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A mixed occurrence of *Hypnum lacunosum* and *H. cupressiforme* provides evidence that the two are genetically distinct

*Lars HEDENÄS**

Swedish Museum of Natural History, Department of Cryptogamic Botany, Box 50007, SE-104 05 Stockholm, Sweden

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Abstract – Plants with *Hypnum cupressiforme* Hedw. and *H. lacunosum* (Brid.) Brid. appearance that were collected in direct association with a mixed collection of the two differed only in leaf length and leaf lamina cell length, besides differences in habit and overall size. These leaf characters belong to the few that potentially differentiate these taxa, and they were studied among 97 samples representing four different shoot types found within the morphological span of these taxa. Statistically significant differences were found among the four different plant types and mostly between the two taxa, as defined by overall plant appearance, in leaf lamina cell length (not between taxa), leaf length, and leaf lamina cell length corrected for leaf length. When leaf lamina cell length was corrected for leaf length, this increased the precision of cell length as a distinguishing character. The occurrence of many intermediates between plant types and a great overlap in measurements among plant types and taxa suggests that additional evidence independent from morphology is required to decide about the taxonomic treatment of *H. lacunosum* in relation to *H. cupressiforme*. The pseudoparaphyllia were studied in 15 specimens of each taxon, but their appearance showed too much overlap to safely distinguish the two.

Bryophyta / Hypnaceae / Leaf lamina cell length / Leaf length / Pleurocarpous mosses

INTRODUCTION

The complex of species around *Hypnum cupressiforme* Hedw. has for a long time puzzled bryologists, even if several of the included taxa are nowadays relatively well understood from a morphological point of view. One member of this complex is *Hypnum lacunosum* (Brid.) Brid., which has been variously treated as a distinct species, as a variety, or a synonym of *H. cupressiforme* (Table 1); sometimes a var. *tectorum* (Brid.) J.-P.Frahm is recognized under *H. lacunosum* (e.g., Frahm, 1976; Smith, 1997). During my own studies of *H. cupressiforme* and related species in Europe, Madeira, and tropical Africa (Hedenäs, 1987, 1991, 1992, 1994, 2005), I have refrained from dealing with *H. cupressiforme* vs. *H. lacunosum* in detail, partly because the characters that supposedly differentiate these (e.g., Ando, 1989; Smith, 1997) are quantitative and appear to vary continuously. For most of the other taxa, which are now commonly

* Correspondence and reprints: lars.hedenas@nrm.se

Table 1. Different published treatments of *Hypnum cupressiforme* Hedw. and *Hypnum lacunosum* (Brid.) Brid., by authors treating European members of the *Hypnum cupressiforme* complex

Two distinct species, without (A) or with (B) recognition of *H. lacunosum* var. *tectorum*
A: (Frey *et al.*, 2006)
B: (Frahm, 1976; Smith, 1997, 2004; Cortini Pedrotti, 2006)

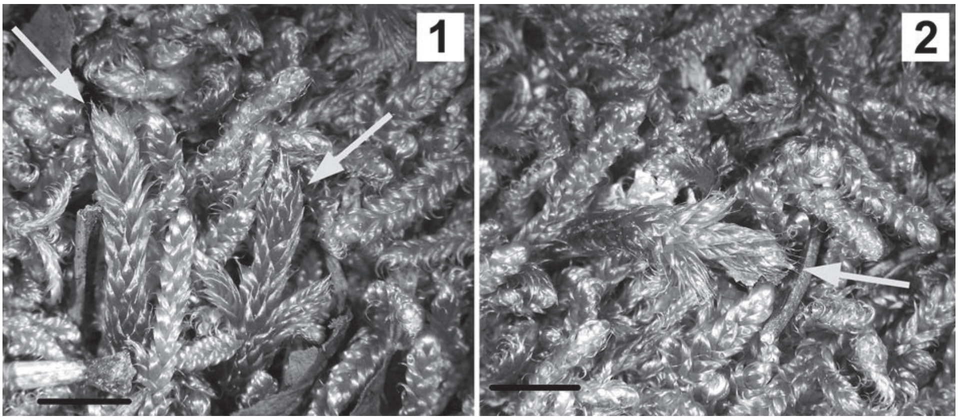
Hypnum cupressiforme* with var. *lacunosum*, without (A) or with (B) recognition of var. *tectorum
A. (Mönkemeyer, 1927; Nyholm, 1965; Orbán & Vajda, 1983; Ando, 1989; Grims, 1999; Dierssen, 2001; Sauer, 2001; Ochyra *et al.*, 2003; Ignatov & Ignatova, 2004; Müller, 2004; Casas *et al.*, 2006; Meinunger & Schröder, 2007)
B: (Limpricht, 1895-1904; Dixon, 1924)

One species, no formally recognized subspecific taxa
(Touw & Rubers, 1989)

Unclear treatment, but *lacunosum* distinguished
(Atherton *et al.*, 2010)

recognized as distinct species within the *H. cupressiforme* complex, mixed occurrences are found occasionally. Thus, Smith (1997) reported mixed occurrences of *H. cupressiforme-H. andoi* A.J.E.Sm., *H. cupressiforme-H. resupinatum* Taylor, *H. andoi-H. resupinatum*, *H. andoi-H. uncinulatum* Jur., and *H. andoi-H. jutlandicum* Holmen. I have seen all these mixtures except *H. andoi-H. resupinatum*, and, in addition, several occasions of *H. cupressiforme-H. jutlandicum*. From these observations it seems clear that the different morphological expressions also represent genetically separate entities, and since each has its distinct habitat requirements and characteristic geographical distribution, recognition at the species level seems warranted. Smith (1997) did not find mixed collections of *H. cupressiforme-H. lacunosum* (or between *H. lacunosum* var. *lacunosum* and var. *tectorum*), and suggested that this was due to too strong ecological differentiation between these. However, mixed collections would also be lacking if we have a single, strongly plastic species with a wide niche. I have searched for mixed occurrences of *H. cupressiforme-H. lacunosum* during more than 20 years, and when I finally found one on the Swedish island Gotland, in the Baltic Sea, in late spring 2011, this conclusively showed that there must be a genetic component in the observed variation also in this case (Figs 1-2).

Although the mixed collections show that the morphologically defined taxa within the *H. cupressiforme* complex have a genetic background, Spagnuolo *et al.* (2008) reported that in northern Italy only *H. jutlandicum* could be distinguished from the rest of the *H. cupressiforme* complex based on non-coding ITS and *trn*L sequence data and ISSR (inter simple sequence repeats) information. However, the voucher specimens for their sequenced specimens that I have seen belong to rather typical *H. cupressiforme* (e.g., Fig. 3), except for the samples of *H. jutlandicum* and *H. imponens* Hedw. The last one turned out to belong to *Ctenidium molluscum* (Hedw.) Mitt. In a subsequent expanded investigation of the *H. cupressiforme* complex, these authors still included some of their earlier incorrectly identified specimens (Terracciano *et al.*, 2012) and no information was provided regarding how the identity of the added specimens was verified. The results of the only molecular study of the *H. cupressiforme* complex that included a sufficient number of specimens to potentially resolve at least some of the relationships should therefore be treated with caution.



Figs 1-2. Two portions of a mixed occurrence, with arrows indicating (**1**) two shoots and (**2**) one shoot of *H. lacunosum* kind growing among typical *Hypnum cupressiforme* (Sweden. Gotland, *L. Hedenäs*, S; B183373). Scale: 3.5 mm.

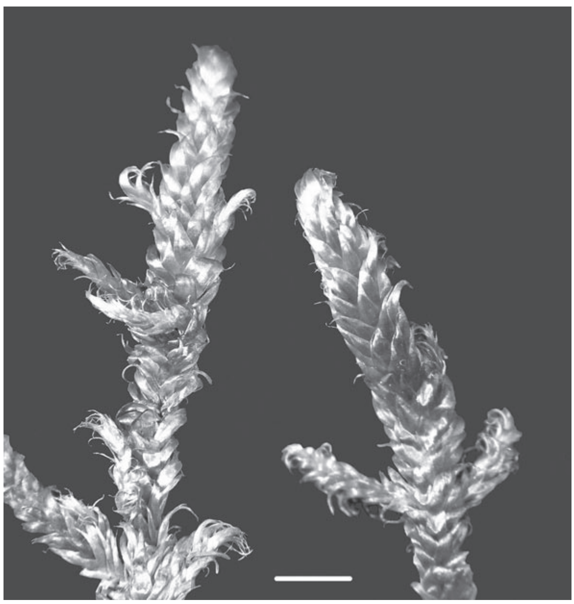


Fig. 3. Two shoots of the voucher of *H. lacunosum* from Basilicata, Italy, which was sampled for the nuclear ITS1+2 and the chloroplast *trn*L intron by Spagnuolo *et al.* (2008) in their study of the *H. cupressiforme* complex. This specimen belongs to morphological type "c" or in small portions "bc" (Table 2, Fig. 3). Scale 1.5 mm.

In view of the found mixed occurrence, which provides evidence for genetic differentiation at some level, the morphological characters that have been reported to potentially distinguish *Hypnum cupressiforme* and *H. lacunosum* need to be scrutinized. This obviously is important to make sure that future molecular studies use material corresponding with the correct morphological concepts of the taxa. During the last 40 years the problems concerning European *H. cupressiforme* and *H. lacunosum* were studied in detail by Ando (1985, 1989), Frahm (1976), and Smith (1997). Of these authors, H. Ando probably spent most time on solving the challenge that these two taxa pose and in addition he had a global overview. It is therefore interesting to first look at the characters he considered relevant to distinguish them. According to Ando (1989), who treated the taxa as varieties, var. *lacunosum* is rather distinct, although it sometimes intergrades with large phenotypes of var. *cupressiforme* and is not always easy to separate from the latter. The var. *lacunosum* has larger plants than var. *cupressiforme* (leaf length 1.7-2.5 vs. 1.5-2.0 mm), its branches are thick-complanate to julaceous and swollen, and the leaves are straight or only weakly falcate and have a short acumen (Ando, 1989). Compared with var. *cupressiforme*, the lamina cells are wider and especially shorter ((40-)50-70(-80) vs. (50-)60-80 µm long), even if this character should not always be constant. In var. *lacunosum* the sporophytes should also be small in relation to the plant size. Plants of var. *tectorum* should be somewhat smaller than in var. *lacunosum*, and be regularly pinnately branched with wider, ovate-oblong, and more shortly pointed leaves (Ando, 1989). According to Frahm (1976), *H. lacunosum* is in addition distinguished by large, orange, swelling alar groups, and erect shoots with rhizoids only at the base, and based on studies of six specimens of each species Smith (1997) reported that *H. lacunosum* has simple pseudoparaphyllia, whereas 50% of these are bilobed in *H. cupressiforme*. Whereas Ando (1989) did not distinguish var. *tectorum* (except as a form), both Smith (1997) and Frahm (1976) separated *H. lacunosum* var. *lacunosum* from var. *tectorum* by differences in colour, plant size, erect and more or less unbranched versus creeping and irregularly pinnately branched shoots, and a curved and gradually tapering rather than weakly curved to straight and abruptly tapering leaf acumen. *Hypnum lacunosum* var. *lacunosum* and var. *tectorum* have not been found growing together, and like Smith (1997) argued for *H. lacunosum* and *H. cupressiforme*, Frahm (1976) argued that this is because of their different habitat preferences. Finally, based on numerous measurements, Zubel (2007) reported that *H. lacunosum* has larger leaves than *H. cupressiforme* although it is unclear how specimens were referred to either species within the overlapping ranges of leaf sizes.

Hypnum lacunosum grows most frequently in calcareous or base-rich and often sunny habitats, both on rocks and loose substrates, rarely on wood or tree bases, in grasslands, heaths, sand dunes, and forests (Frahm, 1976; Ando, 1985). When var. *tectorum* is recognized, this should occur on solid, neutral to weakly acid substrata, such as rocks and roofs (Frahm, 1976; Ando, 1989).

In the present study the value of several characters for distinguishing *Hypnum cupressiforme* and *H. lacunosum* are explored, including measurements of leaf length (as a measure of plant size) and leaf lamina cell length. The measurements are compared with the general shoot appearance, because the different taxa were characterized both by the overall shoot habit and the measured features (see above) and one should therefore expect that these are correlated with each other. Orange alar cells are found now and then in specimens representing the entire range of appearances within *H. cupressiforme* to *H. lacunosum*, most often in exposed habitats, and this character is thus not further evaluated here. Finally, the reliability of the pseudoparaphyllia type to distinguish *H. cupressiforme* from *H. lacunosum* is evaluated. Because plants with the appearance of *H. lacunosum* are relatively frequent in Europe, but quite rare or even absent in some other regions (Ando, 1985, 1989), the present investigation is restricted to plants from Europe and Turkey.

MATERIAL AND METHODS

The microscopic features of shoots having *H. cupressiforme* and *H. lacunosum* appearance and that were collected in direct association with the newly found mixed occurrence were thoroughly studied. Besides the general habit, leaf size, here represented by stem leaf length, and stem leaf lamina cell length were the only characters that reliably differentiated the two intermixed plant types. These characters were therefore measured in three stem leaves from one shoot in each of 97 specimens from Europe and Turkey, representing the phenotypic variation included within these two names. Each studied shoot was scored as belonging to one of the four morphological shoot types in Table 2 and Fig. 4. In some cases a shoot was not possible to unambiguously refer to either of these shoot types; such shoots were scored as intermediate between two categories. Based on the characterization of *H. lacunosum* in the literature cited in the introduction, the shoots were grouped as *H. lacunosum* if they belonged to morphological shoot types “a”, “ab”, or “b” (Table 2) and as *H. cupressiforme* if they belonged to types “c”, “cd”, or “d”. Intermediates between “b” and “c” were excluded in the comparison between *H. lacunosum* and *H. cupressiforme*. From now on this is how the two taxa are defined in the present paper. Pseudoparaphyllia were studied in 15 specimens of *H. lacunosum* and 15 of *H. cupressiforme*. For each specimen, four outer pseudoparaphyllia were studied around three branch primordia in each of two shoots. These sets of 24 pseudoparaphyllia for each specimen were scored in the classes 0% branched, $>$0-25% branched, and $>$25-50% branched.

For the leaf lamina cell length, measured as lumen plus one end-wall, and leaf length, minimum and maximum measurements were searched for and the median of these were used in the calculations. The measurements of leaf lamina cell length and leaf length were used both directly for comparisons and with

Table 2. The four distinguished morphological shoot types, a-d, of *Hypnum cupressiforme* s.l. See also Fig. 4. Intermediates between two types are indicated by two letters, e.g. “ab” for intermediates between “a” and “b”. n: number of specimens belonging to the morphological category. Morphological types “a”, “ab”, and “b” are interpreted as *H. lacunosum* and “c”, “cd”, and “d” as *H. cupressiforme*, whereas “bc” are counted as intermediate between the two taxa

a	Shoots turgid, not flattened. Leaves strongly concave, straight or almost straight, ± homogeneous on all sides of stem. Upper portion of leaves forming a more or less distinctly set off, narrow acumen. Fig. 3A. (n = 6)
ab	Intermediate between **a** and **b**. (n = 4)
b	Shoots turgid, not flattened. Leaves strongly concave, falcate-secund, curved towards ventral side. Leaves more or less gradually narrowed upwards, or acumen set off but not as sharply as in **a**. Fig. 3B. (n = 34)
bc	Intermediate between **b** and **c**. (n = 13)
c	Shoots not turgid, not flattened. Leaves concave, falcate-secund, curved towards ventral side. Leaves gradually narrowed upwards. Fig. 3C. (n = 29)
cd	Intermediate between **c** and **d**. (n = 1)
d	Shoots not turgid, more or less distinctly flattened. Leaves concave or slightly so, falcate-secund, curved towards ventral side or rarely in branches turned slightly upwards. Leaves gradually narrowed upwards. Fig. 3D. (n = 10)

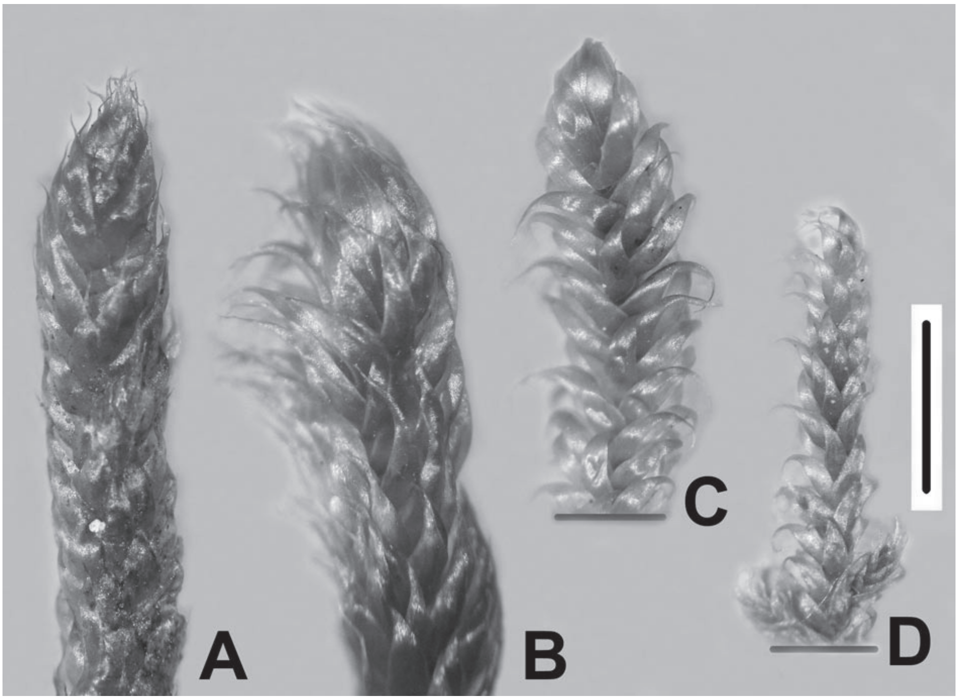


Fig. 4. The four scored kinds of *Hypnum cupressiforme* s.l. shoots **A-D.** Corresponding with the descriptions a-d in Table 2 (A: Germany. Rheinland-Pfalz, *Korneck & Frahm*, S; B185906. **B.** Sweden. Öland, *L. Hedenäs*, S; B183219. **C.** Sweden. Gotland, *L. Hedenäs*, S; B183372. **D.** France. Aude, *J.L. De Sloover 45207*, S; B186127). Scale: 2.0 mm.

lamina cell length adjusted for leaf length by dividing the median cell length value with the corresponding one for the leaf length (cf., Hedenäs, 1996, 1997, 1998). The pair-wise relationships of the measured leaf characters were evaluated by linear regression. Before comparisons were made among the morphological shoot types or between shoots classified as *H. lacunosum* and *H. cupressiforme* (Table 2), it was checked if the data were normally distributed, with Shapiro Wilks W test and by studies of the distribution of residuals in a preliminary Analysis of variance (ANOVA). Leaf lamina cell length and leaf length were both normally distributed, and differences among categories were therefore evaluated by ANOVA with a planned post-hoc pair-wise comparison of the four morphological shoot types by means of the LSD-test. The values of the ratio leaf lamina cell length / leaf length were not normally distributed and for this parameter the Kruskal-Wallis ANOVA by ranks (multiple comparisons) or the Mann-Whitney U-test (pair-wise comparisons) were employed. The statistical calculations were made with STATISTICA 8.0 (StatSoft, 2008).

RESULTS

In the total data set, leaf lamina cell length is statistically significantly positively correlated with leaf length (Fig. 5A). When lamina cell length is divided by leaf length to adjust for leaf length, the adjusted cell length is negatively correlated with leaf length (Fig. 5B). The adjusted cell length shows no correlation with un-adjusted cell length (Fig. 5C).

Both the four morphological shoot types and specimens referred to *H. cupressiforme* and *H. lacunosum* based on this show a tendency to have measurements in one portion or end of the ranges for leaf length and adjusted leaf lamina cell length, even if the overlap is great (Fig. 5). The shoot types differ statistically significantly among each other in the measured quantitative characters (Table 3A; Fig. 6A, C, E) and this is the case also for *H. cupressiforme* and *H. lacunosum*, except in leaf lamina cell length (Table 3B; Fig. 6B, D, F). None of the morphological shoot types were distinguished by leaf lamina cell length in the planned pair-wise post-hoc comparisons (Table 4). Leaf length distinguished shoot type “b” from types, “a”, “c”, and “d”, and shoot type “c” from “d”, and the adjusted lamina cell length separates shoot type “b” from types, “c” and “d” (Table 4). The studied specimens that Ando (1989) referred to *H. cupressiforme* var. *lacunosum* are found within the *H. lacunosum* ranges, but several are within the portions of the ranges that overlap with *H. cupressiforme* (Fig. 5). The two

Table 3. A: Comparison of morphological shoot types, excluding intermediates (see Table 2); B: Comparison between shoots with *H. cupressiforme* and *H. lacunosum* appearance (Table 2). Results of ANOVA for leaf lamina cell length and leaf length, and Kruskal-Wallis Anova by ranks (A) or Mann-Whitney U-test (B) for the ratio leaf lamina cell length/leaf length. n.s.: not significant; NA: not applicable

A: Morphological shoot types

Character	*SS*	*df*	*MS*	*F*	*H*	*P*
Leaf lamina cell length	454.844	3	151.615	2.878	NA	< 0.05
Leaf length	5.995	3	1.998	20.704	NA	< 0.001
Ratio leaf lamina cell length/leaf length	NA	NA	NA	NA	36.496	< 0.001

B: *H. cupressiforme* vs. *H. lacunosum*

Character	*SS*	*df*	*MS*	*F*	*U*	*Z*	*p*
Leaf lamina cell length	2.685	1	2.685	0.048	NA	NA	n.s.
Leaf length	3.832	1	3.832	32.455	NA	NA	< 0.001
Ratio leaf lamina cell length/leaf length	NA	NA	NA	NA	217.000	– 5.938	< 0.001

Table 4. Bonferroni corrected significance levels for the comparisons among the morphological shoot types, excluding intermediates (Table 2). For each comparison between morphological shoot types the following order of characters is followed: Leaf lamina cell length (LSD test)/Leaf length (LSD test)/Ratio leaf lamina cell length to leaf length (Kruskal-Wallis ANOVA by ranks). * p < 0.008333 (corresponds with 0.05), ** p < 0.001667 (0.01), *** p < 0.000167 (0.001); n.s.: not significant

	b	*c*	*d*
a	n.s./**/n.s.	n.s./n.s./n.s.	n.s./n.s./n.s.
b		n.s./***/***	n.s./***/***
c			n.s./**/n.s.

specimens directly associated with the mixed collection are found within the exclusive portions of the *H. cupressiforme* and *H. lacunosum* ranges, respectively, except for the *H. lacunosum* sample in Fig. 5C.

Among the specimens referred to *H. lacunosum* 60% had invariably unbranched pseudoparaphyllia and 40% a sparse occurrence of branched ones (Fig. 7). Among *H. cupressiforme* specimens, 60% revealed a sparse occurrence of branched pseudoparaphyllia, whereas 20% had only unbranched ones and in another 20% branched ones were more abundant (Fig. 7).

DISCUSSION

Plant size, leaf orientation and concaveness, and leaf lamina cell size are features that should differentiate *H. lacunosum* from *H. cupressiforme* (Frahm, 1976; Ando, 1985, 1989; Smith, 1997), although both Ando (1985, 1989) and Smith (1997) noted that cell size in *H. lacunosum* is sometimes variable. Specimens that were here referred to *H. lacunosum* based on the general plant habit have on the average got longer leaves than *H. cupressiforme*. Interestingly, leaf lamina cell length did not differ significantly between *H. lacunosum* and *H. cupressiforme* (Fig. 6B) whereas cell length adjusted for leaf length gives clearly lower values in *H. lacunosum* than *H. cupressiforme* (Fig. 6F). Thus, the precision of the character leaf lamina cell length increases by considering the size of the leaves where the cells are measured, which implies that leaf length is at least partly a function of cell length. Relatively long leaves are then long to a large extent because compared with shorter leaves they have longer and not more numerous cells along the longitudinal axis of the leaf. An increase in precision for quantitative characters like lamina cell length or costa strength by correcting for the size of the studied leaves was observed also for species of *Drepanocladus* (Hedenäs, 1996, 1997, 1998). While both members of the Amblystegiaceae and Hypnaceae show similar correlations of leaf characters with leaf size, and this occurs within the Brachytheciaceae as well (Hedenäs *et al.*, in prep.), it appears to be a general phenomenon among pleurocarpous mosses. To increase the precision in morphological characterizations of very similarly looking pleurocarpous species that can be distinguished mainly by quantitative characters it therefore seems like a good idea to adjust features such as lamina cell size and costa width by dividing the measurements of these by leaf length and width, respectively. It is clear from the present data that the measured leaf lamina cell length cannot be used as a proxy for the adjusted lamina cell length (Fig. 5C).

The found mixed collection shows that genetic differences exist among at least some specimens with *Hypnum cupressiforme* and *H. lacunosum* morphology. Further, the comparisons of leaf length and leaf lamina cell length among the four shoot types and between specimens classified as *H. cupressiforme* and *H. lacunosum* based on their general shoot appearance show that statistically significant differentiation occurs among plant types for these characters. On the other hand, the overlap between the categories is great, and neither these measured features nor the presence or absence of branched pseudoparaphyllia can be used to reliably distinguish among shoot types or between taxa.

Leaf lamina cell length did not differentiate the morphological shoot types among the specimens classified as *H. lacunosum* or *H. cupressiforme*, respectively. However, both shoot types “a” and “b”, which could potentially correspond with *H. lacunosum* var. *lacunosum* and var. *tectorum* (cf. Frahm, 1976;

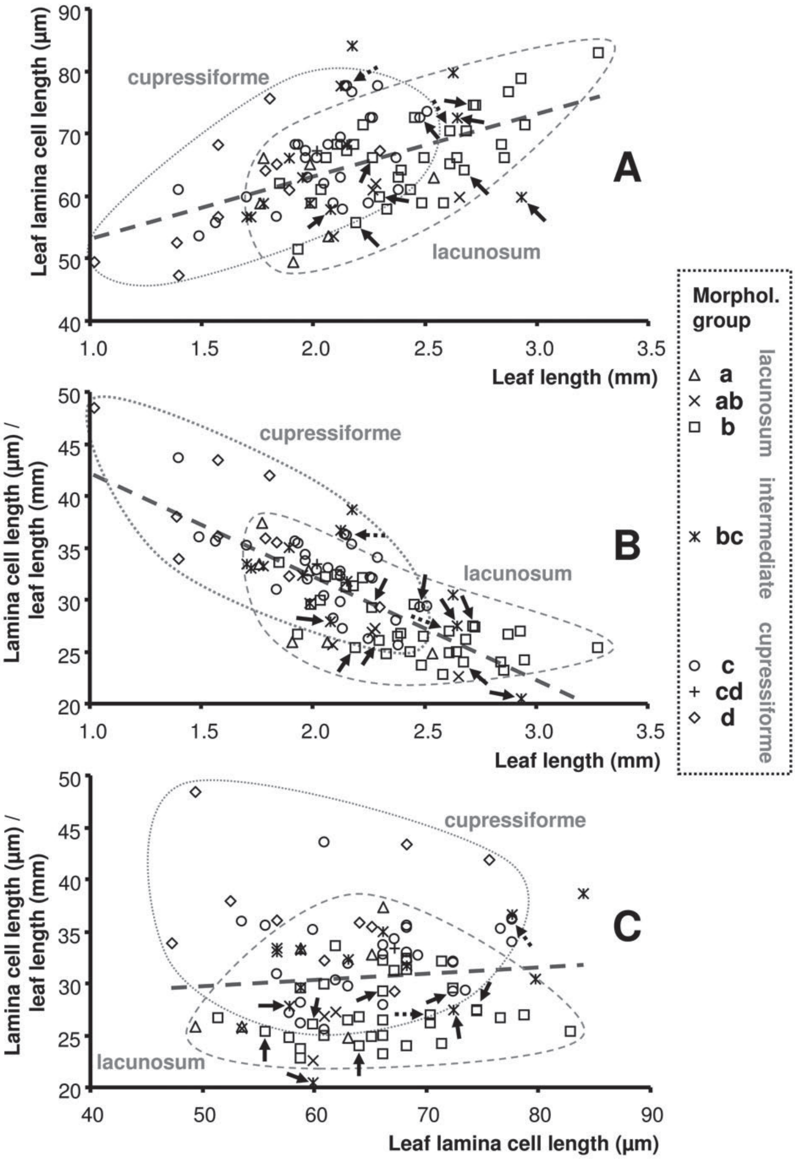


Fig. 5. Correlations between, **A.** leaf lamina cell length (µm) and leaf length (mm) ($y = 9.9612x + 43.1789$; $r^2 = 0.2660$; $r = 0.5158$; $p < 0.001$); **B.** the ratio leaf lamina cell length (µm)/leaf length (mm) and leaf length (mm) ($y = -9.9543x + 52.1855$; $r^2 = 0.6077$; $r = -0.7795$; $p < 0.001$); and **C.** the ratio leaf lamina cell length (µm)/leaf length (mm) and leaf lamina cell length (µm) ($y = 0.0603x + 26.6148$; $r^2 = 0.0083$; $r = 0.0913$; $p = 0.3740$). Median values were used for all measurements. The morphological groups a-d (Table 2; with numbers of specimens) and their intermediates as specified by two letters are indicated by different symbols and those corresponding with the concepts of *Hypnum cupressiforme* and *H. lacunosum* (Table 2) are indicated by gray text and encircled samples. Arrows indicate studied specimens referred to *H. lacunosum* by Ando (1989) and dashed arrows show the two samples directly associated with the mixed occurrence from Gotland, Sweden (see text).

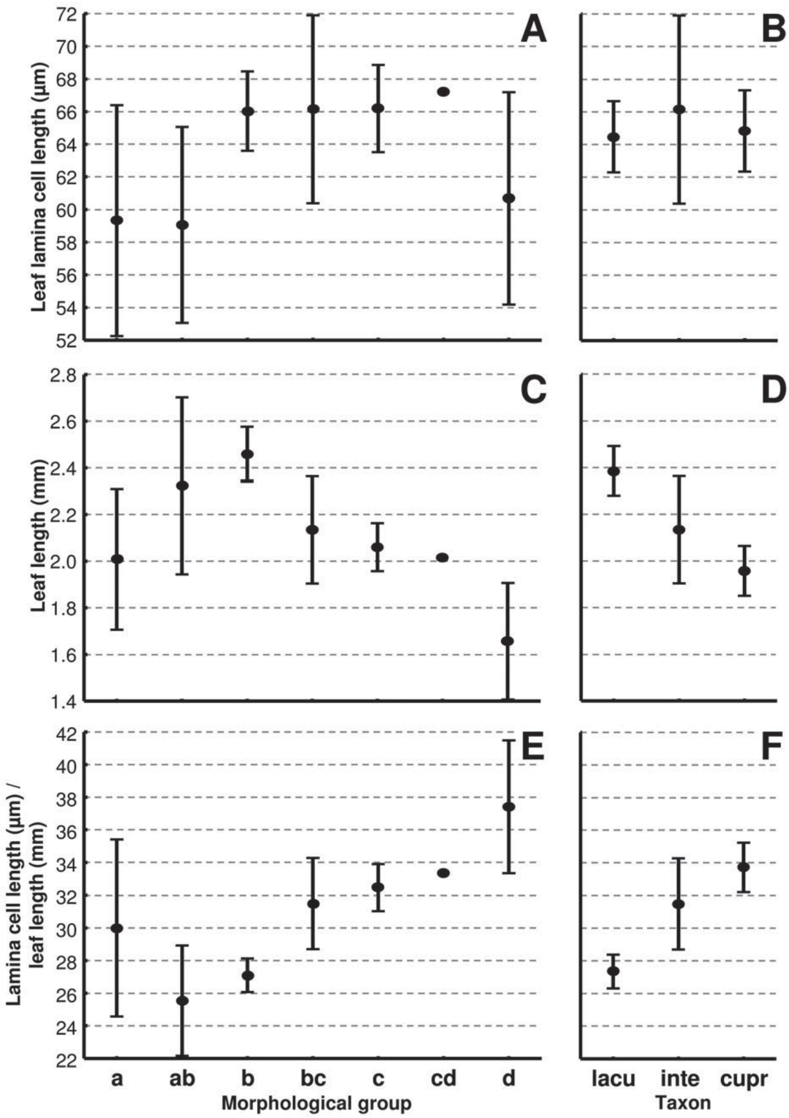


Fig. 6. Mean values and 95% confidence intervals for **A, B.** leaf lamina cell length (µm); **C, D.** leaf length (mm); and **E, F.** the ratio leaf lamina cell length (µm)/leaf length (mm). **A, C, E.** Specimens belonging to the morphological groups a-d (Table 2; with numbers of specimens) and their intermediates as specified by two letters; **B, D, F.** specimens corresponding with the concepts of *Hypnum cupressiforme* and *H. lacunosum* (Table 2).

Smith, 1997), and "c" and "d", within *H. cupressiforme*, differed from each other in size. Thus, if var. *tectorum* should be recognized based on the differences in leaf orientation and size, the same could be argued for the plant types within *H. cupressiforme*. The great variation and overlap even between *H. lacunosum* and *H. cupressiforme*, where the mixed specimen provides evidence for genetic

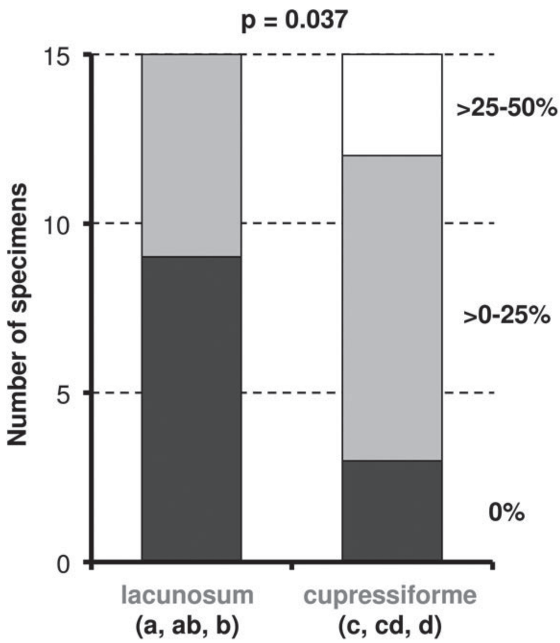


Fig. 7. Number of specimens with different frequencies of branched pseudoparaphyllia in plants referred to *H. lacunosum* (n = 15) and *H. cupressiforme* (n = 15) (cf. Table 2).

differentiation in at least some cases, suggests that it is premature to give taxonomic recognition to entities based on even smaller morphological differences without additional evidence.

In view of the great overlap in leaf length and leaf-length-adjusted leaf lamina cell length among plant types, and the fact that plant phenotypes intermediate between *H. cupressiforme* and *H. lacunosum* exist (cf. Table 2), it is not evident that the two should be treated at the species level, despite the found mixed collection and the found statistically significant differences in the mentioned characters. Without further evidence, independent from morphology, that the plant types here referred to the respective species – not only those of the mixed occurrence – do indeed correspond with two independently evolving lineages, it is a matter of taste whether these two are treated as species, subspecies, or varieties. The status of the two entities that were here classified as *H. cupressiforme* and *H. lacunosum* needs to be tested by molecular data based on material reliably referred to either kind before we can reach a better founded conclusion regarding a correct treatment of these taxa.

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Appendix 1. Studied specimens with *Hypnum cupressiforme* or *H. lacunosum* morphology. All specimens are located in S and the "B" numbers are the S registration numbers. Each specimen is referred to a morphological type **a-d** according to the definitions in Table 2. Types **a**, **ab**, and **b** are interpreted as *H. lacunosum* and **c**, **cd**, and **d** as *H. cupressiforme*, whereas **bc** are counted as intermediate between the two taxa. Duplicates of specimens that were referred to *H. cupressiforme var. lacunosum* by Ando (1989) are indicated by '**AN**' and the two specimens that were collected in direct association with the mixed collection mentioned in the text by "**MM**".

Austria: Niederösterreich, Johannesbachklamm, *J.Froehlich*; B186134: **d**, -. Steiermark, Niedere Tauern, *J.Froehlich*; B186133: **a**, -. Tirolen, Achensee, *T.Suse*; B186046: **b**, -. **Denmark:** E Jutland, Djursland, *M.H.G.Gustafsson*; B152040: **b**, -. Jutland, Kaersgård Klit, *E.Nyholm*; B185192: **bc**, **AN**. **Estonia:** Livland, Ösel, *J.Mikutowicz (Bryoth. Baltica 665a)*; B186035: **ab**, -. **Finland:** Alandia, Lemland, *V.F.Brotherus (Bryoth. fennica 292)*; B186030: **bc**, -. **France:** Alpes Maritimes, Sospel, *G.Een, P.Een*; B062865: **c**, -. Bretagne, Plouharnel, *B.O.van Zanten* 3460; B185191: **b**, **AN**. Dép. Haut-Rhin, Bollenberg, *J.-P.Frahm (Bryoph. Vogesiaca Exs. 45)*; B186078: **ab**, -. Tarn et Garonne, St. Antonin, *G.Een*; B186031: **a**, -. **Germany:** Brandenburg, Sperenberg, *H.Kuhlbrodt (W.Migula: Krypt. Germaniae, Austriae et Helvetiae exs. "Moose" 347)*; B185196: **bc**, **AN**. Erlangen, *P.Reinsch*; B185195: **bc**, **AN**. Rheinland-Pfalz, Cochem-Zell, *Korneck & Frahm*; B185906: **a**, -. Rheinland, Ahreifel, Waldbachtal, *R.Düll*; B186128: **d**, -. **Greece:** Kríti, Lassíthi, *G.Een*; B185771: **c**, -. **Hungary:** Aggtelek National Park, W of Jósvafö, *L.Hedenäs*; B104397: **c**, -. Aggtelek National Park, W of Jósvafö, *L.Hedenäs*; B104441: **d**, -. Salgocz, *Koehler*; B186130: **c**, -. **Ireland:** Connemara, Galway, *K.H.Rechinger 0-2361a*; B186034: **b**, -. Donegal, Dundoran sanddunes, *Etsmitage 590b*; B186032: **b**, -. **Italy:** Emilia-Romagna, Gessi Bolognesi, *M.H.G.Gustafsson 1076*; B173840: **d**, -. Etruria. Villa Pozzolatico, *E.Bacci*; B186132: **c**, -. Veneto, Delta of Po, *M.H.G.Gustafsson 1023*; B173803: **bc**, -. Vid Lago di Como, *M.Fries*; B186048: **c**, . **Montenegro:** Ad claustrum St. Sava prope Ipek, *J.Andrasovszky*; B186131: **c**, -. **Norway:** Ad oppidium Ekersund, *N.Bryhn*; B185193: **b**, **AN**. Finnmark, Hammerfest, *L.Hedenäs*; B176663: **bc**, -. Rogaland, Strand, *L.Hedenäs*; B186079: **a**, -. **Poland:** Golecinie w Poznaniu, *S.Lisowski 41b*; B186036: **c**, -. Malopolska Upland, Sandomierz-Opatów Upland, *J.Wójcicki (Musci Poloniae exs. 691)*; B185194: **c**, **AN**. Nord de l'île de Wollin Kunowo, *J.L.De Sloover 16647*; B186037: **b**, -. Prov. Westpreussen, Schwiedt (Tuchel), *Grebe*; B186045: **b**, -. Silesian Lowland, Opole Plain, *A.Stebel M244 (Musci Macror. Merid. Poloniae Exs. 531)*; B186104: **c**, -. Silesian Lowland, Opole Plain, *K.Jedrzejko, J.Zarnowiec, H.Klama M-2 (Musci Macror. Merid. Poloniae Exs. 524)*; B186103: **d**, -. Western Carpathians, Beskid Wyspowy Mts., *A.Stebel (Musci Macror. Merid. Poloniae Exs. 1222)*; B109757: **d**, -. Western Sudetes, Góry Opawskie Range, *A.Stebel (Musci Macror. Merid. Poloniae Exs. 1477)*; B157626: **c**, -. **Portugal:** Paredes de Guardao, *S.Birger*; B186102: **c**, -. **Russia:** Krasnodar territory, Anapa district, *M.Ignatov, E.Ignatova (Mosses of Russia 20)*; B113885: **c**, -. Krasnodar territory, Caucasian Nature Reserve, *M.Ignatov, E.Ignatova (Mosses of Russia 30)*; B113886: **d**, -. Pskov Province, Pushkinie Gory Settlement, *O.M.Afonina*; B119470: **c**, -. **Spain:** Extremadura, Cáceres, *G.Een*; B185772: **c**, -. Extremadura, near Trujillo, *G.Een*; B035680: **a**, -. **Sweden:** Dalarna, Rättviks, *E.v.Krusenstjerna*; B186080: **c**, -. Gotland, Bunge, *L.Hedenäs*; B183376: **b**, -. Gotland, Fårö, *H.Hesselman*; B185198: **b**, -. Gotland, Fleringe, *L.Hedenäs*; B183382: **b**, -. Gotland, Fleringe, *L.Hedenäs*; B183383: **b**, -. Gotland, Rute, *L.Hedenäs*; B183371: **b**, **MM**. Gotland, Rute, *L.Hedenäs*; B183372: **c**, **MM**. Gotland, Rute, *L.Hedenäs*; B183375: **b**, -. Gotland, Sundre, *L.Hedenäs*; B083161: **ab**, -. Gotland, Väskinde, *H.Hesselman*; B185197: **b**, -. Halland, Skrea, *S.Svenson*; B185189: **b**, **AN**. Hälsingland, Hög, *M.H.G.Gustafsson*; B179044: **c**, -. Jämtland, Kall, *L.Hedenäs*; B106815: **d**, -. Medelpad, Borgsjö, *L.Hedenäs*; B115551: **c**, -. Närke, Mosjö, *N.Hakelier*; B186094: **c**, -. Öland, Alvaret vid Ottenby lund, *J.Christoffersson*; B109415: **b**, -. Öland, Ås, *E.Nyholm*; B185188: **b**, **AN**. Öland, E of Skogsby, *L.Hedenäs*; B174812: **c**, -. Öland, Mensalvaret (Binnerbäck), *L.Hedenäs*; B185131: **a**, -. Öland, Resmo, *L.Hedenäs*; B174814 (**large plant**): **b**, -. Öland, Resmo, *L.Hedenäs*; B174814 (**small plant**): **bc**, -. Öland, Sandby, *L.Hedenäs*; B174803: **b**, -. Öland, Stenåsa, *L.Hedenäs*; B183219: **b**, -. Öland, Stenåsa, *L.Hedenäs*; B174639: **b**, -. Skåne, Sofiero, *J.Christoffersson*; B109417: **b**, -. Skåne, Torekov, *E.Nyholm*; B087677: **b**, -. Skåne, Viken, *L.Hedenäs*; B136376: **b**, -. Småland, Ålem, *L.Hedenäs*; B186096: **c**, -. Småland, Skärstad, *L.Hedenäs*; B186095: **bc**, -. Södermanland, Mörkö, *L.Hedenäs*; B185979: **b**, -.

Södermanland, Utö, *A.Crundwell, E.Nyholm*; B100222: **b**, -. Södermanland, Utö, *L.Hedenäs*; B183589: **c**, -. Södermanland, Utö, *L.Hedenäs*; B183596: **bc**, -. Uppland, Djurö, *G.Een*; B050526: **b**, -. Uppland, Djurö, *L.Hedenäs*; B183483: **bc**, -. Värmland, Filipstad, *L.Hedenäs, G.Odelvik*; B177807: **c**, -. Värmland, Gåsborn, *L.Hedenäs, G.Odelvik*; B177731: **c**, -. Västergötland, Dala, *A.Hülphers*; B186029: **b**, -. Västergötland, Högstena, *A.Hülphers*; B185190: **b**, **AN**. Västergötland, Vilske Kleva, *A.Hülphers*; B185986: **b**, -. Västmanland, Sala, *L.Hedenäs*; B184542: **c**, -. **Switzerland:** Aargau, Turgi, *G.Schellenberg*; B014819: **b**, -. Graubünden, Lai-Obervatz, *N.C.Kindberg*; B014807: **bc**, -. Splügen, *F.Areschoug*; B014806: **c**, -. Ticino, Muralto, *L.Hedenäs*; B087948: **d**, -. **Turkey:** Prov. Aydin, SW of Davutlar, *N.Ayedem, A.C.Crundwell, E,Nyholm 166/71*; B185774: **c**, -. Prov. Mugla, Oyukudag, *N.Ayedem, A.C.Crundwell, E.Nyholm 590/71*; B185773: **bc**, -. Zwischen Kilyos und Saryer, *K.H.Rechinger (18) 23.877*; B186049: **b**, -. **United Kingdom:** England, County Norfolk, *A.C.Crundwell*; B186033: **ab**, -. England, Cumbria, *E.M.Lind*; B186129: **c**, -. England, Shropshire, *L.Hedenäs*; B144760: **cd**, -. England, Shropshire, *L.Hedenäs*; B144675: **b**, -. England, Shropshire, *L.Hedenäs*; B144680: **bc**, -. England, Shropshire, *L.Hedenäs*; B144780: **d**, -.