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## Morphology supports the setaphyte hypothesis: mosses plus liverworts form a natural group

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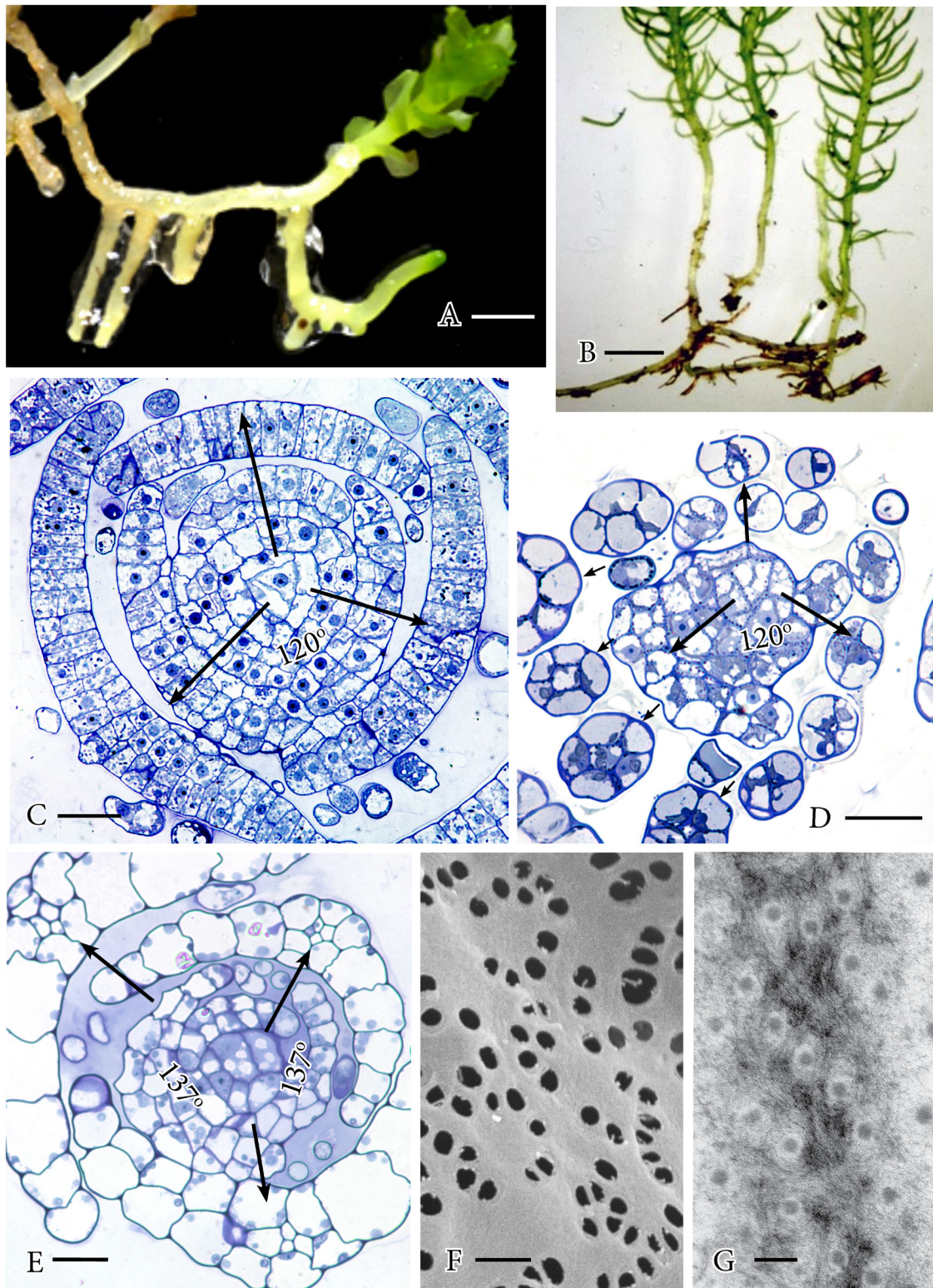
The origin and early diversification of land plants is one of the major unresolved problems in evolutionary biology. Occurring nearly half a billion years ago, the transmigration of green organisms to land changed the landscape and provided the food source for terrestrial life to invade a vast uninhabited space, adapt and radiate. Although bryophytes (mosses, liverworts and hornworts) are often regarded as the earliest terrestrial organisms, the order of their divergence remains contentious even as molecular analyses become more conclusive with expanded taxon sampling, massive genetic data and more sophisticated methods of analysis (Cox *et al.* 2018; Morris *et al.* 2018). Indeed, virtually every combination of relationships among bryophytes has been proposed based on molecules (Qiu *et al.* 2006; Wickett *et al.* 2014; Cox *et al.* 2018). Fortunately, in 2018 it appears that we are approaching a consensus based on molecules, and that is that although bryophytes may or may not be monophyletic, mosses plus liverworts form a natural group (Puttick *et al.* 2018). In this essay, we point out that this inference is neither new nor surprising as it has been the fundamental conclusion of morphological analyses for over 25 years starting with an exhaustive cladistic analysis of characters associated with motile cell development in green plants (Garbary *et al.* 1993).

In an attempt to resolve the seemingly intractable relationships among the three bryophyte groups, Puttick *et al.* (2018) reanalyze an exhaustive transcriptomic dataset from Wickett *et al.* (2014) using gene concatenation and coalescent analyses based on models that allow for compositional site heterogeneity. The study revisited and assessed hypotheses of monophyly and paraphyly of liverworts, mosses and hornworts. Puttick *et al.* (2018), followed by Rensing (2018), claim that the moss/liverwort relationship is well-supported based on their analysis, and that they were the first to name a ‘setaphyte’ assemblage in recognition of this group. We support this primary conclusion and point out that the term ‘setaphyte’ was proposed by Renzaglia and Garbary in 2001 to refer to the same moss plus liverwort clade. To quote from Renzaglia & Garbary (2001), a paper not cited in either Puttick *et al.* (2018) or Rensing (2018):

“We introduce the word ‘setaphytes’ as a common name for the moss plus liverwort clade. Seta refers to the unbranched stalk that bears the solitary terminal sporangium on each sporophyte, and phyte is a suffix commonly used to refer to green plants. Although moss and liverwort sporophytes have different developmental modalities, we consider them fundamentally homologous.”

Following our comprehensive cladistic analysis of characters associated with motile male gametogenesis in 1993, a series of morphological studies in our laboratories robustly supported the setaphyte hypothesis (Garbary & Renzaglia 1998; Renzaglia *et al.* 1999, 2000, 2007; Renzaglia & Garbary 2001). A sister group relationship of mosses and liverworts was consistently recovered when more complete datasets were analyzed that 1) incorporated spermatogenesis from more genera of pteridophytes and bryophytes (Maden *et al.* 1997; Renzaglia *et al.* 1999), 2) were based on morphology and development of gametophytic and sporophytic life history phases (Garbary & Renzaglia 1998), and 3) combined molecular and non-molecular characters (Renzaglia *et al.* 2000).

As can be gleaned by the recurring inference of a moss-liverwort sister relationship that is supported by cladistic analyses, there are a number of morphological features that are shared between these two bryophyte clades. Here we will focus on two lines of evidence that illustrate this relationship. The first line of study relates to the striking morphological features that are shared by the earliest divergent taxa of both clades: *Takakia* S. Hattori & Inoue (1958: 133) and *Haplomitrium* Nees (1833: 109) (Fig. 1).



**FIGURE 1.** A. *Haplomitrium gibbsiae* plant showing underground axis with upward-growing leafy shoots. Modified from Carafa *et al.* (2003). B. *Takakia lepidozoioides* plant showing underground axis with upward-growing leafy shoots. Image from digital museum Hiroshima. C. *Haplomitrium*. Cross section showing 120° angle segmentation of triangular apical cell that produces three rows of leaves. D. *Takakia*. Cross section showing 120° angle segmentation of triangular apical cell that produces three rows of leaves (phyllids); each leaf is composed of (one to) four terete segments (small arrows). E. *Physcomitrella patens*. Cross section showing 137° angle segmentation from obovoidal apical cell that produces spiraled leaves. F. *Haplomitrium*. SEM of plasmodesmatal-derived pores in end walls of water conducting cell. G. *Takakia*. TEM cross section of plasmodesmata that will develop into pores in end walls of water conducting cell. Bars: A, B = 1.0 mm; C = 5.0  $\mu$ m; D, E. = 20  $\mu$ m; F = 300 nm; G = 100nm.

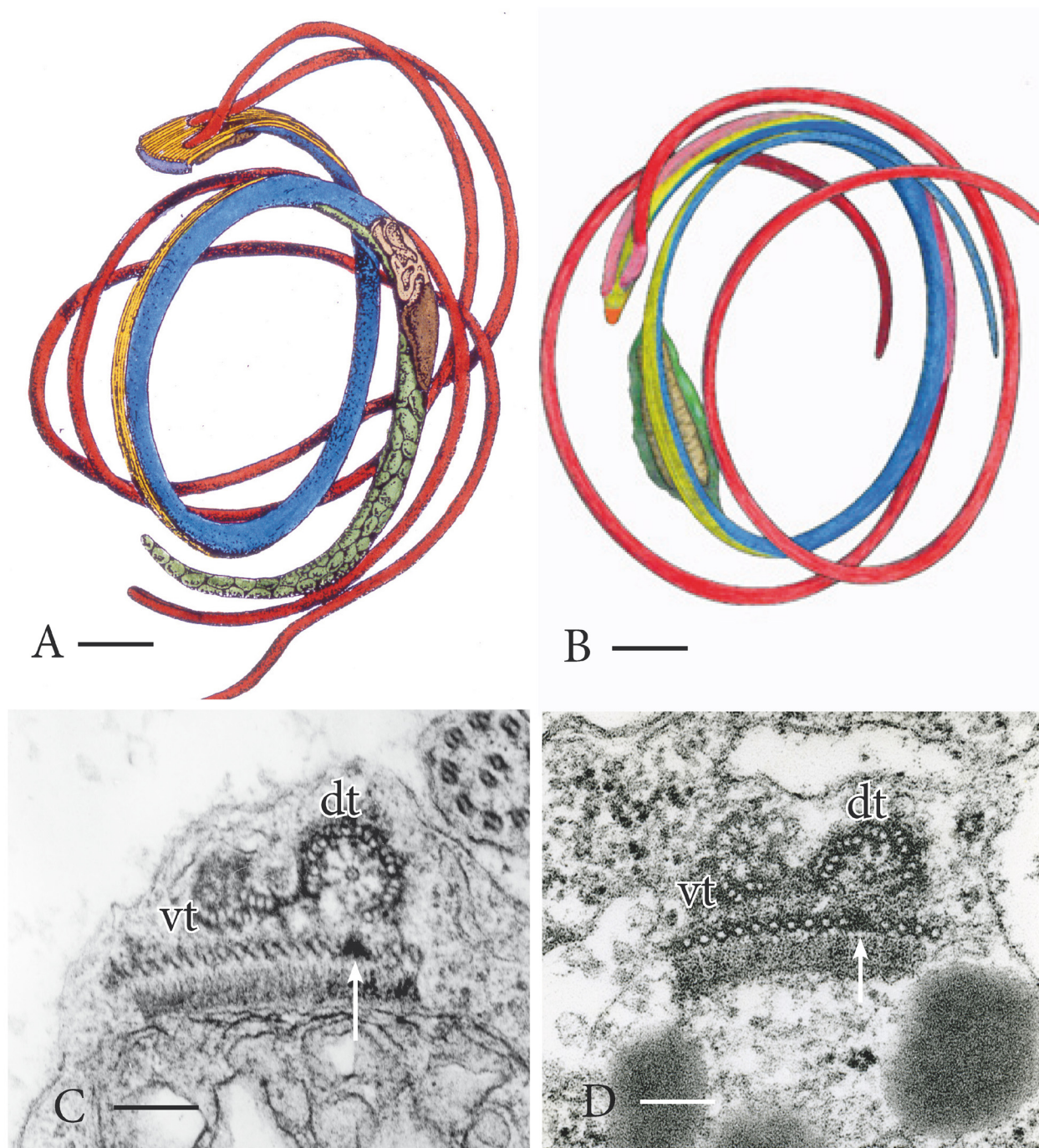
From the circumscription of the genus *Takakia* in 1958 (Hattori & Inoue 1958), this peculiar taxon was of questionable affinity. The habit of *Takakia* is unparalleled in other plants, providing few hints to its affinities. The erect green plant produces irregular leaves (phyllids) composed of one to four terete segments that may or may not fuse at the base (Inoue 1961; Mizutani 1967). Among bryologists, the most widely viewed placement for *Takakia* was as the sister to *Haplomitrium* in the Haplomitriales, an isolated order of liverworts (Schuster 1966, 1984). This placement was based on vegetative gametophytes of *Takakia* and *Haplomitrium* that uniquely bear rhizomatous stems or “roots” devoid of rhizoids (Proskauer 1962; Grub 1970; Schuster 1984) (Fig. 1A, B). Both rhizome and shoot develop from a single generative cell that in *Takakia* and *Haplomitrium* (and sister taxon *Treubia* Goebel (1890 :1) is tetrahedral and appears three-sided in cross section (Fig. 1C, D). Tetrahedral apical cells are restricted to *Haplomitrium* (Fig. 1C) and *Treubia* among early divergent liverworts and are decisively liverwort-like in *Takakia*. The apical cell of *Takakia* segments along three parallel sides at 120° angles and produces segmented leaves (phyllids) that are three-ranked, precisely as occurs in liverworts (Fig. 1D). The three-ranked nature of leaves is readily illustrated in cross section of the apex of both *Haplomitrium* (Fig. 1C) and *Takakia* (Fig. 1D). In all other mosses, apical cell segmentation is slightly off from parallel at roughly 137° angles, producing leaves in a spiral phyllotaxy (Crandall-Stotler 1981; Shaw & Renzaglia 2004) (Fig. 1E). This pattern of development from three cutting faces is responsible for the signature habit of leafy liverworts with three rows of leaves, including the frequently reduced ventral row of underleaves (Shaw & Renzaglia 2004).

Water conducting cells also unify *Takakia* and *Haplomitrium*. Although widespread among mosses, water conducting cells are restricted in liverworts to a few simple thalloid liverwort lineages and *Haplomitrium* (Smith 1964; Ligrone *et al.* 2000). However, among all bryophytes, only *Takakia* and *Haplomitrium* produce water conducting cells that have perforated pores in their end walls that are derived from primary plasmodesmata (Fig. 1E, F). Although this is a simple means of opening passage-ways between cells, it is nonetheless a feature that is shared only by this one moss and one liverwort taxon.

For over 30 years from its circumscription, *Takakia* was known only from female gametophytes that demonstrated affinities with both liverworts, e.g., gametangia shape and location, and mosses, including mucilage hairs (Hattori & Inoue 1958; Murray 1988). With the discovery of antheridia and sporophytes in *Takakia*, a new suite of morphological features was added to the known diversity of capsule architecture in extant bryophytes (Smith & Davison 1993; Renzaglia *et al.* 1997). Antheridial development and embryology are clearly moss-like, while capsule structure and dehiscence are unique among living plants but shared with early fossil embryophytes. Sporophyte dehiscence via separation along a single longitudinal suture is unknown in other mosses but is shared with some liverworts, including *Haplomitrium*; the difference is in the spiraled arrangement of the former and linear nature of the latter. One to several simple sutures is the plesiomorphic sporangial dehiscence mechanism in land plants and may be interpreted as homologous across liverworts and mosses (Shaw & Renzaglia 2004; Ligrone *et al.* 2012a, 2012b).

A second line of inquiry related to morphology and development that presents compelling evidence for a setaphyte group is found in the fine details of sperm cell development and structure, and especially the locomotory apparatus. As the only motile cells in the land plant life cycle, and a source of a multitude of shared characters across early land plants and green algae, male gamete development and structure track a particularly strong phylogenetic signal (Garbary *et al.* 1993; Renzaglia & Garbary 2001). The mature sperm cells of mosses and liverworts are strikingly similar in composition and organization (Fig. 2A, B). Both are thin and coiled with two flagella and a long cylindrical nucleus. A thin band of microtubules underlies the plasmalemma on the outside of the cell and forms the scaffolding for organelles to be positioned and for the cell to coil. The reduced complement of organelles includes a single starch-laden plastid and two mitochondria. One mitochondrion is located at the cell anterior and is intricately associated with the locomotory apparatus; the other mitochondrion is located near the end of the cell. A fundamental difference between the two sperm cells is that although the plastid is positioned more posteriorly in both, this organelle terminates the cell in liverworts but rests on the central part of the nucleus in mosses.

Similarities between the moss and liverwort locomotory apparatus are striking and provide compelling evidence of common origin. Indeed, the highly elaborate locomotory apparatus that includes centrioles, flagella, and unique microtubule and lamellar arrays is virtually indistinguishable in developing spermatids of mosses and liverworts (Fig. 2A–D). Only in mosses and liverworts are the centrioles (basal bodies) asymmetrical and staggered in position, resulting in a staggered insertion of flagella along the cell body. Remarkably, the staggering of centrioles is brought about by the growth of the same specific microtubule triplets on the centrioles in both plant groups. Similarly, the asymmetric basal bodies are positioned in the exact same location over the subtending microtubular band and lamellar strip. Given the multitude of proteins associated with centrioles and flagella (Pazour *et al.* 2005; Azimzadeh & Marshall 2010; Hodges *et al.* 2010), it can be speculated that hundreds (perhaps thousands) of genes regulate the development of this highly specialized complex of structures, the construction of which is found exclusively in mosses and liverworts.



**FIGURE 2.** A. Liverwort (*Blasia*), B. Moss (*Atrichum*). Reconstruction of sperm cells. Similarities between moss and liverwort spermatozooids include coiling, number, kind and position of organelles, stagger between position of the basal bodies and stagger in emergence of flagella on the cell body. The plastid terminates the sperm cell of liverworts, while the nucleus extends to the cell posterior in mosses. Red/ pink, flagella and basal bodies; Blue, nucleus; Yellow, microtubules; Green, plastid; Brown, mitochondrion. C. Liverwort (*Blasia*). D. Moss (*Aulacomnium*). Transmission electron micrographs of the locomotory apparatus showing identical dimorphic basal bodies in mosses and liverworts. Right basal body overlies an aperture in the microtubule band (arrow) and has dorsal triplets (dt). Left basal body consists of ventral triplets (vt) that grow forward and reposition the basal body toward the rear of the cell, resulting in a stagger in emergence of the two flagella. Bars: A, B = 1.5  $\mu\text{m}$ ; C, D = 200 nm

The lack of acceptance of a well-supported liverwort-moss clade since our initial demonstration in 1993, and then formal proposal in 2001, can be attributed to the lack of understanding of the spermatogenesis and morphological features on which we (Garbary *et al.* 1993) made our initial and subsequent analyses, and the assumption that only molecular data can provide insight into such fundamental questions. Even the summary phylogenetic trees in Garbary

*et al.* (1993) and Renzaglia & Garbary (2001) included monophyly of bryophytes, similar to the topology supported by the most comprehensive and highly regarded molecular analyses to date (Cox *et al.* 2014; Wickett *et al.* 2014; Puttick *et al.* 2018; Rensing 2018). The single major discrepancy between Garbary *et al.* (1993) and the recent molecular analyses is in the placement of *Selaginella* P. Beav., (1805:101) which was resolved in an anomalous position at the base of a bryophyte clade, independent of other vascular plants. This placement was based on incomplete data for *Selaginella* that was later corrected with a more complete evaluation of spermatogenesis (Renzaglia *et al.* 1999). Evidence from spermatogenesis initially supported other seemingly dubious relationships between plants that were subsequently confirmed (and accepted) by molecular analyses. For example, the architecture of the locomotory apparatus of *Blasia* L. (1753: 1138) clearly identified this simple thalloid liverwort as a member of the complex thalloid lineage (Pass & Renzaglia 1995; Renzaglia & Garbary 2001) long before the position of *Blasia* as sister to the remaining complex thalloids was affirmed with molecular data (Forrest & Crandall-Stotler 2005; Villarreal *et al.* 2016). Similar examples of morphology identifying seemingly inexplicable relationships across other plant groups include *Equisetum* L. (1753 : 1061) and *Psilotum* Sw. (1800: 8) as eusporangiate monilophytes (Garbary *et al.* 1993; Renzaglia *et al.* 2000, 2001).

We anticipate that with even more comprehensive and sophisticated molecular analyses the relationship between mosses and liverworts will be more robustly supported and setaphytes will be accepted as a natural group. This fundamental insight should facilitate new research in molecular genetics relating to developmental mechanisms that lead to morphological similarities both uniting setaphytes and setting them apart from hornworts and other land plant lineages.

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