Homologous Versus Antithetic Alternation of Generations and the Origin of Sporophytes

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Abstract The late-nineteenth/early-twentieth century debate over homologous versus antithetic alternation of generations is reviewed. Supporters of both theories, at first, used *Coleochaete* as a model for the origin of land-plant life cycles. The early debate focused on the morphological interpretation of the sporophyte and on whether vascular cryptogams had bryophyte-like ancestors. The terms of the debate shifted after the discovery that the alternation of morphological generations was accompanied by an alternation of chromosome number. Supporters of homologous alternation now promoted a model in which land plants had been derived from an algal ancestor with an isomorphic alternation of haploid and diploid generations whereas supporters of antithetic alternation favored a model in which land plants were derived from a haploid algal ancestor with zygotic meiosis. Modern evidence that embryophytes are derived from charophycean green algae is more compatible with an updated version of the antithetic theory.

Keywords Alternation of Generations · Apogamy · Apospory · *Coleochaete* · *Dictyota* · Embryophytes · Gametophyte · Sporophyte

Introduction

For more than a century, theories of the 'antithetic' origin of sporophytes have been juxtaposed with theories of their 'homologous' origin. During this same period, there have been profound changes in our knowledge of the phylogeny of land plants and of mechanisms of inheritance. The opposing theories have not remained static but have been reformulated in the light of new discoveries and as implicit assumptions changed. Modern versions of the homologous theory, in particular, now bear little resemblance to the original theory. The vocabulary of nineteenth-century botanists can be deceptively familiar: familiar because we still use many of the same terms; deceptive because these terms are used with different connotations, arising from different conceptual and theoretical assumptions. Without a historical perspective, it is often difficult to know what botanists are arguing about.

My discussion will focus on the debate among British botanists that was initiated by Scott's (1895) advocacy of homologous alternation as an alternative to Bower's

(1890) hypothesis of antithetic alternation. My historical review will end with the Meeting of the Linnean Society of London on February 18th, 1909 (Lang et al., 1909) at which the major British protagonists of the rival theories expressed their views. During this period, North American botanists mostly viewed the debate from the side-lines: Campbell (1903; 1905, chapter XV) was a strong champion of the antithetic theory whereas Coulter (1899) favored the homologous theory. Farley (1982) provides a good historical overview of the period, placing botanical progress in the wider context of changing views of the nature of sexual reproduction. Farley also emphasizes the importance of advances in microscopy and staining techniques during the nineteenth century that made visible what had previously been unseen. Blackwell (2003) reviews the debate after the period covered in this paper.

Prelude

Steenstrup (1845) defined *alternation of generations* as "the remarkable, and till now inexplicable phenomenon of an animal producing an offspring, which at no times resembles its parent, but which, on the other hand, itself brings forth a progeny, which returns in its form and nature to the parent animal, so that the maternal animal does not meet with its own resemblance in its own brood, but in its descendants of the second, third, or fourth degree of generation" (p. 1). Steenstrup's definition comes from the English translation of the Preface to the German version of a Danish original. *Alternation of generations* was a translation of *Generations-wechsel*, itself, in turn, a translation of *vexlende Generationsrækker* (Steenstrup, 1842a, b, 1845). It is possible that the final step in the translation into English was influenced by Chamisso's (1819, p. 10) earlier use of *alternatio generationum* in his description of the life cycle of salps.

Although *alternation of generations* initially referred to the alternation of sexual and asexual forms in animals, the term is now almost exclusively associated with the life cycles of plants, specifically with the alternation of haploid gametophytes and diploid sporophytes. Hofmeister (1862) wrote that mosses and ferns "exhibit remarkable instances of a regular alternation of two generations very different in their organization. The first generation—that from the spore—is destined to produce the different sexual organs … The object of the second generation is to form numerous free reproductive cells—the spores—by the germination of which the first generation is reproduced." Hofmeister's synthesis was pre-Darwinian (the German version of his treatise appeared in 1851) and he did not view the correspondences that he had identified among the life cycles of bryophytes, ferns and gymnosperms as evidence of common descent (Goebel, 1926; p. 60). Hofmeister's investigations were also 'pre-cytological'. Chromosomes were not identified until the 1880s. Thus, Hofmeister was unaware that the alternation of morphological generations was associated with an alternation of chromosome number.

One question, left unanswered by Hofmeister, was how the alternation of generations of the 'higher cryptogams' or archegoniates related to the life histories of 'lower cryptogams' or thallophytes. Thallophytes (a group that included fungi as well as algae) were known to produce both spores and eggs. An egg required fertilization to produce a new individual (sexual reproduction) whereas a spore could form a new individual by

itself (asexual reproduction). Therefore, an individual that produced spores was recognized as a representative of an asexual or *neutral* generation, whereas an individual that produced eggs (or sperm) was recognized as the representative of a sexual generation. For many thallophytes, sexual and asexual individuals were otherwise indistinguishable. In some thallophytes, motile cells that looked like zoospores could fuse with other motile cells and, by this criterion, were sexual rather than asexual. A resolution of the morphological homologies between 'higher' and 'lower' cryptogams was perceived as central to understanding the origin of land plants.

The ensuing debate focused on the origin of the asexual generation of land plants (i.e., the sporophyte) and is conventionally characterized as a conflict between theories of *antithetic* and *homologous* alternation of generations. This debate initially took place in the context of a common belief in the direct inheritance of form. A distinction between form and the inherited determinants of form—what we now call phenotype and genotype—emerged gradually in Weismann's concept of the germ-plasm (Weismann, 1891) and then in the belated appreciation of Mendel's experiments. Many botanists were slow to adopt the new ideas, however. Plant morphologists tended to emphasize gradual transformations and to view ontogeny as providing direct evidence about how morphology was transformed during phylogeny.

The protagonists of homologous and antithetic alternation sought clues to the origin of the sporophyte in the life cycles of thallophytes. The great diversity of thallophyte life cycles meant examples could be found that appeared to fit either theory. I will not enter into the details of these arguments because most of these taxa are now known to be distant relatives of embryophytes. However, I will discuss various interpretations of the life cycle of *Coleochaete*, an alga whose life cycle had been described by Pringsheim (1860).

Coleochaetes were freshwater algae that grew as epiphytes on other plants. Multicellular thalli developed from zoospores (*Schwärmsporen*). A thallus could be asexual, and produce zoospores; could be a sexual male, and produce sperm (*Samenkörper*); or be a sexual female, and produce oogonia (*Oogonien*). After fertilization of an oogonium, the resulting oospore was retained on the female thallus and underwent a number of cell divisions to produce a multicellular 'fruit'. In some coleochaetes, the female thallus produced a cellular 'rind' that grew around and enclosed the fruit. All cells derived from the oospore then transformed into zoospores that dispersed to establish new thalli (Pringsheim, 1860). This life cycle was characterized by a succession of asexual thalli interspersed with occasional sexual thalli. The interpretation of the fruit was controversial. Some morphologists recognized a similarity between this zoospore-producing fruit, developing *in situ* upon a female thallus, and the spore-producing asexual generation of mosses. Thus, *Coleochaete* was thought by many to exhibit a close analogy, and perhaps homology, to the life cycle of land plants.

Homologous and Antithetic Alternation Expounded

My discussion will focus on the debate in the English language because of my own linguistic limitations. However, I have made some effort to understand the arguments of two papers written in German that were cited by the chief British

protagonists as prefiguring their own views. Bower (1890) derived his concept of 'antithetic alternation' from Celakovsky (1874). Scott (1895) ascribed his hypothesis of 'homologous alternation' to Pringsheim (1876b).

Celakovsky's (1874) purpose was to present an accurate classification of the alternation of generations (*Generationswechsel*). His classification distinguished between antithetic and homologous alternation on the basis of whether two generations obeyed the same growth-laws (*Wachsthumgesetze*). Each of these categories was further broken down into alternation of bionts (*Biontenwechsel*) and alternation of shoots (*Sprosswechsel*). Celakovsky interpreted shoots to be simple individuals (or generations) that remained attached one to another. If the individuals became detached, they qualified as bionts (free-living beings) rather than shoots. In his view, the difference between budding and some forms of asexual reproduction by special cells was sufficiently slight that the exclusion of *Sprosswechsel* from *Generationswechsel* could not be justified (Celakovsky, 1874; pp. 22–24, 42).

Celakovsky proposed that the spore-producing asexual bionts and egg-producing sexual bionts of algae are morphologically similar because they obey the same growth-laws. Therefore, these generations are *homologous*. By contrast, the asexual and sexual generations of mosses and vascular cryptogams obey quite different growth-laws. Therefore, these generations are *antithetic* (Celakovsky, 1874; pp. 31–32). The precise connotations that Celakovsky attached to the adjectives 'homologous' and 'antithetic' are unclear. A tempting interpretation would be that 'homologous' simply referred to generations that were 'similar in form' (isomorphic), whereas 'antithetic' referred to generations that were 'contrasting in form' (heteromorphic). Against such a simple interpretation, Celakovsky classified the production of a leafy gametophore from a moss protonema as an alternation of homologous shoots.

Celakovsky believed that *Coleochaete* exhibited *both* antithetic and homologous alternation. That is, *Coleochaete* possessed three kinds of generations that succeeded each other in the order A, B, C. Generation A was represented by vegetative asexual bionts that produced zoospores; generation B by vegetative sexual bionts that produced oospores; and generation C by a rudimentary antithetic generation that developed from the fertilized oospore. Asexual generation A and sexual generation B followed the same growth-law and were thus homologous, whereas asexual generation C (the 'fruit') followed a different growth-law and was thus antithetic to A and B. The crux of Celakovsky's arguments with respect to land plants was that the asexual generations of mosses and vascular cryptogams were of the same nature as generation C, and were therefore antithetic to the sexual generation. In land plants, generations A and B had sunk to the level of mere shoot-generations of a single biont. The protonema (*Vorkeim*) of mosses corresponded to asexual generation A whereas the leafy moss-plant corresponded to sexual generation B (Celakovsky, 1874; p. 32).

Pringsheim (1876b) presented a contrary interpretation of the connection between alternation of generations in thallophytes and mosses. He found no use for Celakovsky's distinction between antithetic and homologous alternation, nor for Celakovsky's treatment of *Sprosswechsel* as a form of *Generationswechsel*. In Pringsheim's view, there were two series of phenomena that should be kept separate:

shoot-alternation, which belonged entirely to the field of vegetative propagation, and true sexual alternation of generations, which belonged to the field of fructification (Pringsheim, 1876b; pp. 890, 911). Pringsheim denied that the fruits of thallophytes were in any sense homologous to the asexual generation of mosses. Rather, the asexual and sexual generations of mosses were directly homologous to the free-living asexual and sexual generations of thallophytes. Since the latter were clearly homologous to each other, this meant that the moss seta (asexual generation) was homologous to the moss stem (sexual generation), as confirmed by observations of the vegetative sprouting of the seta (apospory).

In Pringsheim's (1876b) experience, the *first* neutral generation of thallophytes (i.e., the spore-producing thallus that develops from the fertilized egg) often proceeded directly to spore-production, with greater or lesser suppression of the vegetative parts relative to subsequent neutral generations. In his view, the first neutral generation had a different habitus from the succeeding generations because it initiated development while firmly held and enclosed by tissues of the female sexual thallus. Thus, Pringsheim interpreted the multicellular fruit of *Coleochaete* as a reduced asexual generation that was fundamentally similar to a free-living asexual thallus. The life cycle of mosses differed from that of *Coleochaete* principally in the elimination of all but one neutral generation. That is, the spores of the first neutral generation of mosses always developed into sexual plants, never into asexual plants (Pringsheim, 1876b; pp. 907–908: there is an apparent contradiction with Pringsheim's earlier statement (p. 872) that the fruits of thallophytes were in no way homologous to the neutral generation of cormophytes).

Bower (1890) viewed the alternation of generations of archegoniates as arising from the adaptation of an initially aquatic organism for the land. That is, the life cycle could "be distinguished as an *amphibious alternation*, which finds its morphological expression in the difference of external form and internal structure between the more ancient gametophyte and the more recent sporophyte." In his view, the sporophyte arose by the "*interpolation* of a new development between successive gametophytes." Bower (1890) suggested that this could be styled *alternation by interpolation*. But, rather than introduce new terms, he chose to refer to his hypothesis as *antithetic alternation* after Celakovsky (1874).

Bower (1890) defined *antithetic alternation* as an alternation "of two generations phylogenetically distinct, i.e., where a new stage (sporophyte) has been interpolated between pre-existing generations (gametophytes)." By contrast, he defined *homologous alternation* as an alternation "of two or more generations phylogenetically similar to one another, but differing in the presence or absence of sexual organs." Antithetic alternation, he believed, had probably arisen independently in several distinct phyla, including the Archegoniatae, the green Confervoideae (a taxon that included *Coleochaete*), the Florideae (red algae), and the Ascomycetous Fungi. Homologous alternation occurred in most thallophytes and "might be described as a mere differentiation—often a very slight one—of successive gametophytes." In support of his theory, Bower disputed the hitherto generally accepted homology between the zoospores of thallophytes and the spores of archegoniates.

[Many years later, Bower (1935) regretted his youthful decision to describe his theory as one of antithetic alternation. He now proposed that the old terminology, of theories of 'antithetic' versus 'homologous' alternation, should be dropped in favor

of theories of '*interpolation*' versus '*transformation*'. This change would accentuate the alternative routes that were proposed for the origin of the asexual generation of land plants (Bower, 1935; p. 491).]

In an obituary of Pringsheim, Scott (1895) championed Pringsheim's opinion that the free-living sexual and asexual forms of thallophytes were homologous, and that their alternation was the phylogenetic precursor to the alternation of gametophytic and sporophytic generations in archegoniates. In Scott's view, the great advantage of Pringsheim's interpretation was that it "would enable us to understand the existence of the immense and unbridged gulf which separates the sporophytes of the Muscineæ from that of the Vascular Cryptogams. The latter might well have been derived from ancestors, in which the 'first neutral generation' had never suffered the extreme reduction which characterise it in the Moss series, but had always retained its vegetative organs."

Scott (1896) returned to these themes in a presidential address to the British Association's botanical section. The principal obstacle to accepting the antithetic theory was the implication that the free-living sporophyte of a fern had been derived from something that resembled the physiologically-dependent sporophyte of a moss. The homologous theory got rid of the need to intercalate a new generation and required only the modification of the already existing sexual and asexual forms of thallophytes. Scott wrote "There is no reason to believe that the Bryophyta, as we know them, were the precursors of the vascular Cryptogams at all. … If we accept the homologous theory of alternation, we may fairly suppose that the sporophyte of the earliest Pteridophyta always possessed vegetative organs of some kind." He was dismissive of the alternative, "The sudden appearance of something completely new in the life-history, as required by the antithetic theory, has to my mind, a certain improbability. *Ex nihilo nihil fit*." [Bower (1898) used his own presidential address for a detailed rebuttal: "to me the zygote is not 'nothing'; it is a cell with all the powers and possibilities of a complete cell."]

Later in his address, Scott (1896) made reference to some botanists who "even go so far as to propose making the number of chromosomes the criterion by which the two generations are to be distinguished. Considering that the whole theory rests at present on but few observations, I venture to think this both premature and objectionable; for nothing can be worse for the true progress of science than to rush hastily to deductive reasoning from imperfectly established premises." Here, Scott referred to recent discoveries that had shaken a strictly morphological interpretation of the alternation of generations, and that had "dropped as a bombshell" (Bower, 1935; p. 486) into the controversy over homologous versus antithetic alternation.

The bombshell was primed by Overton (1893) who reported that pollen mother cells possessed a reduced number of chromosomes relative to archesporial cells. (Overton believed that the reduction of chromosome number occurred at synapsis not, as we now know, in the subsequent nuclear division.) He wrote, "It will be a matter of great morphological as well as physiological interest, to establish beyond the possibility of a doubt that the alternation of generations, which is so remarkable a feature in the life-history of plants, is dependent on a change in the configuration of the idioplasm; a change, the outward and visible sign of which is the difference in the number of the nuclear chromosomes in the two generations."

The bombshell dropped when Strasburger (1894) reported that the asexual generation of ferns had twice the number of chromosomes of the sexual generation.

Strasburger considered "Weismann's conception of the id, as an element in the nucleus which is charged with all the hereditary characteristics of the species, to be felicitous." He would later propose the nouns *Haploid* (haplo-id) and *Diploid* (diplo-id) to refer to *animals* with single and double chromosome numbers, corresponding to the gametophytes and sporophytes of plants (Strasburger, 1906: "*Ich erlaube mir zu diesem Zwecke die Worte Haploid und Diploid, bezw. haploidische und diploidische Generation vorzuschlagen*").

Interlude

Changing Categories

Nineteenth-century botanists distinguished asexual (spore-producing) generations from sexual (gamete-producing) generations. From a twenty-first-century perspective, the category 'asexual generation' grouped together haploid individuals producing haploid spores by mitosis, diploid individuals producing diploid spores by mitosis, and diploid individuals producing haploid spores by meiosis. The category 'sexual generation' encompassed haploid individuals producing gametes by mitosis and diploid individuals producing gametes by meiosis. After the discovery of the alternation of chromosome number, geneticists recognized the fundamental distinction as occurring between haploid and diploid generations rather than between sexual and asexual generations. Some botanists adopted the new dichotomy as primary, some retained the old, and many were muddled in what they considered to be the 'same kind' of generation.

Debates about alternation of generations in the early twentieth century can be confusing because three ways of classifying 'generations' co-exist (sexual vs. asexual, gametophyte vs. sporophyte, haploid vs. diploid) and are often treated as synonymous. There have been a couple of attempts to diagnose the resulting confusion. Wahl (1945, 1965) argued that continued support for the homologous theory in the twentieth century was based on an explicit or implicit assumption of homology between meiotic spores and mitotic (vegetative) spores. For Roe (1975), a supporter of homologous alternation, the "fundamental misconception" was the erroneous equation of the asexual generations of algae with the sporophytes of land plants and the equation of the sexual generations of algae with gametophytes.

Apogamy and Apospory

Farlow (1874) reported the development of fern plantlets directly from prothalli, without the production and fertilization of an egg (apogamy = without sexual union). Soon after, Pringsheim (1876a) reported the experimental induction of leafy outgrowths from a moss seta without the intervening production of spores (apospory = without spores). The interpretation of these phenomena was a major point of dispute between the proponents of antithetic and homologous alternation.

Apogamy and apospory demonstrated that gametophytes could transform into sporophytes, and vice versa, without the intervention of specific cells (eggs or spores). Pringsheim (1876b) and Scott (1895) believed that these transformations

strongly supported the homology of gametophytes and sporophytes. By contrast, Bower (1887a) interpreted these phenomena as "mere sports" without "deep morphological meaning." These were "phenomena of a teratological nature, and [were] not to be taken as evidence with regard to the evolutionary relations of the sporophyte and the gametophyte" (Bower, 1890).

After the discovery of the alternation in chromosome number, Bower (1898; p. 91) suggested that apogamy and apospory would probably be associated with changes in chromosome number. Farmer and Digby (1907), however, showed that these processes usually occurred without changes in chromosome number. Supporters of the homologous theory likely felt vindicated, even though Farmer and Digby cautioned that their results proved that no necessary correlation existed "between the periodic reduction in the number of the chromosomes and the alternation of generations … therefore the problem of alternation and its nature must be settled by an appeal to evidence other than that derived from the facts of meiosis."

Homologous Alternation Revised

The discovery of an alternation of nuclear phase shifted the debate on the alternation of morphological generations and, in particular, changed the way in which the homologous theory was presented. This shift can be illustrated with the example of *Coleochaete*. Celakovsky (1874) had recognized three generations in the life cycle of *Coleochaete*: zoospore-producing thalli (A); gamete-producing thalli (B); and the multicellular body produced from the fertilized oospore (C). Celakovsky (1874) and Bower (1890) believed generation C was an antithetic generation intercalated into the life cycle, whereas Pringsheim (1876b) and Scott (1895) believed generation C was merely a reduced version of generation A (Fig. 1). After Strasburger's (1894) description of the alternation of nuclear ploidy, it was soon realized that generations A and B probably had the same (reduced) number of chromosomes. Therefore, asexual generation A could not correspond cytologically to the asexual generation (sporophyte) of land plants. However, if it were assumed that chromosome reduction occurred immediately before the production of zoospores by generation C, then generation C would be analogous, perhaps even homologous, to the sporophyte of mosses (i.e., a multicellular body with the doubled number of chromosomes growing attached to a sexual generation with the reduced number of chromosomes). Thus, the alternation of chromosome numbers was initially seen as strengthening the antithetic theory.

Supporters of the homologous theory, however, were soon able to invoke cytological discoveries in algae to bolster their own theory but, in the process, they abandoned *Coleochaete* as an exemplar of homologous alternation. Williams (1904) reported that the brown alga *Dictyota dichotoma* underwent an isomorphic alternation between tetraspore-producing individuals (with 32 chromosomes) and gamete-producing individuals (with 16 chromosomes). The former developed from fertilized eggs, the latter from tetraspores. Thus, *Dictyota* provided an example of a regular alternation between a haploid sexual and diploid asexual generation that were "in all morphological respects … perfectly similar to one another" (Scott, 1908).
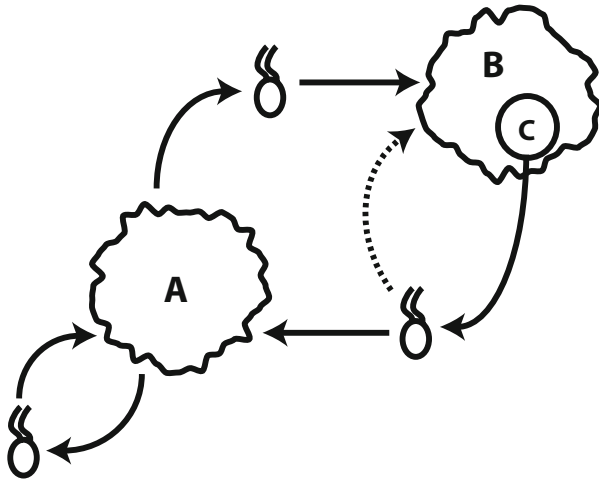
Fig. 1 The life cycle of *Coleochaete* used to illustrate the different interpretations of the antithetic theory and the early version of the homologous theory. An asexual thallus (*A*) produces zoospores that germinate to produce another asexual thallus or a sexual thallus (*B*). Sexual thalli produce gametes. Zygotes are retained on female thalli and develop into an asexual 'fruit' (*C*) that releases zoospores. Bower (1890) and Scott (1895) agreed that *A* and *B* were homologous and that an archegoniate life cycle could be derived by eliminating *A* (*dashed arrow*). Bower interpreted *C* as a new structure *interpolated* into the life cycle whereas Scott interpreted *C* as a *modified* version of *A*

Soon after, Lang (1909) presented an *ontogenetic theory of alternation* that he believed placed the relation of the two generations in a new light. He regarded gametophytes and sporophytes "as homologous, in that they correspond to regularly succeeding individuals (sexual and asexual), developed from germ-cells which are similar in their morphogenetic powers." In his view, the spore and fertilized egg had the same developmental potential but produced different plant-bodies because they developed under different environmental influences. Spores develop free, in direct contact with soil, water and light, whereas the fertilized eggs of archegoniates develop enclosed within cells of the preceding sexual generation. Lang believed that the descent of land plants could "fairly be assumed to have been from forms in which a sexual (haploid) and asexual (diploid) generation of similar form alternated regularly." The change from a dispersed to a retained egg probably accompanied the transition to land. "Once the dependent relation of the diploid generation was established, profound and probably sudden changes might be expected to follow, resulting in the difference in the body form between sporophyte and gametophyte."

Lang presented these ideas at a meeting of the Linnean Society of London (February 18th, 1909) at which Bower and Scott (among others) were present (Lang et al., 1909). In response, Bower argued that the most stringent criterion of homology was identical phyletic history. He wished to "retain the old idea of the historical distinctness of the two alternating phases" and he did not "feel prepared to concede the full morphogenetic unity of the spore and zygote."

Scott, on the other hand, believed that Lang had merely restated the homologous doctrine "as it had taken shape … since the discovery of the cytological facts in *Dictyota*. These discoveries had shown that cytological differences did not preclude the two generations being homologous, and had thus completely removed the value

of the cytological distinction as supporting the antithetic theory." The homologous theory had assumed the form in which it is best known today: land plants had descended from an alga with isomorphic alternation of haploid and diploid thalli (Fig. 2).

The green alga *Ulva* replaced the brown alga *Dictyota* as the favored algal exemplar of the homologous theory (Graham, 1985; Blackwell, 2003) after Föyn (1929) and Hartmann (1929) described isomorphic alternation of generations in *Ulva* and *Enteromorpha*. It should be noted, however, that Föyn and Hartmann considered they had demonstrated *antithetic* alternation of generations because haploid sexual plants and diploid asexual plants differed in inner constitution although they resembled each other in outward form. Clearly, one botanist's antithetic alternation was another botanist's homologous alternation.

Homologous and Antithetic Alternation Compared

Rather than review the sometimes-heated debate that followed Bower's and Scott's respective support of antithetic and homologous alternation, I will try and clarify the different phylogenetic histories of the sporophyte that the two theories implied. Then, in the subsequent section, I will revisit the question of the origin of embryophyte life cycles from the perspective of our modern understanding of the phylogeny of embryophytes and their algal relatives.

Bower's antithetic theory was developed at length in *The origin of a land flora* (Bower, 1908) and updated in *Primitive land plants* (Bower, 1935; a book that Bower dedicated to Scott's memory). The successive presentations of Bower's theory attempted to incorporate progress in the understanding of meiosis, while holding firm to the basic model of the interpolation of a new generation into the life cycle. Bower proposed that archegoniates were derived from a haploid alga in which chromosome-reduction followed immediately upon formation of a zygote that

Fig. 2 The 'late' version of the homologous theory. Pteridophyte life cycles were derived from an alga with free-living haploid and diploid generations (*upper panel*) by retention and development of the zygote on the maternal gametophyte (*lower panel*)
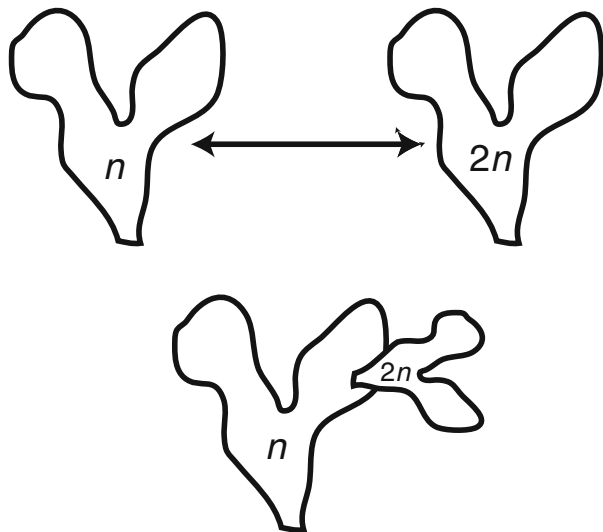
remained attached to the maternal thallus. The sporophyte originated from cellular proliferation of the still-attached zygote. All of these cells were initially sporogenous. That is, chromosome-reduction initially occurred in every cell of the intercalated diploid generation. This post-zygotic proliferation was advantageous on land because of the relative rarity of opportunities for sexual reproduction. By this means, the plant could produce many spores from a single fertilization event. The further elaboration of the sporophyte was accompanied by the sterilization of formerly sporogenous cells to perform vegetative and other functions. The free-living sporophytes of ferns and lycopods were derived from the dependent sporophytes of a bryophyte-like plant by further proliferation and sterilization, and the *acquisition* of physiological independence from the gametophyte. The latter was facilitated by the evolution of a root that allowed the sporophyte to obtain its own supply of water and mineral nutrients.

Bower had "thought that the fruit-body of *Coleochaete* supplied a prototype of an undifferentiated mass of cells, all fertile, such as this theory contemplates," but he was forced to retreat from this position because "it has now been shown that in *Coleochaete* reduction occurs at the first segmentation of the zygote, and accordingly the old comparison is no longer permissible" (Bower, 1908; p. 260). Bower, here, referred to the work of Allen (1905) who had observed highly condensed bivalents at the first division of *Coleochaete scutata* zygospores but less condensed, filamentous chromosomes at the second division. Allen, therefore, identified the first two divisions of the zygospore as the heterotypic and homotypic divisions of chromosome reduction (i.e., meiosis I and meiosis II). The third and subsequent divisions were consequently assumed to be mitotic, although Allen did not observe these divisions. Allen considered his observations to have decisively rejected the analogy between the fruit of *Coleochaete* and the sporophyte of mosses.

Pringsheim (1876b) and Scott (1895, 1896) proposed that archegoniates evolved from an alga with multicellular asexual and sexual thalli that were fundamentally alike. The first asexual, or neutral, generation differed from subsequent asexual generations because it developed while attached to the preceding female sexual generation. The strict alternation of gametophytes and sporophytes originated through the suppression of all except the first asexual generation. Like Bower's theory, this theory proposed that the sporophyte developed from a zygote attached to a female gametophyte. Unlike Bower's theory, the homologous theory proposed that the zygote already produced a multicellular thallus in the algal ancestor of archegoniates.

The above can be considered the homologous theory in its early form. The evolutionary scenario of this theory shifted after Williams (1904) elucidated the alternation of nuclear phases in *Dictyota*. The eggs of *Dictyota*, unlike those of *Coleochaete*, are dispersed before fertilization. Therefore, the 'first neutral generation' of *Dictyota* does not grow attached to a sexual generation. Proponents of homologous alternation thereafter usually proposed descent of land plants from an alga with a life cycle resembling *Dictyota*. In this new guise, the theory required the suppression of egg-dispersal in land plants so that an originally independent diploid generation came to grow attached to the preceding maternal haploid generation.

The alacrity with which Scott substituted *Dictyota* for *Coleochaete* as a model for the ancestor of archegoniates argues that the nature of this ancestor was not his

principal objection to Bower's ideas. As Bower recognized, the dispute was between viewing the sporophyte as the interpolation of a new structure into the life cycle as opposed to the transformation of an existing structure. Scott (1896) wrote: "Nature is conservative, and when a new organ is to be formed it is, as every one knows, almost always fashioned out of some pre-existing organ. Hence I feel a certain difficulty in accepting the doctrine of the appearance of an intercalated sporophyte by a kind of special creation."

A specific point of disagreement was Bower's proposal that pteridophytes had been derived from a bryophyte-like ancestor. For Scott, the sporophytes of bryophytes and pteridophytes had been independently derived from an asexual algal thallus. In the case of bryophytes, the evolution of the sporophyte was associated with a *loss* of vegetative functions as the sporophyte grew to maturity while nourished by the maternal gametophyte. Scott's skepticism about the derivation of a pteridophyte sporophyte from a bryophyte sporogonium was widely shared. A number of botanists were prepared to countenance an *antithetic* origin for the sporophyte of bryophytes, but only if a *homologous* origin was conceded for the sporophyte of pteridophytes (Coulter, 1899; Tansley, 1907, 1912; Fritsch, 1916).

Retrospect

Homology

Bower (1898) wrote that *homology* was "a word which is probably explained to every class of elementary students; it is one of those terms a meaning of which is revealed to the babes of the science, while those who teach are not at one as to its definition." Much the same could be said today. The fact that definitions of morphological homology are still debated suggests to this writer that there is a fundamental problem with the concept.

Homology was initially an intuitive concept. Morphologists recognized that some resemblances indicated two organs belonged to the same class of things, whereas other resemblances were deceptive and did not indicate affinity. The former were homologies, the latter mere analogies. Shortly before the *Origin of Species*, Berkeley (1857) wrote: "Analogy … is always liable to seduce an inattentive or ignorant observer into wrong notions as to the relation of beings between which it exists." whereas "Homology is of far more value; for when true it is founded on a deep knowledge of structure, and is indicative of either close or remote relation." He defined analogy as "resemblance of function" and homology as "correspondence of structure or origin." Homologous structures were "identical in essence and origin." (*Origin* in these definitions probably refers to ontogeny rather than ancestry.)

For many morphologists, the theory of descent with modification provided a rationale for the concept of homology: two structures were homologous if they were descended from the same structure in a common ancestor. Bower (1887b, 1890, 1898; in Lang et al., 1909), for one, was a consistent champion of phylogeny being the ultimate criterion of homology. For Bower (1887b), the 'leaves' of mosses and ferns were analogous, not homologous, because the former occurred in the gametophyte generation whereas the latter occurred in the sporophyte generation.

In his view, homology had no intelligible meaning without the theory of descent (Bower, 1898: p. 67).

Not all morphologists accepted a phylogenetic redefinition of homology. Lang (1915), for example, fully recognized "the interest of the phyletic ideal, but [was] unable to regard it as the exclusive, or perhaps as the most important, object of morphological investigation. To accept the limitation of morphology to genealogical problems is inconsistent with the progress of this branch of study before the acceptance of the theory of descent, and leaves out many of the most important problems that were raised and studied by earlier morphologists." He was prepared to abandon any attempt to base homology on homogeny (common ancestry). Two structures were homologous if they were shaped by common causes. The 'leaves' of mosses and ferns had evolved in parallel but exhibited "homology of organization."

At the same time as homology was successfully redefined as common ancestry, advances in genetics have challenged the very concept of *morphological* homology. The genetic determinants of form are inherited, not the forms themselves. Organs are constructed by the interaction of many genes, and, over the course of evolution, old genes are expressed in new locations and acquire new interactions with novel partners (Jaramillo and Kramer, 2007). Therefore, there can be no one-to-one correspondence between genes and organs. Two DNA sequences have a common ancestor if at some time in the past they were copied from the same physical template, but there is no unequivocal criterion for deciding whether two organs are derived from the same ancestral organ. What we really need to know are the genetic networks that underlie the development of a character and how these networks have been transformed in different lineages over evolutionary time. In practice, such information is often unavailable and judgments of morphological homology still need to be made, but such judgments are inherently imprecise.

If one accepts that the sporophyte was *interpolated* into the life cycle by post-zygotic mitosis, then it is probable that most genes used to *construct* the sporophyte were old genes, with roles in the gametophyte, that were now employed in new locations and in new ways: "Genes do not arrive *de novo*, and there is thus only one source from which the sporophyte could derive its genes, viz. the gametophyte" (Pincher, 1937). Does this mean the two generations are homologous or antithetic? The question is anachronistic because concepts and definitions have changed since the two theories were formulated. Rather than continue to update the score-card of Bower vs. Scott, it would be more productive to focus on questions that can now be answered: What proportion of genes are expressed in both generations? And, to what extent do gametophyte development and sporophyte development use common genetic networks?

Phylogeny

Phylogenetic knowledge has greatly improved in the century since Bower and Scott propounded their theories. We now know that embryophytes are a monophyletic group derived from within the charophycean green algae (Karol et al., 2001; Turmel et al., 2002). Extant members of this group have haploid life cycles with zygotic meiosis (see below). Therefore, land plants did not evolve from within any of the groups of algae in which extant members exhibit isomorphic alternation of generations. Moreover, most molecular studies suggest that tracheophytes are derived from within a paraphyletic

grouping of 'bryophytes' (Qiu et al., 1998; Karol et al., 2001). The deepest dichotomy in the embryophyte clade appears to separate liverworts from other embryophytes, with hornworts the sister group of tracheophytes (Samigullin et al., 2002; Groth-Malonek & Knoop, 2005). These phylogenies constrain possible scenarios for the origin of the sporophyte. In particular, hypotheses that sporophytes were independently derived in vascular plants and bryophytes are distinctly non-parsimonious. Similarly, scenarios that posit 'bryophytes' were derived from an ancestor with a free-living, polysporangiate sporophyte require that monosporangiate 'parasitic' gametophytes have evolved independently in mosses, liverworts, and hornworts.

Despite these advances, there are still many uncertainties about how embryophyte life cycles were derived from a charophycean life cycle. These uncertainties arise because the macrofossil record is poor for the critical period in earth history, because consensus has not been reached on which charophytes are most closely related to embryophytes, and because charophycean life cycles are still poorly known.

Charophycean Life Cycles

In this section, I will briefly summarize the limited data available about the life cycles of *Coleochaete*, *Chaetosphaeridium*, and stoneworts (Charales), and then relate this information to the evolution of embryophyte life cycles. These taxa probably include the closest living relatives of embryophytes. In the molecular phylogeny of Karol et al. (2001), stoneworts are resolved as the extant sister-group of embryophytes, with Coleochaetales (*Chaetosphaeridium* and *Coleochaete* spp.) as the sister-group to the stonewort-plus-embryophyte clade (other analyses favor different phylogenies: e.g., Turmel et al., 2006).

Earlier sections have discussed the life cycle of *Coleochaete* in some detail. The conclusion that meiosis occurs in the zygote is based, in large part, on a single paper that is now more than hundred years old. Allen (1905) observed differences in chromosome compaction between the first two divisions of *Coleochaete* zygospores and interpreted these divisions as meiosis I and meiosis II. Despite Allen's observations, the timing and nature of chromosome reduction in *Coleochaete* remain uncertain. Hopkins and McBride (1976) reported that gametophytic nuclei of *C. scutata* contain either the 1C or 2C amount of DNA (by reference to 1C in sperm nuclei), but zygotic nuclei contain from 2C to 8C. These data are compatible with a 2C zygote undergoing two rounds of DNA replication without cell division, followed by reduction from 8C to 1C over the course of three divisions without DNA replication. One might call these divisions meiosis I, II, and III.

Oltmanns (1898) observed that the zygotic chloroplast of *Coleochaete pulvinata* divided three times, without nuclear division, before the zygote accumulated food-reserves and entered winter-dormancy. In spring, the zygotic nucleus divided three times, without chloroplast division, such that each of eight nuclei came to be associated with a single chloroplast. This sequence of three plastid divisions followed by three nuclear divisions resembles the sequence of two plastid divisions followed by two nuclear divisions observed in the monoplastidic meiosis of bryophytes and lycophytes (Brown & Lemmon, 1997).

Even less is known about the life cycle of *Chaetosphaeridium*. Thompson (1969) reported that *Chaetosphaeridium globosum*, unlike *Coleochaete*, expels its ova before fertilization. A wall is deposited around the zygote, after fertilization, but the germination of the zygote has not been described.

The conclusion that stoneworts have zygotic meiosis is based largely on Oehlkers (1916) and the lack of plausible alternative interpretations. Oehlkers described the first nuclear divisions of the *Chara foetida* zygote after the breaking of winter dormancy. The zygotic nucleus divided twice to produce four nuclei in a common cytoplasm. A wall was then formed separating the apical nucleus from the three lower nuclei. The lower nuclei degenerated and the new plant developed from divisions of the apical nucleus. Oehlkers reported extraordinary difficulty in counting the number of chromosomes during the first division. However, the haploid number was present in telophase nuclei of the first and second division. By a process of elimination, he inferred that reduction occurred at the first division. Oehlkers' work was cut-short by the outbreak of war. His paper contains a simple sketch of the sequence of divisions and no further figures.

Coleochaete, *Chaetosphaeridium*, stoneworts, and embryophytes all produce a multicellular haploid body, and all produce large non-motile 'female' gametes and small motile 'male' gametes. Therefore, the last common ancestor of these plants is likely to have been oogamous and to have produced a multicellular 'gametophyte'. Post-fertilization provisioning of the zygote (matrotrophy: Graham & Wilcox, 2000) occurs in stoneworts, embryophytes, and *Coleochaete*, but is absent in *Chaetosphaeridium*. If we accept the phylogeny of Karol et al. (2001), these data suggest that matrophy was present in the last common ancestor of embryophytes and stoneworts, but evolved independently in *Coleochaete* (or was lost in *Chaetosphaeridium*).

Coleochaete and embryophytes retain their zygotes on the maternal gametophyte, whereas *Chaetosphaeridium* expels its ova before fertilization. Whether stoneworts retain their zygotes depends on how this character is defined. Stoneworts disperse 'nucules' (Vines, 1878), a zygote surrounded by a layer of gametophytic cells. A nucule could therefore be interpreted either as a dispersed zygote or as a detached gametophyte fragment with a retained zygote. The expulsion of ova in *Chaetosphaeridium* suggests that zygote retention evolved independently in *Coleochaete* and embryophytes (or was lost in *Chaetosphaeridium*). No clear statement can be made about whether zygotes were retained in the common ancestor of stoneworts and embryophytes.

Meiosis is reported to occur in the zygotes of *Coleochaete* (Allen, 1905) and *Chara* (Oehlkers, 1916). If these old reports are accurate, neither *Coleochaete* nor *Chara* possesses a 'sporophyte'. This implies that interpolation of a multicellular diploid phase, between syngamy and meiosis, evolved after the divergence of stoneworts and embryophytes. Other, less parsimonious interpretations, are of course logical possibilities. Remy (1980), for example, argues that stoneworts evolved from an ancestor with isomorphic alternation of generations, but secondarily lost the diploid phase.

In summary, the last common ancestor of stoneworts and embryophytes can tentatively be proposed to have possessed a multicellular, oogamous, haploid gametophyte that did not produce zoospores (absent in *Chara* and embryophytes,

present in *Coleochaete*). In this ancestor, the diploid phase was limited to a matrotrophic zygote that underwent meiosis without intervening mitotic divisions. Whether meiosis occurred in a retained zygote or after dispersal of the zygote is unclear.

These phylogenetic comparisons of extant forms allow no clear conclusions about whether a multicellular diploid phase evolved before, or after, retention of the zygote. The simplest interpretation is that retention of the zygote preceded post-zygotic mitosis. The resulting sporophyte would have depended on the gametophyte for its nutrition. In vascular plants, the dependent sporophyte evolved to gain physiological independence as it matured. This scenario corresponds to the antithetic hypothesis of Bower (1890, 1908, 1935), as updated and championed by Graham and Wilcox (2000) and Blackwell (2003).

Modern defenders of the homologous theory (e.g., Remy, 1980; Remy & Hass, 1991) argue that post-zygotic mitosis first evolved in an embryophyte ancestor that dispersed its zygote. Mitotic divisions of the zygote would produce a free-living diploid plant that resembled the free-living haploid plant. Then, at some later stage, the zygote germinated precociously, before, rather than after, dispersal. This hypothesis implies that 'bryophytes' are descended from ancestors with free-living sporophytes.

Homologous Alternation Redux

Isomorphic Alternation in the Devonian

Remy (1980) proposed that modern bryophytes and vascular plants have all descended from an ancestor with an isomorphic life cycle in which haploid gametophytes dispersed zygotes that germinated to produce diploid sporophytes. Reconstruction of this life cycle was based on three principal observations. First, free-living gametophytes of some Devonian land plants morphologically resembled their putative free-living sporophytes. Second, these gametophytes produced archegoniophores that elevated archegonia above the substrate. Third, no gametophytes have been found with attached sporophytes (Remy, 1980; Remy et al., 1993; Taylor et al., 2005).

For purposes of further discussion I will assume that Remy's reconstruction of the 'rhyniophyte' life cycle is correct, as are modern phylogenetic reconstructions in which embryophytes and tracheophytes are monophyletic, but 'bryophytes' are paraphyletic. Two contrasting hypotheses, the 'retained-zygote' hypothesis and the 'dispersed-zygote' hypothesis, are the modern successors of the old antithetic and homologous theories.

The retained-zygote hypothesis proposes that the sporophyte initially evolved by mitotic divisions of a zygote that was retained on a maternal haploid plant. The sporophyte was initially dependent for its nutrition on the maternal gametophyte. This condition is maintained in modern bryophytes. In an ancestor of vascular plants, the physiologically-dependent sporophyte was reduced to a transitory embryonic phase that matured into a free-living diploid plant. The simplest version of this hypothesis requires a single origin of zygotic retention, a single origin of free-living

sporophytes, and a loss of zygotic retention in the rhyniophyte lineage after this diverged from the ancestry of modern forms.

The dispersed-zygote hypothesis includes all scenarios in which modern embryophytes descended from ancestors with free-living haploid and diploid phases, linked by two dispersal stages (zygote and spore). The hypothesis is taken to include variants in which 'nucules' (zygotes surrounded by haploid cells) or early embryos are dispersed instead of naked zygotes. The simplest version of this hypothesis requires a single origin of zygotic retention, in an ancestor of modern embryophytes that did not include rhyniophytes among its descendants. The hypothesis also requires that the dependent, monosporangiate sporophytes of liverworts, mosses, and hornworts have evolved independently in the three lineages. Current versions of this hypothesis do not address how an isomorphic alternation of generations was derived from the basically haploid life cycles of charophycean algae.

The key feature that distinguishes these hypotheses is whether embryophytes had an ancestor with zygotic dispersal, not whether gametophytes and sporophytes were ever 'isomorphic'. It is probable that genes responsible for vegetative development of the gametophyte were co-opted to produce the vegetative sporophyte, whenever a free-living diploid plant evolved. Therefore, a resemblance between free-living gametophytes and sporophytes is compatible with either hypothesis. The retained-zygote hypothesis appears somewhat more plausible, although the dispersed-zygote hypothesis cannot be refuted definitively.

Isomorphic Alternation in Modern Tracheophytes

Pteridophytes are usually conceptualized as having short-lived, simple gametophytes with long-lived, complex sporophytes. This generalization uses the leptosporangiate ferns as the implicit model of pteridophyte life-cycles (but even among leptosporangiate ferns there are taxa in which gametophytes are longer-lived than sporophytes and reproduce vegetatively: Dassler & Farrar, 1997). However, modern ferns possess gametophytes that are morphologically simpler than those of their Devonian ancestors (Kenrick, 1994).

Hints of an earlier stage of 'isomorphic' alternation in vascular plant life-cycles can be found in studies of the lesser-known gametophytes of modern Lycopodiales, Psilotales, and Ophioglossales. Gametophytes of some lycopods produce gemmae that allow indefinite asexual reproduction of gametophytes (Treub, 1886a) and, in some cases, *young* sporophytes morphologically resemble their associated gametophyte (Fig. 3; Treub, 1884, 1886b; Holloway, 1915; Chamberlain, 1917). Subterranean gametophytic and sporophytic axes of *Psilotum* are morphologically similar, both produce gemmae, and both sometimes contain vascular tissues (Holloway, 1939; Moseley & Zimmerly, 1949; Bierhorst, 1953, 1954). Holloway (1921, 1939) emphasized the difficulty of distinguishing between sporophytic and gametophytic 'objects' of *Tmesipteris* and *Psilotum* in the absence of sexual organs. Pant et al. (1984) noted that the form and color of the subterranean gametophytes of Ophioglossales "are so much like that of root or rhizome fragments that it is difficult and cumbersome to recognize them from such sporophytic fragments."

Bierhorst (1969) similarly reported difficulty in distinguishing between subterranean gametophytes and sporophytes of the fern *Stromatopteris moniliformis*. He

wrote, "In all qualitative aspects the primary axes of the sporophyte are identical to the gametophytic axes save for the presence of gametangia on the latter." *Stromatopteris* is a gleicheniaceous fern (Pryer et al., 2004). Therefore, the similarity in form of gametophytes and young sporophytes must be secondarily derived, presumably because of the exigencies of a similar subterranean, mycotrophic existence.

All of the modern forms discussed above possess mycotrophic gametophytes. An interesting possibility—of a non-photosynthetic ancestry for the gametophytes of tracheophytes—emerges when the modes of nutrition of free-living gametophytes are considered. Most lycopods have non-photosynthetic gametophytes that are associated with an endophytic fungus. The Psilotales and Ophioglossales also possess subterranean, non-photosynthetic gametophytes, whereas *Equisetum* and most ferns (*Stromatopteris* is an exception) have photosynthetic gametophytes. Therefore, it would be equally parsimonious to invoke an acquisition of non-photosynthetic

Fig. 3 Isomorphic alternation of generations in modern lycopods: **a** *Lycopodium* (now *Lycopodiella*) *laterale* (from Chamberlain, 1917); **b** *Lycopodium* (now *Huperzia*) *phlegmaria* (from Treub, 1886b)
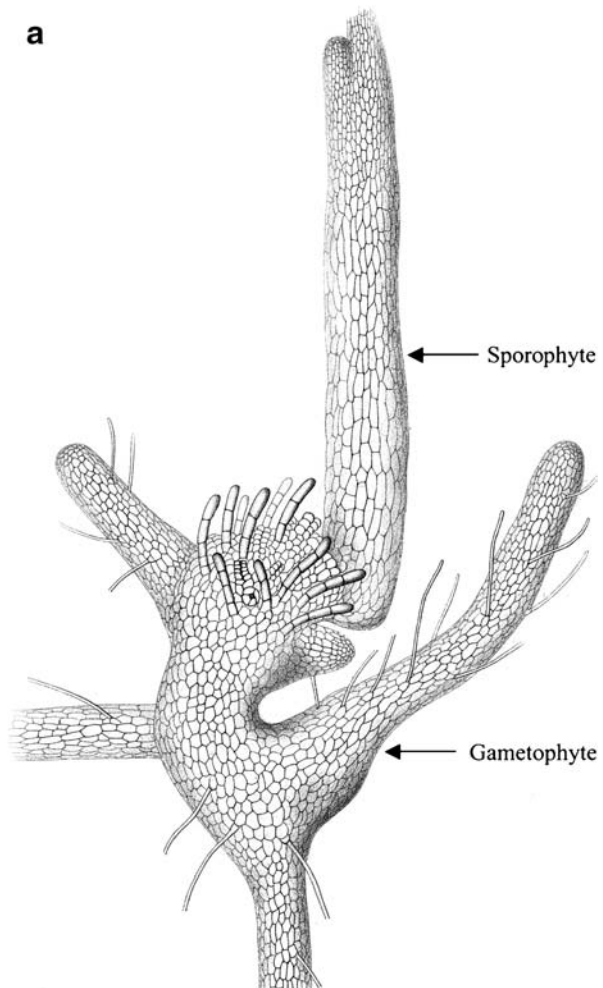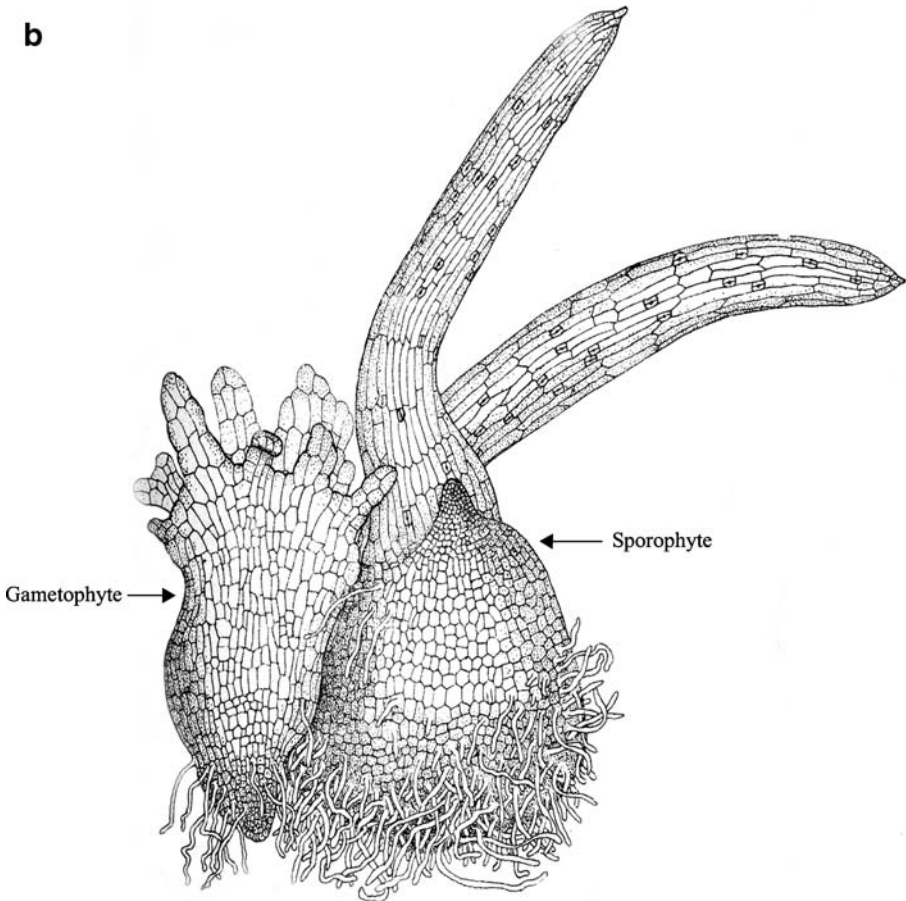
Fig. 3 (continued)

gametophytes in an ancestor of extant tracheophytes, with a reversion to photosynthesis in the *Equisetum*/fern lineage, as to invoke two separate origins of non-photosynthetic gametophytes, one in lycopods and the other in a common ancestor of Psilotales and Ophioglossales.

A less radical hypothesis would be to posit some key character (or characters) in ferns that enabled them to dominate most niches available for reproduction via photosynthetic gametophytes, thereby excluding other 'pteridophytic' lineages from this ecological space. As a result, the only members of non-fern lineages to survive until the present possessed gametophytes with alternative modes of nutrition.

Summary

Celakovsky (1874) introduced a distinction between homologous and antithetic alternation of generations. In Celakovsky's scheme, two generations were homologous if they obeyed the same growth-law but were antithetic if they obeyed

different growth-laws. Thus, *Coleochaete* possessed both forms of alternation: gamete-producing (sexual) and zoospore-producing (asexual) thalli were homologous, whereas the multicellular (asexual) body that developed from the zygote was antithetic to these generations. With respect to archegoniates, Celakovsky considered the asexual generation (sporophyte) to be antithetic to the sexual generation (gametophyte).

Pringsheim (1876b) rejected the distinction between homologous and antithetic alternation. He interpreted the 'fruit' of *Coleochaete* as a rudimentary asexual thallus that developed while attached to the previous sexual thallus. In his view, the 'fruit' and a free-living, zoospore-producing thallus were different manifestations of an asexual generation that was homologous to the gamete-producing sexual generation. The life cycle of a moss could be derived from a life cycle resembling that of *Coleochaete* by the suppression of all except the first asexual generation.

Bower (1890) believed that the sporophyte was a fundamentally new structure that had been *interpolated* into the life cycle between successive gametophytes. He borrowed Celakovsky's terminology and called this antithetic alternation of generations. Scott (1895), by contrast, believed that the sporophyte had been derived from an asexual algal thallus. He called this homologous alternation of generations. Scott favored independent algal origins of bryophytes and vascular cryptogams.

The homologous theory can be considered to have had an early and a late version. In the early version, *Coleochaete* was used as a model for the algal ancestor of land plants. *Coleochaete* was considered to show an isomorphic alternation of sexual and asexual thalli. The first asexual thallus differed from the others because it developed while attached to a sexual thallus. The life cycle of archegoniates could be derived from such a life cycle by suppressing all except the first asexual generation. The discovery that the alternation of generations in land plants was accompanied by an alternation of chromosome number (Strasburger, 1894) weakened this version of the homologous theory because it accentuated the distinctiveness of gametophytes and sporophytes.

In the late version of the homologous theory, first *Dictyota*, then *Ulva*, replaced *Coleochaete* as the model for the algal ancestor of land plants. This version of the theory proposed that land-plants were derived from an alga with an isomorphic alternation of haploid and diploid generations. *Dictyota* (unlike *Coleochaete*) disperses its eggs. Therefore, this version of the theory assumed that the diploid generation was initially free-living, rather than retained on the haploid maternal plant.

The early and late versions of the homologous theory mark a shift in the debate over homologous versus antithetic alternation. In the early debate, the proponents of both theories could use *Coleochaete* as a model for the algal ancestor of archegoniates. Their disagreement was not about the nature of this algal ancestor but about the morphological interpretation of the sporophyte (as something new or something modified) and about the evolutionary relationship between the 'parasitic' sporogonium of bryophytes and the free-living sporophyte of pteridophytes. In the later debate, the two theories proposed different kinds of algal ancestor for archegoniates. This shift in the terms of the debate partially reflected a shift in emphasis from questions of morphology to questions of phylogeny.

We now know that embryophytes were derived from within the charophycean green algae, and that the closest extant relatives of embryophytes possess a multicellular haploid body but lack a multicellular diploid body. Therefore, the sporophyte has been interpolated into a basically haploid life cycle. One could interpret this conclusion as a vindication of the antithetic theory championed by Bower (1908) and as a rejection of the late version of the homologous theory. However, debate continues about whether the sporophyte originated from a dispersed zygote or from a zygote that was retained on a maternal gametophyte.

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