

Paleozoic mosses: Small, but no longer inconspicuous

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The next time you stroll in a wooded area and spot small, green clumps of soft-looking plants, perhaps next to a rotting log or near the bank of a stream, you will probably have found one of several tens of thousands of species of mosses. Today these plants frequent moist areas that extend from the Equator to mountain tops, but they can also be found in extreme environments such as deserts. Like all land plants, they have an alternation of generations that results in the formation of an embryo (Kenrick and Crane, 1997), but unlike vascular plants, it is the leafy green gametophyte that is the larger, more conspicuous phase, with the spore-producing part of the life cycle (sporophyte) wholly dependent on the gametophyte. The fact that these plants exist in a diverse number of habitats is in part related to the fact that they are poikilohydric. This physiologic condition means that mosses are capable of tolerating the loss of a high percentage of their body water and still rehydrate when environmental conditions change (Oliver et al., 2005; Proctor et al., 2007). As part of poikilohydry, however, mosses (and bryophytes in general) lack a structural means to prevent desiccation, such as the cuticle of land plants.

Mosses, together with liverworts, comprise the bryophytes (Bryophyta), plants that lack vascular tissues and several other features of vascular land plants. The hornworts, a poorly known group that has been considered part of the bryophytes in the past, are often classified into a separate group (Anthocerotophyta), and in some phylogenies, resolve as sister to the vascular plants (e.g., Ligrone et al., 2012). Which of these groups of plants is the oldest has been debated for many years (Newton et al., 2000; Ligrone et al., 2012), but both molecular and combined morphological phylogenetic analyses suggest that these plants were some of the first on land, and certainly preceded plants with vascular tissue (Renzaglia et al., 2007; Ligrone et al., 2012). The fossil record of early terrestrial plants consists of Ordovician–Silurian spores and occasional sheets of cuticle-like material; some of the latter may derive from liverworts (Taylor et al., 2009). These unusual spores, termed cryptospores, are generally interpreted to represent a liverwort grade of evolution (e.g., Rubinstein et al., 2010; Wellman, 2010), and the liverworts are considered to be the earliest diverging group of land plants (e.g., Qiu et al., 2006). Evidence of spores with liverwort wall structure within a fragment of sporangial wall from the Upper Ordovician of Oman supports this view (Wellman et al., 2003).

But what of the mosses? What did early mosses look like? How old were they, where did they live, and why don't we know more about them? The answers to some of these questions can only be found in the fossil record. While there have been reports of fossil mosses, especially in Cenozoic and younger deposits (Taylor et al., 2009), the general paucity of Paleozoic discoveries is typically attributed to their poor preservational potential (delicate tissues that simply do not preserve), a lack of training in the study of the group, and the difficulty in recognizing fossils belonging to this group (e.g., if preserved as impressions, they may be mistaken for lycopsids). By the Permian, mosses were both geographically widespread (Antarctica to Siberia) and diverse, including some modern orders (Neuburg, 1960; Smoot and Taylor, 1986; Ignatov, 1990), thus suggesting an earlier origin than the late Paleozoic. As Hübers and Kerp point out in this issue of *Geology* (2012, p. 755), the macrofossil plants from Carbonifer-

ous mire environments have been so extensively studied (for >100 yr) that it is difficult to imagine moss diversity has not previously been recognized.

Hübers and Kerp provide a major step forward in understanding the occurrence and distribution of mosses in ancient ecosystems. They identify three types of fossil mosses from Middle Mississippian shales of eastern Germany. The age of the rocks is based on radiometric and palynological dates that place the fossils at ca. 330 Ma, and they are thus the oldest known reliable macrofossils of this group. The fossils consist of leaf fragments a single cell layer thick, except for one specimen that is bilayered, and probably represents the costal (midrib area) of the leaf. In the strict sense, mosses do not have true leaves, as these single-cell-layer structures lack vascular tissue. In some of the fossil specimens, there is evidence of cell dimorphism, with the shape and pattern of the cells similar to bryophytes reported from the Permian (e.g., Ignatov, 1990).

Hübers and Kerp's type III fossils are sufficiently well preserved so that several features can be identified on the leaves, leaving no doubt as to their systematic affinities. These fossils are remarkable in their similarity to modern members of the Sphagnales, an order of ~350 extant species with complex morphology and anatomy that today includes the peat mosses. The vast modern peat bogs in the Northern Hemisphere, unlike many peats in the geologic record, are made up almost exclusively of mosses of the genus *Sphagnum*; these are used commercially for fuel, in horticulture as a soil conditioner, and in packing material. Modern *Sphagnum* plants consist of a main stem and branches with scattered leaves; each leaf has two types of cells, narrow ones with chloroplasts (green or photosynthetic cells) and larger dead translucent (hyaline) cells, termed hyalocysts (or leucocysts or hyaline cells; Crandall-Stotler and Bartholomew-Began, 2007), that have large water-absorption and storage capacities. These cells, like tracheids in vascular plants, are dead at maturity, and have secondary walls with spiral thickenings (fibrils; Kremer et al., 2004), as well as air pores, unlike tracheids. *Sphagnum* plants, like almost all mosses, depend exclusively on passive capillary action to move water throughout the plant, most of it moved on the surface, so there is no 'control' over the movement of water, as there is in vascular plants (Thompson and Waddington, 2008). These hyaline cells are designed to expand and contract as water availability changes, and the secondary walls of spiral thickenings no doubt provide some structural rigidity during this process. Modern *Sphagnum* is capable of absorbing 20–30 times its weight in water (Yoshikawa et al., 2004). The complement of features in the fossils described by Hübers and Kerp suggests that by the early Carboniferous, mosses were already well diversified, and that some of the physiological processes found in mosses today existed in the bryophytes that grew in those ancient peat-accumulating environments.

Paleobotany, like many disciplines of science, sometimes undergoes a paradigm shift because a new fossil is discovered or there is a new interpretation of specimens already in collections. This also happens when a new technique is used to extract a different type of information, or when an old technique is improved or modified in some way. The use of various types of acid to macerate rocks to free plant cuticles and tissues has been employed for a long time in paleobotany (and palynology), sometimes with great success even in Paleozoic rocks (e.g., Doran, 1980), although it has more commonly been used with Cenozoic sediments. The technique as used by Hübers and Kerp relied on sieving the macerates using a larger

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screen size to capture larger fragments, and subsequently mounting the specimens for microscopic examination. The discovery of at least three types of mosses from a single collecting locality by these authors indicates that the use of this simple bulk maceration process has the potential to provide a far more accurate picture of the total floral composition, including inconspicuous plants such as bryophytes, in certain Paleozoic paleoecosystems.

The colonization of the land by plants is generally thought to have occurred in stages (e.g., Steemans et al., 2009; Rubinstein et al., 2010), beginning in the early Paleozoic with liverworts and liverwort-like plants (e.g., extinct forms such as the nematophytes; Taylor et al., 2009) and continuing until vascular land plants dominated terrestrial ecosystems in the Devonian. The effects of this invasion on weathering rates and the global carbon cycle have been extensively studied (e.g., Algeo et al., 2001; Beerling and Berner, 2005). To date, the mosses were not thought to have played much of an important role in this transition, but the diversity of forms in the early Carboniferous presented by Hübbers and Kerp suggests that perhaps this group of land plants has been overlooked until now. What is equally exciting is that, for the first time, it is now possible to add the dimension of a well-preserved and thus readily interpretable Paleozoic fossil record of mosses to phylogenies based mostly on molecular data (e.g., Newton et al., 2000) or poorly preserved fossils, and thereby to more accurately comprehend the evolution of this widespread but inconspicuous and ancient group of plants.

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