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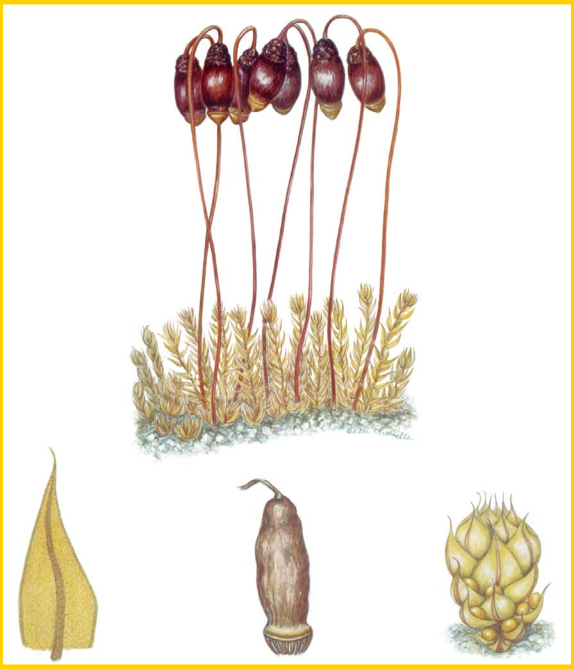

Introduction to Mosses

H.P.Ramsay

INTRODUCTION TO MOSSES

Helen P. Ramsay[1]

Classification

Before the late-eighteenth century, the nature of bryophytes and their relationships to the rest of the Plant Kingdom were poorly understood. Although Carl Linnaeus (1707–1778) described eight genera of mosses (Linnaeus, 1753), only *Sphagnum* survives in modern bryophyte systematics. Johann Hedwig (1730–1799) interpreted the functions of antheridia, archegonia and the sporophyte, including the peristome, and his use of microscopic as well as macroscopic characteristics greatly influenced subsequent bryophyte systematics and taxonomy. Hedwig provided a well-illustrated and essentially complete and accurate account of the bryophyte life history (see Schofield, 1985), and his *Fundamentum* (Hedwig, 1782) included descriptions and illustrations of many taxa. Using three characters — the presence or absence of peristome, the form of the male inflorescence, and the form of peristome — Hedwig distinguished 25 moss genera, later expanded to 35, this work being published posthumously as *Species Muscorum Frondosorum* (Hedwig, 1801). Hedwig's herbarium was later acquired by Christian Friedrich Schwägrichen (1775–1853) who published many additional moss names (Schwägrichen, 1811–1842). Margadant (1968) has provided a detailed review of early theories of sexuality in bryophytes and bryophyte relationships.

The concept of alternation of gametophytic and sporophytic generations was first clearly documented by Wilhelm Hofmeister (1851). Wilhelm Schimper (1808–1880) contributed to an understanding of European bryology, including a significant advance in interpreting the taxonomy of *Sphagnum* (Schimper, 1856). During this period, Johann Karl (Carl) August Müller (1818–1899) published extensively on mosses, dividing them into three classes: Schistocarpi (having capsules with longitudinal valves), Cleistocarpi (capsules without an operculum) and Stegocarpi (capsules with an operculum). He further divided Stegocarpi into Acrocarpi and Pleurocarpi in his *Synopsis Muscorum Frondosorum* (Müller, 1848–1851).

With the recognition of the inflorescence characters (principally the sporophyte as it is recognised today) and the elucidation of the structure of the peristome (endostome, exostome and horizontal, basement membrane), peristome structure and sexuality became accepted as being of greater diagnostic importance than gametophyte characters such as habit, leaves and branching patterns. A key to 33 British genera was produced by Hooker & Taylor (1818) based on the peristome, the position of the sporophyte and calyptra form. Other researchers continued to give sporophytic characters prominence, and the terms acrocarpi (terminal sporophyte) and pleurocarpi (lateral sporophyte) were introduced by Bridel (1818) as primary character states in true mosses. Bridel (1826, 1827) recognised 91 genera of acrocarpous and 31 genera of pleurocarpous mosses.

Classifications began to follow what was called a 'Natural System', e.g. Bridel recognised a hierarchical system of classes, orders and families. Müller (1848–1851) and Schimper (1856) separated cleistocarpous and stegocarpous mosses while also recognising acrocarpi and pleurocarpi. Schimper, although largely unrecognised for his contribution, was the first to introduce the concept of families of bryophytes in the modern sense (Buck & Crum, 1990).

William Mitten emphasised peristome characters, dividing true mosses into Arthrodonti (with a peristome of two parts: an external layer of 16 articulated cells and an internal layer comprising a folded membrane) and Nematodonti (with a peristome of non-articulated

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[1] c/- National Herbarium of New South Wales, Royal Botanic Gardens and Domain, Mrs Macquaries Road, Sydney, New South Wales 2000.

filaments) (Mitten, 1859). He was critical of Bridel's and Schimper's use of growth form characters, noting that in some genera (e.g. *Fissidens*) the sporophyte might be borne on various parts of the stem.

Significant advances in moss nomenclature and classification were made by Max Fleischer (1861–1930) in *Die Musci Flora von Buitenzorg* (Fleischer, 1900–1923). Meanwhile, Viktor Brotherus (1849–1929) refined Fleischer's classification in *Die Natürlichen Pflanzenfamilien* (Brotherus, 1901–1909, 1924–1925) which remains the only attempt to treat all known families, genera and species of mosses, i.e. a global flora. The number of moss genera rose to 660 in the time of Brotherus, with the acrocarps accounting for 43 per cent of species and the pleurocarps 57 per cent (see Buck & Crum, 1990). Many bryologists (e.g. Grout, 1928–1940 for North America; Sim, 1926 for South Africa) have followed the classifications of Fleischer and Brotherus (see Vitt, 1984).

A paper by Henri Philibert on peristome structure (Philibert, 1884) had a profound impact on moss classification, especially following its translation into English (Taylor, 1962). Philibert recognised Mitten's (1859) terms 'nematodontous' and 'arthrodontous' as the two primary types of peristome. He further divided the arthrodontous peristomes into haplolepidous and diplolepidous types based on the origin of the peristome layers.

Peristome attributes have been used widely as the basis for moss classification because they reflect phylogeny (Dixon, 1932; Crosby, 1974, 1980; Vitt, 1984; Vitt *et al.*, 1998). Modern classifications are based on "…what might be called the Philibert-Dixon principle: in constructing a classification of mosses primary weight should be given to characters of the sporophyte particularly the peristome; mosses with similar gametophytes but different peristomes must not be grouped together with mosses that have similar peristomes…" (Crosby, 1974). Peristomial characters are valuable in phylogenetic speculation, and basic developmental patterns in moss peristomes are reliable indicators of higher systematic relationships, probably above the rank of family (Buck, 1991; Goffinet & Buck, 2004). However, a strong reliance on peristomial attributes and superficial morphology is inappropriate for pleurocarpous families where gametophytic characters are more reliable and provide a more stable basis for familial classification (Buck, 1991; Hedenäs, 1998). The position of the perichaetium and sporophyte, as used by Bridel and Schimper, appears to represent parallel evolution, as pleurocarpous forms occur among acrocarpous taxa. Capsule dehiscence as a taxonomic character (Müller, 1848–1851) has been shown to be artificial with cleistocarpous forms occurring in a number of unrelated taxa, this being an adaptive response to xeric habitats (Vitt, 1984).

Detailed morphological and Scanning Electron Microscopy (SEM) studies have facilitated a more accurate interpretation of peristome structure (Edwards, 1984) and have added considerably to the understanding of intra- and interspecific variation (e.g. Vitt, 1984; Shaw, 1985a, b; Shaw *et al.*, 1987; Lewinsky, 1989, 1990; Bruggeman-Nannenga & Berendson, 1990; Bruggeman-Nannenga & Roos, 1990, Buck & Goffinet, 2000).

The first systematic arrangements of genera, families and orders since Brotherus were based on refined taxonomic concepts using evidence from peristome morphology (Edwards, 1984) as well as analysing other data such as gametophyte structure using cladistic methods (Vitt, 1982a, 1984). The classification of pleurocarpous mosses has been further reviewed by Buck & Vitt (1986) and Hedenäs (1994, 1995, 1996a, 1996b, 1998). More recent studies by Vitt *et al.* (1998), Buck & Goffinet (2000) and Goffinet & Buck (2004) have incorporated additional molecular and morphological data to develop more accurate phylogenies for the mosses.

Data from other techniques have also being used to clarify relationships: electrophoresis (Wyatt *et al.*, 1989b, 1993; Stoneburner *et al.*, 1991b); cladistic analysis (Vitt, 1984; Buck & Vitt, 1986; Buck, 1993; Hedenas, 1994, 1995, 1996a, 1996b, 1996c, 1998; Goffinet & Buck 2004); molecular techniques (Mishler *et al.*, 1992; Goffinet & Buck, 2004); ultrastructural studies (Duckett, 1986; Duckett & Renzaglia, 1988; Ligrone & Gambardella, 1988; Brown & Lemmon, 1993); cytogenetics, reproduction and population genetics (Newton, 1984a, 1988; Wyatt & Anderson, 1984; Wyatt *et al.*, 1993; Newton & Mishler, 1994; Wyatt, 1994; Cove, 2000); and chemotaxonomy (Mues, 1990, 2000; Zinsmeister & Mues, 1990).

Cladistics has shown that many genera and families are polyphyletic rather than monophyletic as was previously assumed. This has led to new concepts of individual families, genera and species, e.g. in Orthotrichaceae (Goffinet & Vitt, 1998) and Pottiaceae (Zander, 1993). The recent improvement in techniques for extracting, amplifying and sequencing DNA from fresh as well as older herbarium material has enabled the analysis of chloroplast, mitochondrial and nuclear DNA and the use of increasing numbers of different loci.

Enthusiasm for new molecular tools and techniques of analysis should not, however, mean the abandonment of older, well-established methods. While most studies are rigorous in confirming the identity of specimens sampled, errors can result in inconsistencies between studies. These can be traced to, for instance, the misidentification of herbarium collections, e.g. *Mittenia* in Goffinet *et al*. (2001), while errors in checking the matrix in which the *rps*4 sequence for *Pleurophascum* was incomplete led to this genus being mistakenly transferred to the Bryales (Buck & Goffinet, 2000; Goffinet *et al.*, 2001). There is still considerable debate as to whether molecular or morphological features are inherently better sources of information for estimating phylogeny (Goffinet *et al.*, 2004b). According to Goffinet & Buck (2004), "…it is, indeed, the history of morphological transformation that defines taxa or of the distribution ranges of the species that justify the investment into phylogenetic approaches. A revival of critical morphological and anatomical studies is, however, imperative if major clades are to be diagnosed by characters rather than their genomes."

In bryophyte classification, the dilemma has always been to determine the relative importance of the gametophyte and sporophyte generations, and this is influenced by interpretations of evolutionary processes. Thus, for example, parallel evolution resulting from adaptation might result in similar features occurring in unrelated taxa (Vitt, 1981; Hedenäs, 1998). Whereas, in the past, emphasis was placed on either the sporophyte (particularly the peristome) or gametophyte, more recent classifications have tended to view both generations as having equal weight. Crosby (1980) considered that orders could best be characterised by peristomial attributes, whereas families and infrafamilial taxa are better defined with reference to gametophytic characters. This is borne out in Goffinet & Buck's (2004) most recent scheme of classification.

Two recent, highly significant publications, *Bryophyte Biology* (Shaw & Goffinet, 2004) and *Molecular Systematics of Bryophytes* (Goffinet *et al.*, 2004b), include discussion of molecular methods and the evolution of bryophytes and other land plants. New information has led to revised classifications of mosses, and Buck & Goffinet (2000), further modified by Goffinet & Buck (2004), have reassigned many genera into different or newly described families. Streimann & Klazenga (2002) have based their classification of Australian mosses on Buck & Goffinet (2000) with a few more recent modifications.

The classification of mosses continues to come under review at all levels. Modern, global studies are increasingly concerned with higher level classification as well as familial and generic concepts among acrocarpous and pleurocarpous taxa. The taxonomic level at which a 'group' is now recognised, e.g. class, subclass, order, family, genus etc., can vary, and while there is some broad agreement among bryologists concerning the higher level classification, there is often disagreement regarding the most appropriate taxonomic rank (Klazenga, 2005). For example, while Vitt (1984) recognised a single class of mosses (Bryopsida) with three subclasses, Schofield (1985) acknowledged a single class Bryopsida (Musci) with seven subclasses. Smith (1978), Magill (1981) and Eddy (1988–1996) documented three classes (Sphagnopsida, Andreaeopsida and Bryopsida), while Crandall-Stotler (1986) gave them divisional status. Mishler & Churchill (1984) and Mishler *et al.* (1992) have applied cladistic methods in an attempt to clarify the phylogenetic relationships of bryophytes. They recognise 6 orders of mosses: Sphagnales, Andreaeales, Tetraphidales, Polytrichales, Buxbaumiales and Bryales (see also Goffinet & Vitt, 1997).

The recent classification of Buck & Goffinet (2000), updated by Goffinet & Buck (2004) to incorporate additional information based on molecular studies, has introduced new categories, namely Superclasses I–V:

Superclass I, comprising Class Takakiopsida (one order, one family);

Superclass II, comprising Class Sphagnopsida (two orders, two families);

Superclass III, comprising Class Andreaeopsida (one order, one family);

Superclass IV, comprising Class Andreaeobryopsida (one order, one family);

Superclass V includes the majority of mosses in four classes: Oedipodiopsida (one order, one family); Polytrichopsida (one order, one family); Tetraphidopsida (one order, one family); and Bryopsida, with many subclasses, orders and more than 100 families.

Life History, Morphology and Terminology

Mosses are eukaryotic, chlorophyllose, leafy, annual or perennial plants. Their life histories are characterised by the alternation of a ‘haploid’, autotrophic organism (the gametophyte), with an attached and partially dependent, ‘diploid’ generation (the sporophyte). The sporophyte has a terminal capsule which, although it is photosynthetic until spore dispersal, is short-lived and of determinate growth. Meiosis takes place within the capsule to produce haploid spores that are discharged and dispersed to give rise to the next gametophyte generation.

The gametophyte reproduces sexually before sporophyte production; it often also reproduces asexually or by fragmentation. This, and the ability to regenerate in some cases from a single cell, allows mosses to be readily dispersed and enables rapid colonisation of pioneer niches even in the absence of sexual reproduction.

Stages of the gametophyte generation

A. A haploid *spore* is the first cell of the gametophyte generation,

B. The spore germinates to produce a richly branched, filamentous or plate-like *protonema*,

C. Buds arise from the protonema to produce leafy *gametophores* (moss plants). Mature gametophores are attached to the substratum by *rhizoids* (no true roots are developed),

D. The gametophyte produces sex organs by mitosis: the *antheridium* containing sperm (‘male’) and the *archegonium* containing the ovum (‘female’),

E. A biflagellate sperm with whiplash flagella moves down the neck of the archegonium in a film of water to fertilise the ovum,

F. Following fertilisation, the *calyptra* (derived from archegonial tissue) covers and protects the apex of the sporophyte during capsule development.

Stages of the sporophyte generation

G. The diploid, embryonic sporophyte develops from the fertilised ovum. The mature sporophyte consists of a *foot* embedded in the gametophore and a *seta* (or stalk) with a terminal *capsule*,

H. The capsule consists of a complex, protective wall surrounding the *spore sac* and a central *columella*. In most mosses, a *peristome*, which can assist in spore dispersal, surrounds the capsule mouth. The peristome is covered by a terminal *operculum* or lid until the spores are ready to be shed,

I. Within the spore sac, *sporocytes* (spore mother cells) undergo meiotic division to produce haploid *spores*. The spores enlarge and form a protective wall before being dispersed after the operculum is shed.

The nature of the two generations, the absence of lignified tissues in mosses (Geiger, 1990) and the requirement of water for sexual reproduction have imposed restrictions on the size of these plants. Evolutionary processes, such as mutations and natural selection, can operate at any stage of development and have resulted in many adaptations for reproduction, dispersal and survival.

Morphology and terminology

A appreciation of the morphology and anatomy of mosses is essential for distinguishing between species. Moss specimens are among the easiest to collect and preserve, and guidelines and useful hints can be found in Scott & Stone (1976), Catcheside (1980), Schofield (1985) and Meagher & Fuhrer (2003). In spite of their comparatively small size, the morphology of mosses is complex, and structural as well as physiological adaptations have enabled mosses to adapt to a broad range of habitats.

Well-illustrated publications providing useful information on morphology include Flowers (1973), Watson (1974), Hébant (1977), Schofield & Hébant (1984) and Schofield (1985). The summary of morphology provided by Buck & Goffinet (2000) is particularly useful for those intending to study mosses. The basic reference for terminology is *Glossarium Polyglottum Bryologie* (Magill, 1990), while a richly illustrated, comprehensive glossary of bryological terms has also been published (Malcolm & Malcolm, 2000). Moreover, Buck *et al.* (2002) and Meagher & Fuhrer (2003) illustrate the broad range of morphological and anatomical variation in Australian mosses, while a glossary of technical terms is also found in the current volume.

The Gametophyte

Morphological characteristics of the gametophyte important for the identification of mosses include habit, growth form and branching pattern, stem anatomy and surface features, reproductive structures and sexuality, leaf characteristics including laminal anatomy and costal structure, rhizoids and the calyptra, spore size and ornamentation.

Spores

The moss spore, the first stage of the gametophyte generation, is usually a single cell consisting of a protective wall (often distinctively ornamented and containing sporopollenin similar to pollen grains), a nucleus, chloroplasts, stores of lipid, starch and protein and other organelles (Mogensen, 1983).

The dimensions of spores and the number produced vary considerably among mosses: 4–16 spores of up to 200 µm diam. in *Archidium*; an estimated 350,000–500,000 spores (each c. 13 µm diam.) in capsules of *Funaria hygrometrica*; 470,000 spores (14 µm diam.) in *Orthotrichum cupulatum*; 1,000,000 spores (10 µm diam.) in capsules of *Tortula muralis*; and 50–80 million spores in *Dawsonia*, each 8–10 µm diam. (Ingold, 1959). Some spores remain viable for only 1–2 hours while others can germinate one or more years after sporogenesis. Moreover, some mosses produce spores of two distinct size classes (e.g. in *Macromitrium* and *Schlotheimia*; Ramsay, 1979). In a few taxa, spores can appear multicellular as a result of pregermination in the capsule (e.g. in *Andreaea*, *Muelleriella*, *Eucamptodon* and *Dicnemon*).

Protonema

The moss protonema is usually ephemeral, but it persists in some groups, e.g. *Mittenia* and *Viridivellus* (Stone, 1961, 1976) and Ephemeraceae (Stone, 1996). The protonema consists of caulonemal cells (lacking chloroplasts), including rhizoids with oblique walls, as well as chloronemal cells (containing chloroplasts). The principal role of the caulonema is colonisation, while rhizoids function in attachment and nutrient uptake during colonisation as well as propagation by tubers. The functions of the chloronema are assimilation and propagation by the production of asexual gemmae (Duckett *et al.*, 1998). Although usually filamentous, the form of the protonema can vary and it is diagnostic in some mosses, e.g. *Mittenia* and *Calomnion*. By contrast, the protonema is plate-like in genera such as *Sphagnum* and *Andreaea*.

The Gametophore

The gametophore originates from a single, usually tetrahedral, apical cell bud on the protonema. This bud gives rise to leaves, lateral buds and the outer section of the stem from outer initials, while the inner initials form the inner stem tissues (Crandall-Stotler, 1980). The gametophore, the structure generally recognised as a ‘moss plant’, is usually perennial and grows by innovations or underground rhizomes. The pattern of growth (e.g. upright, trailing, dendroid or prostrate) can characterise a family or genus, e.g. the trailing growth form of the Meteoriaceae, and the dendroid Hypnodendraceae.

Gametophores range in size from less than 1 mm tall (e.g. *Goniomitrium*) to upright stems 20–60 cm tall (e.g. *Dawsonia*), while prostrate or pendulous forms (e.g. *Papillaria*) or aquatic forms and those in moist habitats (e.g. *Brachythecium*) can be even longer.

Stems

The stem of the gametophore can be upright, prostrate or pendulous, simple or branched, and the stem surface can be smooth, bear paraphyllia or it can be covered with a tomentum of rhizoids. Paraphyllia (stem outgrowths) or pseudoparaphyllia (outgrowths protecting branch primordia) on the stems of some pleurocarpous mosses are either filamentous or leafy, and they can be diagnostic for certain genera. Types of axillary hairs found in some mosses can also be highly distinctive (Griffin, 1990).

Stem anatomy has been much used in differentiating taxa at all taxonomical levels (Buck & Goffinet, 2000). Although some stems contain elongated cells with thickened walls (stereids) and have a conducting system of hydroids for internal movement of water, no true lignin is produced (Schofield & Hébant, 1984; Geiger, 1990; Mues, 2000). Leptoids, involved in the translocation of photosynthates, are found only in members of the Polytrichales. Transverse sections of stems reveal the presence or absence of a central strand (with or without stereids), the epidermis and the type of cortical cells present. Absorption of water and nutrients usually occurs through the surface of the leaves and stems, although the translocation of carbohydrates can also include movement along microtubules in leaf costae and laminal cells (Duckett *et al.*, 1997).

The branching pattern of moss stems can be one of two types: 1) monopodial or indeterminate, e.g. in pleurocarpous mosses where the apical bud persists and lateral growth occurs from axillary buds with gametangia on lateral branches; or 2) sympodial and determinate, where the apical bud is replaced following production of gametangia, and branching is continued by lateral meristems. The latter type is found in most acrocarpous species. See La Farge-England (1996) and Buck & Goffinet (2000) for further details.

Leaves

Important leaf characters include size, shape, colour, insertion on the stem, the nature of the leaf apex, margin and base, and the structure and extent of the costa. Many of these features are well illustrated in Malcolm & Malcolm (2000) and Buck *et al.* (2002). At a microscopic level, accurate identification can sometimes depend on assessing the thickness of the leaves by sectioning (whether comprising one, two or more layers of the cells) and the shape, dimensions and structure of costal, epidermal, marginal and basal laminal cells. Leaf sections are often required for complex leaves, e.g. *Leucobryum* and *Polytrichum*. The presence of lamellae on the leaf surface is characteristic of the Polytrichales, e.g. *Dawsonia* and *Polytrichum*. The arrangement of leaves on the stem (whether spiral, complanate or distichous) and their appearance and stance when wet and dry can also be diagnostic.

Leaf cell anatomy

Leaf cells can be chlorophyllose, pigmented or hyaline. Cells of different size, shape, orientation and wall thickness can occur in different parts of the lamina (e.g. margin, upper lamina, basal lamina or juxtacostal), while specialised alar cells can sometimes be seen in the basal corners of the leaf, e.g. in Sematophyllaceae, Dicranaceae and Dicnemonaceae. Cell surfaces can be smooth (Bryaceae), mammillose or papillose (Orthotrichaceae and Pottiaceae), while papillae themselves can have a simple or quite complex structure.

Leaf costa

A costa (or leaf vein/midrib) can be present (Bryaceae, Dicranaceae) or absent (Sematophyllaceae, Hypnaceae). When present, it can be single or double (two distinct costae), and it can extend part of the way up the lamina, reach the apex (percurrent), or even extend well beyond the apex (excurrent) as a hairpoint. Costal cells range from uniform to markedly heterogeneous and thin- or thick-walled. Details of costal anatomy (best seen in transverse section) can also be diagnostic. In *Leucobryum*, the costa occupies most of the leaf and consists of large hyaline cells enclosing a central layer of chlorophyllose cells. In *Campylopus*, the costa occupies up to one-third of the laminal width at its base and had a complex structure; in the Polytrichales, longitudinal, chlorophyllose ridges or plates are found on the adaxial surface of the costa.

Rhizoids

Filamentous rhizoids anchor the protonema and gametophore in the substratum. They can be present only at the stem base or they can form a dense, felt-like tomentum covering large areas of the stem (Buck & Goffinet, 2000). Rhizoids are smooth (Sematophyllaceae) or papillose (Bryaceae, Bartramiaceae), with thin or thick, often oblique walls, and they are often pigmented (Crundwell, 1979). Some have asexual reproductive structures such as tubers (Bryaceae).

Asexual reproductive structures

Mosses produce a range of specialised, vegetative propagules on protonemata, rhizoids, leaves, stems or in stem axils (e.g. in Bryaceae, Pottiaceae, Calymperaceae and some Orthotrichaceae; Lewis & Smith, 1977; Duckett & Ligrone, 1992). Occasionally, stem apices are themselves deciduous and propagative (e.g. in *Campylopus clavatus*), or flagelliform shoots with reduced leaves can be produced (e.g. in *Wijkia extenuata*). Leaf fragments and fragile or deciduous leaves can sometimes regenerate new gametophores, and such structures can be taxonomically informative, e.g. in *Pohlia* and Bryaceae, Pottiaceae and Calymperaceae.

Gametangia and sexuality

The sexuality of a moss is determined by the type of sex organs (gametangia) present and their arrangement and position on the gametophore. An ovum is produced in the basal venter of a flask-shaped archegonium. Archegonia, often intermixed with sterile paraphyses, are aggregated in a perichaetium sheathed by specialised perichaetial leaves that persist after fertilisation and sheath the base of the developing sporophyte. Their shape and structure, especially the inner perichaetial leaves, can differ significantly from the vegetative leaves of the same species (e.g. in *Eucamptodon* and *Holomitrium*). The perichaetia (and eventually the sporophyte) are produced from the shoot apex (acrocarpous) or on lateral branches (pleurocarpous).

Male gametes (antherozoids) are produced in stalked antheridia, mixed with paraphyses, which are usually grouped into the perigonium surrounded by perigonial leaves. Perigonial leaves sometimes differ from vegetative leaves, and in some mosses (e.g. Polytrichales, *Bryum* and *Breutelia*) the perigonium forms a splash cup enabling sperm to be more readily and effectively dispersed by raindrops.

Mosses with perichaetia and perigonia on separate plants are termed *dioicous*; those in which both occur, but separately, on the same plant are *autoicous*. Among autoicous species, those known as *cladautoicous* have the perichaetia and perigonia on different branches of the same plant, whereas in *gonioautoicous* mosses the perichaetia and perigonia occur on the same branch, while *rhizoautoicous* forms have the male sex organs produced on rhizoids at the base of the female (Buck & Goffinet, 2000). In *synoicous* mosses, the antheridia are mixed with archegonia in the same perichaetium, while in *paroicous* species the perigonia and perichaetia are not mixed but occur in different leaf axils of the same plant. Some taxa have a mixture of sexual arrangements, subtle variations can occur, and the terminology and classification of sexual conditions in mosses can also be confusing (Wyatt & Anderson, 1984; Wyatt, 1985; La Farge-England, 1996; Buck & Goffinet, 2000; Malcolm & Malcolm, 2000). In dioicous species, the male and female plants can be dimorphic, the most extreme manifestation of which has the male reduced to an epiphytic dwarf plant (*pseudoautoicous* or *phyllodiocous*) on the leaves or stems of the female (e.g. in *Macromitrium*, *Racopilum*, *Leucobryum* and Dicnemonaceae).

Calyptra

The embryonic sporophyte is enclosed and protected by a hairy or membranous calyptra which is gametophytic in origin and which grows from the base of the archegonial venter. As the sporophyte forms and the seta elongates, the calyptra usually ruptures near the base, leaving a remnant vaginula, the remainder partly or completely enclosing and being carried up with the developing capsule. The calyptra both protects the young sporophyte and determines its shape, often until maturity, at which time it becomes detached from the capsule. Calyptrae vary in shape, size, surface features and manner of splitting. Two basic types are recognised, *viz*. mitrate (conical and undivided or equally lobed at the base) and cucullate (slit up one side).

The Sporophyte

The sporophyte, consisting of a foot, seta and capsule, is comparatively uniform and diagnostic for groups such as the Sphagnopsida, Andreaeopsida and Polytrichopsida. However, great variation is found among the Bryopsida both at family and genus levels; in the more advanced and specialised taxa a considerable morphological range can occur even within a genus or species. Apart from shape, the most important characteristics of the sporophyte are its position on the gametophore, the type of exothecial cells, the location and type of stomata, the presence or absence of an annulus, the shape of the operculum, and the ontogeny and structure of the mouth of the capsule including the development and structure of the peristome.

Foot

The sporophyte is attached to the stem apex of the gametophore by a anchoring and absorptive ‘foot’. The foot, the stem apex and the adjacent placental region vary in their structure and dimensions and, in all mosses except *Sphagnum*, they contain the transfer cells that are essential for the nutrition of the sporophyte (Ligrone & Gambardella, 1988; Buck & Goffinet, 2000).

Seta

The seta is a simple, leafless, photosynthetic stalk that elevates the capsule above the gametophore. It is usually a solitary structure, although in certain genera (e.g. *Dicranoloma*; Klazenga, 2003), several can originate from the same stem apex. The seta elongates before the capsule begins to expand and before sporogenesis takes place, rather than after sporogenesis, as is the case with liverworts. It has a central conducting system of hydroids (along with leptoids in the Polytrichopsida) and stereids that keep it erect and rigid. Differentiation of surface cells enables it to twist when dry. The seta varies in length, being especially short in taxa with largely immersed capsules (e.g. *Acaulon* and *Ephemerum*). In most mosses, however, the seta carries the capsule well above the gametophore. The pattern of twisting of the seta can be diagnostic, e.g. in some Orthotrichaceae (Goffinet & Vitt, 1998). Transverse sections show the form of the conducting system and the nature of the cell types that determine the seta structure and twisting pattern.

Capsule

The functions of the moss capsule are centred on the production and dissemination of spores. Capsules can be immersed, emergent or exserted, depending on the length of the seta. The internal structure and development of the capsule and the origin and form of the peristome at its mouth are characteristic for different types of moss. In most, the capsule consists of an urn with a complex wall composed of a thickened, non-chlorophyllose outer layer of exothecial cells subtended by one or several layers of chlorophyllose cells.

The capsule wall encloses an amphithecium that gives rise to the exothecium and the layers at its apex from which the peristome is derived. The endothecium produces the spore sac in which spores are formed following meiosis as well as a central, non-sporogenous region, the columella (Buck & Goffinet, 2000). An apophysis (or swelling) can sometimes be seen at the point of attachment to the seta (e.g. in *Trematodon*). Immersed or superficial stomata are often present, especially at the base of the capsule, and these are diagnostic for some groups, e.g. the Orthotrichaceae. The mouth of the capsule is usually surrounded by an annulus or ring of cells, and a lid-like operculum covers the mouth until the spores are ready to be shed.

In most mosses, the peristome forms a ring around the mouth of the capsule. Spore dispersal in peristomate species is regulated by hygroscopic movement of the peristome teeth; in cleistocarpous species spores are shed following the breakdown of the capsule wall; while gymnostomous species lack a peristome, and spores are released from the more rudimentary capsule mouth.

Peristome

The peristome comprises 4, 8, 16, 32 or 64 teeth arranged in one or two, rarely multiple, rings inside the mouth of most moss capsules. However, there is considerable variation in the morphology, anatomy and action of the peristome (see Edwards, 1984; Shaw & Robinson, 1984).

Nematodontous peristomes occur in the Polytrichopsida and Tetraphidopsida. In the former, each tooth is composed of several, whole elongate cells, and the peristome consists of 16–64 short, rigid, multicellular teeth in a single circle. In the Polytrichales (except *Dawsonia*), the apex of the columella is expanded to form a plate-like epiphragm. Expansion and contraction of the epiphragm opens and closes the space between the teeth, possibly regulating spore dispersal.

Arthrodontous peristomes occur in all members of the Bryopsida and are derived from the cell walls only (not whole cells) of the three innermost layers of the apical amphithecial tissue: the *inner peristomial layer* (IPL) proximally continuous with the spore sac; the middle or *primary peristomial layer* (PPL); and the *outer peristomial layer* (OPL). The peristome usually consists of one or two rings of triangular or linear appendages (exostome teeth and endostome segments). These are formed from differentially thickened periclinal wall-pairs that remain standing after the breakdown of the rest of the cells (Edwards, 1984). Cell patterns on the face of peristome teeth provide the simplest and most reliable method of establishing homologies between taxa. A peristomial formula indicates the number of cells from each of the layers (OPL, PPL, IPL) involved in the production of each tooth or segment (Edwards, 1984; Buck & Goffinet, 2000). The final divisions of the innermost peristomial layer determine the different types of arthrodontous peristomes (Shaw & Robinson, 1984; Buck & Goffinet, 2000).

In arthrodontous peristomes, the columella does not expand at its apex, but is attached to the operculum and usually breaks when the operculum is shed. Hygroscopic movement of the exostome teeth frequently plays an role in hindering or facilitating spore release, while the endostome is generally considered to play only a minor role in spore release (Miller & Neumann, 1988). Although arthrodontous peristomes have diverged into many different forms, two major types can be recognised: diplolepidous (with an exostome and endostome) and haplolepidous (with an endostome only). A heterolepidous type, found in *Encalypta*, is thought to be intermediate (Goffinet & Buck, 2004).

Diplolepidous peristomes are found in families such as Bryaceae, Mniaceae, Rhizogoniaceae, Hypnaceae and Hookeriaceae, and consisting of two concentric circles of teeth. The teeth in one circle can be opposite to or alternate with those of the second.

The outer circle (exostome) consists of 16 robust, triangular teeth (sometimes as 8 pairs) each with trabeculae derived from the cross walls of a single column of cells on the inner face, and two columns of plates separated by a zig-zag line on the outer face (Edwards, 1984). The exostome teeth, derived from wall-pairs between the OPL/PPL, can be highly ornamented on the outer and/or inner surface. The type of ornamentation, the number of teeth and the extent to which they are fused are often diagnostic. The inner circle (endostome) consists of a delicate inner membrane bearing a network of cell patterns on each side. This membrane, derived from wall-pairs of the PPL/IPL, is divided above into 16 often perforated segments. Between the endostome segments are 16 groups of 2–4 fine cilia also attached to the basement membrane (Buck & Goffinet, 2000). The endostome segments usually alternate with the exostome teeth or, more rarely, oppose them (*Funaria*-type). The number of segments and cilia and their ornamentation on both faces can also be diagnostic.

Haplolepidous peristomes: These are characteristic of the Dicranaceae and Fissidentaceae, are always of one layer, and are homologous with the endostome (Buck & Goffinet, 2000). Each of the 16 teeth consists of two concentric layers of fused cell walls derived from thickening of the contiguous wall-pairs derived from the PPL/IPL. The outer surface of each tooth consists of a single tier of cells, while the inner surface has 1.5 cells per tooth. The 16 teeth of this single ring sometimes split into 32.

Reproductive Biology, Cytology and Genetics

While some mosses reproduce only sexually and lack specialised asexual structures, others rarely reproduce sexually but have one or more asexual or vegetative means of reproduction. Only a few taxa reproduce exclusively by vegetative means.

Sexual reproduction

A range of sexual reproductive systems maintains a high degree of genetic flexibility in mosses (Longton, 1976). The breeding systems and degree of mating success at the time of fertilisation influence the success of the species (Wyatt, 1982) and can also provide important diagnostic characters (Longton, 1982).

Dioicous mosses are slightly more common than monoicous taxa (Wyatt & Anderson, 1984), and most Australian monoicous mosses are autoicous. However, the ancestral sexual form is widely considered to be dioicous (Longton & Schuster, 1983; Vitt, 1984) since dioicy is more widespread among the ‘primitive’ mosses (Anderson, 1980; Smith, 1979).

Sexuality is usually consistent within a species but often differs between species of the same genus, e.g. in *Bryum s. lat.* spp. (dioicous, synoicous or autoicous), *Grimmia* spp. (dioicous or autoicous) and *Macromitrium* spp. (dioicous, including pseudautoicous and phyllodioicous, or autoicous). The basis for sexuality can be related to cytological factors, and doubling of the chromosome number can shift a species from dioicy to monoicy (Vitt, 1968; Smith, 1978; Longton, 1982; Ramsay & Berrie, 1982; Ramsay & Spence, 1996). Moreover, the phenomenon of epiphytic dwarfism in males, widespread in the mosses (Ramsay & Berrie, 1982), is sometimes related to anisospory, e.g. in *Macromitrium* (Ramsay, 1979), and it may also have a cytological basis.

The potential advantage of dioicy is that it promotes outcrossing and increases genetic variability thus providing greater adaptability to environmental change (Mishler, 1988). It also enables mosses to specialise as either male or female parents on slightly different environmental resources (e.g. dwarf males) thereby reducing intraspecific competition. In males, the production of splash cups (e.g. in Polytrichidae and Bartramiaceae) can facilitate the dispersal of gametes, while females plants can be taller to enhance spore dispersal. Dwarfism of males that are epiphytic on the female, increases the possibility of outcrossing in epiphytic species at least for the first generation (Ramsay, 1983; Ramsay & Vitt, 1984).

Selection acts directly on the gametophyte and, being haploid, there is apparently no heterozygosity except for the cytological evidence that initial duplication (functional polyploidy) has occurred at some time in the past to produce gametophytic chromosome numbers such as 10, 11, 12, 13, etc. (Ramsay, 1983; Newton, 1986). The gametes, produced by mitosis, are genetically identical on any one plant. In monoicous species, particularly synoicous and paroicous forms, obligate self-fertilisation and inbreeding can result from close proximity of male and female gametangia. Therefore, it is no more valuable than vegetative reproduction, unless species are protandrous or protogynous to ensure outcrossing. However, the majority of monoicous species are autoicous, and often the distance between perigonia and perichaetia is such that the likelihood of outcrossing is enhanced (Longton & Miles, 1982). Monoicy is favoured where there is a low density of reproductive individuals in the population, e.g. in colonising or weedy species, and it is thought to have a better potential for long-range dispersal. Other isolating mechanisms, such as genetic incompatibility, can also promote outcrossing in monoicous species, for example *Weissia* clones can have different numbers of *m*-chromosomes (Anderson & Lemmon, 1974; Anderson & Snider, 1982).

Ecological trends in breeding systems can be related to environmental pressures. Thus, monoicy is common in drier habitats such as dry deserts, polar deserts and dry micro-environments in otherwise mesic habitats, while dioicy is more frequent where water availability is dependable (Wyatt, 1982).

In Australia, very little research has been carried out on the phenology and reproductive biology of mosses, and we know little of the mechanisms and importance of reproduction in individual species. Some studies have been published for *Macromitrium* (Ramsay, 1988a, 1988b; Ramsay & Vitt, 1986) and *Dicranoloma* (Ramsay, 1985; Milne, 1997), while research has yet to be undertaken on the many different mechanisms that ensure reproductive success among arid zone and epiphytic mosses.

Asexual reproduction

Asexual reproduction is very common in mosses, and while it contributes little to increased genetic variation within species, it enables rapid colonisation and expansion of moss colonies at times when sexual reproduction does not or cannot occur. Increase in size and in numbers of individuals in a clone results from the production of new stems, fragmentation of an existing colony or death of older parts and regeneration from new apices at the edges. In some cases, diaspores that are not dispersed can grow to form new shoots among old or dead plants (e.g. *Archidium, Campylopus* and *Bryum s. lat.*).

Experimental studies suggest that vegetative diaspores or gemmae of various kinds, including filamentous structures in Calymperaceae, *Tortula papillosa*, *T. pagorum* and *Macromitrium brachypodium*, and bulbils or tubers in Bryaceae (Egunyomi, 1984; Schofield, 1985; Imura & Iwatsuki, 1990; Ramsay, 1988b; Spence & Ramsay, 1996) are often more likely to be successful than spores in the spread of a moss colony (Miller, 1984; Longton, 1988). Diaspores are produced in great numbers in transient, open, extreme or unpredictable environments as well as by epiphytic species for which colonisation and rapid population growth are essential (Wyatt, 1994). Diaspore viability varies depending on the species, but it has been calculated from 2–12 months (Egunyomi, 1984). Leaf fragments and fragile or deciduous leaves can also regenerate new gametophores. In some species, several different forms of asexual reproduction can occur simultaneously, e.g. in *Dicranella cardotii*, *Gemmabryum eremaeum* and *G. pachythecum* (Bergstrom & Selkirk, 1987; Duckett & Ligrone, 1992, Spence & Ramsay, this volume).

Cytology and genetics

Bryophytes have contributed significantly to the broad understanding of cytology and genetics. The comparatively high incidence of heterochromatin, specialised *m*-chromosomes, sex chromosomes and certain other meiotic attributes distinguish bryophyte cytology from that of vascular plants (Anderson, 1984). The fundamental cytological differences between the major bryophyte groups are of particular interest in view of the similarities in their life histories. The Hepaticopsida (liverworts) are relatively conservative and stable with respect to chromosome number (n = 8, 9 or 10; 75 per cent with n = 9) with limited polyploidy, while the Anthocerotopsida (hornworts) have n = 5 or 6 (Fritsch, 1991; Goldblatt & Johnson, 1994–2003). By contrast, mosses are more diverse in terms of chromosome number and in cytological behaviour. The Sphagnopsida have a unique chromosome number ($n = 19 + 2m$) with some polyploidy. The Andreaeopsida have $n = 10$ or 11 while the Takakiopsida have $n = 4$ or 5. Cytological uniformity is seen in Polytrichopsida which have numbers based on $n = 7$ large chromosomes or its multiples 14 and 21. The Tetraphidopsida have $n = 7$ or 8 chromosomes (Fritsch, 1991; Goldblatt & Johnson, 1994–2003).

In the highly diverse Bryopsida, chromosome numbers can vary within families, genera or even species (Fritsch, 1991) with numbers such as n = 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 and multiples to 66 (Pottiaceae) the commonest being n = 6, 7, 10, 11, 13, 14 and 20. The relatively uniform chromosome numbers of the diplolepidous, alternate, pleurocarpous mosses (56 families; $n = 10$ or 11) suggest a close relationship for these highly derived taxa, in contrast to diplolepidous, acrocarpous or cladocarpous species which have more diverse chromosome numbers, and which Vitt (1984) considered to be an older and more heterogeneous group.

While chromosome numbers appear to support some major taxonomic categories and are consistent within smaller, tightly defined taxonomic groups such as Polytrichopsida and Sphagnopsida, they are unpredictable in large families of colonising species such as the Pottiaceae, Bryaceae and Funariaceae. The amount of polymorphism in chromosome numbers, particularly in the Bryopsida, can usually be accounted for by cytological changes similar to those in vascular plants, e.g. hybridisation, polyploidy, aneuploidy and structural rearrangements (Newton, 1979, 1984b, 1986; Anderson, 1984).

Levels of ploidy rarely exceed three (n, $2n$ and $3n$) (e.g. in *Funaria hygrometrica* Hedw., 14, 28, 56), but levels are higher in some Pottiaceae and Bryaceae (Fritsch, 1991). Differences in chromosome number, particularly polyploidy and aneuploidy, act as highly effective sterility barriers for the different cytotypes and comprise “intersterile breeding units” (Smith, 1978). Because intraspecific polyploidy and aneuploidy are so frequent in mosses, it is difficult to infer evolutionary directions of change based on chromosome number alone (Anderson, 1964, 1984).

Chromosome data can be used as characters in bryophyte taxonomy in conjunction with traditional morphological ones (Anderson, 1984). Karyotype analyses and Geimsa C-banding (Newton, 1984a) have been used to elucidate the relationships among mosses with the same chromosome number (Inoue *et al.*, 1978; Ramsay, 1982, 1983). Most cytological studies on Australian mosses have been carried out by Ramsay (1964–1998; unpublished data), but there is still much to be done.

Some studies have addressed the genetics of individual taxa and populations (Wyatt, 1992, 1994), with methods such as electrophoresis revealing that bryophytes can differ substantially in their degree of genetic variation (Wyatt *et al.*, 1989a; Stoneburner *et al.*, 1991b), and isozyme analyses interpreting relationships between taxa (Wyatt *et al.*, 1989b, 1993; Goffinet 1995; van Zanten & Hofman, 1995; Goffinet & Buck, 1998). Electrophoretic studies on some genera, e.g. *Racopilum* (de Vries *et al.*, 1989; van Zanten & Hofman, 1995), *Plagiomnium* (Odrzykoski *et al.*, 1993; Wyatt *et al.*, 1989a) and *Atrichum* (Cummins & Wyatt, 1981), have allowed the recognition of the degree of genetic polymorphism within populations and, in some cases, by distinguishing unique diagnostic alleles, have determined the genetic differences between related species. Improvements in molecular techniques such as RAPDs and DNA sequencing have enabled significant research on the genetic diversity of Antarctic mosses, including tracing mutations within colonies in extreme climates (Skotnicki *et al.*, 1998a, 1998b, 2000, 2004) to resolve taxonomic uncertainties.

In recent years there has been analysis of genome size and karyotype in mosses (Cove, 2000). Where polyploid series are thought to exist it has been confirmed that there may be a correlation between chromosome number and genome size in some taxa (Volgmayr & Greilhuber, 1999; Cove, 2000). Studies on 132 moss taxa has demonstrated an approximately 12-fold variation in DNA content of haploid genomes in mosses compared with 1,000-fold range in the diploid genomes of angiosperms (Volgmayr & Greilhuber, 1999; Cove, 2000).

The traditional view of bryophytes as genetically impoverished organisms with limited potential for response to natural selection is not supported (Cummins & Wyatt, 1981; During & van Tooren, 1987; Shaw, 1991, 1992). “It is clear that both mosses and liverworts are genetically variable, that they possess considerable evolutionary potential and cannot be considered in any way unsuccessful or relict groups” (Smith, 1978).

Ecology, Distribution and Biogeography

Ecology

The early radiation of mosses was due to their ability to tolerate environmental conditions unsuitable for many other plants (Schofield, 1985). Today, mosses are widely distributed in many ecosystems including those at Arctic and Antarctic latitudes, alpine environments, the wet-tropics, arid regions and aquatic habitats (Schofield, 1981, 1985). Indeed, they are often important components of the vegetation in wet sites (rainforests, mires, streams) and dry habitats (rock faces, boulders, screes, fellfields), and at environmental extremes where, in the absence of strong competition from vascular plants, they can sometimes dominate the vegetation. In general, bryophytes have adapted a strategy of evolving desiccation tolerance, photosynthesising and growing during moist periods and reducing or suspending metabolism during times of drought (Proctor, 2000).

Many mosses have preferences for particular habitats. Although none are truly marine, some are markedly salt-tolerant, occurring in or above the supralittoral zone, e.g. *Muelleriella crassifolia*, *Grimmia maritima* and *Pottia heimii*. Others, such as *Mitthyridium obtusifolium* and *Taxithelium merrillii* are found in mangrove communities where they are often splashed with brackish water (Windolf, 1989). Some specialists (e.g. *Mittenia plumula*) inhabit extremely deep shade, and a suite of species such as *Encalypta vulgaris*, *Grimmia pulvinata*, *Gigaspermum repens* and *Orthotrichum cupulatum* occur primarily on limestone or on calcareous rocks or soils (Downing *et al.*, 1991, 1995, 1997; Downing, 1992; Downing & Selkirk, 1993; Downing & Coveny, 1995). Others (e.g. *Mielichhoferia mielichhoferiana* and *Scopelophila cataractae*) are abundant on copper-rich soils or those containing high levels of heavy metals, sometimes accumulating them and having potential in geobotanical prospecting and air quality monitoring (Richardson, 1981; Chopra & Kumra, 1988).

In sites where they are abundant, mosses can have a substantial and distinctive influence on the functioning of ecosystems. They contribute to nutrient transfer within ecosystems, as sources of nutrients, and in the translocation and internal redistribution of nutrients. Being poikilohydric, the absence of roots and a cuticle has implications for mineral nutrition as well as water-relations. High water-holding capacity, direct uptake of mineral nutrients from precipitation and low thermal activity, combined with comparative immunity to grazing and slow decomposition resulting in accumulation of humus and peat, can have a greater impact on nutrient cycling, soil temperature and moisture regimes and the range of habitats available to other organisms, than is commonly recognised (Longton, 1984; Jury *et al.*, 1990; Bates, 2000).

Although relatively inconspicuous, mosses, along with other bryophytes and lichens, play a significant role in nutrient cycling and water drainage control in mires, bogs, rainforest and soil crusts. In humid forests, bryophytes often form a carpet on the forest floor, sheath tree trunks, form pendulous curtains from branches or even encrust the surfaces of evergreen leaves. The trapping of rain by epiphytic bryophytes in tropical rainforest has been well documented (e.g. Pócs, 1982; Richards, 1984; Frahm, 1990). Although corticolous epiphytes are more diverse than any other ecological group of bryophytes, only some aspects of their ecology have been studied in detail. Pócs (1982) demonstrated a positive correlation between the biomass of epiphytes and surplus rainfall in forest climates in Africa. Their capacity within rainforests to absorb minute quantities of nutrients from rainwater, exudates from forest leaves and the excrement of insect larvae, and to release these as leachates over time gives bryophytes an important role in the maintenance of the forest. Bates & Bakken (1998) stressed the need to increase research on the bryophyte-rich types of tropical forest where nutrient cycling via terrestrial and epiphytic bryophytes might be far more influential than in other communities. The mossy covering makes bryophyte-rich forests important watersheds, reducing the damaging effects of torrential rains and regulating the release of water and nutrients slowly over time (Bates, 1992). The diversity of bryophytes in Australian rainforest and eucalypt forest has been discussed by, among others, Ashton & McCrea (1970), Chapman & King (1983), Vitt & Ramsay (1985b), Ramsay *et al.* (1987), Jarman & Fuhrer (1995), Fensham & Streimann (1997), Pharo & Beattie (2002), Ramsay & Cairns (2004) and Turner & Pharo (2005).

As a component of microbiotic soil crusts in semi-arid and arid Australia, bryophytes play an important role in controlling infiltration of water and in preventing erosion (Downing & Selkirk, 1993; Eldridge, 1993; Eldridge *et al.*, 1995; Eldridge & Tozer, 1996, 1997). Mosses assist in increasing insulation at the soil surface, they enhance nutrient cycling, contribute to soil stability, and provide niches for soil invertebrates. Soil function is promoted by the acceleration of physical and chemical weathering, the trapping of windblown sediments, and by the direct contribution to organic matter in the soil. In Antarctic, alpine and semi-arid environments, bryophytes colonise substrata and contribute to consolidation of soil particles on rock surfaces and bare soil thus facilitating colonisation by other plants (Selkirk *et al.*, 1990; Eldridge & Tozer, 1996). In these environments, the trapping of wind-blown particles in moss cushions is more significant in soil development than is the weathering of rock (Longton, 1984).

The evolution of certain physiological attributes had allowed some mosses to metabolise even during extreme drought (Vitt, 1989). The requirement for water for survival and reproduction does not restrict these plants to humid environments because, being poikilohydric, they can utilise water when and where it is available, often being able to withstand long periods of drought and desiccation (Proctor, 1981, 1982, 2000). Some mosses dry out to a water content of 10 per cent or less of their dry weight, and they can tolerate desiccation sometimes for years on end (Proctor, 1984). Physiological adaptations enable rapid recovery, with respiration beginning almost at once on remoistening of dried leaves (Proctor, 1979). Photosynthesis recovers more slowly but the compensation point is reached within minutes (Valanne, 1984). While photosynthesis and respiration can return to normal within 12–24 hours of rewetting, recovery can take longer following prolonged desiccation. Furthermore, the structure of cell organelles (mitochondria, chloroplasts, vacuoles) changes after drying out, but normal structure can be restored within a few hours of wetting (Proctor, 1984).

While physiological adaptations are of considerable importance for survival, behavioural and morphological adaptations can also be influential in protecting mosses from desiccation and high light intensities. The arrangement and stance of moss leaves and their behaviour as they dry out promote water retention. Many xerophytic species have small or long and narrow cells with thick, often papillose walls, dense contents and small vacuoles, e.g. Pottiacaeae, Orthotrichaceae, Grimmiaceae (Bell, 1982). The advantage of thick cell walls for water economy relates to the important role of apoplastic storage and movement of water in mosses (Schofield, 1985). Most members of the Polytrichaceae have rows of lamellae on the leaf surface to increase the surface area for photosynthesis. As they dry out the leaves roll inwards and lie parallel to the stem thus reducing water loss (van Zanten, 1973; Smith, 1982). Hyaline hairpoints, common in Grimmiaceae, Pottiaceae and some other families, and papillae on cell walls in Pottiaceae and Orthotrichaceae, can reduce the rate of evaporation and provide capillaries for rapid wetting and water movement (Edwards, 1984). They also protect the leaves from high light intensities and divert heat from the surface of the plant.

In most mosses the movement of water and nutrients occurs over the surfaces of leaves and stems. These ectohydric species predominate on substrata such as rock and bark and in other nutrient-poor microhabitats (Proctor, 1984). External conduction is facilitated in a variety of ways: spaces among rhizoidal tomentum (*Breutelia* and *Dicranoloma*), paraphyllia (in pleurocarpous mosses), sheathing leaf bases (Calymperaceae and Pottiaceae), interstices between surface papillae (Pottiaceae and Orthotrichaceae), and the lumina of empty, porous or laminal cells (Sphagnaceae and Leucobryaceae). In contrast, endohydric mosses (e.g. many Polytrichales) have comparatively well-developed, internal conducting tissues (Hébant, 1977; Schofield & Hébant, 1984), and these are more common on substrata and in habitats that are more reliably moist and rich in nutrients.

In Australia, some colonising species are adapted for recovery after fire (Duncan & Dalton, 1982), or even after burial in sand-dunes (Moore & Scott, 1979). Indeed, a number of strategies, demonstrated experimentally, are involved in sand-dune recolonisation (Moore & Scott, 1979). These include apical innovations (*Barbula torquata*), monopodial growth (*Tortula antarctica* and *Rosulabryum billarderi*), lateral buds (*Barbula calycina* and *Triquetrella papillata*), persistent rhizoids and primary protonemata (*Barbula torquata*). In many habitats, soil can harbour a diaspore bank that germinates rapidly under suitable conditions (Selkirk, 1984; Bergstrom & Selkirk, 1987).

A significant contribution to a greater understanding of the ecology of mosses has been the recognition of 'life forms' (Gimingham & Birse, 1957; Magdefrau, 1982; Richards, 1984), and the identification of a number of 'life strategies' as proposed by During (1979). The life forms and life strategies of mosses relate to gametophyte longevity, reproductive effort, spore size and other attributes (Longton, 1988).

Life forms

Life form is an ecological concept embracing structural characters, the aggregation of individuals and their relationship to the substratum. Acrocarpy is favoured in unstable or xerophytic habitats where taxa often have ephemeral gametophores (e.g. *Pottia*, *Phascum*, *Eccremidium*, *Goniomitrium*, *Gigaspermum* and *Bryobartramia*), prolific sporophyte production, large spores (often 100 µm in diameter), persistent protonemata, small gametophores, and capsules that are often cleistocarpous and gymnostomous, being immersed on a shortened seta. In contrast, pleurocarpy is generally favoured in sheltered, often forested habitats.

Turfs

Turfs can be short or tall, with short turfs predominant on open, mineral soils (*Ceratodon*, *Barbula* and *Ditrichum*) and tall turfs (*Dicranoloma*, *Campylopus*, *Pyrrhobryum* and much of the family Polytrichaceae) in grassland or as ground cover in temperate forest.

Cushions

Cushions (e.g. of *Andreaea*, *Orthotrichum*, *Tortula* and *Grimmia*) occur in exposed habitats such as bare rock or as epiphytes on bark. Many are xerophytic and have short, straight or curved thick setae, oblong to ovoid, sometimes strongly ribbed capsules, often with large calyptrae (*Schlotheimia*) and a peristome that is reduced or absent (e.g. *Macromitrium*), while others are emergent from long perichaetial leaves (*Eucamptodon* and *Calyptopogon*; Vitt, 1981).

Mats and wefts

Mats (e.g. *Hypnum*) and wefts (e.g. *Thuidium*) are usually pleurocarpous mosses with a prostrate growth form. They are most common in mesophytic, stable ecosystems with broad niche overlap and long growing seasons (Buck & Vitt, 1986).

Pendants, dendroids, tails and fans

These are also pleurocarps restricted to very moist forests. Pendants (Meteoriaceae) occur on branches and trunks, while tails, fans and fan-like forms (Neckeraceae, Pterobryaceae) are found on tree trunks and rocks in sheltered places. Dendroids (Hypnodendraceae, Hypopterygiaceae, *Camptochaete*) are confined to the forest floor and grow on rocks, tree bases or soil on stream banks (Frey & Beever, 1995).

Life strategies

Life strategies (During, 1979) are concerned primarily with the life histories associated with mosses in particular environments.

Annual shuttle species are often present in unstable habitats; for example, some species of *Funaria* have ephemeral gametophores.

Perennial shuttle species have xerophytic gametophores and large diaspores (During & van Tooren, 1987; Longton, 1988), occupy habitats that remain available for long periods and recur predictably within particular ecosystems.

Fugitives are tolerant of severe desiccation, can produce abundant spores and are either annual or biennial (e.g. *Funaria hygrometrica*).

Colonists are primarily turfs and are either tall (e.g. *Dawsonia* and *Pogonatum*) or short (e.g. *Grimmia* and *Schistidium*). They frequently have splash cups to enable sperm to travel farther than would otherwise be possible. In exposed habitats, colonist and fugitive species frequently produce large numbers of diaspores that are dispersed by rainwash or wind.

Perennial stayers predominate in hot or cold, arid environments or as epiphytes with xerophytic gametophytes. These have small spores (less than 20 µm in diameter), long setae and other features that promote dispersal. Examples include many Pottiaceae (species of *Tortula* and *Barbula*).

Epiphytes predominate in rainforest and are often vertically stratified, some also being phorophyte-specific, e.g. *Calomnion* on tree ferns. Many species that occur in the canopy have exceptionally high light tolerance. Epiphytes also exhibit morphological, reproductive, physiological and biochemical specialisations (see Smith, 1982; Richards, 1984; Chopra & Bhatla, 1990) that seem to have evolved comparatively recently (e.g. in *Macromitrium*; Vitt & Ramsay, 1985b). Epiphylls comprise a subgroup that inhabit the surfaces of living leaves.

While ecological studies of mosses have concentrated on adaptations of the gametophyte, the importance of the sporophyte should not be overlooked. Successful spore dispersal is essential for evolutionary progress, and the limited size of the sporophyte and its partial dependence on the gametophyte are, in the long term, a great disadvantage. Sporophytes in fugitive and colonist species contribute more to their own nutrition than do sporophytes in species with other life strategies. Increased reliance on translocation from the gametophore is typical of robust, long-lived, perennial species as well as the more ephemeral, annual shuttle species with simplified capsules (Longton, 1984). Correlations can be observed between, for example, seta length, capsule width, peristome reduction, spore size, length of life history, and habitat. Thus, for example, erect capsules predominate in epiphytic or saxicolous habitats, while species on moist forest floors often have elongate, straight setae and curved, horizontal or pendent capsules that are smooth, cylindrical and have a well-developed peristome. Because this same set of characteristics can occur in related or completely unrelated taxa in the same environment, these are considered to have adaptive value (Vitt, 1981; Shaw & Robinson, 1984).

Distribution

Factors determining the distribution of mosses include the availability of water and suitable conditions for growth and reproduction. Modern distributions have been influenced by past climates, habitat history and the method of dispersal of the species. For species to spread by vegetative, horizontal growth alone, a continuum of suitable habitats and climatic conditions over space and time would be required. Scott (1988) estimated that an acrocarpous cushion type might require one million years to spread 10 km, while a pleurocarp might move ten times farther in the same time. However, distribution of most mosses is not determined by growth alone but by dispersal of spores or vegetative propagules. While fragments and some larger diaspores might be distributed by short-range dispersal, the capacity for smaller diaspores to survive long-range dispersal depends on their vulnerability to desiccation and low temperatures (van Zanten, 1978).

The successful transition from diaspore to new colony requires a suitable niche and the ability to establish in competition with existing vegetation, or to regenerate vegetation after natural disturbances (van Zanten & Pócs, 1981). Spread of a species depends on colony's growth rate and macroclimatic and micro-scale moisture conditions. The estimated primary colony expansion and establishment period can take as long as 30–40 years (Vitt, 1989).

Evidence that mosses are distributed over long distances has been clearly demonstrated in the vegetation of isolated Subantarctic islands such as Macquarie Is. and Heard Is. (Bergstrom & Seppelt, 1988; Selkirk *et al.*, 1990). Short-distance dispersal tends to be most influential among aggressive pioneers of inhospitable areas where competition is minimal, or in non-aggressive species if the vegetation is not saturated (van Zanten & Pócs, 1981).

In Australia, patterns of distribution, determined by both macro- and micro-climate, frequently correspond to gross vegetation types, e.g. rainforest and arid zone vegetation. Factors of particular importance include rainfall and humidity, and many families of pleurocarps (e.g. Meteoriaceae, Sematophyllaceae, Thuidiaceae and Hypnaceae) predominate in moist forests in the eastern coastal regions of the country. Temperate species are distributed widely across southern latitudes from the south-west of Western Australia to coastal South Australia, Tasmania, Victoria, the Australian Capital Territory and southern and eastern New South Wales (Scott & Stone, 1976). Alpine and subalpine species are confined to the Southern Tablelands of New South Wales, parts of the Australian Capital Territory, north-eastern Victoria and Tasmania (Ramsay *et al.*, 1986). Subtropical and tropical species occur as far south as the central coast of New South Wales and north into Queensland, while tropical species occur across northern Australia with the greatest diversity in north-eastern Queensland (Ramsay & Cairns, 2004). The high peaks in this area, Mt Bartle Frere, Mt Bellenden Ker, Thornton Peak and Mt Lewis, have a distinctive bryoflora and include endemics such as *Macromitrium dielsii*, *Clastobryum dimorphum*, *Touwia laticostata* and *Buxbaumia thorsborneae*. Arid and semi-arid species occur west of the Great Dividing Range and in the drier areas of the Northern Territory, South Australia and Western Australia (Catcheside, 1980; Ramsay, 1984; Stoneburner *et al.*, 1993).

The mountain ranges, tablelands and moist forests near the east coast of Australia support a considerable diversity of mosses in contrast to the more arid regions to the west of the Great Dividing Range. Thus, at least 60 per cent of Queensland mosses occur in the wet-tropical forests of the north-east (Ramsay & Schofield, 1987; Ramsay, 1988b; Ramsay & Cairns, 2004). Some are endemic, and the remainder have strong affinities with the bryofloras of New Guinea, New Caledonia or Malesia. The interesting mix of subtropical and temperate species in the *Nothofagus moorei* forests of the border ranges between New South Wales and Queensland represents a rather different bryoflora, while the lowland monsoon forests of the Northern Territory, the north of Western Australia and north Queensland contain different suites of species (e.g. Catcheside & Stone, 1988; Stoneburner *et al.*, 1993).

The cooler and more moist habitats of southern New South Wales, Victoria and Tasmania support a diverse temperate moss flora, and the mountains ranges have distinct alpine and subalpine elements (Ramsay *et al.*, 1986). South-eastern Australian moss floras are more similar to those of New Zealand and Subantarctic Macquarie Is. (Scott & Stone, 1976; Ratkowsky & Ratkowsky, 1982; Ramsay *et al.*, 1986; Selkirk *et al.*, 1990; Seppelt 2004). Of the 54 alpine mosses in Tasmania, 44 also occur in Macquarie Is., 34 in mainland Australia and 38 in New Zealand (Ramsay *et al.*, 1986).

Based on published checklists and more recent data (e.g. Streimann & Klazenga, 2002; Klazenga, 2005) about 26% of the moss species in Australia are thought to be endemic. While endemism was previously considered to be most pronounced in the coastal and montane rainforests of north-eastern Queensland (from south of Cooktown to just north of Townsville), a recent study has shown this to have been exaggerated, with the actual level of endemism in that area being only about 7 per cent of the moss flora (Ramsay & Cairns, 2004). Although the total number of mosses recorded from the Northern Territory is comparatively low (113 taxa), six are thought to be endemic. New South Wales has a higher degree of endemism (70 species, or 12 per cent of the flora), Victoria and Tasmania have significant numbers of endemics (18 and 26 species, respectively), while Western Australia has three species and South Australia does not have any endemic species.

Inland of the Great Dividing Range, moss diversity decreases markedly with increasing aridity (Ramsay, 1984; Stoneburner *et al.*, 1993). Thus, for example, only one of the 21 species of *Macromitrium* (*M. archeri*) in Australia occurs in Western Australia. However, 70 per cent of Western Australian mosses are also found in South Australia, 67 per cent in

New South Wales and 46 per cent in Queensland (Stoneburner *et al.*, 1993). In the semi-arid areas of Victoria, Western Australia and South Australia the most diverse families are the Pottiaceae, Dicranaceae, Bryaceae and Fissidentaceae (Catcheside, 1980, 1982; Stoneburner *et al.*, 1993; Streimann & Klazenga, 2002). Few pleurocarpous taxa occur in these drier areas (only 20 species recorded from Western Australia and 31 from South Australia), but ephemeral, acrocarpous forms are well represented. The distribution of mosses in Western Australia demonstrates a north-south disparity, with 147 species in the south-west and only 29 in the Kimberley Region in the north. While exploration and collecting has been most intensive in the south-west, the low diversity of mosses in the north is unequivocal (G.A.M.Scott, pers. comm; H.Streimann, pers. comm.). The paucity of moss species and low levels of endemism in the south-west of Western Australia is in marked contrast to the very high diversity and endemism of angiosperms in the same area (75–80 per cent; Hopper, 1979).

Surprisingly, Polytrichopsida are absent from Western Australia and the Northern Territory although suitable habitats are available. These mosses are common in the eastern States and in New Zealand, and include many weedy species of roadsides and other disturbed sites.

Mosses are rather poorly represented in ‘typical’ Australian eucalypt forests (see Ashton, 1986; Meagher, 1996). In contrast, diversity and abundance are greatest in the more ancient rainforest elements such as the *Nothofagus* and podocarp forests of southern Australia, the montane rainforest along the Great Dividing Range to northern Queensland (Catcheside, 1982; Ramsay, 1984, 1988b; Ramsay *et al.*, 1986; Ramsay & Cairns; 2004) and in Tasmania (Dalton *et al*., 1991; Jarman & Fuhrer, 1995). Species of *Papillaria* and *Macromitrium* occur from Tasmania to north-eastern Queensland, while some families (e.g. Calymperaceae and Sematophyllaceae) are primarily tropical in origin and are diverse only in north-eastern Queensland, being rather poorly represented elsewhere in Australia. Primary colonisers such as the Fissidentaceae, Bryaceae, Ditrichaceae, Funariaceae and Pottiaceae are present throughout Australia, although species composition varies between different climatic regions. Temperate mosses such as *Bryum s. lat.* and *Tortula* tend to be diverse across southern-temperate Australia but have fewer species in the tropics. However, in the genus *Rosulabryum*, with 14 Australian species, ten occur in north-eastern Queensland and five are endemic to Australia.

Biogeography

The historical and biological factors determining patterns of distribution in bryophytes are rather similar to those that influence vascular plants. However, bryophytes, with their distinctive propagules and long-distance dispersal tend to exhibit broader geographical ranges (van Zanten & Pócs, 1981; Schuster, 1983; Schofield, 1985, 1992).

Hill *et al.* (1999) and Crisp *et al.* (1999) described the tectonic events that shaped the origin and evolution of the Australian angiosperm flora. While mosses were probably already diverse and widespread before the separation of Gondwana and Laurasia, climatic changes and subsequent dry periods fragmented and diversified the existing bryoflora, subjecting it to intense selective pressures with only those species in protected niches surviving. Between the Cretaceous and Mesozoic, selection favoured terrestrial, drought-tolerant genotypes. During the Tertiary, with the rise of the angiosperms, microclimatic and microedaphic shifts opened up forest niches and led to an increase in the diversity of bryophytes, especially epiphytes (Vitt, 1984).

The first detailed analysis of floristic regions for mosses on a global scale was that of Herzog (1926) who delimited six bryogeographical kingdoms which were later mapped and further described by Miller (1982). Wijk *et al*. (1959–1969) recognised 20 floristic regions that have been widely accepted, although Tan & Pócs (2000) suggested that some revision of boundaries is required. Schofield (1992) provided an interpretation of the six Herzog kingdoms: Holarctic, Palaeotropical, Neotropical, Cape or South African, Holantarctic and Australian, the Australian bryoflora having elements of the last two.

The Holantarctic Kingdom developed from the floras of widely separated elements of Gondwana. Floristic affinities are greatest between those fragments that have had most recent direct connections, while floristic richness is most pronounced in those areas with the greatest time of isolation from other floras combined with the greatest niche range (Schofield, 1992). Intercontinental similarities at the species level are most likely the result of long-distance dispersal (van Zanten & Pócs, 1981). Examples of circum-Subantarctic species are especially common in genera such as *Hypnum* (Ando, 1972, 1982), *Campylopus* (Frahm, 1987, 1994) and *Bryum s. lat.* (Ochi, 1982). Floristic affinities between Australia and southern Africa are demonstrated by mosses such as *Ischyrodon lepturus*, *Catagonium nitens*, *Eccremidium exiguum* and *Bryobartramia novaevalesiae* (Scott & Stone, 1976), all of which occur in the drier areas of Victoria, South Australia and Western Australia. By contrast, genera such as *Catagonium*, *Cyrtopus*, *Goniobryum*, *Ptychomnion*, *Weymouthia* and species such as *Dicranoloma menziesii*, *Hypnum chrysogaster*, *Goniobryum subbasilare*, *Campylopus chilensis*, *C. laxoventralis* and *C. modestus* represent links between Australasia and South America. The cool, mesic climate of southern Gondwana provided a refugium for austral bryophytes, and remnants of the Gondwanan bryoflora persist today in high southern latitudes (Miller, 1982; Vitt, 1982b, 1984). Fifty-six species are common to the alpine areas of Australia and New Zealand, but only six are shared between the alpine areas of Australia and Papua New Guinea (Ramsay *et al.*, 1986). Among the species confined to Australia and New Zealand are *Camptochaete arbuscula*, *Cryphaea exannulata*, *Fallaciella gracilis*, *Meesia muelleri*, *Mittenia plumula*, *Rhaphidorrhynchium amoenum*, *Sematophyllum homomallum* and *Tridontium tasmanicum*.

The Australian Kingdom, which occupies most of the continent, lies between the Holantarctic in the south and the Palaeotropical in the north (Schofield, 1992). In the Tertiary, when sea levels were higher, much of Australia was an archipelago of islands, and each of these islands, now connected by dry land, became a reservoir of endemic angiosperm species that had evolved during the isolation. This Kingdom encompasses areas of great climatic diversity, from the wet and humid coastal regions and tablelands along the Great Dividing Range, and alpine and subalpine areas in the south-east, to the arid and semi-arid centre or Eremaean Zone occupying more than one-third of the land area of the continent. Schodde (1989) proposed five biotic regions based on evidence from biogeographical studies of the flora and fauna (see Groves, 1999, p. 323). More than half of Australia experiences seasonal or continuous aridity (Hill *et al.*, 1999). Bryophytes are poorly represented in modern Australian *Eucalyptus* forests, but they are diverse in rainforest with a long geological history. Palaeotropical elements are well represented in northern Australia, and a significant Gondwanan element, including the Hypnodendraceae, Leptostomaceae and some species of *Campylopus*, *Macromitrium* and *Fissidens*, is also present in temperate to tropical habitats.

Tan & Pócs (2000) have a broader view of the Australian region, and they include Australia, New Zealand, New Caledonia and offshore islands in their Australasian zone. With the exception of the Gondwanan element, the strongest affinities of the Australian bryoflora are with the Paleotropical Kingdom (Schofield, 1992) which includes the Indomalayan area, western Melanesia and the oceanic islands of the western Pacific including New Caledonia. Tan & Pócs (2000) defined Malesia as comprising a long chain of peninsular and island countries (Malaysia, Indonesia, the Philippines, Brunei and Papua New Guinea). Moreover, they noted its unique geological history following the collision of the Sahul, Sunda and Australian plates during the mid-Tertiary. Several of the islands, e.g. Sulawesi and the Philippine archipelago, are composite in origin, being the accretion of Laurasian and Gondwanan elements (Hall & Holloway, 1998). Thus, floras that were originally dissimilar have subsequently become integrated (Tan & Pócs, 2000), so that the modern lowland bryoflora is mainly Asiatic, while the montane and eastern Malesian floras have a strong representation of Australian elements.

Parts of the northern Australian bryoflora appears to be of recent Asian-Malesian derivation. While Australia and Papua New Guinea share 50–60 per cent of genera (Ramsay *et al.*, 1986), affinities at the species level are much lower (about 10 species; Hyvönen, 1989). A few species of Australasian affinity extend into Malesia (*Hampeella pallens* and *Dicranoloma billardierei*), some are confined to southern Malesia (e.g. *Thuidium sparsum* and *Sclerodontium pallidum*), while *Glyphothecium sciuroides* and the genus *Leptostomum* extend through temperate rainforest zones of Australasia and South America. Species of Australian origin also occur in the tropical montane forests of Malesia and Sri Lanka with a disjunction in eastern Australia suggesting fragmentation of a previously continuous distribution caused by the increasing aridity of Australia (Touw, 1992). In western Melanesia 35 taxa (mainly Calymperaceae and Meteoriaceae) are shared with Australia, Asia and Oceania and 16 are shared with Asia and Australia (Hyvönen, 1989). Pippo & Koponen (1997) have discussed the affinities of Australian moss species within western Melanesia.

Northern Hemisphere families, such as Hypnaceae and Brachytheciaceae, are poorly represented in Australia. Although Schuster (1983) suggested that the c. 200 million years of Gondwanan isolation resulted in a high degree of endemism at family and genus level in the Southern Hemisphere, endemism of this type is actually low in Australia, the small number of endemic genera including *Bryostreimannia*, *Calymperastrum*, *Mesochaete*, *Stoneobryum* and *Touwia*.

Biogeographical disjunctions within Australia include those between the eastern-coastal region and the rest of the country and between northern and southern latitudes. While some disjunctions are almost complete, there are noticeable areas of overlap between, for example, subtropical and temperate floras of eastern New South Wales. Here, fragments and derivatives of the Gondwanan flora have been enriched at high elevations by Holarctic and Holantarctic elements that have arrived by dispersal in the last 2–3 million years. Supportive evidence is found in Gondwanan groups with restricted Southern Hemisphere distributions (e.g. Hypnodendraceae, Orthotrichaceae, Calomniaceae and some members of the Sematophyllaceae) and the absence of large numbers of Laurasia-derived Hypnobryales (Vitt, 1990).

Primarily pantropical families present in Australia include the Calymperaceae, Sematophyllaceae, Meteoriaceae, Pterobryaceae and Racopilaceae. Pantropical and palaeotropical floristic elements are strongly represented in northern Australia, especially north-eastern Queensland (Ramsay & Cairns, 2004). This diversity is well documented for families such as the Sematophyllaceae (Ramsay *et al.*, 2004), Bryaceae (Eddy, 1996; Spence & Ramsay, 1996; Spence & Ramsay, this volume). The Calymperaceae is represented in north-eastern Australia by 42 species, most of which are palaeotropical (Eddy, 1996; Reese & Stone, 1995).

Apart from the bryogeographical relationships already discussed, Australian mosses include some that are cosmopolitan or bipolar in their distributions. Examples of widespread species include *Brachythecium rutabulum*, *Ceratodon purpureus*, *Bryum argenteum*, *Encalypta vulgaris*, *Grimmia pulvinata*, *Leptobryum pyriforme* and *Polytrichum juniperinum*. Bipolar mosses present in Australia include *Pottia heimii*, *P. truncata*, *Orthodontium lineare*, *Drepanocladus uncinatus* and *Aulacomnium palustre* (Schofield, 1974).

The Australian bryoflora includes taxa with diverse histories and potentials, and those with ancient ancestors as well as comparatively recent colonisers. Knowledge of the current distribution of mosses will improve as taxonomic and ecological studies continue, but "the database for bryogeography is limited, and will remain so, because of the destruction of flora and habitats by human activity and the paucity of fossil evidence, even for relatively recent time" (Schofield, 1992).

Origin and Evolution of Mosses

There is evidence to support the evolution of terrestrial green plants from aquatic ancestors that possessed an alternation of sporophyte and gametophyte generations (Smith, 1986; Goffinet, 2000). Success in the terrestrial environment required the development of physiological and morphological adaptations to prevent desiccation as well as mechanisms for the formation and protection of the diploid embryo. Although all land plants possess the heteromorphic alternation of gametophyte and sporophyte generations, two trends have evolved based on the location and ontogeny of the embryo initial following fertilisation.

In bryophytes, the sporophyte is wholly or partially dependent on the gametophyte for nutrition, and it remains attached to the archegonial venter for a long period. In contrast, the sporophyte of ferns, fern allies, gymnosperms and angiosperms is both independent and photosynthetic.

Bryophytes and green algae have similar photosynthetic pigments, cell wall components, starch as a food reserve and flagellar characteristics. A closer affinity of bryophytes to the vascular plants rather than to the algae is supported by the shared characteristics of conducting tissue elements, stomata, cell division with a spindle at mitosis, multicellular sex organs, cutinised and ornamented trilete spores with sporopollenin in the wall, ultrastructural features (Smith, 1986), the occurrence of lignin-like and flavonoid compounds (Mues, 1990), the close relationship between gametophyte and sporophyte, and the absence of a pyrenoid (except in the hornworts).

An appreciation of the role of bryophytes is critical to an assessment of evolution in the terrestrial environment (Mishler & Churchill, 1985). The fossil record and phylogenetic studies indicate that the major groups of bryophytes are very ancient and probably originated near the time of the earliest land plants (Goffinet, 2000; Jordon, this volume).

The oldest known fossil land plants share some common features with bryophytes. This suggests that the various bryophyte groups may have originated from a diverse gene pool at a level sufficient to achieve partial transmigration to land (Miller, 1979; Crandall-Stotler, 1986; Smith, 1986; Kendrick & Crane, 1991; Mishler *et al.*, 1992). The literature on palaeo-climatology and plate tectonics also supports the notion that some ancestral bryophytes might have arisen with other land-plants and constituted one of several largely unrelated archegoniate lines. Adaptation to similar pressures imposed by the gametophyte-dominated, heteromorphic, archegoniate life history (Crandall-Stotler, 1984) would have been necessary for all bryophytes. Cladistic analyses, morphological, molecular and genetic studies (Mishler & Churchill, 1984, 1985; Mishler, 1986; Mishler *et al.*, 1992; Goffinet, 2000) support a monophyletic origin for land plants, a position hotly debated and not necessarily supported by all (e.g. Waters *et al.*, 1992), with the mosses being a monophyletic sister group to vascular plants and the liverworts a sister group of a moss-vascular plant lineage. Crosby (1980), Mishler & Churchill (1984, 1985) and Crandall-Stotler (1986) considered the bryophytes to represent several lines of evolution separate from vascular plants, although they may share common ancestors since they have similar life cycles and structural organisation of the gametophyte and sporophyte. Recent phylogenetic reconstructions of the relationships support the hypothesis that hornworts are the most basal group with mosses and liverworts forming a monophyletic sister clade to the vascular plants (Goffinet, 2000).

While bryophytes appear anatomically simple when compared with vascular plants, they are not necessarily morphologically primitive (Stoneburner, 1990). Many are uniquely suited to survival at environmental extremes (Schofield, 1985) and, indeed, the complex biochemical nature of mosses (Suire & Asakawa, 1979; Asakawa, 1986; Mues, 1990, 2000), their physiological responses to the environment, levels of genetic variation (Stoneburner *et al.*, 1991; Goffinet, 2000; Cove, 2000) and cytological complexity (Smith, 1978, 1986; Newton, 1986) do not suggest primitiveness.

Evolutionary trends in mosses

Although all mosses share the gametophytic features of an apical cell with 3 cutting faces, leaves originating from stem segments derived from this cell and differentiation of separate leaves, sporophytic attributes suggest distinct evolutionary lines. While trends in the evolution of mosses are reflected in both the gametophyte and sporophyte (Vitt, 1984; Schofield, 1985), it is the development of the capsule and the structure of the mature peristome that best demonstrates relationships.

There are two main evolutionary trends in evidence in the origin and development of the moss peristome. Based on the primary architecture of the teeth, peristomes are either nematodontous or arthrodontous. The former occur in Takakiopsida (not in Australia), Andreaeopsida, Andreaeobryopsida (not in Australia), Sphagnopsida, Polytrichopsida and

(?)Oedopodiopsida (not in Australia). Inferences from morphological data and the nuclear and chloroplast genomes have led to an evolutionary scheme in which *Takakia* and *Sphagnum* form a weakly supported basal lineage, followed by the Andreaeopsida and Andreaeobryopsida and, finally, those mosses with a cylindrical columella. However, none of the ambiguities pertaining to the early diversification of mosses have been clarified, and reconstruction of ancient evolutionary events is still problematic (Goffinet & Buck, 2004).

Nematodontous peristomes

Prior to the discovery of male plants and sporophytes (Smith, 1990), *Takakia* was regarded as a hepatic. However, Hedderson *et al.* (1996, 1998) provided the molecular evidence in support of *Takakia* belonging to the mosses (Class Takakiopsida). Capsules dehisce occurs along a single longitudinal spiral line.

In the Sphagnopsida, the gametophore is highly specialised, but the protonema is simple. Moreover, the unistratose leaves are exceptionally distinctive, with the differentiation of dead hyaline porous cells and living chlorophyllose cells. The unusual branching system with fascicles of lateral branches, the nature of the perigonial branches and the pseudopodium associated with growth of the sporophyte are a morphological rather than a physiological adaptation to drought (Pujos, 1992). The sporophyte has a columella overarched by a specialised sporogenous layer, it lacks an operculum, and there is an explosive dehiscence of the capsule. The recently described Tasmanian moss *Ambuchanania leucobryoides* (Sphagnopsida, Order Ambuchananiales) is highly distinctive in terms of its morphology, and it occupies very different habitat to *Sphagnum* species (Seppelt, this volume). Molecular studies by Shaw (2000) resolved *Ambuchanania* as sister to the remainder of Sphagnopsida.

In the Andreaeopsida, leaf arrangement and structure and the gametangia are comparatively unspecialised; these mosses are characterised by the dehiscence of the capsule by one or more longitudinal sutures as a means of exposing most of the spores for dispersal. Within the Andreaeopsida *s. lat.*, evolution has followed two lines, one leading to the present class Andreaeaopsida and the genus *Andreaea*, and the other to the distinct genus *Andreaeobryum* in the new class Andreaeaobrypsida (Goffinet & Buck, 2004).

A significant contribution of molecular research to our understanding of moss evolution has been the recognition of *Oedipodium* as the sister group to the peristomate mosses. Goffinet & Buck (2004) highlighted its significance by placing it in the monotypic Class Oedipodiopsida. *Oedipodium* lacks a peristome, and whether it is pleisomorphic or the result of secondary loss remains unclear. Peristomate mosses and *Oedipodium* share a cylindrical columella as well as protonemal disc-branch initials (Newton *et al.*, 2000).

There is considerable specialisation in the gametophore of the Class Polytrichopsida, with a well-developed and elaborate water-conducting system in the gametophyte and sporophyte (Hébant, 1977, 1979), sheathing leaf bases, rows of photosynthetic lamellae parallel to the costa on the adaxial surface of the leaves and underground ‘rhizomes’. Differentiation of the conducting system appears to have enabled some tall, free-standing gametophores to reach up to 60 cm or more in height. Species are usually dioicous, and male plants possess a ‘splash-cup’ perigonium to enhance wider distribution of sperm to the tall perichaetium-bearing gametophores, and produce enormous quantities of exceptionally minute spores (Ingold, 1959). In the Polytrichaceae the peristome has 16, 32, or 64 multicellular teeth, while in *Polytrichum* 3 or 4 cell layers contribute to small teeth arranged in a single circle. In *Dawsonia*, teeth are elongate, bristle-like and arranged in several irregular circles, being derived from more than 6 concentric cell rows. A phylogenetic reconstruction of the family Polytrichaceae was provided by Hyvönen *et al.* (1998, 2004). Support for the monophyly of the family is drawn primarily from the chloroplast gene rbcL, while genetic data from DNA give ambiguous support for generic relationships.

The gametophyte of Class Tetraphidopsida, with only five species, shares many features with the Bryopsida. However, it differs in the absence of air spaces in the capsule, a character state shared with the other basal lineages such as *Takakia, Sphagnum* and *Andreaea* (Goffinet *et al.*, 2004a). The multicellular structure of the four peristome teeth places it closer to the nematodontous type of the Polytrichales (Edwards, 1984). Preliminary molecular studies have been unable to resolve the relationships between the Polytrichales and Tetraphidales (Goffinet & Buck, 2004).

Further research is essential to determine the significance of the nematodontous peristome in the evolution of the arthrodontous teeth typical of the Class Bryopsida (*sensu* Buck & Goffinet, 2000). The Bryopsida, with at least 12,000 species, exhibits characters that include dorsiventrally flattened gametophores, multiple costae, elaboration of leaf cell surfaces, diversification of cells in the alar region, production of a range of gemmae and other asexual propagules, elaboration of branching systems, diversity of growth forms, acrocarpy and pleurocarpy, specialisation of perichaetia and perigonia and anisospory. Major evolutionary trends in the gametophyte include differences in life form, growth form, branching pattern and perichaetial position.

Mitten (1859) first recognised the phylogenetic significance of acrocarpy and pleurocarpy. However, the distinction is not always clear-cut, and some acrocarpous groups appear to have prostrate species with laterally displaced branching, e.g. *Macromitrium* and *Schlotheimia* in the Orthotrichaceae, sometimes called “pseudopleurocarpous” (Vitt, 1984), while *Cinclidotus* (Cinclidotaceae) has been described as pseudopleurocarpous (Proctor & Smith, 1995) or cladocarpous (Smith, 1978). Cladocarpy has often been defined as a form of pleurocarpy (Frey, 1971; Magill, 1990; Mishler & De Luna, 1991).

Different interpretations of perichaetial position have resulted in a reassessment of some families and their genera, e.g. Rhizogoniaceae and Spiridentaceae (Buck & Vitt, 1986; Koponen, 1988), Hedwigiaceae (Vitt & Buck, 1984; Buck & Vitt, 1986; Hedenäs, 1994; De Luna, 1995). Using more precise definitions, La Farge-England (1996) demonstrated that cladocarpy is widespread in acrocarpous lineages and that the distribution of perichaetial position in 14 major clades of the Bryopsida divides them into three basic patterns: acrocarpous-cladocarpous, cladocarpous-pleurocarpous and pleurocarpous lineages. The amended definitions of perichaetial position present a framework to enable a more rigorous assessment of the structural organisation of mosses and, consequently, more informative insights into evolutionary relationships (La Farge-England, 1996).

Arthrodontous peristomes

In arthrodontous peristomes, teeth consist of cell-wall remnants rather than whole cells. The haplolepidous, or *Dicranum*-type has the endostome segments composed of a single column of cell plates on their outer surface. Diplolepidous peristomes have two columns of dorsal plates on the outer teeth and usually two rings of teeth. In the two diplolepidous subgroups, the exostome teeth in the outer ring can either be opposite the segments of the inner ring or alternate with them (Vitt, 1981, 1984; Shaw & Robinson, 1984; Buck & Goffinet, 2000).

Goffinet & Buck (2004) recognised several subclasses of Bryopsida. Among these, the Funariidae (with a diplolepidous-opposite peristome) includes four families, Funariaceae, Gigaspermaceae, Disceliaceae and Encalyptaceae. The Dicranidae, with a haplolepidous peristome, comprises 24 families including the speciose Grimmiaceae, Archidiaceae, Fissidentaceae, Calymperaceae, Ditrichaceae and Pottiaceae. The Bryidae includes 15 families with acrocarpous and pleurocarpous forms and a diplolepidous peristome. Significant acrocarpous families in the Australian bryoflora include Orthotrichaceae, Bartramiaceae, Bryaceae and Leptostomaceae, with Hypnodendraceae, Rhizogoniaceae, Pterobryellaceae and Racopilaceae among the pleurocarps. A fourth subclass, the Hypnidae, includes 50 families of pleurocarpous forms with diplolepidous-alternate peristomes. One order, the Hypnales, includes many significant families in the Australian flora, e.g. Amblystegiaceae, Sematophyllaceae, Meteoriaceae, Hypnaceae, Cryphaeaceae, Pterobryaceae, Neckeraceae and Lembophyllaceae.

Because of certain unique attributes, two subclasses of the Bryopsida (*sensu* Goffinet & Buck, 2004), the Buxbaumiidae and Diphysciideae, are now recognised as separate although they share a unique peristomial architecture (Edwards, 1984) with the inner peristome consisting of a high, pleated membrane. In *Buxbaumia*, the reduction of the gametophyte is so pronounced that it consists of a few perichaetial leaves surrounding one or two archegonia in the female, or a perigonium with a single antheridium surrounded by a unistratose sheath in the male. In the Buxbaumiideae the sporophyte is a distinctive shape with the amphithecial layer double that of *Diphyscium*. In the peristome of *Buxbaumia* the walls of one or two outer layers of cells may be thickened and partially resorbed, and thus they form two rows of teeth, even if the outermost row is rudimentary and remains partially attached to the capsule wall. In *Diphyscium*, the gametophores are reduced with ±multistratose, chlorophyllose leaves, and there is little if any differentiation of the stem. The outer peristome is composed of a single row of teeth fused to the inner membrane. The cells surrounding the outer peristome are entire and markedly thickened. The peristome is reminiscent of the nematodontous type, but most of the circles of teeth are remnants of cell walls *not* whole cells, hence they are apparently arthrodontous (Shaw *et al.*, 1987).

Distinctive features of the Order Archidiales, now placed in Subclass Dicranidae (Goffinet & Buck, 2004) although its affinities remain ambiguous, include the multilayered intine (formed by different orientations of intine microfibrils; Brown & Lemmon, 1985) not known to occur in the spore cells of any other moss except *Sphagnum*. Other characteristics include the genesis of cell layers in the embryonic sporophyte with two columns of endothecial cells (instead of four), bilateral instead of radial symmetry of the sporophyte, a dome-shaped spore sac and intercellular airspaces, the absence of an inner spore sac, rudimentary columella, small numbers of sporocytes (4–12), the largest spores known in mosses with thick laminated intine (Stone, 1987) and the absence of a seta and peristome. In some species the protonema is persistent.

Vitt (1984) placed Calomniaceae in the Order Tetraphidales (Polytrichopsida), but in his later revision of *Calomnion* (Vitt, 1995) he suggested that a possible close relationship to Rhizogoniaceae (Bryopsida, Bryidae). The absence of a peristome in Calomniaceae creates uncertainty as to its affinities, but chromosome data tend to support placement in or near the Rhizogoniaceae (Ramsay, 1992; Goffinet & Buck, 2004).

An important trend in the evolution of the gametophyte leads to structural reduction, with the greatest degree of specialisation being the production of multicellular spores (e.g. in some Orthotrichaceae), or massive spores consisting of pregerminated protonemata (e.g. in Dicnemonaceae). Some species with specialised protonemata also show ecological specialisation (e.g. *Mittenia plumula* often found in caves, or *Calomnion complanatum* epiphytic on tree ferns). Size, physiological adaptations and morphological diversity, while restricted by the absence of lignified vascular tissue and the development of roots, have nevertheless led to a great diversification of species.

Evolutionary trends in the sporophyte include reduction in the number of cell layers involved in the production of the peristome and the loss of the exostome, endostome or both. Determination of directions of evolution should be made on consideration of character correlations (Vitt, 1984). Thus, for example, the acrocarpous growth form is most prevalent in taxa with the diplolepidous-opposite and haplolepidous peristomes, while cladocarpous and pleurocarpous growth forms occur in all major lineages and are an evolutionary adaptation to specialised substrata and environmental situations (Vitt, 1984). In mosses of considerable physical length, structural support is given by water; or alternatively they are prostrate or pendant. In some epiphytic mosses, the stems have supportive fibre-like stereids but lack an elaborate conducting system. In spite of the considerable amount of information already accumulated we are only just beginning to understand some of the evolutionary processes involved in the speciation of mosses (Szweykoski, 1984). It is very likely that in many groups vigorous evolution has taken place during the last 20 million years (van Zanten & Pócs, 1981) and isozyme studies provide evidence that it is still occurring (Wyatt *et al.*, 1989b, 1993).

Molecular studies have supported a monophyletic lineage for the haplolepidous peristome (Newton *et al.*, 2000 and others), have revised the interpretation of genera in the Orthotrichaceae (Goffinet *et al.*, 1998), led to the transfer of *Amphidium* to the diplolepidous mosses and excluded *Bryobartramia* from the Dicranales. It has resolved three major clades within the haplolepidous mosses, and has highlighted the polyphyly of families such as the Bryaceae, Sematophyllaceae and Orthotrichaceae. The circumscription of some families has been reassessed and some genera have been moved elsewhere, e.g. *Pohlia* and *Schizymenium* to the Mniaceae and *Orthodontium* to the Orthodontiaceae, while *Campylopus* has been incorporated into the Leucobryaceae. The contribution of molecular data to the systematics of the Bryineae (*sensu* Vitt, 1984) has demonstrated that the acrocarpous and diplolepidous-alternate peristomate mosses gave rise to the pleurocarpous mosses (Goffinet & Buck, 2004).

"As bryologists move into the twenty-first century, all sources of data that allow for better resolution of phylogenetic relationships are needed, and molecular sequences offer the best hope for understanding not only familial circumscriptions and phylogeny, but ultimately also the evolution of morphological characters. It is, indeed, the history of morphological transformations that define taxa or of the distribution ranges of the species that justify the investment into phylogenetic approaches. A revival of critical morphological and anatomical studies is, however, imperative if major clades of mosses are to be diagnosed by characters other than genomes" (Goffinet & Buck, 2004).

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