

Ptychostomum touwii, a new bryophyte species distinguished from *Ptychostomum rubens* by iterative morpho-molecular analysis, and a note on *Bryum microerythrocarpum*

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Key words

DNA barcoding
Imbriobryum microerythrocarpum
Ptychostomum bornholmense
Ptychostomum rubens
Ptychostomum touwii

Abstract – DNA barcoding of Dutch collections of *Ptychostomum rubens* (Mitt.) Holyoak & N. Pedersen as understood in modern Floras revealed two distinct taxa. A morphological study of these specimens recognized several characters which can be used for identification. *Ptychostomum rubens* as well as its synonym *Bryum bomanssonii* Lindb. are lectotyped here. These lectotypes, and hence these two taxa, belong to the same morpho-molecular species. The other species is described here as a new species: *Ptychostomum touwii* Bijlsma, Kruijer & M. Stech. A key to these two species and the closely related *P. bornholmense* (Wink. & R. Ruthe) Holyoak & N. Pedersen is given. Their distribution and ecology in the Netherlands are briefly discussed. *Ptychostomum rubens* is a widespread species in the Netherlands, occurring on disturbed, base-rich, often calcareous and nutrient-rich soils, whereas *P. touwii* is calcifuge and prefers disturbed, less nutrient-rich, sandy soils and loams. The distribution range of the latter species needs to be clarified yet. After studying material from the South American species *Bryum subapiculatum* Hampe, *B. dentiferum* Hampe, and *B. rubrinerve* Cardot & Broth., we propose to exclude these species from the species concept of *B. microerythrocarpum* Müll. Hal. & Kindb. awaiting further molecular research of this variable species complex. Since, based on previous molecular research, *B. subapiculatum* is recently classified in the genus *Imbriobryum* N. Pedersen and *B. subapiculatum* and *B. microerythrocarpum* are closely related, we also make the new combination *Imbriobryum microerythrocarpum* (Müll. Hal. & Kindb.) Bijlsma, Kruijer & M. Stech.

Samenvatting – DNA-barcoding van Nederlandse collecties van *Ptychostomum rubens* (Mitt.) Holyoak & N. Pedersen zoals beschouwd in moderne Flora's heeft twee verschillende taxa aan het licht gebracht. Morfologisch onderzoek van dit materiaal heeft vervolgens kenmerken opgeleverd die gebruikt kunnen worden voor identificatie. Voor zowel *P. rubens* als zijn synoniem *Bryum bomanssonii* Lindb. wordt een lectotype aangewezen. Deze lectotypes, en dus ook deze twee taxa, blijken tot dezelfde moleculair-morfologische soort te behoren. De andere soort wordt hier beschreven als de nieuwe soort *Ptychostomum touwii* Bijlsma, Kruijer & M. Stech. Er wordt een determinatiesleutel gegeven voor deze twee soorten en de nauw verwante *P. bornholmense* (Wink. & R. Ruthe) Holyoak & N. Pedersen. De verspreiding en ecologie in Nederland worden eveneens kort besproken. *Ptychostomum rubens* is een wijd-verspreide soort in Nederland die voorkomt op verstoorde, basenrijke, vaak kalkrijke en voedselrijke bodems. *Ptychostomum touwii* is kalkvliedend en prefereert verstoorde, minder voedselrijke, zandige bodems en leemgronden. Het verspreidingsgebied van de laatste soort moet nog nader worden vastgesteld. Na bestudering van materiaal van de Zuid-Amerikaanse soorten *Bryum subapiculatum* Hampe, *B. dentiferum* Hampe en *B. rubrinerve* Cardot & Broth., stellen wij voor deze soorten buiten het soortconcept van *B. microerythrocarpum* Müll. Hal. & Kindb. te houden, in afwachting van moleculair onderzoek van dit variabele soortcomplex. Omdat, gebaseerd op eerder moleculair onderzoek, *B. subapiculatum* recent is ondergebracht in het geslacht *Imbriobryum* N. Pedersen en *B. subapiculatum* and *B. microerythrocarpum* nauw verwant zijn, maken we ook de nieuwe combinatie *Imbriobryum microerythrocarpum* (Müll. Hal. & Kindb.) Bijlsma, Kruijer & M. Stech.

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INTRODUCTION

Ptychostomum rubens (Mitt.) Holyoak & N. Pedersen in Crundwell & Nyholm's (1964, as *Bryum rubens* Mitt.) circumscription is easily recognized by its unique raspberry-like rhizoidal gemmae, which often are present in leaf axils as well. The species is native to Europe, where it is common on more or less disturbed, neutral to basic soils (Porley 2008) and has probably been introduced elsewhere, e.g., in North America, India, Japan and New Zealand (Crundwell & Whitehouse 1978, Fife 2015, Smith 2004, Spence 2014).

The DNA barcoding project of the Dutch bryophytes, initiated by Naturalis Biodiversity Center and the Dutch Bryological and Lichenological Society (Bryologische en Lichenologische Werkgroep, BLWG) in 2010, however, revealed that the included Dutch *Ptychostomum rubens*-collections represented two distinct taxa at species level. This was investigated further by an iterative morpho-molecular approach to (i) find morphological features that could be used to identify both taxa and (ii) test the morphological species concept by DNA barcoding of additional specimens. The morphological study revealed that both taxa can be successfully delimited by several features. The additional DNA barcoding confirmed the revised morphological species circumscriptions. The two species are *Ptychostomum rubens* s. str. and a new species, which is described here as *Ptychostomum touwii* spec. nov.

Acronyms of herbaria follow Index Herbariorum (Thiers 2019+). Vouchers are preserved at L.

MOLECULAR ANALYSIS

DNA sequences were compiled from 15 specimens that were originally identified as *Ptychostomum rubens*, four specimens of *P. bornholmense* (Wink. & R. Ruthe) Holyoak & N. Pedersen, and two specimens of *P. capillare* (Hedw.) Holyoak & N. Pedersen as out-group representatives, all originating from the Netherlands (Table 1).

Genomic DNA was extracted from single shoots using the NucleoSpin® Plant II kit or the NucleoMag®96 Plant kit (Macherey-Nagel) on the KingFisher™ Flex Purification System (Thermo Fisher Scientific). PCR amplifications were carried out in a final volume of 25 µl and contained 1.5 µl template DNA, 2.5 µl 10× buffer with MgCl₂ (or 1.5 µl 25 mM MgCl₂ added separately), 1 µl 100 mM BSA (for *trnL-F* only), 1.0 µl 2.5 mM dNTPs, 1.0 µl of each primer (10 pMol/µl; *trnL-F*: Cm/Fm, Frey et al. 1999; ITS: 18F/25R, Stech & Frahm 1999), and 1.0–1.25 U (5 U/µl) Taq DNA polymerase (Qiagen). Primers were either untailed or had an M13F or M13R tail attached for sequencing. PCR programs were 2 min 94°C, 40 cycles (1 min 94°C, 1 min 55°C, 1 min 72°C), 5 min 72°C for *trnL-F* and 5 min 95°C, 35 cycles (30 s 95°C, 30 s 50°C, 1 min 72°C), 7 min 72°C for ITS. PCR products were purified and sequenced at Macrogen Inc. or BaseClear B.V. Sequences were assembled and edited using Geneious® v8.1.8 (Biomatters Ltd.), submitted to GenBank (accession numbers in Table 1), and aligned in PhyDE v. 0.9971 (Müller et al. 2006).

Phylogenetic reconstructions based on maximum parsimony (MP) and Bayesian Inference (BI) were performed using PAUP 4.0b10 (Swofford 2002) and MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001), respectively. Both markers were analysed separately and combined, with gaps treated as missing data or coded by simple indel coding (SIC) (Simmons & Ochoterena 2000) using SeqState (Müller 2004). Branch-and-bound or heuristic searches with 1000 addition sequence replicates were carried out under MP. Heuristic bootstrap searches were performed with 1000 replicates, and 10 addition sequence replicates per bootstrap replicate. Best-fit models of nucleotide sequence evolution were TIM3 for *trnL-F* and HKY+ Γ for ITS according to the Akaike information criterion in jModeltest 2.1.4 (Darriba et al. 2012). Since a model with four substitution types such as TIM3 is not implemented in MrBayes, we carried out analyses with two and six substitution types for *trnL-F*. Posterior probabilities under BI were calculated based on the Markov chain Monte Carlo method with the settings nst=2 or nst=6 (and rates=gamma for ITS),

Table 1. Voucher information and GenBank accession numbers of the *Ptychostomum* specimens analysed for the present study.

Species	Voucher no.	Herbarium no.	DNA extract no.	Genbank acc. no. <i>trnL-F</i>	Genbank acc. no. ITS
<i>Ptychostomum bornholmense</i>	Horvers s.n. (NMBT 071979)	L0873021	e25922068	MT614305	MT624300
<i>Ptychostomum bornholmense</i>	Zwarts 2139	L0872956	e30104877	MT614304	MT624299
<i>Ptychostomum bornholmense</i>	Bijlsma 12615	L0872953	e4000477280	MT614306	MT624301
<i>Ptychostomum bornholmense</i>	Nieuwkoop 2011002	L0872955	e4000477304	MT614303	MT624298
<i>Ptychostomum capillare</i>	Bijlsma 12263	L0872963	e30104853	MT614301	MT624296
<i>Ptychostomum capillare</i>	Buiten 24.48.25 2586	L0872965	e4000477227	MT614302	MT624297
<i>Ptychostomum rubens</i>	Luong 13018-3	L0854745	B05	MT614309	MT624304
<i>Ptychostomum rubens</i>	Luong 13017	L0854746	B08	MT614310	MT624305
<i>Ptychostomum rubens</i>	Luong 13026	L0854747	B23	MT614311	MT624306
<i>Ptychostomum rubens</i>	Luong s.n.	L0857491	B46	MT614307	MT624302
<i>Ptychostomum rubens</i>	Luong 13041	L0854748	B48	MT614308	MT624303
<i>Ptychostomum rubens</i>	Nieuwkoop 2008057	L0873018	e4000477341	MT614312	MT624307
<i>Ptychostomum rubens</i>	Bijlsma 16392	L0818585	e4010126785	MT614314	MT624309
<i>Ptychostomum rubens</i>	Bijlsma 16411	L0818586	e4010126797	MT614313	MT624308
<i>Ptychostomum touwii</i>	Luong 13005	L0854749	B49	MT614315	MT624310
<i>Ptychostomum touwii</i>	Smulders s.n.	L0873016	e25922066	MT614317	MT624312
<i>Ptychostomum touwii</i>	Smulders s.n.	L0873017	e25922067	MT614318	MT624313
<i>Ptychostomum touwii</i>	Nieuwkoop s.n.	L0872982	e30104902	MT614316	MT624311
<i>Ptychostomum touwii</i>	Bijlsma 15341	L0255102	e4007593673	MT614319	MT624314
<i>Ptychostomum touwii</i>	Bijlsma 16528	L0818583	e4010126761	MT614321	MT624316
<i>Ptychostomum touwii</i>	Bijlsma 16138	L0818581	e4010126832	MT614320	MT624315

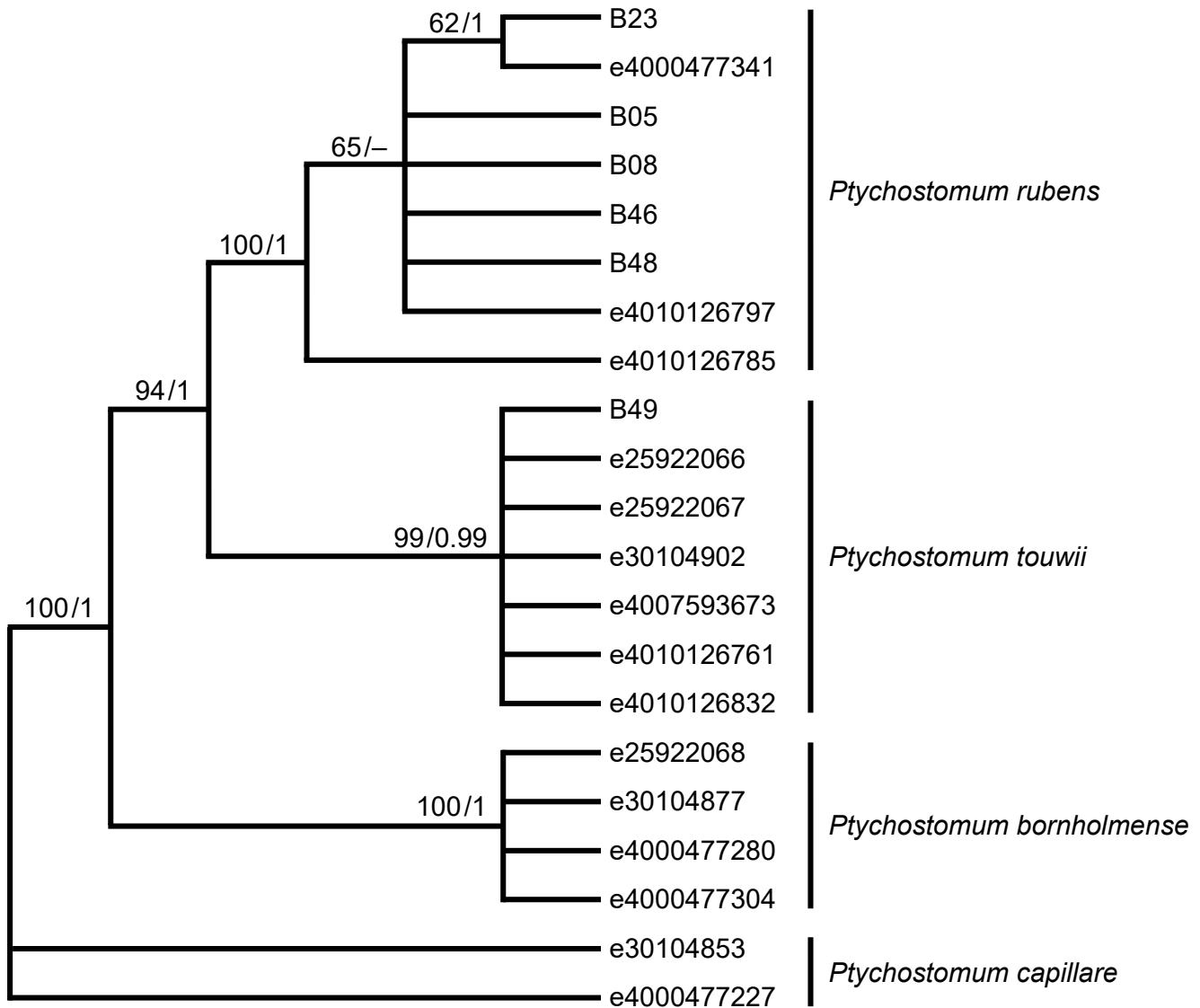


Fig. 1. Maximum parsimony phylogenetic reconstruction of samples of *Ptychostomum bornholmense* (Wink. & R. Ruthe) Holyoak & N. Pedersen, *P. rubens* (Mitt.) Holyoak & N. Pedersen, *P. touwii* Bijlsma, Kruijer & M. Stech, and *P. capillare* (Hedw.) Holyoak & N. Pedersen as outgroup representative, based on combined *trnL-F* and ITS sequences, with indels coded by simple indel coding included. Maximum parsimony bootstrap values >60% and posterior probabilities >0.95 from respective Bayesian Inference analysis are indicated at the branches.

employing the restriction site model ('F81') for the indel matrix, partitions unlinked, four simultaneous Markov chains, 2×10^6 generations, and trees sampled every 1000th generation. Fifty-percent majority-rule consensus trees and posterior probabilities of clades were calculated by combining the four runs and using the trees sampled after the chains converged, excluding the first 25% of trees as 'burnin'.

The combined dataset comprised 1672 characters (*trnL-F* 477 alignment positions/3 indels, ITS 1111 alignment positions/81 indels), of which 156 (*trnL-F* 10/ITS 146) were parsimony-informative. No incongruence with respect to well-supported clades was observed between phylogenetic reconstructions of *trnL-F* and ITS separately, with and without indels coded by SIC included. The combined MP analysis of both markers with indels included yielded 35 most parsimonious trees (length 173, consistency index CI = 0.931, retention index RI = 0.975), of which the strict consensus tree is shown in Fig. 1. Three main ingroup clades were resolved, corresponding to *Ptychostomum bornholmense* (MP bootstrap support [BS] 100%/posterior

probability [PP] from the respective BI analysis 1.00), *P. rubens* (100%/1.00), and *P. touwii* (99%/0.99). The latter two were resolved as sister clades (94%/1.00).

LECTOTYPIFICATION OF *BRYUM RUBENS*

The basionym of *Ptychostomum rubens* is *Bryum rubens* Mitt. When Mitten (1856) described his new *Bryum* species, he did not explicitly mention the localities where he collected material of this species himself. The protologue quite generally states "Throughout the temperate parts of Europe, Asia, and North-west America" and further gives "a summary of the specimens examined". The latter includes collections from Germany (Blankenburg (Harz) and Hamburg), Istria, and Sardinia, which were apparently sent to Mitten under various names. However, the material of *B. rubens* in Mitten's herbarium (NY) contains not only the collections from continental Europe that are cited in the protologue, but also several sheets with packets labelled *B. erythrocarpum* Schwägr.

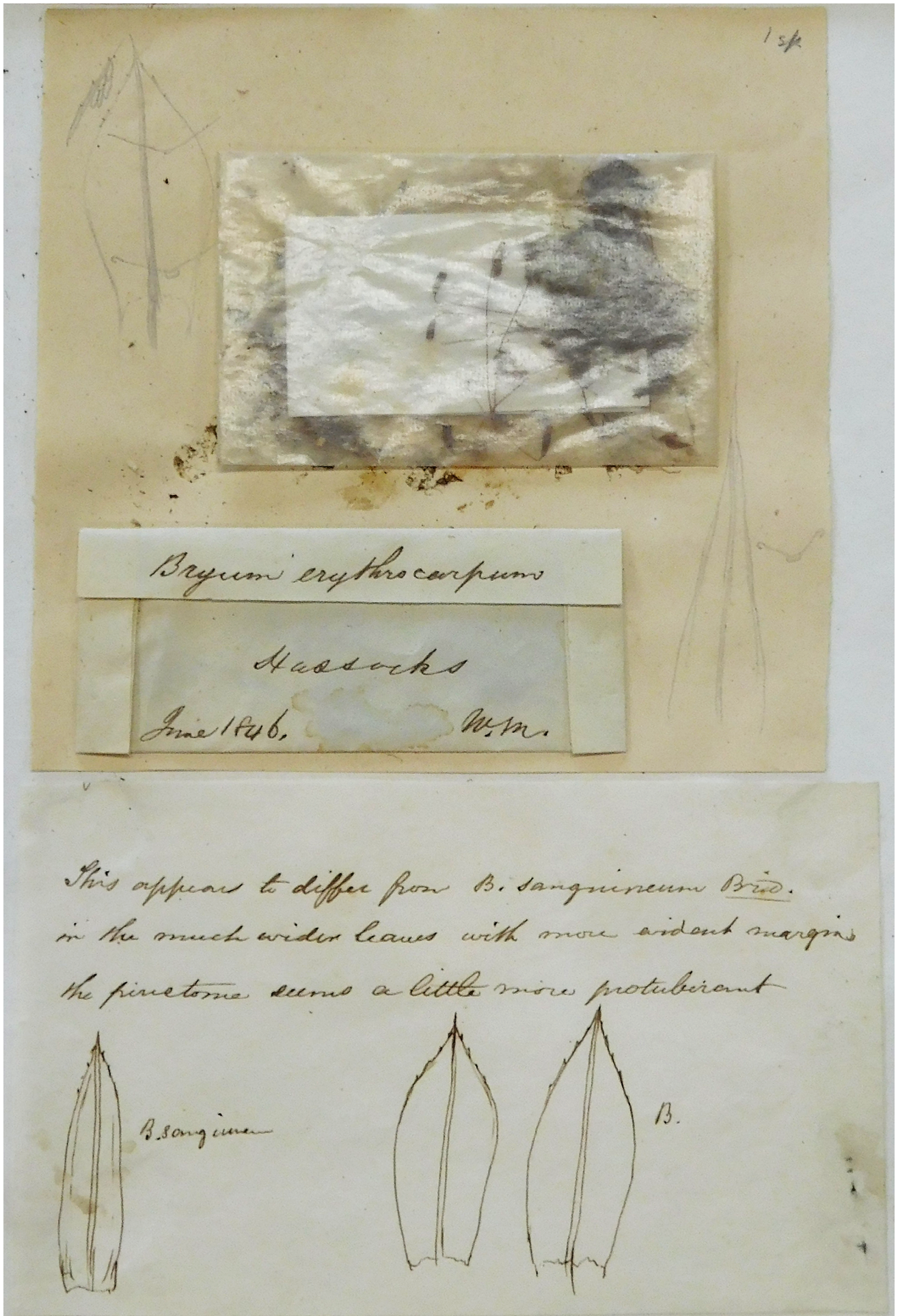


Fig. 2. Lectotype of *Bryum rubens* Mitt. (≡ *Ptychostomum rubens* (Mitt.) Holyoak & N. Pedersen) in NY (Hassocks, June 1846, W.M.), with drawings by Mitten.



Fig. 3. Moistened part of the holotype of *Ptychostomum touwii* Bijlsma, Kruijer & M. Stech (*R.J. Bijlsma 15341*, L [L0255102]). Photo: H.N. Siebel.

that Mitten collected himself in Sussex (Great Britain), not far from where he lived and had his pharmacy. From the collecting dates on the packets it is clear that he revisited a few sites several times. Noteworthy is that not a single specimen, neither from continental Europe nor from Sussex, is labelled as *B. rubens*.

In selecting a lectotype, we focused on material that was collected by Mitten before 1856 and corresponds with his description and discussion of the relationship of his new species with "*Bryum sanguineum* Brid. (*B. erythrocarpum* Schw.)", which is *B. microerythrocarpum* Müll.Hal. & Kindb. as currently understood. According to Mitten (1856), *Bryum rubens* is "easily distinguished" from the latter species "by its leaves being twice as wide and the margin, distinctly not recurved, the serratures larger, the areolation composed of cells of about the same length, but double the width". Indeed, this is an apt description and its main features (leaf shape, serrature, and areolation) were captured by Mitten in fine drawings mounted on the same sheet as the collections from "Hassocks, Hurstpierpoint" and "Danny plantations, Hurstpierpoint" made in 1846. William Mitten (1819–1906) was born at Hurstpierpoint, Sussex. His neighbour, the lichenologist William Borrer, encouraged him to concentrate his botanical interests on mosses and allowed Mitten the use of his library and herbarium (British Bryological Society). Both collections from Hurstpierpoint clearly represent Mitten's *B. rubens*. We select the specimen (packet) from Hassocks as the lectotype of *B. rubens*, which was also indicated as "type" in Crundwell & Nyholm's (1964) publication.

***Bryum rubens* Mitt.**, *Hooker's J. Bot. Kew Gard. Misc.* 8: 232. 1856. — Fig. 2.

Lectotype (designated here): Hassocks, June 1846, W.M. (NY, herb. Mitten, sheet Europe 24/16).

This small packet is mounted above the drawing of two leaves of *Bryum rubens* which are compared with a leaf of *B. sanguineum* (Fig. 2).

LECTOTYPIFICATION OF *BRYUM BOMANSSONII*

Bryum bomanssonii was described as a new species by S.O. Lindberg at a meeting of the Societas pro Fauna et Flora Fennica on 1 March 1884. The minutes of this meeting in *Botaniska Notiser 1884: 67* give a valid description of the species. Lindberg considered *B. bomanssonii* close to *B. erythrocarpum*, from which it was distinguished by its wider leaves with larger cells and more strongly serrated margins. The protologue states that Bomansson collected this species in three locations on Åland (off the coast of Finland) and in Uppland (Sweden). Lindberg's herbarium in H contains several specimens that were collected by Bomansson. We selected a typical specimen from Åland that was collected before 1884 as the lectotype of *B. bomanssonii*. Collections by Bomansson from Åland in G, P, and S are all younger than March 1884 and cannot be selected as lectotype or considered as paratypes. Morphologically, the

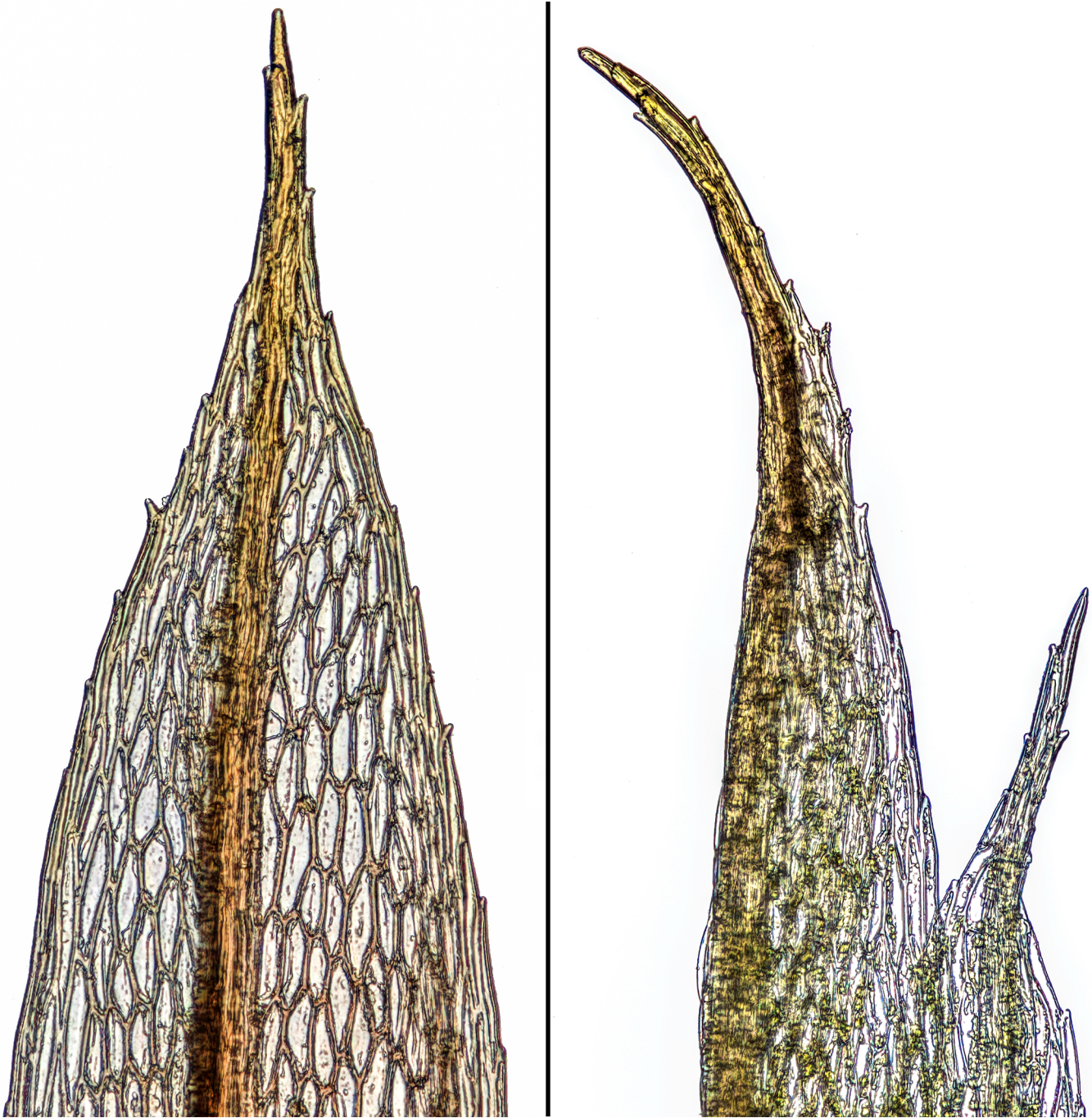


Fig. 4. Leaf apex of *Ptychostomum touwii* Bijlsma, Kruijer & M. Stech in top view (left) and side view (right) (holotype). Photo: D. Haaksma.

lectotype belongs to the same morpho-molecular species as the lectotype of *Bryum rubens*, which makes *Bryum bomanssonii* a synonym of *Ptychostomum rubens* in our restricted sense. *Bryum bomanssonii* has previously been synonymised with *B. rubens* by Crundwell & Nyholm (1964: 629).

***Bryum bomanssonii* Lindb., Bot. Not. 1884: 67. 1884.**

Lectotype (designated here): Åland, [Vengsäda?] i sandiga åkesdiken, 4-8-1874, J.O. Bomansson (H-SOL 390 006).

***Ptychostomum touwii* Bijlsma, Kruijer & M. Stech, spec. nov.**

Dioicous. Sterile shoots and innovations with erect, flexuose or twisted leaves when dry. Leaves erecto-patent when moist, evenly arranged and not much differing in shape along the stem, oblong-lanceolate with acuminate apex gradually narrowed and recurved into a denticulate, excurrent nerve; margin plane or recurved in lower half, bordered with 2–3 rows of incrassate cells, denticulate in upper part; nerve short-excurrent; cells in middle of leaf thin-walled, hexagonal, c. 18 × 60 µm. Rhizoidal gemmae spherical, c. 200 µm when fully developed, abundant and clustered at base of stems and often solitary in leaf axils as well, crimson, red or red-brown, with protuberant more or less evenly sized cells, c. 37 µm wide. Mature sporophytes not seen.



Fig. 5. Moistened plants of *Ptychostomum rubens* (Mitt.) Holyoak & N.Pedersen (*Bijlsma 16411*, herb. R.J. Bijlsma). Photo: H.N. Siebel.

Holotype: Netherlands, Province of Limburg, municipality Gulpen-Wittem, Wylrebos, on bare loess, 28-3-2014, R.J. Bijlsma 15341 (L [L0255102]).

Paratypes:

Netherlands

Province of Gelderland — Municipality Epe, nature restoration area Wisselse Veen, 4-4-2015, R.J. Bijlsma 16528 (L [L0818583]; herb. R.J. Bijlsma); Municipality Rheden, nature restoration area Soerense Broek, 29-11-2014, R.J. Bijlsma 16138 (L [L0818581]; herb. R.J. Bijlsma); Dreumel, Dreumelse Waard, Waal floodplain, 21-8-2011, J. Nieuwkoop s.n. (L [L0872982]).

Province of Noord-Brabant — Schijndel, Achterste Hermalen, arable field, 12-11-2010, M.J. Smulders s.n. (L [L0873016]).

Province of Zuid-Holland — Katwijk, on sand dunes, 19-3-2013, T.T. Luong 13005 (L [L0854749]).

Recently collected specimens have immature sporophytes only. The description of the mature sporophyte awaits a further revision of older collections.

The species epithet is named after the Dutch bryologist Andries Touw, who contributed to Asian and African bryology and co-ordinated a full revision of all Dutch herbarium specimens of mosses, which resulted in a comprehensive Dutch Moss Flora, *De Nederlandse Bladmossen* (Touw & Rubens 1989).

KEY TO *PTYCHOSTOMUM RUBENS*, *P. TOUWII* AND *P. BORNHOLMENSE*

Typical plants of *Ptychostomum rubens* and *P. touwii* can be distinguished by leaf posture and shape of the leaf apex, as given in the key below, which includes the related *P. bornholmense* (see also Crundwell & Whitehouse 2001).

1. Rhizoidal gemmae scattered on long rhizoids, spherical to potato-shaped, up to 330 µm in diameter, dull, orange to brown or red-brown, with smooth outline; cells strongly differing in size. Leaves on older (branched) stems in comal tufts *Ptychostomum bornholmense*
1. Rhizoidal gemmae on short rhizoids clustered at the base of stems and often in leaf axils as well, spherical, up to 260 µm in diameter, often glossy, crimson, red or red-brown; cells evenly sized and protuberant. Leaves not in comal tufts 2
2. Sterile shoots and innovations with evenly arranged leaves; older stems mostly intact (Fig. 3). Leaves not or weakly differing in shape along the stem, oblong-lanceolate, erecto-patent when moist; apex denticulate, gradually narrowed and recurved into excurrent nerve (Fig. 4) *Ptychostomum touwii*
2. Sterile shoots and innovations with upper leaves erect, often bud-like appressed; lower leaves more distant, spreading (Fig. 5); older stems often broken off below the bud-like shoot tip (Fig. 6). Leaves oblong to elliptical; apex clearly delimited; excurrent nerve bent outwards as a short, almost smooth point or hair (Fig. 7) *Ptychostomum rubens*



Fig. 6. Moistened old plants of *Ptychostomum rubens* (Mitt.) Holyoak & N. Pedersen (*H.N. Siebel 2015.139*, herb. H.N. Siebel). Photo: H.N. Siebel.

ECOLOGY AND DISTRIBUTION

Ptychostomum rubens is a species of disturbed, base-rich, often calcareous and nutrient-rich soils. In the Netherlands it is a common species in calcareous coastal dunes, grasslands and fields in limestone and loess areas and in floodplains. It grows frequently together with species such as *Barbula unguiculata* Hedw., *Fissidens taxifolius* Hedw., *Phascum cuspidatum* Schreb. ex Hedw., *Tortula truncata* (Hedw.) Mitt. and *Weissia* species.

Ptychostomum touwii prefers disturbed, neutral to slightly acidic, sandy-loamy soils. In the Netherlands it occurs in cover sand areas, including arable fields, but also in decalcified coastal dunes and sandy soils along the main rivers. Commonly accompanying species are *Bryum microerythrocarpum* Müll. Hal. & Kindb., *Ceratodon purpureus* (Hedw.) Brid., *Ditrichum cylindricum* (Hedw.) Grout, *Leptobryum pyriforme* (Hedw.) Wilson and *Physcomitrium pyriforme* (Hedw.) Hampe.

Sometimes *Ptychostomum rubens* and *P. touwii* grow next to each other in locations with gradients in soil conditions and on soils intermediate in base and nutrient status. Distribution maps and details of the ecology of both species in the Netherlands will be presented in a separate paper.

Ptychostomum bornholmense is restricted to disturbed, dry, nutrient-poor sandy soils or acidic loam in (former) heathland areas and in woodlands, in particular on uprootings, and grows

often together with *Atrichum undulatum* (Hedw.) P. Beauv., *Dicranella heteromalla* (Hedw.) Schimp. and *Polytrichum formosum* Hedw.

A NOTE ON BRYUM MICROERYTHROCARPUM

Bryum rubens and *B. microerythrocarpum* were both included in the *Bryum erythrocarpum*-complex by Crundwell & Nyholm (1964) and have large, red or orange-red rhizoidal gemmae in common. Crundwell & Nyholm (1964) considered *Bryum microerythrocarpum* as “an exceedingly variable species” and did not exclude the possibility that additional species could be separated “after research on a much larger scale than we have been able to undertake”. Ochi (1980, 1994) further synonymised several South American species with *B. microerythrocarpum*, including *B. dentiferum* Hampe, *B. rubrinerve* Cardot & Broth. and *B. subapiculatum* Hampe. The latter is the oldest and now commonly adopted name. Demaret (1993), however, questioned this synonymy and also other authors, by way of precaution, retained the name *B. microerythrocarpum* (Nyholm 1993; Meinunger & Schröder 2007). Based on the examination of herbarium material of *B. subapiculatum*, *B. dentiferum* and *B. rubrinerve* Cardot & Broth. from BM, we conclude that these three South American taxa are conspecific and, albeit being close to *B. microerythrocarpum*, differ consistently from the

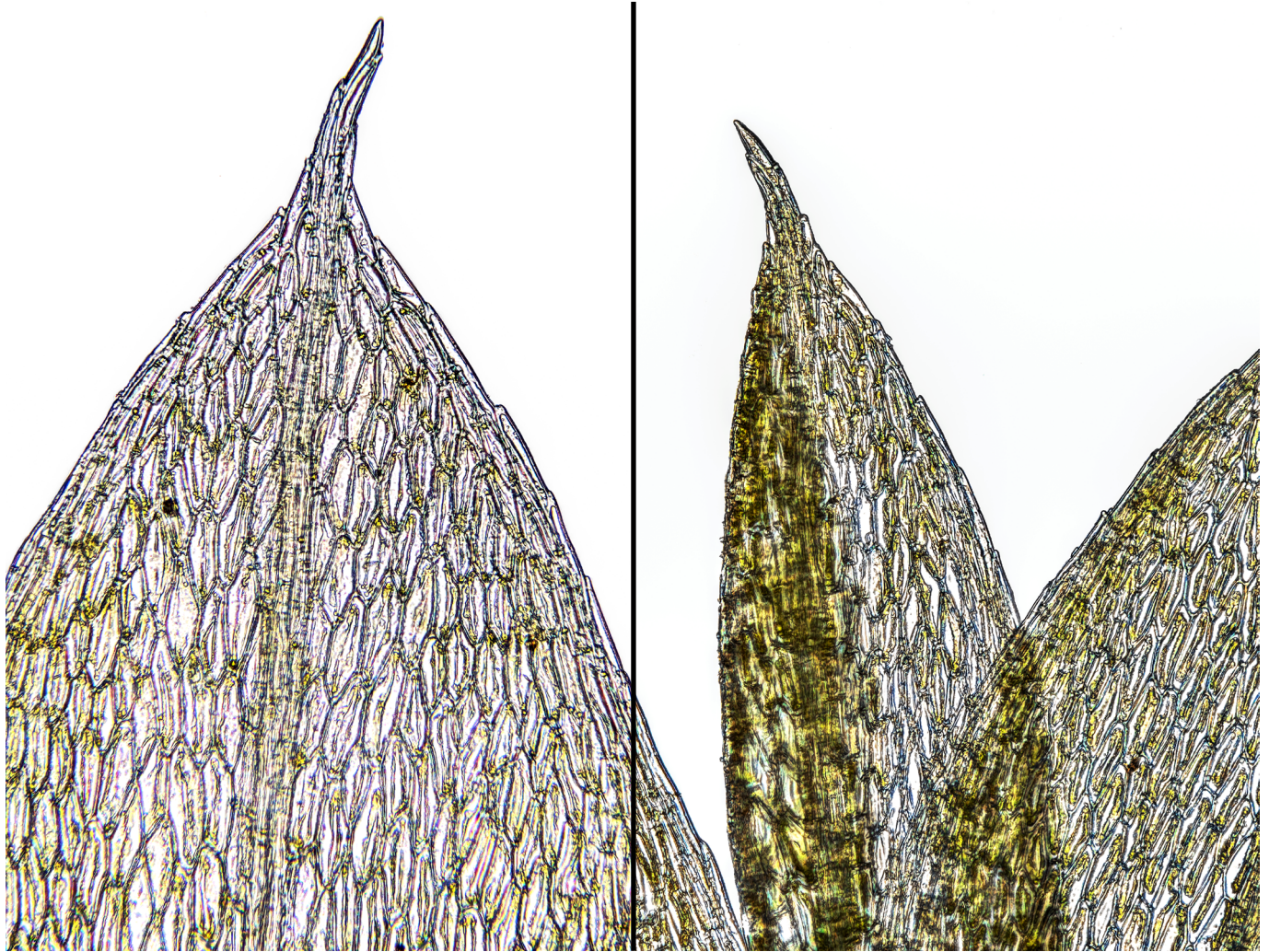


Fig. 7. Leaf apex of *Ptychostomum rubens* (Mitt.) Holyoak & N.Pedersen in top view (left) and side view (right) (*Bijlsma 16411*, herb. R.J. Bijlsma). Photo: D. Haaksma.

latter as understood by us. Material from the South American species shows dense, pale green to yellow-green tufts with rigid shoots bearing ovate, finely serrulate leaves, where *B. microerythrocarpum* in our circumscription mostly occurs in dark green tufts becoming red in exposed conditions, not unlike those of miniature *B. alpinum* Huds. ex With. The leaves of *B. microerythrocarpum* are more lanceolate, often canoe-shaped.

Although we could not study the rhizoidal gemmae and other microscopic details, we propose to exclude these three conspecific South American taxa from the concept of *Bryum microerythrocarpum*. Further molecular research of this group is necessary and should also include other closely related species such as *B. duriusculum* Hook.f. & Wilson from New Zealand (Fife 2015).

Based on previous molecular studies on the phylogeny and morphological evolution of the moss family Bryaceae (e.g., Holyoak & Pedersen 2007, Pedersen et al. 2007), Hodgetts et al. (2020) classified *Bryum subapiculatum*, and *B. tenuisetum* Limpr., in the genus *Imbribryum* N.Pedersen, for which Bell & Holyoak (in Hodgetts et al. 2020) made the combinations *Imbribryum subapiculatum* (Hampe) D.Bell & Holyoak and *I. tenuisetum* (Limpr.) D.Bell & Holyoak. Since *B. microerythrocarpum* is closely related to both *I. subapiculatum* and *I. tenuisetum*, it is safe to assume that *B. microerythrocarpum* belongs to the same genus. Hence we make the following combination to accommodate this species in *Imbribryum*:

***Imbribryum microerythrocarpum* (Müll.Hal. & Kindb.) Bijlsma, Kruijer & M. Stech, comb. nov.** – Basionym: *Bryum microerythrocarpum* Müll.Hal. & Kindb., *Catalogue of Canadian Plants. Part VI. Musci*: 124. 1892.

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