Gametophytic simplicity in Laurasian and Gondwanan Polytrichopsida — the phylogeny and taxonomy of the *Oligotrichum* morphology

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Phylogenetic analyses have largely resolved generic and higher level relationships within the Polytrichopsida, enabling polarisation of characters and the identification of macro-evolutionary trends. Topologies show strong geographic patterning, with major groups having predominantly Northern or Southern Hemisphere distributions and some general morphologies having arisen independently on either side of the equator. While most cases of apparent convergence have been taxonomically visible due to sufficient higher-level characters being present to distinguish unrelated genera, convergent reduction may have resulted in conflation of similar gametophytic morphologies in classification. We present further evidence for the polyphyly of *Oligotrichum* DC. as currently circumscribed, showing how this morphology has probably arisen through reduction on multiple occasions to produce distinct lineages that have lacked taxonomic identity. We present a preliminary arrangement of the species currently recognised in *Oligotrichum*, accommodating selected Southern Hemisphere taxa in *Itatiella* G.L.Sm., and combining *Atrichopsis compressa* (Hook.f. & Wilson) G.L.Sm. and *Oligotrichum tenuirostre* (Hook.) A.Jaeger under *Notoligotrichum* G.L.Sm. For several species that clearly do not belong in *Oligotrichum* but remain of ambiguous affinity to other genera we avoid making new combinations, as ongoing combined molecular and morphological studies have considerable potential to elucidate their relationships in the near future.

Introduction

The Polytrichopsida comprise the only major moss lineage outside of the Bryopsida having significant levels of both species diversity and macro-morphological variation. While recent research (Hyvönen *et al.*, 1998, 2004; Bell & Hyvönen, 2008, 2010a,b) has resolved many generic and higher-level relationships within the class, a striking finding to emerge is that generic-level diversity is phylogenetically partitioned between the Northern and Southern Hemispheres. Although it had previously been apparent that most genera have predominantly Southern or Northern Hemispheric distributions suggestive of Gondwanan or Laurasian paleodistributions respectively, our most recent comprehensive analysis (Bell & Hyvönen, 2010a) shows that all peristomate Northern Hemisphere genera form a monophyletic group, with southern genera occurring as a pectinate series of three or four clades (a grade) subtending it. Meanwhile, the very earliest diverging lineages are a small and distinctive assortment of eperistomate taxa (*Alophosia* Cardot, *Lyellia* R.Br., *Bartramiopsis* Kindb.) with widely scattered and presumably relictual Northern Hemispheric distributions. While the monophyly of most genera is supported, *Oligotrichum* DC., one of the few genera to be well represented at all latitudes, is shown to be unambiguously polyphyletic, indicating that this morphology has very probably arisen independently on at least two separate occasions, perhaps in response to similar adaptive pressures in cool temperate and/or montane regions on either side of the equator.

Species of *Oligotrichum s.l.* are recognised by a combination of features indicative of lesser gametophytic (and to some extent sporophytic) complexity compared to most other genera of Polytrichopsida. Plants are mostly small and lack what has been termed a 'polytrichoid' morphology (e.g. Smith Merrill, 2007), i.e. the leaves do not have an abrupt

transition between a sheathing base and a non-sheathing blade and lack the associated 'hinge tissue'. Adaxial lamellae are few in number, usually not densely packed together, almost always restricted to the costa and very rarely occupy more than half of the width of the lamina. Northern Hemisphere species mostly have some abaxial as well as adaxial lamellae — this is perhaps the only feature of the genus that does not suggest simplicity compared with other Polytrichopsida. Capsules are mostly erect and cylindric (non-angled), although some northern species have ridged sporangia. There are 32 peristome teeth, which may be either simple and acute (Southern Hemisphere species) or mostly compound and linear-obtuse (northern species). Although a few species in other genera have *Oligotrichum*-like gametophytic features, they usually also have other generic synapomorphies and can always be told apart if sporophytes are present. *Atrichum* P.Beauv. species have bordered leaves and rows of teeth on the abaxial lamina as well as being generally more robust with a different leaf shape, while *Psilopilum* Brid. species have narrow walled hyaline cells in parts of the leaf border. Both of these genera as well as *Pogonatum* P.Beauv. have unique and definitive sporophyte morphologies from which generic affinities are always immediately apparent. *Notoligotrichum* G.L.Sm. species usually have more extensive lamellae, most have papillose lamina and/or apical lamellar cells, and capsules are inclined as well as bilaterally compressed or angled, usually distinctly narrowed towards the mouth.

Convergence of habit and morphology has occurred in several different Polytrichopsidan genera in the Northern and Southern Hemispheres, although mostly it has not been sufficiently pronounced to obscure generic boundaries. Species of *Polytrichadelphus* (Müll.Hal.) Mitt. in southern temperate regions and in the Andes, and *Polytrichastrum* G.L.Sm. and *Polytrichum* Hedw., most diverse in the Northern Hemisphere, frequently share similar gametophytic morphologies and ecological niches (in this case, either convergence or plesiomorphic retention is plausible), although they are clearly distinguished by sporophytic synapomorphies as well as some gametophytic characters. Where convergence takes the form of reduction, however, morphological simplification can erase taxonomic characters (e.g. Goffinet *et al.*, 2011) and lead to conflation in classification. The types of molecular characters used in phylogenetic analyses can be highly valuable in these circumstances, as while they are certainly not immune to convergence, they are rarely lost or obscured by reduction.

Some cases of previously obscure generic-level convergence in the Polytrichaceae were identified by careful traditional taxonomic work prior to the advent of molecular data, most notably in *Psilopilum*, which was a fairly sizeable genus with a bipolar distribution until Smith (1971) transferred most of the Southern Hemisphere species to his new genus *Notoligotrichum*. In *Notoligotrichum*, the peristome teeth are almost lanceolate, well separated and pointed and the stomata occur in a discrete and conspicuous band at the base of the capsule, whereas in *Psilopilum s. str.* the teeth are broad, linear, blunt, and close together (see Smith, 1971, Figures 78 and 79). As mentioned above, most *Notoligotrichum* species also have distinctly papillose lamellar and/or lamina cells.

Smith (1971) further noted similar differences between the peristomes of Northern and Southern Hemisphere species of *Oligotrichum* (see SEM images in Bell & Hyvönen, 2010a, Figure 6), and stated that the type elements of *Psilopilum* and *Oligotrichum* (representing the northern subgroups) seemed 'more closely related to one another than to many of the species in their respective genera, and these species, in turn, are evidently more closely related to one another than to the type species of the genus in which they now reside'. In other words, he implicitly recognised that the previously established hierarchy of taxonomic characters was unnaturally inverted. Traditionally, the distinctions between the curved, narrow-mouthed, asymmetric capsules of *Psilopilum* and the cylindrical, symmetrical capsules of *Oligotrichum* were seen as higher-level characters separating two large bipolar or pan-latitudinal genera, within which features of the peristome and stomatal distribution represented lower-level variation. In fact, it now seems that the latter characters indicate higher-level affinities (the closer relationship of the Northern and Southern Hemisphere members of both traditional genera to each other), while the former are convergently evolved features informative at lower levels, defining smaller generic groupings that have arisen independently in both the Northern and Southern Hemispheres. Smith nonetheless implied that all species of *Notoligotrichum*, *Psilopilum*, and *Oligotrichum* form a more or less natural group, with *Oligotrichum s.l.* having evolved from a *Notoligotrichum*-like ancestor and *Psilopilum s. str.* from the derived Northern Hemisphere type of *Oligotrichum* (Smith, 1971, p. 50). He thus retained all species of *Oligotrichum* in a single genus, albeit an implicitly paraphyletic one. In contrast, our results (Bell & Hyvönen, 2010a) demonstrate that the Gondwanan and Laurasian elements of *Oligotrichum* are only very distantly related, and hence that this gametophytic morphology does not indicate generic affinity.

In this study, we aim to further investigate the phylogenetic distribution of the *Oligotrichum* morphology and also take preparatory steps towards an eventual comprehensive worldwide taxonomic

revision of the species currently placed in the genus. Because these small, relatively simple plants often lack taxonomic characters, it is possible that *Oligotrichum s.l.* obscures more than two independent origins of this reduced type. If this is the case, there may be significant phylogenetic diversity (Faith, 1992) 'hidden' within the genus that could be invaluable for informing higher-level relationships within the class that remain unresolved or poorly supported, most notably between the major Northern Hemisphere groupings. Formal taxonomic recognition of previously unrecognised generic-level clades also helps draw attention to phylogenetic diversity that might otherwise be overlooked in conservation efforts. To this end, we have extended sampling and analysis of molecular characters where suitable material has become available, and undertaken a review of the numerous names currently accepted under *Oligotrichum*. Taxonomic changes are made where they can be fully justified at this stage, although we have avoided premature novelties where there is an expectation of more decisive data being obtained in the near future.

Material and Methods
Taxon sampling
Bell & Hyvönen (2010a) included 11 terminals representing nine species of *Oligotrichum s.l.* within a large-scale phylogenetic study of relationships within the Polytrichopsida based on the chloroplast *rbc*L, *rps*4, and *trn*L, mitochondrial *nad*5, and nuclear 18S regions. Of these nine species, five (*O. hercynicum* (Hedw.) Lam. & DC., *O. austroaligerum* G.L.Sm., *O. suzukii* (Broth.) C.C.Chuang, *O. obtusatum* Broth., and *O. parallelum* (Mitt.) Kindb) appeared as a well supported monophyletic group within the large Northern Hemisphere clade of the Polytrichopsida, this being effectively unresolved in relation to other well supported clades representing most of *Polytrichastrum s. str.* (see Bell & Hyvönen, 2010b), *Atrichum/Steereobryon* G.L.Sm./ *Psilopilum*, and *Polytrichum/Pogonatum*. The other four *Oligotrichum* exemplars appeared outside of the Northern Hemisphere clade in a well supported group together with *Notoligotrichum*, *Atrichopsis* Cardot and *Itatiella* G.L.Sm. In the total combined and mitochondrial+chloroplast analyses, *O. riedelianum* (Mont.) Mitt. appeared as sister to *Itatiella*, and *O. tenuirostre* (Hook.) A.Jaeger as sister to *Notoligotrichum*, with *O. canaliculatum* (Hook. & Arn.) Mitt. and *O. afrolaevigatum* (Dixon) G.L.Sm. forming a well supported clade sister to *O. riedelianum/Itatiella*. For the current study, we increased the representation of *Oligotrichum* in our datasets by sequencing all five regions for *O. falcatum* Steere (Russia), *O. aligerum* Mitt. (U.S.A), *O. javanicum* (Hampe) Dozy & Molk. (Papua New Guinea), *O. falcifolium* (Griff.) G.L.Sm. (Nepal), and *O. cavallii*

(G.Negri) G.L.Sm. (Tanzania). In the case of *O. cavallii*, because the results of pilot studies suggested an unexpected phylogenetic placement, we obtained sequences of *trn*L–F and *rps*4 from a second specimen from a different locality. These were used to corroborate the identity and placement of the first specimen and have been made available through GenBank (see Appendix), but were not employed in the final analyses because data from other regions could not be obtained due to the age and condition of the specimen. We further sequenced all of these regions for an as yet unnamed collection of a sterile *Oligotrichum*-like plant found by Professor Terry Hedderson in Northern Pakistan. This material has many features in common with *O. glaciale* C.C.Towns. (itself only known from the type specimen), but does not match the description of that species closely enough to be assigned to it. Finally, we sampled three additional exemplars of *Notoligotrichum* from South Africa in order to test the robustness of the proposed sister relationship of *O. tenuirostre* to *Notoligotrichum*. As detailed in Bell & Hyvönen (2010a), the African representatives of *Notoligotrichum* have also yet to be validly described (as one or more species). However, the early diverging position of our previous single exemplar combined with the relatively reduced gametophytes of some specimens suggested that we should increase sampling from these populations to further test the monophyly of *Notoligotrichum* with respect to *O. tenuirostre*. GenBank accession numbers and voucher specimens for new sequences generated for this study are listed in Appendix, while all others are provided in Bell & Hyvönen (2010a).

Laboratory procedures and phylogenetic analyses
DNA extraction procedures, PCR protocols, sequencing, editing, and alignment were as described in Bell & Hyvönen (2010a), except that in a small number of cases, we used a nested PCR approach to obtain products from the *nad*5 region, using the primers and protocol developed by V. Buchbender and described in Câmara (2008). After adding the new sequences to our matrices, we conducted Bayesian MCMC analyses on the total combined dataset and the mitochondrial+chloroplast datasets using the same data partitions, models, procedures and settings as in Bell & Hyvönen (2010a), other than that in each case we ran three independent runs of eight incrementally heated chains each, rather than two runs of 12 chains each (given the relatively small differences in heating between the 12 chains used previously, eight chains were thought to be sufficient to adequately explore the parameter space while increasing the number of runs provided a further reference point for assessing convergence). We also conducted parsimony and parsimony bootstrap analyses on the total combined

dataset, again using the same methods and settings as in Bell & Hyvönen (2010a). Although a major finding in the latter study was strongly supported incongruence between the 18S nuclear data and the combined chloroplast and mitochondrial data, this was highly localised in particular parts of the phylogeny, and for most relationships, all of the data were congruent and contributed towards increased support values when combined. For relationships among the taxa of interest here, this incongruence is only relevant to a suggested clade appearing in the 18S analyses alone that comprised *Notoligotrichum*, *Atrichopsis*, *Dendroligotrichum* (Müll.Hal.) Broth., *Hebantia* G.L.Merr., *Itatiella*, and *Oligotrichum riedelianum*. However support for this was only marginally significant even from the 18S data alone (which has very few informative sites), and analyses based on the total combined data resulted in the same topology for these taxa as from the chloroplast + mitochondrial data, with most support values increased. Hence, we do not consider *a priori* that these genomic regions are incongruent for the relationships being investigated here.

Results

The alignment of the total combined dataset differed in only minor respects from that used in Bell & Hyvönen (2010a). After exclusion of leading and trailing sections and ambiguous regions, it consisted of 5868 characters, of which 966 were variable. Of the new terminals added, *O. falcatum*, *O. aligerum*, *O. javanicum*, *O. falcifolium*, and the unnamed collection from Pakistan all shared the highly reduced (56–59 bp) P8 region of the *trn*L intron identified in all sampled Northern Hemisphere *Oligotrichum* species by Bell & Hyvönen (2010a), while *O. cavallii* and the three new specimens of *Notoligotrichum* from South Africa had more typical P8 regions of over 150 bp in length. Sequences of the *rps*4 and *trn*L regions from our second specimen of *O. cavallii* (from Tanzania, not used in the final analyses) exactly matched those of the Ugandan specimen, while preliminary parsimony analyses placed the two exemplars together with strong support.

For Bayesian majority consensus topologies within and between clades relevant to the relationships of *Oligotrichum* species, the results of the analyses of the total combined data and the mitochondrial + chloroplast data were identical, other than for some moderately increased support values and resolution in the total combined analysis. The parsimony analysis of the combined dataset resulted in 9216 equally parsimonious trees of length 2197, while the strict consensus was entirely consistent with the Bayesian results, differing only in being less resolved than the Bayesian majority consensus for some relationships

within genera. The consistency index (Kluge & Farris, 1969) was 0.54, the retention and rescaled consistency indices (Farris, 1989) 0.87 and 0.47, respectively. Bootstrap support values generally reflected Bayesian posterior probabilities, other than for a small number of nodes where they were proportionately lower. Henceforth, we will only consider the results of the Bayesian analysis of the combined dataset (a representation of which is provided in Figure 1), other than where significant differences under parsimony were found.

Nine of the sampled *Oligotrichum* species (*O. hercynicum*, *O. aligerum*, *O. falcatum*, *O. austroaligerum*, *O. javanicum*, *O. falcifolium*, *O. suzukii*, *O. obtusatum*, and *O. parallelum*) form a monophyletic group with a posterior probability (pp) value of 1.00 within the large Northern Hemisphere clade. *Oligotrichum cavallii* and the Pakistan specimen also occur within the northern clade, but rather than grouping with the other *Oligotrichum* species they occur as sister taxa within a well supported clade (pp=1.00) together with *Psilopilum*, *Steereobryon*, and *Atrichum*. Within this group, the *Atrichum*/*Steereobryon* clade, *Psilopilum*, and the *O. cavallii*/Pakistan specimen clade are unresolved with respect to each other. Under parsimony, the larger grouping is recovered in the strict consensus although it has less than 50% bootstrap support. The other nine *Oligotrichum* species nonetheless appear as a clade with 100% bootstrap support, excluding *O. cavallii* and the Pakistan specimen.

All of the other *Oligotrichum* exemplars occur outside of the Northern Hemisphere clade together with *Itatiella*, *Notoligotrichum*, and *Atrichopsis* (pp=1.00). The four South African *Notoligotrichum* exemplars form a clade (pp=1.00) that is sister to the remainder of *Notoligotrichum* (including *Atrichopsis*), while *O. tenuirostre* is sister to *Notoligotrichum* (both the combined clade and a monophyletic *Notoligotrichum* have pp values of 1.00). *Atrichopsis* is sister to the temperate South American *N. angulatum* (Cardot & Broth.) G.L.Sm. and *N. minimum* (Cardot) G.L.Sm. (pp=0.82) and part of a larger clade that also includes the Australasian *N. bellii* (Broth.) G.L.Sm., *N. crispulum* (Hook.f. & Wilson) G.L.Sm., and *N. australe* (Hook.f. & Wilson) G.L.Sm. (pp=1.00). *Itatiella* is sister to *O. riedelianum* (pp=1.00), this clade being sister to *O. canaliculatum* together with *O. afrolaevigatum* (pp=1.00).

Discussion

The results of the molecular phylogenetic analyses corroborate the findings of Bell & Hyvönen (2010a) in showing a polyphyletic *Oligotrichum*, while also lending strong support to the hypothesis of a distinct clade of predominantly Northern Hemisphere species that includes the type, *O. hercynicum*. Furthermore,
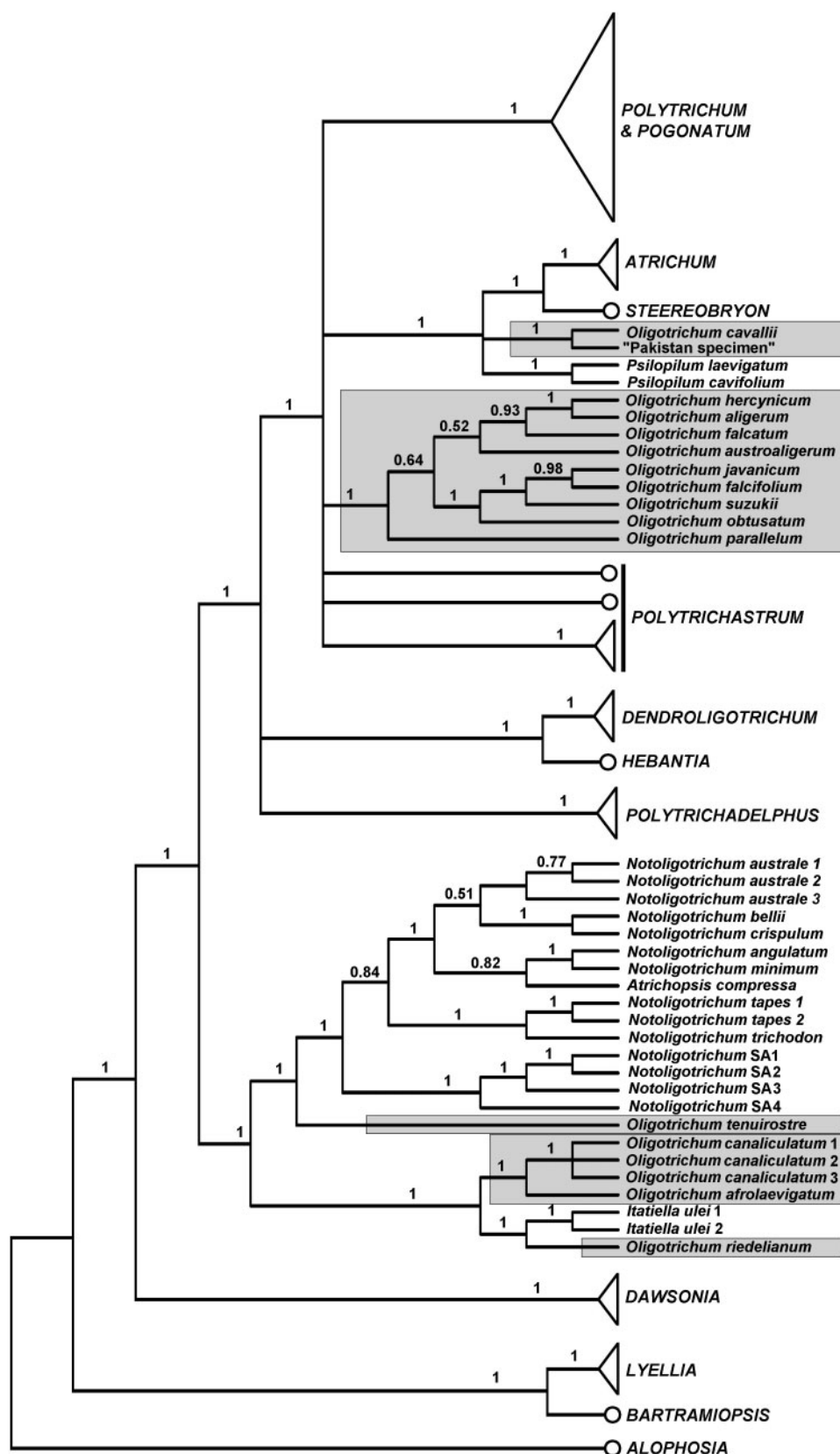
Figure 1 Diagrammatic summary of the Bayesian majority consensus tree based on MCMC analysis of the total combined dataset of 143 terminals using a heterogeneous GTR+I+G model. Monophyletic groups of peripheral interest to the study are represented by triangles where they comprise more than a single species, and by small circles where they are monospecific genera or single species with unresolved positions. Other than in the clades where species level resolution is shown, nodes are collapsed where they have posterior probabilities of less than 0.75. Numbers above branches are posterior probabilities.

assuming that the relatively simple gametophytic morphology that defines *Oligotrichum s.l.* is a product of reduction from a plesiomorphic polytrichoid morphology (see below), it is here shown to have up to four potential independent origins, with *O. cavallii* more closely related to *Atrichum*, *Steereobryon* and

Psilopilum than to *Oligotrichum s. str.*, and *O. tenuirostre* closer to *Notoligotrichum* than to other sampled Southern Hemisphere species of *Oligotrichum*. It is also very plausible that the *Oligotrichum* morphology has arisen on only two or three occasions, depending on plesiomorphic states in the common ancestors of the *Notoligotrichum*/southern *Oligotrichum*/*Itatiella* and *Atrichum*/*Steereobryon*/*Psilopilum*/*Oligotrichum s. str.* clades. Owing to poor phylogenetic resolution among the major clades in the Northern Hemisphere group and as yet fairly limited sampling from Southern Hemisphere *Oligotrichum* spp. we have not conducted ancestral character state reconstruction in this study and thus cannot formally reject the hypothesis of a single origin of the *Oligotrichum* morphology. However, such a scenario seems extremely unlikely as it would require a gametophytically simplified form to have been present in the common ancestors of not only the two aforementioned clades, but also the entire major clade of 'polytrichopsoid' peristomate Polyrichopsida (i.e. the sister group to *Dawsonia* Broth., itself a complex polytrichoid genus), with multiple repeated 're-origination' of more complex polytrichoid forms (with leaf sheath differentiation, hinge tissue and extensive lamellae) throughout the class. As well as being transparently less parsimonious, it is reasonable to assume that multiple losses of complex derived features are more probable than multiple gains. Thus we are broadly in agreement with Smith (1971, p. 24) when he stated that '*…it can be inferred that the extant taxa of Polytrichaceae with broadly lamellate leaves represent the more primitive condition, and that those taxa with lamellae occupying a restricted portion of the leaf surface are derived*'. However, because the earliest diverging member of the order, *Alophosia* (as well as more distant outgroups), lacks any indication of lamellae or lamellar remnants, the lamellar leaf morphology itself may have arisen *de novo* in the stem lineage of the clade that includes *Lyellia*, *Bartramiopsis* and all of the peristomate Polytrichopsida.

The types of reduced gametophytic morphologies found in *Oligotrichum s.l.*, *Psilopilum*, and to a lesser extent *Notoligotrichum* are strongly associated with arctic and sub-arctic, cool oceanic and montane habitats. Lamellar reduction in Polytrichopsida is also found in tropical *Pogonatum* species, where it is associated with shaded forest habitats (see individual species treatments in Touw, 1986), is otherwise atypical for the group. Proctor (2005) demonstrated that for Polytrichaceae subject to high irradiances, CO_2 diffusion is limiting for photosynthesis, with leaf lamellae acting to greatly increase the surface area available for CO_2 uptake and allow efficient use of direct sunlight. It is likely that for tropical *Pogonatum* species in shaded habitats, lamellar reduction is associated with reduced irradiance, as light levels rather than CO_2 uptake become photosynthetically limiting. However, the *Oligotrichum* morphology is usually associated with open habitats, albeit exposed ones subject to high precipitation, strong winds, and low nutrient availability. It seems likely that these life forms represent adaptations to extreme conditions where the potential for CO_2 uptake is less limiting due to other stresses imposing constraints on photosynthesis, rate of growth, or plant morphology. Reduced irradiance levels due to very frequent cloud cover may also be a factor. Such habitats tend to be isolated from each other, either on a global scale in the case of the arctic and cool temperate regions of the Northern and Southern Hemispheres, or on a more local scale for individual mountains, mountain ranges, and oceanic islands. *Oligotrichum s. str.* is most diverse in the northern arctic and temperate regions and especially in the Himalayas and the mountainous regions of China such as Yunnan, while the southern *Oligotrichum* species are very widely scattered in South Africa, New Zealand, Patagonia, Papua New Guinea, Tristan da Cunha, and in the mountainous regions of Brazil and the tropical American Andes. The association of the reduced gametophytic morphology with isolated, extreme habitats is consistent with it having arisen convergently on multiple occasions and without similarly adapted species being forced into competition with each other for the same niches. In a sense, this association could act as an engine for the generation of cryptic or partially cryptic phylogenetic diversity, which is best explored with the aid of molecular level sequence data.

It should not be surprising that in plants such as mosses that are structurally relatively simple to begin with, homoplastic morphological reduction has considerable potential to mislead taxonomy. Unlike other forms of adaptive evolution based on morphological innovation, reduction is almost inevitably convergent to some extent where it occurs in unrelated lineages, because absence by definition erases clues to its own origins. Goffinet *et al.* (2011) very recently described an analogous (if more extreme) situation in *Ephemerum* Hampe and *Micromitrium* Austin, showing that these two highly reduced genera, previously thought to share a common origin, are independently derived from within the Dicranidae. Similarly, it is now well established that reduction of sporophyte (particularly peristome) characters associated with epiphytism in pleurocarpous mosses has been a source of much taxonomic confusion in the past (e.g. Buck *et al.*, 2000; Hedenäs, 2001, 2002; Huttunen *et al.*, 2004; Olsson *et al.*, 2009). Loss of taxonomic characters through simplification often leads to unrelated, reduced taxa being grouped together taxonomically, but it may also lead to unsimplified taxa being combined to form

artificial higher groupings through the phylogenetically inappropriate exclusion of reduced lineages. Probable losses of the dendroid morphology within the Hypnodendrales (Bell & Newton, 2005; Bell *et al.*, 2007) and Hypopterygiaceae (Shaw *et al.*, 2008) have in the past led to artificial generic concepts (of *Hypnodendron* (Müll.Hal.) Lindb. *ex* Mitt. and *Hypoterygium* Brid. respectively), based mainly on the possession of this distinctive but apparently easily lost branching architecture.

In fact, there are ample morphological characters distinguishing the Northern and Southern Hemisphere members of *Oligotrichum s.l.*, (above; Smith, 1971; Bell & Hyvönen, 2010a), although in the past these have been given insufficient weight. Some are gametophytic; most, if not all, true (i.e. northern clade) *Oligotrichum* species have at least some indication of abaxial as well as adaxial lamellae, while abaxial lamellae never occur in the southern species. Similarly many, but not all, southern species have wider nerves supporting rather more lamellae than the typically very narrow, terete nerves of northern species. The most definitive differences are sporophytic however, and as mentioned above, are very similar to the features that separate *Notoligotrichum* from *Psilopilum*. Northern *Oligotrichum* species have mostly compound peristome teeth that are linear, more erect, and less well separated than the simple, acute, more inclined, and widely separated teeth of the southern species, although this distinction is less pronounced than that between the extremely broad and closely spaced teeth of *Psilopilum* and the narrow acute ones of *Notoligotrichum* (which are more or less identical to those of the southern *Oligotrichum* species). Southern *Oligotrichum* species further have the stomata concentrated in a conspicuous narrow band at the base of the capsule, while in northern species, they are more generally distributed at the base.

For largely historical reasons, variation in the peristome/epiphragm complex in Polytrichopsida has not been given the same emphasis in classification as peristome features have in arthrodontous mosses. Part of the reason for this may be that microscopic variations in solid, opaque nematodontous peristomes are more difficult to study using light microscopy than those in semi-transparent arthrodontous ones. Scanning electron microscopy still has considerable potential to expand the range of sporophytic morphological characters available in the Polytrichopsida (Bell & Hyvönen, 2010b).

The position of *Oligotrichum tenuirostre* as sister to *Notoligotrichum* is corroborated by its morphology, which in a number of fundamental respects is closer to *Notololigotrichum* than to the other Southern Hemisphere *Oligotrichum* species (see Frye, 1947 and discussion in Bell & Hyvönen, 2010a). Furthermore, as noted in previous studies (Bell & Hyvönen, 2008,

2010a), *Atrichopsis* has abundant characters supporting its placement in *Notoligotrichum*. In fact, we will argue that although not particularly closely related, these two species share features that expand and clarify the generic concept of *Notoligotrichum*.

Despite the superficial *Oligotrichum*-like appearance of *O. tenuirostre*, many (if not all) specimens, including the type, have distinctly papillose lamina cells at and near the leaf margins, a characteristic feature of *Notoligotrichum* that is also very well developed in *Atrichopsis*, where the leaves are strongly papillose throughout. Furthermore, despite true lamellae in *O. tenuirostre* being few and restricted to a relatively narrow costa (as opposed to numerous and extending to the lamina itself in most *Notoligotrichum* species), the lamina in many specimens has extensive, if often intermittent, bistratose areas (first noted by Frye, 1947). These are reminiscent of the consistently bistratose lamina of *Atrichopsis*, in which lamellae are lacking altogether except on the perigonial bracts (Smith, 1969). In both *O. tenuirostre* and *Atrichopsis*, the leaf margin becomes unistratose in a wide outermost band of cells. The capsule of *O. tenuirostre* is often very slightly curved with hints of two ridges, in this respect being intermediate between *Notoligotrichum* and most of the southern *Oligotrichum* species, while the *Atrichopsis* sporophyte has all of the above mentioned features of *Notoligotrichum*.

Several *Notoligotrichum* species (e.g. *N. bellii* and many forms of the closely related *N. crispulum*) have extensive but very low (as few as one or two cells), small-celled lamellae that sit on top of much larger inflated cells, the latter having been generally interpreted as the upper layer of a bistratose lamina (it could be debated whether they are true lamina cells, a single-layered extension of the nerve, or the highly differentiated lower cells of the lamellae, assuming that such distinctions are developmentally meaningful). *Atrichopsis* has a very similar morphology except that the lamellae themselves are absent despite the bistratose lamina being retained, while in *O. tenuirostre* multi-celled lamellae are found only on the true nerve and a wider bistratose lamina is partially and/or variably present. It is worth noting that in common with *O. tenuirostre*, the South American *N. tapes* (Müll.Hal.) G.L.Sm. also has only a few lamellae restricted to a narrow nerve, while a wider bistratose lamina, arguably a more definitive feature of *Notoligotrichum*, is entirely absent. Additionally, South African 'Notoligotrichum' specimens (as yet undescribed) often have less extensive lamellae than is usual in the genus, although their sporophytes are clearly of the *Notoligotrichum* type. In summary, there is good reason on morphological grounds alone to recognise both *O. tenuirostre* and *Atrichopsis* within an expanded *Notoligotrichum*. An

interesting question for future study is whether the relatively reduced gametophytic morphology of *O. tenuirostre* is derived from a more typical *Notoligotrichum* type (as is presumably the case in *Atrichopsis*), or whether it is truly evolutionarily intermediate between a plesiomorphic southern *Oligotrichum* morphology and the fully developed *Notoligotrichum* form.

The generic treatment of the other Southern Hemisphere species of *Oligotrichum s.l.* is complicated by the phylogenetic position of *Itatiella ulei* (Broth. ex Müll.Hal.) G.L.Sm., the single highly distinctive member of a monotypic genus that appears to be derived from within a clade of species with a more general *Oligotrichum*-like morphology. As well as possessing a unique, globose capsule that lacks both stomata and a peristome, the gametophytic morphology of *Itatiella* is also unusual in that the nerve is very broad relative to the leaf width (around third-fourths of the total), supporting lamellae that further extend onto the lamina. The leaf form is rather reminiscent of small montane examples of some *Notoligotrichum* species, such as *N. australe*. It may, however, be seen simply as a more extreme form of the leaf type found in *O. canaliculatum*, *O. tristaniense* Dixon, and *O. riedelianum*, all of which have nerves that are considerably wider than those of true *Oligotrichum* species and support more lamellae, one or two of which often extend on to the lamina (*O. afrolaevigatum*, however, is much closer to *Oligotrichum s. str.* in having a narrow, more or less terete nerve supporting a small number of tall, spreading lamellae). The only practical taxonomic solution is to extend the generic concept of *Itatiella* to encompass the other sampled species in this wider clade, i.e. *O. canaliculatum*, *O. afrolaevigatum*, and *O. riedelianum*, as well as others that can be confidently assumed to be closely related on morphological grounds (*O. tristaniense* and *O. denudatum* G.L.Merr.). While in some respects, we would have preferred to continue to recognise the unique features of *Italtiella ulei* at the generic level, this would have necessitated the description of at least two new genera, while combining *O. riedelianum* alone under *Itatiella* would have created a genus with no clear morphological identity.

Turning to the species found within the large Northern Hemisphere clade of Polytrichaceae, our analyses based on sequence level data strongly suggest that *O. cavallii* is more closely related to *Psilopilum*, *Atrichum*, and *Steereobryon* than to *Oligotrichum s. str.*, while it appears to have a close relative in an as yet undescribed new species from northern Pakistan. Consistent with this, *O. cavallii* is morphologically an unusual and distinctive plant relative to other Northern Hemisphere species. It is frequently relatively robust, with very large, multicellular marginal teeth and spongy tissue in the neck of the capsule that is the basis of the invalid (if rather euphonic) generic name *Spoggodera* (G.Negri) P.de la Varde & Thér. Although we here informally exclude it from *Oligotrichum* on phylogenetic grounds, we will defer making a new combination until further material has been fully examined with a view to possible description of a new genus.

Annotated list of accepted species recently recognised under *Oligotrichum*

We here provide a list of species recognised in *Oligotrichum* prior to this study, with notes on known distributions and statuses where appropriate. A number of apparently accepted names commonly listed under *Oligotrichum* have previously been reliably synonymised or recombined under different genera, and these are not included. We make taxonomic and nomenclatural changes only where these are likely to be stable, and thus, a number of species (all but one from the Southern Hemisphere) are formally retained in *Oligotrichum* on a temporary basis despite being informally excluded on phylogenetic grounds. Further taxonomy, including the description of new species and possibly other new genera, will be dealt with in future publications. Synonyms are generally only listed for basionyms and for alternative names in use relatively recently.

New combinations under *Notoligotrichum*. As outlined above, *Atrichopsis compresssa* (Hook.f. & Wilson) G.L.Sm. and *O. tenuirostre* should be placed in *Notoligotrichum*. This increases the number of species in the genus to 12, nine of which are sampled in our molecular analysis [the others are *N. mexicanum* (G.L.Sm.) G.L.Sm. and the Tristan da Cunha endemics *N. laxifolium* (Dixon) G.L.Sm. and *N. tristaniense* (Dixon) G.L.Sm.]. At least one further species requires to be described from the South African material (see above).

***Notoligotrichum* G.L.Sm.** Mem. New York Bot. Gard. 21(3): 50. 1971.

Notoligotrichum compressum* (Hook.f. & Wilson) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Polytrichum compressum* Hook.f. & Wilson, London J. Bot. 3: 539. 1844.

Atrichopsis magellanica Cardot, Rev. Bryol. 39: 95. 1912.

Atrichopsis compressa (Hook.f. & Wilson) G.L.Sm., Bull. Torrey Bot. Club 96: 62. 1969.

Distribution: Southern Argentina and Chile (Tierra del Fuego), Falkland Islands.

Notes: See Smith (1969) and Schiavone (1993) for descriptions and illustrations.

Notoligotrichum tenuirostre* (Hook.) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Polytrichum tenuirostre* Hook., Musci Exot. 1: 75. 1818.

Oligotrichum tenuirostre (Hook.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 237 (Gen. Sp. Musc. 1: 699). 1875.

Distribution: New Zealand.

Notes: The species is described and illustrated by Frye (1947).

Oligotrichum s. str. We list species that we consider to belong to a monophyletic group including the type species of *Oligotrichum*, *O. hercynicum*, based on definitive taxonomic characters, molecular phylogenetic evidence, or inference based on both. The genus is in need of a comprehensive worldwide revision and in some cases the statuses of species and the boundaries between them remain unclear.

Oligotrichum DC. Fl. Franc. (DC. & Lamarck), ed. 3. 2: 491. 1805.

Oligotrichum aligerum Mitt. J. Proc. Linn. Soc., Bot. 8: 48. pl. 8. 1864.

Distribution: Western North America, Central America, West Indies, Russia, China, Japan, Taiwan, Philippines, Himalayas (?).

Notes: See Smith Merrill (2007) and Wang *et al.* (2005) for recent descriptions and illustrations.

Oligotrichum aristatulum Broth. Symb. Sin. 4: 132. 1929.

Distribution: China (Yunnan).

Notes: A poorly known species, distinguished from *O. semilamellatum* (Hook. f.) Mitt. by Brotherus by its entire, aristate leaves. The holotype (H-BR) has only a few leaves that are in poor condition, the potentially diagnostic leaf apices often missing, and would be best examined in detail following a thorough study of the range of variation in potentially related species.

Oligotrichum austroaligerum G.L.Sm. Phytologia 18: 403. 1969.

O. magellanicum Card. & Broth., Kongl. Svenska Vetenskapsakad. Handl. 63(10): 71. pl. 4: f. 2. 1923. — Synonymised by Schiavone (1993).

Distribution: Southern Chile (Magellanic Region), Argentina (Tierra del Fuego).

Notes: Unique in being the only true *Oligotrichum* species with a predominantly (exclusively in this case) Southern Hemisphere distribution. See Schiavone (1993) for a description and illustration.

Oligotrichum crossidioides P.C.Chen & T.L.Wan ex W.X.Xu & R.L.Xiong

Acta Bot. Yunnan. 6: 179. f. 5. 1984.

Distribution: China (Yunnan, Xizang/Tibet).

Notes: See Wang *et al.* (2005) for a recent description and illustration.

Oligotrichum falcatum Steere Bryologist 61: 115. f. 1–9. 1958.

Distribution: North America, W. Greenland, E. Russia, China (Xizang/Tibet).

Notes: See Ivanova *et al.* (2005) for the distinctions between this species and *O. hercynicum*. Other recent descriptions are in Smith Merrill (2007) and Wang *et al.* (2005), with an illustration in the latter.

Oligotrichum falcifolium (Griff.) G.L.Sm. Phytologia 18: 403. 1969.

Distribution: Himalayas (including at least Nepal), Philippines.

Polytrichum falcifolium Griff., Calcutta J. Nat. History 2: 475. 1842.

Notes: We have not seen the type specimen of this species, which is highly variable and seems to have been confused in the past with *O. semilamellatum* (Smith 1971, 1972) and possibly *O. javanicum*. Iwatsuki & Tan (1980) and Tan & Iwatsuki (1991) report it from the Mt Canlaon area of the Philippines.

Oligotrichum glaciale C.C.Towns. J. Bryol. 20: 52. f. 2. 1998.

Distribution: India (Kashmir).

Notes: Only known from the sterile type collection, but fairly distinctive in its highly concave, apiculate leaves with markedly undulate-plicate lamellae that are reminiscent of *Psilopilum*. Although we retain this species in *Oligotrichum s. str.*, in some respects (if not others), the plant resembles an as yet undetermined specimen collected by Hedderson in northern Pakistan. Based on our molecular results (above), the latter is closely related to the very different East African *O. cavallii* (below), these two forming a clade that falls outside of *Oligotrichum s. str.* and may be more closely related to *Psilopilum*.

Oligotrichum hercynicum (Hedw.) Lam. & DC. Fl. Franc. (DC. & Lamarck), ed. 3. 2: 492. 1805.

Polytrichum hercynicum Hedw., Sp. Musc. Frond. 94. 1801.

Distribution: North America, Greenland, Europe, Japan, China (?).

Notes: See Smith Merrill (2007) for a recent description.

Oligotrichum javanicum (Hampe) Dozy & Molk. Bryol. Jav. 1: 37. 28. 1856.

Catharinea javanica Hampe, Icon. Musc. (Hampe) 22. 1844.

Distribution: Sumatra, Java, Borneo, Papua New Guinea, Philippines (?).

Notes: See Hyvönen (1986) for a description and illustration, and notes above under *O. falcifolium*.

Oligotrichum nepalense G.L.Sm. J. Hattori Bot. Lab. 41: 420. f. 1–9. 1976.

Distribution: Nepal.

Notes: A very distinct species due to its uniquely dissected lamellae.

Oligotrichum obtusatum Broth. Symb. Sin. 4: 133. 1929.

Distribution: China (Yunnan), Taiwan, Nepal.

Notes: See Wang *et al.* (2005) for a recent description and illustration.

***Oligotrichum parallelum* (Mitt.) Kindb.** Bot. Not. 1896: 191. 1896.

Atrichum parallelum Mitt. J. Linn. Soc., Bot. 8: 48. 1864.

Distribution: Arctic North America, Aleutians, Japan, E. Russia.

Notes: See Smith Merrill (2007) for a recent description and illustration.

***Oligotrichum semilamellatum* (Hook.f. in Hook.) Mitt.** J. Proc. Linn. Soc., Bot. Suppl. 2: 150. 1859.

Polytrichum semilamellatum Hook.f., Icon. Pl. 2: pl. 194A. 1837.

Distribution: China (Yunnan), India, Himalayas.

Notes: See Smith (1971, 1972) for discussion of past confusion between this species and *O. falcifolium*. The species is apparently rare. Smith (1976) reported what was at that time only the second collection (from the Himalayas), although subsequent collections from Yunnan are reported in the Moss Flora of China, where a description and illustration are also provided (Wang *et al.*, 2005).

***Oligotrichum serratomarginatum* J.X.Luo & P.C.Wu** Acta Phytotax. Sin. 18: 125. f. 4: 9–20. 1980.

Distribution: China (Xizang/Tibet).

Notes: We have no knowledge of this species other than the description and it is not included or mentioned in the Moss Flora of China (Wang *et al.*, 2005). The protologue includes a description in Chinese in addition to a shorter Latin diagnosis.

***Oligotrichum suzukii* (Broth.) C.C.Chuang** J. Hattori Bot. Lab. 37: 430. 1973.

Distribution: Taiwan.

Notes: See Wang *et al.* (2005) for a recent description and illustration.

An expanded *Itatiella*. The genus *Italiella* is considerably expanded to encompass many of the Southern Hemsiphere species of *Oligotrichum*. It is likely that further species will be included when their precise affinities have been confirmed (see 'currently unplaced species' below).

***Itatiella* G.L.Sm.** Mem. New York Bot. Gard. 21: 52. 1971.

Itatiella afrolaevigatum* (Dixon) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Psilopilum afrolaevigatum* Dixon, Trans. Roy. Soc. South Africa 8: 207. pl. 11: f. 10. 1920.

Oligotrichum afrolaevigatum (Dixon) G.L. Sm., Phytologia 18: 403. 1969.

Distribution: South Africa.

Itatiella canaliculatum* (Hook. & Arn.) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Polytrichum canaliculatum* Hook. & Arn., Bot. Beechey Voy. 54. 1841 [1832] (Jan–Feb 1832).

Oligotrichum canaliculatum (Hook. & Arn.) Mitt., J. Linn. Soc., Bot. 12: 606. 1869.

Distribution: Chile, Argentina, Brazil.

Notes: See Peralta & Yano (2010) for a recent description and illustration under *Oligotrichum*, although the Brazilian material is not typical; see notes below under *I. tristaniense*.

Itatiella denudatum* (G.L.Merr.) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Oligotrichum denudatum* G.L.Merr. Novon 1: 107. f. 1. 1991.

Distribution: Brazil.

Notes: This species is very similar to *I. riedelianum*, but generally lacks lamellae (Peralta & Yano, 2010, have noted some leaves with very reduced lamellae however). Although we do not have molecular data to support the hypothesis, it seems likely that this is the sister species of *I. riedelianum*. See Peralta & Yano (2010) for a recent description and illustration (also the protologue).

Itatiella riedelianum* (Mont.) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Polytrichum riedelianum* Mont., Ann. Sci. Nat., Bot., sér. 2, 16: 269. 1841.

Oligotrichum riedelianum (Mont.) Mitt. J. Linn. Soc., Bot. 12: 606. 1869.

Distribution: Brazil.

Notes: It is likely that this species, *I. denudatum* and *I. ulei* form a clade that has originated in (and is restricted to) SE Brazil. See Peralta & Yano (2010) for a recent description and illustration.

Itatiella tristaniense* (Dixon) N.E.Bell & Hyvönen *comb. nov.

Basionym: *Oligotrichum tristaniense* Dixon, Results Norweg. Sci. Exped. Tristan da Cunha 48: 47. 1960.

Distribution: Tristan da Cunha group.

Notes: Based on our examination of a paratype in BM (*Christophersen & Mejland*, 840b), this species is sufficiently similar to *I. canaliculatum* to warrant this new combination without reference to molecular data, which would require fresh collections from the extremely remote Tristan da Cunha island group. Both species usually have wide nerves (around one-third of the lamina width or sometimes more) supporting fairly numerous (typically 15–30) tall lamellae, 5–9 cells in height, with often also one or two lamellae to the side of the nerve on the lamina itself (the Brazilian specimens of *O. canaliculatum*, representing the northern extreme of the distribution of the species and described by Peralta & Yano, 2010, would appear to be less well developed). Both also have typically cylindrical *Oligotrichum*-like capsules on fairly short setae (up to 2.5 cm). When describing *O. tristaniense*, Dixon seems not to have compared the material to *O. canaliculatum*, as he considered it quite distinct and only close to the substantially

different *O. laevifolium* (see 'excluded and doubtful species' below). The only clear distinction from *O. canaliculatum* would appear to be the shortly cuspidate, slightly reflexed leaf apex, as contrasted with the more obtuse and slightly incurved apex in *O. canaliculatum*. Dixon described the nerve of *O. tristaniense* as excurrent, although this is not clear in the paratype we examined, which may not be as well developed as the holotype. While it is possible that *I. tristaniense* is conspecific with *I. canaliculatum*, it would be necessary to examine a wider range of material to adequately assess this.

Itatiella ulei (Broth. ex Müll.Hal.) G.L.Sm. Mem. New York Bot. Gard. 21(3): 52. 1971.

Distribution: Brazil.

Currently unplaced species. The following species are informally excluded from *Oligotrichum*, although new combinations are not made at this stage as further study is required to ascertain precise relationships. It is likely that several will be best placed in *Itatiella*. For all of them except *O. novae-guineae* (E.B.Bartram) G.L.Sm. and *O. obtusifolium* Thér., it should be possible to obtain molecular data in the near future (where it does not already exist) to help determine generic placements.

Oligotrichum cavallii (G.Negri) G.L.Sm. Mem. New York Bot. Gard. 21(3): 53. 1971.

Catharinea cavallii G.Negri, Ann. Bot. (Rome) 7: 168. 1908.

Distribution: East Africa — Tanzania, Rwanda, Eastern Congo, Uganda.

Notes: See discussion above. This is the only unplaced species belonging to the large Northern Hemisphere clade of Polytrichaceae.

Oligotrichum erosum (Hampe) Lindb. Not. Sällsk. Fauna Fl. Fenn. Förh. 9: 103. 1867.

Catharinea erosa Hampe, Linnaea 32: 146. 1863.

Distribution: Andes — Colombia, Ecuador, Peru, Bolivia.

Notes: A recent description is provided in the online Andean Bryophyte and Bolivia Bryophyte Projects at the Missouri Botanic Garden (http:// www.tropicos.org/project/anbry, http://www.tropicos. org/project/bmp).

Oligotrichum gymnostomulum (Müll.Hal.) Kindb. Enum. Bryin. Exot., Suppl. 1. 93. 1889.

Psilopilum gymnostomulum (Müll.Hal.) Paris, Index Bryol. 1040. 1898.

Catharinea gymnostomula Müll.Hal., Linnaea 42: 264. 1879.

Distribution: Bolivia, N. Argentina, Peru (?).

Notes: Smith (1971) considered this species to be best placed in *Oligotrichum*, although it has been treated under *Psilopilum* in recent floras (e.g. the online Andean Bryophyte and Bolivia Bryophyte

Projects at the Missouri Botanic Garden (http:// www.tropicos.org/project/anbry, http://www.tropicos. org/project/bmp). Although the 'asymmetric, obloid capsules' might suggest *Psilopilum*, a placement in this arctic taxon seems highly unlikely. The similarity of the gametophyte to *Itatiella afrolaevigatum* suggests a possible placement in that genus, although the asymmetric capsules imply a possible affinity to *Notoligotrichum*.

Oligotrichum novae-guineae (E.B.Bartram) G.L.Sm. Mem. New York Bot. Gard. 21(3): 49. 1971.

Atrichum novae-guineae E.B.Bartram, Rev. Bryol. Lichénol. 30: 206. 1961.

Distribution: Papua New Guinea.

Notes: This species is only known from the type material (*Robbins* 3035, CAN, FH), which we have recently re-examined, and is an enigma. We are in agreement with Smith (1971) that it resembles *O. tenuirostre* (≡ *Notoligotrichum tenuirostre*, as above), although we do not feel that there is sufficient evidence to justify a placement in *Notoligotrichum*. It shares with that species a narrow nerve bearing a small number (5–10) of short (usually three cells high) lamellae which are restricted to the nerve, contrasting with a broad, ± concave lamina (generally species of *Oligotrichum* and *Itatiella* with few lamellae and narrow nerves have lamellae that are much higher, hence the original description of *O. novae-guineae* under *Atrichum*). The leaf form is similar to *N. tenuirostre* (although the apex is considerably more obtuse), with the same border often bearing distant, blunt teeth comprising single cells. Significantly, although we did observe some papillosity on some of the marginal tooth cells, there is no evidence of bistratose areas on the lamina. The specimen we examined includes a single capsule that is unfortunately both in poor condition and not fully mature, the other sporophytes being only at the 'spear' stage. The capsule is slightly inclined and narrowed towards the mouth, suggesting *Notoliotrichum*, but it is impossible to judge whether the mature capsule would be angled and/or asymmetric, while the peristome cannot be observed. The stomatal distribution is also indistinct, again due to the stage and condition of the capsule. Significant evidence against a close relationship to *N. tenuirostre* comes from the nerve structure. In *N. tenuirostre*, although the nerve is narrow in relation to the lamina, it is widened in section, whereas in *O. novae-guineae*, it is almost terete. Furthermore, in *O. novae-guineae*, despite the smaller nerve, there are effectively two rows of guide cells (the lower one comprised of smaller cells), while in *N. tenuirostre* (as in most *Notoligotrichum* spp.), there is a single well-defined row with only occasional isolated smaller guide cells underneath. In addition, the epidermal cells on the ventral side of the nerve

(from which the lamellae arise) are inflated (larger than the lamellar cells) in *N. tenuirostre*, while in *O. novae-guineae*, they are smaller than the lamellar cells. It is to be hoped that further collections of this species will become available in the future to enable its true relations to be confidently resolved.

***Oligotrichum obtusifolium* Thér.** Rev. Bryol. Lichénol. 7: 167. 1. 1935.

Distribution: Chile (Region XIV, Valdivian province).

Notes: We know nothing of this species other than the description in the protologue and have not seen the type. We are not aware of any other collections. The type locality and description suggest a possible synonymy with *O. atrichopsis* Müll.Hal. (below), which to be confirmed would require identification of the type material of the latter species.

***Oligotrichum wageri* (Broth.) G.L. Sm.** Phytologia 18: 403. 1969.

Distribution: South Africa.

Notes: Known only from a small number of localities in the east of South Africa. As with *O. gymnostomulum*, the asymmetrical sporophyte (in this case also laterally compressed) may indicate affinities to *Notoligotrichum*, although a placement in *Itatiella* seems equally plausible, especially given the similar distribution to *I. afrolaevigatum*

Excluded and doubtful taxa

Oligotrichum atrichopsis Müll.Hal. Gen. Musc. Frond. 167. 1900.

The description of this species simply states that it has a 'blunt tip' and is from Valdivia (Chile). No specimen or collector is cited, although there is potential type material in S ('leg. Hahn, ded. C. Müller 1889'; reviewer, pers. comm.)

Oligotrichum crispatissimum Müll.Hal. Gen. Musc. Frond. 167. 1900.

This species was described only as being from Chile and having a mucronate leaf, again without a specimen or collector cited.

Oligotrichum laevifolium Thér. Revista Chilena Hist. Nat. 28: 134. 1924.

= *Hebantia rigida* (Lorentz) G.L.Merr. J. Hattori Bot. Lab. 80: 247. 1996. *syn. nov.*

An isotype of this taxon in H-BR has been annotated by Seki as corresponding to *O. rigidum* (Lorentz) Broth. (≡ *Hebantia rigida* (Lorentz) G.L.Merr.), and we concur with this. The specimen is underdeveloped and without sporophytes, but there are clusters of thin walled cells in the adaxial stereid bands (Smith, 1971; Smith Merrill, 1996).

Acknowledgements

Taxonomic Additions and Changes: *Notoligotrichum compressum* (Hook.f. & Wilson) N.E.Bell & Hyvönen *comb. nov.*; *Notoligotrichum tenuirostre* (Hook.) N.E. Bell & Hyvönen *comb. nov.*; *Itatiella afrolaevigatum* (Dixon) N.E.Bell & Hyvönen *comb. nov.*; *Itatiella canaliculatum* (Hook. & Arn.) N.E.Bell & Hyvönen *comb. nov.*; *Itatiella denudatum* (G.L.Merr.) N.E.Bell & Hyvönen *comb. nov.*; *Itatiella riedelianum* (Mont.) N.E.Bell & Hyvönen *comb. nov.*; *Itatiella tristaniense* (Dixon) N.E.Bell & Hyvönen *comb. nov.*; *Oligotrichum laevifolium* The'r. (*Hebantia rigida* (Lorentz) G.L.Merr *syn. nov.*).

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Appendix

List of GenBank accession numbers and voucher specimens for new molecular sequences generated for this study. Entries are in the format: name, voucher, herbarium, country of collection, 18S, *nad*5, *rps*4, *rbc*L, *trn*L–F. One specimen (indicated *) was used for comparative molecular studies and exploratory phylogenetic analyses but was not included in the final analyses (see text).

Oligotrichum aligerum, *Norris 83978*, H, USA, JQ639442, JQ639433, JQ639423, JQ639451, JQ639413. *O. cavallii*, *Porely U9150a*, H, Uganda, JQ639443, JQ639434, JQ639424, JQ639452, JQ639414. **O. cavallii*, *Pocs 6976/A*, H 3098627, Tanzania, –, –, JQ639425, –, JQ639415. *O. falcatum*, *Ignatov 97-525*, H, Russia, JQ639444, JQ639435, JQ639426, JQ639453, JQ639416. *O. falcifo-lium*, *Weber B-99372*, H, Nepal, JQ639445, JQ639436, JQ639427, JQ639454, JQ639417. *O. javanicum*, *Koponen 32180*, H, Papua New Guinea, JQ639446, JQ639437, JQ639428, JQ639455, JQ639418. 'Pakistan specimen', *Hedderson 12395*, RNG, Pakistan, JQ639447, JQ639438, JQ639429, JQ639456, JQ639419. *Notoligotrichum* 'SA1', *Hedderson 14275*, BOL, South Africa, JQ639448, JQ639439, JQ639430, JQ639457, JQ639420. *Notoligotrichum* 'SA2', *Hedderson 14283*, BOL, South Africa, JQ639449, JQ639440, JQ639431, JQ639458, JQ639421. *Notoligotrichum* 'SA4', *Hedderson 13675*, BOL, South Africa, JQ639450, JQ639441, JQ639432, JQ639459, JQ639422.