

Box 9.1 | Mr. Hofmeister and the vanishing gametophyte

The evolution of plant life cycles

Sadly, plant life cycles are too often taught, if at all, through memorizing the stages and tissue types in the life cycle of a flowering plant. This is hardly an inspiration to further study in botany. Although the preface states that I assume you know some basic botany, increasingly, given the emphasis on teaching physiology and genetics, it seems that one can no longer presuppose familiarity with the alternation of generations. Yet, the alteration of generations is arguably the most important theory synthesizing life history and evolution in the plant kingdom.

To understand the theory, and its implications for evolution and ecology, we need to begin, not with the flowering plants, but rather with the life cycle of primitive plants such as *Rhynia* (Figure 1.11), *Lepidodendron* (Figure 1.13), or modern seedless plants such as ferns. In these plants, we can still see clearly two entirely different life history phases, the sporophyte (which is diploid) and the gametophyte (which is haploid). The sporophyte has cells that undergo meiosis, producing large numbers of haploid cells (spores). Each spore develops into a gametophyte that produces sperm and/or egg cells. The fusion of egg and sperm then produces a diploid sporophyte. The sporophyte and gametophyte generations therefore alternate. Most vascular plant fossils (e.g., Figures 1.11 and 1.13) represent the sporophyte stage, but gametophytes, while rarer, have also been found (Figure B9.1a).

This alternation of generations would seem to be rather inefficient and improbable. Why should a plant have two life history phases at all? Why should plants that live on land have sperm that must swim through water to reach eggs? The answer illustrates a profound and frequently misunderstood point in evolution: natural selection does not create a perfect solution to environmental hazards. Natural selection can only modify an existing situation by weeding out the worst alternatives. The alternation of generations appears to have been directly inherited from the algae, where it is widespread and appears in many different guises. All early land plants, both extinct forms and those which can be thought of as living fossils, have a conspicuous alteration of generations (Kenrick and Crane 1997, Taylor et al. 2005.) In such plants, the ferns being the best known example, both life history stages are free-living and independent of one another. In theory, one could go into a forest and seek either gametophytes or sporophytes of these species. In practice, the sporophytes are much larger and more obvious, and so they tend to receive most of the attention from botanists. Gametophytes are rarely seen.

Swimming sperm could severely limit reproduction, particularly in drier circumstances. Large areas of land might then have remained largely uninhabited by plants. The history of plant evolution can be viewed as a clash between the stress imposed by drought, and the inherited raw material of an algal life cycle better-suited to water. Seeds and pollen arise as a consequence.

The origin of seeds and pollen

Some living and many fossil plants are heterosporous – that is, the sporophyte produces two types of spores, large ones (megaspores that become female gametophytes) and small ones (microspores that become male gametophytes). *Selaginella* is the common example studied in botany courses. Should some

ancestral plants have delayed dispersal of the megaspores, perhaps by something as simple as an imperfectly-rupturing sporangium, the female gametophytes could have matured while still attached to the sporophyte. This minor aberration could have had multiple short term advantages including (1) protection of the gametophyte from predators, (2) continued provision of water and nutrients by the sporophyte, and (3) a general reduction in the time required for a complete life cycle. A female gametophyte retained upon the sporophyte is the precursor to the ovule and seed.

Microspores which would otherwise have dispersed to the ground, developed into male gametophytes, and released sperm, could equally have been dispersed by wind to adjacent shoots possessing female gametophytes. Male gametophyte dispersal through the air would have been the precursor to pollen. Most of the vascular plants, including the conifers and the flowering plants, now have seeds and pollen.

The vanishing gametophyte

The gametophyte stage is still prominent in the life cycle of most primitive plants. It remains the dominant life history phase in mosses. Early fossils of gametophytes are even larger than those of present plants, with antheridia (sperm producing organs) and archegonia (egg producing organs) borne on stalked gametangiophores (Figure B9.1a). The evolutionary history of plants illustrates continued pressure to reduce the size and complexity of this reproductive stage.

The stages in the reduction of gametophytes are represented by varying living plant groups (Figure B9.1b). In the seedless vascular plants, represented by ferns and their allies, gametophytes are still free living. In general we can reconstruct the following sequence of events: female gametophytes were at first retained within the sporangia of the sporophyte, then reduced to ovules protected within cones, and finally, in the case of flowering plants, reduced to a mere handful of cells in what is cryptically named the "embryo sac." In a less dramatic trend, male gametophytes, became reduced in size until, in the case of flowering plants, they become a mere vegetative nucleus within a pollen grain. One can view this trend in two ways, both of which have value. If we focus upon the extreme modification and reduction in the gametophytes achieved by natural selection, we see a strong and consistent evolutionary trend through the entire plant kingdom. If we focus instead on the continued occurrence of alternation of generations, we see a conserved and unifying algal life cycle in spite of the enormous evolutionary diversification that has occurred in vascular plants.

A unifying theory

Remarkably, this essential unifying theory of plant evolution was largely unraveled by a single botanist, Wilhelm Hofmeister (1824–1877). Hofmeister (Figure B9.1c) was largely self-taught, having left school at the age of 15 to work as an apprentice in a book and music shop in Leipzig. Yet he became "one of the most notable scientists in the history of plant biology" (Kaplan and Cooke 1996). Note that while he did this vital research on plants, Mr. Hofmeister was not a tenured professor – he supported himself, and carried out most of his research on his own time, largely from 4 to 6 in the morning before going to the store (Goebel 1905). He was only 27 when he

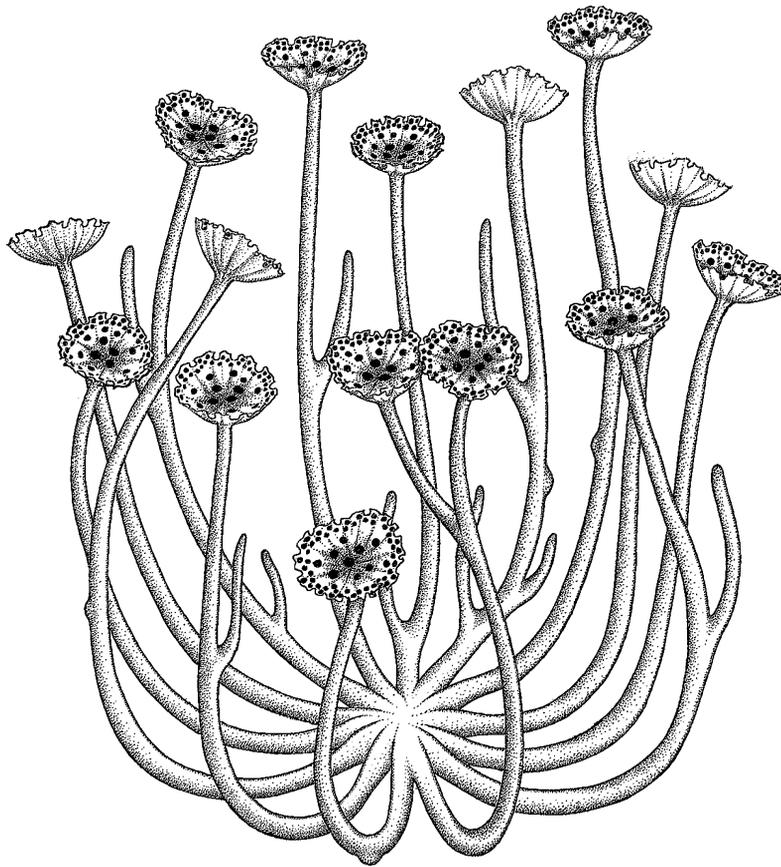


Figure B9.1(a) Reconstruction of a gametophyte preserved as a 400 million year old fossil. The eggs and sperm were produced on top of the stalked structures (termed gametangioophores) in archegonia and antheridia, which can be seen microscopically in slides made from the fossils (Taylor et al. 2005). Note the apparent similarity to modern liverworts like *Marchantia* that are often studied in botany courses (from Kenrick and Crane 1997).

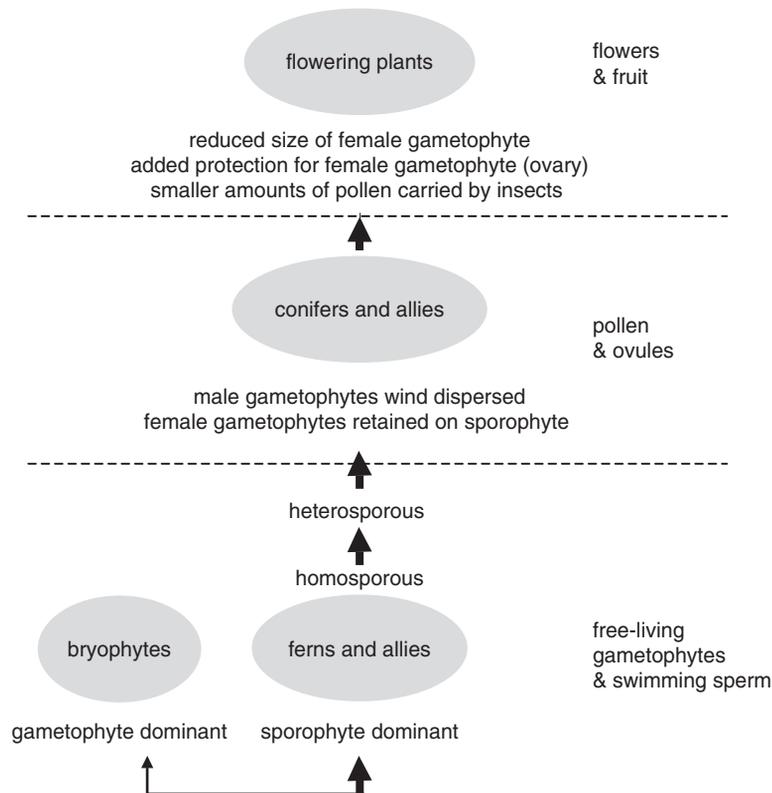
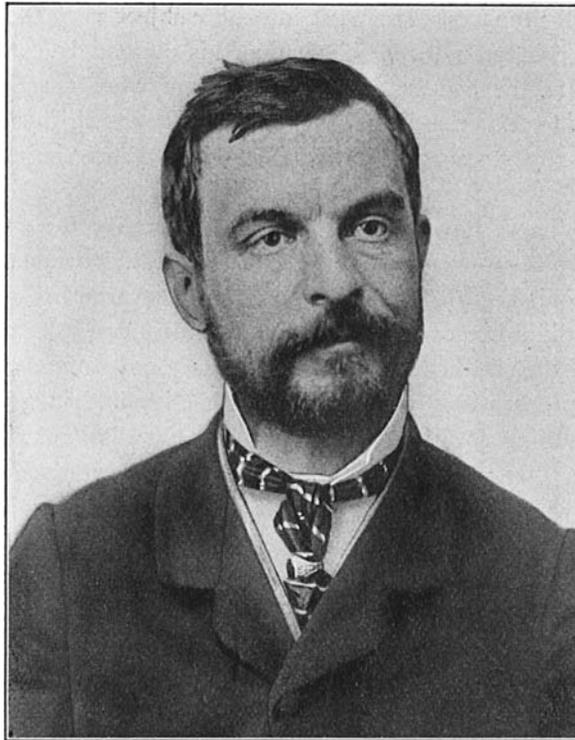


Figure B9.1(b) Major trends in the evolution of the alternation of generations, beginning at the bottom with the free-living gametophytes and swimming sperm typical of early land plants. (Although the diagram shows that the early land plants were homosporous, the spores apparently developed into male and female gametophytes (Taylor et al. 2005).)

Figure B9.1 (c) Wilhelm Hofmeister (1824–1877) uncovered the alternation of generations in plants and published a monograph on the topic in 1851 (from Goebel 1905).



published his ground-breaking monograph that documented the alternation of generations in plants. This appeared in 1851, eight years before Darwin published *The Origin of Species*. Not until 1863 (at the age of 39) was Hofmeister employed as a professor.

9.3 | $>10^4$ years: the Pleistocene glaciations

The Pleistocene is the second to last epoch in the Earth's history; it was a period of climatic instability that began about 2 million years ago during which extensive ice sheets and other glaciers formed repeatedly (e.g., Delcourt and Delcourt 1991, Levin 1994). For this reason, its popular name is the "Ice Age." The Pleistocene and the Holocene (the last 10 000 years) together comprise the Quaternary Period. Although there have been many ice advances and retreats in the Earth's history, much of its surface has been shaped by the last great period of glacial advance and retreat – a period which ended only about 10 000 years ago. No student of plant ecology can afford to be ignorant of the effects that the last ice advance had upon the landscape. The effects are often very local and their results may vary from heavily scoured landscapes lacking soil, to great terminal moraines, to