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Fruiting material of *Chenia lorentzii* (Bryophyta, Pottiaceae) found in Argentina and an evaluation of the sporophyte taxonomic value in the genus *Chenia*

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Summary: In the present contribution, the sporophyte of *Chenia lorentzii* is described in detail and microphotographs are provided. In addition, the role of sporophytic characters is discussed in a phylogenetic context. To accomplish this task, first, a phylogenetic analysis of a reduced dataset of Pottiaceae genera was carried out by using molecular data (*nad5, rps4*, *26S*) and combined data (morphology and molecular markers). Then, gametophytic and sporophytic characters were mapped onto the molecular tree and their fit to the phylogeny was assessed on the basis of their extra steps and the number of diagnosed nodes. Results suggest that sporophytic characters should be treated with caution when nomenclatural generic changes are proposed.

Key words: Character reconstruction, morphology, taxonomy.

Resumen: Material fructificado de *Chenia lorentzii* (Bryophyta, Pottiaceae) hallado en Argentina y una evaluación del valor taxonómico del esporofito en el género *Chenia*. En la presente contribución, el esporofito de *Chenia lorentzii* es descrito en detalle y se proveen fotomicrografías. Además, el rol de los caracteres esporofíticos es discutido en un contexto filogenético. Para ello, primero, se lleva a cabo un análisis filogenético de un dataset reducido de géneros de Pottiaceae empleando marcadores moleculares (*nad5, rps4*, *26S*) y datos combinados (morfología y marcadores moleculares). Luego, los caracteres esporofíticos y gametofíticos son mapeados en el árbol de moléculas y su ajuste a la filogenia es medida en base a su *número de pasos extras* y el *número de nodos diagnosticados*. Los resultados sugieren que los caracteres esporofíticos deben ser evaluados con precaución al momento de proponer cambios nomenclaturales a nivel genérico.

Palabras clave: Morfología, reconstrucción de caracteres, taxonomía.

Introduction

Pottiaceae is amongst the most diverse bryophytes families with about 1500 species (Zander, 1993; Werner *et al*., 2004, 2005). Few exceptions aside, it is widely accepted that its morphological account is particularly challenging (Zander, 1993; Guerra & Cano, 2000; Werner *et al.*, 2005). As a consequence of polymorphism, minimal size, and sterility, many species and genera remain as obscure taxonomic entities (Werner *et al.,* 2002, 2004, 2005). Thus, many morphological characters still have an unclear role in the taxonomy of this group. Specifically, the sporophyte has persisted as a confusing source of information for many genera such as *Chenia* R.H. Zander or *Microbryum* Schimp.

Originally, the genus *Chenia* was erected to include two species the Andean *C. subobliqua* (R.S. Williams) R.H. Zander and the weedy *C. rhizophylla* (Sakurai) R.H. Zander, both previously treated as *Tortula* Hedw. The genus was, for gametophyte characters, easily distinguished from other Pottiaceae by the combination of the dentate upper leaf margins, large, epapillose laminal cells (only laterally papillose in the marginal cells), thin costa, and red coloration in KOH. A third species, *C.*

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lorentzii (Müll. Hal.) R.H. Zander, was added to the genus based on an Argentinian collection (Zander, 1993), and has also been recorded for Bolivia (Churchill *et al.*, 2009); however, its sporophyte is only known from few traits given in the original description. More recently, Hedderson & Zander (2008) described *C. ruigtevleia* Hedd. & R.H. Zander as a fourth species from the Cape region of South Africa, characterised by the presence of papillae in the median laminal cells.

The absence of well-defined sporophyte characters has disguised the taxonomic identity of *Chenia* since Zanders' proposal (1989). Arts & Sollman (1991), for instance, agreed with Müller (1888) in placing *C. leptophylla* (Müll. Hal.) R. H. Zander [= *Tortula rhizophylla* (Sakurai) Z. Iwats. & K. Saito] under *Phascum leptophyllum* subgen. *Leptophascum*. Even so, they recognised that gametophyte characters in *Chenia* hardly fitted the concept of *Phascum* Hedw. Similarly, Guerra & Cano (2000) preferred to establish a new combination *Leptophascum leptophyllum* (Müll. Hal.) J. Guerra & M. J. Cano. This approach was based on the unlikely association with *Tortula* regarding both gametophyte and sporophyte characters. As *Chenia* included both cleistocarpous and stegocarpous species, the placement of *C. lorentzii* within it was also rejected. *Chenia ruigtevleia* Hedd. & R. H. Zander, the lastest described species of *Chenia*, also lacks a sporophyte. In this sense, the taxonomic distinction between the species of *Chenia* and the related genera rested mainly on gametophyte features, whereas sporophyte traits were subjected to a rough discussion of their taxonomic value (Zander, 1989; Arts & Sollman, 1993; Guerra & Cano, 2000).

Recently, while working on the "Bryophyta Genera from the Northwest of Argentina" we found, mixed with *Didymodon umbrosus* (Müll. Hal.) R.H. Zander, a large fertile population of *Chenia lorentzii* collected in 1946. Further examination of the isotype of *Tortula amphidiifolia* (Müll. Hal.) Broth. (recently synonymised with *C. lorentzii*; Cano & Gallego, 2008) revealed some plants with degraded capsules or only with setae present, leaving us to study some sporophyte features.

In this paper, sporophytic characters of this interesting moss are described and photographed in detail for the first time. Finally, a brief discussion on their taxonomic information content is presented by mapping those characters onto a reduced phylogeny of species that are conflictive concerning sporophyte traits.

Materials and Methods

Morphological studies

We studied samples collected in Argentina and other specimens deposited in LIL and LIL-Matteri. The specimens were analysed morphologically with conventional techniques for bryophytes and mounted in Hoyer's solution (Anderson, 1954).

Phylogenetic character reconstruction of sporophyte

In order to discuss the role of the sporophyte on *Chenia* taxonomy, sporophytic characters were mapped onto a phylogenetic tree of Pottiaceae genera. However, none of the taxonomic sampling of previous molecular focused on conflicting taxa regarding sporophytic traits. Therefore, to reduce the number of missing entries, a phylogenetic analysis of a reduced taxon dataset was carried out. It is well-known that the final topology depends on the number of analysed taxa. However, the rationale of our methodology is that if the final tree reflected similar relationships to that of the recent comprehensive phylogenies (Werner *et al.,* 2002, 2004, 2005), then a reliable evaluation of the characters taxonomic value could be conducted.

Given the poor state of the material of *C. lorentzii*, it was not possible to obtain reliable DNA samples. Even so, with the purpose of mapping sporophyte characters, a molecular phylogeny was reconstructed by employing three molecular markers available from Genbank (*nad5*, *rps4*, and *26S*). The dataset consisted of eight outgroup species: two species of Timmiellaceae [*Timmiella barbuloides* (Brid.) Mönk. and *Luisierella barbula* (Schwägr.) Steere] and Ephemeraceae (*E. minutissimum* Lindb. and *E. serratum* (Schreb. ex Hedw.) Hampe) and one species of Dicranaceace [*Braunfelsia dicranoides* (Dozy & Molk.) Broth.], Ditrichaceae [*Rhamphidium dicranoides* (Müll. Hal.) Paris], and Pleurophascaceae [*Pleurophascum grandiglobum* Lindb.]. *Bartramia stricta* Brid. was employed as root. Ingroup included 17 Pottiaceae species from 16 genera (Table 1).

Table 1. Genbank Accession (*nad5/rps4/26S*) numbers and specimens vouchers. Specialised literature of reference is also informed.

TAXA	Genbank Accession (nad5/rps4/26S)	Voucher/Literature of reference
INGROUP		
Aloina rigida (Hedw.) Limpr.	AY908819/AY908024/HM751528	*G. Suárez 1591* (LIL)/Zander, 1993
Aloinella cucullifera (Mitt.) Steere	-/AY908071/HM751548	/Zander, 1993
Aschisma carniolicum (F. Weber & D. Mohr) Lindb.	AY908851/AY908054/AY796270	/Guerra & Cano, 2000
Chenia leptophylla (Müll. Hal.) R.H. Zande	AY908815/JX679982/JX679958	-/Zander, 1989, Zander, 1993, Hedderson & Zander, 2008
Chenia lorentzii (Müll. Hal.) R.H. Zande	-/-/-	Digilio-Grassi 777 (LIL)/Zander, 1989; Zander, 1993; Hedderson & Zander, 2008
Chenia subobliqua (R.S. Williams) R.H. Zander	-/-/-	-/Zander, 1989; Zander, 1993; Hedderson & Zander, 2008
Dolotortula mniifolia (Sull.) R.H. Zander	AY908824/AY908036/HM751535	*G. Suárez 124* (LIL), *S. Churchill & M. Schiavone 20031* (LIL, MO)/Suárez *et al*., 2005; Zander, 1989.
Erythrophyllopsis andina (Sull.) R.H. Zander	AY908831/AY121425/HM751539	*G. Suárez 635, 679* (LIL)/Zander, 1993
Ganguleea angulosa (Broth. & Dixon) R.H. Zander	AY908970/AY908068/HM751713	-/Zander, 1993
Gymnostomiella vernicosa (Hook. ex Harv.) M. Fleisch.	AY908837/AY908066/HM751572	-/Zander, 1993
Hyophila involuta (Hook.) A. Jaeger	KJ195515/KJ195508/KJ195501	*M. Schiavone 3295* (LIL)/Zander, 1993
Microbryum davallianum (Sm.) R.H. Zander	AY908825/AY908033/HM751710	-/Zander, 1993
Microbryum curvicolle (Hedw.) R.H. Zander	-/JX679986/JX679969	-/Zander, 1993
Plaubelia sprengelii (Schwägr.) R.H. Zander	KJ195519/KJ195513/KJ195506	-/Zander, 1993
Pseudosymblepharis guatemalensis (E.B. Bartram) B.H. Allen	AY908850/AY908056/-	-/Zander, 1993
Tortula atrovirens (Sm.) Lindb.	-/EU274587/JN544712	*G. Suárez 939* (LIL)/Zander, 1993
Trichostomum brachydontium Bruch	-/AY950390/-	*G. Suárez 1089* (LIL, MA)/Zander, 1993
Weisiopsis anomala (Broth. & Paris) Broth. & Paris	AY908864/AY908070/HM751583	-/Zander, 1993
Weissia controversa Hedw.	AY908849/JX679984/HM751566	*G. Suárez et al. 1487* (LIL)/Zander, 1993
OUTGROUP		/
Bartramia stricta Brid.	AY312870/ EU301607/ AY330428	-/Matteri, 1983
Braunfelsia dicranoides (Dozy & Molk.) Broth.	AY908879/ AY908102/-	-/Bartram, 1957
Ephemerum minutissimum Lindb.	-/JX679985/JX679966	-/Zander, 1993
Ephemerum serratum (Schreb. ex Hedw.) Hampe	AY908848/AY908061/HM751716	-/Zander, 1993
Luisierella barbula (Schwägr.) Steere	AY908975/AB853085/-	-/Zander, 1993
Pleurophascum grandiglobum Lindb.	AY908961/AY908101/-	-/Zander, 1993
Pleurophascum occidentale R.E. Wyatt & A.H. Stoneb.	-/-/-	-/Zander, 1993
Rhamphidium dicranoides (Müll. Hal.) Paris	AY908867/AY908089/HM751582	*G. Suarez 1608; 1651* (LIL)/-
Timmiella barbuloides (Brid.) Mönk.	-/AB914723/-	*G. Suárez 137* (LIL)/Zander, 1993

The three molecular markers (*nad5*, *rps4*, and *26S*) were aligned with MAFFT (Katoh *et al.*, 2002). The alignment was then edited by omitting those sites which had more than 50% gaps. Tree searches were performed in TNT 1.5 (Goloboff *et al.*, 2008; Goloboff & Catalano, 2016) with parsimony as optimality criterion, by using Ratchet (Nixon, 1999) and Tree Drifting (Goloboff, 1999). Extended implied weighting (Goloboff, 2014), a novel method useful when analysing molecular characters, was applied to weight entire partitions considering the average homoplasy of their characters.

A morphological matrix [consisting of gametophytic and sporophytic character partitions; modified after Zander (1993)] was considered for both character mapping and carrying out a combined analysis. Regarding character mapping, gametophytic and sporophytic characters were exclusively optimised onto the molecular tree. The number of nodes from the molecular tree having at least a single morphological synapomorphy was calculated for both the gametophytic and sporophytic groups of characters. Since the gametophytic partition was larger than the sporophytic partition, the number of nodes which recovered at least one synapomorphy could be biased by the number of characters of each group. To discard this effect, a randomisation test was additionally performed. This involved sampling 19 gametophytic characters (i.e. the total number of sporophytic ones) at random, collapsing those nodes unsupported by these characters and calculating the number of non-collapsed nodes. This procedure was repeated 1000 times and the p-value was computed. A p-value below 0.005 meant that patterns were not related to partition size.

Finally, the mean extra steps (homoplasy) of the gametophytic and sporophytic characters were also assessed. Certain correlation between homoplasy and the number of nodes with synapomorphies is expected. That is, a character may be informative for as many nodes as extra steps it has. However, these two measures represented different aspects of a set of characters: their optimality and their taxonomic information content. Given a relatively low number of extra steps and a high number of nodes with synapomorphies, most of the apomorphic changes will be concentrated on internal branches. In contrast, most of the changes will be autapomorphic if a low number of synapomorphies and high number of extra steps is depicted for a character set.

The final dataset and results are freely available at Morphobank (http://www.morphobank.org; Project: 2566). Taxa vouchers and Genbank accession numbers are provided in Table 1.

Results

Taxonomic description

Chenia lorentzii (Müll. Hal.) R.H. Zander, Bulletin of the Buffalo Society of Natural Sciences 32: 258. 1993. = *Tortula lorentzii* (Müll. Hal.) Broth., Die Natürlichen Pflanzenfamilien I(3): 403. 1902. = *Barbula lorentzii* Müll. Hal., Linnaea 42: 346. 1879. Type citation: Argentinia subtropica, Siambon, 1873, cum *Barbula pernana* associata, in limosis. (NY, S). (Fig. 1, 2)

Tortula amphidiifolia (Müll. Hal.) Broth., Die Natürlichen Pflanzenfamilien I(3): 430. 1902. = *Barbula amphidiifolia* Müll. Hal., Linnaea 42: 332. 1879. Type: Argentinia Cordobensis, Ascochinga, cum *Barbula* sedifolia et Trichostomo acaule Aprili 1871, terrestris. (*Isotipus* LIL-Matteri!). First synonymized by Cano & Gallego 2008.

Plants forming turfs, green to yellow-green, pale. Stem 3-10 mm, branched, in transverse section rounded, central strand strong, sclerodermis present, hyalodermis absent; axillary hairs small, of 3-5 hyaline cells. **Leaves** contorted when dry, erect to spreading when moist, ligulate to spathulate, 1.5-2.5 mm in length, margins plane above, recurved from the middle to basin, dentate to sharply crenulate; **apex** rounded, apiculate, with thick-walled cells, marginal cells often smaller than medial, with a weak simple papilla; costa weak, ending 10-12 cells before the apex, costa with lamina inserted laterally, costal transverse section rounded, stereid band present, ventral and dorsal epidermis present, guide cells 2 in 1 layer, hydroid strand present; upper laminal cells large, hexagonal to isodiametric, 9-18 µm, walls thin, weakly trigonous, papillae absent, basal cells rectangular.

Dioicous. Perichaetia terminal, perichaetial leaves little different from the cauline, slightly shorter. **Seta** 0.5-1.0 cm in length, 1 per

perichaetium, reddish, twisted clockwise; capsule 2 mm in length, cylindrical, exothecial cells 37.5-50 X 18.75-25 µm, rectangular to isodiametric, thin-walled, **stomates** phaneropore at base of theca, annulus of 2 layers of vesiculose cells, persistent, **peristome** present, teeth 32, filamentous, densely spiculose, 480 µm in length, twisted, basal membrane 25 µm in height, spiculose. **Operculum** long-conic, 900 µm in length, cells twisted weakly counterclockwise. **Caliptra** cucullate, smooth. **Spores** 7.5 µm in diameter, nearly smooth. Laminal KOH colour reaction red.

Examined material. Argentina. *Tucumán*: Yerba Buena, 11 VIII 1946, Digilio-Grassi 777A (LIL).

Reference tree and character reconstruction

Searches concluded in two MP trees and a

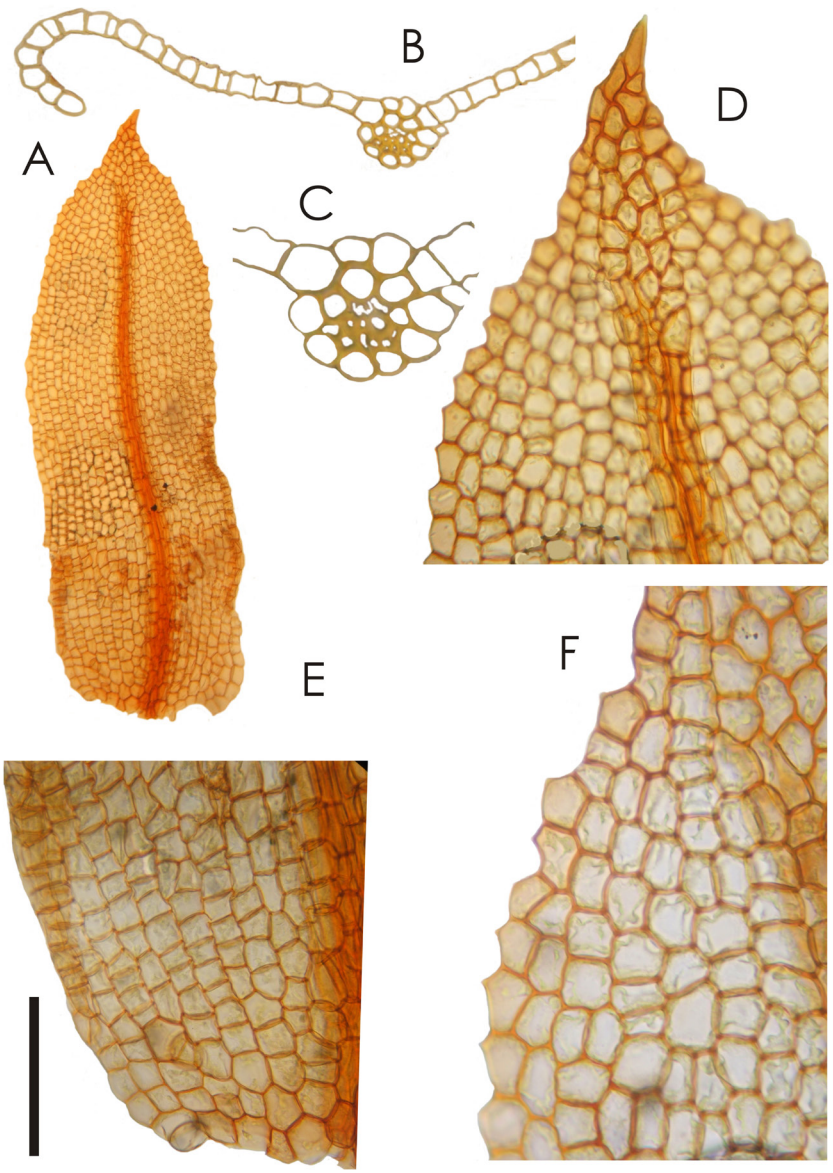

Fig. 1. *C. lorentzii*. A. leaf. B. Leaf cross-section. C. Detail of *B* at the costa level. D. Leaf apex. E. Basal cells group. F. Leaf margin. Scale bars: A: 0.5 mm; B: 15 µm; C: 30 µm; D: 60 µm; E: 70 µm; F: 40 µm.

relatively well-resolved consensus (Fig. 3A). Most of the recognised groups, as well as the recently defined relationships, were retrieved as such (Werner *et al.* 2002, 2004, 2005). Particularly, Timmiellaceae and the nested position of Ephemeraceae within Pottiaceae were recovered. As in Werner *et al.* (2002), *Microbryum davallianum* (Sm.) R. H. Zander and *M. curvicolle* (Hedw.) R. H. Zander were not sister species. Contrary to previous assumptions (Werner *et al.*, 2004), there was low conflict between morphology and molecules. The general topology of the molecular tree is retained when wildcard taxa [*Aschisma carniolicum* (F. Weber & D. Mohr.) Lindb., *Pseudosymblepharis guatelmalensis* (E.B. Bartram) B.H. Allen, *Trichostomum brachydontium* Bruch, *Weissia controversa* Hedw.] are removed from the combined tree (Fig. 3B). In this regard, differences were mainly a consequence of the lack of data for some species either in the morphological or some molecular partitions. Because of the general agreement of the current reference molecular tree with previous phylogenies, such a topology provided a solid basis upon which the contribution of the sporophytic characters could be far tested.

The comparison between the fit of the gametophytic and sporophytic characters onto the molecular topologies revealed that gametophyte characters were slightly more homoplastic than sporophyte traits (Fig. 4). However, gametophytic features recovered a larger number of nodes from the molecular phylogenies (half of the nodes of the molecular consensus tree). The same pattern was obtained when the randomisation test was performed, indicating that this difference was not related to partition size (6.32 ± 1.003; p-value < 0.005).

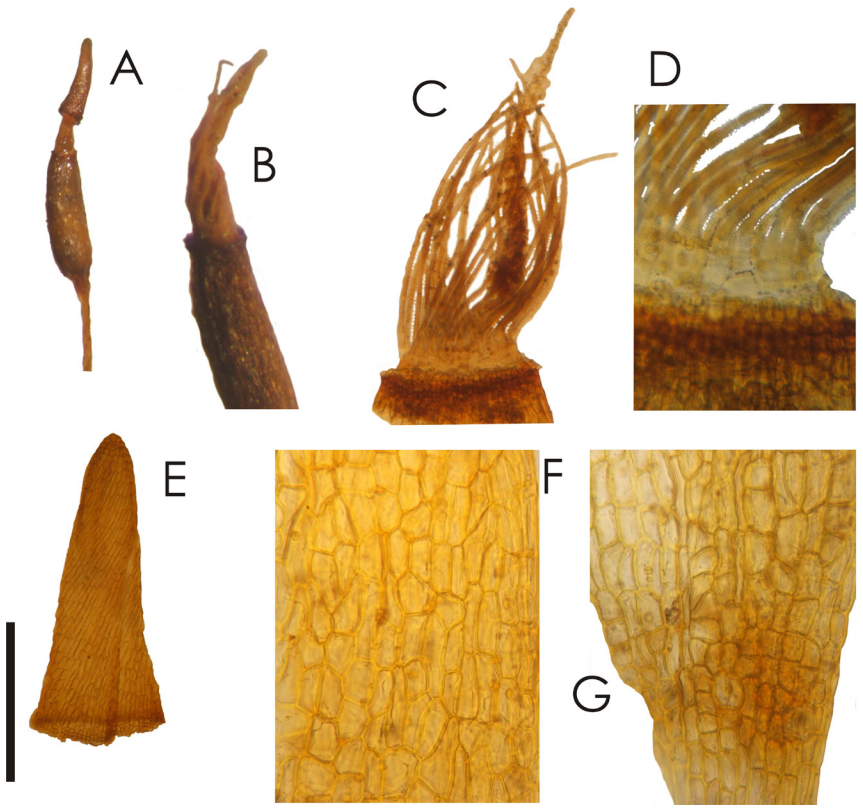

Fig. 2. *C. lorentzii*. A. Complete sporophyte. B. Teeth in dry. C. Teeth detail in wet. D basal membrane. E Opercula. F exothecial cells. C. Neck with stomata. A: 2.2 mm; B: 450 µm; C: 200; D, F, G: 100µm; E: 400 µm.

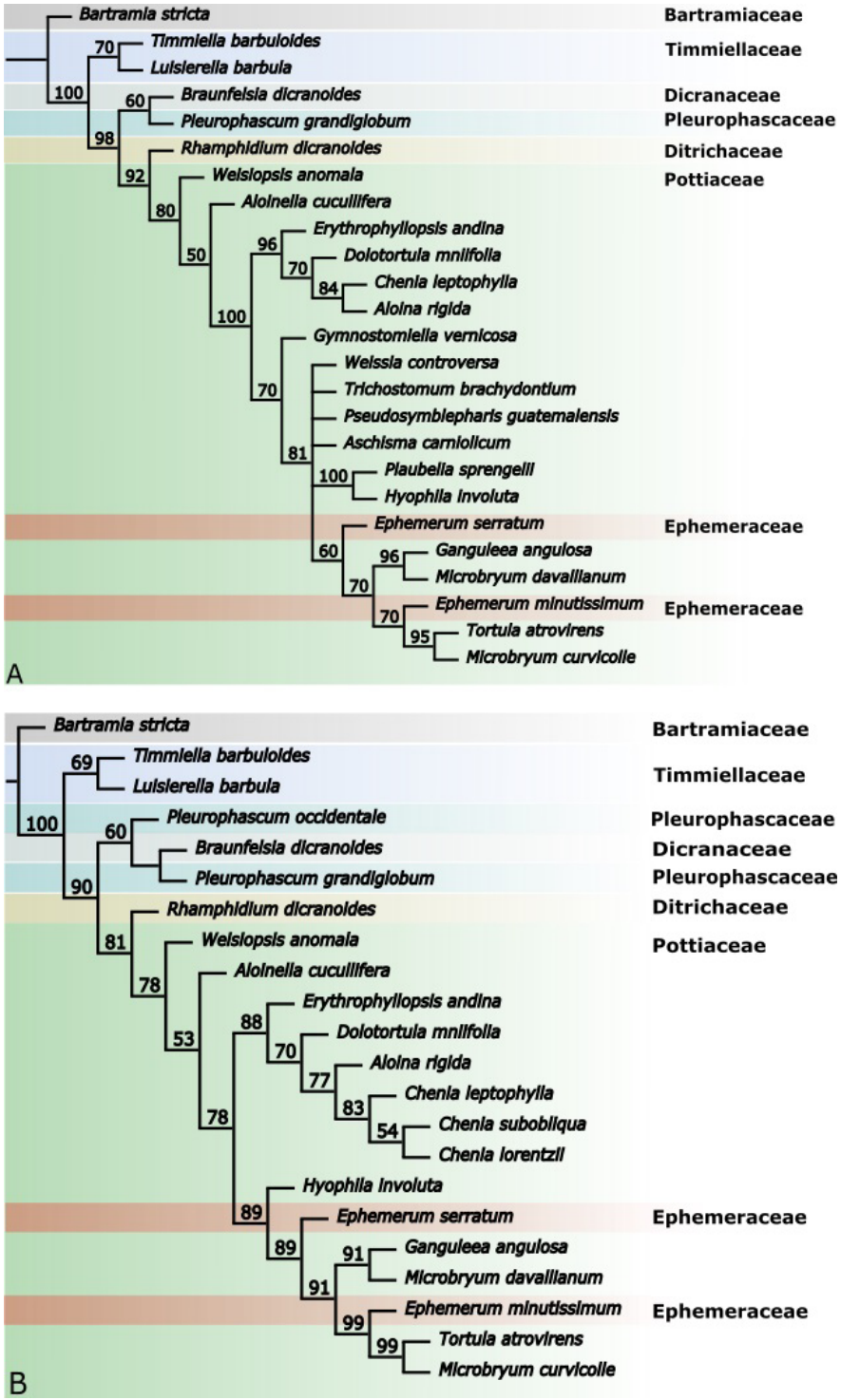

Fig. 3. A. Strict consensus of the two MP trees. B Combined tree after pruning wildcard taxa [Zander's (1993) modified *morphological matrix* + *nad5* + *rps4* + *26S*]. Bootstrap values ≥50 are shown above branches. Family membership is illustrated in colour. See text for details.

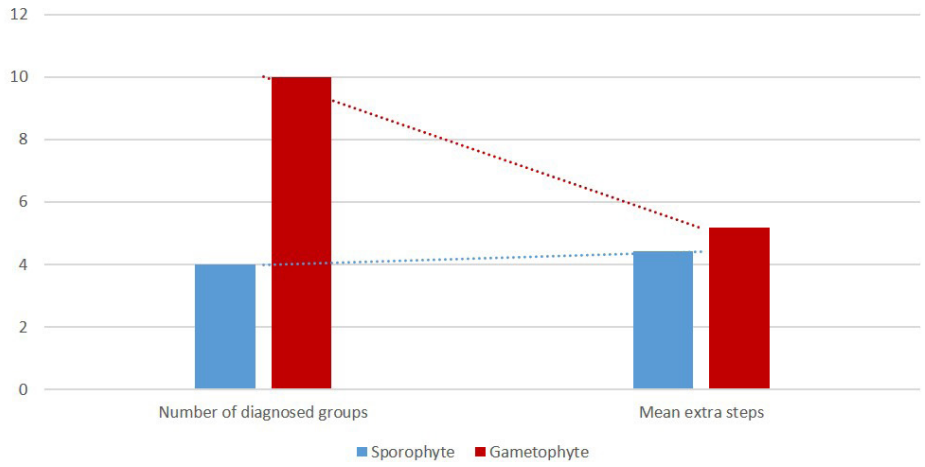

Fig. 4. Column plot. Right columns: mean extra steps (homoplasy) of the gametophytic and sporophytic characters. Left columns: number of diagnosed nodes (i.e. nodes with at least a single synapomorphy). Dotted line: linear tendency line.

Discussion

Sporophyte systematic value on Pottiaceae and Chenia taxonomy

Most of the current knowledge of Pottiaceae systematics is based on the revisions of Zander (1989, 1993). Besides the several taxonomical improvements Zander made, a key issue concerns the sporophyte usefulness to discriminate genera and species within Pottiaceae. Previously, different authors (Chen, 1941; Corley *et al.*, 1981; Saito 1975) provided dissimilar schemes regarding suprageneric classification. These proposals, and in particular Saito (1975), considered sporophytic characters to establish relationships among genera. However, only a few sporophytic traits were apparently reliable to link taxa. Indeed, reduction series of several sporophyte features were already observed by Saito (1975). At the present, this sporophyte simplicity is a puzzle for the systematic and taxonomy of many genera within Pottiaceae.

The taxonomic identity of *Chenia* species has been certainly discussed since the revision of Pottiaceae (Zander, 1989). After Zander distinguished *Chenia* from *Tortula* mainly on the basis of a combination of gametophytic characters (Zander, 1989), different authors made use of the sporophyte to reject *Chenia leptophylla*. As stated before, Arts & Sollman (1991) retained *Phascum leptophyllum* on the base of sporophytic characters. However, up to that moment, a description of the sporophyte was only known from the type specimen (Müller, 1888). Guerra & Cano (2000) specifically stressed the fact that *Chenia*, as defined by Zander (1989), involved stegocarpous and cleistocarpous capsules. Therefore, as a practical choice, *Leptophascum leptophyllum* was raised including the cleistocarpous *C. leptophylla*.

The presence of stegocarpous and cleistocarpous species within the same genus is not necessarily infrequent in the Pottiaceae. *Microbryum*, for example, encompasses both stegocarpous and cleistocarpous species. According to Guerra & Cano (2000), stegocarpous species of *Microbryum* could also be disaggregated from this genus. Although the monophyletic status of *Microbryum* should be clarified, molecular phylogenies disagree with such approach. The stegocarpous *Microbryum rectum* (With) R. H. Zander and the cleistocarpous *Microbryum davallianum* were found to be closely related species (Werner *et al.*, 2002). An even more important example is that of the diverse genus *Tortula*. Despite its polyphyly, many stegocarpous and cleistocarpous were allied in the phylogenetic analysis by Werner *et al.* (2002).

In his revision, Zander (1993) emphasised the information content of the characters of

the gametophyte. However, there is still a lot of controversy about the recognition of genera on their sporophytic characters. In this sense, the comparison between gametophytic and sporophytic characters showed that the number of diagnosed groups is considerably larger for gametophytic traits at the expense of a slightly larger homoplasy (Fig. 4). Furthermore, when 19 gametophytic characters are taken at random, the average number of diagnosed groups is higher than for the sporophytic characters. This suggests that, at least for this dataset, sporophytic characters are not able to distinguish genera not because of being highly homoplastic but as a consequence of being lowly variable. This reinforces the notion that the sporophyte may be only useful for linking particular groups of species (e.g. within *Tortula*; Zander, 1993; Werner *et al.*, 2002). Additionally, this also casts doubts on the approach of postulating new genera exclusively on the ground of sporophytic characters. In fact, characters such as the cleistocarpous or stegocarpous capsules were not depicted as synapomorphies at any level. Therefore, taxa such as *Leptophascum* should be taken with caution.

Conclusion

The sporophyte of *Chenia lorentzii* was shown to be prominently different from that of *C. leptophylla*. In turn, this underlined the fact that species which contrasting sporophytes types may be properly defined within the same genus. Even more, gametophytic traits were shown to be more informative than sporophytic ones. Thus, the present results strengthen the idea that sporophytic characters are valuable at associating specific taxa (Zander, 1989; Werner *et al.*, 2002) while gametophytic features are preferable to elucidate relationship at genera level. These findings discourage the recognition of *Leptophascum leptophyllum* (Guerra & Cano, 2000), as it was defined mainly by its cleistocarpous condition, but suggest the species should be retained in *Chenia*. Additional evaluations should consider a broader taxonomic sampling in order to address both the extension of the current patterns and whether autapomorphic changes persist as such under the extended taxonomic sampling.

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