obtusifolium          | CP; J.T. Wynns 2842    | Germany: Hochschwarzwald, Schauinsland | KF882230 | KF882330   |
| P. denticulatum var. obtusifolium          | UC barcode 1724036     | USA: WA                         | KY550279  | KY513984   |
| P. denticulatum fo. pungens                | DUKE barcode 0150010   | USA: Alaska, Simonof Island     | KY550280  | KY513985   |
| P. japonicum                               | DUKE barcode 0172241   | USA: Alaska, Simonof Island     | KY550291  | KY513996   |
| P. lamprostachyi                           | S-B54613               | Australia: VIC                  | KY550284  | KY513989   |
| P. lamprostachyi                           | DUKE barcode 0156846   | Australia: VIC                  | KY550285  | KY513990   |
| P. lamprostachyi                           | S: H. Streimann 47719  | Australia: NSW                  | KY550282  | KY513987   |
| P. longisetum                              | Wolski 12              | Poland                          | MN077502  | MN311137   |
| P. longisetum                              | Wolski 14              | Poland                          | MN077503  | MN311138   |
| P. longisetum                              | Wolski 15              | Poland                          | MN077504  | MN311139   |
| P. longisetum                              | Wolski 19              | Poland                          | MN077506  | MN311141   |
| P. membranosalum                          | BONN; j.-P. Frahm 7756 | Democratic Republic of the Congo | KY550310 | KY514015   |
| P. membranosalum                          | S-B78514               | South Africa                    | KY550303  | KY514008   |
| P. membranosalum                          | DUKE barcode 0016754   | South Africa                    | KY550304  | KY514009   |
| P. nemorale                                | CP; J.T. Wynns 3044    | Germany: Farnberg, Schwarzwald-Baar | KF882239 | KF882339   |
| P. nemorale                                | CP; J.T. Wynns 2684    | Germany: Mooswald, Kaisersruh   | KF882237  | KF882337   |
| P. nemorale                                | Miebler 3835           | Iran: Sisangan National Park, Manzandaran Prov. | KF882238 | KF882338   |
| P. ovalifolium                             | DUKE barcode 0188886   | Chile                           | KY550314  | KY514019   |
| P. platyphyllum                            | C; J. Lewinsky et al. s. n. | Finland: Haluna, Nilssie, Savonia borealis | KF882241 | KF882341 |
| P. ruthei                                  | CP; J.T. Wynns 1997    | Denmark: Sjælland, Lyngby Aamose | KF882242  | KF882342   |
| P. talbottii                               | W.B. Schofield, S.S. Talbot 120206, MO 5925637 (dupl. UBC B193528) | USA: Alaska, Aleutian Island | OM337522 | OM311940 |
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where two parallel Markov Chain Monte Carlo (MCMC) runs for four million generations each, with trees sampled every 1000 generations. The average standard deviation of split frequencies in both cases remained below 0.01 for the last 1000 generations and posterior probabilities were estimated from the 50% majority-rule consensus tree after elimination of the first 25% of samples as burn-in. The alignment and tree files were submitted to the figshare online database (https://doi.org/10.6084/m9.figshare.18586082.v1).

Haplotype network analysis was performed using Median Joining Network in PopART v. 1.7 with gap coding as a single event, irrespective of length and haplotype geographic distribution (Leigh and Bryant 2015).

Results and discussion

Phylogenetic analyses using the concatenated ITS-rpl16 matrix placed this Alaskan specimen within the sister branch of the sect. Plagiothecium clade with high support from Bayesian Inference (PP = 0.99), but slightly lower support from Maximum Likelihood (BS = 87) (Fig. 1). Although the topology of the tree shows clear distinction of the examined material, the closest representative with maximum support from BI to P. talbotii is the specimen BONN: O.M. Afonina s.n. described as P. denticulatum.

The haplotype network (Fig. 2) also confirms a closer relationship of P. talbotii with sect. Plagiothecium than with representatives from sect. Orthophyllum; however, the position of P. talbotii is isolated. The lowest number of mutational steps to P. talbotii as mentioned earlier is the specimen BONN: O.M. Afonina s.n. of P. denticulatum. This material was collected from the Far East of Russia – from Chukotka (Table 1), a geographic region adjacent to Alaska.

Although DNA analysis places the tested specimen as a sister clade to the clade represented by taxa from section Plagiothecium, it is morphologically different from most of the representatives of this section.

The shape of the decurrent angular cells is one of the most important features that divide the taxa of this genus into individual sections (Wynns et al. 2018; Wolski et al. 2021a, b). Almost all taxa from sect. Plagiothecium form distinct auricles, but not P. talbotii. The alar regions in this species are long and composed of sometimes inflated cells, a feature common to both P. talbotii and P. platyphyllum (Nyholm 1965; Lewinsky 1974; Smith 2001).

Table 2. Summary of partitions for ITS-rpl16 matrix (1526 bp) evolutionary model selection and phylogenetic interference using PartitionFinder2.

|             | ITS1 | 5.8S gDNA | ITS2 | rpl16 intron | rpl16 codon |
|-------------|------|-----------|------|--------------|-------------|
| ML          | F81  | JC        | 5.8S | JC           | F81         |
| BI          | F81  | JC        | HKY  | HKY +I       | GTR         |

Having leaves shrunken in a dry condition and symmetrical make P. talbotii resemble, amongst the Northern Hemisphere of Plagiothecium, the previously-mentioned P. platyphyllum (Lewinsky 1974; Smith 2001). However, P. talbotii is distinguished from P. platyphyllum by the size of the leaves; lack of serration near leaf apex; lack of a group of
eroded, thin-walled cells (nematocysts) and rhizoids near the leaf apex; dimensions of laminar cells; and habitat occupied by the species (Nyholm 1965; Lewinsky 1974; Smith 2001).

Amongst the Northern Hemisphere species belonging to sect. *Plagiothecium* at present, there is only one species characterised by a symmetrical leaf: *P. schofieldii*. However, for example, the size and appearance of the turf; the lack of shrinkage and leaf shape, i.e. their concavity and serration and the shape of the decurrent angular cells differentiates this species from *P. talbotii* (Wolski et al. 2021b).

**Figure 1.** Phylogenetic tree of *Plagiothecium* taxa (sect. *Plagiothecium* [upper] and *Orthophyllum* [lower clade] with *Isopterygiopsis pulchella* as the outgroup, based on concatenated nuclear (ITS1-5.8S-ITS2) and chloroplast (*rpl*16) DNA markers (total 1526 bp). The tree presents the position of the studied specimen from Alaska amongst *Plagiothecium*. Numbers on branches indicate bootstrap values from ML followed by posterior probabilities from BI analysis. An asterisk (*) indicates 100 (ML) and 1.00 (BI), while a minus sign (-) indicates values below 75 (ML) and 0.95 (BI). The topology of the tree was based on ML analysis.
Other species of this section are characterised by asymmetrical to slightly asymmetrical leaves and a completely different set of features when compared with *P. talbotii* (e.g. Lewinsky 1974; Smith 2001; Wolski et al. 2021b).

Taking into account the above facts, we believe that this species belongs to *Plagiothecium* sect. *Plagiothecium*. Thus, we consider that all the above morphological data, supported by molecular studies, warrant the recognition of the Aleutian samples as a new species.

**Taxonomy**

*Plagiothecium talbotii* G.J.Wolski & W.R.Buck, sp. nov.

**Type.** U.S.A. Alaska, Attu Island, Lake Elwood area, under tall herbs on slope, 52°51’N, 173°10’E, 14 Sep 2002, W.B. Schofield and S.S. Talbot 120206, **holotype** MO 5925637, **isotype** UBC B193528.

**Description.** Plants large, dark green, without metallic luster, forming loose mats. Stems erect, julaceous in the lower part, more complanate above, 3.0–5.0 cm long (Fig. 3), very thick, in cross-section rounded, with a diameter of 500–700 μm, the central strand very well developed, epidermal cells 16–43 (M 25) × 12–39 (M 25) μm, the parenchyma thin-walled, 25–50 (M 36) × 18–60 (M 37) μm; leaves large, concave, symmetrical, ovate, imbricate, in wet condition, rather closely arranged on the stem,
Figure 3. The most important taxonomic features of *Plagiothecium talbotii*. Stem (A) in dry condition; leaves from the middle of the stem (B), dimensions of cells from the apex (C), the middle (D) and basal part of the leaf (E). Drawing by G.J. Wolski from the holotype (*W.B. Schofield and S.S. Talbot 120206, MO 5925637* [dupl. UBC B193528]). Scale bars: 1 cm (A); 1000 μm (B); 100 μm (C–E).
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shrunken and sticking out when dry, those leaves from the middle of the stem 3.8–5.0 (M 4.4) mm long and the width measured at the widest point 1.9–3.1 mm (M 2.4); the apex obtuse and apiculate, entire, not denticulate; costae two, thick, strong and very large, extending usually more than ½ of the leaf length, reaching 1.0–3.0 mm (M 2.0); laminal cells rather symmetrical, in unregulated transverse rows, the length and width very variable, but dependent on location: 83–137 (M 101) × 17–22 (M 19) μm at apex, 100–175 (M 139) × 18–32 (M 24) μm at mid-leaf and 88–197 (M 132) × 22–35 (M 28) μm towards insertion, cell areolation loose; decurrencies very long, 700–1000 μm, composed of 3–4 rows of rectangular, at least some gently inflated cells, 90–216 (M 143) × 24–34 (M 28) μm. Sporophytes unknown so far.

**Etymology.** The present species is named in honour of Stephen S. Talbot who spent decades studying the northern regions of North America, including the Aleutian Islands and who, with Wilfred B. Schofield on 14 September 2002, collected the specimen (No. 120206), chosen here as the holotype of *Plagiothecium talbotii*.

**Distribution and ecology.** *Plagiothecium talbotii* so far has only been recorded from Attu Island in Alaska. In this area, it has been recorded in a non-forested area, on a slope, under tall herbs.

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