

Why do bryophytes seem to lack extensive diversity?

Bryophyte diversity is expressed in a wide array of biochemical and physiological adaptations, and to date we have barely looked at these. Consider the abilities of bryophytes to withstand cold, heat and desiccation, or to deter herbivory and disease. There might exist a wide array of microspecies that may or may not be able to interbreed. The rate of genetic change in bryophytes has been as rapid as in higher plants. Furthermore, a haploid organism is able to express every gene innovation without the overriding effect of a complementary dominant gene. Asexual reproduction permits new genes, if not lethal, to be reproduced in populations without the need for compatibility in sexual reproduction.

Having exposed the caveat that hidden diversity exists in bryophytes, consider what might limit their morphological diversity. That limitation seems largely restricted by size, and sporophyte size is limited by lack of structural support due to absence of true lignin. Flowering plants exemplify the epitome of miniaturized gametophytes. But those structures are hardly suitable for comparison with the free-living gametophytes of bryophytes. Flowering plant sporophyte morphology is diverse, with insect pollination driving diversity and specialization through a multitude of paired gene combinations. Meanwhile, bryophyte sporophytes rely on non-lignified gametophytes for physical support and nutrition, largely confined to genes that work best for gametophytes.

Being small is often an advantage – witness the modern lycopods and horsetails that require less water with their small size, permitting them to survive among the ferns and seed plants with branched veins. In animals, miniaturization is most often accompanied by simplification or loss of morphological structures. Tropical miniature frogs demonstrate this very well through loss of teeth, fewer toes, and a reduced laryngeal apparatus. These structures simply don't fit in the smaller organism. Grasses have reduced flower parts, an innovation resulting in simplification. Lack of space may cause whole

organ systems to disappear, sometimes through embryonic crowding that alters development. Similarities among unrelated miniature organisms often result, as in unrelated beetles, flies and wasps that evolved featherwings in response to size reduction, presumably because that is all that worked. Bryophytes may be limited in complexity because what they have is all that works, or all that is needed to make them work.

While many flowering plants were evolving a multitude of adaptations to insect pollination, bryophytes evolved a multitude of secondary compounds to avoid being eaten by insects and other herbivores, a necessity with their mostly slow growth rate, but also costing energy that might otherwise be diverted to growth and complexity. Bryophytes, through morphological, physiological and biochemical adaptations, have found niches in which they thrive and where tracheophyte competition is low.

I still wonder why bryophytes with horizontal growth, where support seems unimportant, have not developed more morphological specialization. Small size arises from early cessation of growth or by reduction in growth rate. Perhaps bryophytes, or some of them, have 'limiting genes' that restrain their growth rates. Gerson showed that a diet of certain bryophytes could prevent the mite *Ledermuelleria frigida* from reproducing, suggesting the possibility of an inhibitor.

Consider alternatives to the current bryophyte strategy. What might be lost if bryophytes were larger or more morphologically diverse? Could they still develop easily from fragments if they had large, showy reproductive organs or complex leaves? Would thick cuticles make regeneration from a leaf impossible, or at least improbable? Would a faster growth rate be at the expense of secondary compounds that prevent herbivory?

The limits to morphological diversity might be clearer if a mathematical model that considers reproductive rates and constricting factors could be constructed. But that needs a lot more data!

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