Journal of Bryology

ISSN: 0373-6687 (Print) 1743-2820 (Online) Journal homepage: http://www.tandfonline.com/loi/yjbr20

Description and phylogenetic investigation of Pogonatum shevockii N.E.Bell & Hyvönen (Polytrichaceae), a new East Asian species with a unique leaf morphology

Neil E. Bell, Jaakko Hyvönen, Kuei-Yu Yao & Wen-Zhang Ma

To cite this article: Neil E. Bell, Jaakko Hyvönen, Kuei-Yu Yao & Wen-Zhang Ma (2017): Description and phylogenetic investigation of Pogonatum shevockii N.E.Bell & Hyvönen (Polytrichaceae), a new East Asian species with a unique leaf morphology, Journal of Bryology, DOI: 10.1080/03736687.2017.1312732

To link to this article: http://dx.doi.org/10.1080/03736687.2017.1312732

Description and phylogenetic investigation of *Pogonatum shevockii* N.E.Bell & Hyvönen (Polytrichaceae), a new East Asian species with a unique leaf morphology

Neil E. Bell [1], Jaakko Hyvönen [2], Kuei-Yu Yao [3], Wen-Zhang Ma [4]

[1]Royal Botanic Garden Edinburgh, Edinburgh, Scotland, UK, [2]Botanical Museum & Department of Biosciences, Viikki Plant Science Centre, University of Helsinki, Helsinki, Finland, [3]Taiwan Endemic Species Research Institute, JiJi, Nantou County, Taiwan, [4]Herbarium, Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China

We describe *Pogonatum shevockii* from Taiwan, a new species with a number of unusual features. A single collection from Yunnan is treated as conspecific, although further sampling is required to confirm whether morphological and molecular differences from the Taiwanese material are sufficiently consistent to be recognised taxonomically. The plants have a remarkable leaf structure with a 3-stratose lamina including a central row of large hyaline cells that may be responsible for the abaxial surfaces of leaves appearing distinctly pale-glaucous when dry. These cells often have globular inclusions that appear variously dark or speckled yellow-brown/blue-green depending on magnification. In fresh material of Taiwanese specimens the calyptra hairs are often distinctly green, another unusual feature in the Polytrichaceae. Molecular phylogenetic analyses including exemplars from 75% of *Pogonatum* species strongly support the monophyly of the new taxon and tentatively place it as sister to a clade including five species with geminate apical lamellar cells, namely the exclusively Central and Southern American *P. campylocarpum*, *P. neglectum*, *P. comosum* and *P. procerum* and the Asian *P. microstomum*.

Keywords: Bryophyte, Glaucous, Leaf structure, Mosses, Phylogenetics

Introduction

Pogonatum P.Beauv. is the most diverse genus within the Polytrichaceae containing more than 50 species (Hyvönen, 1989; Hyvönen & Wu, 1993; Koskinen & Hyvönen, 2004). Morphologically very well circumscribed by characters of the sporophyte, it is either monophyletic, or else includes a monophyletic group in which all but a few of the species occur [18S data suggest that *P. urnigerum* (Hedw.) P.Beauv., *P. perichaetiale* (Mont.) A.Jaeger, *P. dentatum* (Menzies *ex*. Brid.) Brid. and *P. japonicum* Sull. & Lesq. might be outside of a clade in which *Polytrichum* Hedw. is sister to the majority of *Pogonatum* species, although this is contradicted by chloroplast and mitochondrial data; Bell & Hyvönen, 2010]. In November 2012 Jim Shevock and the third author, accompanied on one occasion by En-Liang Chu and with colleagues from the Taiwan Endemic Species Research Institute (TAIE), collected an unusual *Pogonatum* at three locations in Chiayi and Nantou Counties in the mountains of central Taiwan. The plants were growing at altitudes of between 2000 and 2300 m on small, smooth-surfaced boulders on semi-exposed forested ridges in dense hardwood-conifer forest (Figure 1) and notably had green, hairy calyptras and leaf surfaces that when dry were glaucous-white abaxially and green adaxially. These specimens were examined by the fourth author in May 2013 during a visit to the California Academy of Sciences, and brought to the attention of the first two authors when they could not be referred to a named species based on the synopsis of the genus (Hyvönen, 1989). During subsequent excursions in 2014, 2015 and 2016, further specimens were found at similar sites in Chiayi, Nantou and Yunlin counties (the former at 2350 m and the latter just below 1800 m). Meanwhile, just 10 days before the Yunlin collection was made in October 2015, the fourth author, accompanied by Jim Shevock, Y. L. Yao and X. L. Deng, found a very similar looking plant at 2240 m in the mountains of southern Yunnan, nearly 2000 km to the west.

Correspondence to: Neil E. Bell, Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, Scotland, UK. Email: n.bell@rbge.ac.uk

DOI 10.1080/03736687.2017.1312732

Figure 1 Habitat and living material of *Pogonatum shevockii*. (A) Type locality, at 2125 m altitude on the Sun-Link-Sea Trail, Alishan Township, Chiayi County, Taiwan. The species occurs on the boulder immediately to the left of the trail in the centre of the picture. (B) Gametophores and young sporophytes *in situ*. Although the calyptrae appear yellowish here, when mature, fresh and dry they are usually distinctly green in Taiwanese material.

Our herbarium-based morphological studies confirmed that these collections represent at least one species new to science with a number of unique and remarkable features, this being corroborated by sequence level characters obtained from four of the seven existing specimens. Here we describe *Pogonatum shevockii* and typify it with one of the Taiwanese collections. The single Yunnan specimen, while very similar, is distinct both morphologically and in terms of molecular characters (see below) and could conceivably represent a second closely related species. However, this cannot be determined until more collections become available and we currently regard it as conspecific.

Taxonomy

Pogonatum shevockii N.E.Bell & Hyvönen, ***sp. nov.***

Type: Taiwan: Chiayi County, Alishan Township. Along the 10 km contour route section of the Sun-Link-Sea Trail at the saddle ridge of Lucynshan toward Shueiyang Forest, 23°35′49″N, 120° 48′04.5″E, 8 November 2012, 2125 m, *Shevock, Yao & Chu 41562* (**holotype** TAIE, **isotypes** CAS, H [dup. E], KUN, MO, NY). (Figures 3, 4)

Paratypes: Taiwan: Chiayi County, Alishan National Forest Recreation Area. Along the lower ridge of the trail to Tashan, less than 0.5 km above junction of Mianyue and Jhushan sections of the historic Alishan Railway. Open secondary *Cryptomeria* D.Don and *Chamaecyparis* Spach forest. On metamorphic boulders in filtered light, 23°31′40″N, 120°48′53′E, 20 October 2016, 2350 m, *Shevock, Yang, Yao & Schäfer-Verwimp 49629* (CAS, E, TAIE); Nantou County. Jhushan Township, Sun-Link-Sea Forest Recreation Area. Along the 4 km trail near the summit ridge of Jinganshu Mountain, 23°38′29″N, 120°48′50.4″E, 7 November 2012, 2090 m, *Shevock & Yao 41505* (CAS, H [dup. E], NY, TAIE); Sun-Link-Sea Trail along ridge forming boundary between Nantou and Chiayi counties at summit of Lucynshan, 23°36′03″N, 120° 47′28.5″E, 9 November 2012, 2290 m, *Shevock & Yao 41614* (CAS, H [dup. E], KUN, MO, TAIE); Sun-Link-Sea Trail under the saddle ridge of Lucynshan toward Shueiyang Forest, 23°35′52.3″N, 120° 47′59.6″E, 14 November 2014, 2090 m, *Yao 6092* (TAIE); Yunlin County, south route trail to Mt. Shihbi and Jiananyun Peak on divide just below summit of Jiananyun Peak, 23°36′39.5″N,

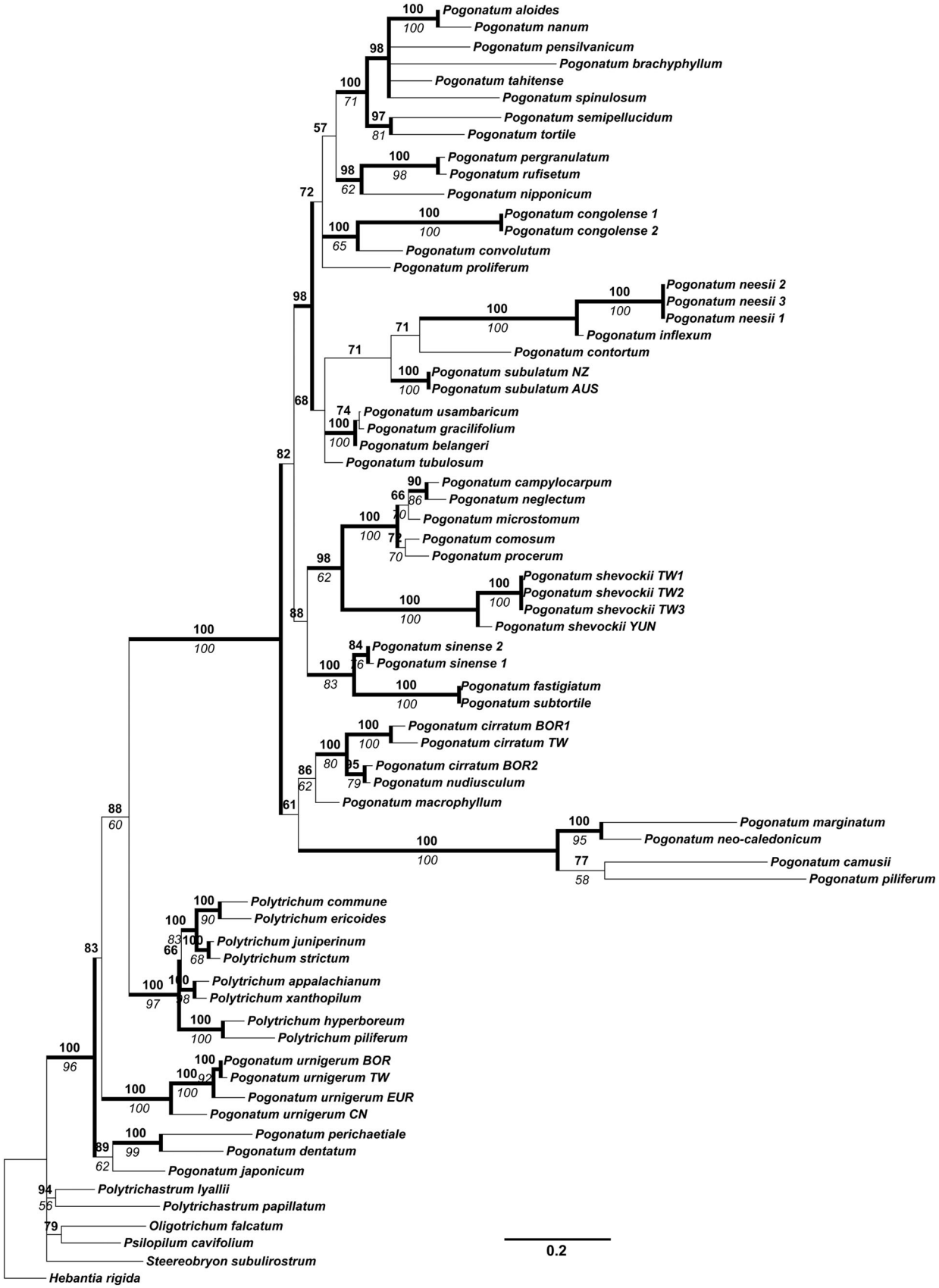

Figure 2 Bayesian 50% majority consensus phylogram resulting from the MrBayes analysis of the combined dataset. Numbers above branches are posterior probabilities, numbers in italics below branches are bootstrap values for corresponding branches of the maximally likely topology resulting from the RAxML analysis of the same dataset.

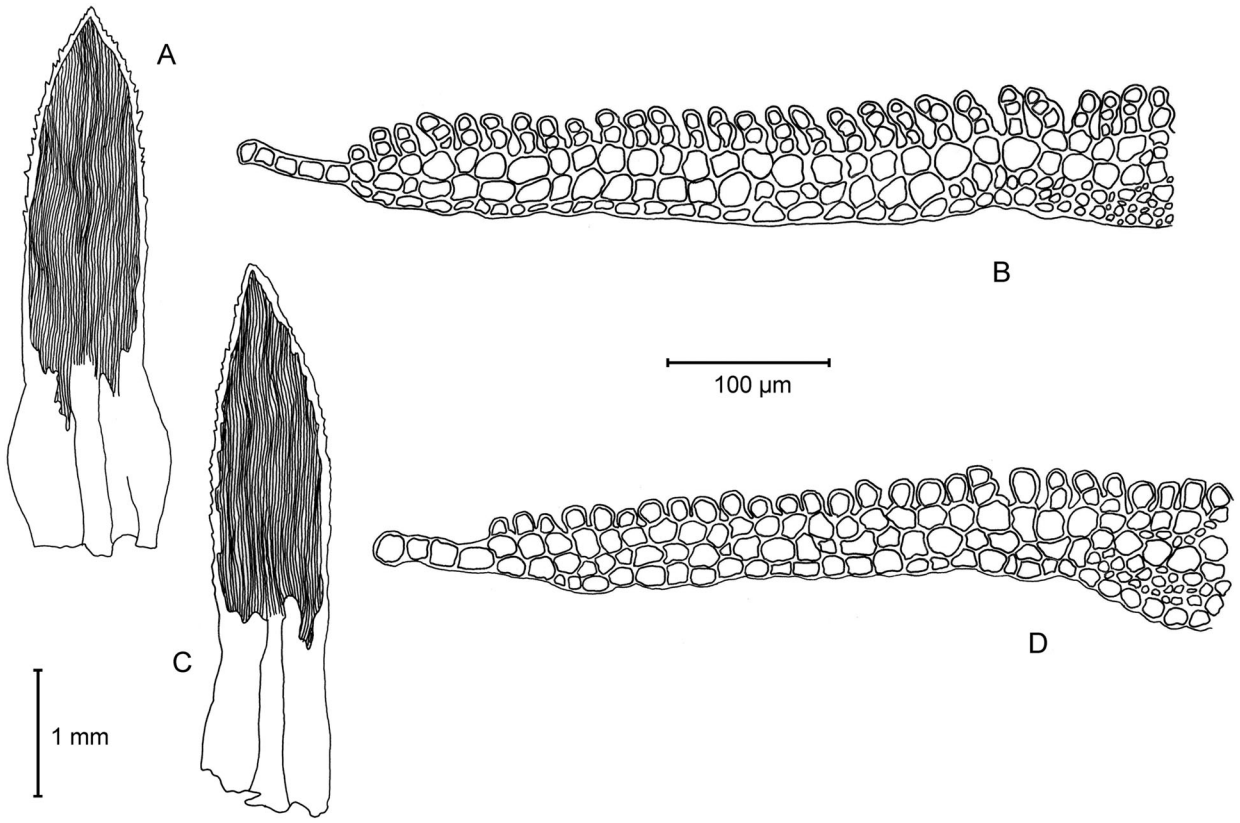

Figure 3 ***Pogonatum shevockii*** **N.E.Bell & Hyvönen. (A, C) Leaves. (B, D) Transverse sections of leaves. (A, B) from** ***Shevock, Yao & Chu 41562*****, Taiwan (isotype, H). (C, D) from** ***Shevock & Yao 47925*****, Yunnan (E).**

120°43′50″E, 10 October 2015, 1795 m, *Shevock & Yao 47925* (CAS, E, TAIE); YUNNAN: Jin-Ping County, Liang-Zi Village, Fen Shui-Ling National Nature Reserve, Xi-Long Mountain, on granitic rock along trail in old growth broadleaved forest, 22°40′10″N, 102°46′48″E, 30 September 2015, 2240 m, *Ma, Yao & Deng 15-7040* (CAS, E, KUN, PE, TNS).

Etymology: The species is named in honour of James R. (Jim) Shevock in recognition of his outstanding contribution to knowledge of tropical bryophyte diversity, particularly through his extensive fieldwork in East Asia.

Plants small to medium sized with short unbranched shoots developing from a persistent protenemal mat. Well-defined polytrichoid central strand lacking. Dioicous, male plants unknown. Female plants mostly 4–6 mm high, comose, generally with only 8–10 mature leaves present. Perichaetial leaves mostly not distinctly differentiated from upper vegetative leaves. Leaves when moist erecto-patent to spreading, moderately soft in appearance. Dry leaves in different specimens ranging from erect to moderately incurved with tips slightly curled but not clearly twisted, to distinctly incurved and somewhat twisted and contorted (this variation more or less inversely correlating with lamellar height). Abaxial sides of leaves when dry appearing distinctly glaucous-white to very pale green, with some darker areas (margins and nerve as well as single longitudinal rows of cells elsewhere) strongly contrasting. Adaxial surfaces uniformly deep green.

Leaves (2.7)3.5–5(5.5) mm long, (0.7)0.8–1.1(1.3) mm wide at widest point. Sheathing lamina variable in relative length, comprising 20–40% of total leaf length, (0.8)1–1.3 mm wide at base. Nerve as visible in sheathing lamina from above or below (150)200–550 µm wide at insertion. Chlorophyllose and sheathing laminae well differentiated, hinge cells not clearly differentiated. Chlorophyllose lamina obovate-lanceolate, narrowed towards junction with sheath; sheath ovate-subtriangular to oblong. Adaxial cells of lamina with thin walls, approximately 15–25 µm in central part. Margin of chlorophyllose lamina ± prominently toothed from $(\frac{1}{4})\frac{1}{3}$–$\frac{1}{2}$ of distance from base upwards, teeth multicellular, mostly with enlarged, pointed end-cells, these becoming spinose and often brown-orange coloured towards leaf apex. Lamina/nerve not toothed abaxially (occasionally some very low projections at extreme apex). Lamellae (30)40–52, extending over most of lamina surface, lamina with single-stratose border (3)4–7(8) cells wide. Lamellae 1–3(4) cells high (*not* including enlarged basal cell corresponding to upper surface of multistratose part of lamina), apical cells undifferentiated. In lateral view lamellae straight, ± smooth (not

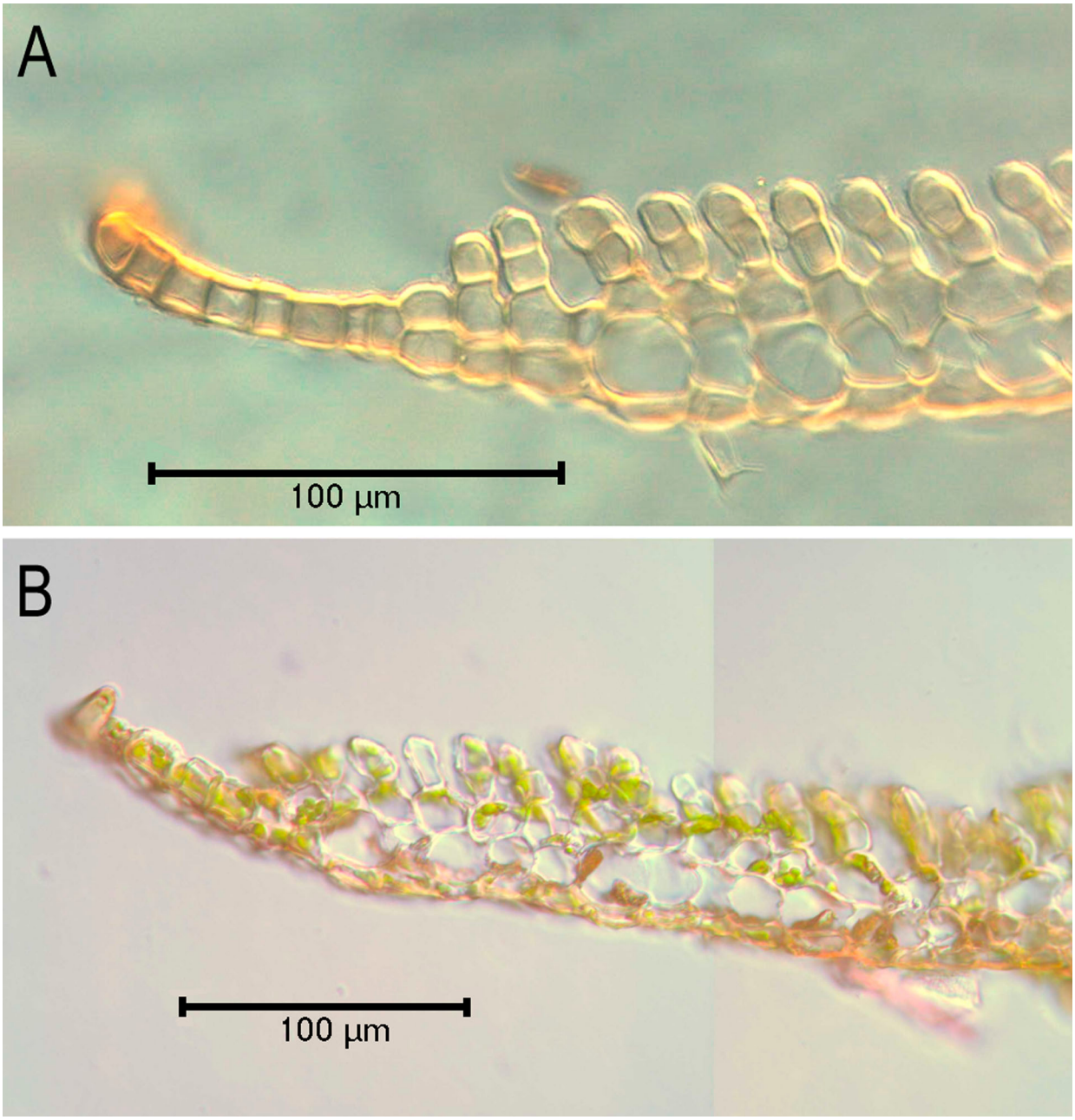

Figure 4 Transverse sections of leaves of ***Pogonatum shevockii*** **N.E.Bell & Hyvönen. (A) From *Shevock, Yao & Chu 41562*, Taiwan (holotype, TAIE). (B) From *Shevock, Yao & Chu 41562*, Taiwan (isotype, H); composite image from two separate photographs. The orange-brown inclusions that can be seen clearly in one of the large hyaline cells in the centre of image (B) are often much more abundant, and appear distinctly dark-coloured at lower magnifications.**

crenate). Leaves in TS showing distinct, thickened central nerve, relatively narrow compared to some other 'polytrichoid' (Smith, 1971) taxa, this fairly abruptly transitioning into extensive 3-stratose lamina underlying the lamellae and extending fully or almost fully to transition with unistratose border. Practically only an abaxial stereid band of cells with firm walls present, only few scattered cells with incrassate walls adaxially. Adaxial layer of 3-stratose lamina comprising markedly enlarged chlorophyllose cells forming bases of lamellae, 12–25 µm. Abaxial layer comprising smaller chlorophyllose cells, 10–17(19) µm, with ± incrassate cell walls often orange-brown in defined central part of nerve. Central layer of generally large (10–25 µm) cells sandwiched between adaxial and abaxial layers, these being mostly hyaline, but (in reasonably fresh material at least) often with numerous agglutinated globular inclusions that appear black under lower-power light microscopy and speckled brown-yellow/blue-green under 100× oil-immersion objective. Cells of unistratose border mostly 8–15 µm wide viewed from above or below, square to irregularly short-rectangular or oval. Sheath cells long-rectangular or long-hexagonal at

insertion, 40–100 μm long, becoming progressively shorter (to 16–30 μm) towards contracted junction with chloroplyllose lamina.

Calyptrae densely and robustly hairy, with hairs longer than mature capsule and forming a thick mat considerably wider than capsule itself; often distinctly green when fresh, gradually becoming golden-yellow in herbarium specimens. *Sporophytes* observed in all specimens but (±) fully mature only in three, including the holotype (*Shevock, Yao & Chu 41562*, *Shevock & Yao 41505*, *Shevock & Yao 41614*). Seta 10–14 mm, pale orange-brown when mature, straight to sinuose. *Capsules* ±2 mm, short-cylindrical, erect to inclined, terete (occasionally with ±5 slight angles), usually slightly contracted immediately below wide mouth. *Exothecium* slightly scabrous but not distinctly papillose or mamillose, outer cells isodiametric square-hexagonal to short-rectangular or short-hexagonal, only moderately incrassate, 22–65 × 18–40 μm. *Peristome* 150–215 μm high, individual teeth 100–200 μm. Teeth ±32, double, red-orange with yellow-brown margins when dry. *Operculum* flat to slightly convex, rostrate, with rostrum slightly curved. *Spores* (7.5) 9–10 μm in diameter.

Phylogeny

Materials and methods

We assembled a matrix of 51 exemplars of *Pogonatum* from 41 species (approximately 75% of currently accepted species), comprising partial sequences of the nuclear 18S and ITS2 regions, the chloroplast *rbc*L and *rps*4 genes, the chloroplast *rps*4-*trn*S intergenic spacer, the chloroplast *trn*L-F region (including the *trn*L group I intron, the *trn*L-F intergenic spacer and parts of the *trn*L and *trn*F exons) and the mitochondrial *nad*5 gene (including the group I intron). Most of the sequences were generated for previous studies by the authors (e.g., Koskinen & Hyvönen, 2004; Bell & Hyvönen, 2010; Daniels *et al.*, 2016), with a small number being previously unpublished (see Appendix 1). A further 14 species of Polytrichaceae were included as outgroups along with four exemplars of *P. shevockii*, resulting in a matrix of 69 terminals in total. One or several of the regions sampled were unavailable for most terminals (Appendix 1) and this is likely to have negatively affected resolution and support values. The precise manner in which missing data affect the results of different types of phylogenetic analyses is still debated (e.g., Wolsan & Sato, 2010; Wiens & Morrill, 2011; Simmons, 2012; Simmons & Goloboff, 2014), although it is clear that this is not a simple problem with a single solution but has many aspects, both practical and theoretical (Wheeler, 2012). Our own experience suggests that missing data are unlikely to result in high support values for erroneous phylogenetic reconstructions using model-based methods where sufficient informative characters have been sampled and the data are appropriately partitioned.

For *P. shevockii* all seven sampled regions were obtained for all four exemplars, except that the 18S region was only sequenced for a single Taiwanese specimen. Genomic DNA was isolated using the Invisorb spin plant mini kit (Invitek, Berlin, Germany) and eluted DNA stored in the supplied buffer. PCR amplifications were performed either in 50 μl reactions with 1.25 U Fermentas DreamTaq polymerase and DreamTaq buffer (Fermentas, Burlington, Ontario, Canada), 200 μM dNTPs and 0.3 μM of each primer, or else in 20 μl reactions with 0.15 μl of Biotaq DNA polymerase (Bioline, London, UK), 2 μl of the supplied 10× reaction buffer, 1 μl of 50 mM $MgCl_2$, 0.75 μl of each primer at 10 μM and 2 μl of dNTPs at 200 μM. Protocols for PCR and primer sequences for all regions other than ITS2 were as detailed in Bell & Hyvönen (2010). For ITS2, the protocol consisted of an initial step of 95° for 4 min, followed by 35 cycles of 94° for 1 min, 55° for 1 min, 72° for 1 min 30 s and then a final extension step of 72° for 7 min. Primers were seqITS2 (Olsson *et al.*, 2009) and ITS4bryo (Stech *et al.*, 2003). Sequencing of PCR products was carried out either by Macrogen Europe (Amsterdam, The Netherlands) or by the Genepool facility at the University of Edinburgh using the sequencing primers detailed in Bell and Hyvönen (2010), and the above PCR primers in the case of ITS2.

Sequences of 18S, *rbc*L, *rps*4, the *rps*4-*trn*S intergenic spacer, the *trn*L-F region and *nad*5 were manually aligned following the methods described for these same regions in Bell *et al.* (2015). There was little alignment ambiguity for these regions although a small number of short areas were excluded from 18S, the *rps*4-*trn*S spacer, the *nad*5 intron and the *trn*L-F region as described in detail in Bell *et al.* (2015). The ITS2 region was considerably more variable and alignment was accomplished using MUSCLE (Edgar, 2004), with areas of significant alignment ambiguity subsequently excluded. Phylogenetic analysis of the concatenated matrix was conducted using maximum likelihood (ML) and Bayesian model-based methods in addition to parsimony as an optimality criterion. Further separate ML analyses of the 18S region, the ITS2 region and the concatenated chloroplast and mitochondrial data were undertaken to screen for possible supported incongruence between either of the two nuclear regions and the exclusively maternally inherited chloroplast and mitochondrial data (which itself is invariably congruent in studies of the family, e.g., Bell & Hyvönen, 2010). Seven partitions were defined

corresponding to each of the aforementioned regions. MrModeltest v.2.2 (Nylander, 2004) was used to estimate the best-fitting model for each partition using the Akaike information criterion (AIC; Akaike, 1974), although we chose not to implement models specifying both a gamma parameter (G) for rate variation between sites and a proportion of invariant sites (I) due to concerns that these parameters may influence each other's correct estimation (e.g., Mayrose *et al.*, 2005), or at least make a stable estimation (and thus run convergence) time consuming under Bayesian analysis. For analysis of the concatenated datasets under both ML and Bayesian methods the same model was applied to all compartments, this being the one with the highest AIC score for the majority of the regions after I + G models were excluded.

ML analyses were conducted using RAxML v.7.4.2. (Stamatakis, 2006) with the raxmlGUI v.1.3 front end (Silvestro & Michalak, 2012). The 'ML + thorough bootstrap' option within the raxmlGUI (RAxML option '-b' followed by an ML search) was used on the partitioned dataset, with 50 runs and 500 replications. Bayesian phylogenetic analyses were conducted using MrBayes v.3.1.2 x64 (Ronquist & Huelsenbeck, 2003). Partitions were unlinked to allow parameters other than topology to vary independently. In each analysis, three independent runs using the default prior settings, each with five chains ('temp' parameter = 0.1), were run simultaneously for 2.5×10^7 generations with trees sampled every 1000 generations. Adequate sampling from the cold chain at stationarity and convergence of independent runs was assessed by checking that the average standard deviation of split frequencies was <0.01, potential scale reduction factor values were near 1.00, effective sample sizes for each parameter were meaningful, and sampling from the posterior probability (PP) distribution was accurate as assessed by examination of log-likelihood trace files in Tracer v.1.6.0. The first 60% of trees (including those from the burn-in phase) were discarded and a majority-rule consensus tree constructed using the remaining sample of 10,000 trees.

Parsimony analyses were performed using Nona (Goloboff, 1994) within the WinClada shell (Nixon, 2002), and TNT (Goloboff *et al.*, 2003, 2008). The molecular matrix used for the model-based analyses was supplemented with 49 morphological characters (Appendix S1) following Koskinen & Hyvönen (2004), but with the addition of two further characters and two character states as follows: character 9 was supplemented with a state (2) to describe apices typical for some species of *Polytrichum* (costa excurrent, margins folded over lamellae) and character 39 with a state (3) to describe capsules with 4(–5) angles, while a new character 32 described the walls of lamellar marginal cells as either thin to firm (0), outer walls incrassate (1) or all walls incrassate (2), and a new character 44 the position of stomata as either scattered (0) or restricted to the apophysis/basal part of the capsule (1). Note that these additions change the numbering sequence of characters 32 onwards as compared to Koskinen & Hyvönen (2004). Prior to these analyses we used the WinClada command 'Mop uninformative characters'. This resulted in a matrix of 741 characters. Nona analyses were performed using processor time as a seed to randomise the order of the terminals with the following settings: hold 30,000 (holding a defined number of trees), 100 replications (search performed with multiple tree bisection–reconnection algorithm mult*max*), and hold/3 (to define the starting trees for each replication). This was supplemented by another search with 1000 replications and the number of starting trees defined as 20. Jackknife (Farris *et al.*, 1997) support values were obtained with 100 replications of ten search replications (mult*10) and with one starting tree per replication (hold/1). As with the search for most parsimonious trees these analyses used processor time as a seed for randomisation and the tree bisection–reconnection algorithm (max*).

Results

After exclusion of areas of significant alignment ambiguity the concatenated matrix comprised 5850 characters, distributed among the sampled regions as follows: 18S—1693, ITS2—338, *nad*5—1780, *rbc*L—619, *rps*4—536, *rps*4-*trn*S spacer—356, *trn*L—528. The optimal models of nucleotide substitution for each compartment selected using the Akaike criterion within MrModeltest (excluding I + G models, as above) were GTR + I, HKY + G, GTR + I, GTR + I, GTR + G, GTR + G and GTR + G respectively, thus a GTR + G model was applied to all compartments in the combined analyses. For independent analysis of the 18S, ITS2 and combined chloroplast / mitochondrial datasets in RAxML the models applied were GTR + I, GTR + G and GTR + G (the HKY model is not implemented in RAxML). The only supported topological incongruence between the results of the independent RAxML analyses (incompatible clades supported with 70% BS values or above in both topologies) was the expected paraphyly of *Pogonatum* in the 18S analysis compared with its monophyly in the analysis of the combined organellar data (see Bell & Hyvönen, 2010), and the grouping of *P. neesii* (Müll.Hal.) Dozy with *P. shevockii* (84% BS) in the 18S analysis and with *P. inflexum* Sande Lac. (99% BS) in the chloroplast and mitochondrial analysis. However, as *P. neesii* has an

extraordinarily large number of autapomorphies in the 18S region (confirmed by sequencing of multiple exemplars), and a correspondingly long branch (more than six times longer than any other branch in the 18S topology and nearly 10 times longer than the next longest terminal branch), this result can fairly confidently be attributed to long branch attraction (Felsenstein, 1978) in the 18S dataset. We thus repeated the RAxML analysis of the 18S data with *P. neesii* excluded, resulting in an otherwise identical topology. As the incongruence of 18S with the other data regarding the monophyly or otherwise of *Pogonatum* only affects single nodes in each topology and does not extend to relationships within the large clade in which the majority of species occur (as also found previously, see Bell & Hyvönen, 2010), we considered it appropriate to perform the final analyses on the total combined data.

Topologies resulting from the ML and Bayesian analyses of the concatenated data were completely consistent, other than that *Pogonatum usambaricum* (Broth.) Paris grouped with *P. gracilifolium* Besch. in the Bayesian analysis (74% PP) and with *P. belangeri* (Müll.Hal.) A.Jaeger using ML (BS <50%), while *P. contortum* (Menzies *ex* Brid.) Lesq. was sister to the *P. neesii* / *P. inflexum* clade under Bayesian (71% BS) and to the *P. aloides* (Hedw.) P.Beauv. / *P. nanum* (Hedw.) P.Beauv. / *P. spinulosum* Mitt. / *P. pensilvanicum* (Bartram *ex* Hedw.) P.Beauv. / *P. brachyphyllum* (Michx.) P.Beauv. / *P. tahitense* Schimp. / *P. semipellucidum* (Hampe) Mitt. / *P. tortile* (Sw.) Brid. clade under ML (BS <50%). Figure 2 shows the Bayesian majority consensus tree with PP values as well as BS values from the ML analysis on corresponding nodes.

Pogonatum shevockii is resolved as monophyletic (100% PP & BS) with the three Taiwanese specimens forming a clade (100% PP & BS) distinct from the single Yunnan exemplar. It is tentatively placed (98% PP, 62% BS) as sister to a clade (100% PP & BS) of five species with geminate apical lamellar cells [*P. campylocarpum* (Müll.Hal.) Mitt., *P. neglectum* (Hampe) A.Jaeger, *P. microstomum* (R.Br. *ex* Schwäegr.) Brid., *P. comosum* (Müll.Hal.) Mitt. and *P. procerum* (Lindb.) Schimp.], four of which are exclusively Central and Southern American and one of which (*P. microstomum*) is widespread in South and South East Asia. This larger clade in turn is very tentatively supported (88% PP, BS <50%) as sister to a well-supported (100% PP, 83% BS) clade of three other SE Asian / Sino-Himalayan species [*P. sinense* (Broth.) Hyvönen & P.C.Wu, *P. fastigiatum* Mitt. and *P. subtortile* (Müll.Hal.) A.Jaeger]. As in the 18S topology, but contrary to the signal from the organellar data, *Pogonatum* itself appears as paraphyletic with the majority of species forming a well-supported (100% BS & PP) clade with a relatively long branch that is tentatively supported (88% PP, 60% BS) as sister to *Polytrichum* but excludes *Pogonatum urnigerum*, *P. dentatum*, *P. perichaetiale* and *P. japonicum*.

The topology obtained from parsimony analysis based exclusively on sequence level data (not shown) was to a large extent unresolved. Several clades are shared with the topology found in the model-based analyses but resolution is lacking for deeper nodes. Nonetheless, the new species was found to be monophyletic. When the matrix was supplemented with morphological characters 36 equally parsimonious trees of length 1857 steps were found with a CI (consistency index) of 0.41 (Kluge & Farris, 1969) and RI (retention index) of 0.73 (Farris, 1989). The (strict) consensus of these trees (see Supplementary Figure S1) deviates in many respects from the one obtained in the model-based analyses, although in all cases of incongruence within the ingroup jackknife support values are low or below 50%. *Pogonatum shevockii* is resolved in a clade together with four diminutive Asian species with persistent protonema [*P. piliferum* (Dozy & Molk.) Touw, *P. camusii* (Thér.) Touw, *P. neo-caledonicum* Besch. and *P. marginatum* Mitt.], while these together form the sister clade to the group of five species with geminate apical cells (see above).

Discussion

The general habit of *Pogonatum shevockii* is reminiscent of *P. microstomum*, a common (and normally distinctly larger) plant of the same region. However, it is quite distinct from all other known species of the genus in combining lamellae that are smooth (not crenate) when viewed laterally together with a number of other features, including low lamellae, a narrow nerve, undifferentiated and non-geminate lamellar apical cells, lack of abaxial teeth and a lack of heavily incrassate cells with rounded lumens on the back of the lamina (as are found in *P. cirratum* (Sw.) Brid. *s.l.*, and *P. convolutum* (Hedw.) P.Beauv., other species with low, smooth, non-geminate lamellae). Furthermore the 3-stratose structure of the leaf in TS with the abaxial surface glaucous when dry is unknown in any other species. The green calyptrae (when fresh) of the Taiwanese collections are also unusual and distinctive. This is corroborated by the molecular analyses, which strongly support monophyly and distinctness of the new taxon in a dataset that includes sampling from around 75% of all known species of *Pogonatum* (Figure 2). In parsimony analyses including morphological characters *P. shevockii* is placed as sister to a group of diminutive plants from SE Asia [recognised as section *Racelopus* (Dozy & Molk.) Touw by Touw (1986)]. Features shared with these species include persistent

protonema, small size, absence of the well-defined (polytrichoid) central strand, dorsal stereid band present only in costa in the central part of the leaf and low adaxial leaf lamellae. Whether *P. shevockii* also possesses the echinoid spore surface structure that this group shares with the genus *Polytrichum* is, as yet, unknown. However, this placement is at odds with the results of the model-based analyses of the molecular dataset, and thus it is possible that these shared features represent convergence of characters associated with small plant size.

The single collection from Yunnan differs from all of the Taiwanese specimens most notably in its lower lamellae; excluding the enlarged basal cell in the lamina these are mostly only one cell high (with a few being two cells high), as opposed to 2–4 (mostly 3) cells high in the Taiwanese material). Other differences are leaves that are more strongly incurved and twisted when dry, a generally longer leaf sheath that is oblong and less sharply differentiated from the chlorophyllose lamina, and slightly larger cells in the unistratose border (12–20 μm) and the lamellae (Figure 3). This is consistent with the strongly supported monophyly of the Taiwanese exemplars in the molecular phylogeny (Figure 2) and the relatively long branch separating these samples from the Yunnanese plant, which is comparable to the degree of molecular difference separating many other species within the genus. However, with only a single specimen from Yunnan available it is impossible to say at this stage whether any population level structure within the taxon has a geographical basis, and also whether the morphological differences observed are consistent. The distinct morphology of the Yunnanese plant is similar to infraspecific morphotypes that occur in other species and are unsupported by molecular data (e.g., the laxer forms of the recently recombined *Delongia cavallii* (G.Negri) N.E.Bell, Kariyawasam, Hedd. & Hyvönen; Bell *et al.*, 2015). Nonetheless, if increased future sampling continued to support reciprocal monophyly of the Yunnanese and Taiwanese populations as well as consistent morphological differences between them, recognition of a second species in Yunnan would be justified.

The most distinctive macro-morphological feature of *Pogonatum shevockii* is the abaxial (lower) surfaces of the leaves appearing dramatically pale-glaucous when dry, this contrasting with the deep green adaxial surfaces. This is presumably related to the unique leaf structure as seen in TS, in which an 'extra' layer of large, hyaline cells is sandwiched between the layer of similar-sized adaxial chlorophyllose cells underlying the lamellae and the smaller chlorophyllose cells forming the abaxial surface (Figures 3–4). In other Polytrichaceae with extensive lamellae and/or wide nerves, there may be one or two rows of large empty cells (deuters) together with small, heavily incrassate cells (stereids) in the multistratose central part of the nerve, but to the extent that these can be said to extend into the rest of the lamina (outside the multistratose zone containing stereids) they could only be equated with the large cells immediately underlying the lamellae. Thus either there are only two layers of cells in the extended lamina, or else (in more robust species such as many *Polytrichum* spp.) a fully differentiated nerve including stereids may extend to most of the width of the leaf. In *P. shevockii* the great majority of the lamina is uniformly 3-stratose, lacking stereids but with the central layer composed of large hyaline cells. We hypothesise that transmission of reflected light through these hyaline cells is responsible for the glaucous appearance of the leaves abaxially (where they are only obscured by a single layer of small chlorophylose cells, whereas adaxially they are comprehensively obscured by the lamellae). Of further note are the agglutinated, dark, globular inclusions that can often be seen inside these enlarged hyaline cells under low- and medium-power light microscopy and appear as brown-yellow masses (Figure 4) with blue-green speckles under a high-power oil-immersion objective. While we speculated that these might represent an algal or fungal endosymbiont, in the lack of further evidence it seems most likely that they are simply cellular debris, a byproduct of the senescence process that produces the hyaline cells. They rather resemble dead chloroplasts (J. Duckett, pers. comm.). It seems that these inclusions may disappear or become more difficult to observe in some older specimens, although this has yet to be confirmed. They are certainly deserving of further investigation.

Pogonatum shevockii represents a further addition to the rich polytrichaceous flora of China and Taiwan (Hyvönen & Lai, 1991), demonstrating that even in regions that are relatively well known, with a long history of exploration (e.g., Cardot, 1906; Noguchi, 1934; Ihsiba, 1935), species new to science can still be found. *Pogonatum shevockii* clearly belongs within *Pogonatum s. str.*, and based on the results of our model-based analyses it is sister to a clade containing *P. microstomum* and a number of American species that were already considered to be closely allied by Hyvönen (1989). The general appearance of the new species hints at this affinity, but its undifferentiated lamellae readily distinguish it from all other species of the group. Although currently analyses including morphological characters and using the parsimony optimality criterion disagree with this phylogenetic placement, we are confident that with further sampling of both terminals and characters this uncertainty will be resolved. While as mentioned

above the overall habit of the plant closely resembles much larger species such *P. microstomum*, many morphological details are shared with the group of diminutive species previously placed in *Racelopus* and allied taxa.

Biogeographically *P. shevockii* represents a further link between Taiwan and the eastern Himalayas. This type of disjunction is already known in a number of bryophyte species as well as in other plant groups such as conifers (Lu *et al.*, 2001; Chung *et al.*, 2004; Wei *et al.*, 2010), while recent findings in angiosperms further strengthen the link, as exemplified by new records of *Begonia grandis* Dry. from Taiwan (Nakamura *et al.*, 2015). That these two regions should share some biotic elements is not surprising given the high elevation of some of the Taiwanese mountains, the great diversity of habitats available, and the relatively recent isolation (5 Ma approx.) of the island from the mainland (e.g., Sibuet & Hsu, 2004). Furthermore it seems that for some plants at least, genetic interchange between Taiwanese and mainland populations has continued in spite of the considerable geographical distances involved (Chung *et al.*, 2004).

Online Supplementary Material

Supplementary material is available at [10.1080/03736687.2017.1312732].

Acknowledgements

We thank Jim Shevock for kindly sending us material of the new species as well as staff at E and H for proving facilities and support. The Royal Botanic Garden Edinburgh is supported by the Scottish Government's Rural and Environment Science and Analytical Services Division. During 2017 we are also grateful for the support of players of People's Postcode Lottery towards our scientific research. Field work in Yunnan by the fourth author was supported by the National Geographic Society (Grant Number 9697-15).

Taxonomic Additions and Changes: *Pogonatum shevockii* N.E.Bell & Hyvönen, *sp. nov.*

ORCID

Neil E. Bell http://orcid.org/0000-0002-2401-2968
Jaakko Hyvönen http://orcid.org/0000-0001-7559-8295
Kuei-Yu Yao http://orcid.org/0000-0002-3737-6832
Wen-Zhang Ma http://orcid.org/0000-0003-3144-001X

References

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19: 716–23.

Bell, N.E. & Hyvönen, J. 2010. Phylogeny of the moss class Polytrichopsida (BRYOPHYTA): generic-level structure and incongruent gene trees. *Molecular Phylogenetics & Evolution*, 55: 381–98.

Bell, N.E., Kariyawasam, I.U., Hedderson, T.A.J. & Hyvönen, J. 2015. *Delongia* gen. nov., a new genus of Polytrichaceae (Bryophyta) with two disjunct species in East Africa and the Himalaya. *Taxon*, 64: 893–910.

Cardot, J. 1906. Mousses de l'île Formose. *Beiheft zum Botanischen Centralblatt*, 19: 85–148.

Chung, J.D., Lin, T.P., Tan, Y.C., Lin, M.Y. & Hwang, S.Y. 2004. Genetic diversity and biogeography of *Cunninghamia konishii* (Cupressaceae), an island species in Taiwan: a comparison with *Cunninghamia lanceolata*, a mainland species in China. *Molecular Phylogenetics & Evolution*, 33: 791–801.

Daniels, A.E.D., Kariyappa, K.C., Hyvönen, J. & Bell, N. 2016. The first Indian record of *Pogonatum marginatum* Mitt. (Polytrichaceae) from the Western Ghats. *Bryophyte Diversity & Evolution*, 38: 41–46.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32: 1792–7.

Farris, J.S. 1989. The retention index and the rescaled consistency index. *Cladistics*, 5: 417–9.

Farris, J.S., Albert, V.A., Kallersjo, M., Lipscomb, D. & Kluge, A.G. 1997. Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12: 99–124.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology*, 4: 401–10.

Goloboff, P.A. 1994. Nona: a Tree-searching Program. Available at: www.cladistics.com/aboutNona.htm.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. 2003. TNT: Tree Analysis Using New Technology. Available at: www.lillo.org.ar/phylogeny/tnt/.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774–86.

Hyvönen, J. 1989. A synopsis of genus *Pogonatum* (Polytrichaceae, Musci). *Acta Botanica Fennica*, 138: 1–87.

Hyvönen, J. & Lai, M.-J. 1991. A synopsis of family Polytrichaceae (Musci) in Taiwan (China). *Journal of the Hattori Botanical Laboratory*, 70: 119–41.

Hyvönen, J. & Wu, P.-C. 1993. The identity of *Microdendron sinense* (Polytrichaceae). *Bryologist*, 96: 631–4.

Ihsiba, E. 1935. Index Muscorum Formosarum. *Transactions of Tropical Agricultural Society Taihoku Imperial University*, 7: 197–204.

Kluge, A.G. & Farris, J.S. 1969. Quantitative phyletics and the evolution of Anurans. *Systematic Zoology*, 18: 1–32.

Koskinen, S. & Hyvönen, J. 2004. *Pogonatum* (Polytrichales, Bryophyta) revisited. In: B. Goffinet, V. Hollowell, & R. Magill, eds. *Molecular systematics of bryophytes. Monographs in systematic botany* from the Missouri Botanical Garden, vol. 98, pp. 255–69. St. Louis: Missouri Botanical Garden.

Lu, S.Y., Peng, C.I., Cheng, Y.P., Hong, K.H. & Chiang, T.Y. 2001. Chloroplast DNA phylogeography of *Cunninghamia konishii* (Cupressaceae), an endemic conifer of Taiwan. *Genome*, 44: 797–807.

Mayrose, I., Friedman, N. & Pupko, T. 2005. A Gamma mixture model better accounts for among site rate heterogeneity. *Bioinformatics*, 21: 151–8.

Nakamura, K., Wang, Y.-F., Ho, M.-J., Chung, K.-F. & Peng, C.-I. 2015. New distribution record of *Begonia grandis* (Begoniaceae, section *Diploclinium*) from Taiwan, with subspecies assignment based on morphology and molecular phylogeny. *Taiwania*, 60: 49–53.

Nixon, K.C. 2002. WinClada ver. 1.00.08. Available at: www.cladistics.com/aboutWinc.htm.

Noguchi, A. 1934. Contributions to the moss flora of Formosa. *Transactions of the Natural History Society of Formosa*, 24: 289–97.

Nylander, J.A.A. 2004. MrModeltest, version 2.2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. Available at: https://github.com/nylander/MrModeltest2

Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L., Huttunen, S. & Quandt, D. 2009. Miyabeaceae, a new family of pleurocarpous mosses. *Bryologist*, 112: 447–66.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19: 1572–4.

Sibuet, J.C. & Hsu, S.K. 2004. How was Taiwan created? *Tectonophysics*, 379: 159–81.

Silvestro, D. & Michalak, I. 2012. raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution*, 12: 335–7.

Simmons, M.P. 2012. Misleading results of likelihood-based phylogenetic analyses in the presence of missing data. *Cladistics*, 28: 208–22.

Simmons, M.P. & Goloboff, P.A. 2014. Dubious resolution and support from published sparse supermatrices: the importance of thorough tree searches. *Molecular Phylogenetics & Evolution*, 78: 334–48.

Smith, G.L. 1971. A conspectus of the genera of Polytrichaceae. *Memoirs of the New York Botanical Garden*, 21: 1–83.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22: 2688–90.

Stech, M., Quandt, D., Lindlar, A. & Frahm, J.-P. 2003. The systematic position of *Pulchrinodus inflatus* (Pterobryaceae, Bryopsida) based on molecular data. Studies in austral temperate rainforest bryophytes 21. *Australian Systematic Botany*, 16: 561–8.

Touw, A. 1986. A revision of *Pogonatum* sect. *Racelopus*, sect. nov., including *Racelopus* Dozy & Molk., *Pseudoracelopus* Broth., and *Racelopodopsis* Thér. *Journal of the Hattori Botanical Laboratory*, 60: 1–33.

Wei, X.-X., Yang, Z.-Y., Li, Y. & Wang, X.-Q. 2010. Molecular phylogeny and biogeography of *Pseudotsuga* (Pinaceae): insights into the floristic relationship between Taiwan and its adjacent areas. *Molecular Phylogenetics & Evolution*, 55: 776–85.

Wheeler, W.C. 2012. *Systematics: a course of lectures*. New York: Wiley-Blackwell.

Wiens, J.J. & Morrill, M.C. 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Systematic Biology*, 60: 719–31.

Wolsan, M. & Sato, J.J. 2010. Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). *Cladistics*, 26: 168–94.

Appendix 1

GenBank accession numbers for terminals used in the molecular phylogenetic study, including voucher information for newly sequenced material (asterisked). Voucher specimens are held in the Botanical Museum of the Finnish Museum of Natural History, University Helsinki (H) or the Royal Botanic Garden, Edinburgh (E).

Taxon; (voucher); 18S, *rbc*L, *rps*4 / *rps*4-*trn*S intergenic spacer, *trn*L, *nad*5, ITS2.

Hebantia rigida* (Lorentz) G.L.Merr.**; GU569594, GU569416, GU569770, GU569679, GU569502, —. ***Oligotrichum falcatum* Steere**; JQ639444, JQ639453, JQ639426, JQ639416, JQ639435, —. ***Pogonatum aloides* (Hedw.) P.Beauv**. GU569615, GU569437, GU569791, GU569703, GU569526, —. ***Pogonatum belangeri* (Müll.Hal.) A.Jaeger**; GU569616, GU569438, GU569792, GU569704, GU569527, AY396474. ***Pogonatum brachyphyllum* (Michx.) P.Beauv.**; —, —, AY396515, AY396497, —, AY396473. ***Pogonatum campylocarpum* (Müll.Hal.) Mitt.**; GU569617, GU569439, GU569793, GU569705, GU569528, AY396455. ***Pogonatum camusii* (Thér.) Touw**; —, KU852692, KU852695, KU852698, —, —. ***Pogonatum cirratum* (Sw.) Brid**. (Borneo 1); GU569618, GU569440, GU569794, GU569706, GU569529, —. ***Pogonatum cirratum (Borneo 2); GU569619, GU569441, GU569795, GU569707, GU569530, —. ***Pogonatum cirratum*** (Taiwan); AY126966, AY118246, AY137691, AF545018, AY137733, —. ***Pogonatum comosum* (Müll.Hal.) Mitt.**; —, —, AY396503, AY396481, —, AY396446. ****Pogonatum congolense* Cardot** (1); Shevock 40093, São Tomé and Príncipe, H; KY793641, KY793619, KY793653, KY793628, KY793646, —. ****Pogonatum congolense*** (2); Shevock 40161, São Tomé and Príncipe, H; KY793642, KY793620, KY793654, KY793629, KY793647, —. ***Pogonatum contortum* (Menzies *ex* Brid.) Lesq.**; AY126967, AY118247, AF208425, AF545019, AY137734, —. ***Pogonatum convolutum* (Hedw.) P.Beauv.**; GU569620, GU569442, GU569796, GU569708, GU569531, —. ***Pogonatum dentatum* (Menzies *ex* Brid.) Brid.**; GU569621, GU569443, GU569797, GU569709, GU569532, AY396454. ***Pogonatum fastigiatum* Mitt.**; —, —, —, —, —, AY396447. ***Pogonatum gracilifolium* Besch.**; —, —, AY396507, AY396488, —, AY396462. ***Pogonatum inflexum* (Lindb.) Sande Lac.**; —, —, —, AY396486, —, AY396459. ***Pogonatum japonicum* Sull. & Lesq.**; GU569622, GU569444, GU569798, GU569710, GU569533, AY396463. ***Pogonatum macrophyllum* Dozy & Molk.**; GU569623, GU569445, GU569799, GU569711, GU569534, AY396443. ***Pogonatum marginatum* Mitt.**; —, KU852693, KU852696, KU852699, —, —. ***Pogonatum microstomum* (R.Br. *ex* Schwägr.) Brid.**; GU569624, GU569446, GU569800, GU569712, GU569535, —. ***Pogonatum nanum* (Hedw.) P.Beauv.**; —, —, AY396506, AY396484, —, AY396456. ***Pogonatum neesii* (Müll.Hal.) Dozy** (1); GU569625, GU569447, GU569801, GU569713, GU569536, AY396449. ****Pogonatum neesii*** (2); Zündorf 26860, Georgia, H; KY793643, KY793621, KY793655, KY793630, —, —. ****Pogonatum neesii*** (3); Zündorf 26054, Georgia, H; KY793644, KY793622, KY793656, KY793631, —, —. ***Pogonatum neglectum* (Hampe) A.Jaeger**; —, —, AY396510, AY396491, —, AY396466. ****Pogonatum neo-caledonicum* Besch.**; Bell 07.11.08.007, New Caledonia, H; —, KY793623, KY793657, KY793632, KY793648, AY396471. ***Pogonatum nipponicum* Nog. & Osada**; GU569626, GU569448, GU569802, GU569714, GU569537, AY396460. ***Pogonatum nudiusculum* Mitt.**; —, —, AY396505, —, —, AY396451. ***Pogonatum pensilvanicum* (Bartram *ex* Hedw.) P.Beauv.**; —, —, —, AY396477, AY137740, AY396442. ***Pogonatum pergranulatum* P.C.Chen**; —, —, AY396514, AY396496, —, —. ***Pogonatum perichaetiale* (Mont.) A.Jaeger**; GU569627, GU569449, GU569803, GU569715, GU569538, AY396461. ***Pogonatum piliferum* (Dozy & Molk.) Touw**; —, —, AY396512, —, —, AY396469. ***Pogonatum procerum* (Lindb.) Schimp.**; —, —, AY396508, AY396489, —, AY396464. ***Pogonatum proliferum* (Griff.) Mitt.**; GU569628, GU569450, GU569804, GU569716, GU569539, AY396465. ***Pogonatum rufisetum* Mitt.**; —, —, —, AY396479, —, AY396444. ***Pogonatum semipellucidum* (Hampe) Mitt.**; —, —, AY396511, AY396492, —, AY396467. ****Pogonatum shevockii* N.E.Bell & Hyvönen** (Taiwan 1); Shevock 41505, Taiwan, H; —, KY793625, KY793659, KY793634, KY793650, KY793638. ****Pogonatum shevockii*** (Taiwan 2); Shevock 47925, Taiwan, E; —, KY793627, KY793661, KY793636, KY793652, KY793640. ****Pogonatum shevockii*** (Taiwan 3); Shevock 41562, Taiwan, H; KY793645, KY793624, KY793658, KY793633, KY793649, KY793637. ****Pogonatum shevockii*** (Yunnan); Ma, Yao & Deng 15-7040, China, E; —, KY793626, KY793660, KY793635, KY793651, KY793639. ***Pogonatum sinense* (Broth.) Hyvönen & P.C.Wu** (1); KP901278, KP901283, KP901289, KP901295, KP901301, —. ***Pogonatum sinense*** (2); DQ120780, DQ120779, —, —, DQ120778, AY396445. ***Pogonatum spinulosum* Mitt.**; AY126974, AY118254, AY137698, AF545026, AY137741, AY396457. ***Pogonatum subtortile* (Müll.Hal.) A.Jaeger**; —, —, —, AY396493, —, AY396468. ***Pogonatum subulatum* (Menzies *ex* Brid.) Brid.** (Australia); GU569629, GU569451, GU569805, GU569717, GU569540, AY396453. ***Pogonatum subulatum*** (New Zealand); GU569630, GU569452, GU569806, GU569718, GU569541, —. ***Pogonatum tahitense* Schimp**;. —, —, —, AY396483, —, AY396452. ***Pogonatum tortile* (Sw.) Brid.**; —, —, AY396501, AY396476, —, AY396441. ***Pogonatum tubulosum* Dixon**; —, —, —, AY396485, —, AY396458. ***Pogonatum urnigerum* (Hedw.) P.Beauv.** (Borneo); GU569631, GU569453, GU569807, GU569719, GU569542, —. ***Pogonatum urnigerum*** (China); GU569632, GU569454, GU569808, GU569720, GU569543, —. ***Pogonatum urnigerum*** (Europe); AF208406, AY118256, AF208426, AF545028, AJ291554, AY396472. ***Pogonatum urnigerum*** (Taiwan); AY126970, AY118250, AY137694, AF545022, AY137737, —. ***Pogonatum usambaricum* (Broth.) Paris**; GU569633, GU569455, GU569809, GU569721, GU569544, —. ***Polytrichastrum papillatum* G.L.Sm.**; GU569652, GU569474, GU569828, GU569744, GU569567, —. ***Polytrichastrum lyallii* (Mitt.) G.L.Sm.**; EU927331, AY118241, AF208423, AF545011, AY137726, AY908802, —. ***Polytrichum appalachianum* L.E.Anderson**; GU569644, GU569466, GU569820, GU569735, GU569558, —. ***Polytrichum commune* Hedw.**; GU569663, GU569485, AF208428, AF545035, GU569578, —. ***Polytrichum ericoides* Hampe**; GU569664, GU569486, GU569839, GU569755, GU569579, —. ***Polytrichum hyperboreum* R.Br.**; GU569665, GU569487, GU569840, GU569756, GU569580, —. ***Polytrichum juniperinum* Hedw.**; EU927329, EU927317,

EU927342, GU569757, GU569581, —. ***Polytrichum piliferum* Hedw.**; AY126981, AY118263, AY137706, AF545037, AY137752, —. ***Polytrichum strictum* Menzies *ex* Brid.**; GU569666, GU569488, GU569841, GU569758, GU569582, —. ***Polytrichum xanthopilum* Wilson *ex* Mitt.**; GU569660, GU569482, GU569836, GU569752, GU569575, —. ***Psilopilum cavifolium* (Wilson) I.Hagen**; EU927330, EU927318, EU927343, GU569761, GU569585, —. ***Steereobryon subulirostrum* (Schimp. *ex* Besch.) G.L.Sm.**; AY126984, AY118265, AY137708, AF545040, AY137755, —.