Circumscription, classification, and taxonomy of Amblystegiaceae (Bryopsida) inferred from nuclear and chloroplast DNA sequence data and morphology

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Results from a previous broad-scale analysis employing *trnL-trnF* sequence data for 168 Hypnalean and 11 Hookerialean taxa, and an analysis employing two chloroplast regions, *trnL-trnF* and *atpB-rbcL*, one nuclear region, the internal transcribed spacers of 18S-26S rDNA, plus 68 morphological characters for a reduced data set of 54 Hypnalean taxa, were used to circumscribe Amblystegiaceae. The analyses provided two well-supported main clades including taxa traditionally included in Amblystegiaceae s.l. and recognized as Amblystegiaceae s.str. [*Anacamptodon*, *Amblystegium*, *Campyliadelphus*, *Campylium*, *Cratoneuron*, *Cratoneuropsis*, *Drepanocladus* s.str., *Gradsteinia*, *Hygrohypnum* s.str. (including the type species, *H. luridum*, but excluding a number of other species previously accommodated in the genus), *Hypnobartlettia*, *Leptodictyum*, *Palustriella*, *Pseudo-calliergon*, and *Serpoleskea*] and Calliergonaceae stat. nov. (*Calliergon*, *Hamatocaulis*, *Loeskypnum*, *Straminergon*, and *Warnstorfia*). *Scorpidium* and "*Hygrohypnum*" *ochraceum* were closely related to Calliergonaceae but were not included in the family because of the lack of support. All these genera but *Anacamptodon* have previously been included in Amblystegiaceae s.l. The sporophytic features of *Anacamptodon*, which contrast with those of all the other members of Amblystegiaceae, are interpreted as adaptations to an epiphytic habitat and suggest, together with other recent taxonomic works in Hookeriales, that characters related to sporophytic specializations are among the most homoplastic. Several other taxa (*Calliergonella*, *Campylophyllum*, *Conardia*, *Donrichardsia*, "*Hygrohypnum*" *smithii*, *Platydictya*, *Sanionia*), previously included in Amblystegiaceae s.l., appeared more closely related to other Hypnalean families. Recircumscribed Amblystegiaceae, and several clades within the family, have no identifiable morphological synapomorphies. A new system of classification for recircumscribed Amblystegiaceae, including morphological delimitation of presented clades based on maximum likelihood reconstruction of ancestral character states, is proposed and appropriate nomenclatural changes made.

KEYWORDS: Amblystegiaceae, Calliergonaceae, molecular phylogenetics, pleurocarpous mosses, taxonomy.

INTRODUCTION

Amblystegiaceae G. Roth are one of the most problematical moss families in terms of separation from other families and division into genera and species (Andrews, 1957). The source of this difficulty lies primarily in the great variability of the plants. Most members of Amblystegiaceae grow associated with damp or aquatic conditions, and even slight differences in ecological conditions induce variations in morphology (Mönkemeyer, 1906, 1909; Loeske, 1907, 1928; Kanda, 1975; Hedenäs, 1996). Sporophytes of Amblystegiaceae are in most features similar to those of species in other families, including Thuidiaceae Schimp. and temperate members of Hypnaceae Schimp. (Fleischer, 1904–1923; Hedenäs, 1989a, 1995, 1998; Nishimura & al., 1984), and offer little information about familial circumscription and relationships. Amblystegiaceae have consequently been subject to conflicting taxonomic treatments since Roth (1899) established the family (contrast, e.g., Crum & Anderson, 1981; Vitt, 1984; Ochyra & al., 1991; Buck & Goffinet, 2000).

In a previous study, Vanderpoorten & al. (in press) employed DNA sequence data and morphological characters for studying morphological evolution in a monophyletic Amblystegiaceae of revised circumscription.

The focus of the present paper is to discuss the taxonomic implications of those analyses in Amblystegiaceae in order to propose a new system of classification for the family.

CIRCUMSCRIPTION AND CLASSIFICATION OF AMBLYSTEGIACEAE

Circumscription of Amblystegiaceae. — The strict consensus of five equally most parsimonious trees based on the analysis of *trnL-trnF*, *atbB-rbcL*, ITS sequence data and morphology (see Vanderpoorten & al., in press for details) is presented in Fig. 1. The analysis, based on 371 informative characters (67 morphological and 304 molecular characters), provided two well-supported main clades. The clades include taxa traditionally included in Amblystegiaceae, and recognized as Amblystegiaceae s.str. (clade A in Fig. 1) and Calliergonaceae stat. nov. (clade B in Fig. 1). The topology was congruent with the results of a broad-scale analysis of the pleurocarps employing *trnL-trnF* sequence data for 168 Hypnalean and 11 Hookerialean taxa used as outgroups (see Vanderpoorten & al., in press).

Our phylogenetic results thus contradict a monophyletic interpretation of Amblystegiaceae as traditionally circumscribed by Roth (1899), Fleischer (1920), Kanda (1975, 1976), and Vitt (1984), and clearly suggest that Amblystegiaceae, in the broad sense, are polyphyletic. Several authors have attempted to define an Amblystegiaceae of narrower circumscription (Ochyra & al., 1991; Buck & Goffinet, 2000), and erected Donrichardsiaceae Ochyra, Hypnobartlettiaceae Ochyra (Ochyra, 1985), Cratoneuraceae Mönk., Helodiaceae Ochyra (Ochyra, 1989), and Campyliaceae (Kanda) W.R. Buck (Buck & al., 2000) to accommodate the excluded taxa. However, many of the proposed family circumscriptions are not supported by our data. The families were defined by such characters as the presence of foliose paraphyllia (Cratoneuraceae), or elongate laminal cells and inflated alar cells (Campyliaceae), characters that are precisely those that appear to be the most labile or homoplastic, or which correlate to habitat conditions (Vanderpoorten & al., in press).

Amblystegiaceae s.str. include *Hypnobartlettia* Ochyra, *Cratoneuropsis* (Broth.) M. Fleisch., *Drepanocladus* (Müll. Hal.) G. Roth, *Pseudo-calliergon* (Limpr.) Loeske, *Cratoneuron* (Sull.) Spruce, *Amblystegium* Schimp., *Palustriella* Ochyra, *Leptodictyum* (Schimp.) Warnst., *Campylium* (Sull.) Mitt., *Campyliadelphus* (Kindb.) R.S. Chopra, *Hygrohypnum* Lindb. s.str. [including the type species, *H. luridum* (Hedw.) Jenn., but excluding a number of other species previously accommodated in the genus], *Anacamptodon* Brid., and *Serpoleskea* (Limpr.) Loeske. *Gradsteinia andicola* Ochyra, nested within a clade including *Amblystegium serpens* in a previous study (Stech & Frahm, 2000), was included in an analysis of ITS plus morphological characters (not shown). The genus, monotypic since the transfer of *G. torrenticola* Ochyra, C. Schmidt & Bültmann into *Platyhypnidium* M. Fleisch. (Ochyra & Bednarek-Ochyra, 1999), was nested within Amblystegiaceae in a well-supported clade including *Cratoneuropsis* and *Drepanocladus* s.str. and is tentatively included within the circumscription of Amblystegiaceae presented here.

All these genera but *Anacamptodon* have previously been included in Amblystegiaceae s.l. *Anacamptodon* is an epiphyte usually included within the family Fabroniaceae (e.g., Crum & Anderson, 1981) whose peculiar sporophyte features including straight capsules, low endostome membrane and recurved peristome teeth when dry, strongly contrast with those of all the other members of Amblystegiaceae. The phylogenetic relationship of *Anacamptodon* and *Campylium* was previously suggested by *rps4* and *trnL-trnF* chloroplast sequence data (Buck & al., 2000). The erect capsules and reduced endostome of *Anacamptodon* are interpreted as adaptations to an epiphytic habitat (Vanderpoorten & al., in press) and suggest, together with other recent taxonomic works in the Hookeriales (Whittemore & Allen, 1989; Tan & Robinson, 1990; Hedenäs, 1997), that characters related to sporophytic specializations are among the most homoplastic (Buck, 1991; Hedenäs, 1999).

Calliergonaceae include *Hamatocaulis* Hedenäs, *Loeskypnum* H.K.G. Paul, *Straminergon* Hedenäs, *Calliergon* (Sull.) Kindb., and *Warnstorfia* Loeske. *Scorpidium* (Schimp.) Limpr. and "*Hygrohypnum*" *ochraceum* (Turner ex Wilson) Loeske were closely related to Calliergonaceae, but were not included in the family because of the lack of support. A clade including *Calliergon*, *Loeskypnum*, *Straminergon*, and *Warnstorfia* was also well supported in the morphology- and ecology-based analyses of Hedenäs (1998) and Hedenäs & Kooijman (1996). However, *Tomentypnum* Loeske and *Conardia* H. Rob., which were nested within the monophyletic resolved clade of Hedenäs & Kooijman (1996), appeared unrelated to Calliergonaceae in our analyses.

Several other taxa previously accommodated in Amblystegiaceae s.l. or segregated families did not appear closely related to either Amblystegiaceae or Calliergonaceae. *Donrichardsia* H. A. Crum & L. E. Anderson, a monospecific endemic aquatic moss genus from Texas, was originally described as a species of *Amblystegium* (Grout, 1933) because of its aquatic habitat, robust habit, and broad costa. Subsequently, the taxon was transferred to the genus *Platyhypnidium*, Brachytheciaceae (Crum, 1969), then its own genus,

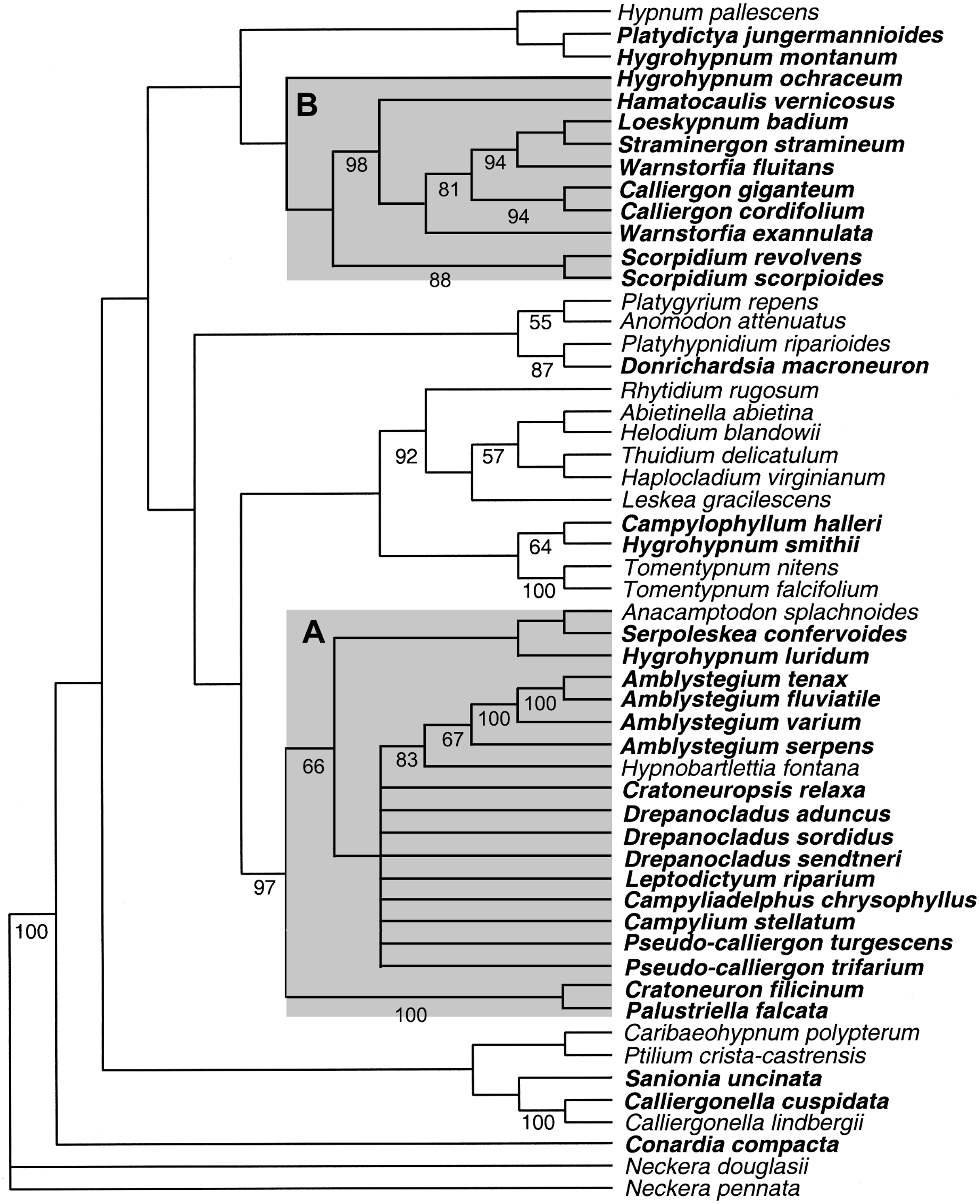

Fig. 1. Strict consensus tree of five equally parsimonious trees (L = 1383, CI = 0.38, RI = 0.58) for 54 taxa of Hypnales from combined molecular and morphological partitions, using *Neckera* spp. as outgroups. Numbers below branches are bootstrap support percentages >50%. Taxa traditionally included within Amblystegiaceae appear in bold. A = Amblystegiaceae s.str.; B = Calliergonaceae and closely related taxa.

Donrichardsia, within Amblystegiaceae (Crum & Anderson, 1979), and finally described in its own family, Donrichardsiaceae, because of its peculiar multistratose leaf lamina and thick costa (Ochyra, 1985). Our results strongly support the transfer of *Donrichardsia* into the genus *Platyhypnidium*, which was recently recircumscribed to include taxa with thick costae and multistratose leaf laminae (Ochyra & Vanderpoorten, 1999).

Calliergonella cuspidata (Hedw.) Loeske and *Hypnum lindbergii* Mitt., two taxa traditionally accommodated in different families (e.g., Corley & al., 1981; Crum & Anderson, 1981), shared numerous molecular synapomorphies and were characterized by three morphological synapomorphies, namely complanate to subcomplanate stem leaves, absence of a costa, and appendiculate cilia. The results strongly support the transfer of *H. lindbergii* to *Calliergonella* (Hedenäs, 1990a).

Limbella tricostata (Sull.) Müll. Hal. ex E.B. Bartram was shown to be unrelated to Amblystegiaceae in a phylogenetic survey of the pleurocarps based on *rbcL* sequence data (Arikawa & Higuchi, 1999) and was subsequently transferred to Thamnobryaceae Margad. & During based on its morphological features (Ochyra, 1987a). Another *Limbella* species, *L. pachyloma* (Mont.) Müll. Hal., for which only partial data were available, was accommodated in its own genus *Vittia* Ochyra and family Vittiaceae Ochyra (Ochyra, 1987b). Hedenäs (1995), conversely, interpreted the taxon as a specialized *Amblystegium* with a few autapomorphic adaptive characters. An assessment of *Vittia*'s taxonomic status is currently in progress.

Lastly, *Conardia compacta*, *Sanionia* Loeske, "*Hygrohypnum*" *smithii* (Sw.) Broth., *Campylophyllum halleri* (Sw. ex Hedw.) M. Fleisch., and *Platydictya jungermannioides* (Brid.) H. A. Crum were also found to be unrelated to Amblystegiaceae s.str. In addition, a Tatra endemic, *Ochyraea tatrensis* Vana, shown to be closely related to "*Hygrohypnum*" *smithii* and *Calliergonella cuspidata* in an analysis of ITS and *trnL-trnF* sequence data (Stech & Frahm, 2001), is therefore not a member of Amblystegiaceae either. These results support previous statements that the genera *Hygrohypnum* Lindb., *Campylium*, and *Platydictya* Berk are, in the broad sense, polyphyletic (see Vanderpoorten & al., 2001, for review). The position of these taxa within the Hypnales is, however, uncertain [contrast, e.g., the affinities of *Sanionia* with "*Hygrohypnum*" *ochraceum* and *Scorpidium* based on ITS sequence data for a more reduced data set by Stech & Frahm (2001) and Vanderpoorten & al. (2001) with its position in the present analysis]. The phylogenetic relationships of these taxa need to be addressed in the context of a larger phylogeny of the pleurocarps.

Classification of Amblystegiaceae s.str. — The strict consensus of eight equally-parsimonious trees from an analysis focusing on Amblystegiaceae s.str., which included 207 informative characters (41 morphological characters and 166 molecular characters), is presented in Fig. 2 (see Vanderpoorten & al., in press, for details). Amblystegiaceae are divided into two subfamilies (Table 1): Cratoneuroideae (Mönk.) stat. nov. and Amblystegioideae. Amblystegioideae are further divided into two tribes: Campylieae (Kanda) stat. nov. and Amblystegieae. Campylieae include two subtribes: Campylinae, including *Leptodictyum*, *Campylium*, and *Campyliadelphus*; and Anacamptodinae subtribe nov., including *Serpoleskea*, *Anacamptodon*, and *Hygrohypnum luridum*. Amblystegieae also include two subtribes: Drepanocladinae (Kanda) stat. nov., including *Cratoneuropsis*, *Drepanocladus* s.str., *Pseudo-calliergon* and, tentatively, *Gradsteinia*; and Amblysteginae, including *Hypnobartlettia* and *Amblystegium*.

The infra-familial classification of Amblystegiaceae presented here contrasts with the traditional definition of the two subfamilies, Calliergonoideae, including *Calliergon* s.l. (thus including *Pseudo-calliergon* and related genera); see, e.g., Smith, 1978; Corley & al., 1981) and Drepanocladoideae, including *Sanionia*, *Drepanocladus* s.l., and *Scorpidium* (see, e.g., Kanda, 1976; Tuomikoski & Koponen, 1979; Shlyakov, 1989). The present results provide strong support for the hypotheses that *Pseudo-calliergon trifarium* and *P. turgescens* should be removed from *Calliergon* and *Scorpidium*, respectively (Hedenäs, 1989b), and that *Drepanocladus* s.str. and *Pseudo-calliergon* (sensu Hedenäs, 1990b) form a well supported clade, sister to *Amblystegium* and *Cratoneuron*. The genus *Scorpidium* (sensu Hedenäs, 1989b) is closely related to the *Calliergon*-*Warnstorfia* complex.

Within *Amblystegium*, the genus *Hygroamblystegium* Loeske, including *H. fluviatile* (Hedw.) Loeske, *H. tenax* (Hedw.) Jenn. and sometimes *H. varium* (Hedw.) Mönk. (Buck, 1998), has been distinguished from *Amblystegium* based on costal characters and habitat, but must be rejected. Indeed, recognition of *Hygroambly-stegium* would lead *Amblystegium* to be paraphyletic. *Amblystegium humile* (P. Beauv.) Crundw., which has been transferred into the genus *Leptodictyum* (Ochyra, 1981; followed by Anderson & al., 1990) due to the existence of populations showing distinctly complanate habit, is clearly a member of *Amblystegium*. The nomenclatural combination, *A. humile*, made by Crundwell (1981), should therefore be adopted.

Amblystegium tenax var. *spinifolium* (Schimp.) H.A. Crum & L.E. Anderson (*Amblystegium irriguum* var. *spinifolium* Schimp.), a segregate of *A. tenax* distinguished by strong, excurrent costa (Crum & Anderson, 1981), appeared nested in the present analyses within *Cratoneuron*. A study of the type material of

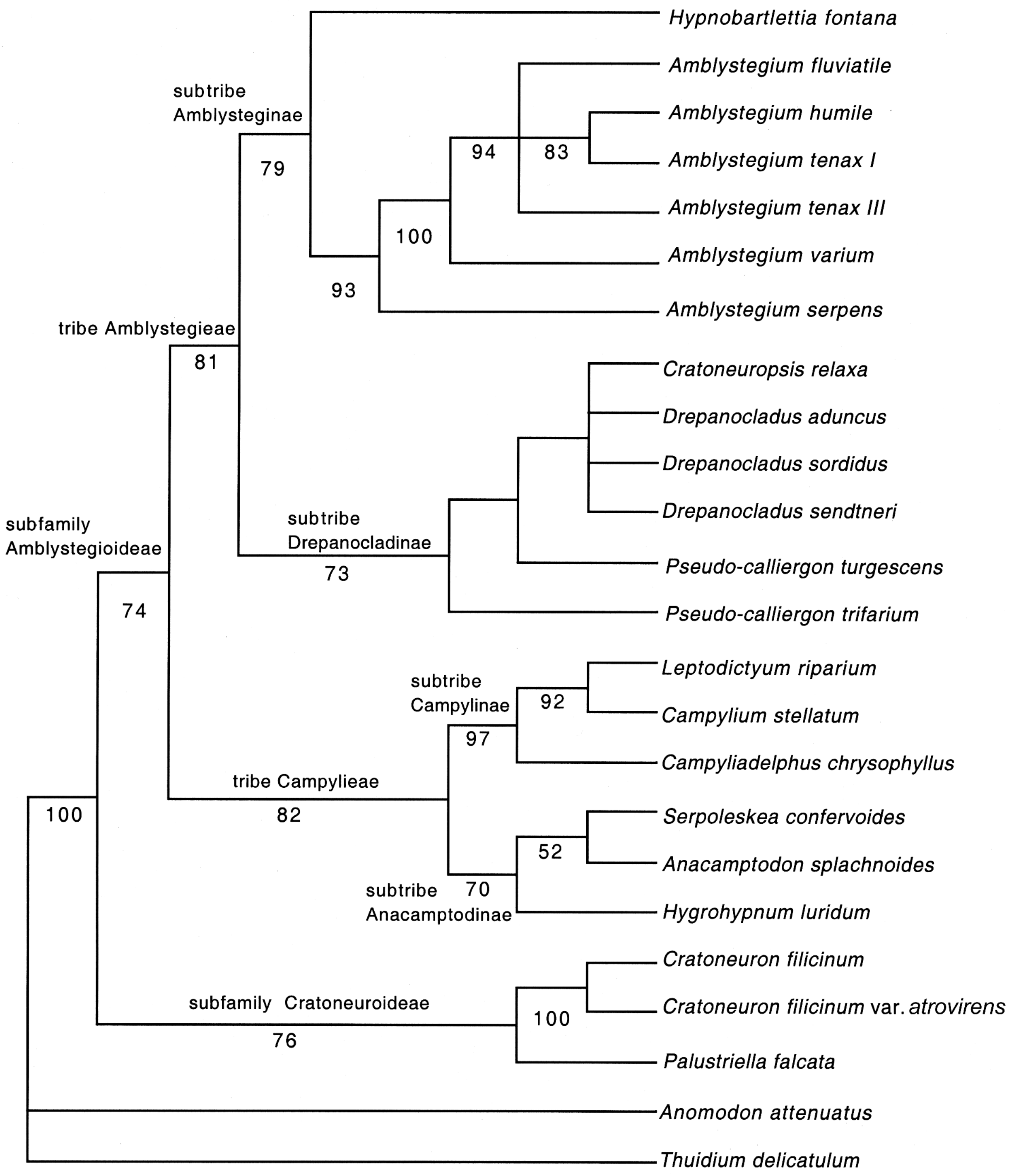

Fig. 2. Strict consensus tree of eight equally parsimonious trees (L = 412, CI = 0.59, RI = 0.71) for 22 taxa of Amblystegiaceae from the combined molecular and morphological partitions using *Anomodon* and *Thuidium* as outgroups. Numbers below the branches are the bootstrap support percentages >50%.

Amblystegium irriguum var. *spinifolium* revealed that it belongs to *Cratoneuron filicinum* based on the presence of a few inflated alar cells, though considerably smaller than in the terrestrial expression of the species, and the fine serrulation of the laminar border. The phenotype of *Amblystegium tenax* var. *spinifolium* differs strongly

Table 1. Synopsis of classification of Amblystegiaceae. Characters listed are resolved morphological synapomorphies for each group (when known).

Amblystegiaceae G. Roth emend. Vanderpoorten & al.

Subfamily **Cratoneuroideae** (Mönk.) Vanderpoorten & al., **stat. nov.** [Basionym: family Cratoneuraceae Mönk. in Pascher, Süsswasserflora 14: 116. 1914. Type genus: *Cratoneuron* (Sull.) Spruce]. Basal alar cells thin-walled; alar cells ontogeny of "exannulata-kind" (see Hedenäs, 1987); decurrent leaves; large spores.

Cratoneuron (Sull.) Spruce (incl. *Callialaria* Ochyra and *Amblystegium tenax* var. *spinifolium* (Schimp.) H.A. Crum & L.E. Anderson). Costa percurrent to excurrent; axillary hairs few per leaf axil.

Palustriella Ochyra. Stem leaves longitudinally plicate; laminal cells narrow, distally prorate; warty-papillose rhizoids.

Subfamily **Amblystegioideae** [Type genus: *Amblystegium* Schimp.].

Tribe **Campylieae** (Kanda) Vanderpoorten & al., **stat. nov.** [Basionym: family Amblystegiaceae subfamily Campylioideae Kanda, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 15: 250. 1976. Type genus: *Campylium* (Sull.) Mitt.].

Subtribe **Campylinae**. Type genus: *Campylium* (Sull.) Mitt. Cilia appendiculate.

Campyliadelphus (Kindb.) R.S. Chopra. Leaves decurrent; margin of inner perichaetial leaf shoulder ciliate; exostome margin entire to slightly dentate.

Campylium (Sull.) Mitt. Pseudoparaphyllia narrow; leaves squarrose, ecostate; basal alar cells inflated; axillary hairs numerous per leaf axil; costa of inner perichaetial leaves short.

Leptodictyum (Schimp.) Warnst. Plants monoecious; pseudoparaphyllia narrow.

Subtribe **Anacamptodinae** Vanderpoorten & al., **subtrib. nov.** [Diagnosis: Campylinae similes sed ciliis non appendiculatis et peristomio saepe deminuto]. Type genus: *Anacamptodon* Brid.

Serpoleskea (Limpr.) Warnst. Leaves ecostate; laminal cells short; stem central strand absent; costa of inner perichaetial leaves short.

Anacamptodon Brid. Laminal cells short; capsules erect; lid rostrate, separating annulus absent; exostome teeth reflexed when dry; basal membrane of endostome low; endostome cilia vestigial or absent.

Hygrohypnum Lindb. s.str. [including the type species, *H. luridum* (Hedw.) Jenn., but excluding a number of other species previously accommodated in the genus]. Leaves secund; spores large.

Tribe **Amblystegieae**. Type genus: *Amblystegium* Schimp.

Subtribe **Drepanocladinae** (Kanda) Vanderpoorten & al., **stat. nov.** [Basionym: family Amblystegiaceae subfamily Drepanocladoideae Kanda, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 16: 47. 1977. Type genus: *Drepanocladus* (Müll. Hal.) G. Roth. Morphological synapomorphies: plants dioecious; axillary hairs numerous per leaf axil; inflated, linear to shortly rectangular basal alar cells.

Cratoneuropsis (Broth.) M. Fleisch. Leaves squarrose; basal laminal cells of stem leaves longer than median laminal cells; paraphyllia present; rhizoids warty-papillose; margin of inner perichaetial leaves entire; cilia appendiculate; exothecial cells collenchymatous.

Drepanocladus (Müll. Hal.) G. Roth. Leaves secund; cilia appendiculate.

Gradsteinia Ochyra (This genus is only tentatively included due to the limitation of our data).

Pseudo-calliergon (Limpr.) Loeske.

Subtribe **Amblysteginae**. Type genus: *Amblystegium* Schimp.

Amblystegium Schimp.

Hypnobartlettia Ochyra. Costa percurrent to excurrent; leaf lamina bistratose.

Calliergonaceae (Kanda) Vanderpoorten & al., **stat. nov.** [Basionym: subfamily Calliergonoideae Kanda, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 16: 79 (1976). Type genus: *Calliergon* (Sull.) Kindb.]. Alar cells inflated.

Calliergon (Sull.) Kindb.
Hamatocaulis Hedenäs
Loeskypnum H.K.G. Paul
Straminergon Hedenäs
Warnstorfia Loeske

from that of the traditional expression of *Cratoneuron filicinum* in possession of long lanceolate stem leaves, very sparse paraphyllia, and few reduced alar cells. Inflated alar cells constitute a character state strongly correlated with swampy habitats (Vanderpoorten & al., in press) but are lost by marshy species when grown totally submerged (Zastrow, 1934). Therefore, the phenotype of this taxon is interpreted in terms of morphological convergence with *Amblystegium tenax* under rheophilous conditions. *Amblystegium tenax* var. *spinifolium* perfectly matches the circumscription of *Cratoneuron filicinum* var. *atrovirens* (Brid.) Ochyra (Ochyra, 1989). *Amblystegium tenax* var. *spinifolium* must therefore be reduced into synonymy with *Cratoneuron filicinum*.

At the species and population level, the present results suggest, together with previous results from AFLP markers (Vanderpoorten & Tignon, 2000), that *Amblystegium* forms a genetic complex whose morphological expression is variable and labile. ITS sequence data suggest that *A. tenax* is polyphyletic (Vanderpoorten & al., 2001). Taxonomic reassessment within this complex is therefore premature, and hence Ochyra (1998) was not followed in accommodating *A. varium* in its own genus *Orthotheciella* Ochyra, since the results of the present study do not support such an arrangement.

MORPHOLOGICAL CHARACTERIZATION OF AMBLYSTEGIACEAE

Morphological ancestral character states were reconstructed to identify the synapomorphies of each clade. Synapomorphies were inferred from a study of morphological evolution using maximum likelihood reconstruction of ancestral character states (see Vanderpoorten & al., in press, for details), which approach allows the assessment of the accuracy of the estimates, and takes branch lengths into account (see Schluter & al., 1997; Cunningham, 1999). When a character had an equal probability to be at either state at a node, it could not be determined along which internode the change in state actually occurred; hence the reconstruction was ambiguous and the synapomorphy could not be defined.

The recircumscribed Amblystegiaceae, and also several clades within the family, are undefined by synapomorphies based on the suite of morphological characters studied. Hence, a typical diagnosis of these clades is not possible. At present, the characters that define these taxa are all molecular. Dealing with well supported clades based on molecular data without being able to provide morphological synapomorphies is an increasing problem in taxonomy (Swann & al., 1999). Here, we attempt a necessarily imprecise morphological diagnosis of Amblystegiaceae and several infra-familial taxa and suggest that our results provide a framework for additional morphological studies.

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