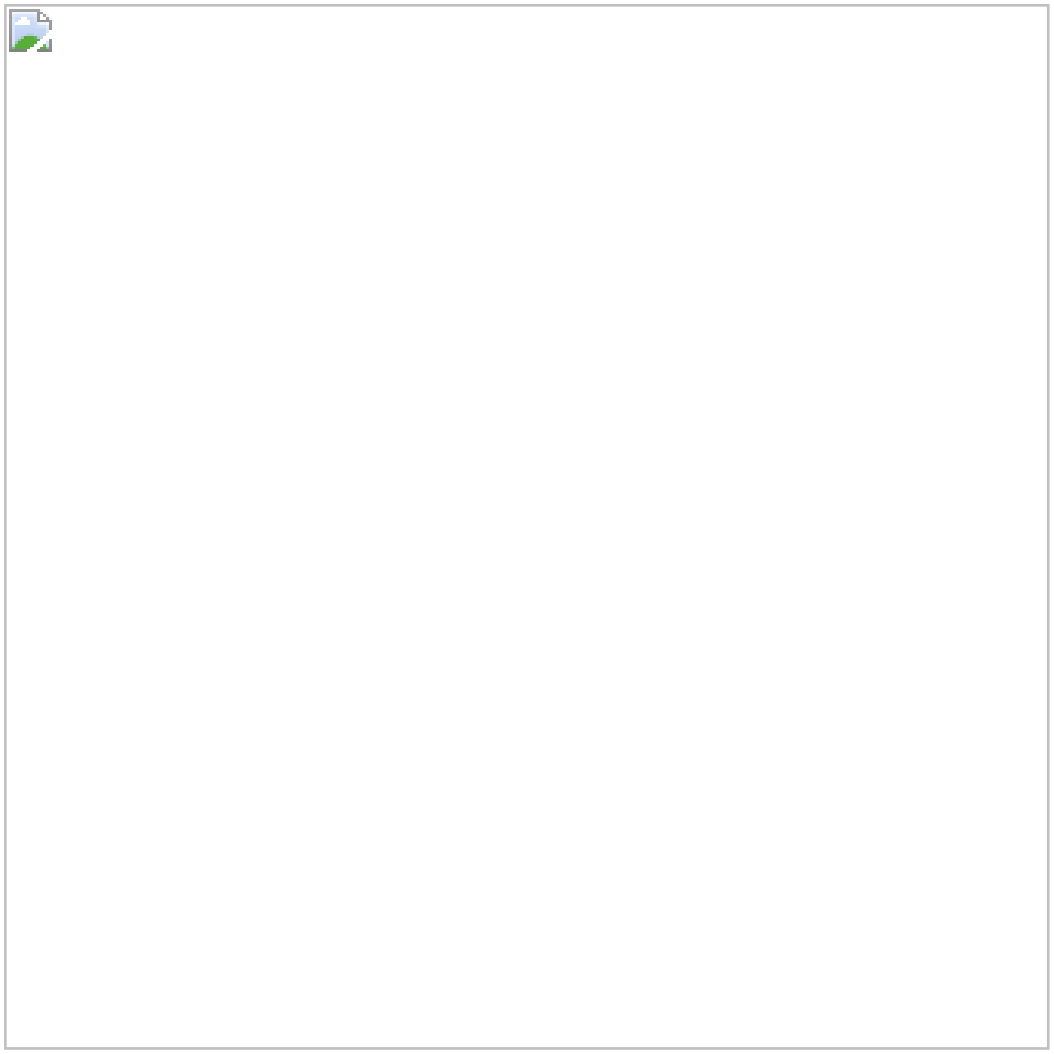

Oxyrrhynchium hians (Brachytheciaceae, Bryophyta) includes several morphologically distinct and cryptic species in northwestern Europe

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Research article

Oxyrrhynchium hians (Brachytheciaceae, Bryophyta) includes several morphologically distinct and cryptic species in northwestern Europe

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A study of the variable species *Oxyrrhynchium hians* s.l. in NW Europe based on nuclear ITS, and plastid *rpl*16 and *trn*L*trn*F, as well as morphology, revealed unsuspected species level diversity. Three taxa are distinguishable by morphology: *O. distichum* with complanate or sub-complanate branch leaves and long and narrow leaf lamina cells, *O. hians* with cordate or broadly ovate, concave leaves that are evenly arranged around the stems and branches, and *O. swartzii* with mostly complanate or sub-complanate branch leaves and compared with *O. distichum* relatively short and wide leaf lamina cells. In Sweden *O. distichum* grows almost exclusively on base-rich or calcareous rocks and has been recorded from a belt stretching from the Baltic Sea islands of Öland and Gotland to Dalarna and southernmost Norway, whereas the other two species grow on various substrates and have wider distributions. *Oxyrrhynchium hians* grows in more nutrient-rich habitats than *O. swartzii* and is therefore absent from regions with relatively poor soils. *Oxyrrhynchium swartzii* occurs northwards to Sør-Trøndelag in Norway and Jämtland and Medelpad in Sweden and includes two semi-cryptic species that differ slightly in size and may have relatively more western and eastern distributions, respectively, in Fennoscandia.

Keywords: assemble species by automatic partitioning (ASAP), geographic distributions, importance of species recognition, NeighborNet (NN) split network, semi-cryptic species

Introduction

The somewhat twisted history of *Oxyrrhynchium* (Schimp.) Warnst., both in relation to *Eurhynchium* Schimp. and *Kindbergia* Ochyra and concerning its typification, was detailed by Ignatov and Isoviita (2003), who proposed the conservation of *Oxyrrhynchium* with *Oxyrrhynchium hians* (Hedw.) Loeske as its conserved type.

This proposal was later adopted (https://naturalhistory2.si.edu/botany/codes-proposals/display_new.cfm; checked 7 March 2023). The well-known, apparently European-North American (Ignatov et al. 2022), *O. hians* and its close relatives are pretty similar to each other in appearance, with at least some phenotypes having sparsely inserted stem leaves, complanate or sub-complanate ovate or oblong-ovate branch leaves, often with a strong costa, and, except in *O. vagans* (A.Jaeger) Ignatov & Huttunen, a rough seta. Ignatov and Huttunen (2002), Huttunen and Ignatov (2004) and Wynns et al. (2009) all observed that several morphologically deviating aquatic species form a clade sister to the species around *O. hians*, and Wynns et al. (2009) made some of the formal combinations for such species within *Oxyrrhynchium*.

The history of what we today call *O. hians* is also contorted. Until the study by Touw and Knol (1978) the nomenclature of this taxon was frequently confused with that of *Kindbergia praelonga* (Hedw.) Ochyra. These authors considered *O. hians* to be the correct name of what had previously been called *Eurhynchium swartzii* (Turner) Curn. [*Oxyrrhynchium swartzii* (Turner) Warnst.] in Europe. The Pennsylvanian specimen of *Hypnum hians* Hedw. in Hedwig's herbarium that Touw and Knol (1978) studied was later designated as the lectotype of this name by Hedenäs and Geissler (1999).

Oxyrrhynchium hians, as currently understood in Europe, is highly variable morphologically and both subspecific and closely related species-level taxa have often been recognized (Limpricht 1895–1904, Brotherus 1923, Dixon 1924, Nyholm 1965). Further, based on nuclear ITS, Ignatov et al. (2022) found two subgroups of *O. hians*. Considering the wide range of habitats inhabited and the wide morphologic variation in European *O. hians*, this suggests that it is worth exploring the species in more detail. In the present study especially its NW European variation is examined based on a combination of molecular and morphological information.

Material and methods

Study species and material

As the species is currently usually understood, *O. hians* s.l. is a small or medium-sized pleurocarpous moss that typically grows in loose mats composed of irregularly to pinnately branched shoots. While the stem leaves are erecto-patent to spreading and mostly evenly arranged around the stem, the branch leaves vary from evenly arranged around the branch to appearing distichous with one leaf surface facing upwards (complanate or sub-complanate). Leaf shape and whether the leaves are plane or concave varies considerably. However, mostly the costa ends in a distinct spine on the back, especially in the branch leaves, and the leaf margin is more or less strongly denticulate. It is dioicous and sporophytes are found occasionally. *Oxyrrhynchium hians* s.l. colonizes bare or sparsely vegetated moist soil, both in fields and on forest ground and often in nutrient-rich habitats, but it may also grow on rock surfaces, especially on basic rocks or limestone.

For the molecular portion of this study, 32 specimens of *O. hians* s.l. from Sweden, six from Norway, and three from Switzerland were included. One specimen each of the two closely related species *O. schleicheri* (R.Hedw.) Röll and *O. speciosum* (Brid.) Warnst., two other unambiguous members of *Oxyrrhynchium* (Ignatov and Huttunen 2002, Ignatov and Isoviita 2003), were included as outgroup.

Five specimens of each lineage identified in the molecular results were subjected to detailed morphological studies. The remaining molecularly identified specimens, when available, were used to test the potential morphological differences found between lineages. After the entities possible to identify by morphology were established, type material of potential names was checked. Thereafter, the Fennoscandian material (825 specimens, excluding duplicates) and selected European specimens (87) filed under *O. hians* in S were checked to get an idea of the geographical distribution patterns and habitats for each identified entity.

Molecular study

Total DNA was extracted using the NucleoMag Plant kit for DNA isolation from plant tissue (Macherey-Nagel) with the KingFisher Duo magnetic particle processor. Double stranded DNA templates were prepared by polymerase chain reaction (PCR). PCR was performed using IllustraTM Hot Start Mix RTG (GE Healthcare) in a 25 µl reaction volume according to the manufacturer's instructions.

In all cases, the specified PCR programs were initiated by a denaturation step of 5 min at 95°C and followed by a final extension period of 10 min at 72°C. The PCR programs were, for the nuclear internal transcribed spacers 1 and 2 (ITS), 4 cycles of 30 s at 95°C, 40 s at 55°C, and 1 min at 72°C, 4 cycles of 30 s at 95°C, 30 s at 53°C, and 1 min at 72°C, 35 cycles of 30 s at 95°C, 30 s at 50°C, and 1 min at 72°C, with the primers 'ITS4bryo' (Stech 1999) and 'ITSbryoR' (Hedenäs 2014). For the plastid *rpl*16 G2 intron (*rpl*16), 43 cycles of 30 s at 95°C, 30 s at 58°C, and 1 min 15 s at 72°C, with the primers 'F71' (Jordan et al. 1996) and 'rpl16-antR2' (Hedenäs 2008), and for the plastid *trn*LUAA intron plus *trn*-LUAA-*trn*FGAA spacer (*trn*L-*trn*F), 4 cycles of 30 s at 95°C, 40 s at 57°C, and 1 min at 72°C, 4 cycles of 30 s at 95°C, 30 s at 55°C, and 1 min at 72°C, 35 cycles of 30 s at 95°C, 30 s at 52°C, and 1 min at 72° C, with the primers 'trnC' and 'trnF' (Taberlet et al. 1991).

The amplified PCR products were purified from excess primers and nucleotides by adding 1 µl of Exonuclease I (20U μl^{-1}) and 4 µl of FastAP Thermosensitive Alkaline Phosphatase (1U μl^{-1}) (Thermo Scientific) and incubating at 37°C for 30 min followed by an enzyme inactivation step at 80°C for 15 min. The purified PCR products, together with the same primers used for PCR amplification, were subsequently sent to Macrogen Europe B.V (Amsterdam, the Netherlands) for single-stranded sequencing on an Applied Biosystems 3730XL sequencer.

Sequence editing and analysis

Nucleotide sequence fragments were edited and assembled for each DNA region using PhyDE 0.9971 (http://www.phyde.de/index.html; accessed 17 February 2023). The assembled sequences were aligned manually in PhyDE. Regions of partially incomplete data in the beginning and end of the sequences were identified and were excluded from subsequent analyses. Gaps were coded using the simple indel coding of Simmons and Ochoterena (2000) in SeqState (Müller 2005). Gaps provided additional information and this was included in the analyses. The sequence alignments used in the analyses are uploaded at doi: 10.5061/dryad.d2547d88m. GenBank accession numbers are listed in Table 1.

The ITS chromatograms included in this study did not show 'messy' patterns or noise that could indicate paralogy (Košnar et al. 2012, Hedenäs et al. 2019), and the 5.8S gene was invariable (Shaw et al. 2002, Feliner and Rosselló 2007). The found variation in ITS was therefore considered to be among homologous haplotypes.

Reticulation was revealed using TCS (Clement et al. 2000), and relationships among specimens were therefore evaluated in a network context. The relationships were evaluated in NeighborNet (NN) split networks, produced in SplitsTree 4.12.6 (Huson and Bryant 2006) and in TCS networks, and potential support for lineages in a tree context was tested by jackknife analyses (1000 replications) performed with the program TNT (Goloboff et al. 2003). Because visual inspection of jackknife results and NN split networks revealed no conflicts between well-supported structures in the nuclear and plastid NN split networks, the data sets were combined. The online assemble species by automatic partitioning (ASAP) tool (Puillandre et al. 2019; https://bioinfo.mnhn.fr/abi/public/asap; accessed 6 October 2021), using the default settings, was used to aid in assessing which entities to potentially recognize within *O. hians* s.l.

Table 1. Specimen data and GenBank accession numbers for the sequences. The data are arranged as: **Sample no**.[* = leaf and selected sporophyte characters measured in the detailed morphological study; (A–B) = *O. swartzii* lineage according to Fig. 1]: locality,; coll. year, collector (LH = L.Hedenäs) [collector's number]; Herbarium acronym: herbarium registration No.; GenBank accession numbers for ITS, *rpl*16, *trn*L-*trn*F.

***Oxyrrhynchium distichum* (J.E. Zetterstedt) Hedenäs: D1521*:** Sweden, Södermanland, Mörkö; 2020, L. Hedenäs; S: B299325; OR725727, OR728069, OR739721. **D1522*:** Sweden, Södermanland, Mörkö; 2020, L. Hedenäs; S: B299328; OR725728, OR728070, OR739722. **D1526*:** Sweden, Dalarna, Norrbärke; 1990, T. Hallingbäck *3137*; S: B300152; OR725732, OR728074, OR739726. **D1540*:** Sweden, Värmland, Färnebo; 2020, L. Hedenäs; S: B301022; OR725746, OR728088, OR739740. **D1541*:** Sweden, Värmland, Färnebo; 2020, L. Hedenäs; S: B301029; OR725747, OR728089, OR739741. ***Oxyrrhynchium hians* (Hedw.) Loeske: D1517*:** Sweden, Skåne, Östra Vram; 2016, C.-A. Andersson CAA41879/CAA4077; S: B302789; OR725723, OR728065, OR739717. **D1520*:** Sweden, Skåne, Kropp; 2018, R. Åkesson RÅk 55870; S: B302792; OR725726, OR728068, OR739720. **D1523*:** Sweden, Södermanland, Sorunda; 2020, L. Hedenäs; S: B301659; OR725729, OR728071, OR739723. **D1529*:** Sweden, Västergötland, Skövde; 2002, T. Hallingbäck 38045; S: B300150; OR725735, OR728077, OR739729. **D1537:** Sweden, Småland, Hakarp; 2006, T. Hallingbäck 43697; S: B300151; OR725743, OR728085, OR739737. **D1599*:** Sweden, Uppland, Singö; 2021, L. Hedenäs; S: B304522; OR725755, OR728097, OR739749. ***Oxyrrhynchium swartzii* (Turner) Warnst.: D1515* (A):** Sweden, Skåne, Strövelstorp; 2017, R. Åkesson RÅk 48062; S: B302787; OR725721, OR728063, OR739715. **D1516* (A):** Sweden, Skåne, Kattarp; 2017, R. Åkesson RÅk 48237; S: B302788; OR725722, OR728064, OR739716. **D1518* (B):** Sweden, Skåne, Billinge; 2012, L. Birkedal & T. Tyler 946; S: B302790; OR725724, OR728066, OR739718. **D1519 (A):** Sweden, Skåne, Ekeby; 2017, T. Tyler et al. 239; S: B302791; OR725725, OR728067, OR739719. **D1524 (B):** Sweden, Södermanland, Sorunda; 2020, L. Hedenäs; S: B301660; OR725730, OR728072, OR739724. **D1525* (B):** Sweden, Dalarna, Boda; 2018, L. Hedenäs; S: B288146; OR725731, OR728073, OR739725. **D1527 (B):** Sweden, Uppland, Skå; 2018, P. Engström; S: B289369; OR725733, OR728075, OR739727. **D1528* (B):** Sweden, Södermanland, Mörkö; 2020, L. Hedenäs; S: B301251; OR725734, OR728076, OR739728. **D1530 (B):** Sweden, Småland, Järeda; 2019, T. Nilsson et al. 4060; S: B299351; OR725736, OR728078, OR739730. **D1531* (A):** Sweden, Västergötland, Angered; 2006, T. Hallingbäck 44325; S: B300157; OR725737, OR728079, OR739731. **D1532 (B):** Sweden, Småland, Tveta; 2017, T. Nilsson & J. Rundberg 3545; S: B289475; OR725738, OR728080, OR739732. **D1533* (B):** Sweden, Bohuslän, Kungälv; 1975, T. Hallingbäck 3136; S: B300149; OR725739, OR728081, OR739733. **D1534* (A):** Sweden, Bohuslän, Torp; 1974, T. Hallingbäck 3134; S: B300154; OR725740, OR728082, OR739734. **D1535* (A):** Sweden, Skåne, Helsingborg; 2011, T. Hallingbäck 5663; S: B300155; OR725741, OR728083, OR739735. **D1536 (A):** Sweden, Skåne, Brunnby; 1978, T. Hallingbäck 3131; S: B300156; OR725742, OR728084, OR739736. **D1538 (B):** Sweden, Södermanland, Utö; 2021, L. Hedenäs; S: B302449; OR725744, OR728086, OR739738. **D1539* (B):** Sweden, Halland, Steninge; 2006, K. Georgson Hal-394; S: B301431; OR725745, OR728087, OR739739. **D1542 (B):** Sweden, Västmanland, Hällefors; 2020, L. Hedenäs; S: B300999; OR725748, OR728090, OR739742. **D1543 (B):** Sweden, Södermanland, Mörkö; 2020, L. Hedenäs & I. Bisang; S: B301136; OR725749, OR728091, OR739743. **D1544 (B):** Switzerland, Kt. Appenzell A. Rh., Urnäsch; 1990, I. Bisang 90054; S: B302177; OR725750, OR728092, OR739744. **D1545 (A):** Switzerland, Kt Tessin, Comologno; 1985, I. Bisang 85614; S: B302182; OR725751, OR728093, OR739745. **D1546 (A):** Switzerland, Cte. Ticino, Novaggio; 1988, I. Bisang 238, *B6*; S: B302184; OR725752, OR728094, OR739746. **D1597 (B):** Sweden, Södermanland, Botkyrka; 2021, L. Hedenäs; S: B303504; OR725753, OR728095, OR739747. **D1598 (B):** Sweden, Södermanland, Vårdinge; 2021, L. Hedenäs; S: B303916; OR725754, OR728096, OR739748. **D1600 (B):** Norway, Akershus, Ås; 2014, T. Høitomt M2206Høi & S. L. Olsen; TRH: B-91681; OR725756, OR728098, OR739750. **D1601 (A):** Norway, Telemark, Porsgrunn; 2014, T. Høitomt M2313Høi; TRH: B-91975; OR725757, OR728099, OR739751. **D1602 (A):** Norway, Rogaland, Vindafjord; 2018, S. O. B. Drangeid et al.; TRH: B-109270; OR725758, OR728100, OR739752. **D1603 (A):** Norway, Hordaland, Fusa; 2016, T. Høitomt et al. M3433Høi; TRH: B-89857; OR725759, OR728101, OR739753. **D1604 (A):** Norway, Østfold, Halden; 2014, T. Høitomt M2172Høi & K. A. Lye; TRH: B-91650; OR725760, OR728102, OR739754. **D1605 (A):** Norway, Telemark, Porsgrunn; 2016, T. Høitomt M3954Høi & R. Solvang; TRH: B-12619; OR725761, OR728103, OR739755. **OUTGROUP: *Oxyrrhynchium schleicheri* (R. Hedw.) Röll: D1513:** Sweden, Skåne, Vittskövle; 2000, T. Hallingbäck 16647; S: B300159; OR725719, OR728061, OR739713. ***Oxyrrhynchium speciosum* (Brid.) Warnst.: D1514:** Sweden, Skåne, Norra Vram; 2017, T. Tyler et al. 23195; S: B302793; OR725720, OR728062, OR739714.

Morphological study and analysis of measurements

After the molecular relationships among the 32 *O. hians* s.l. specimens had been clarified, the morphology of five specimens from each identified lineage was studied in detail. When more than five specimens were available from a lineage, the five specimens were arbitrarily selected. Both standard comparisons of qualitative and quantitative characters and detailed measurements of selected gametophyte features were performed, employing dissecting and compound microscopes.

Specimens for which selected gametophyte features were measured in detail are indicated with an asterisk (*) in Table 1. For each of these specimens, measurements (Table 2) were taken from each of three vegetative stem leaves and from each of three branch leaves from the middle of branches adjacent to the respective sampled stem leaves, sampled from two shoots (2 stem and branch leaves, respectively, from one shoot, and 1 from the other, to avoid sampling all leaves from an atypical shoot for the specimen). An Olympus SC50 digital camera and the Olympus cellSens Standard 1.13 software (Olympus Corporation) for automatic and continuous image stacking were used to produce temporary images of leaves and cells. Measurements were taken from these leaf and cell images, using the Olympus cellSens Standard 1.13 software.

Comparisons of the detailed measurements among the lineages within *O. hians* s.l. are based on two approaches. First, measurements were compared between the molecularly identified groups. To test for potential influence of leaf size on lamina cell size, these were in addition evaluated by adjusting cell sizes to a standard leaf length of 1.00 mm for stem leaves and 0.75 mm for branch leaves, and a width of 0.75 mm for stem leaves and 0.5 mm for branch leaves, by dividing the actual leaf lengths or widths with these values and multiplying the resulting values with the cell lengths and widths, respectively (Table 2). For all measurements except cell sizes, Shapiro Wilks W-test was not significant for most measurements, indicating that the data met the criterion of normality, and potential differences between the lineages were tested by analysis of variance (ANOVA). For the measurements of leaf cells, Shapiro Wilks W-test (normality) was significant for most measurements, indicating that the data were not normally distributed and the nonparametric Kruskal–Wallis Anova by ranks for multiple comparisons was used to compare the measurements among or between the groups, respectively. Second, the leaf and leaf cell measurements (in total 60 measured leaves) were subjected to a principal component analysis (PCA) to see whether the combined information corresponds with the molecularly identified groups. The following were included in the PCA: stem leaves: leaf length and width; costa length, and width near base; mean leaf lamina cell length and width; mean marginal denticle length; branch leaves (those adjacent to the respective stem leaf): leaf length and width; mean leaf lamina cell length and width. The statistical calculations were made in STATISTICA 12 (StatSoft 2013). Bonferroni corrections were applied in cases of multiple statistical comparisons.

Because two lineages differed only in quantitative characters, branch leaf length was further evaluated for the remaining nine and eleven molecularly identified specimens belonging to these two lineages to estimate the extent of overlap. The ranges in branch leaf length for these specimens were noted.

Table 2. Measured and derived characters in each of five molecularly identified specimens from each of the four *Oxyrrhynchium hians* lineages.

a.	**Sll.** Stem leaf length, mm, from three arbitrarily selected leaves from two well-developed stems.
b.	**Slw.** Stem leaf width, mm from same leaves as in **a**.
c.	**Sll/w.** Stem leaf length / width ratio from same leaves as in **a**.
d.	**Bll.** Branch leaf length, mm, from three arbitrarily selected leaves from middle of well-developed branches from two different shoots.
e.	**Blw.** Branch leaf width, mm, from same leaves as in **d**.
f.	**Bll/w.** Branch leaf length / width ratio, from same leaves as in **d**.
g.	**Slcol.** Stem leaf costa length, % of leaf length, from same leaves as in **a**.
h.	**Slcow.** Stem leaf costa width at base, µm, from same three leaves as in **a**.
i.	**Sld.** Stem leaf marginal denticle length along distal denticle margin, µm, from same three leaves as under **a**. Mean of five consecutive denticles at mid-leaf.
j.	**Slcl.** Stem leaf lamina cell length, µm, from 20 mid-leaf lamina cells per leaf. Same leaves as under **a**.
k.	**Slcw.** Stem leaf lamina cell width, µm, from same 20 mid-leaf lamina cells as in **j**.
l.	**Slcl/w.** Stem leaf lamina cell length / width ratio, from same 20 mid-leaf lamina cells as in **j**.
m.	**Blcl.** Branch leaf lamina cell length, µm, from 20 mid-leaf lamina cells per leaf. Same leaves as in **d**.
n.	**Blcw.** Branch leaf lamina cell width, µm, from same 20 mid-leaf lamina cells as in **m**.
o.	**Blcl/w.** Branch leaf lamina cell length / width ratio, from same 20 mid-leaf lamina cells as in **m**.
p.	**SlclA.** Stem leaf lamina cell length, adjusted to a leaf length of 1 mm, µm, from same 20 mid-leaf lamina cells as in **j**.
q.	**SlcwA.** Stem leaf lamina cell width, adjusted to a leaf width of 0.75 mm, µm, from same 20 mid-leaf lamina cells as in **j**.
r.	**Slcl/wA.** Stem leaf lamina cell length / width ratio, based on the adjusted leaf length and width, from same 20 mid-leaf lamina cells as in **j**.
s.	**BlclA.** Branch leaf lamina cell length, adjusted to a leaf length of 0.75 mm, µm, from same 20 mid-leaf lamina cells as in **m**.
t.	**BlcwA.** Branch leaf lamina cell width, adjusted to a leaf width of 0.5 mm, µm, from same 20 mid-leaf lamina cells as in **m**.
u.	**Blcl/wA.** Branch leaf lamina cell length / width ratio, based on the adjusted leaf length and width, from same 20 mid-leaf lamina cells as in **m**.

Results

Molecular relationships

Four lineages could be molecularly recognized within *O. hians* s.l., and the names of those recognizable by morphology, as suggested by the present study, will be used from now on to facilitate the presentation of the results and the following discussion (Fig. 1).

The total number of aligned ITS sites in the 43 molecularly studied *Oxyrrhynchium* specimens, including the two outgroup specimens, after deletion of regions at the beginnings and ends that were incomplete for some specimens, was 753. Of these, 43 (11 in *O. hians* s.l.) sites were variable, with 9 (8) of the variable ones parsimony-informative; 19 (1) indels were present, with 1 (1) informative. For *rpl*16, the length was 723, 28 (10) sites were variable, and 9 (8) were parsimony-informative; 6 (2) indels with 2 (1) informative. For *trn*L-*trn*F, the length was 447, 17 (7) sites were variable, and 7 (5) of these were parsimony-informative; 2 (1) indels with 1 (1) informative. The lengths of the sequences were, for *O. distichum* (n = 5): ITS: 706, *rpl*16: 712–722, *trn*L-*trn*F: 439; *O. hians* (n = 6): 705, 722, 447; *O. swartzii* A (n = 14): 705, 722–723, 439; *O. swartzii* B (n = 16): 705, 722, 439.

The NN split network revealed four distinct lineages within *O. hians* s.l. (Fig. 1) and three of these received moderate to high jackknife support (75–93). Recognition of the same four groups received the lowest score, 1.5, in the ASAP analysis (Fig. 2).

Morphological evaluation

The PCA based on the detailed measurements of *O. hians* s.l. suggests that all four taxa are possible to distinguish in most cases (Fig. 3A). Most of the measured features correlate with the first axis, but both stem and branch leaf

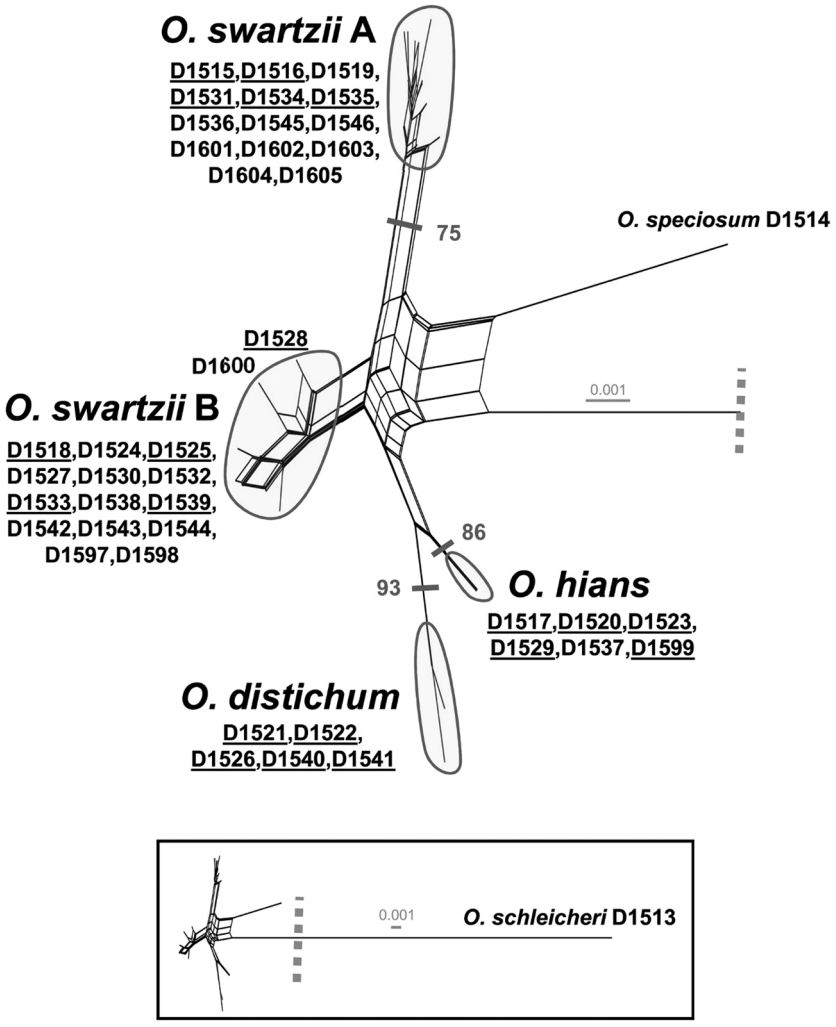

Figure 1. NeighborNet split network for *Oxyrrhynchium hians* s.l. based on nuclear ITS and plastid *rpl*16 and *trn*L-*trn*F in combination. *Oxyrrhynchium speciosum* and *O. schleicheri* were used as outgroups to root the network. Jackknife support of at least 75 is indicated in grey. Specimens are indicated according to their numbers in Table 1, and numbers of specimens selected for the first morphological evaluation are underlined.

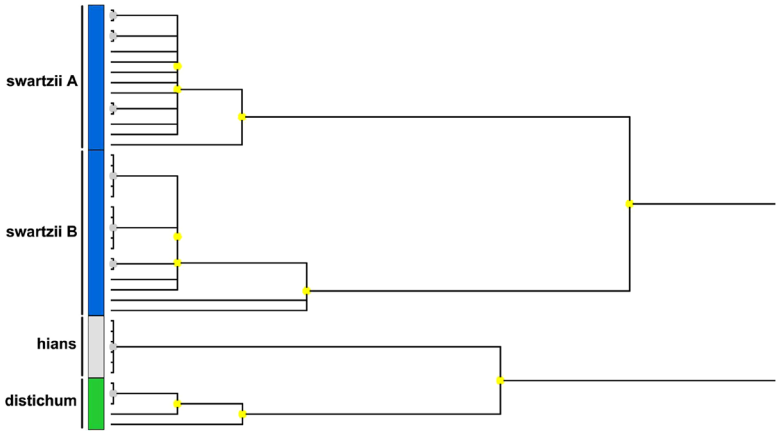

Figure 2. ASAP results based on nuclear ITS and plastid *rpl*16 and *trn*L-*trn*F in combination. Only the result with the lowest ASAP score, 1.5, is shown.

lamina cell lengths correlate with the second axis (Fig. 3B). *Oxyrrhynchium distichum* and *O. hians* are most strongly differentiated from each other, and also differ in almost all individual measured characters, also when these are adjusted to standard leaf sizes (Fig. 4). These two species also differ from one or both of *O. swartzii* A and B in several measurements, whereas found differences between *O. swartzii* A and B were mainly in size (Fig. 4, Table 3). When branch leaf length, the feature which differentiated *O. swartzii* A and B most strongly in the detailed study, was measured in the remaining nine (A) and eleven (B) specimens that were included in the molecular study it turned out that A specimens varied between ca 0.7–1.2 mm and B specimens between ca 0.5–1.0 mm (Fig. 5). A high proportion of the specimens could not be distinguished by this character.

Aside from these measurements, *O. distichum* had shorter and more narrowly decurrent stem leaves than the other species and *O. hians* was the only species to have distinctly concave leaves, also in the branches, and a frequently twisted leaf apex.

Geographical distribution and habitat

In Fennoscandia, *O. distichum* has the most restricted distribution (Fig. 6A) and only a few finds are as yet known from outside Fennoscandia. Its primary habitat seems to be vertical faces of base-rich to calcareous rocks (Fig. 7A). *Oxyrrhynchium hians* is moderately common along the southern coasts and also in the inland lowlands from the Stockholm Archipelago to the Swedish west-coast (Fig. 6B). This species is widespread in Europe. Its distribution in Fennoscandia coincides with that of relatively nutrient- and base-rich soils, where it is relatively often found in forests, also on decomposing wood (Fig. 7B). *Oxyrrhynchium swartzii*, including both A and B, is clearly the most common and widespread species in Fennoscandia (Fig. 6C), as well as in Europe. The molecularly identified specimens suggest that A may have more western distribution than B (Fig. 8). This species grows primarily on soil and is the most common species of the three on soil in habitats without trees or shrubs (Fig. 7C).

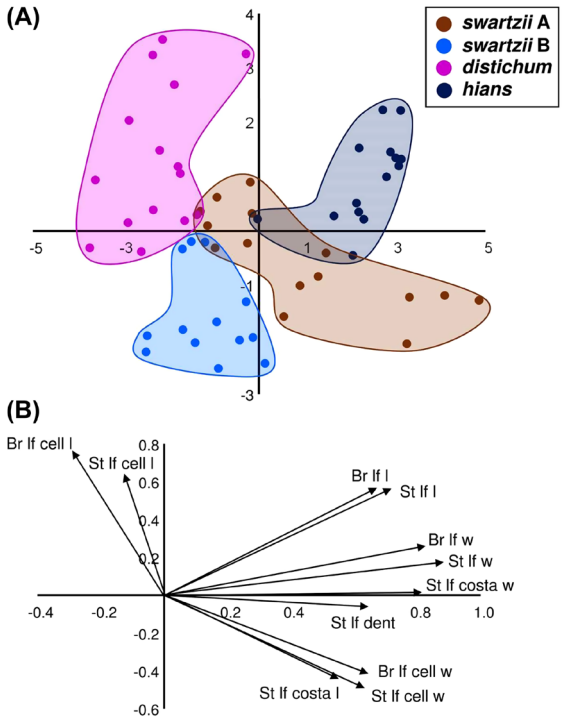

Figure 3. PCA based on five specimens from each lineage identified in the NeighborNet split network of *O. hians* s.l. (specimens with numbers underlined in Fig. 1). (A) The positions of samples based on leaf and leaf lamina cell sizes, along the first two axes in a PCA. Each sample consists of a stem leaf plus a leaf from the closest branch, and three such samples were taken from each specimen. Factors 1 and 2 explain 42.97% and 21.19% of the variation, respectively. (B) Explanatory factors in the plane of factors 1 and 2 in (A). This PCA is based on the following, for each stem plus closest branch leaf: stem leaf length (St lf l) and width (St lf w), branch leaf length (Br lf l) and width (Br lf w), stem leaf costa length (St lf costa l) and width (St lf costa w), stem leaf marginal denticle length (St lf dent), stem leaf cell mean length (St lf cell l) and width (St lf cell w), and branch leaf mean cell length (Br lf cell l) and width (Br lf cell w). Mean values of cell measurements are based on 20 measurements.

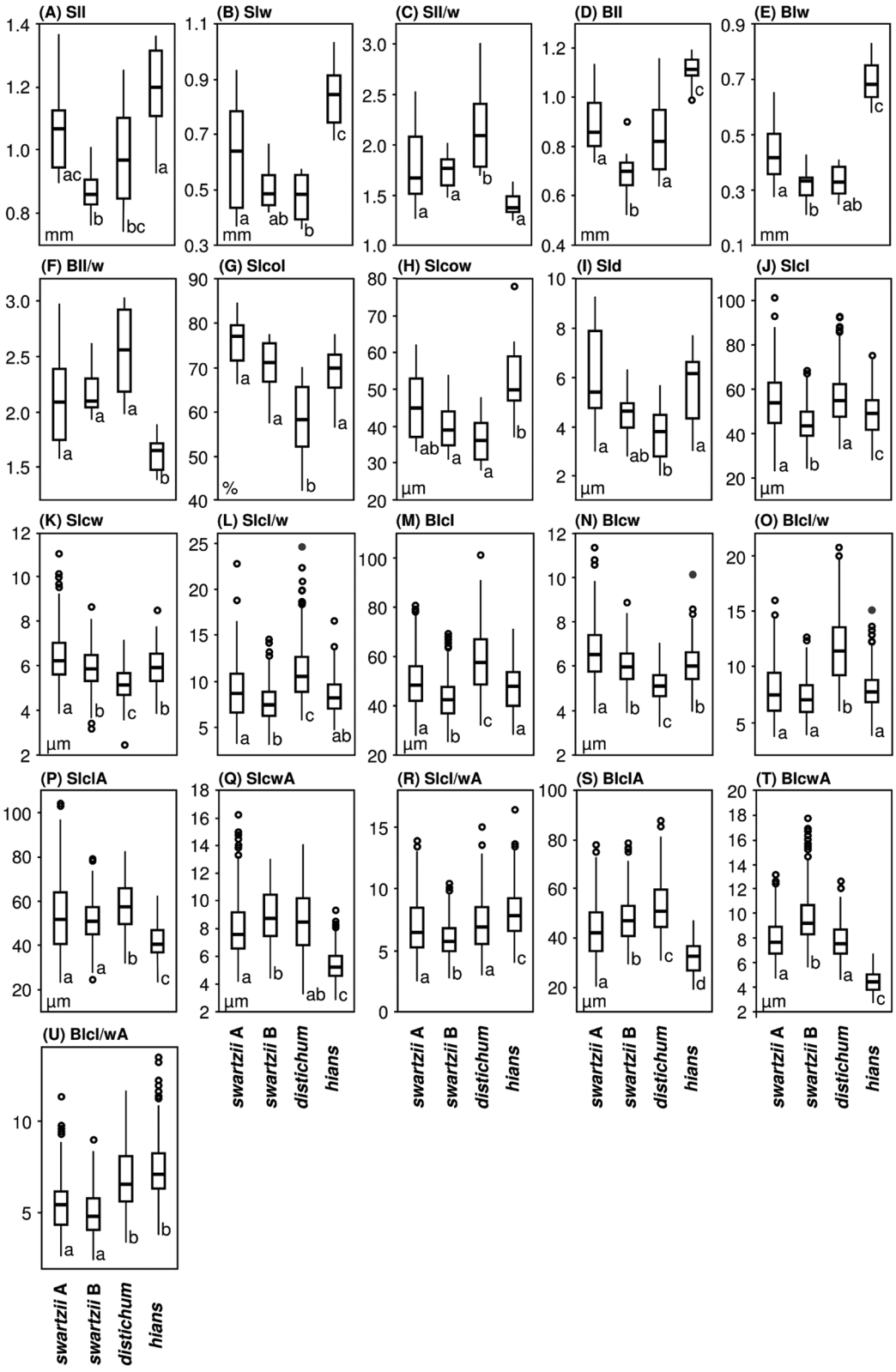

Figure 4. Medians, quartiles, and ranges for the measured and derived characters in Table 2, where the characters are also described. Outliers are indicated by circles and extreme outliers by grey dots. Lineages for which the means (cf. Table 3) are significantly different according to Bonferroni corrected p corresponding with 0.05 are indicated by different letters (a–d). Potential differences were tested by Anova for (A)–(I) and Kruskal–Wallis Anova by ranks for (J)–(U).

Table 3. Descriptive statistics for measured and derived characters in the four *Oxyrrhynchium* species. For characters a–i, n = 15 measurements per lineage, for characters j–u, n = 300 measurements per lineage. SE: Standard error. *Mi*-10-**Med**-90-*Ma*: *Minimum value*-limit of 10th Percentile-**Median**-limit of 90th Percentile-*Maximum value*. Statistically significant differences between the lineages are indicated in Fig. 4.

		Oxyrrhynchium swartzii A		*Oxyrrhynchium swartzii* B		*Oxyrrhynchium distichum*		*Oxorhenium hians*	
		Mean (SE)	*Mi*-10-Med-90-*Ma*	Mean (SE)	*Mi*-10-Med-90-*Ma*	Mean (SE)	*Mi*-10-Med-90-*Ma*	Mean (SE)	*Mi*-10-Med-90-*Ma*
a.	**Sll**	1.0 (0.0)	*0.9*-0.9-**1.1**-1.2-*1.4*	0.9 (0.0)	*0.8*-0.8-**0.9**-1.0-*1.0*	1.0 (0.0)	*0.7*-0.7-**1.0**-1.2-*1.3*	1.2 (0.0)	*0.9*-1.0-**1.2**-1.3-*1.4*
b.	**Slw**	0.6 (0.0)	*0.4*-0.4-**0.6**-0.8-*0.9*	0.5 (0.0)	*0.4*-0.4-**0.5**-0.6-*0.7*	0.5 (0.0)	*0.4*-0.4-**0.5**-0.6-*0.6*	0.8 (0.0)	*0.7*-0.7-**0.8**-1.0-*1.0*
c.	**Sll/w**	1.8 (0.1)	*1.3*-1.3-**1.7**-2.3-*2.5*	1.7 (0.0)	*1.5*-1.5-**1.8**-1.9-*2.0*	2.1 (0.1)	*1.7*-1.7-**2.1**-2.7-*3.0*	1.4 (0.0)	*1.2*-1.3-**1.4**-1.6-*1.6*
d.	**Bll**	0.9 (0.0)	*0.7*-0.7-**0.9**-1.1-*1.1*	0.7 (0.0)	*0.5*-0.5-**0.7**-0.8-*0.9*	0.8 (0.0)	*0.6*-0.6-**0.8**-1.2-*1.2*	1.1 (0.0)	*1.0*-1.0-**1.1**-1.2-*1.2*
e.	**Blw**	0.4 (0.0)	*0.3*-0.3-**0.4**-0.5-*0.7*	0.3 (0.0)	*0.2*-0.2-**0.3**-0.4-*0.4*	0.3 (0.0)	*0.2*-0.3-**0.3**-0.4-*0.4*	0.7 (0.0)	*0.6*-0.6-**0.7**-0.8-*0.8*
f.	**Bll/w**	2.1 (0.1)	*1.6*-1.6-**2.1**-2.9-*3.0*	2.2 (0.1)	*1.9*-2.0-**2.1**-2.5-*2.6*	2.5 (0.1)	*2.0*-2.0-**2.6**-3.0-*3.0*	1.6 (0.0)	*1.4*-1.4-**1.6**-1.8-*1.9*
g.	**Slcol**	76.1 (1.4)	*66.3*-66.9-**77.2**-81.5-*84.7*	70.6 (1.5)	*57.3*-63.3-**71.2**-77.0-*77.7*	57.4 (2.4)	*42.0*-42.4-**58.3**-69.1-*70.2*	69.4 (1.5)	*56.5*-62.4-**70.1**-76.5-*77.6*
h.	**Slcow**	46.1 (2.5)	*33.0*-36.0-**45.0**-62.0-*62.0*	39.8 (1.6)	*31.0*-33.0-**39.0**-48.0-*54.0*	36.5 (1.6)	*28.0*-28.0-**36.0**-47.0-*48.0*	52.8 (2.5)	*37.0*-43.0-**50.0**-63.0-*78.0*
i.	**Sld**	6.1 (0.5)	*3.0*-3.4-**5.4**-8.3-*9.3*	4.5 (0.2)	*2.8*-3.2-**4.7**-5.7-*6.3*	3.8 (0.3)	*2.0*-2.6-**3.8**-5.2-*5.7*	5.7 (0.4)	*3.0*-3.9-**6.2**-7.1-*7.7*
j.	**Slcl**	54.5 (0.8)	*22.9*-37.4-**53.9**-72.1-*101.4*	44.2 (0.5)	*24.3*-34.7-**43.6**-54.7-*69.1*	56.3 (0.7)	*33.1*-43.4-**54.8**-72.9-*93.2*	49.3 (0.6)	*27.8*-37.3-**49.0**-62.3-*75.7*
k.	**Slcw**	6.4 (0.1)	*3.9*-5.0-**6.2**-8.2-*11.1*	5.9 (0.1)	*3.2*-4.8-**5.9**-7.1-*8.7*	5.2 (0.0)	*2.5*-4.3-**5.1**-6.2-*7.2*	6.0 (0.0)	*3.8*-5.0-**5.9**-7.1-*8.5*
l.	**Slcl/w**	8.9 (0.2)	*3.2*-5.3-**8.7**-12.1-*22.8*	7.7 (0.1)	*3.1*-5.5-**7.5**-10.4-*14.5*	11.1 (0.2)	*5.8*-7.8-**10.5**-14.9-*24.6*	8.4 (0.1)	*4.7*-6.1-**8.2**-10.8-*16.5*
m.	**Blcl**	49.7 (0.6)	*27.6*-37.9-**48.5**-63.6-*80.4*	42.9 (0.5)	*25.2*-32.5-**42.6**-53.6-*69.2*	58.4 (0.8)	*32.0*-42.5-**57.8**-76.1-*101.2*	47.5 (0.5)	*28.4*-35.8-**48.0**-59.2-*71.2*
n.	**Blcw**	6.7 (0.1)	*3.9*-5.1-**6.5**-8.3-*11.4*	6.0 (0.1)	*3.9*-4.9-**6.0**-7.3-*8.9*	5.1 (0.0)	*3.3*-4.2-**5.1**-6.1-*7.0*	6.1 (0.1)	*3.9*-5.0-**6.0**-7.5-*10.1*
o.	**Blcl/w**	7.8 (0.1)	*3.7*-5.0-**7.4**-10.9-*16.1*	7.3 (0.1)	*3.8*-5.3-**7.0**-9.9-*12.7*	11.6 (0.2)	*5.9*-7.9-**11.4**-15.3-*20.8*	8.0 (0.1)	*3.8*-5.9-**7.7**-10.4-*15.1*
p.	**SlclA**	53.2 (0.9)	*22.9*-34.7-**51.8**-75.2-*104.3*	51.1 (0.5)	*24.5*-40.0-**50.7**-63.5-*79.1*	57.9 (0.6)	*31.8*-43.5-**57.4**-73.3-*82.7*	41.7 (0.4)	*23.1*-32.7-**40.6**-52.6-*62.5*
q.	**SlcwA**	8.1 (0.1)	*4.1*-5.8-**7.6**-11.3-*16.2*	8.9 (0.1)	*4.4*-6.4-**8.8**-11.4-*13.1*	8.6 (0.1)	*3.2*-6.0-**8.5**-11.5-*14.1*	5.4 (0.1)	*2.8*-4.1-**5.3**-6.9-*9.3*
r.	**Slcl/wA**	6.8 (0.1)	*2.5*-4.4-**6.5**-9.5-*14.0*	5.9 (0.1)	*2.7*-4.2-**5.7**-8.0-*10.4*	7.1 (0.1)	*2.9*-4.3-**6.9**-10.1-*15.1*	8.0 (0.1)	*4.0*-5.7-**7.8**-10.6-*16.4*
s.	**BlclA**	43.1 (0.6)	*20.1*-29.9-**42.1**-56.5-*77.9*	47.3 (0.6)	*29.0*-35.9-**46.8**-60.8-*78.7*	52.5 (0.6)	*30.6*-38.6-**50.6**-67.3-*87.8*	32.2 (0.4)	*19.0*-23.7-**32.5**-40.3-*47.3*
t.	**BlcwA**	8.0 (0.1)	*4.7*-6.1-**7.6**-10.5-*13.2*	9.7 (0.1)	*5.6*-7.4-**9.2**-12.6-*17.8*	7.8 (0.1)	*4.6*-6.2-**7.6**-9.9-*12.7*	4.5 (0.0)	*2.7*-3.4-**4.4**-5.6-*6.7*
u.	**Blcl/wA**	5.5 (0.1)	*2.7*-3.8-**5.5**-7.6-*11.4*	5.0 (0.1)	*2.5*-3.6-**4.8**-6.6-*9.0*	6.9 (0.1)	*3.4*-4.9-**6.6**-9.3-*11.7*	7.4 (0.1)	*3.8*-5.4-**7.1**-9.7-*13.5*

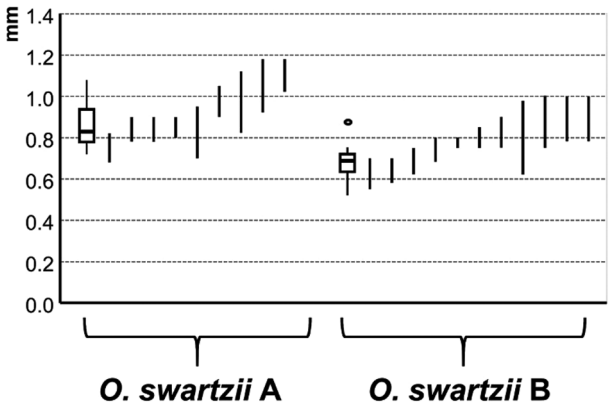

Figure 5. Ranges in branch leaf lengths for molecularly identified *Oxyrrhynchium swartzii* A and B specimens that were not included in the detailed measurements (not underlined in Fig. 1). Sample numbers of A: D1602, D1603, D1605, D1519, D1545, D1601, D1604, D1546, D1536; B: D1530, D1524, D1542, D1532, D1597, D1598, D1527, D1543, D1538, D1544, D1600. Medians, quartiles, and ranges from Fig. 4, for the specimens included for the detailed measurements, are shown to the left of the present measurements.

Discussion

The molecular relationships within *O. hians* s.l., supported by the ASAP analysis, suggest the recognition of four distinct entities. These have different geographical distributions, partly different habitat preferences, and the three entities, *O. distichum*, *O. hians*, and *O. swartzii* (A + B), can be reliably identified by morphology. All these features suggest recognition at the species level. The two molecular entities A and B within *O. swartzii* are only distinguishable by morphology to some degree, since 60% of the 20 molecularly identified samples that were used to test the main difference found in the detailed study could not be reliably assigned to either species by morphology. These two entities are therefore best treated as semi-cryptic species within *O. swartzii*. Semi-cryptic species, displaying minor but strongly overlapping morphological differentiation that prohibits certain identification of a high proportion of the specimens have also been found in, for example, *Andoa berthelotiana* (Mont.) Ochyra (Martins et al. 2021) and *Neckera pennata* Hedw. (Appelgren and Cronberg 1999). Semi-cryptic species, like cryptic ones, need to be included in biodiversity studies and conservation contexts (Hedenäs 2018, Hodgetts et al. 2019), since they have the same biological and other values as species that are more easily recognizable by morphology. The name *Hypnum swartzii* Turner most likely belongs to entity B, since this molecular entity was the only one found in the Stockholm area (SE Sweden), where the type was once collected in the end of the 18th century. If additional molecularly identified samples confirm the distributions of the semi-cryptic species A and B of *O. swartzii*, A could be described as a separate species based on molecular evidence and a morphology that partly deviates from that of B.

It is important to understand which species exist for our interpretation of species diversity and of species' habitat preferences, but this is not the only reason why it is important.

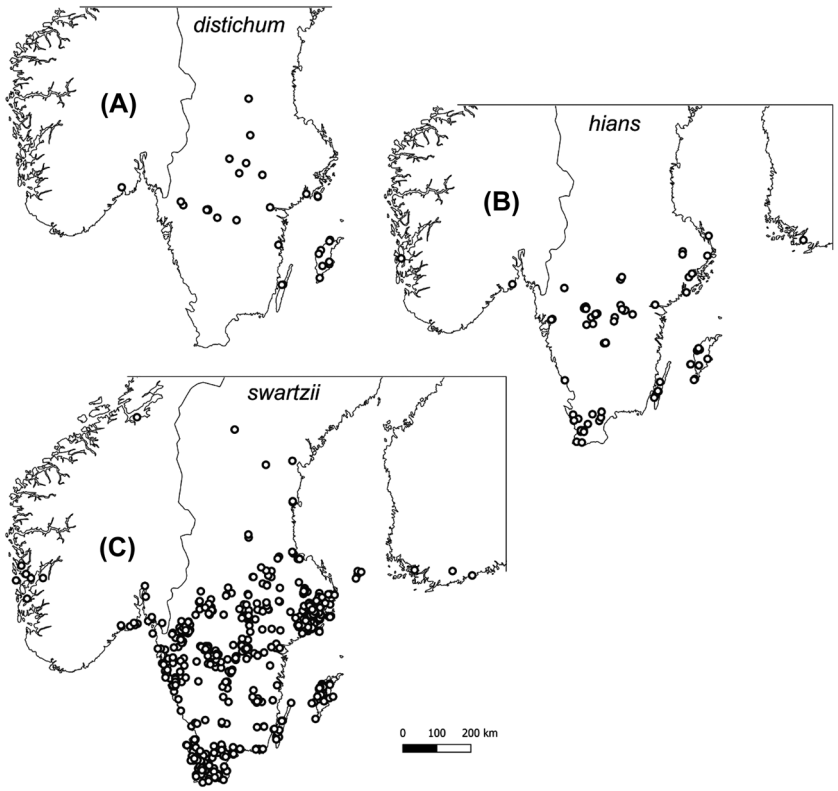

Figure 6. Fennoscandian distributions of studied specimens of (A) *O. distichum*, (B) *O. hians*, and (C) *O. swartzii*.

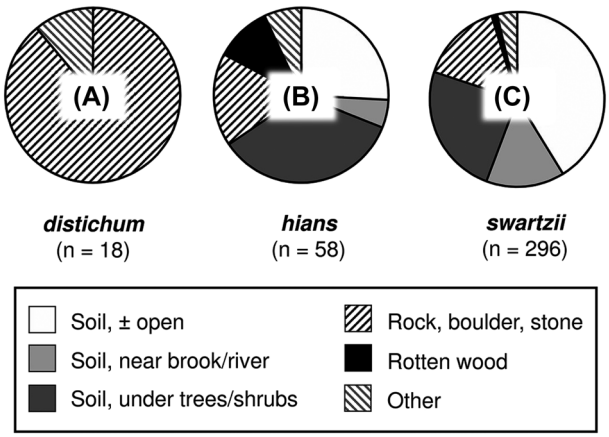

Figure 7. Distributions among habitats where the *Oxyrrhynchium* species were collected, according to label information. (A) *O. distichum*, (B) *O. hians*, and (C) *O. swartzii*. n = number of specimens.

A recent study found that different morphologies and water storing capacities depended on the origin of *O. hians* s.l. plants (Thielen et al. 2021). The new information presented here suggests that these results in their study could potentially have resulted from the inclusion of two different species. The four species found in the present study differ in features that are likely to affect water holding capacity, such as size, leaf shape and concaveness, leaf orientation, and cell size. Also in other contexts it may be wise to check which of the four *O. hians* s.l. species were included, for example, in studies of bioaccumulation of various elements (Gorelova et al. 2016) and antibiotic properties of moss species (Karpiński and Adamczak 2017).

Taxonomy

Key to the morphologically recognizable species of *Oxyrrhynchium hians* s.l. in Europe

Identification note: Select well-developed shoots and avoid stoloniferous shoots. The latter may have leaves that differ strongly from leaves of well-developed shoots. Since no differences between the species were found in sporophyte characters, only gametophyte features relevant for the identification of the species are included in the key and descriptions.

1. Stem leaves concave, rarely slightly so, cordate or broadly ovate, ± strongly narrowed at insertion, above narrowed to a set-off and sometimes twisted acumen that constitutes 10–15(30)% of leaf length, decurrent or long-decurrent, often broadly so. Branch leaves evenly arranged around branch, 0.6–0.8 mm wide and 1.4–2.0 times as long as wide ..... ***O. hians***
– Stem leaves plane or at most slightly concave, mostly varying around ovate, rarely cordate, strongly narrowed at insertion or not, mostly gradually narrowed to acuminate apex, narrowly or very narrowly decurrent. Branch leaves often complanate or sub-complanate, occasionally evenly arranged around branch, 0.2–0.5(0.7) mm wide and 1.6–3.0 times as long as wide..... 2
2. Branch leaf mid-leaf lamina cells relatively long and narrow, (32.0)42.5–76.0(101.0) × (3.0)4.0–6.0(7.0) µm, (5.9)7.9–15.3(20.8) times as long as wide. Costa ending 40–70% way up leaf. Almost exclusively on base-rich or calcareous rocks ..... ***O. distichum***
– Branch leaf mid-leaf lamina cells relatively short and wide, (25.0)32.5–63.5(80.5) × (4.0)5.0–8.5(11.5) µm, (3.7)5.0–10.9(16.1) times as long as wide. Costa ending 60–85% way up leaf. On various substrates ..... ***O. swartzii***

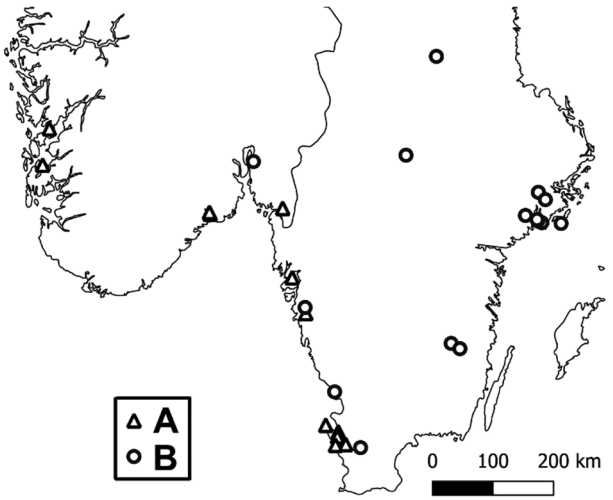

Figure 8. Scandinavian distributions of the molecularly studied specimens of *O. swartzii* semicryptic species A and B.

Oxyrrhynchium distichum (J.E.Zetterst.) Hedenäs, comb. et stat. nov. Fig. 9–10)

Basionym: *Eurhynchium praelongum* fo. *distichum* J.E.Zetterst., Nova Acta Regiae Soc. Sci. Upsal., ser. 3, 7(1): 32. 1869. ≡ *Eurhynchium praelongum* var. *distichum* (J.E.Zetterst.) J.E.Zetterst., Kongl. Svenska Vetensk. Acad. Handl., n.s. 13(14): 29. 1876. Type: 'Eurhynchium praelongum var. distichum Zett., Öland, Köpings branter, 26/6 1867, leg. J. E. Zetterstedt' [lectotype (designated here) in Herb. J. E. Zetterstedt in UPS: B-566651!; isolectotype in Herb. Axel Elof Jäderholm in S: B314990!]. Note: Herbarium J. E. Zetterstedt in UPS holds three syntypes of *Eurhynchium praelongum* fo. *distichum* J.E.Zetterst., all from Öland, Sweden. One was collected in Ottenbylund (UPS: B-566652), one in Köpings branter (B-566651), and one in Borgholms slottsbranter (B-566650). In S there is an isosyntype from Köpings branter (S: B314990). The specimen from Ottenbylund belongs to *Oxyrrhynchium swartzii* (Turner.) Warnst., whereas the other specimens fit the concept of *E. praelongum* fo. *distichum*, and the UPS one collected in Köpings branter is here selected as lectotype for the name.

Plants small, irregularly or irregularly pinnately branched. Stem with narrow central strand and a cortex of 2–3 layers

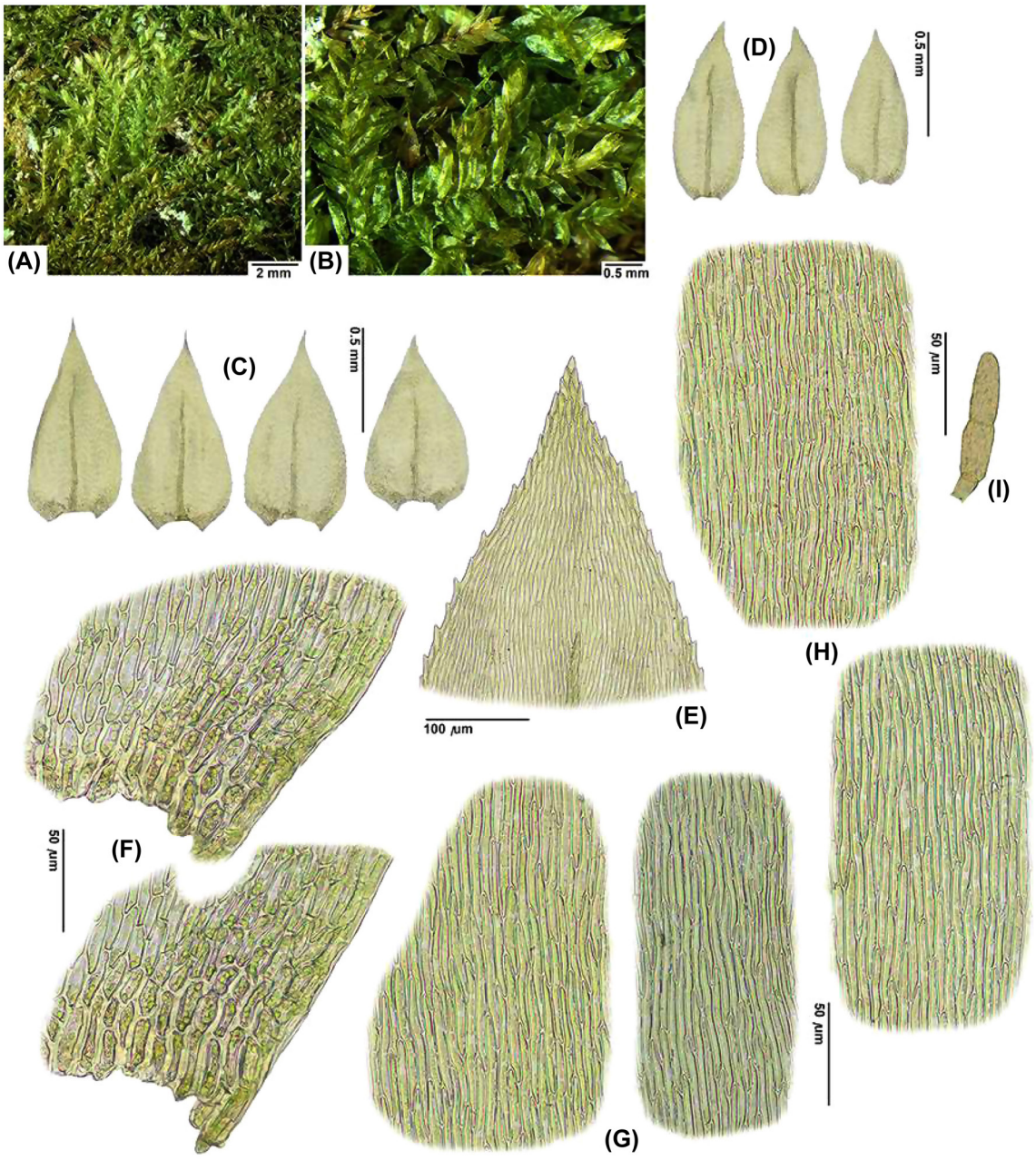

Figure 9. *Oxyrrhynchium distichum*, specimen S: B299325. (A, B) Habit, (C) stem leaves, (D) branch leaves, (E) branch leaf apex, (F) alar cells, (G) mid-leaf lamina cells, stem leaf, (H) mid-leaf lamina cells, branch leaf, (I) axillary hair.

of small and incrassate cells. Axillary hairs with 1–2 upper, rectangular, sometimes bulging, hyaline cells, 9–15 µm wide, basal cell pale brownish. Stem leaves ovate, triangular-ovate, or oblong-ovate, 0.7–1.2(1.3) mm long, 0.4–0.6 mm wide, 1.7–2.7(3.0) times as long as wide, moderately narrowed at insertion, gradually narrowed upwards to acuminate apex or occasionally suddenly narrowed to set-off acumen, to 25% of leaf length), slightly concave, leaves very narrowly decurrent, decurrency often only one cell wide; costa ending 40–70% way up leaf, 28.0–47.0(48.0) µm wide near base; margin denticulate, denticles (2.0)2.5–5.0(5.5) µm long; mid-leaf lamina cells (33.0)43.5–73.0(93.0) × (2.5)4.5–6.0(7.0) µm, (5.8)7.8–14.9(24.6) times as long as wide; basal cells shorter and wider than in mid-leaf, incrassate, occasionally porose; alar cells quadrate or rectangular, occasionally shortly linear, distinctly incrassate, forming an ovate or sometimes rounded group along basal leaf margin. Branch leaves mostly complanate or sub-complanate, sometimes evenly spreading, oblong, oblong-ovate, or ovate, 0.6–1.2 mm long, (0.2)0.3–0.4 mm wide, 2.0–3.0 times as long as wide, shortly or sometimes gradually narrowed to acuminate, shortly acuminate, or acute apex; mid-leaf lamina cells (32.0)42.5–76.0(101.0)

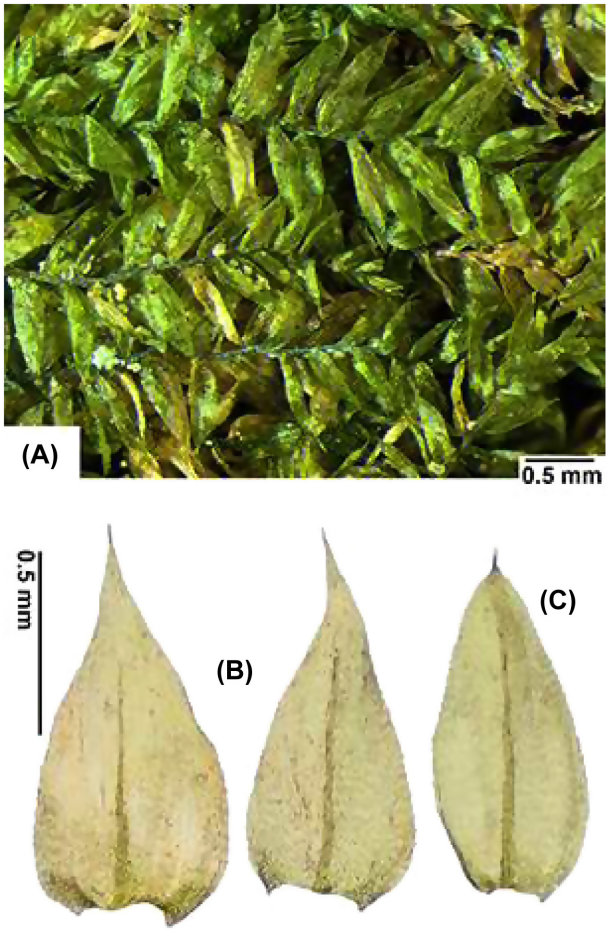

Figure 10. *Oxyrrhynchium distichum*, specimen S: B301022. (A) Habit, (B) stem leaves, (C) branch leaf.

× (3.0)4.0–6.0(7.0) µm, (5.9)7.9–15.3(20.8) times as long as wide.

Typical expressions of this species have distinctly complanate or sub-complanate branch leaves, and due to the long and narrow leaf lamina cells the plants are glossier than the other two species (Fig. 9A–B, 10A). Thanks to its distinct appearance and its special habitat, specimens can frequently be referred to this species in the field.

Oxyrrhynchium distichum is known from a wide belt across southern Scandinavia (Fig. 6A) and from a few localities in Germany and Switzerland. Most likely the species occurs at additional localities in and around the Alps. The typical habitat of this species is shaded, vertical limestone rock walls (Fig. 7A).

Selected specimens studied: Norway, Telemark, Porsgrunn, 1895, E. Jäderholm, S: B317737. Sweden, Dalarna, Osmundberget, 1854, S. O. Lindberg, S: B317716. Dalsland, Bäcke, 1917, P. A. Larsson, S: B316527. Dalsland, Gunnarsnäs, 1945, P. A. Larsson, S: B316526. Gotland, Ardre, 2014, L. Hedenäs et al., S: B205076. Gotland, Etelhem, 1954, Å. Hovgard, S: B315083. Gotland, Hall, 1953, Å. Hovgard, S: B315081. Gotland, Kräklingbo, 1965, J. Christoffersson, S: B87146. Gotland, Visby, 1935, P. A. Larsson, S: B315085. Gotland, Västerhejde, 1888, K. Johansson 117, S: B315092. Småland, Kvistrum, 1879, M. Huss, S: B311443. Södermanland, Utö, 2010, L. Hedenäs, S: B176719. Västergötland, Medelplana, 1922, A. Hülphers, S: B316300. Västergötland, Skövde, 1917, A. Hülphers, S: B315554. Västmanland, Arboga, 1860, O. G. Blomberg, S: B317008. Västmanland, Guldsmedshyttan, 2000, L. Hedenäs, S: B39600. Västmanland, Vikers, 1960, G. Een, S: B79511. Öland, Köpings branter, 1867, J. E. Zetterstedt, S: B314990. Östergötland, Kvillinge, 1880, N. C. Kindberg, S: B316336. Östergötland, Rogslösa, 1946, H. Persson, S: B312901. Germany, Regensburg, Minoritenhof, 1903, I. Familler (Fl. exs. Bav., Bryophyta 581), S: B318240. Switzerland, Ct. Valais, Monthey, 2022, L. Hedenäs, S: B317669. Ct. Ticino, Monte Generoso, 1892, N. C. Kindberg, S: B318226.

Figure 11. Portion of lectotype of *Hypnum hians* Hedw. in G: 00040213. Photo: Isabella Valette.

Oxyrrhynchium hians (Hedw.) Loeske (Fig. 11–13)

Verh. Bot. Vereins Prov. Brandenburg 49(1): 59. 1907. ≡ *Hypnum hians* Hedw., Sp. Musc. Frond. 272–273, pl. 70, f. 11–14. 1801. *Eurhynchium hians* (Hedw.) Sande Lac., Ann. Mus. Bot. Lugduno-Batavi 2: 299. 1866. Type: the fertile specimen at the upper left on the sheet labelled 'In Pensylvania ad Lancaster lectum' [lectotype (Hedenäs and Geissler 1999) in herb. Hedwig-Schwaegrichen, G: 00040213!].

= *Hypnum praelongum* var. *meridionale* Boulay, Musci Gall. 10: n. 480. 1873. Type: '*Eurhynchium praelongum*

Sch. var. *meridionale* Boul., Hypnum. L. Collines calcaires, à Beaucaire (Gard.). Septembre, Boulay (Husnot, Musci Galliae 480)' [Lectotype (designated here) in S: B318327; isolectotype in Herb. N. C. Kindberg in S: B318177].

= *Eurhynchium swartzii* var. *robustum* Limpr., Laubm. Deutschl. 3: 202. 1896. ≡ *Eurhynchium robustum* (Limpr.) Loeske, Verh. Bot. Vereins Prov. Brandenburg 46: 200. 1904. Type: *Eurhynchium swartzii* (Turn.) Curn. forma major. Bolgen bei Bärwalde u/m, Am Ton, […], 2, 66, R. Ruthe' [lectotype (designated here) in S: B318232; isolectotype in Herb. G. Roth in S: B318231].

Note: in addition to the lectotype of *Hypnum hians* Hedw., there exist two 'Mühlenberg 2225' specimens collected in North America ('Ex America boreali') in herbarium Swartz in S (reg. no. B318601, B318602) that are possible isolectotypes of *Hypnum hians* Hedw. These two specimens look similar to the lectotype in Hedwig's herbarium (G). That they are indeed isolectotypes is possible since Muhlenberg sent many specimens to Hedwig for identification (Mears 1978), and Hedwig and Swartz were in close contact with each other, as evidenced by citations of Swartz material in several of Hedwig's works (Hedwig 1791–1792, 1797, 1801).

Plants medium-sized or robust, irregularly or regularly pinnately branched. Stem with strong central strand and a cortex of 2–3 layers of small and incrassate cells. Axillary hairs with 1–4 upper, rectangular, slightly bulging, hyaline cells,

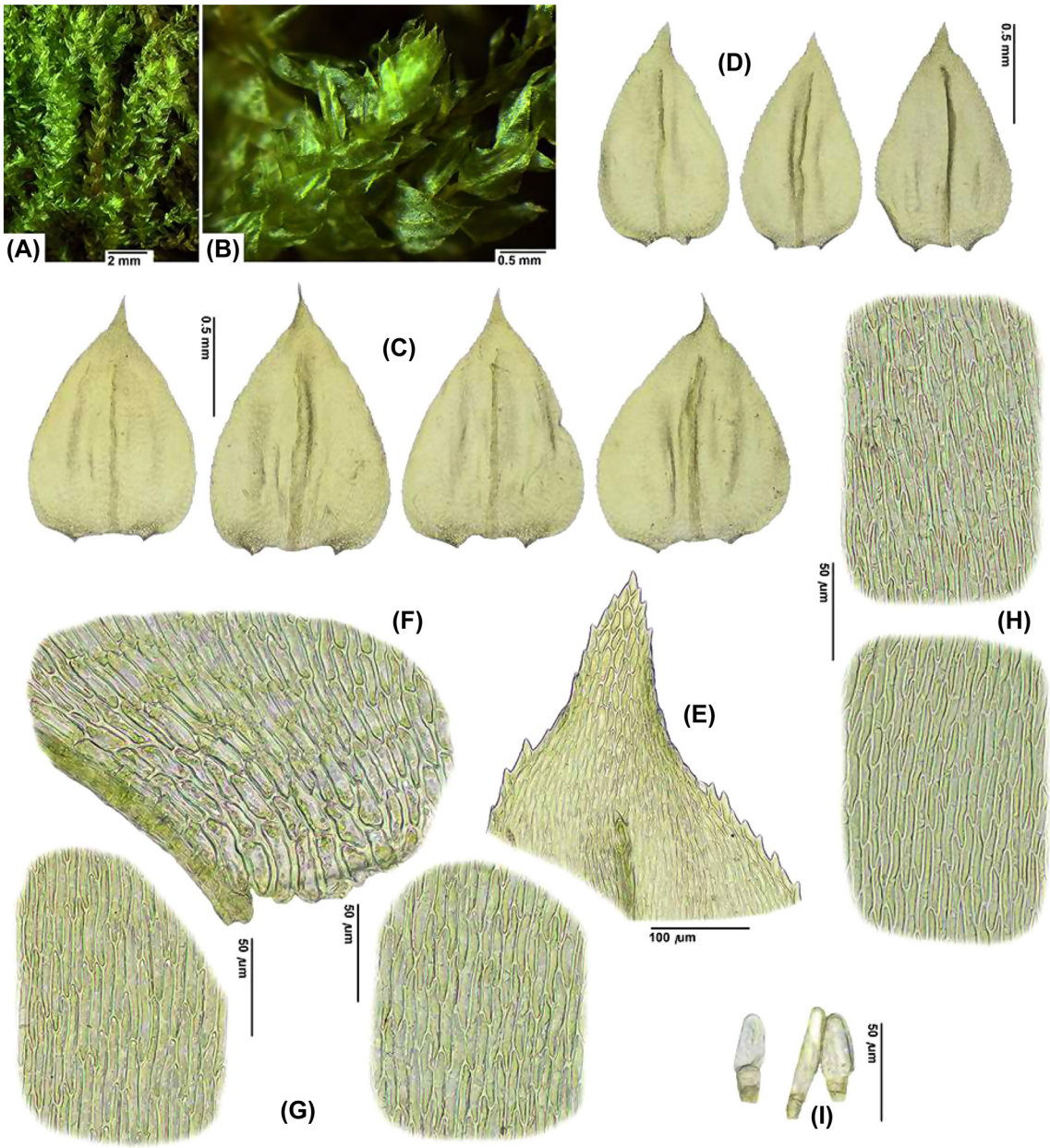

Figure 12. *Oxyrrhynchium hians*, specimen S: B301659. (A–B) Habit, (C) stem leaves, (D) branch leaves, (E) branch leaf apex, (F) alar cells, (G) mid-leaf lamina cells, stem leaf, (H) mid-leaf lamina cells, branch leaf, (I) axillary hairs.

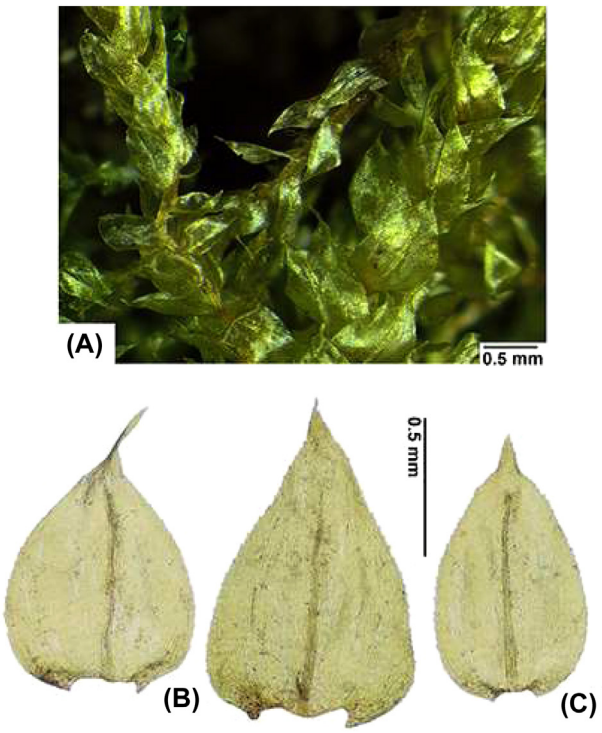

Figure 13. *Oxyrrhynchium hians*, specimen S: B304522. (A) Habit, (B) stem leaves, (C) branch leaf.

10–16 µm wide, basal cell pale brownish. Stem leaves cordate or broadly ovate, (0.9)1.0–1.3(1.4) mm long, 0.7–1.0 mm wide, (1.2)1.3–1.6 times as long as wide, strongly narrowed at insertion, concave, with set-off and often twisted acumen constituting 10–15(30)% of leaf length, apex acuminate, decurrent or long-decurrent; costa ending 55–80% way up leaf, (37.0)43.0–63.0(78.0) µm wide near base; margin denticulate, denticles (3.0)4.0–7.0(7.5) µm long; mid-leaf lamina cells (28.0)37.5–62.5(75.5) × (4.0)5.0–7.0(8.5) µm, (4.7)6.1–10.8(16.5) times as long as wide; basal cells shorter and wider than in mid-leaf, incrassate, porose or not; alar cells rectangular or shortly so, incrassate or strongly so, forming an ovate group along basal leaf margin or group transversely triangular. Branch leaves not complanate, broadly ovate, cordate-ovate, or oblong-ovate, 1.0–1.2 mm long, 0.6–0.8 mm wide, 1.4–1.8(2.0) times as long as wide, gradually or suddenly narrowed to broadly acuminate or acute apex; mid-leaf lamina cells (28.5)36.0–59.0(71.0) × (4.0)5.0–7.5(10.0) µm, (3.8)5.9–10.4(15.1) times as long as wide.

This is the on the average largest species of the three treated here, and well-developed plants are usually recognizable by their wide and distinctly concave leaves that are evenly arranged around stems and branches (Fig. 12A–B, 13A).

Oxyrrhynchium hians is widespread in coastal areas in southern Sweden and in a belt from southern Finland to southern Norway (Fig. 6B), and is otherwise widespread in Europe. In southern Scandinavia it seems not to occur in the central regions located at higher elevations. This species occurs mainly on soil, but also on rocks and rotten wood (Fig. 7B), primarily in nutrient-rich habitats.

Selected specimens studied: Denmark, E Jutland, Havskov, 2009, M. H. G. Gustafsson 913, S: B160305. Möen, Klintholm, 1914, O. Hagerup, S: B318027. Seeland, Allindelille, 1990, L. Hedenäs, S: B87515. Faroe Islands, Østerø/Eusturoy, 2014, T. Hallingbäck 47781, S: B306900. Finland, Varsinais-Suomi, Särkisalo, 1975, M. Ohenoja 15, S: B314908. Norway, Hordaland, Bömlö, 1967, E. Nyholm, S: B86644. Hordaland, Moster, 1967, G. Een, S: B81114. Norveg. merid., Sandefjord, 1890, E. Jörgensen, S: B314907. Sweden, Bohuslän, Uddevalla, 1899, P. Larsson, S: B314354. Dalsland, Edsleskog, 1920, P. A. Larsson, S: B314390. Gotland, Sundre, 2014, L. Hedenäs et al., S: B204958. Halland, Falkenberg, 1912, S. Svensson, S: B314351. Närke, Hidinge, 1968, N. Hakelier, S: B314392. Skåne, Lund, 1941, S. Waldheim, S: B230494. Småland, Jönköping, 1865, J. E. Zetterstedt, S: B315204. Uppland, Solna, 1889, H. Hamberg, S: B317379. Västergötland, Högstena, 1945, A. Hülphers, S: B314373. Öland, Mörbylånga, 1912, R. Sterner, S: B314983. Östergötland, Vreta kloster, 1889, N. C. Kindberg, S: B314375. Austria, Nieder-Österreich, Ebreichsdorf, 1948, J. Froehlich, S: B318225. France, Beaucaire, 1873, Boulay, S: B318216. Germany, Bärwalde, Bolgen, 1866, R. Ruthe, S: B318232. Flensburg, Clues-Ries, 1878, Prahl, S: B318244. Hungary, Comit. Abauj-Torna, Jósvafő, 1952, A. Boros, S: B196633. Comit. Pest. Ócsa, 1928, A. Boros, S: B318290. Italy, Emilia Romagna, San Lazzaro di Savena, 2021, M. H. G. Gustafsson 2821, S: B305684. Prov. Como, Nino, 1901, F. A. Artaria (Bauer, Musci Eur. Exs. 791), S: B318358. Sicily, Imtumetu, 1907, Zodda, S: B318362. Trentino-Alto Adige, Trento, 1898, T. Suse, S: B318222. Latvia, Livland, Riga, 1906–1909, J. Mikutowicz (Bryotheca Baltica 562a), S: B318281. Poland, Pogórze Slaskie Foothills, Goleszów, 2004, A. Stebel (Musci Macroreg. Merid. Poloniae exs. 1380), S: B99137. Russia, Adygeia Republic, Kamennomostskij, 1999, M. Ignatov, S: B114165. Switzerland, Kt. Uri, Erstfeld, 1990, I. Bisang 90004, S: B299399.

Oxyrrhynchium swartzii (Turner) Warnst (Fig. 14–17)

Krypt.-Fl. Brandenburg, Laubm. 784. 792 f. 4. 1905. ≡ *Hypnum swartzii* Turner, Muscol. Hibern. Spic. 151, pl. 14, f. 1. 1804. ≡ *Eurhynchium swartzii* (Turner) Curn., Bryoth. Eur. 12: 593. 1862. Type: 'Hb. Turner: *H. swartzii*, *H. atrovirens* Dicks., Dr. Swartz', right tuft [lectotype (Ignatov et al. 2005) in BM: 00725149 n.v.; isolectotypes in BM: 00725152 n.v.; S: B314451].

≡ *Hypnum praelongum* var. *atrovirens* Brid., Muscol. Recent. Suppl. 2: 104. 1812. [*Hypnum atrovirens* Dicks. ex Brid., Muscol. Recent. 2(2): 153. 1801, non *Hypnum praelongum* var. *atrovirens* Brid. = *Pseudoleskea incurvata* (Hedw.) Loeske]. Type: see *Hypnum swartzii* Turner (above).

= *Eurhynchium distans* Bryhn, Kongelige Norske Videnskabers Selskabs Skrifter 1892: 217. 1893. (Kongel. Norske Vidensk. Selsk. Skr. (Trondheim)); nom. nov. for *Hypnum distans* Lindb., Musci Scandinavici 34. 1879. (Musci Scand.) hom. illeg. (non *Hypnum distans* Brid.). Type: '*Hypnum distans* Lindb., c.fr., Finlandia, Helsingfors,

Hort. Botan., 11/6 1867, leg. S. O. Lindberg, Herb. S. O. Lindberg' (syntype in S: B317806). Additional syntypes likely exist in H-SOL (n.v.).

Note (1): the full label information of the S isolectotype of *Hypnum swartzii* Turner is more complete than for the BM lectotype (cf. Swartz 1798): 'Hypnum atrovirens dicksoni – dill. XLIII. F. 67, In horto ad Bergielund ad terram, [illeg.] Julio 1795' with later text additions: 'O. Swartz scripsit' and the even later 'Hypum Swartzii' plus 'J. E. Wikström scripsit'. Another specimen in herbarium Swartz in S (B76788) is a possible additional isolectotype of *H. swartzii* Turner, although the label information is too sparse for certainty ('*Hypnum atrovirens* S., Sw.'). This specimen looks very similar to the confirmed S isolectotype.

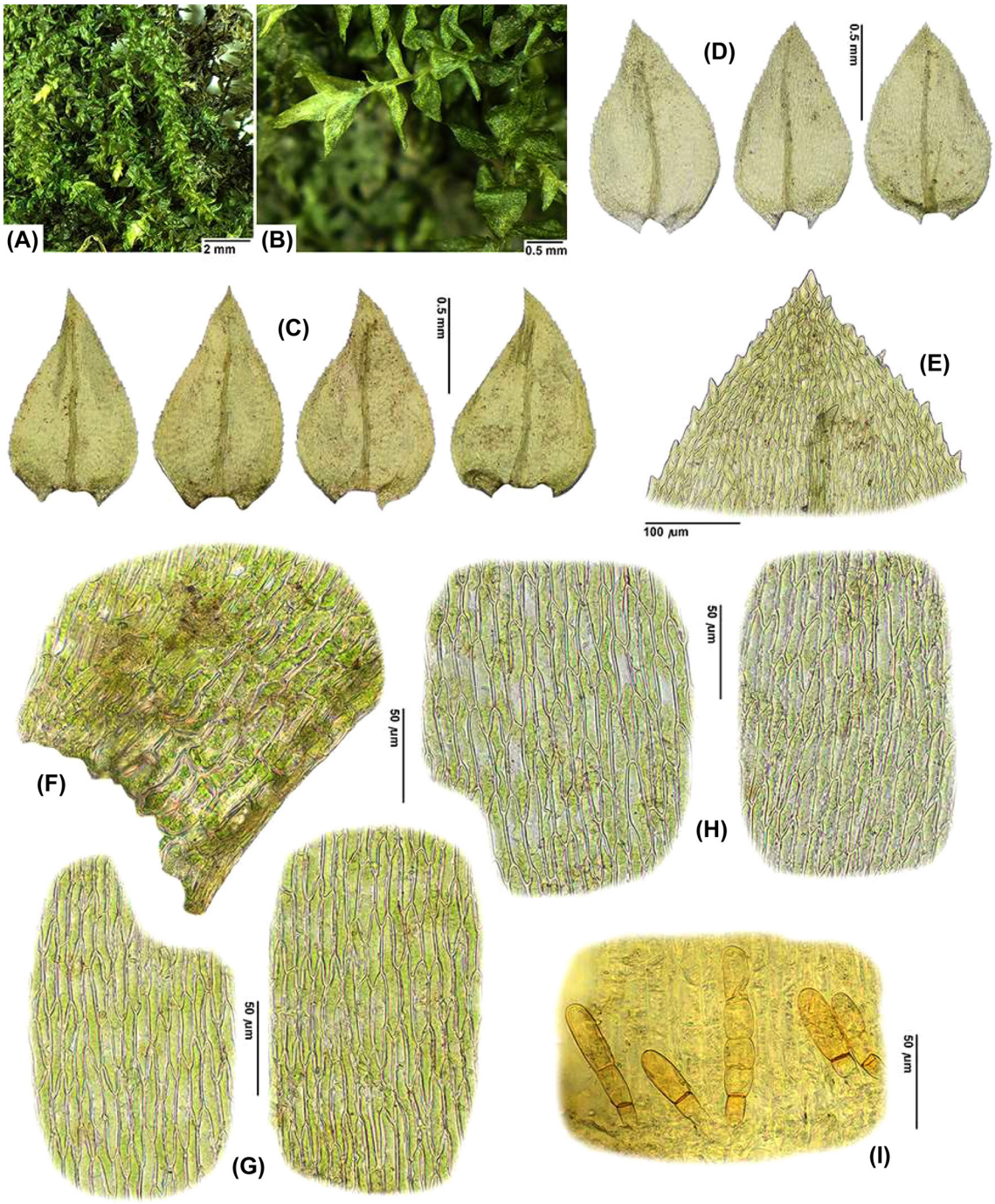

Figure 14. *Oxyrrhynchium swartzii*, lineage A, specimen S: B302787. (A–B) Habit, (C) stem leaves, (D) branch leaves, (E) branch leaf apex, (F) alar cells, (G) mid-leaf lamina cells, stem leaf, (H) mid-leaf lamina cells, branch leaf, (I) axillary hairs.

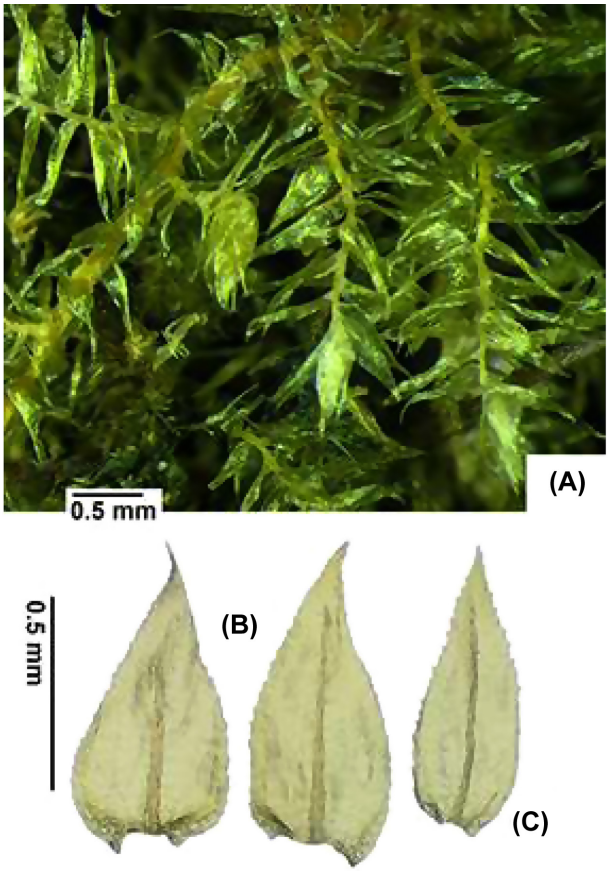

Figure 15. *Oxyrrhynchium swartzii*, lineage A, specimen S: B300154. (A) Habit, (B) stem leaves, (C) branch leaf.

Note (2): *Hypnum praelongum* var. *atrovirens* Brid. is a homotypic synonym of *Hypnum swartzii* at variety level, and may be the oldest variety level name of *Hypnum swartzii*.

Plants medium-sized, irregularly or irregularly pinnately branched. Stem with narrow central strand and a cortex of 1–3 layers of small and incrassate cells. Axillary hairs with 1–4 upper, shortly to longly rectangular, bulging, hyaline or pale brownish cells, 8–18 µm wide, basal cell pale brownish. Stem leaves ovate, broadly ovate, cordate-ovate, or cordate, 0.8–1.2(1.4) mm long, 0.4–0.8(0.9) mm wide, 1.3–2.3(2.5) times as long as wide, strongly or moderately narrowed at insertion, gradually narrowed upwards to acuminate apex or acumen slightly set off, plane or slightly concave, narrowly decurrent; costa ending 60–85% way up leaf, (31.0)33.0–62.0 µm wide near base; margin denticulate, denticles 3.0–8.5(9.5) µm long; mid-leaf lamina cells (23.0)34.5–72.0(101.5) × (3.0)5.0–8.0(11.0) µm, (3.1)5.3–12.1(22.8) times as long as wide; basal cells shorter and wider than in mid-leaf, incrassate, eporose; alar cells shortly rectangular to shortly linear, incrassate or slightly so, forming an ovate or shortly ovate group along basal leaf margin. Branch leaves complanate, sub-complanate, or evenly spreading, narrowly ovate, ovate, or oblong-ovate, 0.5–1.1(1.2) mm long, 0.3–0.5(0.7) mm wide, 1.6–2.9(3.0) times as long as wide, more suddenly narrowed to apex than stem leaves and acuminate, shortly acuminate, or narrowly acute; mid-leaf lamina cells (25.0)32.5–63.5(80.5) × (4.0)5.0–8.5(11.5) µm, (3.7)5.0–10.9(16.1) times as long as wide.

Oxyrrhynchium swartzii differs from *O. distichum* in its somewhat shorter and wider leaf lamina cells, in the somewhat longer costa, and in many cases by having its branch leaves evenly arranged around the branches. It differs from *O. hians* in its narrower and plane or almost plane leaves. In addition, specimens with complanate branches belong to *O. swartzii* rather than *O. hians*. *Oxyrrhynchium swartzii* includes two semi-cryptic species, of which A appears to have a more western distribution than B (Fig. 8) and is on the average slightly larger than the latter. However, there is great size overlap between the two semi-cryptic species, and they cannot be safely distinguished even by microscopic features.

Oxyrrhynchium swartzii is widespread in southern Finland and the southern half of Scandinavia, but its occurrences are scattered in the northern half of this area (Fig. 6C). It is otherwise widespread in Europe. This is the most common species in the *O. hians* complex in Europe. This species occurs predominantly on soil, but sometimes also on rocks (Fig. 7C), both in relatively nutrient-poor and nutrient-rich habitats.

Selected specimens studied: Denmark, Bornholm, Almindingen, 1886, E. Nyman, S: B318082. E Jutland, Århus, 2009, M. H. G. Gustafsson 921, S: B160313. Fyn, Lindeskov, 1898, A. Hansen, S: B318043. Mön, Klintholm, 1914, O. Hagerup, S: B87143. Själland, Allindelille Skov, 1880, C. Jensen, S: B318034. Faroe Islands, Bordö, Graverdal, 1896, C. Jensen, S: B318094. Finland, Åland, Sund, 1928, H. Möller, S: B317805. Nyland, Helsingfors, 1870, S. O. Lindberg (Brotherus, Musci Fenn. Exs. 93), S: B317799. Varsinais-Suomi, Parainen, 1974, M. Ohenoja IV, S: B317801. Norway, Hordaland, Os, 1968, N. Hakelier, S: B317744. Östfold, Fredrikstad, 1888, E. Ryan, S: B317757. Sör-Tröndelag, Trondhjem, 1890, I. Hagen, S: B317748. Vestfold, Sandefjord, 1890, E. Nyman, S: B317756. Sweden, Blekinge, Asarum, 1919, S. Medelius, S: B314977. Bohuslän, Klövedal, 1945, O. H. Selling, S: B315403. Dalarna, Garpenberg, 2011, L. Hedenäs et al., S: B186488. Dalsland, Edsleskog, 1920, P. A. Larsson, S: B316635. Gästrikland, Ovansjö, 2000, G. Odelvik, S: B45257. Gotland, St. Karlsö, 1943, H. Persson, S: B312924. Halland, Ölmevalla, 1984, T. Hallingbäck, S: B315314. Hälsingland, Hälsingtuna, 2009, M. H. G. Gustafsson 1091, S: B176106. Jämtland, Frösön, 1880, F. Lönnkvist, S: B317733. Medelpad, Borgsjö, 2006, L. Hedenäs, S: B115678. Närke, Längbro, 1931, S.Waldheim, S: B316978. Öland, Vickleby, 1920, C. Stenholm, S: B314982. Östergötland, Godegård, 2022, L. Hedenäs, S: B313525. Skåne, Gråmanstorp, 1916, S.Medelius, S: B230294. Småland, Gränna, 1913, A. Arvén, S: B315222. Södermanland, Grödinge, 1985, L. Hedenäs, S: B88650. Uppland, Djurö, 2021, L. Hedenäs & I. Bisang, S: B304178. Värmland, Filipstad, 1884, N. C. Kindberg, S: B316751. Västergötland, Fröjered, 1929, A. Hülphers, S: B315621. Västmanland, Viker, 1924, C. A. Tärnlund, S: B317063. Austria, Niederoesterreich, Wienerwald, 1951, J. Froehlich & H. Persson, S: B318214. Belgium, Prov.

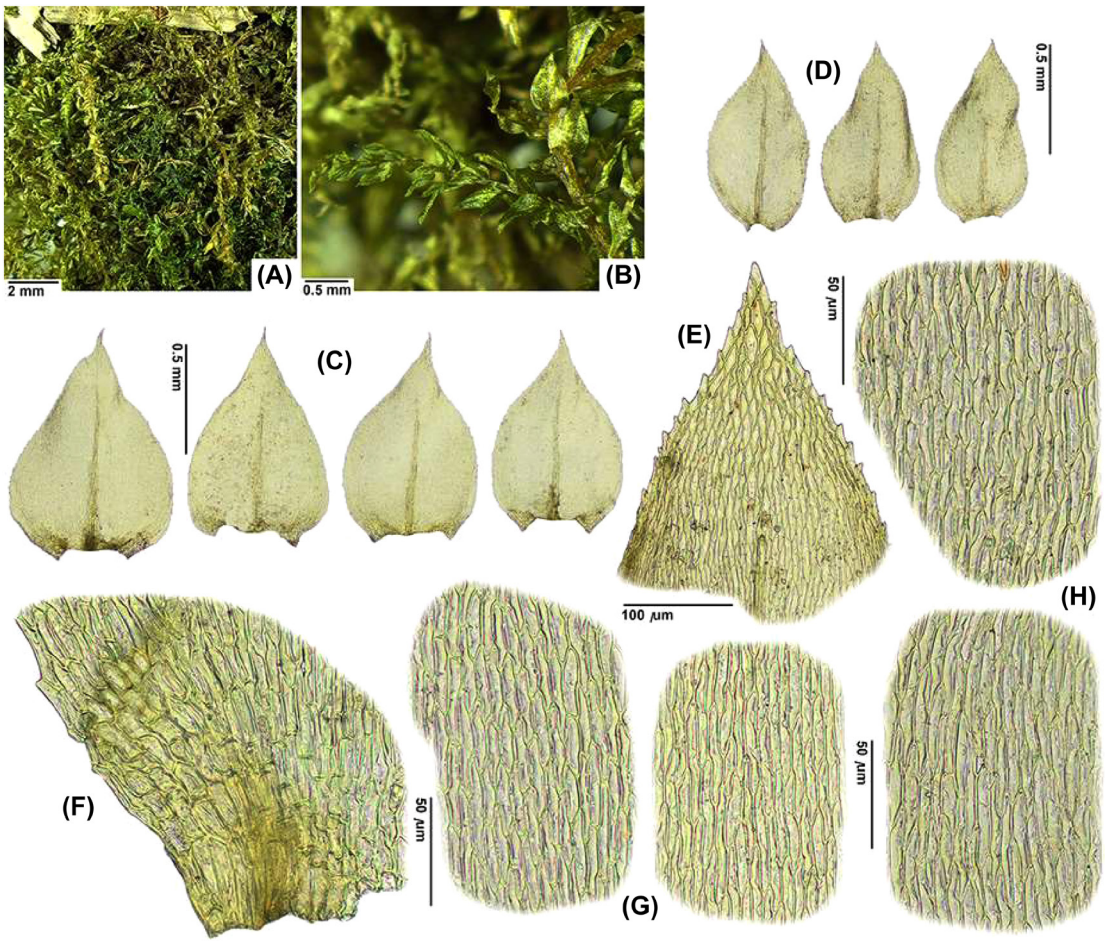

Figure 16. *Oxyrrhynchium swartzii*, lineage B, specimen S: B300149. (A–B) Habit, (C) stem leaves, (D) branch leaves, (E) branch leaf apex, (F) alar cells, (G) mid-leaf lamina cells, stem leaf, (H) mid-leaf lamina cells, branch leaf.

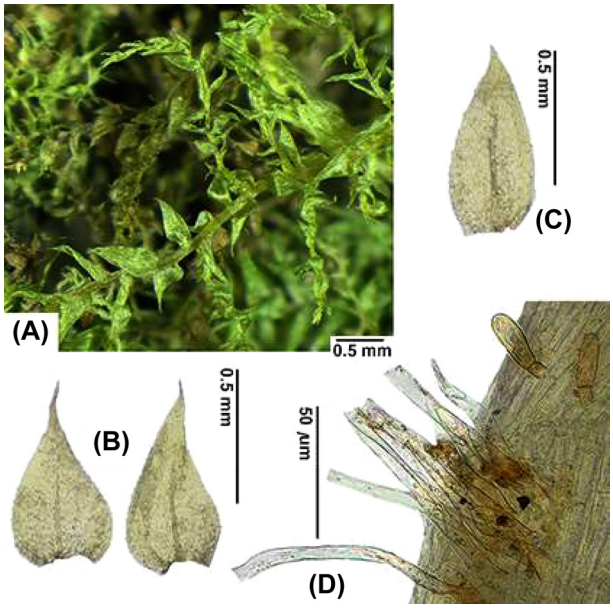

Figure 17. *Oxyrrhynchium swartzii*, lineage B, specimen S: B288146. (A) Habit, (B) stem leaves, (C) branch leaf, (D) portion of stem with rhizoids and axillary hairs.

Liège, Royseux, 1943, Demaret 3989, S: B318220. Croatia, Dalmatien, Zara, 1913, J. Baumgartner, S: B318315. Istrien: Galizana, 1889, Glowacki, S: B318224. Czech Republic, Bohemia, Beroun, 1962, J. Vana, S: B199914. Moravia, Dèvicky nad Dol. Vistonicemi, 1920, J. Podpera, S: B318319. Estonia, Haapsalu, Puhtu, 1989, L. Hedenäs E-7, S: B318288. France, Corte, Haure-Corse, 1993, I. Bisang 93087a, S: B302185. Savoie: Mont Cenis, 1965, G. Een, S: B64030. Germany, Baden-Württemberg, Heidelberg, 1855, N. C. Kindberg, S: B318229. Bayern, Hohengebraching, 1904, J. Familler (Krypt. Germ., Austr. Helv. Exs. 365), S: B318228. Greece, Crete, Distr. Selinos, 1943, G. Bickerich 15037, S: B318368. Laconia, Sparti, 1964, K. H. Rechinger 26347, S: B318369. Hungary, Budapest, Csepel, 1892, Förster, S: B318318. Zemplén Mts, Füzer, 2005, L. Hedenäs, S: B104432. Italy, Como, Valle di S. Martino, 1899, F. A. Artaria, S: B318348. Emilia Romagna, San Lazzaro di Savena, 2021, M. H. G. Gustafsson 2800, S: B305683. Marche, Parco S Bartolo, 2014, M. H. G. Gustafsson 2071, S: B208435. Trentino-Alto Adige, Trento, 1898, T. Suse, S: B318223. Latvia, Césis, old castle ruin, 1989, L. Hedenäs L-20, S: B318286. Moldova, Nicoliza (Jassy), 1923, C. Papp, S: B318320. Netherlands, Prov.

Gelderland, Arnhem, 1979, P. Sollman, S: B318219. Zuid-Holland, Bergambacht, 1990, L. Hedenäs, S: B199921. Poland, Western Carpathians, Pogórze Wielickie Foothills, 2002, K. Jedrezejko & E. Walusiak (Musci Macroreg. Merid. Polon. exs. 1119), S: B110106. Romania, Langental, Sibenbürgen, 1871, J. Barth, S: B318317. Russia, Moscow, Park Fili-Kuntzevo, 1990, E. A. Ignatova & M. S. Ignatov, S: B318325. Pskovskaya oblast, Pushkinskie Gory, 2005, O. M. Afonina, S: B200176. Serbia, prope Sv. Petka ad Nis, 1910, J. Podpera, S: B318321. Slovakia, Gau Kaschau, Snina, 1925, E. Bauer, S: B318322. Spain, Catalogne, Hostalets, 1905, Héribaud, S: B318350. Süd-Spanien, Alhambra, 1873, R. Fritze, S: B318352. Switzerland, Kt. Graubünden, Lugnez, 1982, I. Bisang 82395, S: B302179. Ct. Neuchatel, Val-de-Travers, 2017, L. Hedenäs, S: B263222. Ct. Valais, Monthey, 2022, L. Hedenäs, S: B316388. Cte. Ticino, Locarno, 1985, I. Bisang 85037, S: B302183. Kt. Luzern, Kottwil, 1982, I. Bisang 8272, S: B302181. Kt. St. Gallen, Alt St. Johann, 2006, L. Hedenäs, S: B116646. United Kingdom, England, Shropshire, 2008, L. Hedenäs, S: B144766. Scotland, Clyde, 1950, A. C. Crundwell, S: B318096.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d2547d88m (Hedenäs 2024).

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