Darwiniana
ISSN: 0011-6793
sdenham@darwin.edu.ar
Instituto de Botánica Darwinion
Argentina

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Darwiniana, vol. 5, núm. 1, 2017, pp. 51-64
Instituto de Botánica Darwinion
Buenos Aires, Argentina

DARWINIANA
www.ojs.darwin.edu.ar
NUEVA SERIE
ISSN 0011-6793 impresa - ISSN 1850-1699 en línea

DARWINIANA, nueva serie 5(1): 51-64. 2017
Versión final, efectivamente publicada el 31 de julio de 2017
DOI: 10.14522/darwiniana.2017.51.728

CLADISTIC ANALYSIS OF THE FAMILY CRYPHAEACEAE (BRYOPHYTA) WITH EMPHASIS ON *CRYPHAEA*: A STUDY BASED ON A COMPREHENSIVE MORPHOLOGICAL DATASET

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Abstract. Flores, J. R.; S. A. Catalano & G. M. Suárez. 2017. Cladistic analysis of the family Cryphaeaceae (Bryophyta) with emphasis on *Cryphaea*: a study based on a comprehensive morphological dataset. *Darwiniana*, nueva serie 5(1): 51-64.

The first comprehensive phylogenetic analysis of the Cryphaeaceae (Bryophyta), a pleurocarpic moss family, is conducted on the basis of morphological characters. The data set comprised 73 characters: 10 continuous and 63 discrete. Taxon sampling involved nine genera and 46 species of Cryphaeaceae, 32 species belonging to *Cryphaea*. Outgroup sampling included 23 species from 21 genera and 13 families of pleurocarpous mosses. The phylogenetic analyses were conducted using parsimony as the optimality criterion following an implied weighting approach. The results did not support the monophyly of Cryphaeaceae as it excluded *Dendroalsia abietina* from the family. The clade composed of the remaining genera (clade A) was diagnosed by a short seta (0.26-0.30 mm), costa present throughout the innermost perichaetial bract, conical operculum and appressed leaves in dry condition. The analyses furthermore recovered *Cryphaea* as paraphyletic and *Dendrocryphaea* as polyphyletic. *Cryphaea* included *Schoenobryum concavifolium*, *Cyptodontopsis leveillei*, and *Dendrocryphaea lamyana* which were thereby separated from the other species of *Dendrocryphaea*. Character mapping revealed that, as a consequence of the unexpected placement of crucial species, diagnosis should be considerably modified.

Keywords. Implied weighting; parsimony; pleurocarpous mosses; systematics; taxonomy.

Resumen. Flores, J. R.; S. A. Catalano & G. M. Suárez. 2017. Análisis cladístico de la familia Cryphaeaceae (Bryophyta) con énfasis en *Cryphaea*: un estudio basado en un conjunto integral de datos morfológicos. *Darwiniana*, nueva serie 5(1): 51-64.

El primer análisis filogenético de Cryphaeaceae (Bryophyta), una familia de musgos pleurocárpicos, se lleva a cabo sobre la base de caracteres morfológicos. El conjunto de datos consta de 73 caracteres: 10 continuos y 63 discretos. El muestreo de taxa incluye 9 géneros y 46 especies de Cryphaeaceae, 32 especies pertenecientes a *Cryphaea*. El grupo externo, incluye 23 especies de 21 géneros y 13 familias de musgos pleurocarpous. Los análisis filogenéticos se realizaron utilizando parsimonia bajo pesos implicados. Los resultados no apoyan la monofilia de Cryphaeaceae ya que excluye a *Dendroalsia abietina* de la familia. El clado compuesto por los géneros restantes (clado A) fue diagnosticado por una seta corta (0,26-0,30 mm), costa presente en todas las hojas periqueciales internas, opérculo cónico y hojas adpresas al estado seco. Los análisis además recuperaron *Cryphaea* como parafilético y *Dendrocryphaea* como polifilético. *Cryphaea* incluye *Schoenobryum concavifolium*, *Cyptodontopsis leveillei*, y *Dendrocryphaea lamyana* que se separaron de las otras especies de *Dendrocryphaea*. El mapeo de caracteres reveló que, como consecuencia de la ubicación inesperada de especies cruciales, la diagnosis debería ser considerablemente modificada.

Palabras clave. Parsimonia; pesos implicados; musgos pleurocárpicos; sistemática; taxonomía.

Original recibido el 14 de septiembre de 2016, aceptado el 7 de abril de 2016
Editora Asociada: Lone Aagesen

INTRODUCTION

In recent years, traditional systematic schemes in bryology were subjected to a harsh review. Although some pre-cladistics schemes were reconsidered by analysing morphological data sets (Hedenäs, 1994, 1996 a,b), major taxonomic modifications are currently established based on the results of molecular studies (Capesius & Stech, 1997; Cox & Hedderson, 1999). Pleurocarpous mosses, a distinctive group of bryophytes, were reviewed on the basis of both morphology (Buck, 1988; Hedenäs, 1994, 1995, 1996 a, b) and molecules (Buck et al., 2000; De Luna et al., 1999). However, the monophyly of some internal groups has been scarcely evaluated. This is the case of the family Cryphaeaceae Schimp. Although this taxon is considered to be crucial for the understanding of the evolution of pleurocarpy (Buck et al., 2000; LaFarge-England, 1996), no comprehensive phylogenetic study has been conducted in order to test its monophyly. Proposals about its monophyly and phylogenetic placement were always done in the context of higher taxonomic level phylogenies, with a limited taxon sampling for this family (Buck et al., 2000; Cox et al., 2010; Maeda et al., 2000; Quandt et al., 2004).

Historically, the taxonomy of Cryphaeaceae as well as its most diverse genus, *Cryphaea* D. Mohr, has been challenging. Such a conundrum is reflected in the copious number of studies which propose conflicting schemes of classification at both family and genus level (e.g. Brotherus, 1903; Fleischer, 1906, 1914; Flores & Suárez, 2014; Robinson, 1972; Schimper, 1856; Suárez & Schiavone, 2004, 2010; Table 1). As pointed out by Buck (1998) and Rao (2000, 2001), taxa within Cryphaeaceae are highly variable and divergent in aspect. Consequently, the definition of these taxa is not an easy task. Plants within the family have been characterized as species which constitute tufts or have pendulous strands; stems are differentiated in a creeping leafless primary stem and an erect or pendent secondary stem: leaves vary in size and form, from ovate leaves with acute apex and plane margins to acuminate with serrulate margins. Manuel (1974, 1981, 1982) proposed a combination of three characters to distinguish the main genera within the Cryphaeaceae. Nevertheless, some of these characters were not helpful to separate problematic genera (Manuel, 1981, 1982), such as *Cyptodon* (Broth.) Paris & Schimp. ex M. Fleisch. and *Dendrocryphaea* Paris & Schimp. ex Broth. A further taxon with dubious taxonomic position identified by Manuel was *Cyptodontopsis* Dixon, which was considered as a "transitional" genus between *Dencrocryphaea* and *Cyptodon*. Despite some features being constant throughout the family (Maeda et al., 2000).

Table 1. Cryphaeaceae concept according to different authors.

Brotherus (1905)	Manuel (1982)	Buck (1998)	Buck & Goffinet (2000)
Acrocryphaea B.S.B. Ex Broth. (= *Schoenobryum* Dozy & Molk.)	*Schoenobryum* Dozy & Molk.	*Schoenobryum* Dozy & Molk.	*Schoenobryum* Dozy & Molk.
Cryphaea D. Mohr	*Cryphaea* D. Mohr	*Cryphaea* D. Mohr	*Cryphaea* D. Mohr
Cryphidium (Mitt.) A. Jaeger	*Cyptodontopsis* Dixon	*Cyptodon* (Broth.) Paris & Schimp. ex M. Fleisch.	*Cryphidium* (Mitt.) A. Jaeger
Dendrocryphaea Paris & Schimp. ex Broth.	*Dendrocryphaea* Paris & Schimp. ex Broth.	*Dendrocryphaea* Paris & Schimp. ex Broth.	*Cyptodon* (Broth.) Paris & Schimp. ex M. Fleisch.
Dendropogon Schimp.	*Dendropogonella* E. Britton	*Cryphidium* (Mitt.) A. Jaeger	*Cyptodontopsis* Dixon
Pilotrichopsis Besch.	*Cyptodon* (Broth.) Paris & Schimp. ex M. Fleisch.	*Dendropogonella* E. Britton	*Dendroalsia* E. Britton ex Broth.
	Pilotrichopsis Besch.	*Pilotrichopsis* Besch.	*Dendrocryphaea* Paris & Schimp. ex Broth.
	Sphaerotheciella M. Fleisch.	*Dendroalsia* E. Britton ex Broth.	*Dendropogonella* E. Britton
			Pilotrichopsis Besch.
			Sphaerotheciella M. Fleisch.

Cryphaeaceae were traditionally regarded as members of the Leucodontales based on their pleurocarpic habit and a sympodial branching pattern (Buck, 1998). However, Buck et al. (2000) found evidence to include Leucodontales as part of Hypnales, so Cryphaeaceae are classified within the latter order in the system proposed by Goffinet et al. (2009). Until the last decade, relatively few advances were done to clarify the phylogenetic status of the family. Maeda et al. (2010) carried out the most extensive molecular phylogenetic analysis of Leucodontineae up to that moment. That study included 25 taxa of Leucodontineae and three genera of Cryphaeaceae, and obtained a close relationship between the species of Cryphaeaceae and the family Leucodontaceae. By analysing three molecular markers (ITS2, trnL-F and psbT-H) Quandt et al. (2004) transferred *Cryphaeophilum molle* (Dusén) M. Fleisch. from Meteoriaceae to Cryphaeaceae. Recently, Cox et al. (2010) carried out one of the largest studies concerning Bryophyta in terms of taxonomic sampling, where a considerable number of pleurocarpous families were resolved as paraphyletic.

Cryphaea, widely distributed throughout the Old and New World (Rao, 2001), is the most specious genera of the family Cryphaeaceae. Weber (1813) gave account of the mitriform calyptra of *Cryphaea* as a defining feature. Later, Bridel (1819) took into account the immersed capsule, double peristome of 16 teeth and the smooth calyptra. After several taxonomic changes, Brotherus (1905, 1924) recognised ovate to elliptic laminar cells, erect secondary stem, capsule shape and spore size as diagnostic generic characters. Following Gradstein et al. (2001), the genus *Cryphaea* can be identified by its erect habit, lateral sporophytes, ovoid almost sessile capsules, and papillose exostome teeth. In addition, Buck (1998) had previously suggested unicostate leaves as a distinctive feature of the genus. However, some of these characters are highly variable. In this sense, pseudoparaphyllia were described as foliose (Buck, 1998) or as filamentous (Rao, 2001). Therefore, an extensive morphological study should be conducted in order to consider the wide variability of the genus, and to evaluate the phylogenetic information content of that variation.

Until Rao's (2001) monographic studies, no phylogenetic analysis had been conducted in *Cryphaea*. Based on that cladistic analysis and previous taxonomical studies, Rao adjusted the definition of *Cryphaea* by including only species with diplolepidous peristome and epiphytic habit. In that study, Rao also retrieved the monophyly of *Cryphaea* and relocated *Cryphaea lamyana* (Mont.) Müll. Hal. to *Dendrocryphaea lamyana* (Mont.) P. Rao, the latter decision being grounded on the aquatic habit and the cladocarpous position of the sporophyte of *C. lamyana*. Although the meticulously labour of Rao (Rao 2000, 2001; Rao & Enroth, 1999) is, undoubtedly, a key for the understanding of *Cryphaea* taxonomy, some cautions must be taken about the results of the phylogenetic hypothesis (Rao, 2001) as the analysis presented a limited taxon sampling and included a very restricted number of outgroups.

Because of the possible relevance of Cryphaeaceae for the study of pleurocarpy and the lack of a comprehensive morphological phylogenetic analysis, the purpose of the present paper is to evaluate for the first time the monophyletic status of Cryphaeaceae focusing on *Cryphaea*. The results presented herein provide a first insight into the status of and relationships within the family Cryphaeaceae based on an extensive morphological dataset.

MATERIALS AND METHODS

Taxon and Character Sampling. The present study included 69 species (46 ingroup species of Cryphaeaceae and 23 outgroup taxa; Table 2). The outgroup taxa include 12 families and 17 species from the Hypnales and, two families and six species from Hookeriales. Among these, *Cyclodictyon lorentzii* (Müll.Hal.) W. R. Buck & Schiavone was selected for rooting. Ingroup taxa include all the genera of Cryphaeaceae (Goffinet et al., 2009), and a total of 46 species, 32 of them belonging to *Cryphaea*. Of these, eight species are included in a morphological phylogenetic analysis for the first time: *Cryphaea lorentziana* Müll. Hal., *Cryphaea furcinervis* Müll. Hal., *Cryphidium leucocoleum* (Mitt.) A. Jaeger., *Dendrocryphaea tasmanica* (Mitt.) Broth., *Dendrocryphaea cuspidata* (Sull.) Broth., *Dendrocryphaea latifolia* D. G. Griffin, Gradst. & J. Aguirre, *Dendrocryphaea gorveana* (Mont.) Paris & Schimp. and *Cryphaeophilum molle*. For voucher information see Supplementary appendix online (http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/728/728).

Table 2. Species included in the current study. Parenthesis refer to the number of species included. "*" denote taxa already present in Rao's (2001) phylogenetic analysis.

Order	Family	Species
Hookeriales (6)	Pilotrichaceae	*Cyclodictyon lorentzii* (Müll. Hal.) Buck & Schiavone
		Cyclodictyon albicans (Hedw.) Kuntze
		Cyclodictyon varians (Sull.) Kuntze
		Lepidopilum polytrichoides (Hedw.) Brid.
	Daltoniaceae	*Daltonia stenophylla* Mitt.
		Leskeodon palmarum (Mitt.) Broth.
Hypnales (63)	Neckeraceae	*Neckera villa-ricae* Besch.
		Neckeropsis undulata (Hedw.) Reichardt
	Leptodontaceae	*Forsstroemia coronata* (Mont.) Paris
	Anomodontaceae	*Anomodon attenuatus* (Hedw.) Huebener
		Herpetineuron toccae (Sull. & Lesq.) Cardot
		Thelia hirtella (Hedw.) Sull.
	Pterobryaceae	*Orthostichopsis tenuis* (A. Jaeger) Broth.
		Pterobryon densum Hornsch.
	Prionodontaceae	*Prionodon densus* (Sw. ex Hedw.) Müll. Hal.
	Phyllogoniaceae	*Phyllogonium viride* Brid.
	Lepyrodontaceae	*Lepyrodon tomentosus* (Hook.) Mitt.
	Leucodontaceae	*Leucodon julaceus* (Hedw.) Sull.
	Meteoriaceae	*Meteorium deppei* (Müll. Hal.) Mitt.
		Meteoridium remotifolium (Müll. Hal.) Manuel
	Thuidiaceae	*Thuidium delicatulum* (Hedw.) Bruch & Schimp.
		Rauiella praelonga (Besch.) Wijk & Margad.
	Leskeaceae	*Haplocladium microphyllum* (Hedw.) Broth.
	Cryphaeaceae	*Cyptodontopsis leveillei* (Thér.) P. Rao & Enroth *
		Cryphaeophilum molle (Dusén) M. Fleisch.
		Schoenobryum concavifolium (Griff.) Gangulee *
		Cryphidium leucocoleum (Mitt.) A. Jaeger
		Dendroalsia abietina (Hook.) E. Britton ex Broth.
		Dendrocryphaea gorveana (Mont.) Paris & Schimp.
		Dendrocryphaea latifolia D.G. Griffin, Gradst. & J. Aguirre
		Dendrocryphaea cuspidata (Sull.) Broth.
		Dendrocryphaea tasmanica (Mitt.) Broth.
		Dendrocryphaea lamyana (Mont.) P. Rao *
		Dendropogonella rufescens (Schimp.) E. Britton
		Cryphaea (* all the 30 species analysed by Rao (2001) were considered)
		Cryphaea furcinervis Müll. Hal.
		Cryphaea lorentziana Müll. Hal.
		Sphaerotheciella pinnata (Schimp.) Manuel
		Sphaerotheciella koponenii P. C. Rao
		Pilotrichopsis dentata (Mitt.) Besch.

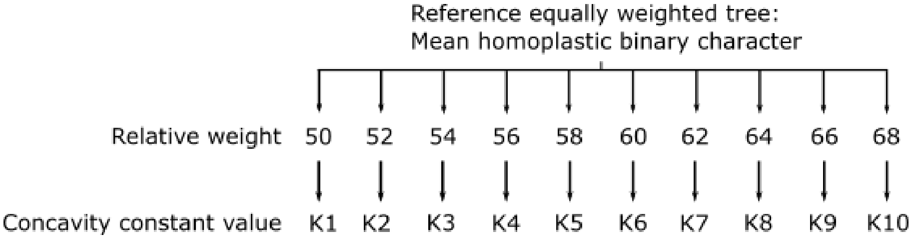

Fig. 1. Different weighted schemes explored in the analysis. Concavity values (*K*) were chosen on the basis of the relative weight they assigned to an equally-weighted mean homoplastic character. Thus, *K1* assigns to such mean character half the weight of a perfectly adjusted binary character. *K10* assigns to an equally weighted, mean character 68% the weight of a perfect binary character (see Mirande, 2009).

Character sampling involved 73 morphological characters (44 gametophytic, 29 sporophytic). Eighteen multistate characters were considered as ordered, based on the different degrees of similarity observed among their states (Lipscomb, 1992). Ten characters, which represented measurements of different structures, were analysed as continuous characters (Goloboff et al., 2006). This is a source of information not usually included in phylogenetics studies of mosses. Continuous characters were standardized in such a way that the full range of each character was equal to one step in a discrete character. Finally, a single character (character 21; perichaetial position) was scored as a Sankoff character (Sankoff & Rousseau, 1975), with symmetrical cost changes among states (1 step from cladocarpous to pleurocarpous and, 2 steps from acrocarpous to cladocarpous/pleurocarpous). Most traits were directly observed and scored from specimens. In those cases where specimens (or parts) were not available, the matrix was completed with data from specialised bibliography (Buck, 1998; Rao, 2000, 2001; Rao & Enroth, 1999). Two species were completely scored from literature: *Daltonia stenophylla* Mitt. and *Leskeodon palmarum* (Mitt.) Broth. (Buck, 1998). The final dataset and complete descriptions of the new characters are in Supplementary appendix online (http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/728/728; Tables S1-S2). Further information on results, character scoring and specimen images is freely available at Morphobank webpage (http://morphobank.org/permalink/?P2411)

Cladistic Analyses. Phylogenetic analyses were run in TNT 1.1 (Goloboff et al., 2008a; Version 1.1 (February 2014)), a free access software, considering parsimony as optimality criterion. Tree searches were performed under implied weighting (Goloboff, 1993). This approach, which weights characters during searches according to their homoplasy, has shown to enhance the results of morphological data analyses when compared with equal-weighted parsimony (see discussion in Goloboff et al., 2008b). Given the lack of an objective criterion to choose a specific strength for downweighting homoplasy (concavity value, *K*), the analyses were repeated considering ten different concavities (*K:* 4.344 – 9.231; *K* selection followed Mirande, 2009; Fig. 1). The main taxonomic results were derived from the topology which remained the less sensitive to parameter variation (concavity value). That is, that topology which was recovered with more frequency across the concavity range was regarded as the final tree. However, in order to achieve more conservative conclusions, the strict consensus from the complete set of trees was also employed. In all cases, the search strategy involved 8 replicates of: 3 rounds of fusing, 10 cycles of drifting and ratchet, and sectorial searches (Goloboff, 1999), hitting at least 3 times the best score (command "xmult"). These cladograms were again submitted to TBR, keeping up to 1.000 trees in memory. Node support was measured with standard Bootstrapping (Felsenstein, 1985), and Jackknifing (Farris et al., 1996).

Constrained searches. Constrained searches (forcing some groups to be monophyletic) were performed in order to evaluate the optimality of taxonomic groups previously proposed in the literature but that were not found as monophyletic in the present analyses. The difference in scores between the best tree *with* and *without* the group under consideration is a measure of how much evidence is contradicting

Table 3. Concavity values explored (*K* values) and trees scores (Tree distortion). Tree score reported as the adjusted homoplasy (distortion), i.e. a convex function to be minimised. Those cladograms which maximised similitude (minimised SPR movements) are marked in bold type.

Number of *K* value explored	*K* value	Tree distortion
1	*K* = 4.344	42.96
2	*K* = 4.706	44.05
3	*K* = 5.099	45.16
4	*K* = 5.529	46.26
5	*K* = 5.999	47.40
6	*K* = 6.516	48.60
7	*K* = 7.088	49.80
8	*K* = 7.723	51.02
9	*K* =8.432	52.26
10	*K* =9.231	53.58

that grouping in the best tree. Since making direct comparisons in terms of fit is not easy to be interpreted, differences in fit were translated to the number of mean homoplastic character with an extra step added (that is, $\bar{x}_{+1}$). A mean homoplastic character ($\bar{x}$) is obtained as the tree length divided by the number of characters. By taking the ratio between the fit differences of topologies ($F_{unconstrained}$, $F_{constrained}$) and mean homoplasious characters ($F_{\bar{x}}$, $F_{\bar{x}+1}$) suboptimality is conceived in light of how many mean homoplastic characters which gained one step are needed to explain that suboptimality $[(F_{unconstrained} - F_{constrained})/(F_{\bar{x}} - F_{\bar{x}+1})]$.

All these procedures (concavity exploration, topology stability assessment and constrained searches) were implemented into TNT scripts available upon request. A detailed description of this methodology is found in the Supplementary appendix online (http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/728/728).

Character mapping.

In order to explore the behaviour of the diagnosing characters, these were mapped along the stable topology. The optimization of continuous characters considered the complete range of reconstructions. That is, in cases where the character had multiple reconstructions at internal nodes, the complete set of possible reconstructions (implied by the extreme values of the optimization) was scrutinised. Thus, overall positive or negative changes at internal nodes were only considered as such when the complete set of reconstruction indicated an increment or decrement, respectively.

RESULTS

Character analysis

Except for the previously excluded species, observation of the available specimens verified Rao's (2001) scoring. Although Rao (2001) did not include *Cryphaea furcinervis* in his analysis, he appealed to the species' protologue for considering its capsule as an oval capsule (character 32). The shape of the capsule of *C. furcinervis*, examined in specimens from Argentina, did not agree with such a description. Scoring was made in accordance with available from type and fresh material of *C. furcinervis*. In addition, other characters were modified in order to include new observations of outgroup taxa not previously incorporated in the matrix. In some cases character state definitions were modified, while in other characters new states were added. This is the case of character 14 and 15.

Phylogenetic analysis

Relationships within Cryphaeaceae

The exploration of concavity values concluded in one fully resolved tree per K value, and their distortion ranged from 42.96 to 53.58 (Table 3). A single topology, obtained in six out of ten *K* values, was found to be the most frequent across the entire range of concavities (i.e. the least sensitive; Fig. 2). Such a topology retrieved a non-monophyletic Cryphaeaceae, and a close association between *Dendroalsia abietina* (Hook.) E. Britton ex Broth. and *Orthostichopsis tenuis* (A. Jaeger) Broth. (Fig. 2).

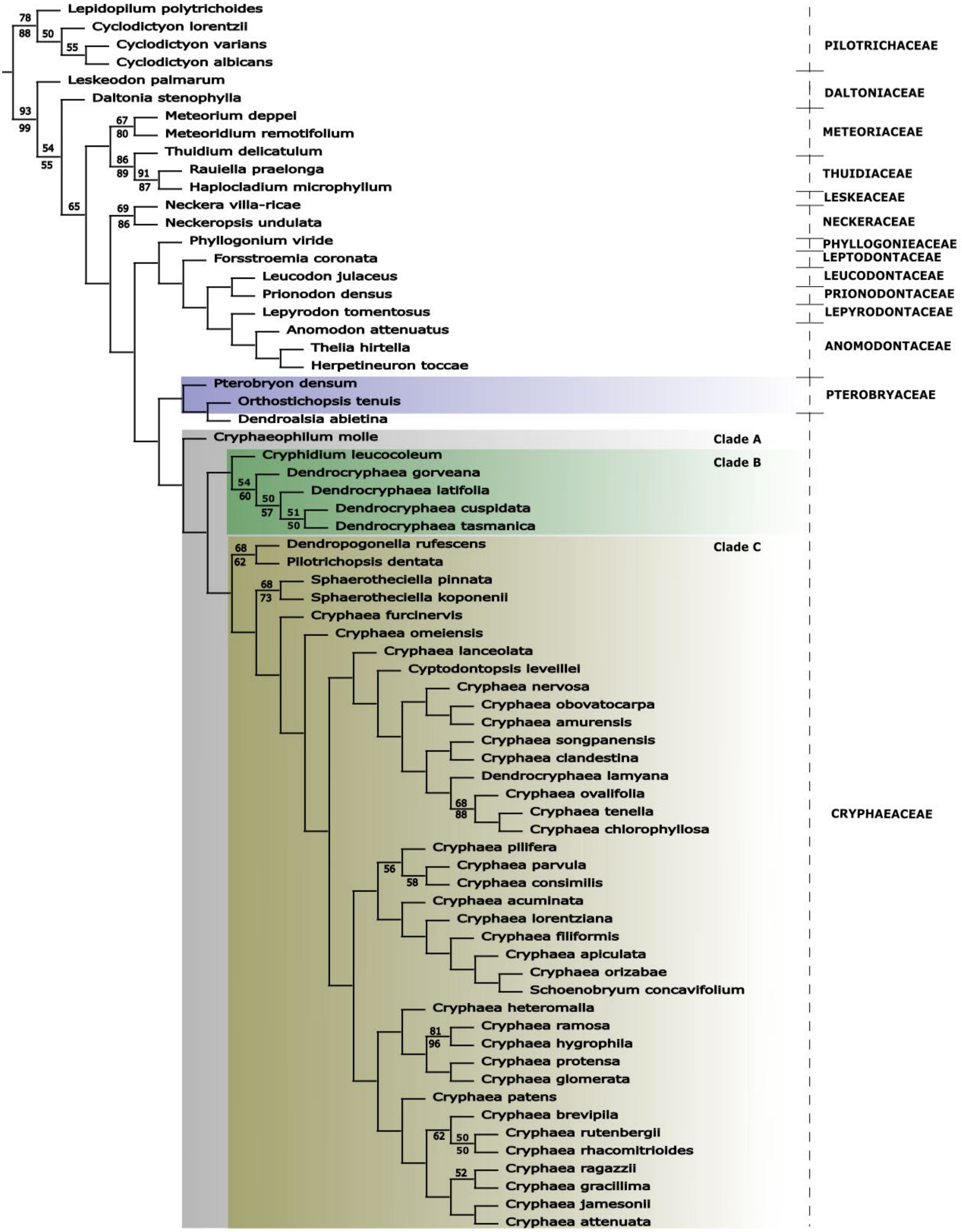

Fig. 2. The most frequent tree, obtained in six out of ten concavities values. Clade A (grey) comprises all the Cryphaeaceae species, excepting *Dendroalsia abietina*. Clade B and C (green and brown) constitutes the two earlier divergences within clade A. Numbers above and under the branches are bootstrap and jackknife values, respectively. See text for details and discussion. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/728/727

Cryphaeophilum molle appeared as the sister taxon of the remaining genera of the family with the exception of *D. abietina* (clade A - Fig. 2). Within clade A, a basal dichotomy separated four of the five *Dendrocryphaea* species and *Cryphidium leucocoleum* (clade B, Fig. 2) from the remaining species (clade C, Fig. 2). The recently recognised *D. lamyana* (Rao, 2001) was nested within clade C, more closely related to *Cryphaea ovalifolia* (Müll. Hal.) A. Jaeger than to any other species of *Dendrocryphaea*. This rendered the genus *Dendrocryphaea* polyphyletic as is currently circumscribed. Within clade C, the clades *Dendropogonella-Pilotrichopsis* and *Sphaerotheciella* successively branched as sister groups to *Cryphaea*, *Cyptodontopsis*, *Dendrocryphaea lamyana* and *Schoenobryum* (Fig. 2). The main genus, *Cryphaea*, was not monophyletic as it included the remaining genera of Cryphaeaceae.

Relationship between Cryphaeaceae and outgroup families

The status and relationship among pleurocarpous families have been hardly elucidated (Buck et al., 2000; Cox et al., 2010). Consequently, no family could be convincingly proposed as the sister group of the Cryphaeaceae (Maeda et al., 2000; Cox et al., 2010). In the present study, many of these pleurocarpous families were non-monophyletic. Indeed, half of the families represented by more than a single species resulted non-monophyletic. In accordance with this pattern, a paraphyletic Pterobryaceae constituted the sister taxon of Cryphaeaceae (Fig. 2). Even though the support values were low, most of the clades found within the Cryphaeaceae-Pterobryaceae node were highly stable and were recovered under more than six concavity values (Fig. 3).

Constrained searches

In spite of the general low support values, forcing monophyly of para- or polyphyletic taxa had a slight to notably impact on the tree score. Forcing Cryphaeaceae monophyly implied that 2.28 characters added an extra step. Similarly, monophyly of *Dendrocryphaea* required an extra step in 2.31 characters. However, in the case of *Cryphaea*, a considerable number of characters added a further step (6.63). Likewise, resultant trees were also suboptimal when the monophyly of the outgroup families was forced. Monophyly of Thuidiaceae implied the smallest difference on the global tree score (1.34). The monophyletic status of Pterobryaceae affected the overall score slightly more (2.20). Surprisingly, the monophyly of Daltoniaceae turned out to be strongly suboptimal (4.91). This difference in optimality was certainly unexpected given that *Daltonia stenophylla* was the species with the maximum number of missing entries, which do not add extra steps when they are optimised.

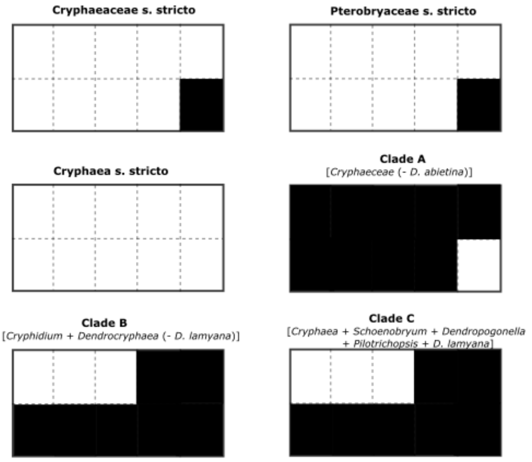

Fig. 3. Sensitivity plots depicting areas of monophyly. Boxes (from left to right) represent differents parameters conditions (K: 1 -10). White (empty) boxes indicate non-monophyly, black boxes indicate monophyly. *Sensu stricto* categories refer to current acceptance: Cryphaeaceae and Pterobryaceae from Goffinet et al. (2009); *Cryphaea* from Rao (2001).

Character mapping

Character mapping indicated that four characters diagnosed clade A (Cryphaeaceae, excluding *D. abietina*; Fig. 4): seta length, costa of the internal perichaetial bracts present, operculum shape, and leaf position when dry. When mapped, the length of the seta showed a progressive decrease. However, at the base of clade A, the seta length suffered a considerable shortening. Consequently, a seta shorter than 0.30 mm diagnosed clade A. A costa present throughout the internal perichaetial bract also characterised this node. However, at internal nodes, the character state reverts as a costa disappearing downwards the bract or completely absent from it. A conical shape of the operculum furthermore diagnosed the clade A, and only Neckeraceae and *Herpetineuron toccoae* (Sull. & Lesq.) Cardot depicted the same state outside clade A. A rostrate condition was secondarily present in some species of *Cryphaea*.

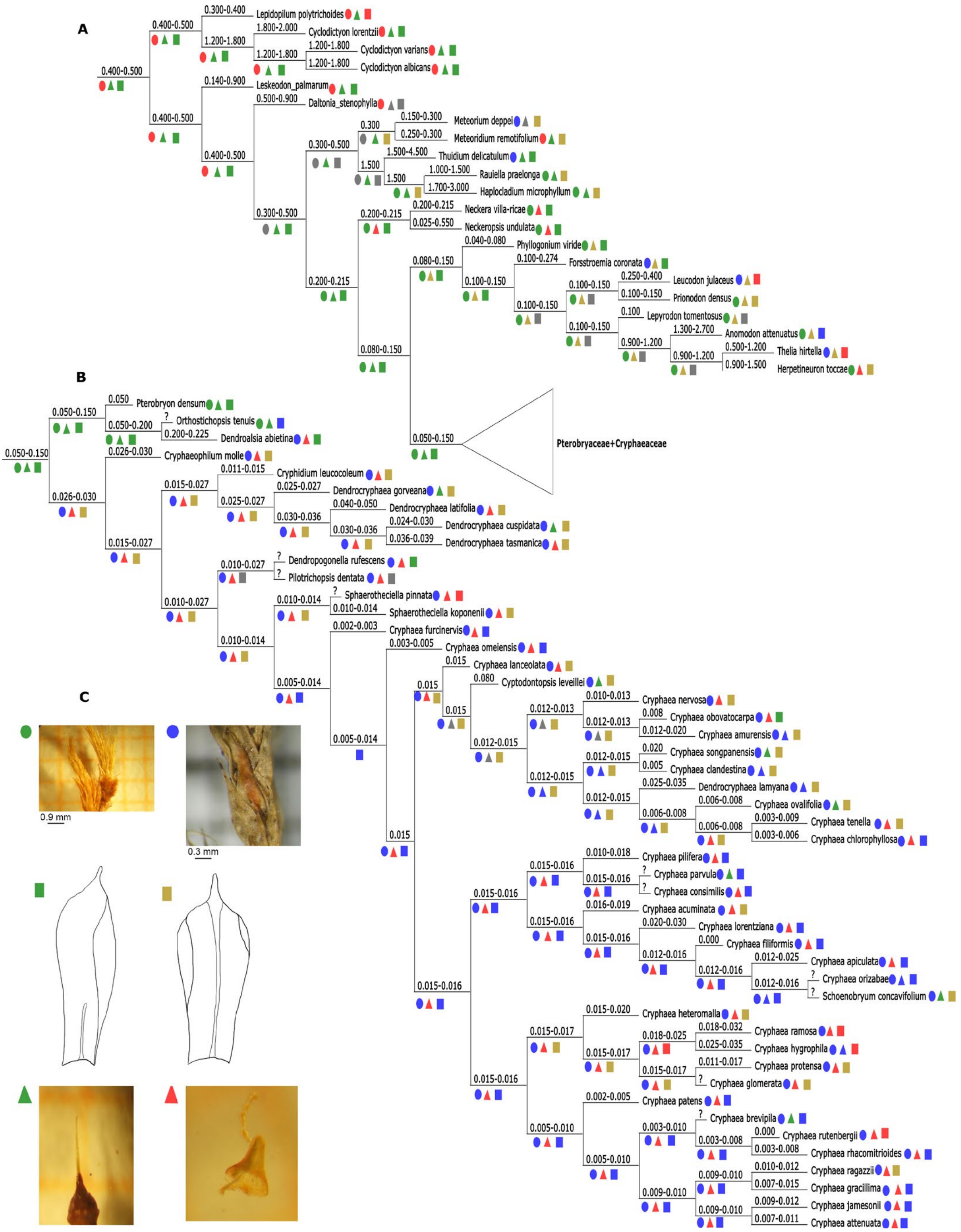

Fig. 4. Optimisation of the characters which diagnosed clade A. **A,** Optimisation along the Hookeriales and the basalmost Hypnales. **B,** Optimisation along the group constituted by Pterobryaceae and Cryphaeaceae. **C,** Examples of character state changes supporting the clade A. Seta length is indicated with numbers above nodes. Leaf position in dry condition (circles): contorted (red circles), markedly apressed (blue circles), spreading (green circles). Operculum shape (triangles): conical operculum (red triangles), rostellate (blue triangles), rostrate (green triangles), sidewards rostrate (brown triangles). Costa of the internal perichaetial bracts (squares): absent (red squares), strong at apex and vanishing below (blue squares), strong at base and vanishing above (green squares), present throughout (brown squares). Grey symbols are ambiguous optimisations, "?" refers to missing entries. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/728/727

Finally, a markedly appressed leaf position was a consistent feature of all the Cryphaeaceae. Nevertheless, this state also arose among the outgroups in *Meteorium deppei* (Hornsch. ex Müll. Hal.) Mitt., *Thuidium delicatulum* (Hedw.) Schimp., *Forsstroemia coronata* (Mont.) Paris, *Leucodon julaceus* (Hedw.) Sull. and *Thelia hirtella (*Hedw.) Sull.

DISCUSSION

Phylogenetic patterns and Taxonomy

In the present study, phylogenetic relationships of the pleurocarpic family Cryphaeaceae were analysed, with a special focus on *Cryphaea*. Because exhaustive or explicit testing of the diagnosis features of this group are infrequent, most of the results presented here impact not only the taxonomical status of genera and families but also their morphological concepts.

One of the most important results obtained in this study was the corroborated non-monophyly of Cryphaeaceae. Until the molecular work of Cox et al. (2010), there was scarce evidence about the status of this family (Buck et al., 2000; Maeda et al., 2000; Quandt et al., 2004). In the study carried out by Maeda et al. (2000), Cryphaeaceae were represented by only three taxa, *Cryphaea sinensis* E.B. Bartram, *Cyptodontopsis obtusifolia* (Nog.) Nog., and *Pilotrichopsis dentate* (Mitt.) Besch.; and its conclusion clarified much of the systematics problems of the Leucodontineae suborder. However, that analysis was unable to elucidate the relationship among the genera included in the Cryphaeaceae. Cox et al. (2010), who provided the most solid evidence about the nature of Cryphaeaceae, found a polyphyletic Cryphaeaceae due to the exclusion of *Dendroalsia* and *Pilotrichopsis*. Besides the inclusion of *Pilotrichopsis* within the clade A, the results presented here were quite in agreement with those of Cox et al. (2010). Concordantly, a monophyletic circumscription of Cryphaeaceae would require excluding, at least, the genus *Dendroalsia*. *Pilotrichopsis*, on the other hand, was well nested within the clade A. Although this fact is not contradicted by the results of Maeda et al. (2000), it is significantly opposed to that of Cox et al. (2010) where *Pilotrichopsis* was placed within Pterobryaceae. Based on the results of Maeda et al. (2000), Cox et al. (2010) and the present ones, it is likely that a more exhaustive sampling of genera within the Pterobryaceae and Leucodontaceae will help to elucidate the position of *Pilotrichopsis*.

Establishing the relationship of the Cryphaeaceae with other families has also been a difficult task (Maeda et al., 2000). As mentioned by Maeda et al. (2000), several authors have proposed alternative hypotheses. Brotherus (1924) and Manuel (1982) indicated that Leucodontaceae and Cryphaeaceae could be related because of their laminar cell shape and the upright position of the capsule. Buck et al. (2000) found a clade established by *Prionodon densus* (Sw. ex Hedw.) Müll. Hal. and *Cryphaea glomerata* Schimp. ex Sull. Simultaneously, Maeda et al. (2000) cast doubts about the relationship between Cryphaeaceae and Pterobryaceae by finding a polytomy involving Cryphaeaceae and Leucodontaceae. Cox et al. (2010) found a main group of Cryphaeaceae (Cryphaeaceae excluding *Dendroalsia abietina*, *Dendropogonella rufescens* (Schimp.) E. Britton, and *Pilotrichopsis dentata* (Mitt.) Besch.) closely related to an assemblage of non-monophyletic families such as Hypnaceae, Leskeaceae, and Hylocomiaceae among others. The present cladogram (Fig. 2), recovered a clade composed of the paraphyltic Pterobryaceae and *Dendroalsia* as the sister node of clade A. This pattern, also retrieved in the consensus of all the trees, somehow resembles that of Cox et al. (2010). However, the paraphyletic or polyphyletic condition of many pleurocarpous families makes difficult to establish a reliable sister relationship.

A further significant result of the present study was the non-monophyly of *Cryphaea*. The definition of this genus has varied since Brotherus (1905) separated *Acrocryphaea* (= *Schoenobryum*), *Dendrocryphaea* and *Dendropogon* (= *Dendropogonella* E. Britton) from *Cryphaea*. After several modifications made by numerous authors, Manuel (1973) transferred *C. ravenelii* to *Cryphaea* so that the genus included both species with single and double peristome. Rao (2001) proposed the genus *Monocryphaea* to accommodate this last species. Consequently, *Cryphaea* would only consist of species with double peristome. However, as a consequence of the restricted species sampling, this taxonomic proposal and the status of *Cryphaea* itself could not be rigorously tested.

In the present study, a paraphyletic *Cryphaea* was recovered. In addition, *Cryphaea* diagnosis might be drastically changed as it embedded *Schoenobryum* and *D. lamyana*. This would leave the genus *Cryphaea* comprised by haplolepidous and diplolepidous species as well as by epiphytic and aquatic species. Hence, the present results as well as those obtained by other authors (Cox et al., 2010) suggest a re-evaluation of *Cryphaea* as defined by Rao (2001).

As in the case of *Cryphaea*, the low taxon sampling in previous phylogenetic studies cast doubts about the nature of *Dendrocryphaea* and *Cryphidium*. In respect to the latter, there has been a long controversy about its nature since the original definition of the genus (Flores & Suárez, 2014; Jaeger, 1876; Mitten, 1869; Robinson, 1972). Rao (2001), as well as Buck (1980), Suárez and Schiavone (2010) and Flores and Suárez (2014), proposed to keep *Cryphidium leucocoleum* as such. In the present study, *C. leucocoleum* appeared as a taxon related to *Dendrocryphaea*. The position of *Dendrocryphaea lamyana* is also controversial. Due to its aquatic habitat, Rao (2001) replaced *Cryphaea lamyana* (Mont.) Müll. Hal. with *Dendrocryphaea lamyana*. This combination was supported by the results of his phylogenetic analysis, where *D. lamyana* was sister to *Cyptodontopsis leveillei* (Rao, 2001). Nevertheless, no other species of *Dendrocryphaea* was included. Consequently, it was not possible to test the identity of *C. lamyana* as a *Dendrocryphaea* in that analysis. Thus, the present results suggest revisiting Rao's transference. Moreover, on the ground of the current results, *Cryphaea lamyana* should be revalidated.

The synapomorphies of Cryphaeaceae outlined in the present analysis were, at least partially, associated with the position of *Cryphaeophilum molle* at the base of the family. Originally, *C. molle* was recognised as *Cryphaea mollis* Dusén (Dusén, 1905). This approach was also taken by Brotherus (1903), who placed it within the section *Cryphaeopsis* Broth. Later, Fleischer (1914) observed differences in leaf anatomy between both genera, and proposed the segregation of *C. mollis* from the family under the designation of *Cryphaeophilum*. Because of the association of *Cryphaeophilum molle* and *Cryphaea heteromalla*, Quandt et al. (2004) proposed to maintain *Cryphaeophilum molle* within the Cryphaeaceae. From the present analysis it is clear that *C. molle* is basally placed within Cryphaeaceae. Thereby, because of both the significant morphological differentiation (Fleischer, 1914; Kühnemann and Gonçalves-Carralves., 1976) and the basal position within the family, the generic distinction between *Cryphaeophilum* and *Cryphaea* seems reasonable.

Morphological trends and Diagnosis

Cox et al. (2010) provided the first evidence of a polyphyletic Cryphaeaceae. This non-monophyletic status, retrieved in the present study as well, suggest not only a taxonomic rearrangement but also a revision of the diagnostic characters. Among several features, Cryphaeaceae has long been described as having oval leaf cells, slightly differentiated alar cells, short seta, immersed capsule, papillose peristome teeth throughout, conic operculum, and mitrate calyptra (Buck, 1998; Sharp et al., 1994). Since *D. abietina* was separated from the other genera of Cryphaeaceae (Fig. 2), most of the apomorphies commonly associated with the family shall be re-defined, discarded, or restricted to groups within Cryphaeaceae. Oval laminal cells were a synapomorphy of the group constituted by the clades B+C. However, the basal position of *Cryphaeophilum molle* implied that oval cells were not a synapomorphy at familial level. Even so, the group of clades B+C comprised genera with secondarily rhombic (e.g. *Cryphaea rhacomitriodes* Müll. Hal.) and linear cells (*Cryphaea ragazzii* (Brizi) Broth., *Cryphaea gracillima* Herzog). Similarly, weakly differentiated alar cells diagnosed the clade B+C though *Cryphaea runtenbergii* Müll. Hal., *Cryphaea rhacomitriodes* and -externally- *Cryphaeophilum molle* had strongly distinct alar cells. A short seta and an immersed capsule are striking features of the Cryphaeaceae (Buck, 1998; Sharp et al., 1994). The exclusion of *D. abietina*, whose seta length is 2-2.25 mm, left the clade A diagnosed by a seta of 0.26-0.30 mm in length. Even more, the group B+C is characterized by a shorter seta (0.15-0.27 mm). Posterior increases were found to distinguish nodes at clade B, but none of them was as long as 2 mm. A mitriform calyptra was shown to be a plesiomorphic character state. However, the conical shape of the operculum appeared to be a synapomorphy of the clade A, depicting secondarily rostrate shape in isolated taxa. The papillose peristome and immersed capsule were plesiomorphic character states that originated within the order.

In short, the placement of several species (*D. abietina*, *C. molle*, *D. lamyana*, *C. leveillei*, *S. concavifolium*) at unexpected nodes affected the diagnosis of the family and the genus *Cryphaea*. Aside from the conic operculum and the costa throughout the inner perichaetial bracts; some of the characters were either circumscribed to a narrower morphological span (seta length), restricted to some inner group (oval leaf cells), or discarded as primitive features (mitrate calyptra).

Sources of conflict with previous hypothesis

Given that Rao's phylogeny (2001) is a cornerstone for the current knowledge of *Cryphaea*, it is worth trying to determine the sources of discrepancies between that study and the present. The first cause of discrepancy may be related to the wider taxon and character sampling of the present analysis. In addition, Rao used *Schoenobryum* in order to root the obtained phylogenetic hypothesis. However, no previous phylogenetic evidence supported that choice. To ensure the reliability of choosing an appropriate root terminal (i.e. a taxon that is, in fact, external to *Cryphaea* and Cryphaeaceae) we decided to select *Cyclodictyon* (Pilotrichaceae, Hookeriales) for rooting and include species from a large number of related families and orders. Another difference between both analyses lies in the characters included in the matrix, some of them considered for the first time for evaluating this group. In order to include a wider range of outgroup taxa; some of the characters defined by Rao were modified. Along with the differences in the evidence from where the phylogenetic hypotheses are derived, both analyses also differ in their methodologies. For instance, the present study was conducted using weighted parsimony while that of Rao considered equal weights for all characters with the purpose of avoiding bias. Additionally, Rao (2001) kept the multi-state characters as unordered with the intention of minimising assumptions about character evolution. The "unweighted approach" really implies that all the characters are equally capable of the explaining the phylogenetic pattern. As this is certainly not true (due to homoplasy), we used implied weights. Coding multi-state characters as non-additive is equivalent to appreciate the several states within them as being equally different. Obviously, this does not need to be the case. In order to make explicit the similarity among characters states we coded them as ordered in cases where we did observe resemblance (Lipscomb, 1992).

CONCLUSIONS

The aim of this paper was to re-evaluate the relationship of the Cryphaeaceae taxa on the basis of under an improved taxon and character sampling. In addition, several doubtful or previously excluded species were incorporated as well as taxa never before included in phylogenetic studies. As a result of this, the Cryphaeaceae appeared non-monophyletic, *Dendroalsia abietina* was disaggregated from the family and *Cryphaeophilum molle* was placed as the sister species of the remaining Cryphaeaceae genera. Contrary to prior hypothesis (Rao, 2001), *Cryphaea* is paraphyletic. Even though, we take the position of conserving current taxonomic status of *Cryphaea* until more evidence confirms the findings presented here.

In lights of present results, taxonomical re-arrangements should be considered. Because of the low support and stability of the results we did not take any taxonomical decisions. As can be seen from previous analyses (Cox et al., 2010; Rao, 2001), low character support in phylogenies of pleurocarpous taxa is not a weakness of the current data solely. This tells us about the necessity of looking for new sources of character for the group, such as ultra-structural, developmental, and molecular. Hopefully these new sources of characters will help us to clarify the phylogenetic relationships within Cryphaeaceae and taxonomical identity of its members.

ACKNOWLEDGEMENTS

Authors are indebted with herbaria curators (LIL, NY, CTES, MO, BA, RB, HBr, CHR and PC) for providing valuable materials for elaborating this work. Lone Aaegesen and J. Salvador Arias provided invaluable suggestions to improve an early version of the manuscript. TNT is freely available thanks to the Willi Hennig Society.

This study was carried out with the financial support of the National University of Tucumán (CIUNT students' scholarship and PIUNT G524), the Consejo Nacional de Investigaciones Científicas y Tecnológicas and the Agencia Nacional de Promoción Científica y Tecnológica (PICT 1838, PICT 0810).

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