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Studies on *Schistidium* (Grimmiaceae, Bryophyta) in Europe, with particular reference to the Alps: II. Description of two new species *S. pratense* and *S. heribertii*

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Abstract

Schistidium pratense and *S. heribertii*, two distinctive and locally abundant components of the Alpine flora, are here formally described as new species from Europe. Although recognised for over two decades, their official taxonomic treatment has been long overdue. This paper provides an integrative account, combining morphological and molecular evidence, outlining their currently known distribution, and discussing their relationships to related species. *Schistidium pratense* is closely allied to *S. dupretii* in both molecular and morphological traits but differs in its larger overall size, including longer shoots and leaves, as well as in the absence of stomata. *Schistidium heribertii* resembles *S. atrofuscum* in its black coloration but is distinguished by its prominent leaf hairpoints and a pruinose appearance on the upper parts of the shoots. Molecular analyses place *S. heribertii* as the sister species to the clade comprising *S. atrofuscum* and *S. helveticum*. Both new species share similar ecological preferences, typically colonising calcareous substrates. *Schistidium pratense* is widespread and locally abundant in subalpine pastures, while *S. heribertii* has a more scattered distribution and predominantly inhabits warm sites across a broad elevational range in valleys with a continental climate. To date, *S. heribertii* is known only from the Alps, whereas *S. pratense* has also been recorded in Scandinavia, the Dinarides, the Apennines and the Black Forest in Germany.

Key words: calciphyte, ITS, mountain mosses, Musci, phylogeography, phylogeny, saxicole, taxonomy

Introduction

In a previous paper, Blom *et al.* (2016) briefly reviewed the state of knowledge of the genus *Schistidium* Bruch & Schimper (in Bruch, Schimper & Gümbel 1845: 99) in Europe with particular attention to taxa added to the European flora since the publication of Blom's (1996) monograph. Since then, no fewer than six species have been added to the European *Schistidium* flora, namely *S. tenuinerve* Ignatova & H.H.Blom (Ignatova *et al.* 2010: 220; Ignatova & Kozhin in Ellis *et al.* 2016), *S. succulentum* Ignatova & H.H.Blom (Ignatova *et al.* 2010: 216; Kiebacher 2020), and the recently described *S. convergens* J.Guerra & M.J.Cano (Guerra *et al.* 2019: 72), *S. memnonium* J.Guerra (Guerra *et al.* 2020: 570), *S. foraminis-martini* Kiebacher, Köckinger & H.H.Blom (2021: 3) and *S. mammillosum* Kiebacher, A.Hodgson & H.H.Blom (Kiebacher *et al.* 2024: 39). Clearly, our understanding of *Schistidium* diversity in Europe remains incomplete, even in well-studied regions such as the Alps in its continental part. Continued research is likely to uncover additional species within the flora.

Prior to the taxonomic revisions by Blom (1996, 1998), the broadly defined and highly variable *Schistidium apocarpum* (Hedwig 1801: 76) Bruch & Schimper (in Bruch, Schimper & Gümbel 1845: 99), along with a few other distinct species such as *S. atrofuscum* (Schimper 1876: 240) Limpricht (1889: 713) and *S. flaccidum* (De Notaris 1836:

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254) Ochyra (1989: 94), were generally accepted as part of the prevailing taxonomy established in the authoritative work *Bryologia europaea* (Bruch *et al.* 1845). This taxonomic tradition led to an overrepresentation of common species in herbaria, while rarer taxa were underrepresented—unlike in genera with more resolved taxonomies, where collection efforts typically focus on rare or conservation-priority species. As a result, some rare and still undescribed European species of *Schistidium* may be poorly represented in major herbaria, if present at all. Additions to the European *Schistidium* flora are most likely to be found among rare taxa, species confined to hard-to-access areas such as high alpine regions, or taxa that closely resemble well-known species. Moreover, new discoveries are more likely to result from dedicated field investigations focusing on *Schistidium*, rather than from herbarium-based studies. Such targeted fieldwork has been carried out by Heribert Köckinger (Weißkirchen, Austria) in various parts of the Austrian Alps. His collections have been invaluable for advancing our understanding of the taxonomy of this challenging genus (Blom *et al.* 2016, Kiebacher *et al.* 2021).

The greatest diversity of *Schistidium* species is found in mountainous regions, with most recent additions to the European *Schistidium* flora occurring in the Alps (Blom *et al*. 2016, Kiebacher *et al.* 2020, 2024). Among the alpine *Schistidium* species of Central Europe, there is a distinct ecological separation between those that prefer siliceous rocks and those that grow on calcareous substrates. In this paper, we formally describe two new species that inhabit calcareous rocks and are both widespread in the Alps. Their previous misidentification or oversight is likely due to a combination of the earlier conservative species concepts in *Schistidium* and their strong overall resemblance to well-known species. Furthermore, these species are largely confined to alpine and subalpine habitats—regions that are generally less explored than lowland areas—and one of them appears to be relatively rare. Notably, conservative species concepts framed the understanding of the diversity of the genus for a very long time. Until the mid-1990s, when Hans Blom published his taxonomic revisions for Scandinavia, incorporating numerous collections from continental Europe, Asia, and North America (Blom 1996, 1998), no more than 7–8 species of *Schistidium* were generally accepted to occur in Europe (Corley *et al.* 1981; Düll 1984). This concept was essentially an inherited legacy of Bruch and Schimper's (1845) treatment of this genus in *Bryologia europaea*, which for over a century and a half served as an authoritative source for the taxonomy of European and, more broadly, Holarctic mosses.

Since the examination of Central European specimens by the first author in the 1990s, both species have been mentioned in the literature, making their formal description thus long overdue. Blom (1997) reported *Schistidium pratense* as taxon 'C', reporting it from two locations in the Swiss Alps and analysing its elevational range in the Göschener Valley, canton of Uri (Blom *op. cit*. Table 1). As a provisional name, Köckinger *et al*. (2008) mapped the distribution of *S. pratense* in Carinthia, Austria, and provided brief notes on its ecology and morphology. Subsequent records include reports from the Austrian province of Vorarlberg (Amann *et al.* 2013, Schröck *et al*. 2013) and distribution mapped in the province of Upper Austria (Oberösterreich; Schlüsslmayr & Schröck 2013). The species was also illustrated—though still undescribed—in the photographic atlas of European mosses (Lüth 2019, p. 256).

Schistidium heribertii was first recorded from a single locality in the canton of Valais, Switzerland (Blom & DeZuttere 2002). Its distribution in Carinthia, Austria—where it was referred to as *S. atrofuscum* "haartragende Sippe"—was mapped by Köckinger *et al*. (2008: 229), who also included a brief note on its ecology and its morphological distinctions from *S. atrofuscum* in this region. Detailed morphological and anatomical characteristics of the species were later illustrated in the photographic Flora of European mosses (Lüth 2019, p. 245).

Material and Methods

This study is primarily based on specimens loaned to the first author from several herbaria (see Acknowledgements), with particular emphasis on collections by Heribert Köckinger and those gathered by Thomas Kiebacher from various regions of the Alps. The material was examined and described using standard anatomical and morphological methods employed in the study of Grimmiaceae (Frisvoll 1983, 1988, Blom 1996, Bednarek-Ochyra 1995, 2006). Microscopic examinations and measurements were conducted using a Zeiss light microscope, focusing on mature leaves located just below the perichaetial leaves. Illustrations were made with the aid of a Nikon drawing tube, initially rendered in pencil, then inked and assembled into plates.

Data sets for phylogenetic inference. To investigate the phylogenetic relationships between the two taxa, we targeted the nuclear ITS region, the most commonly used molecular marker in the genus *Schistidium* (e.g., Ignatova *et al.* 2010, Kiebacher *et al.* 2021, Kiebacher & Blom 2024). We first generated ITS sequences for four specimens of *S. heribertii*—one each from Austria and Italy, and two from Switzerland—and for three specimens of *S. pratense*, representing Austria, Italy, and Switzerland (Tables 1–2).

To identify closely related taxa for inclusion in the phylogenetic analysis, we performed standard nucleotide BLAST searches using one ITS sequence from each of the two focal taxa against the NCBI database (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Both BLAST results and morphological comparisons indicated that *S. heribertii* and *S. pratense* are distantly related. Consequently, we compiled two separate datasets to ensure accurate alignments and allow inference of phylogenetic relationships at a low taxonomic rank. For the *S. heribertii* dataset, we sequenced samples of *S. atrofuscum*, *S. crassipilum* H.H.Blom (1996: 224), *S. elegantulum* H.H.Blom subsp. *elegantulum* (1996: 233) and *S. helveticum* (Schkuhr 1811: 48) Deguchi (1979: 434). We also included two accessions of *S. papillosum* Culm. (1918: 386) retrieved from GenBank as outgroup taxon (Table 1). For the *S. pratense* dataset, we sequenced samples of *S. dupretii* (Thériot 1907: 63) W.A.Weber (1976: 106) and *S. robustum* (Nees von Esenbeck & Hornschuch 1827: 123) H.H.Blom (1996: 149). Additional accessions retrieved from GenBank included *S. foraminis-martini*, *S. memnonium*, *S. submuticum* subsp. *arcticum* H.H.Blom (1996: 255), *S. tenuinerve*, and *S. frigidum* H.H.Blom (1996: 181) as outgroup taxon (Table 2).

Laboratory protocols. Genomic DNA was extracted from dried plant material using the NucleoSpin Plant II Mini kit (Macherey-Nagel, Germany). The nuclear ITS region—comprising partial sequence of the 18S rRNA gene, ITS1, 5.8S rRNA gene, ITS2, and a partial sequence of the 26S rRNA gene—was amplified using external and internal primers as described by Kiebacher *et al.* (2024). The reagents, volumes, and thermal cycling conditions for the PCR reaction were according to Kiebacher *et al.* (2024).

TABLE 1. Specimens used to infer the phylogenetic relationships of *Schistidium pratense*, including GenBank accession numbers of ITS sequence data.

Taxon	Country	Voucher Information	Isolate and Sample ID	GenBank Acc.No.
S. dupretii	Italy	Cuneo, Pontechianale, Chianale, Col de St. Veran, 14.VII.2021, *T. Kiebacher 3015* (STU-BR-0070088)	I0159-TK3015	PV455462
S. dupretii	Italy	Südtirol, Mühlbach/Vintl, Vals, am Südhang der Wurmaulspitze, 07.X.2016, *T. Kiebacher 1293* (STU-BR-0070086)	I0543-TK1293	PV455463
S. dupretii	Italy	Südtirol, Mühlbach, Vals, along path between Fane Alm and Brixner Hütte, 01.X.2019, *T. Kiebacher* 2360 (STU-BR-0070087)	I0111-TK2360	PV455464
S. dupretii	Switzerland	Obwalden, Engelberg, Mt. Titlis, W-ridge, 03.IX.2021, *T. Kiebacher 4162* (STU-BR-0070089)	I0346-TK4162	PV455465
S. pratense	Austria	see below (STU-BR-0070101)	I0470-TK1891	PV455466
S. pratense	Italy	see below (STU-BR-0070103)	I0472-TK3073	PV455467
S. pratense	Switzerland	see below (STU-BR-0070102)	I0471-TK2614	PV455468
S. robustum	Austria	Osttirol, Prägraten, between Hinterbichl and Johannishütte, 03.VIII.2024, *T. Kiebacher 4932* (STU-BR-0070110)	I0578-TK4932	PV455469
S. robustum	Italy	Südtirol, Mühlbach, Vals, along path between Vane Alm and Brixner Hütte, 01.X.2019, *T. Kiebacher 2359* (STU-BR-0070106)	I0579-TK2359	PV455470
S. robustum	Italy	Südtirol, Tramin, Summit area of Mt. Roen, E-facing rock outcrops just below the summit, 07.X.2020, *T. Kiebacher 2725* (STU-BR-0070108)	I0439-TK2725	PV455471
S. robustum	Switzerland	Glarus, Glarus-Süd, am Segnespass (Kantonsgrenze), 05.VII.2018, *T. Kiebacher 2045* (STU-BR-0070104)	I0033-TK2045	PV455472
S. robustum	Switzerland	Graubünden, Silvaplana, Julierpass. Ca. 200 m W Fuorcla Alva, 15.VIII.2018, *T. Kiebacher 2075* (STU-BR-0070105)	I0034-TK2075	PV455473
S. robustum	Switzerland	Grisons, Trun, Nadels Davon, 06.VII.2023, *T. Kiebacher 4223* (STU-BR-0070109)	I0347-TK4223	PV455474
S. robustum	Switzerland	Solothurn, Selzach, Ridge between Stallflue and Wandflue, 10.V.2020, *T. Kiebacher 2562* (STU-BR-0070107)	I0440-TK2562	PV455475

TABLE 2. Specimens used to infer the phylogenetic relationships of *Schistidium heribertii*, including GenBank accession numbers of ITS sequence data.

Taxon	Country	Voucher Information	Isolate and sample ID	GenBank Acc.No.
S. atrofuscum	Austria	Osttirol, Prägraten, W facing slope above Johannishütte, 05.VIII.2024, *T. Kiebacher 4967* (STU-BR-0070079)	I0537-TK4967	PV455476
S. atrofuscum	Norway	Vestland, Luster, W of Jærgolagjelet, Engjadalen, Gaupne , 10.VII.2017, *H. Blom s.n.* (TRH B-35609)	I0225-TK3399	PV455477
S. atrofuscum	Switzerland	Uri, Attinghausen, Hermisalp, 24.VIII.2017, *T. Kiebacher 1657* (STU-BR-0070077)	I0207-TK1657	PV455478
S. crassipilum	Austria	Styria, Haselbach, Raabklamm, 01.VII.2022, *T. Kiebacher 3468* (STU-BR-0070081)	I0541-TK3468	PV455479
S. crassipilum	Great Britain	East Midlands, Derbyshire, above High Peak Quarry, Longcliffe, 29.VIII.2024*, A. Hodgson 16/981 & T. Blockeel* (STU-BR-0070084)	I0590-TK5026	PV455480
S. crassipilum	Great Britain	East Midlands, Derbyshire, above High Peak Quarry, Longcliffe, 29.VIII.2024, *A. Hodgson 16/982 & T. Blockeel* (STU-BR-0070085)	I0588-TK5028	PV455481
S. crassipilum	Italy	Friuli-Venezia Giulia, Pordenone, Polcenigo, Parco San Floriano, 19.V.2024, *T. Kiebacher 4602* (STU-BR-0070083)	I0584-TK4602	PV455482
S. crassipilum	Spain	Islas Baleares, Mallorca, 18.X.2023, *T. Kiebacher 4340* (STU-BR-0070082)	I0371-TK4340	PV455483
S. crassipilum	Switzerland	Bern, Lenk, am Weg vom Talschluss zu den Siebe Brünne, 13.V.2017, *T. Kiebacher 1746* (STU-BR-0070080)	I0542-TK1746	PV455484
S. elegantulum subsp. *elegantulum*	Austria	Tirol, Wilder Kaiser, X.2010, *T. Kiebacher 120* (STU-BR-0070090)	I0580-TK120	PV455485
S. elegantulum subsp. *elegantulum*	Italy	Friuli-Venezia Giulia, Pordenone, Polcenigo, Parco San Floriano, 24.III.2019, *T. Kiebacher 2013* (STU-BR-0070091)	I0022-TK2013	PV455486
S. elegantulum subsp. *elegantulum*	Norway	Hordaland, Tysnes, 24.V.2019, *T. Kiebacher 2093* (STU-BR-0070093)	I0021-TK2093	PV455487
S. elegantulum subsp. *elegantulum*	Switzerland	St. Gallen, Walenstadt, am Wanderweg zwischen Walenstadt und Quinten, 06.IV.2019, *T. Kiebacher 2038* (STU-BR-0070092)	I0023-TK2038	PV455488
S. helveticum	Greece	Achaia, Nordpeloponnes, nordwestl. des Chelmosmassivs, Strasse Egio Kalavriton (von Aigio nach Kalavrita), 02.III.2020, *F. Roloff s.n.* (STU-BR-0070095)	I0398-TK3034	PV455489
S. helveticum	Switzerland	Solothurn, Bettlach, Ca. 250m E of ruin Grenchen, 10.V.2020, *T. Kiebacher 2566* (STU-BR-0070094)	I0397-TK2566	PV455490
S. helveticum	Switzerland	Valais, Niedergesteln, Along path between Hohtenn and Ausserberg, Lüegilchi, 09.V.2021, *T. Kiebacher 3043* (STU-BR-0070096)	I0399-TK3043	PV455491
S. heribertii	Austria	see below (STU-BR-0070097)	I0314-TK1022	PV455492
S. heribertii	Italy	see below (STU-BR-0070098)	I0315-TK1941	PV455493
S. heribertii	Switzerland	see below (STU-BR-0070100)	I0317-TK3347	PV455494
S. heribertii	Switzerland	see below (STU-BR-0070099)	I0316-TK2998	PV455495

Alignment and phylogenetic analyses. Raw sequences were edited using GeneStudio v2.2.0.0. (available at www.genestudio.com). Edited sequences were aligned using the E-INS-i strategy in the online interface of MAFFT v7.511 (Katoh & Standley 2013), followed by manual refinement. Indels were scored using the simple coding method (Simmons & Ochoterena 2000) and phylogenetic analyses were conducted using Bayesian inference (BI) implemented in MrBayes v3.2.6 (Ronquist *et al.* 2012) and maximum likelihood (ML) in RAxML v8.2.4 (Stamatakis 2014).

For the BI analysis, we applied the GTR+G+I substitution model, with a sampling frequency of 100 and default settings for all other parameters. Convergence between the two runs was assessed in Tracer v1.6.0 (Rambaut *et al.* 2013), ensuring that all effective sample size (ESS) values exceeded 200. A 50% majority-rule consensus tree was generated after discarding the first 25% of trees as burn-in in MrBayes. For ML analysis, we also used the GTR+G+I model and conducted 50 independent ML runs. Node support was evaluated using the thorough bootstrapping algorithm, applying extended majority-rule bootstopping criterion. Support values from both BI and ML analyses were summarised using TreeGraph 2 (Stöver and Müller 2010), with the BI topology used as the reference tree.

Results

The alignments used to analyse the phylogenetic relationships of *Schistidium pratense* and *S. heribertii* spanned 889 and 954 nucleotide positions, respectively, and included 107 and 90 variable sites, and 96 and 86 parsimony-informative sites. *Schistidium pratense* was grouped with strong support (posterior probability = 1; bootstrap support = 99) alongside accessions of *S. dupretii* (Fig. 1) in a clade that is sister to *S. robustum*. Within this clade, accessions of *S. dupretii* formed a moderately supported subgroup (0.74; 82), while accessions of *S. pratense* clustered with low support (0.57) in BI and appeared unresolved at the base of the *S. dupretii* clade in the ML analysis. Accessions of *S. heribertii* formed a strongly supported clade (0.99; 98), which was sister to a clade containing *S. atrofuscum* and *S. helveticum* (Fig. 2). The results of the morphological analysis are presented in the taxonomy section.

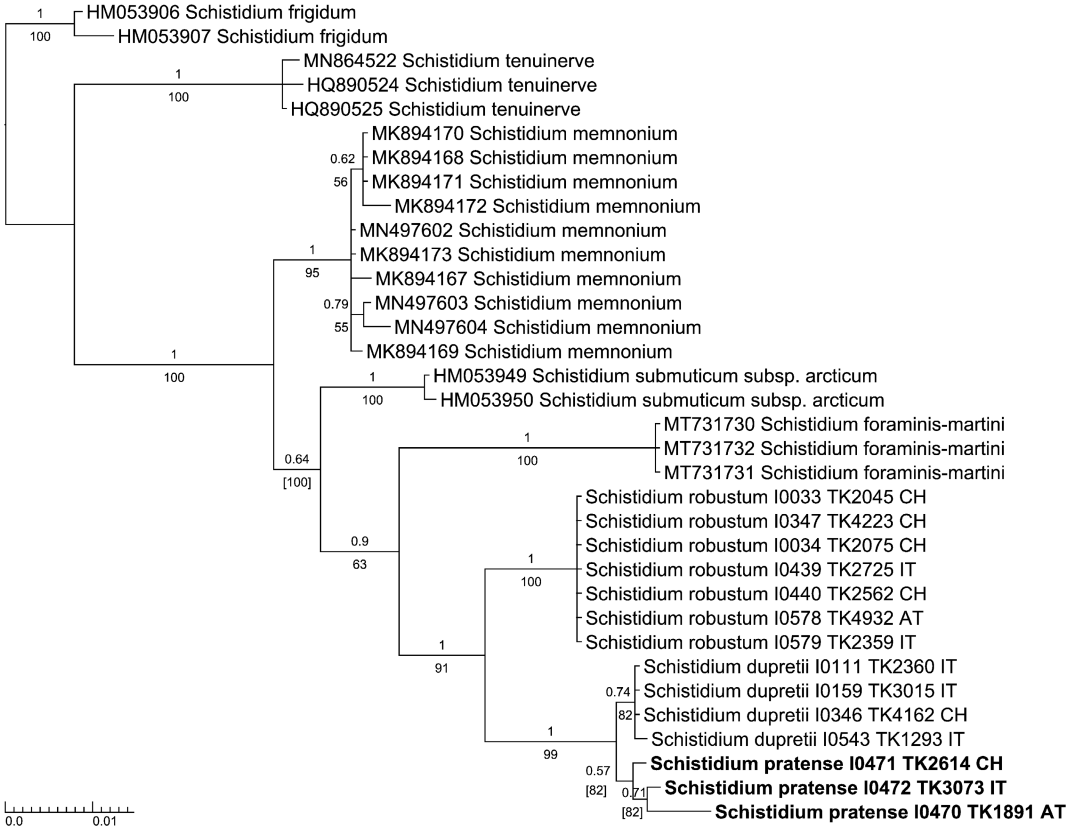

FIGURE 1. Bayesian inference (50% majority rule consensus tree) on the nuclear ITS region of *S. pratense* and taxa identified as similar to it in a BLAST search. Numbers above branches are posterior probabilities, numbers below branches are bootstrap support values ≥ 50 obtained from maximum likelihood analysis of the same dataset. *Schistidium pratense* is highlighted in bold. Newly generated sequences are followed by isolate (I) and sample (TK) IDs and ISO country codes (Table 2). Accessions retrieved from GenBank are preceded by the accession number.

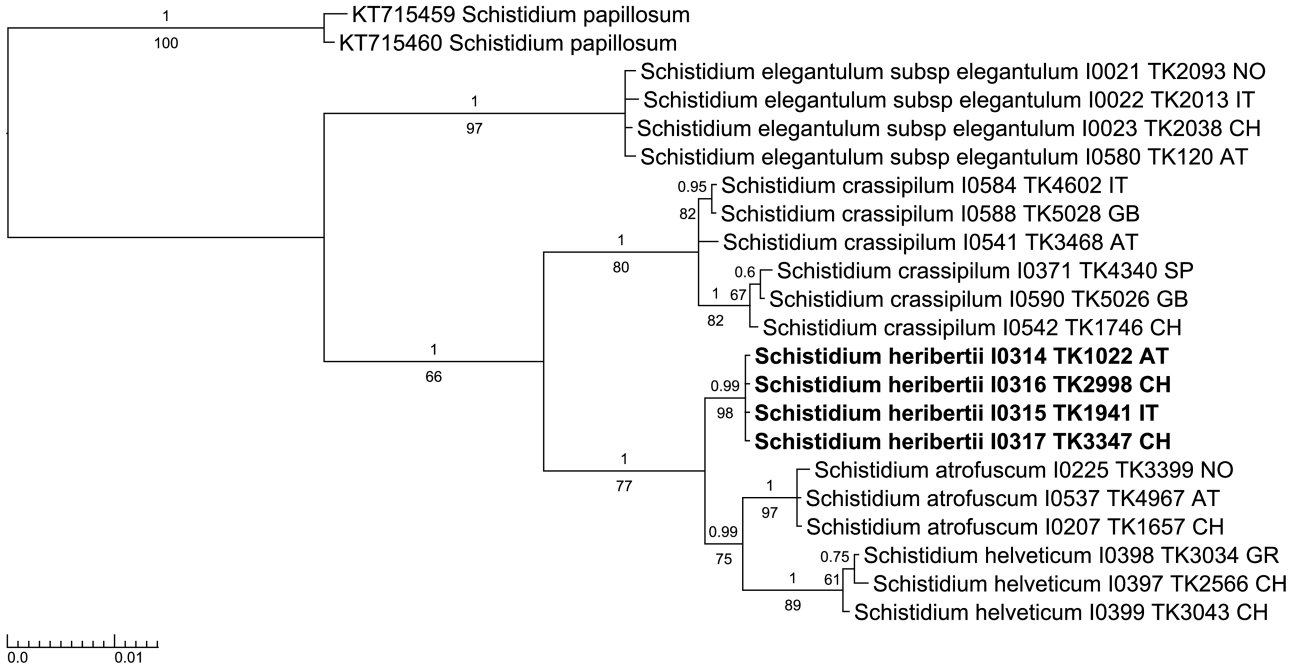

FIGURE 2. Bayesian inference (50% majority rule consensus tree) on the nuclear ITS region of *Schistidium heribertii* and taxa identified as similar to it in a BLAST search. Numbers above branches are posterior probabilities, numbers below branches are bootstrap support values ≥ 50 obtained from maximum likelihood analysis of the same dataset. *Schistidium heribertii* is highlighted in bold. Newly generated sequences are followed by isolate (I) and sample (TK) IDs and ISO country codes (Table 1). Accessions retrieved from GenBank are preceded by the accession number.

Taxonomic Treatment

Schistidium pratense H.H.Blom, Kiebacher, Bedn.-Ochyra & Ochyra *sp. nov.* Figs 3–5

Diagnosis:—*Species haec* Schistidio dupretii *similis sed statura majore*, *foliis nitidis*, *stomatibus nullis et sporis majoribus facillime dignoscenda*.

Type:—AUSTRIA. Kärnten: Karawanken, Mt. Hochobir, [lat. 46°32′22″N, long. 14°29′14″E], S-side, Simon-Rieger-Steig, ca. 1700 m s.m.; sunny limestone boulders on a pasture, soc. *Tortula ruralis*, *T. norvegica*, *Pseudoleskea inc.*, *Pseudoleskeella catenulata*, *Tortella bambergeri*, *T. tortuosa*, *Orthotr. anomalum*, 25.5.1999, Qu.: 9552/2, leg. & det. *Köckinger* Nr.: *99-331* (Holotype TRH 126522, isotype KRAM B-283071).

Plants medium-sized, glossy or occasionally dull, olivaceous, brownish or dark green, brownish or, more rarely blackish in the lower parts, forming loose or dense, sometimes extensive tufts. *Stem* 1.0–4.5 cm, intricately branched; epidermis of 2–3 rows of small, thick-walled cells; cortical cells with slightly thickened walls; central strand usually large and distinct. *Leaves* ovate-lanceolate to ovate-triangular, acute to acuminate, tapering into a fine point, sharply keeled, (1.8–)2.0–2.7 × 0.5–0.8 mm. *Hairpoint* usually short but rarely absent on all leaves, to 0.3 mm long, narrow, thin, ± terete, straight or slightly irregularly bent, not or rarely shortly decurrent, weakly denticulate with only slightly protruding spinulae, often brownish at base. *Costa* smooth or very rarely with a few papillae near apex, ending below apex to percurrent, often indistinctly delimited towards apex, dorsally convex and hemispherical to subrectangular in transverse section, in upper and central parts 42–73 µm wide and 3–4-stratose, in lower part 57–78 µm wide and 4-stratose, narrower in basal part. *Margins* often plane on one or both sides in basal part, strongly recurved to revolute in lower ¾–⅘ leaf length; in upper part bistratose for 1(–2) rows, in central part bistratose for 1 row or unistratose, unistratose in lower parts. *Lamina* smooth, unistratose with bistratose strips or patches in upper and central parts. *Laminal cells* smooth, moderately thick-walled, in upper part from transversely ovate to shortly oblong with orange walls, mostly esinuose, 8–11 µm wide, in central and lower parts shortly oblong to rectangular, slightly to distinctly sinuose, 10–13 µm wide and up to 15–26 µm long; *basal cells* rectangular with yellowish walls, 11–14 µm wide and up to 26–55 µm long; *basal marginal cells* chlorophyllose, square or shortly rectangular to transversely rectangular. *Perichaetial leaves* erect to erecto-patent, ovate-lanceolate to narrowly elliptical, sometimes with shoulders, acuminate,

2.9–3.4 × 0.8–1.0 mm. Margins recurved in upper ⅓–⅔(–¾) leaf length. *Hairpoint* as in vegetative leaves but sometimes reflexed, to 0.8 mm long, and, from not decurrent to long decurrent. *Calyptra* narrow, cucullate.

Monoicous. *Sporophytes* present in all studied specimens, abundant, immersed. *Seta* narrow**,** of same colour as urn**,** 0.2–0.5(–0.7) mm. *Urn* slightly glossy, yellow-brown to reddish-brown, obloid-cylindrical, abruptly or broadly conically narrowed to the seta, becoming striated or shallowly furrowed soon after dehiscence, 0.7–1.2(–1.7) × 0.5–0.6(–0.7) mm; length/width ratio 1.4–2.1(–2.5). *Exothecial cells* predominantly oblong with curved, unevenly thickened longitudinal walls. *Stomata* absent. *Peristome teeth* 270–370 µm long, dark red, squarrose, becoming revolute when old, ± straight but twisted half-way around the axis, tapering to a fine point, entire or with few narrow slits, smooth in basal part, above distantly to densely and coarsely papillose with decumbent comb-like or knob-like papillae arranged in ± distinct horizontal to oblique rows. *Columella* long and narrow, permanently attached to the conic-convex operculum with an erect or oblique, straight rostrum, 0.22–0.28 mm long. *Spores* greenish or brownish, almost smooth, (10–)11–15(–16) µm.

Etymology:—The epithet refers to its most common and characteristic habitat: subalpine and low alpine meadows.

Relationships and differentiation:—The species belongs to *Schistidium* sect. *Robusta* Ochyra (2003: 132), based on several diagnostic features, including strongly recurved leaf margins in the upper part of the leaf, obloid-cylindrical urns with curved and unevenly thickened exothecial cell walls, and nearly straight peristome teeth that become squarrose shortly after dehiscence. Its placement within sect. *Robusta* is supported by nrITS region analyses (Fig. 1), where it clusters in a clade that also includes *S. dupretii*, which is sister to a clade containing *S. robustum.* Despite several clear and consistent morphological traits that distinguish *S. pratense* from *S. dupretii* (see below), the molecular differentiation between them is surprisingly low. One possible explanation is a relatively recent divergence. It is plausible that *S. pratense* evolved from *S. dupretii* during the Holocene, potentially in response to human activities that created or expanded open pastures in the subalpine zone—habitats where the species is most abundant today. Under natural conditions, these areas would mostly be forested, offering very limited opportunities for *Schistidium* species to establish due to low light levels within closed stands.

Schistidium pratense is the only known species within this section in which the urns lack stomata. The presence of small bistratose areas in the upper part of the leaf lamina suggests additional morphological similarity with species of sect. *Atrofusca* Ochyra (2003: 133).

Schistidium pratense closely resembles *S. dupretii* in both gametophyte and sporophyte characteristics, and the two species are often found growing together in the field. As a result, *S. pratense* may easily be mistaken for *S. dupretii*. However, *S. pratense* is a considerably larger moss, with longer stems (1.0–4.5 cm vs. 0.5–1.5(–1.9) cm in *S. dupretii*) and longer leaves (2.0–2.7 mm vs. 1.1–2.1 mm). In addition to its larger size, the glossy leaves of *S. pratense* help distinguish it from *S. dupretii* in the field. Microscopically, the two species are easily distinguishable: the urns of *S. pratense* lack stomata, while those are present (usually 6) in *S. dupretii*. Moreover, the spores of *S. pratense* are, on average, larger—(10–)11–15(–16) µm compared to 8–11 µm in *S. dupretii*. The hairpoints of *S. pratense* often have a brown base, and the leaf margins below the hairpoint are sometimes crenulate-denticulate. In contrast, *S. dupretii* lacks a brown base at the hairpoint, and its leaf margins below are smooth. Additionally, the base of the capsule in *S. pratense* is often conical when dry, as opposed to the broadly rounded shape found in *S. dupretii* and most other species of the genus. However, this feature is not present in all specimens.

Schistidium confusum shares a similar growth habit and size with *S. pratense*, and the two species sometimes occur together in mixed stands. However, *S. confusum* can be readily distinguished by its dull leaves, caused by the presence of papillae on the laminal cells, as well as by its typically shorter and more uniformly shaped exothecial cells.

Ecology and distribution:—*Schistidium pratense* grows on calcareous rocks in exposed locations or open woodland stands. It is a characteristic species of boulders and outcrops in subalpine pastures and heaths, where it often dominates the bryophyte vegetation. The species also occurs on man-made rock walls and concrete structures. *Schistidium pratense* is found in the Alps, the Jura Mountains, the Dinarides and the Central Apennines. Further north, it is known from a locality in the Black Forest, Germany and another in the Scandes of southern and northern Norway (Fig. 6). In the Alps, the species occurs at elevations ranging from approximately 1300 to 2600 m, with most records between 1600 and 2100 m. The Black Forest locality, which is on an artificial wall, is at 660 m, while the Norwegian localities are found at elevations between 560 and 725 m.

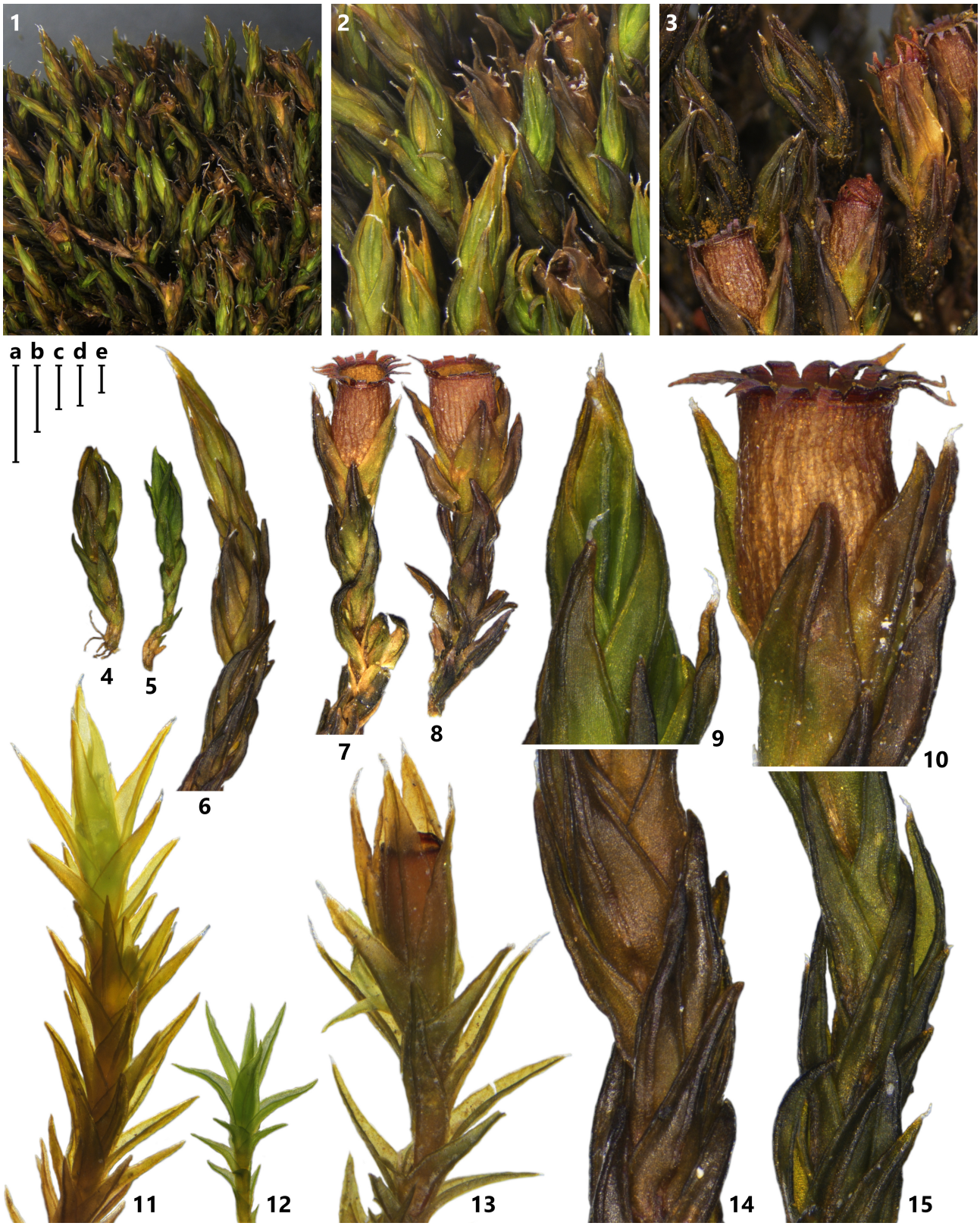

FIGURE 3. *Schistidium pratense*: 1. Tuft; 2–3. Shoots within tufts; 4–8, 9–10, 14–15. Individual fertile and vegetative shoots in dry state: Fertile shoots with enlarged perichaetial leaves, and vegetative shoots and part of vegetative shoots with muticous or shortly hairpointed leaves; 11–13. Shoots in moist state. 1, 2, 4–6, 9, 11–12, 14–15. From *Kiebacher 3073*; 3, 7–8, 10. *Kiebacher 2557*; 13. *Kiebacher 2625*. Scale bars: a. 0.5 mm (4–8, 11–13); b. 0.25 mm (9–10, 14–15); c. 0.5 mm (2); d. 1 mm (3); e. 1 mm (1).

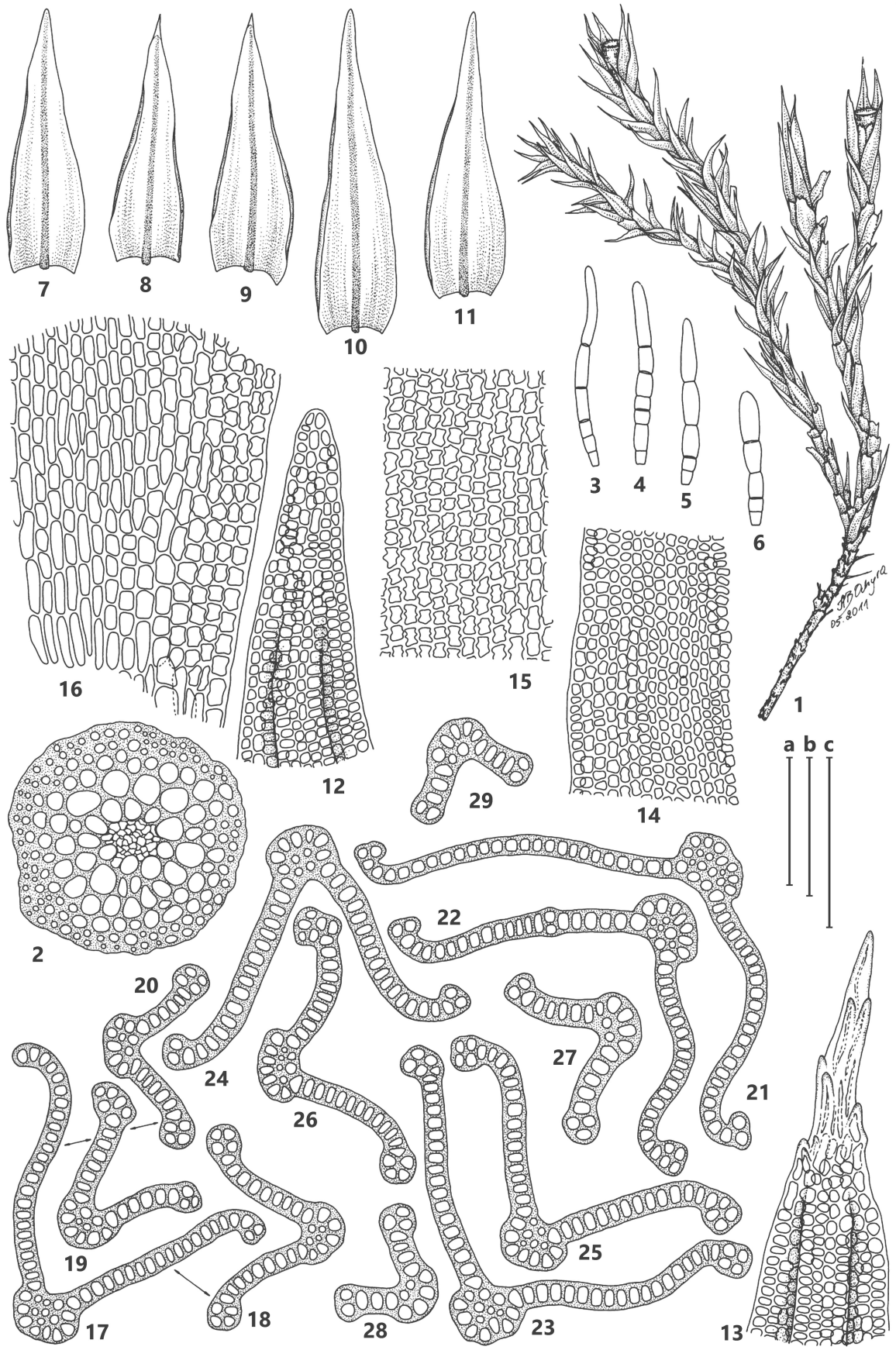

FIGURE 4. *Schistidium pratense*. 1. Habit, wet; 2. Transverse section of stem; 3–6. Axillary hairs; 7–11. Vegetative leaves; 12. Muticous leaf apex; 13. Leaf apex with hairpoint; 14. Mid-leaf cells; 15. Supra-basal cells; 16. Basal cells 17–29; Transverse sections of leaves, sequentially from base to apex (17–20, 21–29). 1, 7–9, 13, 21–29. From *Köckinger 99-331*, isotype; 2–6, 10–12, 14–20. *Köckinger 98-276*, paratype (both in KRAM). Scale bars: a. 100 µm (2–6, 12–29); b. 1 mm (7–11); c. 0.5 cm (1).

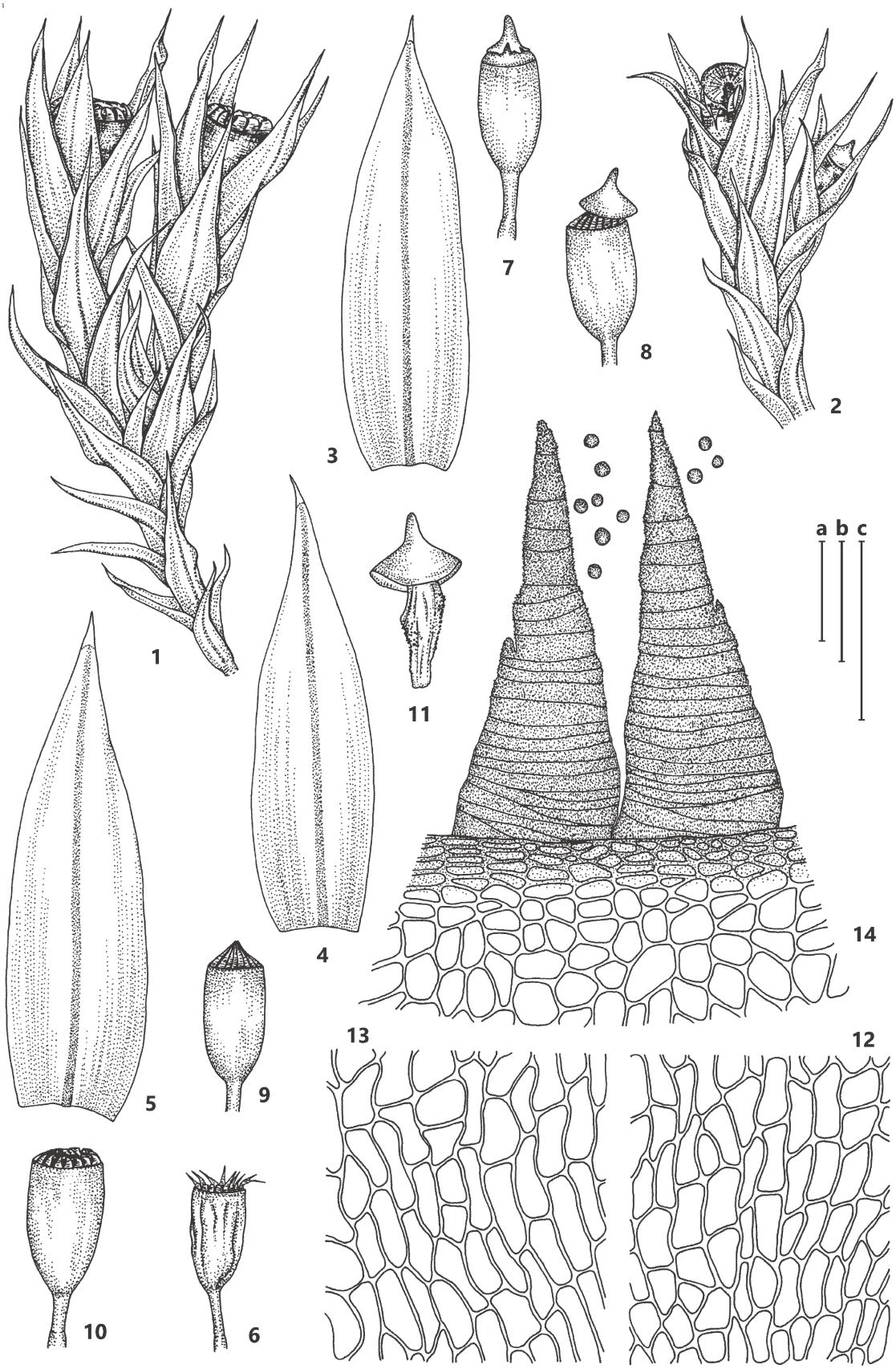

FIGURE 5. *Schistidium pratense*. 1. Portion of branches with perichaetia and sporophytes, wet; 2. Same, dry; 3–5. Perichaetial leaves; 6. Deoperculate capsule, dry; 7. Operculate capsule with calyptra, wet; 8. Capsule with detaching operculum, wet; 9–10. Deoperculate capsules, wet; 11. Operculum with attached columella; 12. Exothecial cells at base of urn; 13. Exothecial cells in middle of urn; 14. Exothecial cells at mouth, peristome and spores. 1–2, 6–14. From *Köckinger 99-331*, isotype; 3–5. *Köckinger 98-276*, paratype (both in KRAM). Scale bars: a. 1 mm (1–2, 6–10); b. 100 µm (11–14); c. 1 mm (3–5).

FIGURE 6. Distribution map for *Schistidium pratense*.

Additional specimens examined (paratypes):—AUSTRIA**. Kärnten**: Karnische Alpen, Frohnalm S of Maria Luggau, between Ingridhütte and Luggauer Törl, 15.VI.2004, *Köckinger 12345* (TRH B-148358); Karawanken, Mt. Petzen, ridge E of Feistritzer Spitze, 4.VI.2003, *Köckinger 12347* (KRAM B-283070, TRH B-148360); Hohe Tauern, SE Grossglockner, between Salmshütte and Stockerscharte, 15.VIII.1997, *Köckinger 97-814* (TRH B-126506); Leitertal SE Grossglockner, 13.VIII.1997, *Köckinger 97-760* (TRH B-148370); NW Heiligenblut, between Böser Platte and Priccius-Kapelle, 1995, *Köckinger 95-763* (with *S. brunnescens* subsp. *brunnescens*, *S. brunnescens* subsp. *griseum* and *S. subflaccidum*; TRH B-148374). **Niederösterreich**: Rax massif, E. Klobedntörl, alt. *ca* 1600 m a.s.l., limestone boulder below *Pinus mugo*, 08.07.2010, *Köckinger 14885* (KRAM B-283068). **Osttirol**: Venedigerguppe, Kl. Nilmalm above Obermauern, 9.VIII.1998, *Köckinger 98-613* (TRH B-148366); Venedigergruppe, above Obermauern near Virgen, 9.VIII.1998, *Köckinger 98-622* (TRH B-126509). **Steiermark**: Eisenerzer Alpen, Mt. Zeritzkampel, 23.VI.1998, *Köckinger 98-302* (TRH B-148367), 23.VI.1998, *Köckinger 98-308* (TRH B-148369); Mt. Eizenerzer Reichenstein, 26.VI.1998, *Köckinger 98-341* (TRH B-148364); Reichenstein, near Krumpensee, 25.VI.1998, Köckinger *98-343* (TRH B-126507); NW Wald by Schoberpass, *Köckinger 98-276* (KRAM B-283067, TRH 126523); Ennstaler Alpen, between Mt. Totenköpfl and Mödlinger Hütte, 23.VII.1998, *Köckinger 98-426* (TRH B-148361). **Salzburg**: St. Wolfgang, Schafberg, Gipfelbereich, 08.IX.2018, *Kiebacher 1891* (STU-BR-0070101).

Tirol: Zillertal, Gerlossteinwand, *Townsend 79/116a* (E). **Voralberg**: Grosses Walsertal, WNW Metgertobel Alm, 20.VI.2011, *Kiebacher 265* (priv. herb.). Verwall, Davenna massif, Itonskopf, northern slope, alt. *ca* 1850 m a.s.l., limestone boulder in pasture, 24.07.2009, *Köckinger 14892* (KRAM B-283069).

CROATIA. **Lika-Senj:** Ca. 5 km W Krasnov, 26.V.2025. *Volkers Br-2014, Br-2015* (priv. herb., STU-BR-0070140, STU-BR-0070141).

GERMANY. **Baden-Württemberg:** Schwarzwald, Schramberg, Berneck, Road turn to Kappelhof below Ramstein, *Lüth 1547* (priv. herb.).

ITALY. **Marche**: Sibillini mountains, below Mt. Borghese. 1993 *Bertolani* (CAME). **Molise:** Pagana valley, 3.VII.1989 *Cortini & Aleffi* (CAME, with S. *brunnescens* ssp. *griseum*); Venafrana valley, 5.VIII.1989 *Aleffi* (CAME). **Südtirol**: Ratschings, along path between Plattner and Mt. Ratschinger Kreuz, 09.X.2021, *Kiebacher 3058* (BOZ-BRYO-9767); Ratschings, ca 1 km E Mareiter Stein, 09.X.2021, *Kiebacher 3073* (STU-BR-0070103). **Trentino:** Vigo di Fassa, am Weg 517B zwischen Karerpass und Kleiner Latemarscharte, 04.X.2018, *Kiebacher 1924* (priv. herb.). **Udine:** Alpi Carnici, Plöckenpass SW of Kötschach-Mauthen, ridge between Mt. Kl. Pal and Mt. Freikofel, 18.VI.2004. *Köckinger 12346* (TRH B-148359). **Verona**: Malcesine, summit area of Mt. Cima delle Pozzette, 27.IX.2025. *Kiebacher 5503* (STU-BR-0070139).

NORWAY. **Nordland**: Rana, Hellerfjellet, Langtjønnlia, 29.VIII.2011, *Blom & Heegaard s.n.* (TRH B-126508). **Sogn og Fjordane**, Luster municipality, Engjadalen by Gaupne: below Jærgolagjelet, 10.V.2017, *Blom s.n.* (TRH B-35606); *loc. cit.*, Håvardsete, 11.VII.2017, *Blom s.n.* (KRAM B-243564, TRH B-35567, B-35570); *loc. cit.*, Gjetarknubben, 12.VII.2017, *Blom s.n.* (TRH B-35577); *loc. cit.*, W of Liabakkane, 12.VII.2017, *Blom s.n.* (TRH B-35586); *loc. cit.*, Trolldalsmyri-Øvringane, 13.VII.2017, *Blom s.n.* (TRH B-35597).

SWITZERLAND. **Vaud**: Jura mountains, Vallée de Joux, 30.VIII.1979 *Nyholm* (S). **Uri**: Eingang im Guggithal, 30.IX.1955 *Albrecht* (Z, with *S. dupretii*); Göschener Tal, *Blom 6083, 6091* (TRH B-126505, 148380); Klausenpass, *Blom 6134, 6136, 6149* (TRH B-148381, 148379, 148378). **Bern**: Gemmi, VII.1971 *Albrecht* (Z). **Graubünden:** Luzein, St Antönien, WSW-slope of Mt. Eggberg, ca. 0.6 km SE of Maiensäss, 25.XII.2020, *Kiebacher 2614* (STU-BR-0070102). **Fribourg**: Jaun, Ritzlialp, unterhalp der Hütte, 01.VII.2019, *Kiebacher 2141* (priv. herb.). **Schwyz:** Oberiberg, First, Gross Stärnen, 02.VIII.2018, *Kiebacher 1770* (priv. herb.). **Solothurn**: Selzach, Stallflue, E-ridge, 10.V.2020, *Kiebacher 2557* (Z-000144965).

Schistidium heribertii H.H.Blom, Kiebacher, Bedn.-Ochyra & Ochyra *sp. nov*. Figs 7–9

Diagnosis:—*Nostra species nova* Schistidio atrofusco *proxima*, *sed foliis praesertim perichaetialibus piliferis et laminis foliorum superiorum pruinoso suffusis bene distinguitur*.

Type:—AUSTRIA. **Steiermark:** Niedere Tauern, Gastrumer Ofen near Oberwölz [lat. 47°12′01″N, long. 14°13′50″E], insolated dolomite rock, 3.6.1996, leg. & det. *H. Köckinger 96–301* (Holotype: TRH 126524, isotype: KRAM B-283063).

Plants medium-sized, in upper part bluish green or black, occasionally with a yellowish tinge, black or blackish-brown in lower parts, forming dense, turgid tufts. *Stem* 0.9–2.8(–4.0) cm, with long branches; epidermis of (1–)2–3 rows of thick-walled cells; cortical cell walls gradually thinner towards stem centre; central strand sharply delimited, mostly broad. *Leaves* imbricate, arranged in ± distinct spiral rows, pruinose, concave, straight, keeled, oblong to ovate-triangular, obtuse or subacute, in lower part of stem and on sterile shoots muticous, in upper part of fertile stems with distinct hairpoints, (1.4–)1.6–2.4 × 0.6–0.8(–1.0) mm. *Hairpoint* 0–0.4(–0.7) mm, coarse and stiff but ± flattened, triangular in outline but often abruptly widened shortly above insertion, embracing part of upper lamina and shortly but broadly decurrent, margins laterally finely spinulose-denticulate or almost smooth, dorsally densely spinulose with slightly protruding spinulae. *Costa* smooth, ending just below apex to excurrent, dorsally convex and mostly hemispherical in transverse section, in upper part 45–62 µm wide and 2–3-stratose, in central and lower parts 50–75 µm wide and (3–)4–5-stratose (the fifth stratum represented by few cells). *Margins* broadly recurved in lower ½–⅔(–¾) leaf length on one side and plane or very narrowly and shortly recurved in the broadest part of leaf on the opposite side, in upper and central parts bistratose for 1–3(–5) rows, sometimes with 3-stratose spots, in lower part bistratose for 1–2 rows or unistratose. *Lamina* smooth, irregularly bistratose in upper ½–⅔ leaf length or more rarely predominantly unistratose with several bistratose striae. *Laminal cells* thick-walled and tending to be short and esinuose to weakly sinuose in all parts of the leaf, in upper part ovate, 7–9 µm wide, in central and lower parts predominantly oblong mixed with isodiametric cells, 7–10 µm wide and up to 11–18(–21) µm long; *basal cells* rectangular, 8–11 µm wide and up to 23–39 µm long, forming a small group at the costa; *basal marginal cells* rounded, square and shortly rectangular with ± thickened transverse walls. *Perichaetial leaves* 2.5–3.3 × (0.8–)1.0–1.2(–1.4) mm, concave, gradually tapering to leaf point, with margins narrowly recurved in upper ⅓–⅔ leaf length but often plane near apex, sometimes only recurved

FIGURE 7. *Schistidium heribertii*: 1. Tuft; 2. Shoots in a tuft; 3. Shoot with sporophyte; 4–10, 15–16. Fertile and vegetative shoots, dry: Fertile shoots with hairpoint-wearing perichaetial leaves, and vegetative shoots with muticous leaves; 11–14. Fertile and vegetative shoots, moist. 1, 3, 5–10. From *Kiebacher 3347*; 2. *Kiebacher 1941*; 4, 14. *Kiebacher 1022*. Scales: a. 0.5 mm (9–10, 15–16); b. 0.5 mm (3); c. 1 mm (4–8, 11–14); d. 1 mm (2); e. 1 mm (1).

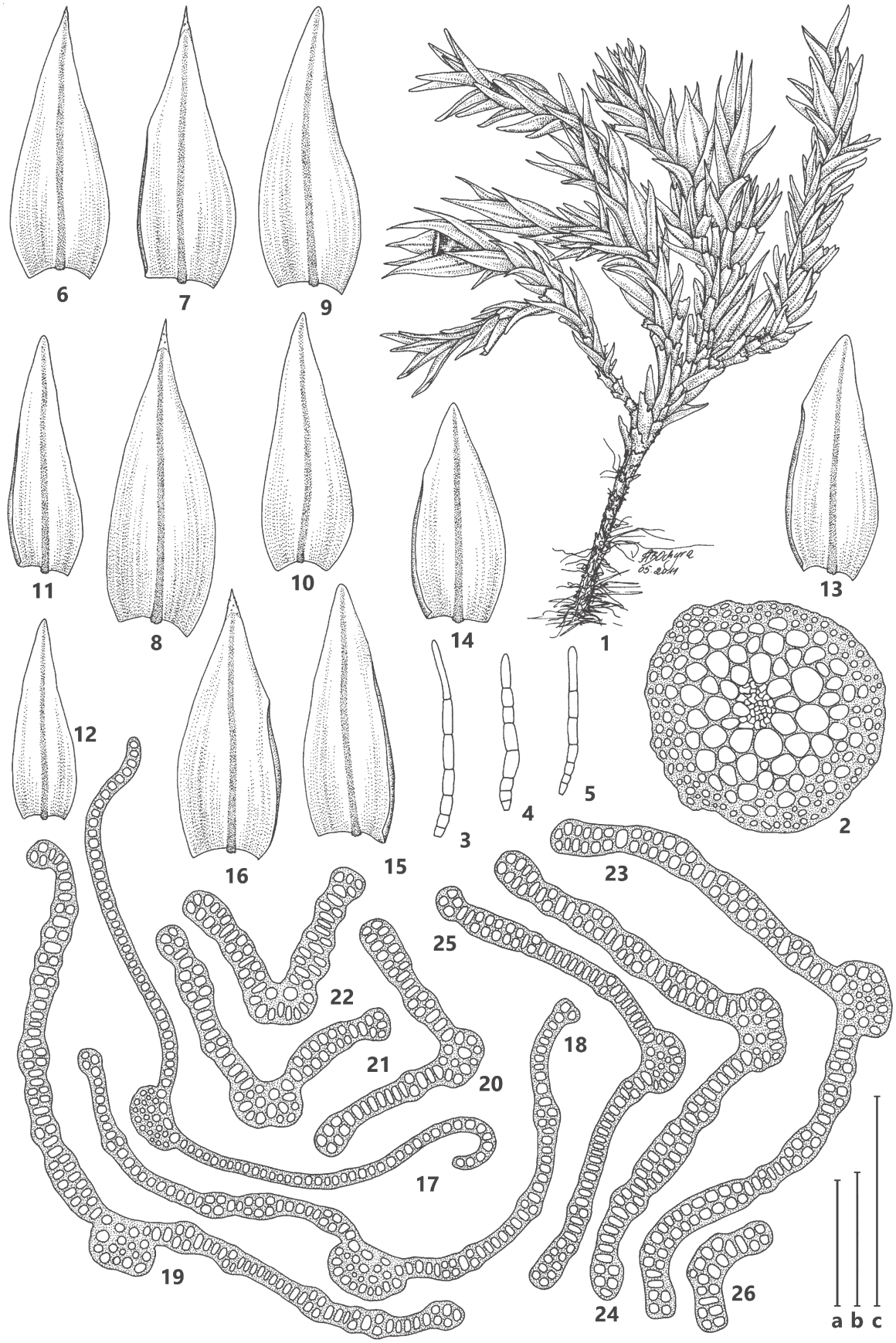

FIGURE 8. *Schistidium heribertii*. 1. Habit, wet; 2. Transverse section of stem; 3–5. Axillary hairs; 6–16. Vegetative leaves; 17–26. Transverse sections of leaves, sequentially from base to apex: 17–22 and 23–26; 1, 3–5. From *Köckinger 96-935b*, paratype; 2, 6–12, 17–22. *Köckinger 96-301*, isotype; 13–16, 23–26. *Köckinger 97-1263*, paratype (all in KRAM). Scale bars: a. 1 mm (6–16) and 100 µm (17–26); b. 1 µm (2–5); c. 0.5 cm (1).

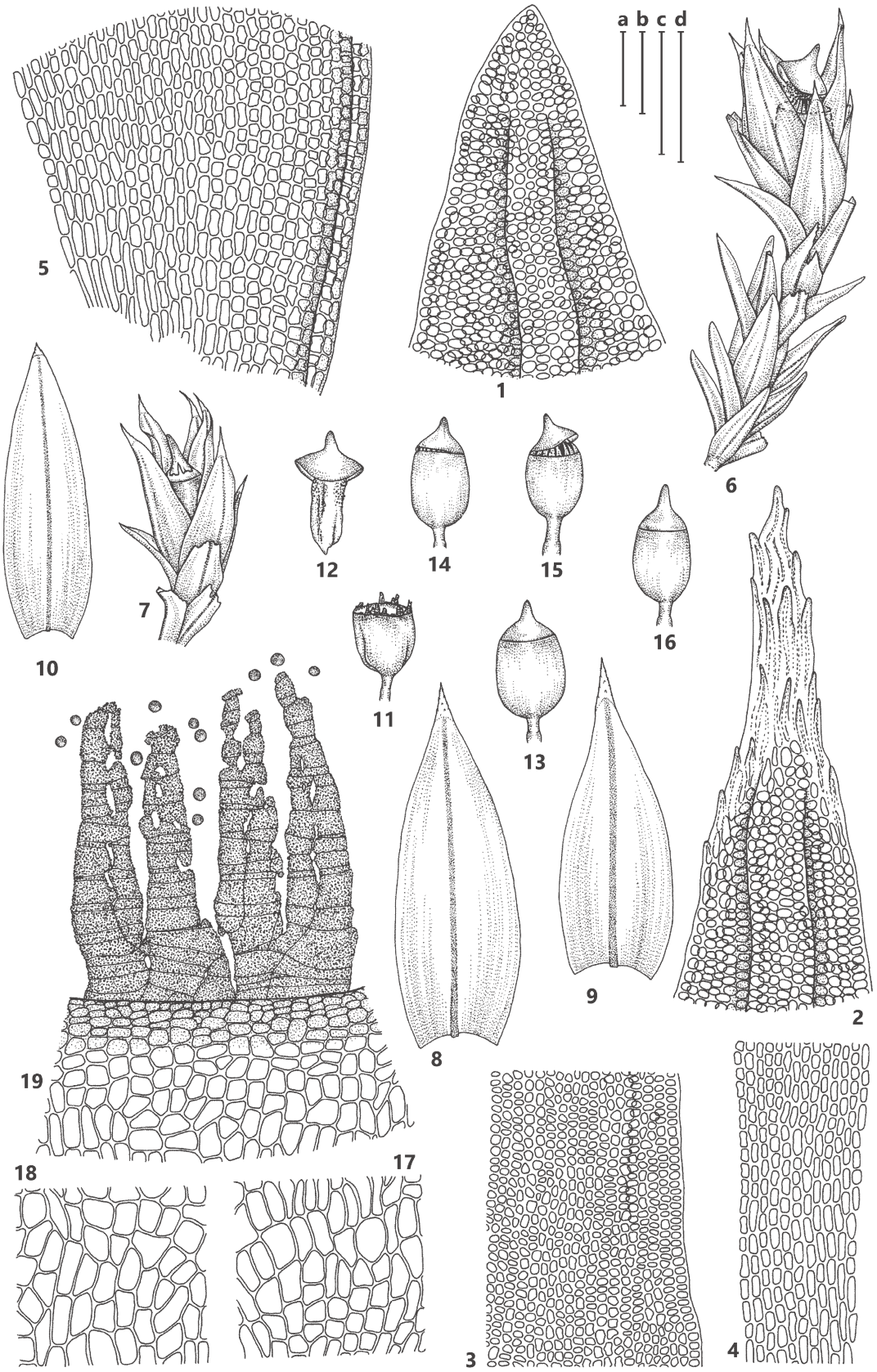

FIGURE 9. *Schistidium heribertii*. 1. Epilose leaf apex; 2. Leaf apex with hair-point; 3. Mid-leaf cells; 4. Supra-basal cells; 5. Basal cells; 6. Portion of branch with perichaetium and sporophyte, wet; 7. Same, including calyptra, wet; 8−10. Perichaetial leaves, sequentially from outer to innermost; 11. Deoperculate capsule, dry; 12. Operculum with attached columella, wet; 13−16. Operculate capsules, wet; 17. Exothecial cells at base of urn; 18. Exothecial cells in middle of urn; 19. Exothecial cells at mouth, peristome and spores. 1, 3−5, 8−10, 17–19. From *Köckinger 96-301*, isotype; 2. *Köckinger 96-437*, paratype; 6−7, 11−16. *Köckinger 96-935b*, paratype (all in KRAM). Scale bars: a. 1 mm (6−7, 11, 13−16); b. 1 mm (12); c. 1 mm (8−10) and 100 µm (17−19); d. 100 µm (1−5).

for short distances in the broadest part, hairpoints 0.3–0.5 mm long, embracing part of the upper lamina, not or shortly decurrent. *Calyptra* cucullate, split in 3 lobes at base.

Monoicous. *Sporophytes* deeply immersed, present in 95% of studied specimens, sparse or abundant. *Seta* rather thick, yellowish, (0.1–)0.2–0.5 mm. *Urn* yellow-brown to orange-brown, yellowish when empty, broadly obovoid, ellipsoid or obloid-cylindrical, (0.4–)0.7–1.1 × (0.3–)0.5–0.9 mm; length/width ratio (1.0–)1.3–1.8. *Exothecial cells* irregular in size and shape, of mixed square, transversely rectangular, rectangular and polygonal cells, walls distinctly and ± evenly thickened in upper part of urn, up to 25–40 µm wide and 38–50(–80) µm long. *Stomata* absent. *Peristome teeth* reduced but hygroscopical, fragile, 100–250 µm long, orange or light red, erect to erecto-patent but becoming recurved when old, irregular in shape and size and often split into two prongs at top, outer face smooth in lower and central parts, but mostly papillose with low knob-like papillae in upper part, inner face papillose throughout with coarse decumbent knob-like papillae in uppermost part. *Columella* broad with erect or rarely oblique, straight, obtuse rostrum, 0.1–0.3(–0.5) mm long. *Spores* thin-walled, finely granulose, 8–11 µm.

Etymology:—This species is named in honour of Heribert Köckinger. His work has been instrumental in fundamentally advancing our comprehension of Alpine bryophytes, across diverse taxonomic groups including *Schistidium*.

Relationships and differentiation:—*Schistidium heribertii* is most likely to be confused with two closely related species, *S. atrofuscum* and *S. helveticum*, which share its characteristic blackish gametophyte coloration. *Schistidium helveticum* typically appears more brownish-black, while *S. atrofuscum* closely resembles *S. heribertii* in colour and often exhibits a similar bluish tinge in the upper parts of the shoots. In *S. atrofuscum*, the leaves are usually muticous, whereas in almost all studied specimens of *S. heribertii*, distinct hairpoints are present on the upper vegetative and perichaetial leaves of fertile stems. However, short hairpoints have also been reported in *S. atrofuscum*, and such forms may in part represent *S. heribertii*. A distinguishing feature of *S. heribertii* is the pruinose (frosted) appearance of its leaves, caused by a waxy coating, typically visible on the upper parts of at least some stems. This feature is absent in *S. atrofuscum*. Both species can develop white lime encrustations, which may be mistaken for the more uniform and sometimes subtle waxy coating that characterises *S. heribertii*.

Schistidium helveticum, apart from coloration, is distinguished by well-formed peristome teeth usually exceeding 300 µm in length (versus reduced and up to 250 µm in *S. heribertii*). However, in some specimens, the peristome teeth may be fragile and prone to breaking, particularly when heavily perforated or cribrose in the upper part. Additionally, the hairpoint on the perichaetial leaves of *S. helveticum* is short – up to 0.25 mm – and remains terete throughout. In contrast, *S. heribertii* typically has a more developed hairpoint on the perichaetial leaves, measuring 0.3–0.6 mm, which is flat and widened at the base. *Schistidium heribertii* is classified in sect. *Atrofusca*, based on its partially bistratose lamina, predominantly isodiametric and only slightly sinuose laminal cells, and stiff hairpoints. ITS sequences analysis supports this taxonomic placement and confirms its close relationship with both *S. atrofuscum* and *S. helveticum*.

Ecology and distribution:—*Schistidium heribertii* predominantly inhabits alpine environments, typically growing on sunny, south-facing ledges of calcareous rocks. It is primarily found in valleys characterised by a continental climate, though it can also descend into the montane zone. In Austria, most specimens have been collected from inclined surfaces of calcareous schists and greenstones, but the species has also been recorded on marble and mortar of man-made walls. According to specimen labels *S. heribertii* is often found growing in association with *Schistidium subflaccidum* (Kindberg 1900: 85) H.H.Blom *et al*. 2006: 193) and *Didymodon subandreaeoides* (Kindberg) R.H.Zander (1978: 23). The species is currently known from the Alps of Austria, Italy, and Switzerland (Fig. 10). However, its full distribution is likely still under-documented, and it may also occur in other mountain ranges. Its elevational range spans from 920 to 2550 m.

Additional specimens examined (paratypes):—AUSTRIA. **Kärnten**: Gurktaler Alpen, Rinsennock. 14.VII.1996, *Köckinger 96-562* (TRH B-148290). Hohe Tauern, Seebachtal NE Mallnitz. *Köckinger 97-1263* (KRAM B-283064); Dösen SE Mallnitz, 1.VIII.1995, *Köckinger 95-361*, 3.VIII.1995, Köckinger *95-394* (TRH B-148288, 148298); Nockberge, Mt. Falkert. 6.IX.1999, *Köckinger 99-1229* (TRH B-148304). **Ost-Tirol**: Hohe Tauern, Mt. Mutanitz. 20.VIII.1996, *Köckinger 96-935b* (KRAM B-283066, TRH 126525); Mt. Mutanitz, 1 km W of Sudetend. Hütte. 20.VIII.1996, *Köckinger 96-936* (TRH B-148390); Mt. Steingruben-Kopf, 11.IX.1997, *Köckinger 97-1187* (TRH B-148297) (with *S. atrofuscum*); Umbaltal W of Hinterbichl, above Iselitzer-Alm, 12.IX.1997, *Köckinger 97-1158* (TRH B-148296); Venedigergruppe, above Obermauern near Virgen, 9.VIII.1998, *Köckinger 98-622* (TRH B-126509). **Salzburg**: Lungau, NW Mauterndorf, Twenger Au., 5.VIII.1996, *Köckinger 96-831* (TRH B-148289); Lungau, W of Muhr, Zalußenalm, S slope, *ca* 1800 m a.s.l., dry syunny, S-facing rock ledges, calcareous schist, 14.09.2006, *Köckinger 12248* (KRAM B-283065, TRH 126526). Radstädter Tauern, Murtal NW of Muhr, 4.VIII.1997, *Köckinger 97-633* (TRH B-148294); Murtal, above Muhr, 24.VII.1997, *Köckinger 97-623* (TRH B-148292); Murtal, between

Öllschützen and Jedl, 24.VII.1997, *Köckinger 97-602* (TRH B-148293). **Steiermark**: Rottenmanner Tauern, Mt. Kl. Geierkogel. 29.VI.1997, *Köckinger 97-49* (with *S. atrofuscum*; TRH B-148291); Oberes Murtal, NW Judenberg, NW Oberkurzheim, 27.VII.1999, *Köckinger* 99-632 (TRH B-148305). **Tirol**: Kitzbühel, am SE-Hang des Kleinen Rettensteins, 28.VIII.2015, *Kiebacher 1022* (STU-BR-0070097).

ITALY. **Südtirol:** Wengen, Rit, 11.X.2018, *Kiebacher 1909* (BOZ-BRYO-9766); Villnöss, am Panoramaweg am S-expon. Hang im Villnösstal ca. 1.5 km WNW St. Magdalena, 27.XII.2018, *Kiebacher 1941* (STU-BR-0070098).

SWITZERLAND. **Valais:** Evolène, Les Haudères vers La Forclaz, *De Zuttere 24301* (CMV); Zermatt, am nördlichen Ortsrand von Zermatt am Lüegelbach, Felsen oberhalb des Schwemmkegels orographisch links, 06.VII.2021, *Kiebacher 2998* (STU-BR-0070099); Vouvry, Le Flon, La Cheseule, 06.VII.2022, *Kiebacher 3347* (STU-BR-0070100); **Graubünden**: Vaz/Obervaz, ca. 0.7 km ENE Creusen, 27.VI.2017, *Kiebacher 1612* (priv. herb.); Chur, roch wall ca. 100 m NW St. Luzikapelle, 12.V.2022, *Kiebacher 3332* (Z-000144966); Domat/Ems, Arabühel, 21.VI.2022, *Kiebacher 3336* (priv. herb.). **Vaud**: Villeneuve, Les Dentaux, 07.VII.2022, *Kiebacher 3358* (priv. herb.).

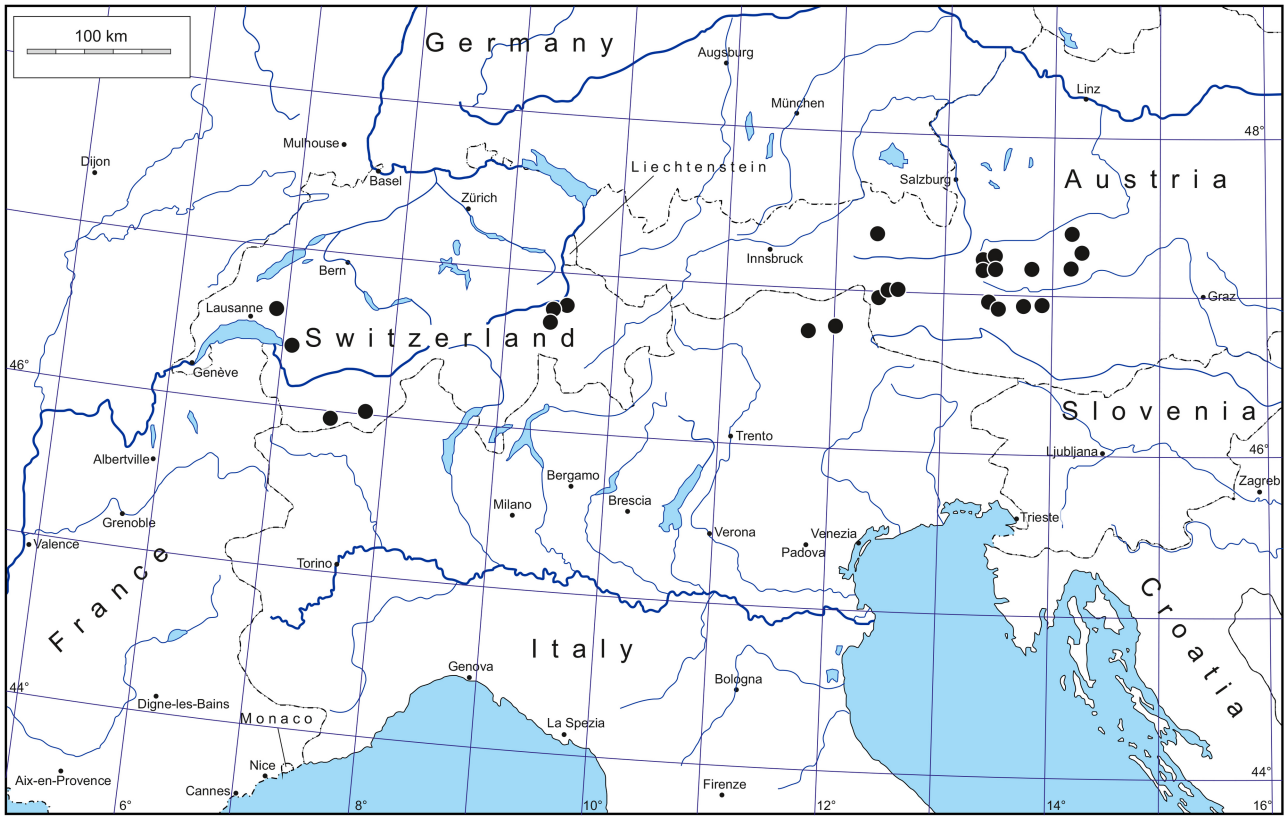

FIGURE 10. Distribution map for *Schistidium heribertii*.

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References

Amann, G., Köckinger, H., Reimann, M., Schröck, C. & Zechmeister, H. (2013) Bryofloristische Ergebnisse der Mooskartierung in Vorarlberg. *Stapfia* 99: 87–140.

Amann, J., Meylan, Ch. & Culmann, P. (1918) *Flore des mousses de la Suisse. Deuxième partie: Bryogéographie de la Suisse*. Herbier Boissier, Genève, 414 pp.

Bednarek-Ochyra, H. (1995) Rodzaj *Racomitrium* (Musci, Grimmiaceae) w Polsce: taksonomia, ekologia i fitogeografia [The genus *Racomitrium* (Musci, Grimmiaceae) in Poland: taxonomy, ecology and phytogeography]. *Fragmenta Floristica et Geobotanica Series Polonica* 2: 3–307. [In Polish with extensive English summary]

Bednarek-Ochyra, H. (2006) *A taxonomic monograph of the moss genus Codriophorus P. Beauv. (Grimmiaceae).* W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 276 pp.

Blom, H.H. (1996) A revision of the *Schistidium apocarpum* complex in Norway and Sweden. *Bryophytorum Bibliotheca* 49: 1–333.

Blom, H.H. (1997) An account on the genus *Schistidium* (Grimmiaceae) in two areas of the Swiss Alps. *Meylania* 12: 27–29.

Blom, H.H. (1998) *Schistidium*. *In*: Nyholm, E. (Ed.) *Illustrated flora of Nordic mosses*, 4. *Aulacomniaceae – Meesiaceae – Catoscopiaceae – Bartramiaceae – Timmiaceae – Encalyptaceae – Grimmiaceae – Ptychomitriaceae – Hedwigiaceae – Orthotrichaceae*. Nordic Bryological Society, Copenhagen and Lund, pp. 287–330.

Blom, H.H. & Darigo, C.E. (2009) *Schistidium viride* (Grimmiaceae), a new name for a common but neglected species in Eastern North America. *The Bryologist* 112: 273–277.
https://doi.org/10.1639/0007-2745-112.2.273

Blom, H.H. & De Zuttere, Ph. (2002) Quelques *Schistidium* intéressants récoltés dans les Alpes française (Savoie et Haut-Alpes) ainsi que suisses (Valais). *Nowellia Bryologica* 23: 36–38.

Blom, H.H., Bednarek-Ochyra, H. & Ochyra, R. (2016) Studies on *Schistidium* (Grimmiaceae, Bryophyta) in Europe, with particular reference to the Alps: I. A description of *S. marginale* sp. nov. *Phytotaxa* 247 (3): 210–218.
https://doi.org/10.11646/phytotaxa.247.3.4

Bruch, Ph., Schimper, W.Ph. & Gümbel, Th. (1845) *Bryologia europaea seu genera muscorum europaeorum monographice illustrata. 3. Schistidium et Grimmia*. E. Schweizerbart, Stuttgart, pp. 93–132 + pls. 231–252, 254–261 [Fasc. 25–28 Monogr.: 1–10, Tab. i–v].

Corley, M.F.V., Crundwell, A.C., Düll, R., Hill, M.O. & Smith, A.J.E. (1981) Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. *Journal of Bryology* 11: 609–689.
https://doi.org/10.1179/jbr.1981.11.4.609

Deguchi, H. (1979) Les veritables caracteres de *Schistidium alpicola* (Sw. ex Hedw.) Limpr. et son nouveau synonyme, *Schistidium agassizii* Sull. et Lesqu. *Revue Bryologique et Lichénologique Nouvelle Série* 45: 425–435.

De Notaris, J. (1836) Mantissa muscorum ad Floram Pedemontanam. *Memorie della Reale Accademia delle Scienze di Torino* 39: 211–258.

Düll, R. (1984) Distribution of the European and Macaronesian mosses (Bryophytina). Part I. *Bryologische Beiträge* 4: 1–113.

Ellis, L.T., Asthana, A.K., Srivastava, P., Omar, I., Rawat, K.K., Sahu, V., Cano, M.J., Costa, D.P., Dias, E.M., Dias dos Santos, N., Silva, J.B., Fedosov, V.E., Kozhin, M.N., Ignatova, E.A., Germano, S.R., Golovina, E.O., Gremmen, N.J.M., Ion, R., Ştefănuţ, S., von Konrat, M., Jimenez, M.S., Suárez, G.M., Kiebacher, T., Lebouvier, M., Long, D.G., Maity, D., Ochyra, R., Parnikoza, I., Plášek, V., Fialová, L., Skoupá, Z., Poponessi, S., Aleffi, M., Sabovljević, M.S., Sabovljević, A.D., Saha, P., Aziz, M.N., Sawicki, J., Suleiman, M., Sun, B.-Y., Váňa, J., Wójcik, T., Yoon, Y.-J., Żarnowiec, J. & Larraín, J. (2016) New national and regional bryophyte records, 46. *Journal of Bryology* 38: 47–63.
https://doi.org/10.1080/03736687.2015.1123344

Frisvoll, A.A. (1983) A taxonomic revision of the *Racomitrium canescens* group (Bryophyta, Grimmiaceae). *Gunneria* 41: 1–181.

Frisvoll, A.A. (1988) A taxonomic revision of the *Racomitrium heterostichum* group (Bryophyta, Grimmiaceae) in N. and C. America, N. Africa, Europe and Asia. *Gunneria* 59: 1–289.

Guerra, J., Jiménez-Martínez, J.F., Cano, M.J., Alonso, M. & Gallego, M.T. (2019) *Schistidium convergens* (Grimmiaceae, Bryophyta), a new species from southern Spain and Morocco. *Nova Hedwigia* 109: 65–80.
https://doi.org/10.1127/nova_hedwigia/2019/0529

Guerra, J., Martínez, M., Jiménez, J.A., Cano, M.J. & Gallego, M.T. (2020) A new species of moss emerges from molecular and morphological data: *Schistidium memnonium* sp. nov. (Grimmiaceae, Bryophyta). *Plant Biosystems* 155: 567–578.
https://doi.org/10.1080/11263504.2020.1762789

Hedwig, J. (1801) *Species muscorum frondosum descriptae et tabulis aeneis LXXVII coloratis illustratae*. Opus posthumum editum a Frederico Schwaegrichen. Sumtu Joannis Ambrosii Barthii, Lipsiae and apud Amand Koenig, Parisiis, vi + 357 pp. + Tab. lxxvii.
https://doi.org/10.5962/bhl.title.26

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
https://doi.org/10.1080/03736687.2020.1784587

Kiebacher, T. (2020) *Schistidium succulentum* Ignatova & H.H.Blom (Grimmiaceae) new to Europe. *Journal of Bryology* 42: 277–280.

Kiebacher, T., Köckinger, H. & Blom, H.H. (2021) *Schistidium foraminis-martini* sp. nov. (Grimmiaceae), a high mountain calcicole from the European Alps molecularly related to *S. agassizii*. *Bryophyte Diversity & Evolution* 44: 1–11.
https://doi.org/10.11646/bde.44.1.1

Kiebacher, T., Yousefi, N., Meier, M., Hodgson, A. & Blom, H.H. (2024) Homoplasy rather than intergeneric hybridisation explains mammillose leaf cells in *Schistidium mammillosum* sp. nov. (Grimmiaceae). *Bryophyte Diversity and Evolution* 47: 31–50.
https://doi.org/10.11646/bde.47.1.7

Köckinger, H., Suanjak, M., Schriebl, A. & Schröck, C. (2008) *Die Moose Kärntens*. Naturwissenschaftlicher Verein für Kärnten, Klagenfurt, 319 pp.

Limpricht, K.G. (1888–1889) Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Abtheilung: Sphagnaceae, Andreaeaceae, Archidiaceae, Bryineae (Cleistocarpae, Stegorcarpae [Acrocarpae]). 69. Gattung: *Schistidium*. *In*: *Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.* Zweite Auflage. Band 4. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. Verlag von Eduard Kummer, Leipzig, pp. 702–718.

Lüth, M. (2019) *Mosses of Europe. A Photographic Flora*. Volume 1. Privately published, Freiburg, 328 pp.

Nees von Esenbeck, C.G.D. & Hornschuch, C.F. (1827) *Bryologia germanica, oder Beschreibung der in Deutschland und in der Schweiz wachsenden Laubmoose. Zweiter Theil. Erste Abtheilung*. Bei Friedrich Fleischer, Leipzig, 182 pp. + Tab. xiii–xxiv.

Ochyra, R. (1989) Lectotypification of *Schistidium pulvinatum* (Hedw.) Brid. (Musci: Grimmiaceae) and its consequences. *Nova Hedwigia* 48: 85–106.

Ochyra, R., Żarnowiec, J. & Bednarek-Ochyra, H. (2003) *Census catalogue of Polish mosses*. Institute of Botany, Polish Academy of Sciences, Kraków, 372 pp.

Rambaut, A., Suchard, M. & Drummond, A. (2013) Tracer v1.6 – MCMC trace analysis package. [http://tree.bio.ed.ac.uk/software/tracer/]

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
https://doi.org/10.1093/sysbio/sys029

Schimper, W.Ph. (1876) *Synopsis muscorum europaeorum praemissa introductione de elementis bryologicis tractante. 2. Specierum descriptio*. E. Schweizerbart, Stuttgart, 886 pp.

Schkuhr, [Ch.] (1811) *Deutschland's kryptogamische Gewächse. Zweyter Theil. Oder vier und zwanzigste Pflanzenklasse. II. Abtheilung, die deutschen Moose enthaltend*. 2. Ernst Fleischer, Leipzig, pp. 41–82, Tab. 20–37.

Schlüssmayr, G. & Schröck, C. (2013) Bemerkenswerte Neu- und Wiederfunde zur Moosflora von Oberösterreich. *Stapfia* 99: 75–86.

Schröck, C., Köckinger, H., Amann, G. & Zechmeister, H. (2013) *Rote Liste gefährderter Moose Voralbergs*. Inatura Erlebnis Naturschau – Rote Listen 8. Inatura – Erlebnis Naturschau, Dornbirn, 236 pp.

Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.
https://doi.org/10.1093/sysbio/49.2.369

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Stöver, B.C. & Müller, K.F. (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* 11: 1–9.
https://doi.org/10.1186/1471-2105-11-7

Thériot, I. (1907) *Grimmia dupretii*, n. sp. *The Bryologist* 10: 62–64.
https://doi.org/10.1639/0007-2745(1907)10[62:GDNS]2.0.CO;2

Weber, W.A. (1976) New combinations in the Rocky Mountain flora. *Phytologia* 33: 105–106.
https://doi.org/10.5962/bhl.part.16783

Zander, R.H. (1978) New combinations in *Didymodon* (Musci) and a key to the taxa in North America north of Mexico. *Phytologia* 41: 11–32.
https://doi.org/10.5962/bhl.part.20773