

ARE *PLAGIOTHECIUM CAVIFOLIUM*, *P. NEMORALE* AND *P. SUCCULENTUM* INDEED VARIABLE SPECIES ?

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Abstract

This article compiles all available morphological and anatomical data on the gametophyte of three species of *Plagiothecium* genus which are considered to be the most taxonomically difficult. It presents a range of variation of all the described characteristics of these species and summarises the characteristics considered by individual researchers as taxonomically important. The article shows that among all the features qualitative characteristics related to stem leaves of the described species dominate. Results suggest not only a wide range of variability of the described features or the overlapping of their ranges, but also a lack of clear criteria which could be used to distinguish *Plagiothecium cavifolium*, *P. succulentum* and *P. nemorale* from one another.

Key words: *Plagiothecium*, *Orthophyllum* section, Range of variability, Taxonomic characteristics.

Introduction

The genus *Plagiothecium* Schimp. is widespread in Europe and in the world. In Europe, it is represented by 13 species (Hill *et al.*, 2006), while in the world the total number of species of this genus is still unknown and needs to be determined.

Researchers suggest that the species representing this genus are highly variable and some are even considered to be complex. Three among the European species: *Plagiothecium cavifolium* (Brid.) Z. Iwats., *P. succulentum* (Wilson) Lindb. and *P. nemorale* (Mitt.) A. Jaeger, belonging to the section *Orthophyllum* Jedl. (Ochyra *et al.*, 2003), are considered to be the most variable and researchers have the greatest taxonomic problems with them (Iwatsuki, 1970; Lewinsky, 1974; Hemerik, 1989; Smith, 2001).

So far, a significant amount of research on the genus *Plagiothecium* or its individual species has been conducted, but usually such studies concern individual European countries or their parts (Lefebvre & Lennes, 1969; Lewinsky, 1974), and they rarely cover a larger area in Europe (Jedlička, 1948, 1950) or other parts of the world (Ireland, 1969, 1986, 1992; Iwatsuki, 1970; Buck & Ireland, 1989).

Most of these studies provide different and often very divergent results concerning not only the ranges of variability of individual characteristics but also indicating different traits as taxonomically important for the described species. This often leads to the situation when the proposed features are excluded or the ranges of variability of these characteristics for each species overlap. None of the mentioned European studies (Jedlička, 1948, 1950; Ireland, 1969, 1986, 1992; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Buck & Ireland, 1989) have provided clear criteria to distinguish *P. cavifolium*, *P. succulentum* and *P. nemorale* from one another. This leads to misunderstandings and makes it difficult to provide clear revisions of studied specimens. Additionally, researchers (Nyholm, 1965; Iwatsuki, 1970; Greene, 1957) mentioned

specimens with intermediate features between the described species, which made correct interpretations of these specimens even more difficult.

Due to existing discrepancies and in order to systematise the current state of knowledge on the taxonomically important characteristics and the range of variability of these characteristics, all available data on morphological and anatomical features of the studied species have been compiled together. The results of this work are presented in this article.

Materials and methods

The article is based entirely on the literature data coming from all papers and handbooks describing *P. cavifolium*, *P. nemorale* and *P. succulentum*. The compiled data on morphological and anatomical parts of the gametophyte of these species were used for further analysis. Additionally, based on available articles and handbooks, the article lists the characteristics considered by authors as taxonomically significant to distinguish these species.

In the description of the range of variation of a given characteristic, the most frequent values were described as "commonly reported".

Results

Among the morphological and anatomical features mentioned in all the cited papers describing the species, qualitative features dominate. Among the 34 qualitative features indicated, the ones that describe the leaves of the studied species. These characteristics include: symmetry, colour, gloss, serration and the shape of the leaf. The features also concern individual leaf structures, such as: the apex (the length, shape and symmetry of the apex), the size of costae, leaf cells (the surface and the width of the walls, presence or absence of protoplast in the leaf cells, the shape of the cells and the arrangement of the transverse rows created by these cells), and decurrent cells (the colour and shape of these cells)

(Jedlička, 1947, 1948, 1950; Nyholm, 1965; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Less often researchers have used quantitative features. In this case, characteristics related to stem leaves of the species also dominate. They describe: the cells from the middle part of the leaves (the length and width of the cells), costae (the number of costae and their length in relation to the length of the leaves), and decurrent cells (the number of rows, the length and width of these cells) (Jedlička, 1947, 1948, 1950; Nyholm, 1965; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Description of *Plagiothecium cavifolium*, *P. nemorale* and *P. succulentum*

Size, colour and lustre of plants: *Plagiothecium cavifolium* is described as a large (Ireland, 1986), medium (Iwatsuki, 1970; Noguchi, 1994; Smith, 2001) to small-size plant (Iwatsuki, 1970) forming dense (Jedlička, 1948, 1950; Iwatsuki, 1970) or loose mats (Jedlička, 1948, 1950). This species forms green (Jedlička, 1948, 1950), pale green (Nyholm, 1965; Ireland, 1969; Iwatsuki, 1970; Noguchi, 1994), yellowish green (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970), yellowish (Jedlička, 1948, 1950; Nyholm, 1965) to even brownish mats (Jedlička, 1948, 1950). Plant are glossy (Ireland, 1969), slightly glossy (Noguchi, 1994), distinctly glossy (Iwatsuki, 1970) or rarely dull (Ireland, 1969).

Plagiothecium nemorale specimens are large (Iwatsuki, 1970) to medium-size (Iwatsuki, 1970; Smith, 2001) forming loose mats (Jedlička, 1948, 1950). The colour of the species ranges from dark green (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994) to yellowish green (Nyholm, 1965; Iwatsuki, 1970), and is usually without metallic lustre (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970).

Plagiothecium succulentum are medium-size plants (Smith, 2001) forming dense or loose mats (Jedlička, 1948, 1950). The colour of the plants ranges from green (Jedlička, 1948, 1950), dark green (Jedlička, 1948, 1950; Nyholm, 1965) to yellowish (Nyholm, 1965), usually with metallic lustre (Jedlička, 1948, 1950; Nyholm, 1965).

Stems: *Plagiothecium cavifolium* stems are irregularly branched (Iwatsuki, 1970; Lewinsky, 1974) or simple (Noguchi, 1994), erect or prostrate (Jedlička, 1948, 1950; Ireland, 1969), densely foliate (Jedlička, 1948, 1950), rarely complanate-foliate, but often flagelliform and attenuate at the apex (Ireland, 1969; Noguchi, 1994). Stems are usually julaceous (Ireland, 1969), from 4.0 mm (Ireland, 1969, 1986) to 15.0 mm long (Noguchi, 1994), and from 1.0 mm (Ireland, 1969, 1986), 2.5 (Noguchi, 1994) to even 4.0 mm wide (Ireland, 1969, 1986). Cross-sections of the stems are round to slightly elliptical, from 0.25 mm (Jedlička, 1948, 1950; Iwatsuki, 1970) to 0.30 mm in diameter (Jedlička, 1948, 1950). The epidermis is constructed of two layers of yellowish-green (Jedlička, 1948, 1950), thin-walled cells (Iwatsuki, 1970), with

dimensions from 13.0 to 15.0 μm wide and from 8.0 to 15.0 μm thick (Iwatsuki, 1970). Parenchyma is composed of large cells (Jedlička, 1948, 1950). In cross-sections of the stems, central strands are present (Jedlička, 1948, 1950; Iwatsuki, 1970).

Stems of *Plagiothecium nemorale* are irregularly branched (Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974), prostrate, densely and complanately leaved, with leaves on the stem loosely arranged (Jedlička, 1948, 1950). Stems are 20.0 mm long and 4.0 mm wide with leaves (Noguchi, 1994). Cross-sections of the stem are round (Iwatsuki, 1970), from 0.3–0.4 (Jedlička, 1948, 1950) to 0.5 mm in diameter (Iwatsuki, 1970). The epidermal layer is composed of two rows (Jedlička, 1948, 1950) with thin-walled cells, with dimensions 18.0–26.0 μm wide and 15.0–20.0 μm thick (Iwatsuki, 1970). Parenchyma is composed of large cells (Jedlička, 1948, 1950), and central strands are developed (Jedlička, 1948, 1950; Iwatsuki, 1970).

Plagiothecium succulentum stems are irregularly branched (Nyholm, 1965; Lewinsky, 1974) or sometimes unbranched (Lewinsky, 1974), with dense foliage (Jedlička, 1948, 1950), in cross-sections from 0.38 to 0.45 mm. The epidermis is composed of two rows of yellowish cells, while parenchyma is composed of large cells (Jedlička, 1948, 1950).

Branches: *Plagiothecium cavifolium* branches are ascending to erect (Greene, 1957; Nyholm, 1965; Ireland, 1969; Iwatsuki, 1970; Smith, 2001), or sometimes prostrate (Ireland, 1969), julaceous (Greene, 1957; Nyholm, 1965; Lewinsky, 1974; Smith, 2001) or usually julaceous (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970) to subjulaceous (Iwatsuki, 1970; Ireland, 1986), rarely somewhat complanate-foliate, but not strongly complanated (Greene, 1957; Ireland, 1969), often complanate near the end of branches (Iwatsuki, 1970) and often flagelliform and attenuate at apices (Ireland, 1969), densely foliate (Iwatsuki, 1970). Branches vary from 0.7 to 1.0 cm long and from 2.0 to 2.5 mm wide (including leaves when moist) (Iwatsuki, 1970).

Branches of *Plagiothecium nemorale* are ascending (Greene, 1957; Iwatsuki, 1970; Smith, 2001), erect, rarely creeping (Iwatsuki, 1970), prostrate (Greene, 1957; Smith, 2001), moderately complanate (Greene, 1957), complanate, but not plicate (Lewinsky, 1974), usually julaceous to subjulaceous (Iwatsuki, 1970). Branches are from 1.5 to 3.0 cm long and about 5.0 mm wide including leaves when dry (Iwatsuki, 1970).

Plagiothecium succulentum branches are prostrate to ascending (Greene, 1957; Smith, 2001), moderately complanate (Greene, 1957), complanate (Lewinsky, 1974), not plicate (Lewinsky, 1974), and densely foliate (Jedlička, 1948, 1950).

Colour and appearance of the leaves: *Plagiothecium cavifolium* leaves are light green or yellowish (Iwatsuki, 1970), with more or less distinct metallic lustre (Iwatsuki, 1970). Leaves are erect-spreading (Ireland, 1969; Noguchi, 1994), rarely distant (Ireland, 1969; Iwatsuki, 1970), appressed (Jedlička, 1948, 1950; Barkman, 1957) and arranged all around the stem (Nyholm, 1965). When dry,

leaves are scarcely shrunken (Iwatsuki, 1970; Smith, 2001), sometimes longly plicate (Jedlička, 1948, 1950; Lewinsky, 1974), but not undulate (Ireland, 1969; Smith, 2001).

Leaves of *Plagiothecium nemorale* are usually dark green to yellowish brown (Iwatsuki, 1970), spreading (Smith, 2001) to erect-spreading when moist (Noguchi, 1994). When dry, leaves of this species are shrunken (Jedlička, 1947, 1948, 1950; Nyholm, 1965; Smith, 2001), or more or less distinctly shrunken (Iwatsuki, 1970; Noguchi, 1994); younger leaves are usually shrunken, while lower leaves are scarcely shrunken (Iwatsuki, 1970).

Plagiothecium succulentum leaves are large (Jedlička, 1948, 1950; Greene, 1957) and spreading (Smith, 2001). When dry, moderately to strongly shrunken (Smith, 2001), slightly or not shrunken (Jedlička, 1948, 1950).

Symmetry and shape of the leaves: *Plagiothecium cavifolium* leaves are symmetric (Jedlička, 1948, 1950; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994), mostly symmetric (Iwatsuki, 1970; Smith, 2001) or sometimes slightly asymmetric (Iwatsuki, 1970; Lewinsky, 1974). Leaves are usually distinctly julaceous (Iwatsuki, 1970), imbricate (Ireland, 1969, 1986; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001) or loosely imbricate (Nyholm, 1965), concave (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), more or less concave (Iwatsuki, 1970), sub-complanate (Smith, 2001), not or slightly complanate (Nyholm, 1965; Ireland, 1969; Noguchi, 1994). Leaves of this species are broad (Greene, 1957) and rounded (Nyholm, 1965), broadly (Smith, 2001) or shortly ovate (Greene, 1957), ovate (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), ovate-lanceolate (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970) to lanceolate (Lewinsky, 1974).

Leaves of *Plagiothecium nemorale* are symmetric (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974), mostly symmetric (Noguchi, 1994; Smith, 2001), almost symmetric (Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994), slightly asymmetric (Jedlička, 1948, 1950; Greene, 1957; Iwatsuki, 1970; Lewinsky, 1974) or asymmetric (Noguchi, 1994). Leaves are complanate (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), more or less concave (Iwatsuki, 1970) to concave (Nyholm, 1965; Noguchi, 1994), not plicate (Lewinsky, 1974). Leaves of this species are broad (Jedlička, 1948, 1950; Greene, 1957), rounded ovate (Lewinsky, 1974), ovate (Greene, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), to ovate-lanceolate (Jedlička, 1948, 1950).

Plagiothecium succulentum leaves are symmetric (Jedlička, 1948, 1950; Nyholm, 1965; Greene, 1957; Lewinsky, 1974) or almost so (Nyholm, 1965; Smith, 2001) to slightly asymmetric (Jedlička, 1948, 1950; Greene, 1957; Lewinsky, 1974), complanate (Nyholm, 1965; Lewinsky, 1974; Smith, 2001), slightly concave (Nyholm, 1965), but not plicate (Jedlička, 1948, 1950; Lewinsky, 1974). Leaves of this species are broad (Jedlička, 1948, 1950; Greene, 1957), ovate (Greene,

1957; Nyholm, 1965; Lewinsky, 1974; Smith, 2001), ovate-lanceolate (Jedlička, 1948, 1950; Lewinsky, 1974; Smith, 2001), long ovate-lanceolate (Jedlička, 1948, 1950) to lanceolate (Lewinsky, 1974).

Margin and apex of the leaves: *Plagiothecium cavifolium* margins are plane (Ireland, 1969, 1986; Iwatsuki, 1970), sometimes narrowly and slightly recurved at the base (Iwatsuki, 1970; Noguchi, 1994) or narrowly recurved near the apex (Ireland, 1969). Margins are usually entire (Jedlička, 1948, 1950; Ireland, 1969, 1986; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001), or seldom with a few denticulations at the apex (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974). The apex is short (Noguchi, 1994; Smith, 2001) and narrow (Noguchi, 1994). Leaves are tapering to acute (Greene, 1957; Smith, 2001), abruptly acute (Ireland, 1969; Iwatsuki, 1970), shortly apiculate (Greene, 1957), or acuminate at the apex (Ireland, 1969; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001). Apex leaves are often reflexed (Ireland, 1969, 1986; Nyholm, 1965; Iwatsuki, 1970; Smith, 2001), hardly changed by desiccation (Iwatsuki, 1970).

Margins of *Plagiothecium nemorale* are plane or rarely slightly recurved below (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001). The margin and apex are entire (Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001), mostly entire (Nyholm, 1965), or denticulate near the apex (Jedlička, 1948, 1950; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001). Leaves of this species are tapering to short or gradually narrowed (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970), acute (Smith, 2001), broadly acute (Greene, 1957; Noguchi, 1994) to acuminate at the apex (Smith, 2001).

Plagiothecium succulentum margins are plane or slightly recurved (Nyholm, 1965). The margin and apex are entire (Jedlička, 1948, 1950; Nyholm, 1965; Lewinsky, 1974; Smith, 2001) or rarely with a few denticulations (Lewinsky, 1974). Leaves of this species are gradually tapering to a narrow acuminate (Greene, 1957; Nyholm, 1965; Smith, 2001) or straight recurved apex (Nyholm, 1965).

Dimensions of the leaves: The length of *Plagiothecium cavifolium* leaves ranges from 1.0 to 3.0 mm (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001), but the most commonly reported are those of 1.0 mm (Jedlička, 1948, 1950; Ireland, 1969, 1986), 1.7 mm (Greene, 1957; Lefebvre & Lennes, 1969; Smith, 2001), or 3.0 mm length (Jedlička, 1948, 1950; Ireland, 1969, 1986). The widest range of variation is given by Jedlička (1947, 1948, 1950) and Ireland (1969, 1986). Other authors give a much narrower range of variation of this character (Fig. 1).

Leaves of this species are largest near the base of the stem (Noguchi, 1994). The width of *P. cavifolium* leaves ranges from 0.3 to 1.4 mm (Jedlička, 1947, 1948, 1950; Greene, 1957; Ireland, 1969; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Noguchi, 1994), the most commonly reported are those of the 0.8 mm width (Greene, 1957; Iwatsuki, 1970). The widest range of variation is given by Ireland (1969, 1986) and Jedlička (1947, 1948, 1950),

other authors give a much narrower range of variation of this characteristic (Fig. 2).

The length of *Plagiothecium nemorale* leaves ranges from 1.4 to 4.0 mm (Jedlička, 1948, 1950; Greene, 1957; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001), the most commonly reported are those of the 2.4 mm length (Lefebvre & Lennes, 1969; Iwatsuki, 1970). The widest range of variation is given by Jedlička (1948, 1950) and Smith (2001), other authors give a much narrower range of variation of this characteristic (Fig. 3). The width of leaves of this species ranges from 1.1 to 1.7 mm width (Jedlička, 1948, 1950; Greene, 1957; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Noguchi, 1994), but the most commonly reported are those of the 1.2 mm width (Lefebvre & Lennes, 1969; Noguchi, 1994). Other authors give a much narrower range of variation of this character (Fig. 4). Leaves of *P. nemorale* are usually the widest near the base and much smaller near the end of branches (Iwatsuki, 1970).

The length of *Plagiothecium succulentum* leaves ranges from 2.0 mm to 3.5 mm length (Jedlička, 1947, 1948, 1950; Greene, 1957; Lefebvre & Lennes, 1969; Smith, 2001), the most commonly reported are those of the 2.0 mm (Jedlička, 1948, 1950; Smith, 2001) or 2.7 mm length (Greene, 1957; Lefebvre & Lennes, 1969). The widest range of variation is given by Jedlička (1948, 1950) and Smith (2001). Other authors give a much narrower range of variation of this characteristic (Fig. 5). The width of leaves of this species ranges from 1.0 mm to 1.4 mm (Jedlička, 1948, 1950; Greene, 1957; Lefebvre & Lennes, 1969), the most commonly reported are those of the 1.0 mm width (Jedlička, 1948, 1950; Greene, 1957). The widest range of variation is given by Jedlička (1948, 1950), other authors give a much narrower range of variation of this character (Fig. 6).

The length and width influence the size of the leaf. Considering the ranges of variation of these characteristics reported in all the cited articles, confirmed an overlapping of their ranges (Fig. 7A). The ranges of variation for the length and width of the leaf given for *Plagiothecium succulentum* practically completely coincide with the ranges of variability of these characteristics given for other species. The leaf sizes for *P. cavifolium* and *P. nemorale* also overlap. Only in extreme ranges, the leaf sizes of this species differ from one another (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Costae of the leaves: *Plagiothecium cavifolium* costae are sometimes poorly developed, appearing single or rarely even lacking (Ireland, 1969), but are usually double (Jedlička, 1948, 1950; Barkman, 1957; Nyholm, 1965; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974), short (Jedlička, 1948, 1950; Barkman, 1957; Nyholm, 1965; Ireland, 1969), usually short (Iwatsuki, 1970), or rather long (Noguchi, 1994). The costa often reaches from 1/5–1/4 (Barkman, 1957), 1/3 (Jedlička, 1948, 1950; Lewinsky, 1974), 1/2 (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001), to 2/3 length of the leaf (Smith, 2001).

Costae of *Plagiothecium nemorale* are broad (Jedlička, 1948, 1950), double (Iwatsuki, 1970; Lewinsky, 1974), and branched (Nyholm, 1965; Iwatsuki, 1970), extending halfway up the leaf (Jedlička, 1948, 1950; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001) or reaching from 1/3 to 1/2 length of the leaf (Lewinsky, 1974).

Plagiothecium succulentum nerves are double (Nyholm, 1965; Lewinsky, 1974), but weak (Jedlička, 1948, 1950), broad at the base (Nyholm, 1965), extending halfway up the leaf (Smith, 2001), 1/2–1/3 (Lewinsky, 1974) or only 1/4 length of the leaf (Jedlička, 1948, 1950).

Shape of leaf cells: *Plagiothecium cavifolium* cells from the middle part of the leaf are thin-walled (Jedlička, 1947, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970), or even thickened (Iwatsuki, 1970), and smooth (Ireland, 1969). Cell contents are lacking in old specimens (Iwatsuki, 1970). Median cells of this species are elongate (Jedlička, 1948, 1950; Noguchi, 1994), almost linear (Iwatsuki, 1970; Noguchi, 1994), flexuose (Iwatsuki, 1970), narrowly linear (Iwatsuki, 1970) to linear-rhomboidal (Smith, 2001). Lower lamina cells are somewhat lax, elongate-hexagonal, hyaline (Noguchi, 1994), with pits in walls (Ireland, 1969), wider and thick-walled (Iwatsuki, 1970).

Plagiothecium nemorale median lamina cells are thin-walled (Iwatsuki, 1970; Noguchi, 1994), and fairly homogeneous throughout the leaves (Nyholm, 1965). Cells are broad (Jedlička, 1948, 1950; Greene, 1957), scarcely overlapping (Greene, 1957; Smith, 2001) and forming regular transverse rows (Greene, 1957; Smith, 2001). Contents of cells often remain in old specimens (Iwatsuki, 1970). Median cells of this species are hexagonal (Greene, 1957; Iwatsuki, 1970), elongate-hexagonal (Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994), narrowly hexagonal (Smith, 2001), hexagono-rhomboidal (Jedlička, 1948, 1950; Noguchi, 1994), rhomboid (Nyholm, 1965; Iwatsuki, 1970), narrowly rhomboidal (Iwatsuki, 1970), elongate rhomboid-hexagonal, rectangular (Noguchi, 1994), but never linear or flexuose (Iwatsuki, 1970). Upper lamina cells are shorter than median cells (Iwatsuki, 1970; Noguchi, 1994), marginal cells are narrower and linear-rhomboidal (Noguchi, 1994), at the base cells are slightly widened (Nyholm, 1965; Iwatsuki, 1970).

Plagiothecium succulentum leaf cells are thick-walled (Jedlička, 1947, 1948, 1950) or thin-walled (Nyholm, 1965), distinctly overlapping (Greene, 1957; Smith, 2001), with a few protoplasts remaining in the cells in old specimens (Jedlička, 1948, 1950). Cells do not form regular transverse rows (Smith, 2001). In the middle of leaves, cells are narrowly hexagono-rhomboidal (Jedlička, 1948, 1950), elongate (Nyholm, 1965), or linear-rhomboidal (Smith, 2001).

Dimensions of leaf cells: *Plagiothecium cavifolium* cells from the middle part of the leaf have the length from 40.0 µm to 161.0 µm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), but the most commonly reported are those of the 120.0 µm length (Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994). The widest range of variation is given by Jedlička (1947, 1948, 1950) and Ireland (1969, 1986), other authors give a much narrower range of variation of this characteristic (Fig. 8).

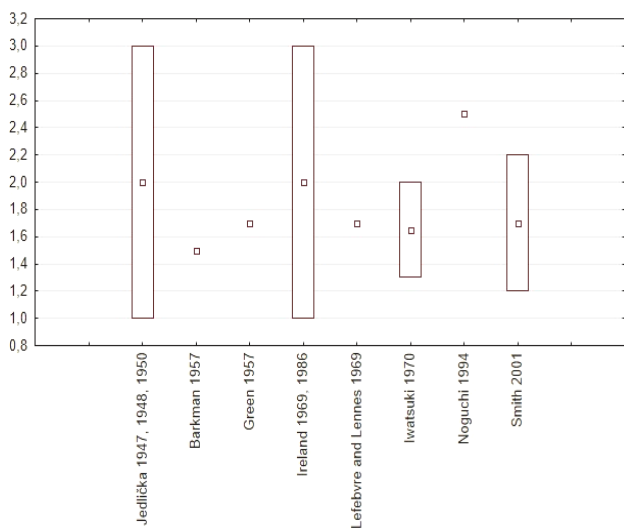


Fig. 1. The range of variation of the *Plagiothecium cavifolium* leaf length noted by individual authors.

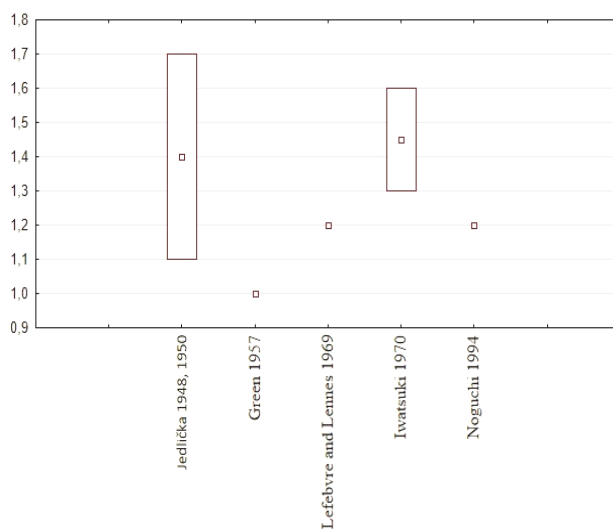


Fig. 4. The range of variation of the *Plagiothecium nemorale* leaf width noted by individual authors.

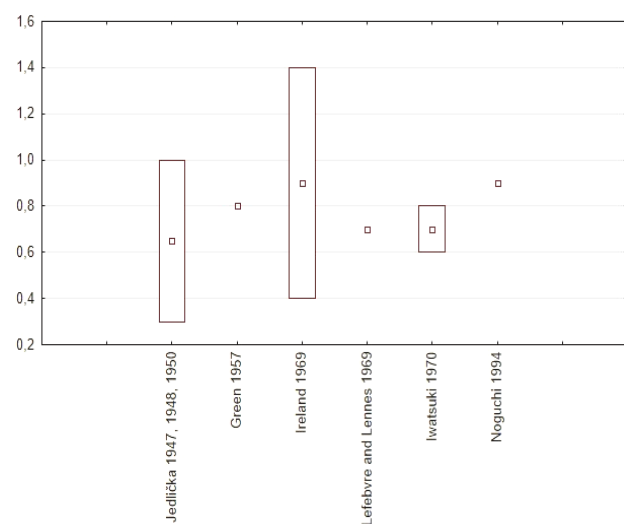


Fig. 2. The range of variation of the *Plagiothecium cavifolium* leaf width noted by individual authors.

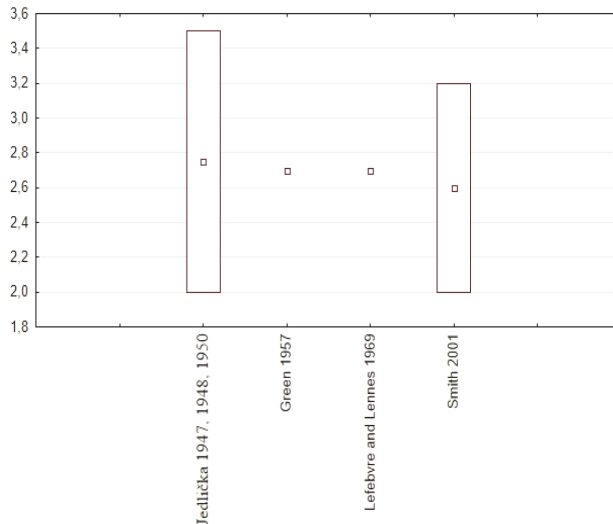


Fig. 5. The range of variation of the *Plagiothecium succulentum* leaf length noted by individual authors.

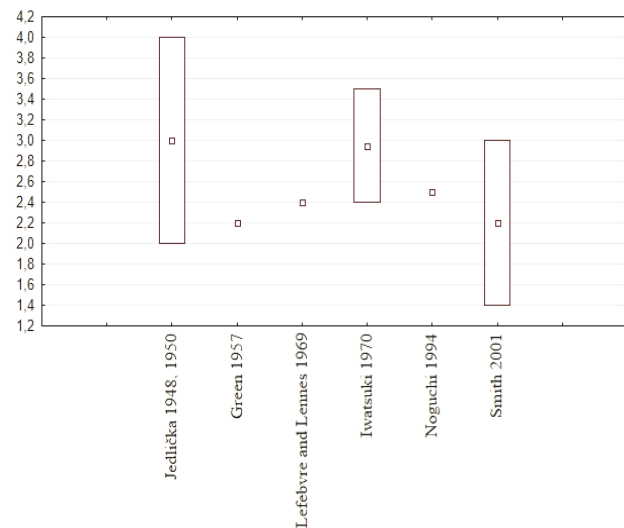


Fig. 3. The range of variation of the *Plagiothecium nemorale* leaf length noted by individual authors.

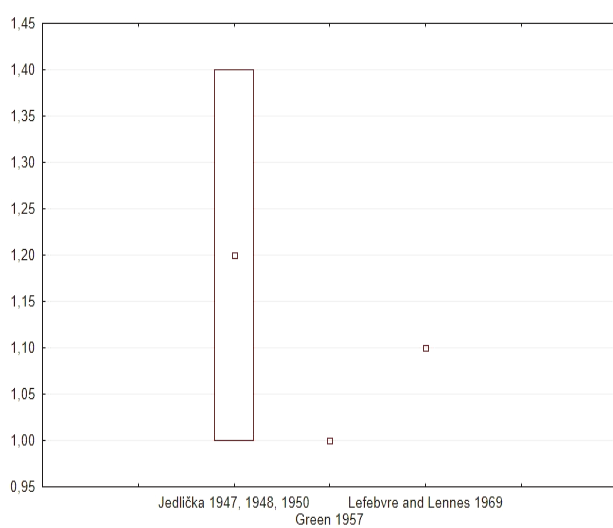


Fig. 6. The range of variation of the *Plagiothecium succulentum* leaf width noted by individual authors.

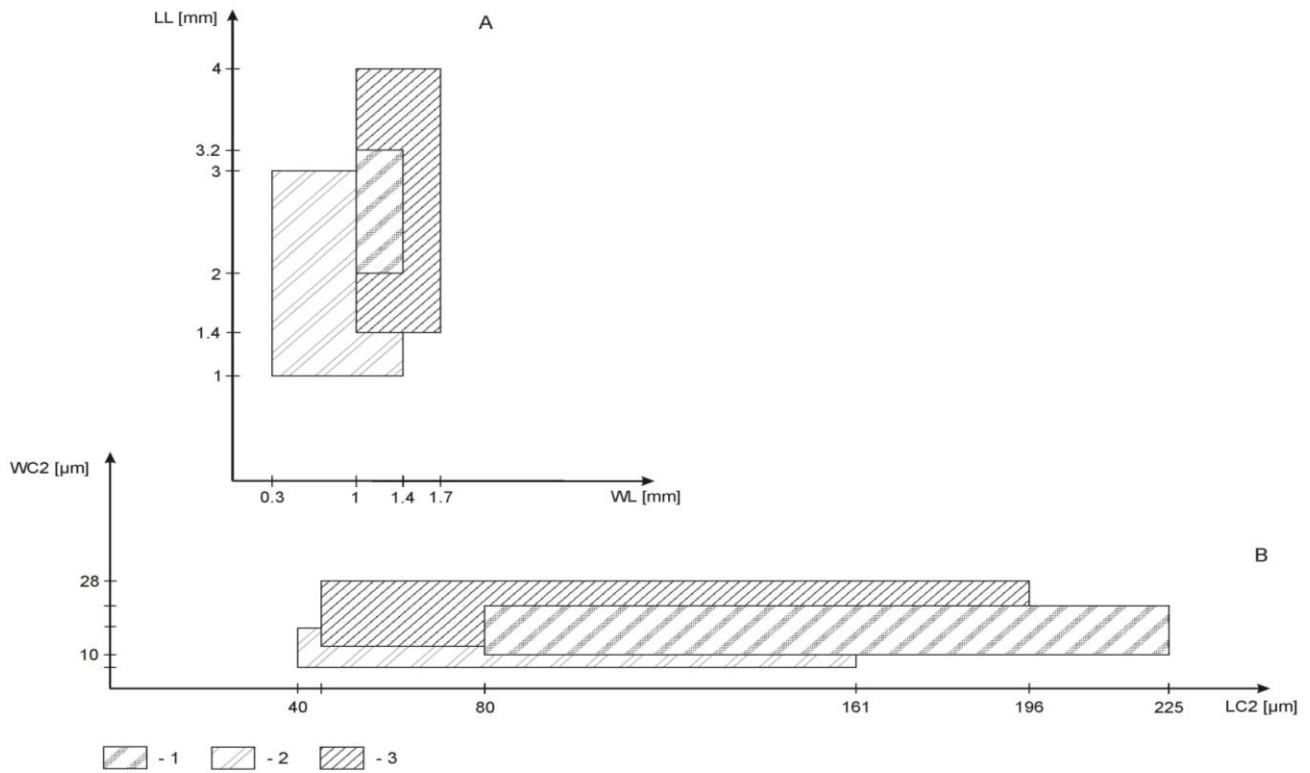


Fig. 7. The range of the length and width of leaves (A) and the range of the length and width cells from the middle part of the leaves (B) of the described species. Explanation: 1 – *Plagiothecium suculentum*, 2 – *P. cavifolium*; 3 – *P. nemorale*.

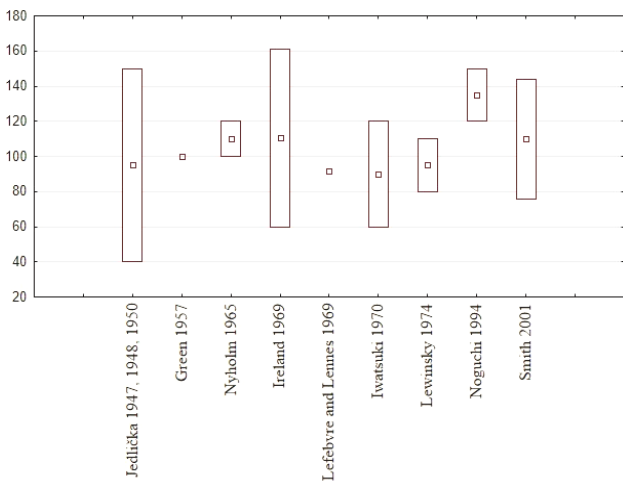


Fig. 8. The range of variation of the length of *Plagiothecium cavifolium* cells from the middle part of the leaf noted by individual authors.

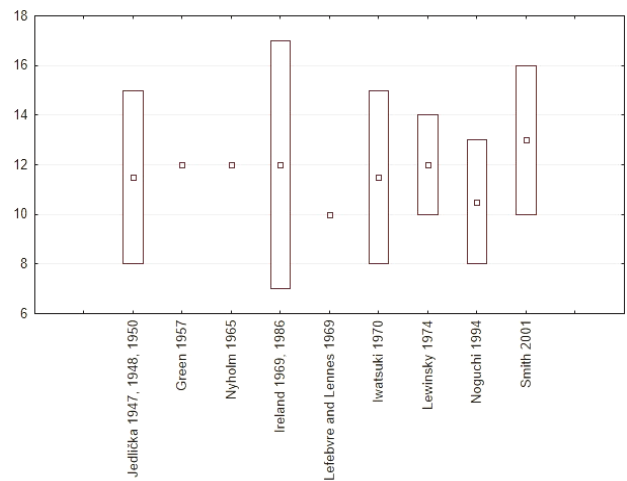


Fig. 9. The range of variation of the width of *Plagiothecium cavifolium* cells from the middle part of the leaf noted by individual authors.

The width of the cells of this species ranges from 7.0 μm to 17.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Ireland, 1969, 1986; Nyholm, 1965; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), the most commonly reported are those of the 12.0 μm width (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965; Iwatsuki, 1970). The widest range of variation is given by Ireland (1969, 1986), other authors give a much narrower range of variation of this characteristic (Fig. 9). The leaf cells of this species are 6–13 (Smith, 2001) or 8–10 (Barkman, 1957) times as long as they are wide, and cells from the top are shorter than cells from the middle part of the leaf (Iwatsuki, 1970).

The length of *Plagiothecium nemorale* cells from the middle part of the leaf ranges from 45.0 μm to 196.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), the most commonly reported are those measuring 80.0 μm (Nyholm, 1965; Lewinsky, 1974; Smith, 2001). The widest range of variation is given by Jedlička (1947, 1948, 1950), other authors give a much narrower range of variation of this characteristic (Fig. 10). The width of these cells ranges from 12.0 μm to 28.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Lefebvre and Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith,

2001), the most commonly reported are those of the 16.0 μm width (Lewinsky, 1974; Nyholm, 1965; Noguchi, 1994; Smith, 2001). The widest range of variation is given by Jedlička (1947, 1948, 1950), other authors give a much narrower range of variation of this characteristic (Fig. 11). The leaf cells of this species are 4–6 times as long as they are wide (Smith, 2001).

Plagiothecium succulentum cells from the middle part of the leaf have the length from 72.0 μm to 225.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Lefebvre & Lennes, 1969; Lewinsky, 1974; Smith, 2001), the most commonly reported are those measuring 200.0 μm (Nyholm, 1965; Smith, 2001). The widest range of variation is given by Jedlička (1947, 1948, 1950) and Smith (2001), other authors give a much narrower range of variation of this characteristic (Fig. 12).

The width of these cells ranges from 8.0 μm to 22.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Lefebvre & Lennes, 1969; Lewinsky, 1974; Smith, 2001), the most commonly reported are those of the 12.0 μm (Nyholm, 1965; Lewinsky, 1974) or 15.0 μm width (Jedlička, 1947; Greene, 1957; Lefebvre & Lennes, 1969). The widest range of variation is given by Smith (2001), other authors give a much narrower range of variation of this characteristic (Fig. 13). Middle leaf cells of this species are 6–10 times as long as they are wide (Smith, 2001), but at the leaf base cells are somewhat shorter and wider (Nyholm, 1965).

The length and width of leaf cells affect their size. Given the cited in the literature ranges of variation of leaf cells, it can be clearly seen that the ranges overlap (Fig. 7B). Literature data show that the cell length is not a good feature in distinguishing individual species, only extreme values of this feature differ *P. cavifolium* and *P. succulentum* from each other (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Decurrent angular cells: *Plagiothecium cavifolium* decurrent angular cells are hyaline to green (Lewinsky, 1974), narrow (Jedlička, 1948, 1950; Barkman, 1957; Greene, 1957; Iwatsuki, 1970; Smith, 2001), and short (Barkman, 1957). They are composed of elongate (Jedlička, 1948, 1950; Barkman, 1957), rectangular (Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), linear (Nyholm, 1965; Iwatsuki, 1970), or enlarged cells (Smith, 2001), but not rounded or forming distinct auricles (Smith, 2001). They consist of 1–2 (Barkman, 1957), 1–3 (Lewinsky, 1974; Smith, 2001), 2–3 (Iwatsuki, 1970) or even 1–5 vertical rows (Ireland, 1969). Decurrent cells are from 28.0 μm (Ireland, 1969), 40.0 (Noguchi, 1994), 55.0 (Noguchi, 1994) to 70.0 μm long (Ireland, 1969), and from 12.0 μm (Ireland, 1969), 13.0 (Noguchi, 1994), 22.0 (Ireland, 1969) to 25.0 μm wide (Noguchi, 1994).

Decurrent cells of *Plagiothecium nemorale* are hyaline (Lewinsky, 1974), pale (Nyholm, 1965) to pale green (Lewinsky, 1974). Leaves of this species are shortly (Noguchi, 1994), narrowly (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001) to broadly decurrent (Jedlička, 1948, 1950; Greene, 1957; Smith, 2001).

Decurrent cells are from rectangular (Greene, 1957; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001), sublinear (Noguchi, 1994), linear (Nyholm, 1965; Iwatsuki, 1970), elongate-rectangular (Noguchi, 1994), enlarged (Smith, 2001) to elongate (Jedlička, 1948, 1950), but never rounded (Noguchi, 1994; Smith, 2001). Leaves are decurrent in 1–3 rows (Lewinsky, 1974; Smith, 2001).

Plagiothecium succulentum decurrent cells are from pale (Nyholm, 1965), pale green to hyaline (Lewinsky, 1974). Leaves are narrowly (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965) or broadly decurrent (Greene, 1957). Decurrent angular cells of this species are elongate (Jedlička, 1948, 1950), rectangular (Greene, 1957; Nyholm, 1965; Lewinsky, 1974; Smith, 2001), linear (Nyholm, 1965), enlarged (Smith, 2001) to elongate, with rounded cell ends (Lewinsky, 1974), but not rounded cells, and they do not form distinct auricles (Smith, 2001). Leaves are decurrent in 1–3 rows (Lewinsky, 1974; Smith, 2001).

Brood bodies: *Plagiothecium cavifolium* fusiform axillary gemmae are common (Iwatsuki, 1970; Lewinsky, 1974), or occasionally present (Ireland, 1969; Smith, 2001), gemmae are from 36.0 μm (Ireland, 1969), 83.0 (Lefebvre & Lennes, 1969) to 110.0 μm long (Ireland, 1969), and from 9.0 μm to 17.0 μm wide (Ireland, 1969), consisting of 2–7 cells (Ireland, 1969).

Brood bodies of *Plagiothecium nemorale* are often abundant at the axis of leaves (Iwatsuki, 1970; Lewinsky, 1974) or sometimes present (Smith, 2001), they are 85 μm long (Lefebvre & Lennes, 1969).

Plagiothecium succulentum fusiform gemmae are often abundant (Lewinsky, 1974) or sometimes present (Smith, 2001), they are 112.0 μm long (Lefebvre & Lennes, 1969).

Taxonomically significant features: Among the taxonomically significant characteristics given by each author, qualitative features dominate. They are related to: the size of the plant, the arrangement of leaves on the stem, as well as the length and width of the stem. These features are also related to leaf cells of the described species, including: the length and width of the median cells of the leaf, its shape, the arrangement of the transverse rows created by the cells, the width of cell walls, presence or absence of protoplast in the leaf cells of the old specimens, the shape of the decurrent angular cells, and the number of rows of these cells. However, they are mainly related to the stem of leaves of the studied species (Jedlička, 1947; Barkman, 1957; Greene, 1957; Ireland, 1969; 1986; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Particular features are connected with: the length and width of leaves, their symmetry, shape, colour, and gloss, as well as the arrangement of leaves on the stem, the shape of the apex leaves, serrations of the margin and leaf apex, the number of the costae and their length in relation to the length of the leaf and the length and width of decurrent cells (Jedlička, 1947; Barkman, 1957; Greene, 1957; Ireland, 1969; 1986; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

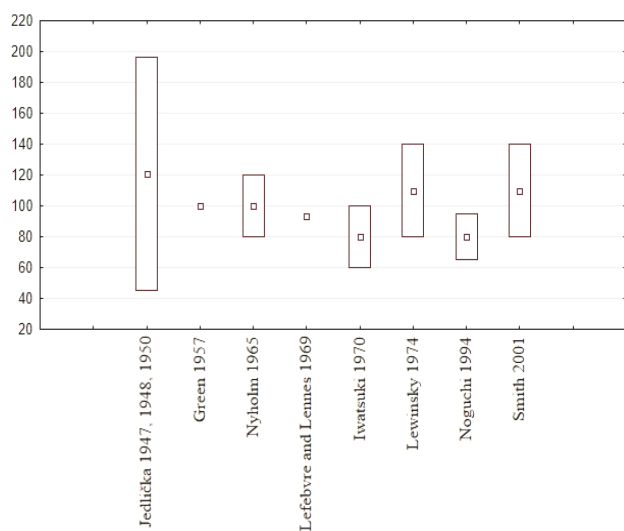


Fig. 10. The range of variation of the length of *Plagiothecium nemorale* cells from the middle part of the leaf noted by individual authors.

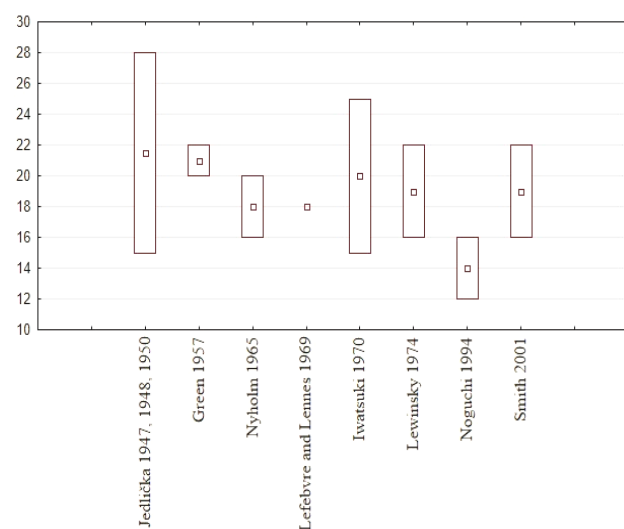


Fig. 11. The range of variation of the width of *Plagiothecium nemorale* cells from the middle part of the leaf noted by individual authors.

Discussion

Most of the species from the *Plagiothecium* genus are not described in detail yet. There is not just a lack of detailed data about their morphological or anatomical characters, but there are no detailed reports in the literature regarding their variability, distribution or ecological preferences covering a large area of their geographical distribution. There are also no in-depth studies describing relationships between individual, closely related species, or characteristics describing particular species.

Among the representatives of the *Orthophyllum* section, *Plagiothecium succulentum* has been the most poorly described so far. Compared to the rest of the species, the least amount of data about its morphological and anatomical features has been found (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith,

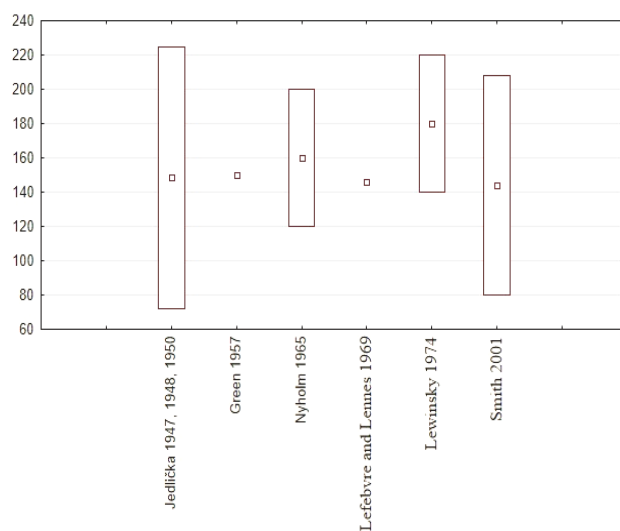


Fig. 12. The range of variation of the length of *Plagiothecium succulentum* cells from the middle part of the leaf noted by individual authors.

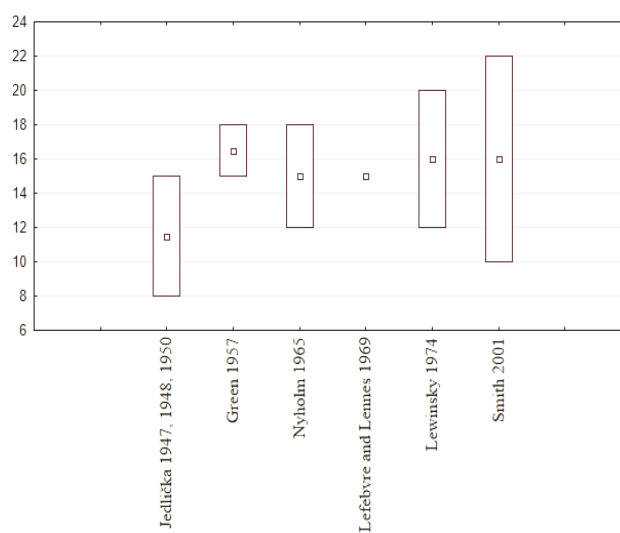


Fig. 13. The range of variation of the width of *Plagiothecium succulentum* cells from the middle part of the leaf noted by individual authors.

2001). Therefore, in my opinion, this species requires detailed research to fill these gaps.

Among all the features describing *Plagiothecium cavifolium*, *P. nemorale* and *P. succulentum*, qualitative characteristics dominate. Individual authors pay considerable attention to leaves of the studied species and structures associated with these leaves. However, in descriptions of the species, many features or structures have been described very sparingly or completely omitted, for example—rhizoids (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001). Therefore, the existing data should be supplemented in order to describe all the species in a similar manner.

Based on the analysis of the available literature, it can be stated that there are not many features which can easily distinguish the three species from one another. Features such as the colour and size of the plant, the

arrangement of branches on the stem, the length and diameter of the stem, the colour, symmetry, shape, length and width of the leaves, the serration of the margin and apex of the leaf, dimensions of leaf cells, decurrent angular cells and brood bodies, as well as the range of variability of these characteristics clearly overlap. Therefore, these features treated separately cannot be a clear criterion distinguishing the three species from one another (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

The leaf shape, which is often treated as a feature that allows easily to distinguish individual species from one another, described in articles or handbooks (particularly in figures), in my opinion, is not such a feature in this case. The described species have the leaf shape ranging from ovate (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001), ovate-lanceolate (Jedlička, 1948, 1950; Ireland 1969; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001) to lanceolate (Lewinsky, 1974).

The length and width of the leaf is also not a good feature for distinguishing the species in question. Although some authors (Jedlička, 1948, 1950; Greene, 1957) state that *Plagiothecium succulentum* has the longest leaves, the summary of the literature shows that *P. nemorale* reaches similar values of this feature. The cited data also confirm the observations of the author of this paper. While the compilation of bibliographic data suggests that *P. cavifolium* has shorter and narrower leaves than *P. nemorale* and *P. succulentum*, the ranges of variation of this characteristic for particular species partially overlap and differ only in extreme cases (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001). While analysing these characteristics, it should be noted that mainly Jedlička (1947, 1948, 1950) Ireland (1969, 1986) and Smith (2001) give a wider range of variation of these qualities than the other researchers.

Another feature which can help to distinguish individual species from one another is the leaf concavity. Generally, there is a view that *Plagiothecium cavifolium* has concave leaves, while other species have flat leaves. However, in my opinion, this feature is not an entirely good criterion, since the literature analysis has confirmed that *P. cavifolium* has leaves from concave (Jedlička, 1947, 1948, 1950; Barkman, 1957; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001) to slightly complanate (Nyholm, 1965; Ireland, 1969; Noguchi, 1994). *P. nemorale* has leaves from complanate (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001) to concave (Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994), while *P. succulentum* from complanate (Nyholm, 1965; Lewinsky, 1974; Smith, 2001) to slightly concave (Nyholm, 1965). Unpublished research of the author of this article confirms the presented data. Examining specimens described as *P. nemorale*, one can record specimens with strongly concave leaves as well as *P. cavifolium* specimens with practically flat leaves.

For many bryologists (Jedlička, 1948; Barkman, 1957; Nyholm, 1965), shrunken leaves of *Plagiothecium nemorale* are a good feature for distinguishing this species from other species, but it is not in accordance with Green's (1957) and Lewinsky's (1974) observations. They believe that *P. succulentum* can have strongly shrunken leaves, too. My observations suggest that leaves of *P. nemorale* and *P. succulentum* may be shrunken in dry conditions, but more often they are shrunken in the case of *P. nemorale*. Hence, this cannot be a clear feature separating the described species.

Another feature which is often considered as helpful in distinguishing *Plagiothecium nemorale* from *P. succulentum* is the serration of the leaf apex. In my opinion, which is also confirmed by the review of literature, this feature is not good to distinguish these species from each other. This is due to the fact that, as the literature review shows, all three species (even *P. cavifolium*) can have the leaf margin entire or usually entire (Jedlička, 1948, 1950; Ireland, 1969, 1986; Nyholm, 1965; Iwatsuki, 1970; Lewinsky, 1974; Smith, 2001), or with a few denticulations at the apex (Jedlička, 1948, 1950; Ireland, 1969; Iwatsuki, 1970; Lewinsky, 1974).

The cited authors describe that the apex leaves of *Plagiothecium cavifolium* are often reflexed (Nyholm, 1965; Ireland, 1969, 1986; Iwatsuki, 1970; Smith, 2001) and they also state that this could be a useful feature for distinguishing this species from others because very often the apex of this species is clearly curved. However, Nyholm (1965) also states that the apex of *Plagiothecium succulentum* is recurved. My observations of specimens described as *P. nemorale* from Central and Eastern Europe also document a gently curved apex for this species. Therefore, this feature should also be treated with some caution.

Another feature considered as a good trait for distinguishing species is the length and width of the cells from the central part of the leaf. Lewinsky (1974) states that the described species differ in terms of aerolation of their leaf cells, *Plagiothecium nemorale* has short and wide cells, *P. succulentum* has long and narrow cells, whereas *P. cavifolium* has short and narrow cells. A summary of the values of these features shows that the ranges of variation of these features overlap and differ only in extreme cases (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

Generally, it is accepted that *Plagiothecium succulentum* has longer cells in the middle part of its leaf than the other species. A summary of collected data shows that similar values are also reached by *P. nemorale* (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001). However, it should be noted that the range of variation of this characteristic, as with the length and width of the leaf, is clearly wider due to the inclusion of the results given by Jedlička (1947, 1948, 1950), Ireland (1969, 1986), and Smith (2001).

The width of cells from the middle part of the leaf given by some authors may also cause a great deal of confusion and problems with an appropriate classification of these species. The cited authors report that this value for *Plagiothecium cavifolium* and *P. succulentum* can take from 7.0 to 8 μm . This fact is excluded from most studies where it is stated that the range of this feature for representatives of the *Orthophyllum* section is bigger rather than smaller than 10.0 μm (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001).

In addition, some researchers, such as Green (1957) or Nyholm (1965), mention specimens with intermediate features between the said species. This information confirms unpublished observations of the author of this article. Specimens with intermediate features occur sometimes and should be subject to separate and detailed research in the near future.

The literature review indicates that only some features distinguish the described species quite well. However, these are features distinguishing one species from the other two, not all three of them from one another. Such a feature is, for example, the metallic lustre which differs *Plagiothecium nemorale* from *P. succulentum* (Jedlička, 1948, 1950; Nyholm, 1965; Iwatsuki, 1970), but not from *P. cavifolium*, as this species may be dull (Ireland, 1969) or glossy (Ireland, 1969; Iwatsuki, 1970; Noguchi, 1994).

Costae, the structure which is the least described among the features associated with leaves of these species, are another such feature (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001). There are reports that *Plagiothecium cavifolium* has rather delicate and short costae, while *P. nemorale* and *P. succulentum* have longer and thicker costae (Jedlička, 1948, 1950; Barkman, 1957; Nyholm, 1965; Ireland, 1969; Iwatsuki, 1970).

Another feature which allows to fairly well distinguish the described species is the height and width of their epidermis cells. Iwatsuki (1970) describes that *Plagiothecium cavifolium* differs from *P. nemorale* by the height and width of these cells. However, it should be noted that small variability of the feature given in such cases does not always mean its small variability in the whole geographical range of this species. It may stem, for example, from a lack of research on this topic, which may be the case, as data on this subject so far have been only provided by Iwatsuki (1970) from Japan.

An interesting feature which may help to distinguish two species from each other is the formation of regular transverse rows by leaf cells, yet in my opinion, this characteristic still requires more detailed research. Researchers report that cells of *Plagiothecium nemorale* form these rows (Greene, 1957; Smith, 2001), and that they do not form on leaves of *P. succulentum* (Smith, 2001). However, none of the above-mentioned researchers says anything about forming regular transverse rows by *P. cavifolium*, therefore, this feature should be examined and carefully described.

The shape of the cells in the middle part of the leaf allows to better distinguish the analysed species, in particular, to distinguish *Plagiothecium cavifolium* from the other two species, although the literature review indicates a wide range of variability of this feature (Jedlička, 1947, 1948, 1950; Greene, 1957; Nyholm, 1965; Ireland, 1969, 1986; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974; Noguchi, 1994; Smith, 2001). Researchers report that *Plagiothecium cavifolium* has cells from elongate, almost linear, narrowly linear, flexuose to linear-rhomboidal (Jedlička, 1948, 1950; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001). While *P. succulentum* has cells from narrowly hexagono-rhomboidal, elongate to linear-rhomboidal (Jedlička, 1948, 1950; Nyholm, 1965; Smith, 2001). *P. nemorale* has cells from hexagonal, elongate-hexagonal, narrowly hexagonal, hexagono-rhomboidal, rhomboid to narrowly rhomboidal, elongate rhomboid-hexagonal, and rectangular, but never linear or flexuose (Jedlička, 1948, 1950; Greene, 1957; Nyholm, 1965; Iwatsuki, 1970; Noguchi, 1994; Smith, 2001).

Cell contents in old specimens are another characteristic related to cells. For *Plagiothecium cavifolium*, Iwatsuki (1970) observes that cell content is lacking, but in cells of *Plagiothecium nemorale* it remains. Jedlička (1948, 1950) adds that a few protooplasts remain in cells of *P. succulentum*. This may be a good indication but not a diagnostic feature, as it only concerns old herbarium specimens.

An important feature characteristic of all the studied species, which also clearly distinguishes them from *Plagiothecium denticulatum* or *P. ruthi*, is the fact that decurrent angular cells of the *Orthophyllum* section are not rounded or forming distinct auricles (Smith, 2001). It is worth remembering this fact and paying attention to this feature while conducting research in order not to confuse these species.

Species representing the *Orthophyllum* section for a long time have been the source of errors and taxonomic uncertainties (Greene, 1957). In addition, none of the previous revisions (Jedlička, 1948, 1950; Ireland, 1969, 1986, 1992; Lefebvre & Lennes, 1969; Iwatsuki, 1970; Lewinsky, 1974) has provided clear criteria and characteristics to distinguish the described species. This could have been due to the fact that so far none of these species has been described in detail in its wide geographical range. This observation is confirmed by Nyholm (1965), who states that features assigned to each species may be more variable than it has been described so far. In addition, researchers state that the representatives of this section are very variable (Greene, 1957; Iwatsuki, 1970) and can easily be confused with one another (Lewinsky, 1974). This is confirmed by the overlapping ranges of variation of all the analysed features.

The presented summary of the ranges of variation of characteristics describing particular species confirms not only that *Plagiothecium cavifolium*, *P. nemorale* and *P. succulentum* are very variable species but also shows gaps in the current state of knowledge and directions that need to be taken to fill the information gaps.

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