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Phylogenetic relationships within the fern genus *Hymenophyllum s.l.* (Hymenophyllaceae, Filicopsida): contribution of morphology and cytology

Sabine Hennequin

Équipe « Classification, Évolution et Biosystématique », laboratoire de paléobotanique et paléoécologie, université Pierre-et-Marie-Curie et IFR 101 CNRS « Institut d'écologie fondamentale et appliquée », 12, rue Cuvier, 75005 Paris, France

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Abstract

The phylogenetic relationships of *Hymenophyllum* and its segregate genera *Cardiomanes*, *Hymenoglossum*, *Rosenstockia*, *Serpyllopsis* and *Microtrichomanes* are addressed, using 31 morphological characters of the sporophyte and one cytological character. As expected, this study reveals considerable morphological heterogeneity within the genus sensu lato, but several apomorphic changes allow support for some clades. Four unresolved taxa, *Cardiomanes*, *Hymenoglossum*, *Diplophyllum* and *Mecodium pro parte* are probably the most basal elements in *Hymenophyllum*. The analysis also suggests the polyphyly of *Mecodium*, and two unexpected associations: *Sphaerocionium* together with *Microtrichomanes*; and a broad clade composed of subg. *Hymenophyllum*, *Hemicyatheon* and *Craspedophyllum*, genera *Rosenstockia* and *Serpyllopsis*, and subsect. *Leptocionium* and *Amphipterum*. These associations appear justified by morphological, cytological or geographical data, and most of them are in agreement with preliminary molecular results. ***To cite this article: S. Hennequin, C. R. Biologies 326 (2003).***

Résumé

Systématique du genre *Hymenophyllum s.l.* (Hymenophyllaceae, Filicopsida) : apport des données anatomo-morphologiques et cytologiques. Afin d'étudier les relations phylogénétiques au sein du genre *Hymenophyllum s.l.*, trente et un caractères anatomiques et morphologiques du sporophyte ainsi que des données cytologiques ont été utilisés. Cette étude prend en compte les genres traditionnellement séparés d'*Hymenophyllum* : *Cardiomanes*, *Hymenoglossum*, *Rosenstockia*, *Serpyllopsis* et *Microtrichomanes*. Le genre ainsi pris au sens large révèle une hétérogénéité morphologique considérable, déjà démontrée par certains ptéridologistes. Plusieurs changements apomorphiques permettent toutefois de soutenir des clades. Quatre taxa, *Cardiomanes*, *Hymenoglossum*, *Diplophyllum* et *Mecodium pro parte*, apparaissent comme les plus basaux au sein du genre. L'analyse suggère aussi la polyphylie de *Mecodium*, ainsi que plusieurs associations inattendues : *Sphaerocionium* et *Microtrichomanes* ; et un vaste clade, composé des sous-genres *Hymenophyllum*, *Hemicyatheon* et *Craspedophyllum*, des genres *Rosenstockia* et *Serpyllopsis*, et des sous-sections *Leptocionium* et *Amphipterum*. Ces résultats apparaissent justifiés au vu des données morphologiques, anatomiques, cytologiques ou géographiques, et la plupart sont en accord avec les résultats moléculaires préliminaires. ***Pour citer cet article : S. Hennequin, C. R. Biologies 326 (2003).***

E-mail address: sabine.hennequin@snv.jussieu.fr (S. Hennequin).

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1. Introduction

The fern genus *Hymenophyllum s.l.* (Hymenophyllaceae, Filicopsida) includes more than 300 species distributed worldwide, mostly in tropical areas, but also in temperate humid areas. It is traditionally distinguished from the sister genus *Trichomanes s.l.* (hereafter called *Trichomanes*) by its bivalved sori, in contrast to the tubular sori of the latter. *Hymenophyllum s.l.* (hereafter called *Hymenophyllum*) is, however, notably variable in sorus morphology, and displays a continuum of shapes ranging from tubular to bivalved [1]. To accommodate the morphological variation observed, several pteridologists proposed a polygeneric classification [2–7] (see Table 1). Using a tree of relationships, Copeland [5,6] and Pichi Sermolli [7] however suggested affinities among their genera. Nevertheless, these systems were found inconvenient by Morton [8] and Iwatsuki [9,10] (see Table 1). According to Morton [8], even if a few species of the family appear intermediate between *Hymenophyllum* and *Trichomanes*, the majority could be placed unambiguously into one genus or the other. Both authors consequently proposed fewer genera for the family, and defined a precise and hierarchical classification by adopting most of Copeland's genera as subgenera, sections, or subsections (Table 1). The problematic intermediate taxa include *Cardiomanes*, *Serpyllopsis* and *Microtrichomanes*. The first two are monospecific, and all three display tubular involucres. Two other taxa, *Hymenoglossum* and *Rosenstockia*, have clear affinities with *Hymenophyllum*, based on soral morphology, but display certain peculiarities that prompted some pteridologists to treat them as monotypic genera. Finally, the paucity of reliable characters for defining groups [4] also complicated the classification of the genus.

Phylogenetic studies have already been performed for the sister genus *Trichomanes s.l.* [11–13], and globally supported Morton's system. More recently, molecular studies [14–16], have revealed the robustly supported monophyly of both genera *Hymenophyllum* and *Trichomanes*, with the inclusion of the segregate genera (*Cardiomanes*, *Hymenoglossum*, *Rosenstockia*, *Serpyllopsis*) and the section *Microtrichomanes* in the *Hymenophyllum* clade. The aim of this unprecedented morphological study is to confront the phylogeny inferred with the one obtained by molecular methods, and with the different classifications proposed in the past century.

2. Material and methods

2.1. Taxa

The operational taxonomic units (OTU) are Morton's sections. Their position in the different classifications is summarized in Table 1, along with their distribution and the number of species they contain. The genera *Hymenoglossum*, *Serpyllopsis*, *Rosenstockia* and *Cardiomanes* were included in this study, as well as the genus *Microtrichomanes sensu* Copeland, whose species were placed by Morton in his 'unclassified' (unplaced sectional name) section *Flabellata*. The name chosen by Copeland was retained here. Two subsections were also selected, *Leptocionium* and *Amphipterum* (placed by Morton in *Sphaerocionium* and *Mecodium*, respectively), because they were treated as genera by Copeland [5,6]. The section *Mecodium* was divided into two groups, based on morphological observations and especially on cytological data, even though they are not available for all taxa. The first, named '*Mecodium* I', is characterised by the chromosome number $n = 28$, and the second, named '*Mecodium* II', by the chromosome number $n = 36$. This distinction allowed reduction of the observed polymorphism within the taxon.

A wide sampling of species representative of the morphological diversity and of the geographical range of the sections was studied to attribute character states to the OTUs. This represented more than one hundred and fifty species of *Hymenophyllum s.l.*, from diverse herbaria ('Muséum national d'histoire naturelle', Paris (P); Natural History Museum, London (BM); Royal Botanic Gardens, Kew (K)) and a personal collection.

Table 1
Comparison of the classifications of Copeland [5,6], Morton [8], Pichi Sermolli [8] and Iwatsuki [9,10], with number of species in the studied sections and distribution

Copeland [5,6]	Morton [8]			Pichi Sermolli [7]	Iwatsuki [9,10]			Number of species	Distribution [7]
Genera	Genera	Sub-genera	Sections	Genera	Genera	Sub-genera	Sections		
Hymenoglossum	*Hymenoglossum*			*Hymenoglossum*	*Hymenoglossum*			1	Ch
Serpyllopsis	*Serpyllopsis*			*Serpyllopsis*	*Serpyllopsis*			1	Ch-Arg
Rosenstockia	*Rosenstockia*			*Rosenstockia*		*Rosenstockia*		1	NC
							Plumosa		
							Pseudomecodium		
Mecodium		*Mecodium*	*Mecodium (2, 3)*	*Mecodium*		*Mecodium*	*Mecodium*	> 100	P
							Diplophyllum	2	Aus-NZ
							Corrugatae		
Craspedophyllum		*Craspedophyllum*		*Craspedophyllum*			*Pachyloma*	2	Aus-NZ
Hymenophyllum	*Hymenophyllum*		*Hymenophyllum*	*Hymenophyllum*	*Hymenophyllum*	*Hymenophyllum*	*Hymenophyllum*	26	C
			Eupectinum				*Eupectinum*	4	Ch-Arg
Amphipterum		*Hymenophyllum*	*(2)*	*Amphipterum*			*Amphipterum*	4	A
Buesia			*Buesia*	*Buesia*			*Buesia*	5	NT
Meringium			*Ptychophyllum*	*Meringium*		*Chilodium*	*Chilodium*	70	P-Oc
Myriodon			*Myriodon*	*Myriodon*			*Myriodon*	1	A
Hemicyatheon		*Hemicyatheon*		*Hemicyatheon*			*Hemicyatheon*	2	Aus, NC
Leptocionium			*(1)*	*Leptocionium*			*Leptocionium*	1	Ch-Arg
Sphaerocionium		*Sphaerocionium*	*Sphaerocionium*	*Sphaerocionium*	*Sphaerocionium*	*Sphaerocionium*		70	P
Apteropteris			*Apteropteris*	*Apteropteris*		*Apteropteris*		2	Aus, NZ
Cardiomanes	*Cardiomanes*			*Cardiomanes*	*Cardiomanes (4)*			1	NZ
Microtrichomanes	*(6)*			*Microtrichomanes*	*(5)*			9	PT

(1) Included in *Sphaerocionium* as a sub-section; (2) included in *Mecodium* as a sub-section; (3) including the sub-section *Diplophyllum*; (4) unique representative of the sub-family Cardiomanoidae; (5) included in *Trichomanes* section *Crepidomanes*; (6) included in *Trichomanes* under the unplaced sectional name *Flabellata*; (7) distribution: A, Asia; Arg, Argentina; Aus, Australia; Ch, Chile; C, Cosmopolitan; NT, Neotropics; NC, New Caledonia; NZ, New Zealand; O, Oceania; P, Pantropics; PT, Paleotropics.

Table 2
Percentage of species studies per section (personal observations) and references used, in addition to those already cited in the text, for the coding of the characters and the preparation of the matrix

Sections/subsections	Percentage of species observed	References
Cardiomanes	100%	[27]
Hymenoglossum	100%	[28,29]
Serpyllopsis	100%	[28,29]
Rosenstockia	100%	[30]
Hymenophyllum	50%	[27–29,31–36,40,44]
Buesia	60%	[37]
Eupectinum	33%	[28,29]
Ptychophyllum	55%	[27,31–35,37,38,44,45]
Myriodon	50%	[37]
Craspedophyllum	100%	[30,31]
Hemicyatheon	100%	[31,35]
Apteropteris	100%	[27,29,35]
Sphaerocionium	30%	[27,32,33,35,38–46]
Leptocionium	100%	[28,29]
Amphipterum	100%	[37]
Mecodium	50%	[27,30–35,38–45]
Diplophyllum		[27,31,35]
Microtrichomanes	100%	[34,35,38]
Cephalomanes	–	[11,34]
Pachychaetum	–	[11,40–42]
Lacosteopsis	–	[11,38,40–42]
Callistopteris	–	[11,30,34]

–, not calculated.

The list of these specimens is not shown (available on request), but the percentage of species studied for each section is given in Table 2, along with references from which additional data were extracted. According to preliminary molecular results [14], a probable outgroup, apart from *Trichomanes*, would be the monotypic *Cardiomanes*. This position was, however, not clearly supported by analyses based on *rps*4 and *rps*4-*trn*S data [15], and accordingly a sample of sections of *Trichomanes* was selected as outgroup. These four sections are considered to be among the most basal ones in *Trichomanes* (Dubuisson, pers. comm.).

2.2. Characters

Thirty-one morphological characters of the sporophyte and one cytological character were selected. These characters were acquired from personal observations and from literature (see Table 2). Uninformative characters were retained for their potential to distinguish morphologically similar taxa and in order to study their appearance in a phylogenetic context. Some characters show different degrees of polymorphism. The utility of each character for the analysis is discussed in Table 3, with the coding of states. The final matrix is reported in Table 4.

2.3. Phylogenetic analyses

Cladistic parsimony analyses were carried out with beta test versions of PAUP* version 4.0b10w [17], run on a Power Macintosh G4. A Branch and Bound search was performed. To test the robustness of the nodes, decay indices were calculated using AutoDecay [18]. Characters were unordered a priori. Bootstrap procedures [19] were not performed in this study both due to the small size of the matrix, and from a cladistic point of view, it was considered more appropriate to discuss the characters present at the nodes. The polarity and evolution of each character were studied a posteriori using MacClade version 3.04 [20].

3. Results

The parsimony analysis yielded 4200 most parsimonious trees of 109 steps (CI = 0.761; RI = 0.822). Fig. 1 shows the strict consensus tree, with each node numbered (in bold front and circled) and decay indices indicated. Inferred evolution of characters and statistic results are described in Table 5.

3.1. Topology

By rooting with selected outgroups, *Hymenophyllum s.l.* (node 1 in Fig. 1) is retrieved as monophyletic with five apomorphic changes: the reduced to dorsiventral stele, the undeveloped base of the involucre, the half-immersed involucres, the presence of lateral veinlets, and the included receptacles. This implies the inclusion of *Cardiomanes*, *Hymenoglossum*, *Rosenstockia*, *Serpyllopsis* and *Microtrichomanes* in *Hymenophyllum s.l.* Within the ingroup, four basal taxa are in an unresolved position: *Cardiomanes*, *Hymenoglossum*, *Mecodium* II and *Diplophyllum*. Apart from these taxa, a clade (node 2) can be proposed, and is further divided in two groups. The first one (node 3, named '*Sphaerocionium s.l.*') regroups *Sphaerocionium*, *Apteropteris* and *Microtrichomanes*. The second clade (node 5) is further divided in a branch leading to

Table 3
Morphological characters used in the cladistic analysis with character state coding

Fronds

1. Texture of the lamina: *normal* (0); *lamina reduced to teeth* (1); *lamina reduced to hairs* (2). The lamina is very reduced and almost absent in two sections: in *Apteropteris* the lamina is reduced to stellate hairs, in *Myriodon* it is reduced to non vascularised teeth.
2. Thickness of the lamina: *1 cell thick* (0); *2–4 cells thick* (1). Members of the Hymenophyllaceae generally have a lamina that is one cell thick, lacking stomata. A few species display a lamina thicker, ranging from 2 (sometimes only partly) to 4 cells thick.
3. Frond size (lamina + petiole): *large* ($>$15 cm) (0); *small to medium* (5–15 cm) (1); *very small* ($<$5 cm) (2).
4. Margin denticulation: *absent* (0); *present* (1). The denticulation observed for some species of *Hymenophyllum* is not in relation with the venation, what is rare within ferns.
5. Frond fractality: simple (0); *simply pinnatifide* (1); *fractal to very fractal* (2).
6. Dark, thick and forked veins: absent (0); present (1). Within *Hymenophyllum s.l.*, one species, *Rosenstockia rolandi-principis*, shows peculiar veins on the segments, the outer curving in a marginal position.
7. Dark brown (not forking) veins: *absent* (0); *present* (1). Two sections, *Sphaerocionium* and *Microtrichomanes*, have a lamina usually brown green, with dark brown veins even in the youngest segments of the frond.
8. Accessory wings along the veins: *absent* (0); *present* (1).
9. Thin and long accessory wings (teeth-like): *absent* (0); *present* (1).
10. Black marginal cells: *absent* (0); *1 row* (1); *2 rows* (2). Copeland distinguished two genera, *Hymenoglossum* and *Craspedophyllum*, based on this probably derived character.
11. Cell walls: *mostly thin and straight* (0); *mostly thick and wavy* (1); *thick and punctuated* (2). Copeland [5] considered this character important for the distinction of his genera.
12. Simple pluricellular pale to dark brown or red hairs on fronds: *absent* (0); *present* (1).
13. Marginal setae: *absent* (0); *present* (1).
14. Stellate hairs: *absent* (0); *present* (1).
15. Marginal unicellular setae: *absent* (0); *present* (1).
16. Marginal paired hairs: *absent* (0); *present* (1).

Stem anatomy

17. Diameter of the rhizome: *thin* ($<$1 mm) (0); *thick* ($\geqslant$1 mm) (1).
18. Anatomy of the stele: *massive* (0); *reduced to dorsiventral* (1); *subcollateral* (2). The rhizome of the Hymenophyllaceae includes a protostele, for which Ogura [47] defined different types: massive, reduced, dorsiventral, subcollateral, collateral, and extremely reduced.

Soral characters

The sorus of the Hymenophyllaceae, always in a marginal position, is composed of a receptacle bearing the sporangia, enclosed by a bivalved or cup-shaped indusium, called involucre.

19. Position of sori: *pantotactic* (0); *paratactic* (1); *epitactic* (2).
20. Position of sori on pinnae: *on most segments* (0); *on short basal acroscopic segments on primary pinnae or secondary pinnules* (1).
21. Sori orientation: *in the same plane as the lamina* (0); *in a perpendicular plane to the lamina, arched at the base* (1).
22. Base of the involucre: *not developed* (0); *small base* (1); *large base* (2); *totally developed* (3). In *Hymenophyllum s.l.*, the involucre is typically bivalved, the valves being a single cell thick. At the base of the involucre the tissue is thickened, forming a base [1], which has the shape of an arch when it is not developed. In some species traditionally described as tubular (*e.g. Cardiomanes*, *Microtrichomanes*), the tubular portion of the involucre is a single cell thick and thus not considered as the base of the involucre, while in *Trichomanes* the whole involucre is formed by a pluricellular tube (*i.e.* base totally developed). Some species in *Hymenophyllum s.l.* display an intermediate feature: the pluricellular base is widened, and forms a tube, which composes up to half of the involucre [1; personal observations].
23. Immersion of the sorus: *sorus shortly immersed to pedicellate* (0); *half-immersed* (1); *entirely or nearly entirely immersed* (2).
24. Fusion of the valves: *not fused* (0); *partially fused* (1). When the involucre is not totally immersed in the lamina, the valves may be fused as to develop a tubular base (as described above).
25. Lateral veinlets: *absent* (0); *present* (1). The sorus emerges from a vein, which extends in the receptacle. In some cases, this fertile vein can give rise to a branch running up each side of the sorus.
26. Denticulation of the lips: *absent* (0); *present* (1).
27. Length of the receptacle: *included and very short* (0); *as long as the valves or slightly extruded* (1); *very extruded* (2). In the family, sporangia develop on a receptacle with basipetal growth [21]. In *Trichomanes s.l.*, the receptacle has an indefinite growth, and is very extruded from the involucre. On the contrary, in *Hymenophyllum*, the receptacle is rarely longer than the size of the valves, but its length varies a lot between sections, and some of them display receptacles extruding a lot from the involucres.
28. Receptacle shape: *globose to claviforme* (0); *capitate* (1); *cylindrical or filiform* (2).

Table 3 (*Continued*)

29. Position of the sporangia on the receptacle: *receptacle not totally covered by sporangia* (0); *receptacle totally covered by sporangia* (1). This character follows the distinction by Diem and Lichtenstein [29] of two types of receptacles: 1) receptacles totally (or nearly so) covered by sporangia, and 2) receptacles partly covered by sporangia, with the base naked.

30. Fertility of the receptacle: *numerous sporangia* (>20) (0); *few sporangia* (2–20) (1).

31. Sporangiophores: *absent* (0); *present* (1). According to Bower [21], the sporangia are uniform in type for both genera *Trichomanes* and *Hymenophyllum*. They are always short-stalked, but can be born on more or less prominent extensions of the receptacle, called sporangiophores.

32. Chromosome number: $n = 36–72$ *chromosomes* (0); $n = 11–22$ (1); $n = 12–24$ (2); $n = 13–26$ (3); $n = 14–28–56$ (4); $n = 18–36$ (5); $n = 21–42$ (6); $n = 33$ (7); $n = 32$ (8). Although cytological data are still lacking for several representatives of the family, the chromosome numbers reported for *Hymenophyllum s.l.* can be classified in several polyploide series: 11–22, 12–24, 13–26, 14–28, 21–42, 28–56 [48–54], 18–36 and 36–72 (the last two ones are considered independent). The chromosome numbers $n = 32$ and $n = 33$ are observed in *Trichomanes*.

Mecodium I, and a clade (node 6) regrouping all the remaining taxa. In this last clade (corresponding roughly to the subg. *Hymenophyllum* and allies, named '*Hymenophyllum s.s.*'), only a robust association including *Rosenstockia*, *Hemicyatheon*, *Amphipterum*, *Ptychophyllum*, and *Myriodon* (node 8) is suggested.

The clade corresponding to node 2 is supported by two synapomorphies (see Table 5): the diameter of the rhizome, which is less than 1 mm, and the protostele of the subcollateral type. *Sphaerocionium s.l.* (node 3) is monophyletic, with three apomorphic changes: the presence of dark brown veins and marginal setae (also shared by *Leptocionium*) and the low number of sporangia (also in other sections). The association of *Sphaerocionium* and *Apteropteris* (node 4) is further supported by an exclusive apomorphy: the presence of stellate hairs, and by the lack of lateral veinlets (also observed in *Mecodium* I and II). The clade regrouping *Mecodium* I and *Hymenophyllum s.s.* (node 5) shows two apomorphic changes: the cytological series 13–26 and cylindrical to filiform receptacles. Only one exclusive autapomorphy, the chromosome number $n = 28$, characterises *Mecodium* I. The large clade *Hymenophyllum s.s.* (node 6) is supported by five apomorphic changes: the denticulation of the margin (with reversals in *Serpyllopsis* and *Craspedophyllum*), the presence of simple pluricellular brown hairs, involucres with a thickened base, the position of sori in short acroscopic segments of pinnae, and the fusion of the valves (not in all taxa). With *Eupectinum* excluded, the remaining clade (node 7) shows five apomorphic changes: the sori orientation in a perpendicular plane (with polymorphism in *Ptychophyllum*), the non-immersion of the involucre (with reversals in *Ptychophyllum* and *Hemicyatheon*), the denticulation of the lips of the involucre (with reversals in *Craspedophyllum* and in some species of *Ptychophyllum*, *Hymenophyllum*, *Amphipterum*, and *Hemicyatheon*), the receptacle totally covered by sporangia (reversal in *Serpyllopsis*) and the absence of sporangiophores. Finally, the clade regrouping *Ptychophyllum, Myriodon*, *Hemicyatheon*, *Amphipterum* and *Rosenstockia* (node 8) is supported by the chromosome number $n = 21$ (however chromosome numbers are unknown for *Amphipterum* and *Hemicyatheon*), by long and extruded receptacles (also found in *Cardiomanes* and *Microtrichomanes*), and by involucres with a large base (also present in *Leptocionium*). In contrast, the other sections of subg. *Hymenophyllum* and the subg. *Craspedophyllum* display a little base.

3.2. Evolution of characters

A posteriori evolution of the characters is reported in Table 5. Out of 24 informative characters, nine appear to be homoplastic changes: the thickness of the lamina, the size and fractality of the fronds, the thick and punctuated cell walls, the entirely immersed involucres, the presence of lateral veinlets and the size, the form and the fertility of the receptacles.

4. Discussion

In agreement with the preliminary molecular results [14–16], this study supports the inclusion, in *Hymenophyllum*, of the segregate genera *Cardiomanes*, *Hymenoglossum*, *Rosenstockia and Serpyllopsis*, and of the problematic section *Microtrichomanes*. A surprising result is the polytomy, at the base of the tree, of *Cardiomanes*, *Hymenoglossum*, *Diplophyllum* and *Mecodium* II. Because of their peculiarities, the first two have been treated as separate genera by Copeland, Pichi Sermolli, Morton and Iwatsuki, while

Table 4
Data matrix with status of character. Details of characters and coding are discussed in Table 3

	Morphological and cytological characters																														
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Hymenoglossum	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	?
Serpyllopsis	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	1	–	1	1	0	1	1	1	1	2	0	0	1	?
Rosenstockia	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	2	1	1	1	2	0	1	1	1	2	2	1	0	1	6
Cardiomanes	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	1	0	2	0	0	0	0	0
Hymenophyllum	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	1	1	0	0,1	1	0,1	1	0,2	1	0	1	1,3,4,5
Eupectinum	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	0	1	1	1	1	0	1	2	0	0	0	?
Buesia	0	0	1	1	2	0	0	1	0	0	1	1	0	0	0	0	0	2	1	1	0,1	1	0	0	1	1	1	0,2	1	0	1	?
Ptychophyllum	0	0	1,2	1	2	0	0	0	0	0	1,2	1	0	0	0	0	0	2	1	1	1	2	0,1	1	1	0,1	2	2	1	0	1	1,3, 6
Myriodon	1	–	1	1	2	0	0	0	0	0	2	1	0	0	0	0	0	2	1	1	1	2	0	1	1	1	2	2	1	0	1	6
Apteropteris	2	–	1	0	2	0	–	0	0	0	0	0	1	1	0	0	0	2	1	0	0	0	1	1	0	0	1	2	0	1	0	0
Sphaerocionium	0	0	0,1,2	0	2	0	1	0	0	0	0	0	1	1	0	0	0	2	1	0	0	0	1,2	0	0	0	0	1	0	1	0	0
Leptocionium	0	0	1	0	2	0	0	0	0	0	1	1	1	0	0	1	0	2	1	1	1	2	0	1	1	1	1	2	1	0	1	?
Craspedophyllum	0	0	2	0	1	0	0	0	0	1	1	1	0	0	0	0	0	2	1	1	1	1	0	0	1	0	1	2	1	1	1	2,3
Hemicyatheon	0	0	1	0,1	2	0	0	0	0	0	1	1	0	0	0	0	0	2	1	1	0	2	0,1	1	1	0,1	2	2	1	0	1	?
Amphipterum	0	0	1	0,1	2	0	0	0	1	0	1	1	0	0	0	0	0	2	1	1	1	2	0	1	1	0,1	2	2	1	0	1	?
Mecodium I	0	0	1,2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	0,1	0	1	2	0	0,1	0	7
Mecodium II	0	0,1	0,1	0	2	0	0	0	0	0	0,1,2	0	0	0	0	0	1	1	1	0	0	0	1	0	0,1	0	0,1	0,1,2	0	0,1	0	0
Diplophyllum	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0,1	0	0	0,1	0	0
Microtrichomanes	0	0	2	0	1	0	1	0	0	0	0	0	1	0	1	0	0	2	1	0	0	0	2	0	1	0	2	1	0	1	0	0
Pachychaetum	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	1	0	1	1	0	3	0	–	0	0	2	1	0	0	0	8
Lacosteopsis	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	3	0	–	0	0	2	1	0	0	0	0
Cephalomanes	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	1	1	0	3	0	–	0	0	2	1	0	0	0	9
Callistopteris	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	3	0	–	0	0	2	1	0	0	0	0
Status	U	I	I	I	I	U	I	U	U	U	I	I	I	I	U	U	I	I	U	I	I	I	I	I	I	I	I	I	I	I	I	I

– = Inapplicable character; U = uninformative; I = informative.

Table 5
A posteriori evolution of characters in relation to the topologies of the most parsimonious trees and characters statistics

Characters	Polarity and status of states	Nodes	CI	RI
1 Lamina texture	0 → 1 autapomorphy of *Myriodon*		1.000	0/0
	0 → 2 autapomorphy of *Apteropteris*			
2 Lamina thickness	0 → 1 *Cardiomanes*, *Diplophyllum*, *Mecodium* II		0.667	0.000
3 Frond size (lamina + petiole)	0 → 1 (polymorphism in *Sphaerocionium*)	2	0.875	0.750
	0 → 2 (2 is homoplastic apomorphy)			
4 Margin denticulation	0 → 1 (reversals in *Serpyllopsis*, *Craspedophyllum*, *Leptocionium*; polymorphism in *Hemicyatheon* and *Amphipterum*)	6	0.750	0.750
5 Frond fractality	2 → 0 (0 is homoplastic apomorphy)		0.400	0.400
	2 → 1 (1 is homoplastic apomorphy)			
6 Dark, thick and forked veins	0 → 1 autapomorphy of *Rosenstockia*		1.000	0/0
7 Dark brown (not forking) veins	0 → 1	3	1.000	1.000
8 Accessory teeth	0 → 1 autapomorphy of *Buesia*		1.000	0/0
9 Accessory wings	0 → 1 autapomorphy of *Amphipterum*		1.000	0/0
10 Black marginal cells	0 → 1 autapomorphy of *Craspedophyllum*		1.000	0/0
	0 → 2 autapomorphy of *Hymenoglossum*			
11 Cell walls	0 → 1 (reversal in *Serpyllopsis, Hymenophyllum*)	6	0.625	0.667
	1 → 2 (2 is homoplastic apomorphy)			
	0 → 2 *Mecodium* II (with polymorphism)			
12 Simple pluricellular hairs	0 → 1	6	1.000	1.000
13 Marginal setae	0 → 1	3	0.500	0.667
14 Stellate hairs	0 → 1	4	1.000	1.000
15 Marginal unicellular setae	0 → 1 autapomorphy of *Microtrichomanes*		1.000	0/0
16 Marginal pair forked hairs	0 → 1 autapomorphy of *Leptocionium*		1.000	0/0
17 Diameter of the rhizome	1 → 0	2	1.000	1.000
18 Anatomy of the stele	0 → 1 *Hymenophyllum s.l.*	1	1.000	1.000
	1 → 2	2		
19 Position of sori	1 → 0 autapomorphy of *Cardiomanes*		1.000	0/0
20 Position of sori on pinnae	0 → 1	6	0.500	0.857
21 Orientation of sori	0 → 1 (reversals in *Hemicyatheon, Ptychophyllum*)	7	0.667	0.857
22 Base of the involucre	3 → 0 *Hymenophyllum s.l.*	1	0.750	0.917
	0 → 1	6		
	1 → 2	8		
	1 → 2 *Leptocionium*			
23 Immersion of the involucre	0 → 1 *Hymenophyllum s.l.*	1	0.714	0.714
	1 → 2 (2 is homoplastic apomorphy)			
	1 → 0 (polymorphism in *Ptychophyllum* and *Hemicyatheon*)	7		
24 Fusion of the valves	0 → 1 (reversals in *Buesia*, *Craspedophyllum*; polymorphism in *Hymenophyllum*)	6	0.400	0.625
	0 → 1 *Apteropteris*			
25 Lateral veinlets	0 → 1	1	0.750	0.800
	1 → 0	4		
	1 → 0 (polymorphism in *Mecodium* I)			
26 Denticulation of the lips	0 → 1 (reversals in *Craspedophyllum*; polymorphism in *Hymenophyllum, Hemicyatheon*, *Amphipterum*, and *Ptychophyllum*)	7	0.833	0.750
27 Length of the receptacle	2 → 1 *Hymenophyllum s.l.*	1	0.571	0.700
	1 → 2 (2 is homoplastic apomorphy)	8		
	1 → 0 (0 is homoplastic apomorphy)			
28 Receptacle shape	1 → 0 (polymorphism in *Mecodium* II)	1	0.857	0.857
	1 → 2 (polymorphism in *Buesia*, *Hymenophyllum*)	5		
	1 → 2 *Apteropteris*			
29 Position of the sporangia	0 → 1 (reversal in *Serpyllopsis*)	7	0.500	0.875
30 Fertility of the receptacle	0 → 1 (1 is homoplastic apomorphy)	3	0.800	0.667

Table 5 (*Continued*)

Characters	Polarity and status of states	Nodes	CI	RI
31 Sporangiophores	0 → 1	7	1.000	1.000
32 Chromosome number	0 → 3 (polymorphism in *Hymenophyllum*, *Craspedophyllum*)	5	1.000	1.000
	3 → 6 (polymorphism in *Ptychophyllum*)	8		
	3 → 4 autapomorphy of *Mecodium*			

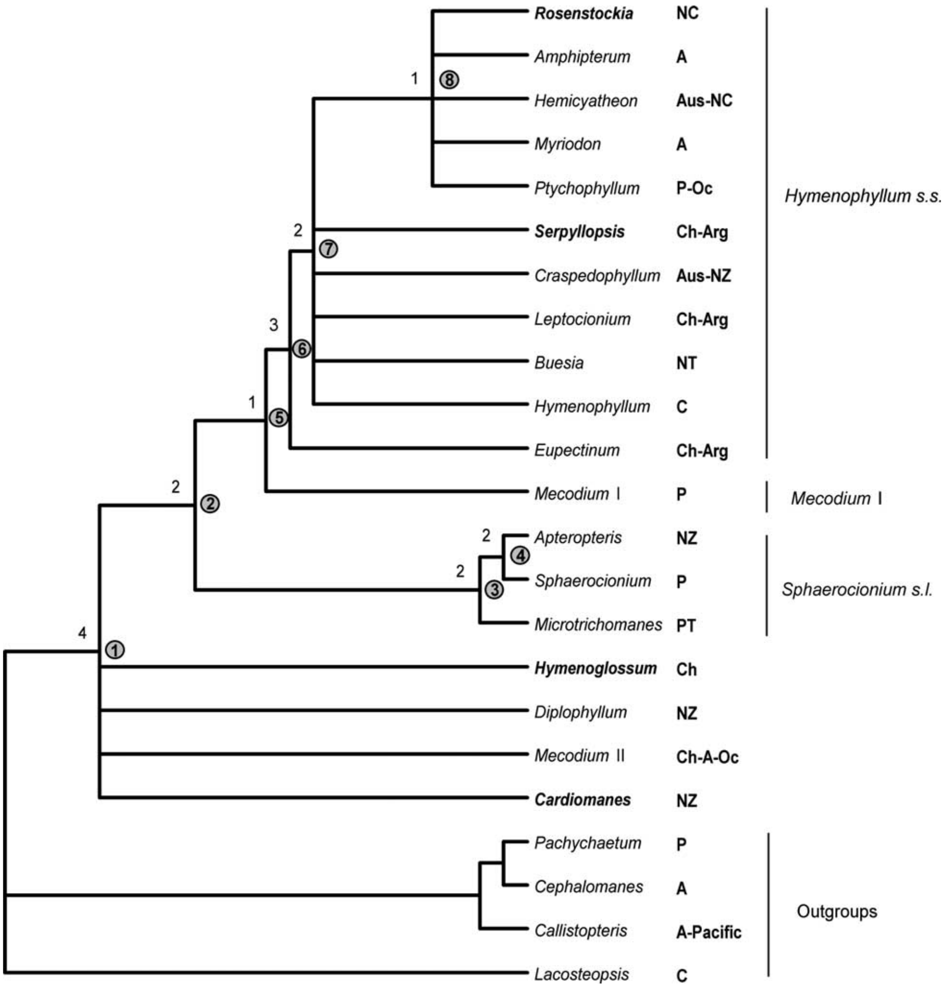

Fig. 1. Strict consensus of 4200 MP trees. Values in bold front and circled are node numbers (used in Table 5); other values are Decay Indices. Names in bold front correspond to the genera separated from *Hymenophyllum* by Morton [8]. Names on the right correspond to the clades discussed. **A**, Asia; **Arg**, Argentina; **Aus**, Australia; **C**, Cosmopolitan, **Ch**, Chile; **NC**, New Caledonia; **NT**, Neotropics; **NZ**, New Zealand; **Oc**, Oceania; **P**, Pantropics; **PT**, Palaeotropics.

Diplophyllum and *Mecodium* II always belonged in *Mecodium* [5–10]. These taxa share characters that appear plesiomorphic for the genus: large fronds, a relatively thick rhizome, a protostele of the reduced or dorsiventral type, and the chromosome number $n = 36$, which is also reported in many species of *Trichomanes*. However, cytological data are still lacking for *Hymenoglossum*. Some of these basalmost taxa are also characterised by a thicker lamina than the one-cell thick one typically found in the family: the lamina is

3–4-cell thick in *Cardiomanes* and bistratose, sometimes only partly, in *Diplophyllum* and in some species of *Mecodium* II. In addition, these taxa share an Austral to Australasian distribution: *Hymenoglossum* and some species of *Mecodium* II occur in southern Chile, *Cardiomanes* and *Diplophyllum* in New Zealand, and most species of *Mecodium* II in Australasian pacific regions (from New Zealand to Indonesia and Tahiti), possibly also in Africa. Bower [21] suggested that *Cardiomanes*, together with some large species of *Hymenophyllum*, such as *H. dilatatum* (type species of *Diplophyllum*), may be held as taking a central position in the family; this hypothesis is congruent with this analysis. Finally, the involucre of *Cardiomanes*, traditionally described as tubular, does not appear homologous to the involucres observed in *Trichomanes*: it is tubular only by complete immersion of the involucre, as the valves are not thickened.

Genus *Sphaerocionium sensu* Iwatsuki [9,10], Pichi Sermolli [7] or Copeland [5,6] is retrieved as monophyletic, but not subgenus *Sphaerocionium sensu* Morton [8], because of the exclusion of *Leptocionium*. This taxon, with a single species, *H. dicranotrichum*, from South Chile and Argentina, is problematic in having the marginal setae of *Sphaerocionium* and the sorus of *Ptychophyllum* [5]. It is here embedded in subg. *Hymenophyllum*, but this does not exclude the hypothesis of a hybridisation between species of these two taxa. Interestingly, *Microtrichomanes* is resolved as sister group to *Sphaerocionium* and *Apteropteris*. This problematic palaeotropical taxon was long considered close to *Trichomanes* [8–10,22,23]. Nevertheless, Copeland [5] suggested that it may be related to *Hymenophyllum*, and, at least for some species, derived from *Sphaerocionium*, based on the marginal setae present in both groups. These results corroborate Copeland's assumption.

Although the morphological uniformity of *Mecodium* has rarely been questioned, this analysis suggests the polyphyly of this taxon sensu Morton [8], Iwatsuki [9,10] or Copeland [5,6]. The two groups created appear quite distantly related, with *Mecodium* II positioned at the base of the tree, close to *Diplophyllum*, and *Mecodium* I sister group to the '*Hymenophyllum s.s.*' clade. Furthermore, the subsection *Amphipterum* defined by Morton is retrieved as embedded in *Hymenophyllum s.s.* The clade *Mecodium* I is supported by a single autapomorphy, which is the chromosome number $n = 28$. Among the other features of *Mecodium* I are the glabrous fronds (while some species of *Mecodium* II display pale pluricellular simple hairs on axes), the entire margins and the bivalved sori with thin cylindrical and included receptacles. This Pantropical clade is based on *H. polyanthos* (Sw.) Sw. from South America, which was the type species attributed to *Mecodium* as a genus by Copeland [4], or as a subgenus by Morton [8] and Iwatsuki [9,10]. In his following treatments of the genus, Copeland [5, 6] however changed the type of *Mecodium* to *H. sanguinolentum* Forst., from New Zealand, the species that Presl [2] mentioned in proposing *Mecodium* as a *nomen nudum*. The choice of the type species of *Mecodium* appears all the more crucial since the chromosome number $n = 28$ (or $n = 27$) has always been reported for *H. polyanthos*, while *H. sanguinolentum* has a chromosome number of $n = 36$ and is thus here included in *Mecodium* II.

With regard to the remaining taxa, the grouping of the sections of subg. *Hymenophyllum* (*Hymenophyllum*, *Buesia*, *Eupectinum*, *Ptychophyllum* and *Myriodon*) by Morton [8] is retrieved. Furthermore, the phylogeny inferred indicates a much broader group than expected, including the genera *Serpyllopsis* and *Rosenstockia*, the subgenera *Hemicyatheon* and *Craspedophyllum* and the subsections *Leptocionium* and *Amphipterum*. This clade regroups taxa from as distant locations as South America, Africa, Europe, Asia, and Oceania, but has nevertheless many representatives in the temperate rain forests of southern areas. *Serpyllopsis*, from South Chile and South Argentina, has often been assumed to belong to *Hymenophyllum s.l.* [5–10, 24,25], although it displays a tubular involucre. With regard to *Rosenstockia*, endemic to New Caledonia, all authorities [6–10,24,26] agreed on its relation to *Hymenophyllum*, and more precisely to *Ptychophyllum* (Copeland's *Meringium*), based on the sorus shape. However, only Iwatsuki has integrated it into his genus *Hymenophyllum*. The present analysis corroborates his treatment, and is in agreement with recent molecular studies [15,16].

The placement of *Hemicyatheon* (Australia, New Caledonia) close to *Ptychophyllum* is in agreement with Iwatsuki [9,10], who included it in his subg. *Chilodium*. As for *Craspedophyllum* (Australia, New Zealand), Copeland [5] and Iwatsuki [9,10] considered it to be related to *Mecodium*. Iwatsuki even integrated it as section *Pachyloma* in his subg. *Mecodium*. Morton [8] proposed no affinities to other groups and attributed the subgeneric rank to the taxon. This study, showing *Craspedophyllum* embedded in *Hymenophyllum*, refutes all these treatments. Finally, the much debated subsections *Amphipterum* and *Leptocionium*, placed by Morton in respectively subg. *Mecodium* and *Sphaerocionium*, are retrieved as related to the subg. *Hymenophyllum*. This supports Copeland's [5,6] suggestions and Iwatsuki's [9,10] treatment.

As Copeland [4] noted, the genus *Hymenophyllum* appears at first to be quite homogeneous in comparison to *Trichomanes*. Nearly always epiphytic, *Hymenophyllum* displays pendant fronds, more or less widely distanced on thin long-creeping rhizomes. Nevertheless, when it is studied in more depth, the genus reveals considerable heterogeneity. This is illustrated by the shape of the involucre, the shape and size of the receptacle, the size of the fronds, etc. Among the characters used in this study, a few are autapomorphies and thus non-informative. Nevertheless, some informative characters are synapomorphies, or if homoplastic, however allow support to a clade. The constructed matrix thus contains structured homoplasy. Pichi Sermolli [7] stated that "probably we attach too great an importance to the characters of the sorus". Indeed, the separation of two types of involucres (tubular/bivalved) is not clear, not only because there are intermediate cases where the involucre has an obconic or tubular base, but also because an involucre described as tubular is not always homologous to the tubular state in *Trichomanes*. In the present study, I consider that the involucre of *Cardiomanes* is different from that of *Serpyllopsis* and that both are different from that of *Trichomanes*. The sori of *Cardiomanes* and *Microtrichomanes* appear more similar. A combination of characters was thus used to describe the soral shape. The results suggest that totally bivalved (with no developed base) involucres may be a plesiomorphic character state for *Hymenophyllum*, with a single transition to involucres with a developed base. The base can then be further developed, leading sometimes to an almost tubular involucre.

The intercontinental southern hemisphere distributions observed for the basal taxa in *Hymenophyllum s.l.* point to possible ancient Gondwanan connections, and would thus corroborate Copeland's [6] hypothesis of an austral origin for the family. Indeed, recent fern phylogenies [55,56] indicate that Hymenophyllaceae have been a distinct lineage at least by the Late Palaeozoic or Early Mesozoic, *i.e.* prior to the break-up of Gondwana. Derived taxa (*Sphaerocionium*, *Mecodium* I, *Ptychophyllum*) display a pantropical distribution, and, as suggested by Iwatsuki [57], the diversification of the family may have occurred in tropical areas. Nevertheless, it is difficult to discriminate the relative roles of dispersal and vicariance in ferns [58]. Probably both processes account for the wide distribution observed in *Hymenophyllum*, and a broader sampling is required for further historical and biogeographical assumptions.

5. Conclusion

This study, based on morphological characters, calls into question the previous classifications of the genus. The results are overall more in agreement, with some exceptions, with Iwatsuki's [9,10] system than with Morton's [8]. Many of Copeland's [5,6] proposed associations are also supported, but his classification is not. Nevertheless, the high number of most parsimonious trees obtained and the poor support illustrate the limitations of the morphological data for the resolution of the systematics of the genus. The cytological data appear useful to justify some suggested relationships, but too many data are still lacking to exploit them fully. Further works should therefore include molecular characters, which may provide greater resolution of the phylogenetic relationships within the genus.

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