SYSTEMATICS OF TRICHOMANES (HYMENOPHYLLACEAE: PTERIDOPHYTA), PROGRESS AND FUTURE INTERESTS

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ABSTRACT

Trichomanes L. sensu lato (s.l.), is a large group of Hymenophyllaceae to which ca. 250 species are attributed, distributed from the tropics to temperate regions around the world. Their life forms and morphology are more diversified than those of the other large filmy-fern genus Hymenophyllum. Phylogenetic analyses were performed based on the rbcL sequences of 81 Trichomanes taxa, covering most of the major groups within the genus, in addition to morphological, anatomical and cytological investigations, that offer a number of insights concerning evolution of the genus. Eight robustly supported clades are recognized within Trichomanes, while some traditional trichomanoid taxa (e.g., Pleuromanes) are transferred to the Hymenophyllum clade.

INTRODUCTION

Because of their simplified morphology among pteridophytes, filmy ferns (Hymenophyllaceae) have attracted the attention of many researchers, especially those interested in evolution and phylogeny. The family’s basal placement among leptosporangiate ferns was already suggested by morphological evidence (oblique annuli of sporangia; Bower, 1926) and supported by recent molecular phylogenetic work (Pryer et al., 2004). In contrast, it is difficult to reconstruct its intrafamiliar lineages from its morphological characters, probably as a result of numerous parallel evolutions (Dubuisson, 1997a). Several different classification systems (e.g., Copeland, 1938; Morton, 1968; Iwatsuki, 1984) are currently in use for this family.

Dubuisson (1997b) first adopted molecular phylogeny to infer intrafamiliar relationships among the Hymenophyllaceae, specifically targeting one of the two largest groups, Trichomanes sensu lato (s.l.), to explore the reliability of the chloroplast rbcL marker at the infrageneric level. The result showed better resolution than for the other group, Hymenophyllum s.l., in which less genetic variation was found for rbcL (Pryer et al., 2001; Ebihara et al., 2002; Hennequin et al., 2003). Trichomanes, however, is a large genus comprising around 250 species (Iwatsuki, 1990) occurring nearly throughout the tropics and extending into the temperate zone, especially the southern latitudes. Despite the study by Dubuisson et al. (2003a) focusing on Neotropical Trichomanes, many distinctive Palaeotropical taxa remained unsampled. Recently, Ebihara et al. have added considerable new rbcL data, making a global revision of the genus possible.
COVERAGE OF SAMPLING

In total, 81 species of *Trichomanes*, approximately a third of the estimated number of extant species, were included in this study, though some traditional trichomanoid taxa (*Microtrichomanes* Copel. pro parte and *Cardiomanes reniforme* (G.Forst.) C.Presl) whose affiliations to the *Hymenophyllum* lineage have already been suggested (Pryer et al., 2001; Ebihara et al., 2004) were not counted as *Trichomanes*. This sampling covered all of Copeland’s trichomanoid genera (*Abrodictyum* C.Presl, *Callistopteris* Copel., *Cephalomanes* C.Presl, *Crepidomanes* (C.Presl) C.Presl, *Crepidopteris* Copel. [= *Reediella* Pic.Serm.], *Davalliopsis* Bosch, *Didymoglossum* Desv., *Feea* Bory, *Gonocormus* Bosch, *Lecanium* C.Presl, *Macroglena* (C.Presl) Copel., *Microgonium* C.Presl, *Nesopteris* Copel., *Pleuromanes* (C.Presl) C.Presl, *Polyplebium* Copel., *Selenodesmium* (Prantl) Copel., *Trichomanes* sensu stricto (s.s.) and *Vandenboschia* Copel.) and most of Morton’s (1968) sections under *Trichomanes*, except for four small sections of the subgenus *Achomanes* C.Presl (sections *Odontomanes* (C.Presl) C.Chr., *Trigonophyllum* (Prantl) C.Chr., *Homoeotes* (C.Presl) C.Chr. and *Ragatelus* (C.Presl) C.Chr.).

A data matrix consisting of 1206 bp fragments of the *rbcL* sequences from 81 *Trichomanes* species as well as 12 other Hymenophyllaceae and 4 non-Hymenophyllaceae (*Polypodium glycyrrhiza* D.C.Eaton, *Matonia pectinata* R.Br., *Osmunda cinnamomea* L. and *Angiopteris evecta* Hoffm.; the last taxon was treated as an outgroup) was analyzed using the maximum-parsimony (MP) method with PAUP*4.0 software (detailed in Ebihara et al.).

EVOLUTIONARY RELATIONSHIP

In the resulting consensus MP tree (Ebihara et al., in prep.; Figure 1), both the *Trichomanes* and *Hymenophyllum* clades are strongly supported, as in Pryer et al. (2001) and Ebihara et al. (2004). *Pleuromanes*, a group which has always been considered a member of *Trichomanes*, is indeed embedded in the *Hymenophyllum* clade and eight robustly-supported subclades (BS > 90) are recognizable in the *Trichomanes* lineage. These groupings do not match any of the existing classifications, but seem to be closely related to the plants’ morphological characters, chromosome base numbers and geographical distributions.

The phylogenetic framework suggests three evolutionary scenarios for the genus: (1) Cytological data reveals that the chromosome base numbers are constant within each “clade,” so the observed diversity in number may originate from aneuploid reduction from the ancestral $x = 36$. (2) Life form data indicate that four monophyletic clades (Cr, Di, Pa and Va in Fig. 1), consisting mostly of epiphytic and epipetric taxa displaying evolutionary traits that tend towards morphological and anatomical reductions, are supported with fairly high reliability (Ebihara et al.). Assuming that the common ancestor of *Trichomanes* was terrestrial, the occurrence of epiphytism related to evolutionary regression was apparently quite a significant event in the genus, and at least four independent evolutionary transitions led to the epiphytic habit. (3) Geographical distribution data show that four of the eight clades are subcosmopolitan; the NT clade is nearly confined to the Neotropics, while the Ca, Ce and Cr clades are confined to the Palaeotropics. Peculiar monotypic trichomanoid “genera” distributed in the southern hemisphere, which formed the basis of the Antarctic origin theory of Hymenophyllaceae (Copeland, 1938, 1939), are all placed in derivative positions in the present phylogeny.
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Figure 1. Evolutionary relationship of Trichomanes: a strict consensus of seven most parsimonious trees retrieved from an unequally weighted rbcL data matrix (3717.96 steps, CI=0.32 and RI=0.74). Bootstrap values ≥50% are shown. Taxon names generally follow the Morton’s (1968) system, and the trichomanoid genera defined by Copeland (1938) are indicated in parentheses.
FUTURE CHALLENGES

Usefulness of rbcL

In the case of Trichomanes, rbcL phylogeny is a useful tool for inferring the “macroevolution” or global relationships among sublineages of the genus. Indeed, eight principal clades have recently been defined as eight distinct genera (Ebihara et al.). Although our results show that there is some useful genetic variation for discussing relationships among species with closely-related rbcL sequences, further consideration is necessary before adopting chloroplast-coding markers for this purpose. If hybridization or reticulate evolution (e.g., Wagner 1954; van den Heede et al., 2003; Ebihara et al., 2005) occurred in a clade, the relationship between the members as reconstructed from chloroplast DNA, which is maternally inherited in ferns (Gastony & Yatskievych, 1992), would not be accurate.

For example, Copeland’s genus Gonocormus, ranging from Africa to the Pacific region, consists of several taxa segregated by leaf shape and proliferation (e.g., Trichomanes saxifragoides C.Presl, T. minutum Blume and T. proliferum Blume); however, Yoroi and Iwatsuki (1977) argued that it should be difficult to recognize such taxa morphologically and tentatively clustered them into a single species, T. minutum (Iwatsuki, 1984). Although much genetic variation is also found in rbcL sequences taken from several specimens of the Gonocormus species collected from various localities, there does not seem to be a clear relationship between their morphological and genetic variation (Ebihara, unpublished data). Considering the fact that diploid, triploid and tetraploid series are reported for Gonocormus (Braithwaite, 1969, 1975; Yoroi & Iwatsuki, 1977), reticulate evolution has probably occurred in this complex. Another example is the Trichomanes (Vandenboschia) radicans complex (the Va clade), which includes the American T. radicans Sw., the European T. speciosum Willd., the African T. giganteum Willd., the Japanese T. orientale C.Chr. and the Asian T. birmanicum Bedd. Our study, utilizing the biparently-inherited nuclear GapCp marker, suggests that hybridization involving at least three biological units occurred in Japan, despite an observed difference in rbcL of up to 1.66% (20/1206 bp; Ebihara et al., 2005) among them. In addition, it is likely that both T. speciosum and T. giganteum are of hybrid origin (Ebihara, unpublished data). Considering the high incidence of allopolyploid hybridization in ferns (Soltis & Soltis, 1999), such examples may be ubiquitous rather than exceptional. These results strongly indicate the importance of biparently-inherited markers in species-level analyses. Analyses using sequences from multiple gene regions are also necessary to clarify relationships among the clades that are unresolved in the present rbcL phylogeny.

Importance of field observations

The evolution of life forms is one of the most interesting topics concerning Hymenophyllaceae. Their habits are usually divided into several types, such as terrestrial, epiphytic, epipetric, hemi-epiphytic and true lianas (Dubuisson et al., 2003b), but in fact their ecological classification is routinely complex and requires careful and precise in situ observations. For example, we have never seen herbarium specimens of T. auriculatum with underground parts (roots). Rather, most herbarium specimens consist only of epiphytic parts, i.e., leaves with climbing rhizomes. Our field observations, however, reveal that the plant germinates on the ground and the rhizomes climb up tree trunks. Field investigations are therefore essential for evolutionary studies.
Diversification history and conservation

Extant filmy ferns exclusively prefer moist and shady environments, but the habitat where their common ancestor acquired its unique one-cell thick lamina in the Triassic or earlier (Axsmith et al., 2001; Pryer et al., 2004) remains unknown for certain. The fact that roughly half of the Hymenophyllaceae species are attributed to the hymenophylloids, which are mostly epiphytic on tree trunks and diversified relatively recently compared to trichomanoids (Hennequin et al., 2003; Schuettpeltz & Pryer, 2006), is consistent with the trend of extant fern diversification in angiosperm forests (Schneider et al., 2004). Our phylogeny also suggests that a few species in _Trichomanes_ with an epiphytic habitat on trees may have recently acquired this habit.

Filmy ferns are one of the fern groups most sensitive to environmental changes, particularly decreased humidity caused by deforestation. Habitat conservation and conservation biology studies of already-endangered species (e.g., Rumsey et al., 1998) are crucial for the future study of this family and to maintain its present diversity.

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