

## Article

# Revision of the *Plagiothecium cavifolium* complex (Bryophyta: Plagiotheciaceae)

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**Abstract:** In the Northern Hemisphere, *Plagiothecium cavifolium* is currently one of the most widely distributed species. This taxon has been described as extremely variable for decades, but the reasons for this variability have not been investigated in detail. The analysis of original materials and diagnoses, as well as a detailed analysis of the history of names considered as synonyms of *P. cavifolium sensu lato*, showed that in terms of qualitative and quantitative characteristics, a number of the names of this complex differ significantly from the diagnosis of *Hypnum cavifolium* (basionym of *P. cavifolium*). The most important features distinguishing individual taxa include: julaceous stems; imbricate leaves, their symmetry, concavity; serration of leaf apices; the length of the cells from the middle part of the leaf; and the orientation of the capsules. Thus, the research conducted within *P. cavifolium sensu lato* made it possible to distinguish seven separate taxa: *P. cavifolium* (= *P. cavifolium sensu stricto*), *P. flaccidum*, *P. tenue* (being a new combination), *P. ikegamii*, *P. subjulaceum*, *P. sakuraii* and *P. otii* (four resurrected species). In addition, the analysis of original materials and the diagnosis of several taxa allowed them to be excluded from the described complex, and here we propose their synonymization with other taxa, such as *P. longisetum* and *Hygrohypnum luridum*. Photographic documentation and a key to distinguishing species within the described complex are attached. For two names (*P. sakuraii* and *P. succulentum* var. *longifolium*) lectotypes are proposed.

**Keywords:** diagnosis; *Hypnum cavifolium*; new combinations; *Plagiothecium flaccidum*; *P. ikegamii*; *P. otii*; *P. sakuraii*; *P. subjulaceum*; *P. tenue*; synonymy; taxonomy



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## 1. Introduction

*Plagiothecium cavifolium sensu lato* is listed from almost all countries of Eurasia and on both coasts of North America. Similarly, the *P. denticulatum* and *P. nemorale* complexes have a comparable distribution in the Northern Hemisphere, and along with *P. cavifolium*, they are the most common and widespread species in the genus [1–3].

The basionym of *Plagiothecium cavifolium* (Brid.) Z.Iwats. is *Hypnum* (*Stereodon*) *cavifolium* La Pyl. ex Brid., which was published in *Bryologia Universa* [4]. In the diagnosis, the author stated, e.g., this species is characterized by concave, entire (not serrate), julaceous leaves and inclined capsules. Now, after almost 200 years, Wolski [5] stated that this taxon is very variable and probably is too broadly interpreted. On the other hand, despite the described outstanding variability, in the latest taxonomic studies, only one infraspecific within it is distinguished—*P. cavifolium* var. *orthocladium* (Schimp.) Z.Iwats. [3].

The abovementioned infraspecific variability of the *Plagiothecium cavifolium* complex affects qualitative and quantitative characteristics [5]. Thus, various individual authors have indicated that this taxon is small, medium to large-sized [6–9]; pale green to yellowish [1,6,8,10–12]; glossy [1,6,8]; with a more or less distinct metallic luster [6]; forming loose



or dense mats [6,10,11]. Stems are ascending to erect or sometimes prostrate [1,6,9,12,13]; julaceous to subjulaceous or rarely complanate-foliate [1,6,7,9–14]. The leaves of *Plagiothecium cavifolium sensu lato* are symmetric or sometimes slightly asymmetric [1,6–8,10,11,13–15]; imbricate or loosely imbricate [1,6–9,12]; concave or slightly complanate [1,7–16]; ovate, ovate-lanceolate to lanceolate [1,6,8–11]; shrunken when dry [6,9] and sometimes plicate when moist [10,11,14]. The leaves are rather small,  $1.0\text{--}3.0 \times 0.3\text{--}1.4$  mm [1,6,8–11,13,15–17]; the apices are usually acute, shortly apiculate or acuminate [1,6,8,9,13]; margins are entire or seldom with a few denticulations [1,6,7,9–11,14]. The cells from the middle part of the leaf of the analyzed taxon are elongate, almost linear, flexuose to narrowly linear or even linear-rhomboidal [6,8–11], and they reach  $40\text{--}161 \times 7\text{--}17$   $\mu\text{m}$  [1,6–15,17].

By comparing the characteristics listed above with the data contained in the diagnosis of *Hypnum cavifolium* [4], it is easy to see that the taxon is now too broadly described and recognized. Thus, taking into account the above facts, research has been undertaken to revise all available types, original materials and diagnoses of all names belonging to *P. cavifolium sensu lato* and to analyze to the fullest possible extent the history of names related to the described taxon.

## 2. Materials and Methods

### 2.1. Taxonomic Analyses

Before starting the research, efforts were made to obtain as many as possible of the types and original materials of names currently considered synonyms of *Plagiothecium cavifolium sensu lato*. Thus, it was revised: *Hypnum roeseanum* Hampe (JE04004196, JE04004197, JE04004199, JE04004198); *H. sullivantiae* Schimp. ex Sull. (PC0132606, PC0132607, PC0132608); *Leskea flaccida* Brid. (B31076701); *Plagiothecium apiculatum* Sakurai in sched. (MAK B115140); *P. attenuatirameum* Kindb. (PC0132687); *P. fujiyamae* Sakurai in sched. (MAK 57198); *P. nakajimae* Sakurai (MAK B57158); *P. otii* Sakurai (MAK B16360); *P. roeseanum* fo. *umbrosa* Mönk. (HBG021131); *P. roeseanum* var. *alpinum* Kern (PC0132603); *P. roeseanum* var. *angustirete* Warnst. (JE4004200); *P. roeseanum* var. *japonicum* Cardot (PC0132574); *P. sakuraii* Reimers (MAK B609; PC0132597); *P. sylvaticum* var. *cavifolium* Jur. in Rabenhorst (PC0132571); and *P. takahashii* Sakurai (MAK B9398). An attempt was made to see all types and authentic material but was unsuccessful in some cases.

Together with original materials, all available diagnoses of names currently considered as synonyms of *Plagiothecium cavifolium sensu lato* were analyzed, e.g., [4,6,10,11,15,18–49]. Moreover, other types in *Plagiothecium* have been revised and are included in the current study: *P. propaguliferum* Broth. in sched. (PC0132610); *P. silvaticum* var. *latifolium* Röhl [26] (HBG21134); and *P. succulentum* var. *longifolium* Mönk. (JE 4004211, JE 4004212).

### 2.2. Statistical Analyses

Original materials and types were examined morphologically for qualitative and quantitative characteristics. The features were selected taking into account those given in the protologue of *Hypnum cavifolium* as well as the currently most important taxonomic revisions of this genus, e.g., [6,14]. A total of 18 specimens (original materials and types) were examined in detail. From each of them, leaves were torn from the middle part of the stem for further examination. Thus, the following characters were analyzed: symmetry (symmetrical or asymmetrical); concavity (concave or flat); serration (serrate or entire) and the folding of the leaves (longitudinal, transverse or not folded); shape of the apex; the presence of decurrencies and the shape of the cells forming them (rectangular and square or round and inflated); length and width of the cells of the central part of the leaves (in this case, five cells from each leaf were randomly measured and subjected to further analysis) and capsule orientation (erect or inclined).

For statistical analysis of the obtained results, the data were summarized. In the case of qualitative traits, depending on the presence or absence of each feature, they were given the value “0” or “1” (“0” when there is an absence, and “1” if the feature is present). However, in the case of quantitative traits to convert continuous into ordinal data, the



range of variability of a given feature was divided into two equal parts, giving “0” for the lower and “1” for the higher values. Therefore, for the length of the cells whose range of variability of studied specimens is from 25 to 175 µm, “0” was adopted for values from 25 to 100 µm, whereas “1” was used for 101–175 µm. Similarly, for cell width, “0” was adopted for values from 6 to 11 µm, whereas “1” was adopted for 12–16 µm.

All source data (Raw data) used in the manuscript are available at the link ([https://drive.google.com/drive/folders/1ZZRoEOiARwqgOyDny0rEw\\_j7jsN8t44?usp=sharing](https://drive.google.com/drive/folders/1ZZRoEOiARwqgOyDny0rEw_j7jsN8t44?usp=sharing), accessed on 18 July 2022). The similarity between the analyzed specimens was calculated in the PAST v. 4.08 program (Øyvind Hammer, Natural History Museum, University of Oslo, Norway); due to the nature of the data (binary data), the Jaccard distance and the UPGMA joining method were used.

### 3. Results

*Plagiothecium cavifolium sensu lato* and the history of this name is primarily related with four names: *H. cavifolium*, *H. sullivantiae*, *P. orthocladium* and *P. roeseanum*. Nevertheless, over the nearly 200-year history of this taxon, dozens of subspecies, varieties and forms have been described. Most of them are related to the four abovementioned species, the others with, e.g., *P. sylvaticum auct. non* (Brid.) Bruch and Schimp. and *P. denticulatum* (Hedw.) Schimp. In addition, until the mid-twentieth century, a dozen species were described that are now considered synonyms of *P. cavifolium*, including, e.g., *Leskea flaccida*, *P. attenuatirameum*, *P. ikegamii*, *P. insigne*, *P. otii*, *P. sakuraii*, and *P. takahashii*. The most important aspects related to the history of the name *Plagiothecium cavifolium sensu lato* are presented below.

#### 3.1. *Hypnum cavifolium*

*Hypnum cavifolium* (Figure 1), as *Hypnum cavifolius*, being the basionym of *P. cavifolium*, was described by Bridel [4]. The author described this species as a plant with ovoid, concave, non-serrate leaves, and with elongate and inclined capsules. Additionally, he compared *H. cavifolium* with other taxa, suggesting that the most important features distinguishing this species from others are the julaceous stem and concave, non-serrate leaves [4].

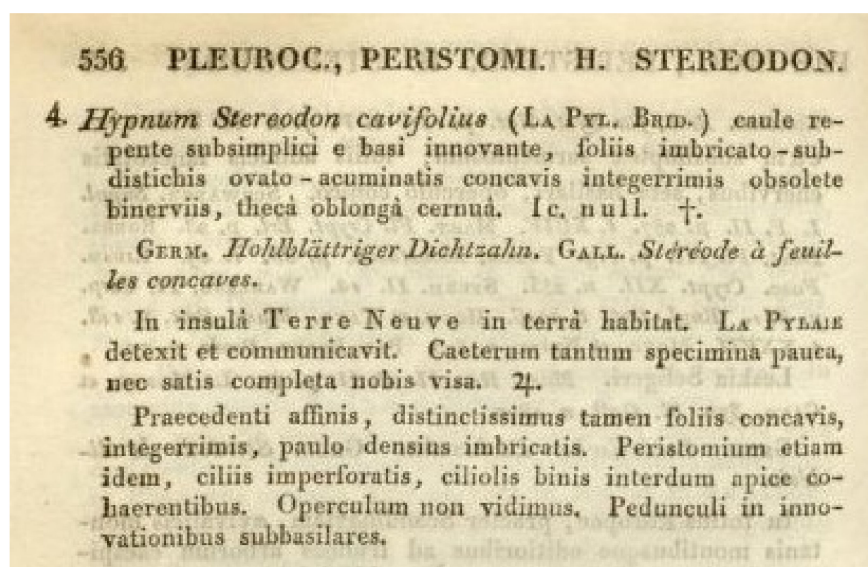


Figure 1. Diagnosis of *Hypnum* (*Stereodon*) *cavifolium* [4].

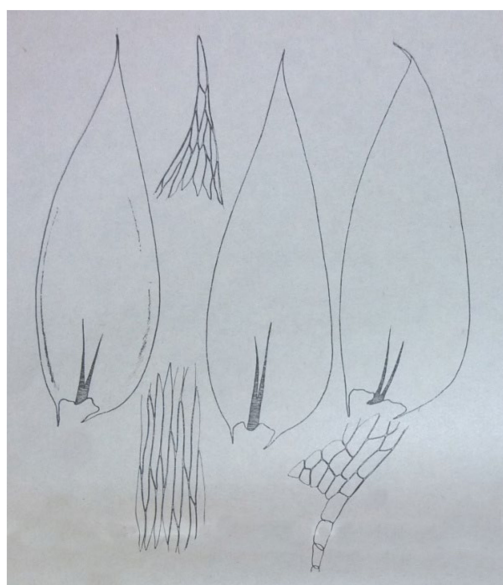
In the 19th century, the name “*cavifolius*”, as “*cavifolium*”, appears at the varietal level of *Plagiothecium sylvaticum*—*P. sylvaticum* var. *cavifolium* Jur. in Rabenhorst [50] and *P. denticulatum*—*P. denticulatum* var. *cavifolium* Röhl [25], but they appear not to be homotypic with *P. cavifolium*. Nevertheless, at the end of the 19th and at the beginning of the 20th



centuries, it was very quickly replaced by a different name (*P. roeseanum*) and forgotten. This state lasted almost to the end of the 20th century until the revision of *Plagiothecium* by Iwatsuki [6].

Iwatsuki [6] studied original specimens of *Hypnum cavifolium* and pointed out that they are identical to the materials called *P. roeseanum*, and because *H. cavifolium* was published earlier, he proposed a new combination for this taxon—*Plagiothecium cavifolium*. Additionally, Iwatsuki [6] indicated that specimens of *H. cavifolium* are characterized by julaceous stems with overlapping very concave symmetrical leaves. These characteristics correspond to the features given by Bridel [4]. However, Wynns [51] described *P. cavifolium* as small plants with erect stems, and concave and folded leaves with short sporophytes and inclined capsules. Moreover, that author claimed that large creeping forms are also present and may resemble *P. succulentum* with concave leaves.

On the other hand, Iwatsuki [6] characterized *P. cavifolium sensu lato* as plants with more or less julaceous stems, almost symmetrical or sometimes slightly asymmetrical leaves, entire or serrate margins at apex and short costae. This variability is reflected in the forms and varieties proposed by him [6]. One of them is *P. cavifolium* fo. *acuminatum* (Jedl.) Z.Iwats. being a new combination of the form described by Jedlička [10]—*P. roeseanum* fo. *acuminatum* Jedl. (Figure 2). Both Jedlička [10] and Iwatsuki [6] characterized this taxon as plants with non-julaceous stems with slightly concave or practically flat leaves. The analysis of the figures attached to these studies also shows that the leaves are more or less asymmetrical.



**Figure 2.** Asymmetrical and flat or almost flat leaves of *P. roeseanum* fo. *acuminatum* from Jedlička [11] (changed).

Another combination proposed by Iwatsuki [6] is *P. cavifolium* fo. *otii* (Sakurai) Z.Iwats., which is characterized as non-julaceous plants with slightly concave serrate and long-decurrent leaves. The basionym of this taxon was proposed in the mid-20th century as *P. otii* [46]. Iwatsuki [6] also proposed a new combination for a taxon described in the 19th century, *P. orthocladium*, treating it as a variety—*P. cavifolium* var. *orthocladium*. However, in his revision, he did not characterize it in any way. Wynns [51], on the other hand, described this variety as plants with lustrous and julaceous stems and folded, ovate leaves; sometimes with wide cells. He also used that name to describe “olivaceous, boreal collections with crispate, spreading leaves.”

Another combination given by Iwatsuki [6] is related to Ireland’s [1] concept, which proposed synonymizing *P. fallax* Cardot and Thér. with *P. roeseanum* (= *P. cavifolium*). Iwatsuki [6] proposed treating this taxon as a variety—*P. cavifolium* var. *fallax* (Cardot and



Thér.) Z.Iwats. However, currently, as indicated by molecular analyzes, *P. fallax* is treated as a separate species unrelated to *P. cavifolium sensu stricto* [3,51,52].

The analysis of the history of names related to *P. cavifolium* ends with a variety proposed at the end of the 20th century—*P. cavifolium* var. *imbricatum* Ukrainka [49]. The author described it as very small, densely foliate plants with imbricate, strongly concave leaves, acute apex and short decurrencies.

### 3.2. *Plagiothecium orthocladum*

This species has been described as a plant with densely foliate stems and ovoid-lanceolate, concave, non-serrate leaves with inclined capsules. Moreover, the analysis of the attached figure shows that the leaves are symmetrical (Figures 3 and 4) [18]. Five years later, Schimper [19] proposed a new combination for this taxon, treating it as a variety of *Plagiothecium sylvaticum*—*P. sylvaticum* var. *orthocladum* (Schimp.). Schimp. thus presented a fairly broad understanding of *P. sylvaticum*, which is now a synonym of *P. nemorale* (Mitt.) A.Jaeger. Some 26 years later, Husnot [53] also considered this taxon as a variety—*H. sylvaticum* var. *orthocladum* (Schimp.) Husn., whereas Hérubaud [34] treated this taxon as a variety of *P. denticulatum*—*P. denticulatum* var. *orthocladum* (Schimp.) Hérub.

Schimper [19], followed by Lindberg [21], recognized this taxon as a variety of *P. sylvaticum* (nom. illeg. orthogr. pro *P. sylvaticum* (Brid.) Bruch and Schimp.) as *P. sylvaticum* var. *β orthocladum* (Schimp.) Lindb. This error was duplicated in many studies and persisted for the next decades, and the name “*orthocladum*” can be found in, e.g., *Synopsis Muscorum Europaeorum* [20], *Les muscinées d’Auvergne* [34] or *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* [54]. This name, as a variety, even appears with *P. denticulatum* as *P. denticulatum* var. *orthocladum* (Schimp.) Warnst. [32].

As mentioned above, Schimper [19], Lindberg [21] and Barkman [15] associated this taxon with *Plagiothecium sylvaticum*, treating it as a form—*P. sylvaticum* var. *neglectum* fo. *orthocladum* (Schimp.) Barkman. They specified additionally that this plant has leaves shrunk when dry; flat, not serrate, asymmetrical; with long costae and long and wide laminal cells (130–225 × 24 µm).

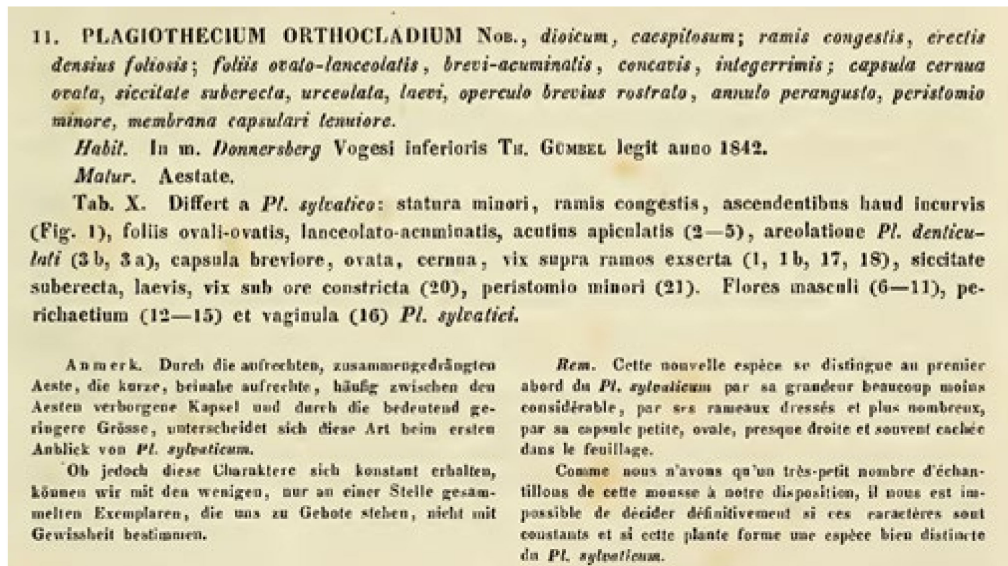


Figure 3. Diagnosis of *Plagiothecium orthocladum* [18].



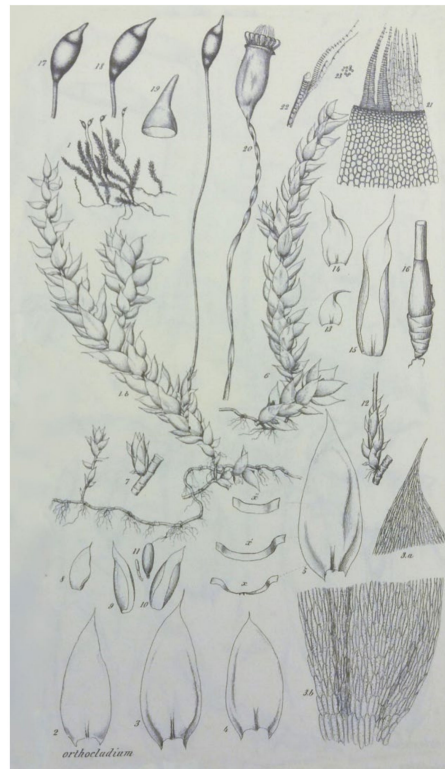


Figure 4. Drawing of *Plagiothecium orthocladum* [18].

In addition, Kindberg [28], as mentioned by Barkman [15], treated *P. silvaticum* very widely and considered the described taxon as a variety—*P. silvaticum* var. *orthocladon* (Schimp.) Kindb. However, he made a mistake in his notation, and the orthographic variant “*orthocladon*” has been used and is found, e.g., in Limpricht [40], who considered it a variety of *P. roeseanum*—*P. roeseanum* var.  $\beta$  *orthocladon* (Hampe ex Schimp.) Limpr. (Figure 5). This author noted additionally that this taxon is characterized by symmetrical and abruptly narrowed leaves. Thereby, the orthographic variant “*orthocladon*” is repeated in many studies and was used in parallel with “*orthocladum*” for the next decades, e.g., [11,33].

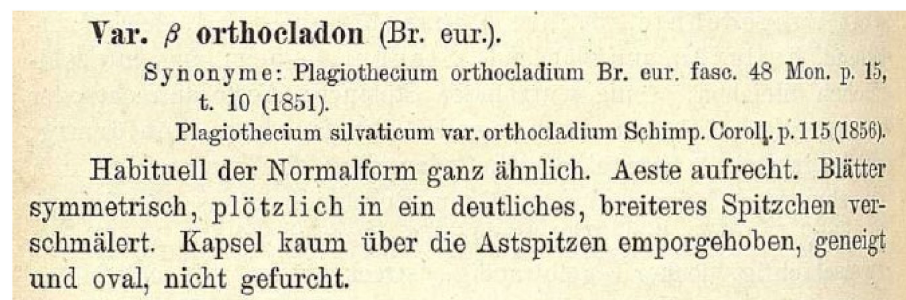


Figure 5. Description of *Plagiothecium roeseanum* var.  $\beta$  *orthocladon* [40].

Limpricht’s [40] point of view mentioned above of regarding this taxon as a variety is also accepted by Jedlička [10], who stated that *Plagiothecium roeseanum* var. *orthocladon* is a plant, e.g., with dense, green or dark yellow, slightly shiny turf; erect, julaceous and densely foliate stems; symmetrical, broadly ovate, concave leaves, with aa abruptly narrowed non-serrate apex; long and narrow laminal cells and short (to 1/3 of the leaf length) costae. Additionally, Jedlička [10] proposed for this taxon a form—*P. roeseanum* var. *orthocladon* fo. *propaguliferum* Jedl., stating in the description that it is characterized only by the presence of gemmae. Some 13 years later, Pilous in Jedlička [48] described a new form for this variety—



*P. roeseanum* var. *orthocladon* fo. *moravicum* Pilous, thus replacing the fo. *propaguliferum* described by Jedlička [10].

### 3.3. *Plagiothecium roeseanum*

Schimper [18] described *Plagiothecium roeseanum* Hampe ex Schimp. based on the unpublished *Hypnum roeseanum* Hampe. In the diagnosis that Schimper gave, these plants are characterized by erect, julaceous, slightly flattened stems; ovate-lanceolate, gently imbricate leaves and almost erect capsules (Figure 6).

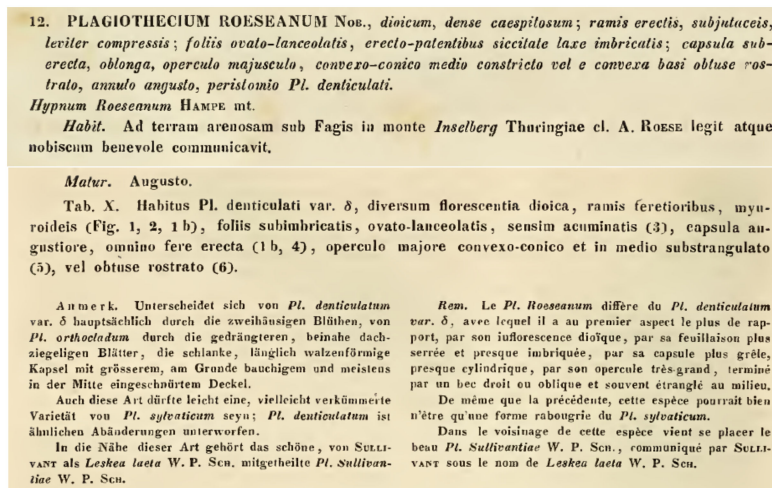


Figure 6. Diagnosis of *Plagiothecium roeseanum* [18].

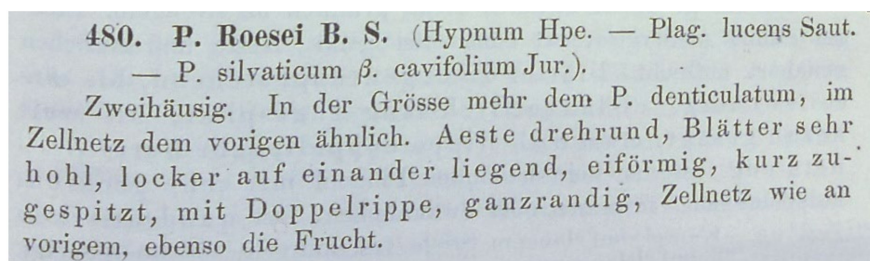
Some 25 years after *P. roeseanum* was described, Schimper [20] wrote this taxon as *P. röseanum*. However, this change (“oe” to “ö”) is only a Germanization for the double-character “oe” in the word *roeseanum*. This way of writing is quite rare in the literature and appears only in a few studies, e.g., in *Index Bryologicus* [55].

For the next decades, *Plagiothecium roeseanum* was used in the literature, e.g., [10,15,33,37,40,56], thus replacing the earlier described *H. cavifolium* [4]. Nevertheless, the understanding of this taxon by individual researchers varied greatly, e.g., Limpricht [40], Mönkemeyer [37] and Barkman [15] interpreted this taxon very narrowly, describing, e.g., that its turf is dense and glossy; its stems are erect or creeping, julaceous, densely foliate; its leaves are imbricate, concave, symmetrical, and entire (non-serrate); its costae are double, very short, reaching  $1/5$ – $1/4$  leaf length with long and narrow cells.

On the other hand, Warnstorf [33] and Jedlička [10] understood this taxon more broadly, sometimes very broadly, but still separately from other species, including *Plagiothecium sylvaticum*. The mentioned researchers reported a very wide range of variability of many taxonomic features of this species, indicating, e.g., that the turf is julaceous or slightly flattened, rarely completely flat; its leaves are mostly symmetrical and very concave or more asymmetrical and less concave and its leaf margins are serrate or not. In Jedlička [10], this concept was particularly reflected in the 21 varieties, forms and subforms of this taxon described by him.

*Plagiothecium roeseanum* was understood differently by Walther and Molendo [57] and Héribaud [34], who treated it as a variety of *P. sylvaticum*—*P. sylvaticum* var. *roeseanum* (Hampe ex Schimp.) Hérib. A similar approach was adopted by Lindberg [21] and Jensen [47], except that the first of them wrote the name incorrectly as *P. sylvaticum*  $\gamma$  *roesei* (Hampe) Lindb. Thus, the orthographic variant “roesei” appeared in many contemporary studies, e.g., [24–28], and the taxon itself was treated as a subspecies—*P. sylvaticum* subsp. *roesei* (Lindb.) Kindb. or a separate species—*P. roesei* (Lindb.) Milde [24] (Figure 7).





**Figure 7.** Description of *Plagiothecium roesei* from Milde [24].

In addition, Braithwaite [35] in his *British moss-flora* adopted Lindberg's [21] point of view regarding this taxon as a variety of *Plagiothecium sylvaticum*, as *P. sylvaticum* var. *β roesii* (Hampe) Braithwaite. The author also made a mistake in the name of basionym of this species, writing it as *Hypnum roesii* (Hampe) Braithwaite [35].

The end of the 19th and the beginning of the 20th century are the times when many new varieties and forms of *Plagiothecium roeseanum* were described. One of them given by Gravet was *P. roeseanum* fo. *laxa* Gravet in Warnstorf, and another by Ruthe [32] was *P. roeseanum* var. *propaguliferum* Ruthe in Warnstorf. On the other hand, Warnstorf [33] also treated this taxon as a form but writing it as *P. roeseanum* fo. *propagulifera* (Ruthe) Warnst.

In his studies, Warnstorf [33,54] proposed further varieties of this taxon: *Plagiothecium roeseanum* var. *flagellaceum* Warnst., *P. roeseanum* var. *angustirete* Warnst. and *P. roeseanum* var. *heterophyllum* Warnst. The first two were characterized as plants sometimes with thin, flagellate stems and symmetrical, concave leaves, while *P. roeseanum* var. *heterophyllum* was described as a plant with flattened, but not julaceous stems; asymmetric, less concave, broadly-ovoid leaves and as a plant similar to *P. sylvaticum* and occupying a similar habitat to that species.

Some 21 years later, Mönkemeyer [37] proposed a new combination of the variety (*Plagiothecium roeseanum* var. *flagellaceum*) described by Warnstorf [33], changing its status to *P. roeseanum* fo. *flagellacea* (Warnst.) Mönk. In his description, Mönkemeyer [37] emphasized, as Warnstorf [33] wrote earlier, that these plants are characterized by long, flagellate stems. The combination proposed by Mönkemeyer [37] was adapted by Jedliček [10], but he wrote it as did Warnstorf [33]—*P. roeseanum* fo. *flagellaceum*. Moreover, he proposed a subform for this taxon—*P. roeseanum* fo. *flagellaceum* subfo. *propaguliferum* Jedl., which was characterized only by the presence of gemmae [10].

In the middle of the 20th century Jedlička [10] proposed a change in the status of the varieties described above, e.g., *P. roeseanum* var. *angustirete* as *P. roeseanum* fo. *angustirete* (Warnst.) Jedl.; *P. roeseanum* var. *heterophyllum* as *P. roeseanum* fo. *heterophyllum* (Warnst.) Jedl. and *P. roeseanum* var. *densum* as *P. roeseanum* fo. *densum* (Warnst.) Jedl., where he pointed out that the latter is characterized by, e.g., julaceous, erect stems and very concave, serrate leaves [10].

At almost the same time, Warnstorf [32,33] and Mönkemeyer [36] proposed a new taxon—*Plagiothecium roeseanum* var. *julaceum* Mönk.—which was characterized as a plant with thick, julaceous stems. However, nine years later Cardot [41] also described a taxon with the same name—*P. roeseanum* var. *julaceum* Cardot (Figure 8). Moreover, this author proposed this variety of the described species—*P. roeseanum* var. *japonicum*. A new variety is also given by Podpěra [38]—*P. roeseanum* var. *basalticum* Podp., which more than half a century later he changed its status to the rank of form—*P. roeseanum* fo. *basalticum* (Podp.) Podp., describing that these plants, e.g., have a loose mesh of cells [39]. The following decades brought a new form described by Mönkemeyer [37], *P. roeseanum* fo. *umbrosa* Mönk., which is characterized as a plant with julaceous foliage but almost flattened at the top of stems.



**Plagiothecium Røseanum** Br. eur. var. nov. **julaceum**  
 Card. — A praecedente ramis julaceis, foliisque valde concavis, late  
 ovatis, abrupte apiculatis distinguitur. Habitu *Rhynchostegio murali*  
 Br. eur. subsimile.  
 Japon : rocher de Zarnishi (n. 3887).

**Figure 8.** Description of the *P. roseanum* var. *julaceum*, hom. illeg. from Cardot [41].

The mid-20th century was a time when many new combinations of *Plagiothecium roseanum* were proposed, with the majority of changes related to transferring taxa at the varietal status to that of form. One of the authors who described many of the types of these new combinations has already been mentioned—Jedlička [10]. His concepts concerned the taxa mentioned above, and also *P. silvaticum* var. *cryptarum* (Renauld and Hérib.) P.Syd. as *P. roseanum* fo. *cryptarum* (Renauld and Hérib.) Jedl. and *P. sylvaticum* var. *filiforme* Broeck as *P. roseanum* fo. *filiforme* (Broeck) Jedl. On the other hand, in the case of *P. roseanum*, Jedlička [10] also proposed a change to *P. roseanum* var. *gracile* Breidler as *P. roseanum* fo. *gracile* (Breidler) Jedl. He described this taxon as plants with loose turf; delicate, long stems and small non-imbricate leaves [10–30]. Moreover, Warnstorf [33] and Mönkemeyer [37] indicated that it is a montane species; additionally, Mönkemeyer [37] and Jedlička [10] reported that it is characterized by round or almost round decurrency cells.

The next combinations proposed by Jedliček [11] were related to the change in the status of the varieties described by Kern [42] and Meylan in Amann [58]. The first concerns the change of status of *Plagiothecium roseanum* var. *alpinum* Kern to *P. roseanum* fo. *alpinum* (Kern) Jedl., which he then proposed as a separate species—*P. alpinum* (Kern) Jedl. Both authors described the plants as alpine, with julaceous stems, very wide and very concave leaves and short costae.

The second combination referred to *Plagiothecium roseanum* var. *subjulaceum* Meylan and its change to the form level—*P. roseanum* fo. *subjulaceum* (Meylan) Jedl. and its subsequent recognition as an independent species, *P. subjulaceum* (Meylan) Jedl. [11]. Jedlička [10,11] described these plants as dense, yellowish or dark green, slightly shiny turf; with short, julaceous, densely foliate stems and broadly ovoid-lanceolate, very concave and folded leaves. However, 11 years later [48] this species was reduced in rank, and once again it reappeared as *P. roseanum* fo. *subjulaceum*.

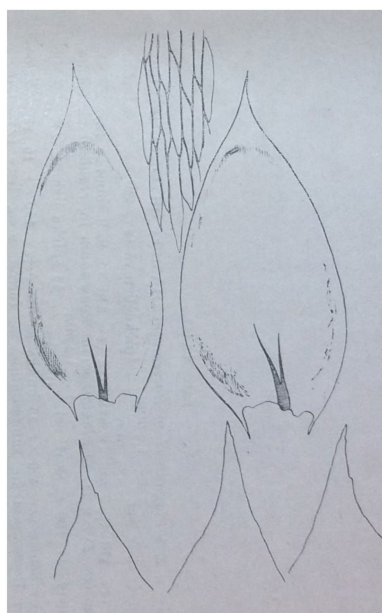
Apart from proposing new combinations, Jedlička [10] described a number of new taxa for *P. roseanum*, including the new forms: *P. roseanum* fo. *rigidum* Jedl., which he described as plants with dense, yellowish-green, shiny turf, julaceous, densely foliate stems and very concave, serrate leaves; *P. roseanum* fo. *tenue* Jedl. (Figure 9) was characterized as creeping, dirty green turf plants, with filamentous, non-imbricate stems and flat leaves [10]. For this taxon, Jedlička [10] also proposed a subform—*P. roseanum* fo. *tenue* subfo. *propaguliferum* Jedl., which is distinguished only by the presence of gemmae. Some 13 years later, Pilous in Jedlička [48] proposed another subform for this taxon—*P. roseanum* fo. *tenue* subfo. *gemmacladum* Pilous with which he synonymized *P. roseanum* fo. *tenue* subfo. *propaguliferum* previously proposed by Jedlička [10].

fo. **tenue** m. forma nova. —  
 Caespites prostrati, densi, plerumque sordide fusco-virides vel  
 fusci. Rami breves usque filiformes, conserti, dilute foliosi. Folia parva,  
 ovato-lanceolata,  $\frac{1-1.2\text{ mm}}{0.5\text{ mm}}$  longa et lata, in acumen peracutum pro-  
 ducta, integra et subplana. Cellulae foliorum typo latiores,  $\frac{9-12\ \mu}{7-8\times}$ .  
 Alae anguste decurrentes. A. g.: Germania, Bohemia, Moravia, Austria,  
 Jugoslavia.

**Figure 9.** Description of *P. roseanum* fo. *tenue* from Jedlička [10].



*Plagiothecium roeseanum* fo. *subdentatum* Jedl. (Figure 10) is yet another form proposed by Jedlička [10]; he characterized this taxon as plants with dense, yellow-green, shiny turf; short, julaceous, densely foliate stems and very concave leaves with a serrate apex. Another taxon at the rank of form proposed by Jedliček [10] is *P. roeseanum* fo. *strenuum* Jedl., in the description of which the author stated that the plants are characterized by dark green, shiny, julaceous and densely foliate turf with large, ovate-lanceolate, concave or nearly flat leaves. Jedlička [10] added that it resembles *P. platyphyllum* Mönk. and proposed a subform—*P. roeseanum* fo. *strenuum* subfo. *propaguliferum* Jedl., stating that it is characterized only by the presence of gemmae [10]. Two years later, Jedlička [11] changed the status of *P. roeseanum* fo. *strenuum* as *P. strenuum* (Jedl.) Jedl. Nevertheless, 11 years later, Pilous in Jedlička [48] still distinguished this taxon proposed by Jedlička [10] at the form level, for which Pilous in Jedlička [48] proposed a subform—*P. roeseanum* fo. *strenuum* subfo. *moravicum* Pilous.



**Figure 10.** *Plagiothecium roeseanum* fo. *subdentatum*, one of the many forms described by Jedlička [10].

The taxa related to *Plagiothecium sylvaticum* and *P. roeseanum* have also been described as related to *P. denticulatum*. Grout [44] treated the latter as a subspecies—*P. denticulatum* subsp. *roeseanum* (Bruch and Schimp.) Grout, which is characterized as plants with julaceous stems and imbricate leaves. Both the abovementioned authors understood *P. denticulatum* quite broadly, but Grout [44] very broadly, because within this species he also included a number of other taxa as subspecies, including *P. sylvaticum*, *P. ruthei*, *P. laetum* and the abovementioned *P. roeseanum*.

### 3.4. *Hypnum sullivantiae*

Schimper [18] in *Bryologia Europea* in the paragraph related to *Plagiothecium roeseanum* mentioned the name *P. sullivantiae*. Four years later in the *Manual of the Botany of the Northern United States* [59], this name appears as *Hypnum sullivantiae* Schimp. ex Sull., where it is described as having imbricate, ovoid, narrowly pointed leaves with a narrow mesh of cells and erect capsules. Some 22 years later, as *P. sullivantiae* (Schimp. ex Sull.) Schimp. ex A. Jaeger, the name was moved into *Plagiothecium* [27].

In the next years, this taxon was no longer distinguished as a separate species but more often as a variety of *Plagiothecium sylvaticum*—*P. sylvaticum* var. *sullivantiae* (Schimp. ex Sull.) Renauld and Cardot, or of *P. denticulatum*—*P. denticulatum* var. *sullivantiae* (Schimp. ex Sull.) Dixon, to function only as a synonym for *P. roeseanum* for the next decades, [1,55].



### 3.5. Other Taxa

Bridel [4] in *Bryologia universa* described *Leskea flaccida*, stating that this species is characterized by, e.g., folded, rather concave, loosely and imbricate leaves with acuminate apex and elongate and erect capsules. This name was synonymized with *P. cavifolium* by Iwatsuki [6]. However, he did not analyze the original materials of this taxon but only indicated that “*Leskea flaccida* is identical to *P. cavifolium*.”

In the following years, a number of taxa currently considered as synonyms of *P. cavifolium sensu lato* were described. Within *P. denticulatum*, the variety *P. denticulatum* var. *gmyurum* Schimp. [18], which Molendo [23] gave as belonging to *P. sylvaticum*—*P. sylvaticum* var. *myurum* (Schimp.) Molendo, was characterized as a julaceous plant. Other taxa associated with *P. sylvaticum* are *P. sylvaticum* var. *pseudoroeseanum* Cardot [41] and *P. sylvaticum* fo. *cavernarum* C.E.O. Jensen [47].

In the *Catalogue of Canadian Plants*, Kindberg in Macoun [28] described *Plagiothecium attenuatirameum* Kindb., which is characterized as plants with shiny turf, short stems, concave leaves and short costae. Two years later, Kindberg [29] proposed to change its status to a subspecies of *P. laetum*—*P. laetum* subsp. *attenuatirameum* (Kindb.) Kindb. On the other hand, Grout [44] indicated that this taxon is a form of *P. latebricola* Schimp., while Ireland [1] and Wynns [51] indicated that the original material of this species is identical to *P. roeseanum* (= *P. cavifolium*).

The last group of species currently considered synonyms of *Plagiothecium cavifolium sensu lato* are the specimens described on the basis of materials from Japan. Two of them were described by Europeans, i.e., Cardot [41]—*P. insigne*, and Reimers [43]—*P. sakuraii*; the other three were proposed by Sakurai [45,46]—*P. otii*, *P. ikegamii* and *P. takahashii*.

The first of them (*P. otii*) is characterized by flattened foliage; rather asymmetrical, concave, transversely folded leaves; serrate apex; large but variable costae, reaching even half of the length of the leaf and narrowly rhomboidal, rather short cells. *Plagiothecium ikegamii* was characterized as a plant with folded, concave, serrate (at apex) leaves and delicate costae, reaching up to 1/3 of the length of the leaf. Whereas *P. takahashii* was described as a pale green plant with densely, julaceous foliage; strongly concave, symmetrical or asymmetrical, ovate or lanceolate, nonserrate leaves and horizontal capsules.

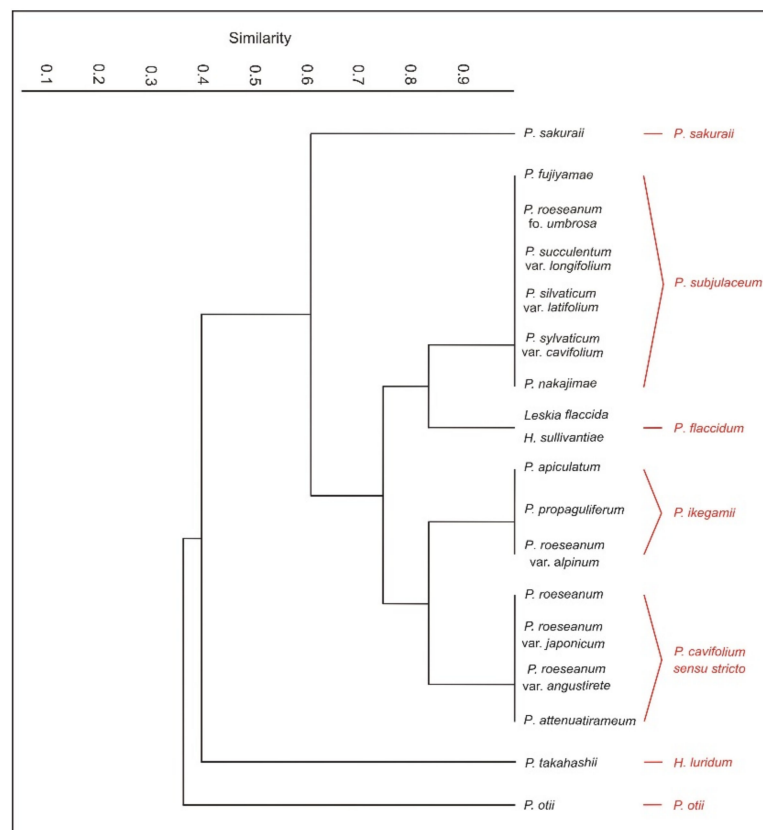
### 3.6. Grouping of Taxa and the Taxonomic Implications

As the above list shows, the analyzed taxa sometimes differ diametrically from each other in terms of many, even taxonomically significant, features. Thus, they do not seem to belong to the *Plagiothecium cavifolium* complex. Others, in terms of the features included in the diagnoses, seem to be more or less consistent with the diagnosis of *H. cavifolium*.

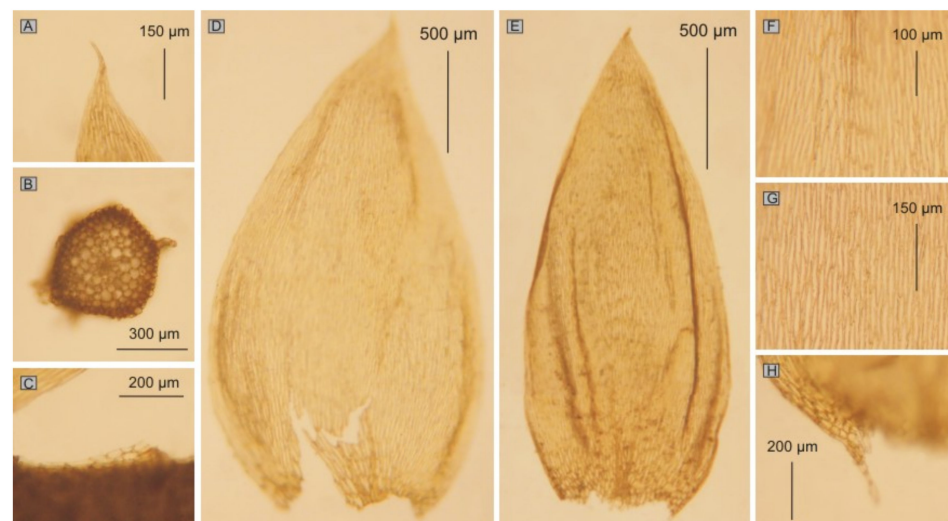
In terms of the analyzed features, the original materials and the analyzed names quite easily form distinguishable groups (Figure 11). Nevertheless, in the grouping below, some of them have been omitted due to the lack (for example in diagnoses) of all the necessary information for the analysis data or lack of a possibility to obtain original materials with these names.

The first group includes taxa characterized by julaceous stems; imbricate symmetrical, concave, non-serrate and more or less folded leaves; the cells from the middle part of the leaf larger than 101 µm in length and inclined capsules. This group contains *P. attenuatirameum* (PC0132687), *P. roeseanum* (*Hypnum roeseanum*) (Figures 11 and 12) (JE04004196, JE04004197, JE04004198, JE04004199), *P. roeseanum* var. *angustirete* (JE04004200) and *P. roeseanum* var. *japonicum* (PC0132574) (Figure 11). On the basis of diagnoses and figures assuming this set of features, in the above group we can also include *P. orthocladium*. The abovementioned features fit perfectly with the diagnosis of *H. cavifolium* and with the description of *P. cavifolium sensu stricto*, thus we propose to consider these taxa as synonyms of *P. cavifolium*.





**Figure 11.** Grouping of the studied specimens using the UPGMA method (Jaccard distance).



**Figure 12.** The most important taxonomic features of *Plagiothecium cavifolium* (= *Hypnum roeseanum*): (A) leaf apex (A. Roese, JE4004199); (B) stem cross section (A. Roese, JE4004199); (C) decurrency cells (A. Roese, JE4004199); (D–E) leaves (D)—A. Roese, JE4004199; (E)—A. Roese, JE4004197; (F) cells from the upper part of the leaf (A. Roese, JE4004197); (G) cells from the middle part of the leaf (A. Roese, JE4004197); (H) cells from the lower part of the leaf (A. Roese, JE4004197).

*Plagiothecium cavifolium* (Brid.) Z.Iwats., J. Hattori Bot. Lab. 33: 360 (1970); *Hypnum* (*Stereodon*) *cavifolium* Brid., Bryologia Universa 2: 556 (1827) ("*cavifolius*"; *Stereodon cavifolius* (Brid.) Brid., Bryologia Universa 2: 824 (1827). Type: in terra habitat in insula Terre Neuve, La Pylaie (B-Brid 915).



*Plagiothecium roeseanum* Hampe ex Schimp., Bryologia Europea 5: 193, 504 (Table X) (1851); *Hypnum roeseanum* Hampe in Bruch, Schimper and W.Gümbel, Bryologia Europea 5: 193, 504 (1851); *P. sylvaticum* var. *roeseanum* (Hampe ex Schimp.) A.W.H. Walther and Moldendo, Laubm. Oberfrank. 177 (1868); *P. denticulatum* var. *roeseanum* (Hampe ex Schimp.) Hérrib., Mém. Acad. Sci. Clermont-Ferrand, sér. 2, 14: 228 (1899); *P. denticulatum* subsp. *roeseanum* (Hampe ex Schimp.) Grout, Moss Fl. N. Amer. 3: 158 (1932). Type: Ad terram arenosam sub *Fagis* in monte Inselberg Thuringiae cl. *A. Roese* legit atque nobiscum benevole communicavit (JE04004196!, JE04004197!, JE04004198!, JE04004199!).

*Plagiothecium orthocladium* Schimp., Bryologia Europea 5: 193, 504 (Table X) (1851); *P. sylvaticum* var. *orthocladium* (Schimp.) Schimp., Corollarium Bryologiae Europaeae 115 (1856); *Hypnum sylvaticum* var. *orthocladium* (Schimp.) Husn., Fl. Mousses Nord. Ouest (ed. 2) 149 (1882); *P. roeseanum* var. *orthocladium* (Schimp.) Limpr., Laubm. Deutschl. 3: 262 (1897); *P. denticulatum* var. *orthocladium* (Schimp.) Hérrib., Mém. Acad. Sci. Clermont-Ferrand, sér. 2, 14: 229 (1899); *P. sylvaticum* fo. *orthocladium* (Schimp.) Barkman, Phytosociol. Ecol. Cryptog. Epiphytes 619 (1958); *P. cavifolium* var. *orthocladium* (Schimp.) Z.Iwats., J. Hattori Bot. Lab. 33: 371 (1970). Type: In m. Donnersberg Vogesi inferioris, Th. Gumbel legit auno 1842 (n.v.).

*Plagiothecium attenuatirameum* Kindb., Catalogue of Canadian Plants, Part VI, Musci 277 (1892); *P. laetum* subsp. *attenuatirameum* (Kindb.) Kindb., Canad. Rec. Sci. 6(2): 72 (1894). Type: Canada, Québec, Chelsea in Gilmour's Park, on rock, J. Macoun 417, 6 September 1889, herb. I. Thériot (PC0132687!).

*Plagiothecium roeseanum* var. *angustirete* Warnst., Verh. Bot. Vereins Prov. Brandenburg 42: 214 (1900); *P. roeseanum* fo. *angustirete* (Warnst.) Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 39 (1948). Type: Germany, Brandenburg, Chorin (Mark), Hohlweg am Bach, am Waldhohlwege im „Forstgarten“ mit *Eurhynchium schleicheri*, L. Loeske, 10 Sep. 1899, herb. H. Dohl (JE4004200!).

*Plagiothecium roeseanum* var. *japonicum* Cardot, Bull. Soc. Bot. Genève, sér. 2, 4: 385 (1912). Type: Japan, Aomori Pref., Faurie 408 (“*P. silvaticum* var. *orthocladum* Sch.”), herb. J. Cardot (PC0132574!); idem, Faurie 418; Kanita, Faurie 1812; Hirosaki, Faurie 1878; Osorezan, Faurie 2104; château d'Akita, Faurie 2904; Nayoro, Faurie 3078 in parte; Sambongi, Faurie 3190; Otaru, Faurie 3753; Tobetsu, Faurie 3761 (KYO).

Taking into account the analyzed features, *P. propaguliferum* (PC0132610) (Figure 13) could be considered a new synonym for *P. cavifolium sensu lato*; however, the difference from the diagnosis of *H. cavifolium* confirms the legitimacy of excluding this name from the described complex. Additionally, with *P. apiculatum* (MAK B115140) and *P. roeseanum* var. *alpinum* (PC0132603), they form another group of specimens characterized by symmetrical, concave, more or less folded leaves, with cells of the central part of the leaf longer than 101 µm. However, these specimens differ from the previous group in the serration of the leaf apex. Assuming this set of features, for this group we can also include *P. ikegamii*, *P. roeseanum* fo. *rigidum*, *P. roeseanum* fo. *subdentatum*, *P. roeseanum* fo. *alpinum* and *P. alpinum*. Thus, taking into account the analysis of original materials and diagnoses, we propose to resurrect *P. ikegamii* as a separate species and consider the other taxa mentioned above as its synonyms.

*Plagiothecium ikegamii* Sakurai, Botanical Magazine (Tokyo), 62: 113, f. 3. (1949). Type: Japan, Etigo Prov., Mt. Renge, ad terram, ca. 2200 m, Y. Ikegami 11270, herb. K. Sakurai 16336, August 1949; Shinano Prov., Mt. Shirouma, 2500 m, N. Takaki in herb. K. Sakurai 16368, August 1949 (n.v.).

*Plagiothecium roeseanum* var. *alpinum* Kern, Jahresber. Schles. Ges. Vaterl. Cult. 91(2b): 64 (1914); *P. roeseanum* fo. *alpinum* (Kern) Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 37 (1948); *P. alpinum* (Kern) Jedl., Spisy Přír. Fak. Masarykovy Univ. 318: 5 (1950). Type: Italy, Felsritzen des Cruschettapasses an der Schweizer Grenze, 2300 m, F. Kern, 30 July 1913 (PC0132603!).



*Plagiothecium roeseanum* fo. *rigidum* Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 37 (1948). Type (authentic specimens cited in Jedlička 1961): Moravia, Jeseníky, Švýcarská, 1300 m, ster., J. Podpěra, H. M. B.; Brno, Bílovice, cfr., K. Doležal, H. U. B., s. *P. denticulatum*; Adamov, in conc. riv. Kateřinský, ster., J. Jedlička, H. J.; Slovakia, Vysoké Tatry, Štrbské Solisko, in *Calamagrostidetum villosae*, solo granitico, 1385 m, ster., Krajina, H. U. P., sub *P. denticulatum* (n.v.).

*Plagiothecium roeseanum* fo. *subdentatum* Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 38 (1948); *P. subdentatum* (Jedl.) Jedl., Spisy Přír. Fak. Masarykovy Univ. 318: 5 (1950). Type (authentic specimens cited in Jedlička 1961): Moravia, Jeseníky, ster. cum *Desmatodon*, Frank H. P., Inter. p. Dalečín et Jimramov, 500 m, ster., J. Podpěra, H. P.; Carp. occid., Rožnov, s. m. Radhošť, versus Kluzov, ster., J. Podpěra, H. P.; Turcia, Salonichi, Kartaš-dagh, 1200 m, ster., J. Podpěra, H. P. (n.v.).

*Plagiothecium propaguliferum* Broth., in sched. Basis: Japan, Sendai, Y. Iishiba, July 1907, herb. J. Cardot, I. Thériot (PC0132610!).

*Plagiothecium apiculatum* Sakurai, in sched. Basis: Japan, Niigata Pref., Toyanao, Y. Ikegami 4256, 2 Apr. 1942 (MAK B115140!).



**Figure 13.** The most important taxonomic features of *P. propaguliferum*: (A,B) leaf; (C) leaves apex; (D) cells from the middle part of the leaf; (E) stem cross section (all from Y. Iishiba, PC0132610).

The quantitative and qualitative characteristics of the original materials also indicate that *P. sylvaticum* var. *latifolium* (HBG21134) and *P. succulentum* var. *longifolium* (JE 4004211, JE 4004212) can be synonymous with *P. cavifolium sensu lato*. However, compared to the diagnosis of *H. cavifolium*, the morphological diversity of these taxa confirms the legitimacy of excluding them from the described complex. The abovementioned specimens, together with *P. fujiyamae* (MAK 57198), *P. nakajimae* (MAK B57158), *P. roeseanum* fo. *umbrosa* (Figure 14) (HBG021131), *P. succulentum* var. *longifolium* (JE 4004211, JE 4004212) and *P. sylvaticum* var. *cavifolium* (PC0132571) form one group of specimens characterized by julaceous stems; imbricate, symmetrical, strongly concave, non-serrate and more or less folded leaves and with inclined capsules. However, they are distinguished from the first group by shorter cells, the length of which does not exceed 100 µm. Assuming this set of features to the above group, we can also include *P. roeseanum* var. *subjulaceum*, *P. roeseanum* fo. *subjulaceum*, and *P. subjulaceum*. Thus, taking into account the analysis of original materials and diagnoses, we propose to resurrect *P. subjulaceum* as a separate species and consider the other taxa mentioned above as its synonyms.





**Figure 14.** The most important taxonomic features of *Plagiothecium subjulaceum*: (A) leaf; (B) leaf apex; (C) cells from the middle part of the leaf; (D) cells from the lower part of the leaf (all from R. Schmidt, HBG021131).

*Plagiothecium subjulaceum* (Meyl.) Jedl., Spisy Přír. Fak. Univ. Masarykovy Univ. 318: 5 (1950); *P. roeseanum* var. *subjulaceum* Meyl. in J.J. Amann, Fl. Mouss. Suisse 2: 328 (1918); *P. roeseanum* fo. *subjulaceum* (Meyl.) Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 38 (1948). Type: No type was specified.

*Plagiothecium roeseanum* fo. *umbrosa* Mönk., Laubm. Eur. 863 (1927). Type: Germany, Thüringen, Finsteres Loch, Rich Schmidt Lips., 20 June 1916 (HBG021131!).

*Plagiothecium sylvaticum* var. *cavifolium* Jur. in Rabenhorst, Bryotheca Europaea 16: 765 (1864). Type: *Bryotheca europaea* 765, Auf nacktem Boden in Buchenwäldern auf Nagelfluhe am Mönchsberge bei Salzburg, Sauter (als. *Plag. Lucens* Sauter n. sp.), distrib. L. Rabenhorst (FH220150, MO406590, PC00132571!).

*Plagiothecium sylvaticum* var. *latifolium* Röhl, Deutsche Bot. Monatsschr. 9: 131 (1891), non Cardot, Bull. Soc. Bot. Genève, sér. 2, 4: 385 (1912), hom. illeg.; *P. sylvaticum* var. *latifolium* Röhl, Hedwigia 56: 229 (1915), hom. illeg. Type: Germany, Thuringia, im Werrthal bei Plankenburg an der hohen Schlaufe bei Ilmenau, J. Röhl (HBG21134!).

*Plagiothecium succulentum* var. *longifolium* Mönk., Laubm. Eur. 863, f. 206b (1927); *P. sylvaticum* fo. *longifolium* (Mönk.) C.E.O.Jensen, Skand. Bladmossfl. 495 (1939); *P. succulentum* fo. *longifolium* (Mönk.) Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 42 (1948). Lectotype (designated here): Germany, Thüringen Wald, am Simmetsberg im Ungeheuren Grund, Hess, Aug. 1872 (JE 4004211!), isolectotype: Germany, Thüringen, Annathal bei Eisenach, Hess, Aug. 1872 (JE 4004212!).

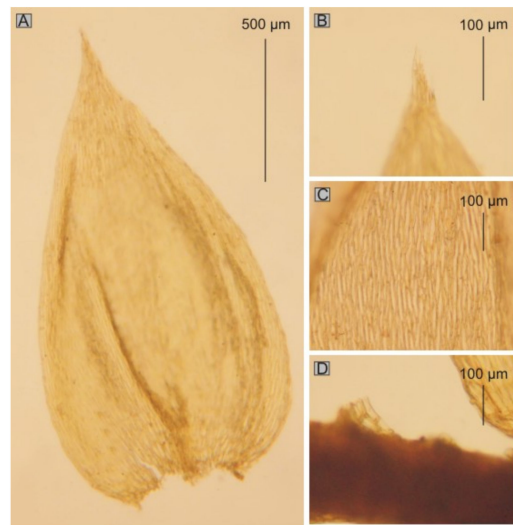
*Plagiothecium fujiyamae* Sakurai, in sched. Basis: Japan, Aokigahara, Fuji, Yamanashi Pref., T. Maede 1462, 9 Nov. 1950, herb. K. Sakurai (MAK 57198!).

*Plagiothecium nakajimae* Sakurai, in sched. Basis: Japan, Chichinu, Nagano, 6 Nov. 1951, herb. K. Sakurai 761 (MAK B57158!).

The next group is created by *Leskea flaccida* (B31076701) (Figure 15), and it represents materials with julaceous stems; imbricate, symmetrical, concave, more or less folded leaves; with the cells of the central part of the leaf shorter than 150 µm. It differs from the rest of the groups by erect capsules. Taking this set of features as a determinant, the analysis of original materials also allows the inclusion in this group of *H. sullivantiae* (PC0132606, PC0132607, PC0132608) and *P. sullivantiae*, while the analysis of diagnoses of individual names also allows the inclusion of *P. roeseanum* var. *orthocladon* fo. *propaguliferum* and *P. roeseanum* var. *orthocladon* fo. *moravicum*. Taking the above into account, we propose a new



combination for this taxon *Plagiothecium flaccidum* (Brid.) G.J.Wolski and W.R.Buck comb. nov., and we propose to consider the abovementioned names as synonyms of this taxon.



**Figure 15.** The most important microscopic features of *Plagiothecium flaccidum* (= *Leskea flaccida*): (A) leaf; (B) leaf apex; (C) cells from the middle part of the leaf; (D) decurrency cells (all from holotype, J. Torrey, B31076701).

***Plagiothecium flaccidum* (Brid.) G.J.Wolski and W.R.Buck, comb. nov.** *Leskea flaccida* Brid., Bryologia Universa 2: 308 (1827). Type: In Republica Massachusetts Americae Foedewatae circa Noveboracum in rupis habitat, caespitosa, caespitum basi e congerie caulium veterarnorum marcescentium constante, Torrey 67, 1820 (B31076701!).

*Hypnum sullivantiae* Schimp. ex Sull., Manual (ed. 2) 680 (1856); *Plagiothecium sullivantiae* (Schimp. ex Sull.) Schimp. ex A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges.t 1876–77: 450 (1878); *P. sylvaticum* var. *sullivantiae* (Schimp. ex Sull.) Renauld and Cardot, Rev. Bryol. 20: 22 (1893). Type: Ohionis et Novae Angliae, in rupium fissuris terra impletis, Musci Boreali-Americani 355 (PC0132606!, PC0132607!); idem Herb. M. Bizot 13157 (PC0132608!).

*Plagiothecium roeseanum* var. *orthocladon* fo. *propaguliferum* Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 39 (1948), *hom. illeg., non* (R.Ruthe) Jaap, Verh. Naturwiss. Vereins Hamburg, ser. 3, 7: 36 (1900); *P. roeseanum* var. *orthocladon* fo. *moravicum* Pilous in Jedlička, Spisy Přír. Fak. Univ. v Brně 422: 214 (1961), *nom. nov.* Type: Moravia, conv. flum. Oslava, ster., Latzel, H.L., observavi (*n.v.*).

The analysis of the diagnoses of the remaining taxa also shows that this respect of features differs significantly from the diagnosis of *H. cavifolium*. Sometimes the differences are importance and basic. Thus, some of the analyzed names were described as not julaceous and characterized by flat, more or less asymmetrical leaves. Taking these features as diagnostic, the analysis of protologues in this group allowed the inclusion of *P. roeseanum* fo. *acuminatum*, *P. cavifolium* fo. *acuminatum*, *P. roeseanum* fo. *Tenue* and *P. roeseanum* fo. *tenue* subfo. *propaguliferum*. Taking into account the above and the fact that the oldest name for this group is *P. roeseanum* fo. *tenue*, we propose a new combination for this taxon—*Plagiothecium tenue* (Jedl.) G.J.Wolski and W.R.Buck comb. nov. and we propose to consider all the abovementioned taxa as synonyms of this species.

***Plagiothecium tenue* (Jedl.) G.J.Wolski and W.R.Buck comb. nov.**; *P. roeseanum* fo. *tenue* Jedl., Spisy Přír. Fak Masarykovy Univ. 308: 38 (1948). Type (authentic specimens cited in Jedlička 1961): Silesia, Cuidowa, Steinberg, ster. Paul, H.M.B.; Bohemia, Beroun, Skryje, in decl. Vosník col. ster., Šmerda, H. Š. (sub *P. denticulatum*). Moravia, Jeseníky, Quarklöcher, pr. Brummlitz, ster. una cum *Barbula rigida* et *Fissidens pusillus*, Latzel, H. L.; Voskovic, in silva umbrosa pr. oppid, 300 m, ster., Doležal, H. P.; Brno, Kuřim, ad col.



Baba, ster. *Doležal*, H. M. B. (sub *P. denticulatum*); Kůňku pr. Obora, str., *Podpěra*, H. P.; Mor. Krumlov, ad rup. perm., 300 m, ster. *Podpěra*, H. M. B.; Carp. occid., in m. Ondřejník, pr. Frýdlant, ster., *Podpěra* H. P.; in m. Lysá in conv. riv. Mazák, ster., *Podpěra*, H. P.; Rajnochovice, Pomořsko, ster., *Podpěra*, H. P.; Rychtářov, in conv., V. Haná, ster., *Podpěra*, H. P.; Unčov, cataract. Řešovský, ster., *Podpěra*, H. P. Austria. Koralpe, Theisseneggergraben, solo granit., 800 m, ster., *Latzel*, H. L.; Pressinggraben, ster. *Latzel*, H. L. (s. *P. Roeseanum gracile*). Jugoslavia, Surdulica, in conv. Vrla reka, ster. *Podpěra*, H. P.; Vrane-Kazandžol, ster., *Podpěra*, H. P. (n.v.).

*Plagiothecium roeseanum* fo. *tenue* subfo. *propaguliferum* Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 38 (1948), *hom. illeg.*; *P. roeseanum* subfo. *gemmacladum* Pilous, Spisy Přír. Fak. Univ. v Brně 422: 212 (1961), *nom. nov.* Type (authentic specimens cited in Jedlička 1961): Suecia, Skåne, Bokeberg, ster., Möller, H. M. B. Germania, Sachsen, Plauen, ad saxa umbr. in conv. Elstertal, ster., Stolle, H. P. (planta pulcherrima!!). Austria, Saualpe, Pöllinggraben, cfr., *Latzel*, H. L. Wien, ad arcem Greifenstein, 300 m, cfr., Baumgartner, *Kryptog. exsicc.* M. N. no. 1788a, H. M. P. Bohemia, Praha, Hasenburg, 250 m, ster., *Bauer*; *Musc. eur. exsicc.* no. 1311, H. P., H. M. B., H. M. P., H. U. B. (sub *P. Roeseanum* fo. *gracilescens*) *Bauer in sched.*; Řevnice, ster. *Podpěra*, H. P. (sub *P. denticulatum*). Nové Město n. Met. ad rup. fylit. Peklo, ster., Šmaeda, H. Š.; Berno, Skryje, ster., cum *Anomodon attenuatus* et *Mnium cuspidatum*, Šmaeda, H. Š. (sub *P. denticulatum propaguliferum*); Tusset, 1000 m, ster., *Podpěra*, H. P. (sub *P. denticulatum*). Moravia, Jeseníky, Švýcarsko, ster. 1300 m, *Podpěra*, H. P.; Hokšár, ster., *Podpěra*, H. P.; Brno, pr. arcem Veverí, ster., *Podpěra*, H. P.; in conv. Bílý potok, sup. Hluboké, ster. *Podpěra*, H. P. (sub *P. Roeseanum umbrosum*); Adamov, in conv. riv., Josefovský, ster., *Podpěra*, H. P.; in conv. rivuli Kateřinský potok, ster., J. Müller, H. U. B.; ad rup. syenit. in conv. flum. Svitava, inter Adamov et Blansko, ster., *Podpěra*, H. P.; Rousínov, Vítocický žleb, *Podpěra*, H. P. (sub *P. Roeseanum gracile* fo. *tenellum*) *Podp. in sched.*; Mor. Krumlov, ad rup. perm., 300 m, ster., *Podpěra*, H. P.; Carp. occid., ad ped. m. Lysá Hora, pr. Staré Hamry, ster., *Podpěra*, H. P.; in m. Hostýn, ster., *Podpěra*, H. P. (n.v.).

*Plagiothecium roeseanum* fo. *acuminatum* Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 40 (1948); *P. cavifolium* fo. *acuminatum* (Jedl.) Z.Iwats., J. Hattorii Bot. Lab. 33: 363. (1970). Type (authentic specimens cited in Jedlička 1961): Austria, Arlingsgraben, ster., *Latzel*, H. L. Bohemia, Praha, ad rup. lydit., 200 m, ster., Šmarda, H. Š.; Babka pr. Řevnice, 400 m, *Bauer*, Bryoth. Bohem. no 255, H. U. P., H. Š., H. M. P. (sub *P. roeseanum typicum*), Mladá Boleslav, in conv. Choboty, cfr., *Podpěra*, H. P. Moravia, Jeseníky, Dolní Lipová, ster., *Latzel*, H. L.; in conv. riv. Seifen pr. Vernířovice, 800 m, ster., *Podpěra*, H. P.; Znajmo, Eisleiten pr. Varanoc, ster., *Podpěra*, H. P.; Senohrady, ad rup., ster., *Podpěra*, H. P.; Unčov, ad cataract. Řešovský, 400 m, ster., *Podpěra*, H. P. Slovakia, Babia Góra, ad lignus putr., ster., Šmerda, H. Š. (sub *P. silvaticum longifolium*); Bielské Tatry, in conv. Havran, 1100 m, cum *Blepharostoma trichophyllum*, ster., Šmerda, H. Š. (n.v.).

An analysis of original materials of *P. otii* (MAK B16360) shows that they are the most different from the previously described groups. Leaves of this specimen are symmetrical or asymmetrical, concave, strongly folded, and strongly serrate at the apex, with quite wide and long cells 100–170 (M 137)  $\times$  10–12  $\mu$ m (M 11) and with very long decurrencies composed of rectangular cells. These features exclude the tested material from the described complex. However, compared to all species of the Northern Hemisphere, this material constitutes a unique set of features. Thus, we propose the resurrection of *P. otii* (Figure 16) as a separate species.

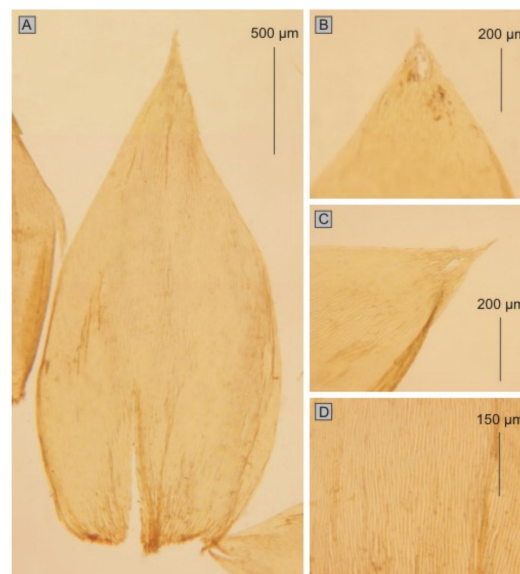
*Plagiothecium otii* Sakurai, Botanical Magazine (Tokyo) 62: 113, f. 5 (1949); *P. cavifolium* fo. *otii* (Sakurai) Z.Iwats., J. Hattori Bot. Lab. 33: 363 (1970). Type: Japan, Prov. Iyo, Mt. Ishizuti, K. Oti, 8 Aug. 1949, herb. K. Sakurai 3388 (holotype: MAK B16360!).





**Figure 16.** The most important taxonomic features of *P. otii*: (A,B) leaves; (C) cells from the upper part of the leaf; (D) cells from the middle part of the leaf; (E) cells from the lower part of the leaf (all from the holotype, *K. Oti*, MAK B16360).

Analysis of the original collection of *P. sakuraii* (MAK B609; PC0132597) allows the observation that this specimen is characterized by symmetrical, folded, concave and serrate leaves. However, it differs from the abovementioned taxa in the length and width of cells from the central part of the leaf [ $87.5\text{--}150$  (M 119)  $\times$   $7\text{--}10$  (M 8.5)  $\mu\text{m}$ ]. Moreover, detailed analysis of this material showed that the leaf apices are eroded (Figure 17). These features exclude the tested material from the described complex; thus we propose to resurrect *P. sakuraii*.



**Figure 17.** The most important taxonomic features of *Plagiothecium sakuraii*: (A) leaf; (B,C) leaf apices; (D) cells from the middle part of the leaf (all from *H. Reimers*, *P. sakuraii* MAK B609).

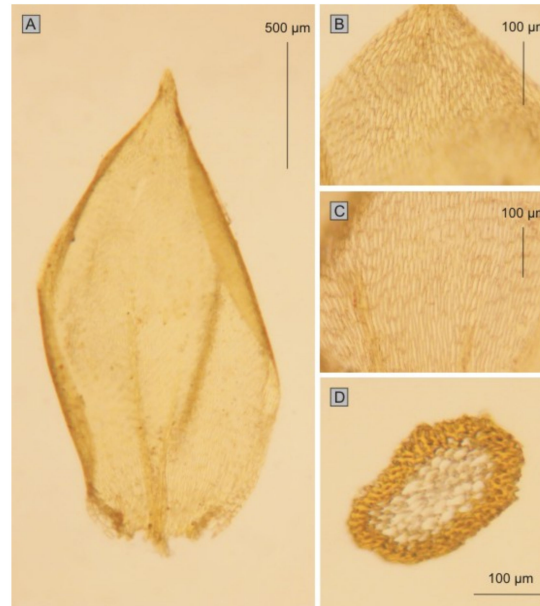
*Plagiothecium sakuraii* Reimers, Bot. Jahrb. Syst. 64: 554, 21 f. 3,4 (1931). Lectotype (designated here): Japan, Honsho, Prov. Hitachi, Mt. Tsukuba, an feuchten Felsen, *K. Sakurai* 609, May 1921, herb. *K. Sakurai* (PC0132597!), isolectotype: (MAK B609!).

The other analyzed names differ even more from the diagnosis of *Hypnum cavifolium* and should be excluded not only from the *P. cavifolium* complex but also (in one case) even from *Plagiothecium*.

Analysis of original collections of *P. takahashii* (MAK B9398) (Figure 18) showed that the leaves of this specimen are strongly rolled; the cells are short and narrow



25–55 (M 40)  $\times$  6–8 (M 7)  $\mu\text{m}$ ; the stems have multiple layers of thick-walled epidermal cells; pseudoparaphyllia are present on the stems. These features not only exclude the analyzed material from *P. cavifolium sensu lato*, but also from the entire genus *Plagiothecium*. However, this set of features clearly indicates that this material belongs to *Hygrohypnum luridum* (Hedw.) Jenn. Thus, we propose to consider *P. takahashii* as a new synonym for this species.



**Figure 18.** The most important taxonomic features of *Hygrohypnum luridum* (= *P. takahashii*): (A) leaf; (B) cells from the upper part of the leaf; (C) cells from the middle part of the leaf; (D) stem cross section (all from the holotype, K. Sakurai, MAK B9398).

***Hygrohypnum luridum* (Hedw.) Jenn.**, Manual Mosses W. Pennsylvania 287 (1913).

*Plagiothecium takahashii* Sakurai, Bot. Mag. (Tokyo) 51: 79 (1937), *syn. nov.* Type: Japan, Miyazaki Pref., Mt. Sobo, 24 June 1935, H. Takahashi 108, herb. K. Sakurai 9398 (holotype: MAK B9398!).

Due to the set of features, the next analyzed names also cannot be classified as *P. cavifolium sensu lato*. Characters such as the asymmetric, broadly ovate leaves with long and wide cells described for *P. sylvaticum* var. *neglectum* fo. *orthocladum*, *P. roeseanum* var. *heterophyllum* and *P. roeseanum* fo. *heterophyllum* bring to mind the recently reintroduced *P. longisetum* Lindb. This is also confirmed by quantitative features and figures.

***Plagiothecium longisetum* Lindb.**, Contr. Fl. Crypt. As., Acta Soc. Sci. Fenn. 10: 232 (1872). Type: Japan, ad Nikosan ins. Kiusiu, [fertile], 16 Junii 1863, S.O. Lindberg s.n. (lectotype: H-SOL 1563 011!, isoelectotype: PC00132572!, S-B160017).

*Plagiothecium roeseanum* var. *heterophyllum* Warnst., Krypt.-Fl Brandenburg, Laubm. 814 (1906), *syn. nov.*; *P. roeseanum* fo. *heterophyllum* (Warnst.) Jedl., Spisy Přír. Fak. Masarykovy Univ. 308: 40 (1948). Type: Germany, Brandenburg, Neurippen, Ruppín, auf Waldboden, Böschungen im “Flössergrunde”, C. Warnstorf; Westprignitz, Forsthaus “Alte Eiche”, auf Waldboden am Standort von *Osmunga regalis*, Janzen and C. Warnstorf; Wittenberge, Westprignitz, am Grunde eines Baumstammes, “Krauses Brack”, C. Warnstorf; Ratzburg, Buchenwälder, Prahl. Poland, Świnoujście, Weg nach Corswant, R. Ruthe (n.v.).

*P. sylvaticum* var. *neglectum* fo. *orthocladum* Barkman, *nom. inval.*, Buxbaumia 11: 23 (1957), *syn. nov.* Type: no type was specified.

Whereas *P. roeseanum* var. *gracile* and *P. roeseanum* fo. *gracile*, described as montane plants characterized by, e.g., loose turf with small, distant foliage and with round or



almost round decurrency cells. This set of characteristics brings to mind *P. denticulatum* var. *obtusifolium* (Turner) Moore or other taxa belonging to the *P. denticulatum* complex. However, it was not possible to obtain the original materials to verify this hypothesis.

Thus, the conducted research, the analysis of all original materials, available diagnoses and the history of the described taxon show that the *Plagiothecium cavifolium* complex consists of *P. cavifolium* (= *P. cavifolium sensu stricto*), *P. flaccidum*, *P. ikegamii*, *P. tenue*, *P. subjulaceum*, *P. sakurarii* and *P. otii*.

Additionally, the research allowed us to propose *P. takahashii* as a new synonym for *Hygrohypnum luridum*, whereas *P. sylvaticum* var. *neglectum* fo. *orthocladum*, *P. roeseanum* var. *heterophyllum* and *P. roeseanum* fo. *heterophyllum* are proposed as new synonyms for *P. longisetum*.

*The key for species belonging to the P. cavifolium complex*

1. Leaves with an eroded apex . . . *P. sakurarii*.
- 1'. Leaves without an eroded apex . . . 2.
2. Symmetrical and asymmetrical leaves on the stem . . . *P. otii*.
- 2'. Stem leaves symmetrical or separately slightly asymmetrical . . . 3.
3. Turf julaceous; leaves imbricate, symmetrical, concave; more or less folded . . . 4.
- 3'. Turf not julaceous, leaves little or not at all imbricate, flat and not folded . . . *P. tenue*.
4. Capsules inclined . . . 5.
- 4'. Capsules erect . . . *P. flaccidum*.
5. Leaves not serrate . . . 6.
- 5'. Leaves serrate . . . *P. ikegamii*.
6. The cells from the middle part of the leaf to 101 µm in length . . . *P. cavifolium sensu stricto*.
- 6'. The cells from the middle part of the leaf more than 101 µm in length . . . *P. subjulaceum*.

#### 4. Discussion

The current taxonomic status of species in *Plagiothecium* Schimp. is undoubtedly influenced by the generic history. Since the mid-20th century in North America, Asia and Europe, *Plagiothecium* has been the subject of quite detailed studies [1,6,7,10,11,48]. This period can be divided into two stages, the first represented by Jedliček's revisions [10,11,48], who described several dozen taxa at the rank of species, subspecies, varieties, forms and subforms among the European species of this genus. The second period is represented by later bryologists—Ireland [1,7] and Iwatsuki [6]—who synonymized most of these and a number of other taxa.

In the entire Northern Hemisphere, this second period not only led to a very significant reduction in the number of species recognized in *Plagiothecium* [9,14,60–62], but also resulted in the fact that some of them (e.g., *P. curvifolium*, *P. nemorale*) turned out to be too widely described and proved to be complexes. Many bryologists, [9,12,14], have written about the outstanding infraspecific variability of *Plagiothecium* taxa, but Ireland's [1,7] and Iwatsuki's [6] concepts persisted in North America, Asia and Europe for almost the next half century [8,9,14,60–62].

Like the taxa mentioned above, *Plagiothecium cavifolium sensu lato* was also described as extremely variable [8,9,12,14]. This variability concerned not only qualitative and quantitative features related to the size or color of the plant, [1,6–12], but also considered to be the most taxonomically significant, including symmetry, concavity, leaf serration, dimensions of the cells and orientation of the capsule [1,7–16]. Thus, comparing the data published in the above-cited articles with the features included in the diagnosis of *Hypnum* (*Stereodon*) *cavifolium* [4], which is the basionym of *P. cavifolium*, it is easy to notice that most of characteristics exclude the taxon described by Bridel [4].

On the other hand, as shown by the latest studies of species from *Plagiothecium*, supported by DNA analysis [52,63–65], all the abovementioned features, are useful traits



to separate closely related taxa from each other [63–65]. Thus, modern analysis methods confirm their highly effective taxonomic utility.

The conducted research within *Plagiothecium cavifolium sensu lato* allowed us to describe groups that differ, among others, in arrangement of leaves on the stem. Most of the specimens were characterized by julaceous stems and imbricate leaves (e.g., *P. cavifolium sensu stricto*, *P. flaccidum*, *P. ikegamii*, *P. subjulaceum*); others are characterized as plants with non-julaceous stems and non-imbricate leaves (*P. tenue*). Similar differences can be observed in closely related Northern Hemisphere species, e.g., *P. denticulatum* and *P. schofieldii* G.J.Wolski and W.R.Buck or *P. cavifolium sensu stricto* and *P. nemorale*. In both of these cases, *P. schofieldii* and *P. cavifolium* are characterized by strongly julaceous and imbricate leaves, while the other two species are characterized by more flattened foliage and less imbricate leaves [3,9,12,14,63].

The characteristics related to leaves, such as symmetry, concavity and serration, are the next important features that distinguish taxa described within *P. cavifolium sensu lato*. These characteristics are important, and even Bridel [4] indicated them in the diagnosis as distinguishing *H. cavifolium* from other species. Most taxa within *P. cavifolium sensu lato* (e.g., *P. cavifolium sensu stricto*, *P. flaccidum*, *P. ikegamii*, *P. sakuraii*, *P. subjulaceum*) are characterized by a clearly symmetrical leaf, while others (*P. otii*, *P. tenue*) have more or less asymmetric leaves. This feature makes it quite easy to distinguish other closely related species, such as *P. longisetum* and *P. nemorale* or *P. angusticellum* G.J.Wolski and P.Nowicka-Krawczyk and *P. nemorale*. In the above case, *P. longisetum* and *P. angusticellum* have asymmetrical leaves, while *P. nemorale* has clearly symmetrical leaves, [3,9,12,14,63].

Although the leaf of *Plagiothecium* species (apart from the costae) consists of one layer of cells, the concavity of the leaves often plays a fairly important role in distinguishing individual species. For *H. cavifolium* described by Bridel [4], this feature is so important that it influenced its name. Among *P. cavifolium sensu lato*, most species (*P. cavifolium sensu stricto*, *P. flaccidum*, *P. ikegamii*, *P. otii*, *P. sakuraii*) are characterized by concave leaves, while others (*P. subjulaceum*) are flat. Thus, it makes it possible to distinguish the latter from the others. The cases of *P. nemorale* and *P. angusticellum* or *P. nemorale* and *P. cavifolium sensu stricto* are similar. These closely related species differ in leaf concavity, with *P. nemorale* being characterized as having flat leaves and the other two by clearly concave leaves, [3,9,12,14,63].

The leaf apex of *Plagiothecium* species may be serrate or not, [9,12,14]. Among the analyzed taxa, some species (e.g., *P. cavifolium sensu stricto*, *P. subjulaceum*) do not have a serrate apex, while others (*P. ikegamii*, *P. otii*, *P. sakuraii*) are clearly serrate. This is another very strong characteristic that distinguishes closely related species from each other. Taking into account other taxa, apical serration distinguishes, among others, *P. denticulatum* from *P. denticulatum* var. *obtusifolium*; *P. nemorale* from *P. longisetum*; or *P. nemorale* from *P. succulentum* (Wilson) Lindb, whereas, *P. denticulatum* and *P. nemorale* have a clearly serrate apex, and *P. denticulatum* var. *obtusifolium*, *P. longisetum* and *P. succulentum* are non-serrate [2,3,9,12,14,63].

The abovementioned features are very helpful in the analysis of material from *Plagiothecium*, and their clear variability may be a premise for further detailed taxonomic studies of individual taxa. However, one of the most important taxonomical features separating the species of *Plagiothecium* are the dimensions of the cells from the middle part of the leaf, [2,9,12,14,63]. Within the *P. cavifolium* complex, species with long (over 101 µm) cells (*P. cavifolium sensu stricto*, *P. ikegamii*, *P. otii*, *P. sakuraii*) and short (less than 100 µm) cells (*P. subjulaceum*) were distinguished. We find similar differences between many other closely related taxa of *Plagiothecium*, incl. *P. nemorale* and *P. longisetum* or *P. nemorale* and *P. succulentum*. The first is characterized by cells shorter than 100 µm, while *P. longisetum* and *P. succulentum* have much longer cells, [2,3,9,14,63].

Taxa of *Plagiothecium* are usually collected sterile [13], and therefore the taxonomically significant features of species from the genus are often focused on the qualitative and quantitative features of the gametophyte [5,66]. However, the sporophyte also plays a very important taxonomic role. The length of the seta allows one to distinguish closely related



*P. nemorale* and *P. longisetum*, while the orientation of the capsule is key to distinguishing, among others, *P. schofieldii* and *P. denticulatum* as well as *P. laetum* and *P. curvifolium*. While *P. schofieldii* and *P. laetum* are characterized by an erect capsule, *P. denticulatum* and *P. curvifolium* have capsules that are inclined to horizontal, [3,9,14,63]. The conducted research shows that within the analyzed complex, most of the described taxa are characterized by inclined capsules, and only *P. flaccidum* is characterized by an erect one.

Differences between all the taxa mentioned above, as well as the taxonomic significance of these features, is clearly confirmed by the currently conducted taxonomic analyzes supported by DNA analysis [52,63–65].

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