Preface

The application of cladistic analysis and molecular data to the study of relationships of organisms has resulted in a revolution in the systematics of many groups of organisms, not least the mosses. We can now propose hypotheses about relationships in an objective manner, and use topologies resulting from analyses to ask questions about the evolutionary processes underlying the observed patterns. At the same time, there has been a paradigm shift, from the traditional, knowledge-based and synthetical methodology, where individuals "knew" the organisms and suggested classifications on that basis, to a data-based, analytical methodology where matrices of characters (molecular or morphological) are assembled and analysed using computers. Although morphological data and the older methods have been responsible for a very large proportion of our current knowledge at all taxonomic levels, some conclusions based on these have been erroneous, and other problems have proved intractable. The circumscription and relationships of the pleurocarpous mosses present a major example where traditional data have accomplished much but also leave much to be desired.

The symposium on pleurocarpous mosses held at Cardiff in September 2004 provided an opportunity for many of the researchers active in the systematics of this group to meet and present the results of their studies. This event was held approximately ten years after the publication of the first major attempt (by Lars Hedenäs, in 1994) to study the relationships of pleurocarpous mosses using cladistic methodology, and gives a broad overview of the progress in our understanding of the relationships of the pleurocarpous mosses. In particular, this book draws on both molecular data and morphology (including morphology of molecules), and synthetical and analytical methodology, to highlight the areas of the pleurocarp phylogeny where there is some resolution, and to identify the regions where there are still intriguing questions to be addressed.

In the introductory chapter, Bill Buck reviews the history of pleurocarp classification, identifying a cyclical pattern in the philosophical principles underlying efforts to resolve the classification of the pleurocarps, which revolved around the relative importance of the gametophyte and sporophyte generations as sources of characters. He notes that the classification of pleurocarpous mosses has traditionally lagged behind that of acrocarps (which is a reflection of the morphological diversity and distinctness of the acrocarp groups, in contrast to the morphological plasticity and close relationships of the pleurocarps). In one of the earliest classifications of mosses, based on sporophyte characters, Hedwig included 30 genera of acrocarps but only five genera of pleurocarps, despite the very similar number of species now recognized in these divisions. Subsequently classifications have alternated between emphasizing gametophyte and sporophyte characters, but the advent of molecular data has allowed bryologists to present classifications independent of morphology. Although initial work using one-gene trees resulted in faulty classifications, multiple-gene trees have refined the process. However, the Hypnales, the largest group among the mosses and a key pleurocarp group, still lacks phylogenetic resolution. A combination of multiple genes with carefully observed morphology should provide us with a stable classification.

The two following chapters explore the relationships of the earliest-diverging lineages of mosses in which pleurocarpous morphology appeared, emphasizing molecular and morphological data, respectively. The majority of taxa in this region of the phylogeny, including the rhizogonian and hypnodendroid mosses, have a primarily Gondwanan distribution centered in Oceania, and represent only about 1% of the species in the pleurocarpous mosses. Terry O'Brien investigates the distribution of the phylogenetic diversity in pleurocarpous mosses through an analysis of a four-gene cpDNA dataset of 58 exemplar taxa. The results indicate that pleurocarpous and non-pleurocarpous members of the Rhizogoniaceae plus the acrocarpous genera *Aulacomnium*, *Calomnion* and *Orthodontium*

Participants at the symposium on Pleurocarpous Mosses: Systematics and Evolution. Group photo taken on the steps of the National Museum of Wales, Cardiff, September 2004, by Misha Ignatov. From left to right: Niklas Pedersen; Lars Hedenäs; Philip Stanley; Ray Tangney; Gisela Oliván; Anastasia Gardiner; Terry O'Brien; Alan Orange; Bill Buck; Sean Russell; Neil Bell; Brian O'Shea; Dolores Gonzalez; Liz Kungu; Angie Newton; Boon-Chuan Ho; Efrain De Luna; Hans Kruijer; Rolf Blöcher; Yelitza León-Vargas; Roy Perry; Katherine Vint; Sanna Huttunen; Nancy Slack; Dietmar Quandt.

are the sister group or near sister group to the hypnodendroid pleurocarps and the Hypnidae (Hypnobryales, Hookeriales and Ptychomniales). These results highlight a marked asymmetry in the phylogenetic distribution of diversity of pleurocapous mosses similar to that found in angiosperms. Looking at the diversity of morphology in these taxa, Neil Bell and Angela Newton examine modular branching structure in exemplars from the rhizogoniaceous grade, in order to isolate discrete architectural types associated with the pleurocarpous condition. These are described and used as a basis for optimization of pleurocarpy *sensu stricto* onto a phylogeny derived from chloroplast and mitochondrial molecular sequence data. Characters closely associated with pleurocarpy in these taxa are also optimized, and the results used to examine scenarios for the evolution of modular form in the basal pleurocarpous clades. The results reveal that there is disproportionate diversity of pleurocarpous architectural types in the rhizogoniaceous grade compared with the hypnodendroid pleurocarps and the Hypnidae, and that these probably represent successive and varied novel adaptive strategies that utilize the potential of the key innovation of pleurocarpy.

Another clade with a position among the early-diverging lineages of pleurocarpous mosses, with affinities to the Hookeriales, is the family Hypopterygiaceae, comprising 21 species distributed among seven or eight genera. These are characterized by a distinctive leaf arrangement and a diversity of branching architectures. In Chapter 4, Hans Kruijer and Rolf Blöcher give an overview of systematic studies in the family and present a phylogenetic study of relationships within the family using a combination of morphological and molecular data. Although their results, based on molecular data for 15 species of Hypopterygiaceae and nine species of related families, show support for monophyly of the family, the traditional circumscription of some of the genera needs to be reviewed. The authors consider that the homoplasy of the morphological characters suggested by the molecular data requires a new view of the morphology and that increased sampling will produce a fuller understanding of the evolutionary history of the family, resulting in a new generic classification of the Hypopterygiaceae. In Chapter 5, Boon-Chuan Ho and Hans Kruijer report on the plasticity of growth patterns in *Calyptrochaeta*, a small genus in the Hookeriaceae (Hookeriales) that grows mainly on decaying wood and tree bases in wet tropical mountain forests in Malesia and adjacent areas. These species display two different growth patterns in which there is no clear differentiation into axes of different hierarchical levels. These growth patterns are characterized by orthotropic axes and sympodial (basal) innovations, and by long plagiotropic axes showing indeterminate growth and monopodial branching. However, observations suggest that the plagiotropic growth pattern represents a character state derived from the orthotropic one, and that their striking difference should not be overestimated in taxonomic research on *Calyptrochaeta*.

In the following section, Chapters 6 to 10 present the results of analyses, primarily of molecular data and using a variety of analytical techniques, to explore the relationships of families within the Hypnales. This group represents about 80% of the pleurocarpous moss species (and a third of all extant moss species) but relationships within and between the families are very poorly known. Sanna Huttunen, Anastasia Gardiner and Michael Ignatov review progress in understanding the Brachytheceaceae, one of the most diverse groups of mosses. Although a backbone phylogeny of the Brachytheciaceae has been suggested, problems remain with some groups. They present new data with additional species, utilizing POY alignment and analysis of the secondary structure of *trn*L intron. Their results highlight extensive parallelisms in the morphology of major lineages associated with ecological specialization. Most lineages within the family have subaquatic members with morphologies convergent across lineages in characters such as leaf shape, leaf orientation and costal structure. Similarly a tendency to epiphytism across lineages has led to homoplasy in peristome morphology. The authors address these repeated patterns of extreme ecological divergence and whether the divergent morphologies of these taxa should be reflected in paraphyletic genera. In the following chapter, Sanna Huttunen and Dietmar Quandt synthesize results from four phylogenetic analyses of the moss family Meteoriaceae and review the current generic relationships within the family. Phylogenies are used to evaluate morphological evolution within the family and to pinpoint the synapomorphies of the major clades. Previous classifications of the Meteoriaceae are seen to be characterized by extensive homoplasy of morphological, particularly cellular, characters. Although more extensive future sampling will be needed to test monophyly of the genera, at the subfamily level major divisions in the family are recognized, including a new subfamily. Important morphological features at this level are orientation of stem leaves and characters of the axillary hairs and peristome. The Trachypodaceae, long associated with the Meteoriaceae, is resolved as a grade basal to the Meteoriaceae.

The Amblystegiaceae have been traditionally circumscribed by their mostly single and long leaf costa, cylindrical and curved spore capsule, and their preference for humid to wet environments. Lars Hedenäs and Alain Vanderpoorten examine the suggestions of late twentieth century studies, analysing comprehensive morphological datasets, that radical reclassification among the Amblystegiaceae was necessary. They found that phylogenetic studies based on both molecular and morphological data resolved many relationships at the generic level and provided strong evidence that the family should be split into the Amblystegiaceae *s. str.*, with the taxa related to *Amblystegium*, *Campylium*, *Drepanocladus*, and *Palustriella*, and the Calliergonaceae, with the taxa around *Calliergon*, *Scorpidium*, and *Warnstorfia*. However, many relationships within the two families and their genera remain uncertain. For example, within *Hygroamblystegium* morphological and molecular evolution appear to be uncoupled, suggesting that several currently recognized morpho-species should be synonymized. A team headed by Michael Ignatov, again using a diversity of analytical methods and data, focuses in Chapter 9 on taxa traditionally classified in the Leskeaceae to reassess the relationships of mosses in the order Hypnales. They identify a basal grade and two main clades, and analyse the circumscription and changes in these and subclades under the different analytical methods. The split between Amblystegiaceae *s. str.* and the Calliergonaceae is again found by these authors although the taxon distribution is not identical. The Leskeaceae as traditionally circumscribed are not monophyletic but found in both main clades. Interestingly, the two main clades have some similarities to the traditional classification of pleurocarpous mosses into Leucodontales and Hypnales, a classification abandoned when earlier analyses of molecular data showed that the epiphytic leucodontalean taxa had been derived repeatedly from within the Hypnales. Relationships within the family Amblystegiaceae are examined in greater detail in Chapter 10, where Gisela Oliván, Lars Hedenäs and Angela Newton use molecular data to explore the phylogeny of *Hygrohypnum* and related taxa. Their results reveal the polyphyly of the genus and demonstrate that the morphological characters traditionally used to circumscribe the genus may reflect convergence. Within the genus there is strong support for two major clades, one with *Hygrohypnum styriacum* and *H. luridum* (the type of the genus) and the two species included as representatives of Amblystegiaceae *s. str.*, while the other clade includes the remaining species of the genus plus *Platydictya jungermannioides*, *Campylophyllum halleri* and the two taxa chosen as representatives of Calliergonaceae, *Calliergon cordifolium* and *Warnstorfia exannulata.* These chapters have gone a long way towards suggesting some major relationships within the Hypnales, but large numbers of taxa are involved and many important families are barely represented. In order to adequately assess relationships of the remaining taxa, additional projects at a similar scale will be required.

Morphology has been the primary source of information regarding pleurocarpous moss relationships in the past approximately 200 years, but has also undergone something of a revolution with the advent of cladistic methodology and the necessity to examine characters in sufficient detail to include them in data matrices. In Chapters 11 to 15 morphological character systems are explored in some depth. Lars Hedenäs, provides a review of morphological characters and their use in pleurocarpous moss systematics. The strategy of using a few "key characters," while highly successful in many groups of organisms, has been distinctly misleading in the pleurocarpous mosses with their high levels of plasticity and parallel evolution of features. Only relatively recently have numerous and more obscure characters been studied systematically in numerous species. He outlines how in the last 20 years cladistics and the inclusion of molecular data for phylogenetic reconstruction have revolutionized our understanding of pleurocarpous moss relationships. As molecular information is largely independent of morphology, the reliability of the latter in reconstructing relationships can now be assessed. He notes that relationships that are well supported by molecular data are frequently suggested by morphology, but that morphology yields more ambiguous results than molecular data, most likely due to incorrect interpretations of homology. The latter is especially serious for taxa with orthotropous (earlier called "erect"), specialized spore capsules. However, morphology sometimes reveals relationships that have not yet been resolved by molecular data. Hedenäs concludes that molecular phylogenies can be fully interpreted only in the light of structural similarities or differences between taxa.

Morphological characters used to delimit taxa within the African Entodontaceae are reevaluated by Elizabeth Kungu and Royce Longton. Characters available in both the sporophyte and gametophyte are described and assessed in the light of the restrictions incurred due to morphological reduction. Gametophyte structures are examined for characters to reinforce the taxonomic boundaries based on peristome ornamentation patterns which provide key characters for delimiting both genera and species within the Entodontaceae. However, the use of peristome ornamentation patterns is confounded by the high level of variation associated with peristome reduction. Examination of internal peristome structure demonstrates a relationship with function and proves that the major differences in surface ornamentation between papillose and striate reflect a difference in internal deposition. Morphology indicates that the family as currently recognized is probably not monophyletic and the status of *Pylaisiobryum* is unresolved.

The homologies of stem structures in pleurocarpous mosses, especially pseudoparaphyllia and similar structures are revisited in Chapter 13 by Michael Ignatov and Lars Hedenäs, where they give an overview of current definitions of different stem structures in pleurocarps. Paraphyllia are usually considered as organs not concentrated around branch initials, but their observations reveal that positional and structural homologies in "paraphyllia" and "pseudoparaphyllia" suggest that the distinctions between paraphyllia, pseudoparaphyllia and proximal branch leaves remain unclear. A set of characters for the description of the diversity of foliose structures found at the base of branches or around branch initials is suggested, replacing the commonly generalized character of pseudoparaphyllia absence versus presence. The two following chapters (14 and 15) examine specific aspects of the branching structure of pleurocarpous mosses. Angela Newton discusses the history and application of the concepts of acrocarpy and pleurocarpy, and the implications of these features for the exploitation of morphological characters in the systematic study of pleurocarpous mosses. The necessity of "deconstructing" branching architecture into modules is emphasized. The components of branching architecture are analysed, described and figured, including case studies of individual species. Ray Tangney emphasizes structural concepts and examines the way in which architectural terms, as used in the analysis of Tracheophytes, have increased our understanding of branching in mosses. He differentiates between monopodial and sympodial growth and discusses repeated growth units. The concept of the architectural unit, not previously applied to mosses, is utilized to help recognize both the type of branching and the hierarchical level at which branching is occurring, aspects of branching analysis that have had insufficient emphasis. In doing so, differences are highlighted between sequential growth (branching that builds architectural units), and reiterative growth (growth that repeats the architectural units).

The origins of pleurocarpous mosses are explored in Chapters 16 and 17, using fossil and molecular data. Reviewing Paleozoic and Mesozoic fossil mosses, Michael Ignatov and Dmitry Shcherbakov address the question of whether pleurocarpous mosses originated before the Cretaceous. They found that some Paleozoic, Triassic and Jurassic fossils are similar to extant pleurocarps in some respects, but that other peculiarities of these fossil mosses make their immediate placement in extant groups problematic. They describe a new genus and species from the Upper Jurassic of Transbaikalia, concluding that this species is probably the fossil most similar to extant pleurocarps among pre-Cenozoic fossils. This new fossil corroborates the conclusions of the team headed by Angela Newton and Niklas Wikström, who explore the patterns of diversification of the pleurocarps and estimate possible dates for their origins using molecular data, calibrated on the fossil date of 450 myr for the origin of land plants. Their results suggest that the earliest-diverging extant lineages in which pleurocarpy is found originated in the mid Jurassic (at 194–161 mya), significantly before the period in which the majority of the extant lineages diversified (about 165–131 mya), probably over a (geologically) short period of time. This radiation coincides with the diversification of the angiosperms in the early Cretaceous and is earlier than the period in which angiosperm forests came to dominate the terrestrial environment in the early Cenozoic, suggesting that pleurocarpous mosses were well established before the appearance of the highly structured forests that now exist.

In the final two chapters evolutionary questions are explored. Niklas Pedersen and Angela Newton use Bayesian inference and maximum likelihood methods, with chloroplast and mitochondrial DNA sequence data, to evaluate phylogenetic relationships within the Ptychomniales. The genus *Glyphothecium* was found to be polyphyletic, and a new genus described. They then use the resulting topology to study evolution of 18 morphological characters, and to test whether the evolution of dwarf males is correlated with morphological variation and the epiphytic habit. Reconstructions of morphological characters using maximum parsimony and maximum likelihood are mostly congruent although maximum likelihood reconstructions indicate high uncertainties at most internal nodes. Correlation tests suggest that the evolution of dwarf males is significantly correlated with twelve of the morphological characters studied. In addition, the correlation tests indicate that the presence of dwarf males may promote morphological evolution.

Continuing the theme of comparison between pleurocarps and angiosperms, in Chapter 19 Ray Tangney examines the distribution patterns of pleurocarpous mosses in the Australasian region. His analysis reveals patterns, also known for angiosperms, that form a network of general distribution tracks and highlight different areas within the region. The combination of this general pattern of distribution with vicariance, the spatial separation of closely related taxa, emphasizes a relationship between taxa and localities stronger than that expected if long-distance dispersal was a major determining factor in forming distributions. This suggests a major role for allopatric evolution, and a distinction is drawn between the timing of the origin of taxa and the time of the origin of the ancestral range. He concludes that differentiation of taxa may occur at different times within ancestral ranges and therefore that taxa of different ages and taxonomic levels may share the same present-day distribution through congruence of ancestral ranges and interaction with regional geological and ecological processes.

Many important families of pleurocarpous mosses could not be included in this symposium, either because they have not been studied in sufficient depth, or through logistical constraints. The sheer size of the pleurocarpous moss clade, combined with the apparent rapid diversification of a large number of individual lineages, makes resolution of the relationships in this group a formidable task. The evidence presented here for the homoplastic nature of many of the morphological characters traditionally used to recognize and circumscribe many of the taxa, especially families, would seem to indicate that use of morphology as a source of systematic data is doomed. Yet at the same time it is evident that by careful examination and critical evaluation of characters, a great deal of useful information can be obtained, that is both interesting in its own right, and as a source of data for systematic and evolutionary studies. Further resolution of the relationships of the pleurocarpous mosses, although challenging, seems to be achievable. As in this symposium volume, building from both directions — dense sampling for genus and family level studies, combined with "backbone" analyses of broadly sampled regions of the topology — will allow us to resolve the relationships of the pleurocarpous mosses, and at the same time, explore some very interesting questions.

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