THE EARLY EVOLUTION OF THE
ARCHEGONIATAE: A RE-APPRAISAL

A. D. J. MEEUSE

(Hugo de Vries Laboratory, University of Amsterdam)

ABSTRACT

After a re-appraisal of the alternative hypotheses concerning the origin and the early evolution of the archegoniate land plants, the postulation of a thalassiophytic group of precursors with free isomorphic alternating generations by Church, Zimmermann, and several others is rejected. Several versions and modifications of this 'homologous' theory, such as Fritsch's suggestion of diminutive filamentous algal being the progenitors of the vascular plants and Jeffrey's idea of an advent of partly emerged (aerial) sporangiate extensions of an aquatic sporophyte, are equally untenable. In the present author's opinion the old and reputedly almost obsolete 'antithetic' theory is much more compatible with the relevant evidence, provided this hypothesis is more precisely formulated. The conquest of the land must have begun with the gradual migration of the *gametophytic* (haploid) generation to semi-terrestrial or temporarily dry habitats *before* the development of a vegetative diploid phase. The first stage after the colonisation of semi-terrestrial and subsequently of terrestrial environments by presumably still prostrate life forms consisting of filamentous algal strands must have been the differentiation of a portion of this haploid type into a more massive parenchymatous soma which remained prostrate in many cases and bore the sessile sporangia. In bryophytes such differentiations of the gametophyte may themselves be more or less erect and thus raise the sporangia into an undeniably aerial position (as in many Musci), or they produce upright extensions on which the gametangia are produced and, later on, the sporangia are inserted (as in *Marchantiales*). Ontogenetically the phylogenetic sequence is frequently recapitulated in that first a filamentous protonema develops from a germinated spore and only afterwards a more important gametophytic structure (typically developed in the *Bryales*). In other instances the sporangium is, or was, not supported and 'lifted' into the air by a part of the haploid plant but by an *intercalated* sporangial stalk (sporangiophore) which is a vegetative diploid structure and constitutes the modest beginning of the large sporophytes of the Higher Cormophyta. The intercalated vegetative diploid structure originated subaerially and was *ab initio* a terrestrial organism, i.e., the sporophyte did not develop out of a submerse aquatic archetype by a process of adaptation as is assumed in the 'homologous' theory. The vegetative sporophyte and, accordingly, the characteristic features of the terrestrial plants such as the vascular (stelic) tissues, on the contrary developed *de novo* and the sporangiophore is consequently *sui generis* in respect of both the gametophytic and the sporangium (representing the phylogenetically older portions of the plant). The *Anthocerotales* are reminiscent of this early evolutionary level of the Hemitracheophyta which must *ab initio* have had, or soon acquired, green and partly independent (photo-autotrophic) sporophytes. The phylogenetic history of the *Bryophyta* and of the *Hemitrachyophyta* is discussed in the light of the new interpretation of the subaerial transmigration Certain pertinent problems of evolution (mono- or polyrheithry) and of homology (morphological equivalence of certain structures versus inhomology through independent, i.e., *sui generis*, origin) are tentatively analysed. These considerations have an important bearing on our views concerning the relationships of various archegoniate groups and reveal flaws in several 'established' ideas some of which concern certain aspects of the Telome Theory.

1. THE ALTERNATIVE HYPOTHESES

Some recent summaries dealing with the origin of the early terrestrial plants (e.g., CHRISTENSEN, 1954, 1957; ZIMMERMAN, 1955, 1959, 1965; ANDREWS, 1960a; AXELROD, 1959; STEWART, 1960, 1964) suggest that the three principal points of inquiry are (1) the "transition" from a non-tracheophytic (or at least a non-archegoniate) precursory phase to the proper terrestrial plants, (2) a monophyletic descent starting from a single group of telomic or pre-telomic organisms resembling the *Psilophytales* (or perhaps the *Anthocerotales*), or a polyrheithric development, and (3) the advent of the first truly tracheophytic forms, which is almost certainly of pre-Devonian, but according to some exaggerated claims even of Cambrian age. In my opinion, the first question is by far the most pertinent, because the possible answers to the other two depend to a large extent on the acceptance of the mode of origin of the terrestrial sporophyte. It is this topic that still needs exhaustive treatment, because there are some controversial issues which are not so apparent, most workers suggesting in their writings that the so-called homologous theory has completely superseded the older "antithetic" hypothesis (see, in addition to the above-cited authors, e.g., TAKHTAJAN, 1953; STEINBÖCK, 1954, 1959; PROSKAUER, 1960). The majority of them accept the so-called thalassiophytic origin of the archegoniate forms, *in extenso* developed by CHURCH (1919), which theory requires the postulation of a group of putative progenitors of the terrestrial plants, the Thalassiophyta, which are supposed to have been rather large marine algae with isomorphic alternating generations (i.e., with a free-living, well-developed sporophyte). Strong adherents of this idea of a descent of the archegoniate plants from such large marine ancestral types are, apart from Zimmermann, e.g., STEWART (1964) and CORNER (1964). Some dissident opinions were expressed by FRITSCH (e.g., 1945) who pointed out, among other things, that, instead of larger precursors invading the land, the possibility of diminutive algal forms migrating to the terrestrial habitat deserves serious consideration. However, he left the question open whether a migration from the sea or from the fresh water must be accepted as the more likely event, although he himself was inclined to postulate the conquest of the land by intertidal marine forms. VISCHER (1953) agrees with Fritsch's ideas in many respects, but decidedly favours fresh water forms as the putative progenitors of the archegoniate plants. CHRISTENSEN (1954) brought a very fundamental point to the fore: irrespective of the primary origin of the archegoniate plants from aquatic organisms with isomorphic generations, the question must be considered whether the originally free-living sporophyte had already become dependent ("parasitic") on the gametophyte (and at the same time had become reduced) before or after subaerial transmigration. Zimmermann and several other authors evade the issue, but, as CHRISTENSEN (1957) re-emphasized, this aspect of the hypothesis of the homologous alternating generations has a considerable bearing on the relative position of the Bryophyta (and especially so of the *Anthocerotales*) in

respect of both the earliest land plants and the various pteridophytic forms. The bryophytic sporophyte may be "reduced" or "advanced" as compared to a common ancestral form of pteridophytes ("tracheophytes") and bryophytes (PROSKAUER, 1960). Such ideas did not change the main theme of the theory, the advent, at some time or another, of a progenitor of the cormophytic plants with isomorphic generations.

The alternative theory, presupposing the alternation of "antithetic" generations, or, in Zimmermann's terminology, the intercalation of a sporophytic generation between the gametophytic ones, is older and goes back to Hofmeister. If one would only go by the opinions expressed by such authorities as Zimmermann, Corner, and several others, the antithetic theory is entirely obsolete.

Indeed, since the publications by WETTSTEIN (1935) and by CAMP-BELL (whose last paper on the subject appeared in 1940), no other botanist seems to have seriously challenged the homologous theory (or "transformation theory" as Zimmermann has it) postulating progenitors with alternation of isomorphic generations. Even JEFFREY (1962), who has pointed out that *"the question of the evolution of land plants is primarily a biological one, of which the evolution of water economies comprises a major part"*, and that this question has been largely ignored in most discussions of the problem, surprisingly still adheres to the idea of isomorphic diplohaplonts being the progenitors of the archegoniatae (although he assumes that the sporophyte develops from the fertilised egg cell *in situ* and is borne on the gametophyte). The present publication, apart from being a compilation of the more recent opinions on the subject, is a re-consideration of exactly these ecological aspects of the evolution of the *Archegoniatae*. The corollary of the ensuing deductions is a plea for the rehabilitation of the old theory of antithetic generations, albeit on somewhat different grounds than those on which the theory was originally conceived by Hofmeister and other protagonists of the "intercalation" theory.

2. SOME FUNDAMENTAL CONSIDERATIONS

As mentioned previously, Christensen and Jeffrey pointed out certain facets of the problem of proto-cormophyte evolution which had not previously been extensively treated in most of the relevant publications. In spite of CHRISTENSEN's (1957) most pertinent statement that this aspect was neglected by ZIMMERMANN (1955), the latter (1959, 1965) did not reconsider the possibility of the conquest of the land by a form with the sporophytic generation ("already") dependent on the gametophyte at the time of sporulation, instead of by some *"Urlandpflanze"* in which the originally isomorphic *gametophyte* had become reduced in size in respect of the sporophyte (see, e.g., ZIMMERMANN, 1955, p. 300, fig. 3; 1959, p. 130, fig. 56 B; 1965, p. 21, fig. 6, and p. 46, fig. 16). This is the crux of the whole problem of the origin of the archegoniate plants, because irrespective of the early history of their still completely aquatic progenitors, their first terrestrial precursors were according to Christensen's interpretation

no longer plants with isomorphic alternating generations. Similarly, JEFFREY's (1962) idea of a partial emergence of the originally sub-merse sporophyte and an increase in size of the subaerial sporangium-bearing portion is an important emendation of CHURCH's original views. There are several other basic assumptions on which the "ho-mologous" theory rests that are not at all convincing and can certainly be challenged. In the first place, the habitat of the putative algal ancestors: was it the marine intertidal zone or the fresh water? The arguments adduced by Jeffrey certainly point to the second alternative. The hypothetical thalassiophytic progenitors are consistently described as fairly large to large green seaweeds, but according to ideas de-veloped by FRITSCH as early as 1916 (and re-published in extenso in 1945) there are several direct and indirect indications pleading in favour of the postulation of small to diminutive prostrate algae living in fresh water (or even on wet ground) being the ancestral forms. JEFFREY (1962) uses the same reasoning (without citing Fritsch's papers) and submitted some relevant ecological evidence. These con-siderations have a considerable bearing on the most probable evolu-tionary sequence of events: did the two generations of the plant (gametophyte and sporophyte) both attain their maximum develop-ment *before* the conquest of the land (followed by the retrograde development of one of them), or did only one of them do so? The *Thalassiophyta* were "modelled" after the highest forms of marine algae (including the predominantly marine *Phaeophyta* and *Rhodophyta*) with a massive parenchymatous soma, but the putative ancestors of all land plants must have been green algae on biochemical and phytochemical grounds, so that neither the structure nor the life-cycles of the other algal groups can possibly have any bearing on the problem under discussion. The evidence provided by the recent green algae is anything but convincing and in point of fact the origin of the land flora must indeed rather be sought among the diminutive green, and still filamentous, oogamous forms of the fresh water or moist soils (VISCHER, 1953). Intimately linked with this deduction is the question of the relative development of the two generations. As I pointed out before, Church and most of the other adherents of the hypothesis of the alternation of isomorphic generations in the thalas-siophytic archetypes of the Archegoniatae imagine free-living and mutually independent haplontic and diplontic phases (see, e.g., Zim-mermann's figures already quoted in this chapter). However, as Fritsch pointed out, there are no recent green algae that could adequately fit the part required by the thalassiophytic theory. Fossil remains of algal forms cannot have any demonstrative force in this connexion because we can only in exceptional cases ascertain the true taxonomic position of these fossils, i.e., whether they were red, brown, or green algae.

The postulation of an alternation of free isomorphic generations of algal precursors in the transformation hypothesis implies that both phases were originally autotrophous plants with practically the same ecological requirements, which in turn requires the assumption that

the gametophyte and the sporophyte migrated simultaneously to the terrestrial environment, or approximately so. None of the recent archegoniate land plants has a completely submerse-aquatic phase combined with a terrestrial alternating generation! However, whereas the sporophyte, in the train of thought of the "homologous" theory, "acquired" the characteristic features of the terrestrial plants (a cuticle, stomatic openings, vascular, or stelic, tissues, non-motile cutinised spores), the gametophyte did nothing of the sort and even became reduced instead. It was exactly this moot point which incited CHRISTENSEN's emendation of the theory and Jeffrey's version of the conquest of the land, the first author explicitly stating (1957) that the common ancestor of the *Bryophyta* and the *Pteridophyta* had a sporophyte which was parasitic on the gametophyte, and the second postulating and initial association of the two phases, the submerged sporophyte forming subaerial sporangiate outgrowths. In all these reconsiderations the sequence of events (the time factor) is of paramount importance. If we start from the plausible assumption that the haploid phase of the generation cycle was the first to develop a vegetative soma of an appreciable size, the diploid phase lagging behind in this respect, many speculations can be simplified or even rendered superfluous by considering the possibility of a migration of the gametophytic plant to the terrestrial habitat *before* the development of a sporophyte of an appreciable size. This amounts to the re-instatement of the intercalation theory, of the hypothesis of antithetic alternating phases, *in optima forma*, as we shall see, and this requires some comment.

3. WHEN DID THE TRANSMIGRATION FROM WATER TO LAND TAKE PLACE?

After the first multicellular green algae had evolved, which must have happened a very long time ago in an aquatic environment, even the early filamentous and perhaps still planktonic forms must gradually have filled other ecological niches: the intertidal marine environment, the fresh water, and subsequently also, via temporarily flooded ground, moist terrestrial habitats. It is very likely that the conquest of the land started from such habitats as shallow freshwater pools drying out periodically. Even to this day algal froms with a primitive organisation, i.e., filamentous form with a hardly developed diploid phase, are by no means rare in semi-terrestrial situations and on dry land (VISCHER, 1953). There are, therefore, no arguments precluding an early adaptation of primitive filamentous forms to a truly terrestrial life. This has already been emphasised by Fritsch, Vischer, Jeffrey, and others, but this simple and logical starting point of our inquiry into the origin of the land flora has up to now been obscured by the assumption that a vegetative sporophyte of at least modest dimensions had developed *before* the gametophytic generation had become completely terrestrial or approximately so. Jeffrey has summed up the ecological and physiological evidence for his contention that a truly terrestrial plant is fundamentally different

from a submerse aquatic form in several respects. As Jeffrey rightly says (l.c., p. 449): "Direct colonisation of the land by littoral inter-tidal algae seems quite improbable". The gradual "adaptive" evo-lution of terrestrial forms is explained by Jeffrey by postulating that a portion of a submerse sporophyte was, so to speak, gradually raised above the water and assumed the characteristics of the terrestrial sporophyte as it became more important by producing additional vegetative soma. In view of the evidence from recent (semi-)terrestrial green algae and pteridophytic prothalli I cannot visualise a migration as suggested by Fritsch, Jeffrey (or Christensen for that matter) for the very same reason, viz., the different physiology and ecology of submerse aquatics and of land plants. The crux of the problem can be expressed by the question why, as suggested in the older hypotheses, the *gametophyte* was induced by some selective evolutionary force to leave the medium to which it was best adapted after it was accom-panied by a vegetative sporophyte. It is much more logical to suppose that the whole development of the vegetative sporophyte took place subsequent to the migration of the gametophyte to a (semi-)ter-restrial environment. As Jeffrey has rightly emphasised, the selective advantage of an aerial diaspore dispersal becomes apparent in per-odically changing habitats (monsoon pools, and the like), but this applies to haplontic forms as well as to diplonts, in other words, the advent of the non-motile cutinized spore was not necessarily coupled with the presence of a vegetative sporophyte of appreciable dimen-sions.

If we take this as the starting point of our deductions and postulate that the colonisation of the land by algae started at the phylogenetic level of a still insignificant diploid phase, the gametophytic gener-ation of the terrestrial algal ancestors of the archegoniate plants must have been a plant of a modest to diminutive stature, most probable consisting of prostrate filaments. The protonemata of the mosses are strongly reminiscent of this early evolutionary phase, in my opinion. Sexual reproduction of these early forms was perhaps rather primitive, as in e.g., Charophyta, but at some time or other the already sessile oocyte must have been retained on the gametophyte to develop into a sessile sporangium. It is rather irrelevant in this connexion whether at this stage the spores were already non-motile or still of the ciliate zoospore type, and if the prostrate filaments had either already evolved into a prostrate frondose (thallose) soma, or became dif-ferentiated into prostrate and more or less erect portions (the latter bearing the archegonia and later the sporangia). The sequence is not so important, but at some time or other there must have been prostrate thallose haploid forms with sessile sporangia, or prostrate gametophytes with erect archegonium-bearing portions which raised, as it were, the sporangia into the air. It is already at this early phy-logenetic stage that the first divergent evolution must have taken place which is conceivably still reflected in the morphology of the gametophytes and the sporophytes of the various groups of the Bryo-phyta at the present-day level. In several cases the erect and more

Salient points	'Homologous' theory (CHURCH, ZIMMERMANN, etc.)	Do. emended by FRI 1945; VISCHER
Suggested progenitors of terrestrial plants.	Marine algae of intertidal zone with alternation of independent isomorphic generations; haploid and diploid phases (fairly) large, evolution monophyletic; this hypothetical group referred to as 'Thalassiophyta'.	Aquatic to terrestrial tous) heterotrichous, with isomorphic gametophytes of mo to diminutive with so (subaerial) branches monophyletic.
Development of gametophyte and sporophyte at the beginning of the conquest of the land.	The gametophyte is supposed to have become reduced before or soon after the adoption of a terrestrial way of life; the sporophyte must have become adapted to a subaerial existence and developed vascular tissues etc. de novo or from a pre-vascular cell differentiation in precursory algal forms.	Do.
Morphology of early subaerial sporophyte.	Very similar to thalassiophytic prototype, but with adaptations to terrestrial existence (cuticle, stomata, stele).	Do.
Evidence from fossils.	No unequivocal records of Thalassiophyta; Eocormophytes are already too diversified to be of decisive importance in any objective judgment of the hypothesis.	Do.
Evidence from recent forms.	Large Chlorophyceae with free-living isomorphic generations and reproducing by means of oogamy unknown, i.e., recent forms fitting the part of the Thalassiophyta are non-existent.	Small heterotrichous with erect or suberec are known, but the eration usually sma tions not isomorphic ed in the theory!).
Adaptation and ecological requirements.	Migration of large marine sporophyte to the land and adaptation to terrestrial life is postulated.	Do. (but origin from algae not precluded).
Position of the Bryophyta.	Bryophytes are supposed to be reduction lines, the gametophytes predominating and the sporophyte having undergone a retrograde development and secondarily dependent on the gametophyte; Anthocerotales not necessarily primitive.	It seems probable tha phyta have followed lutionary line of (FRITSCH, 1945, p. generation supposed come secondarily the gametophyte.

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SCH, 1916, 1953	Do. emended by JEFFREY, 1962	'Antithetic' or 'intercalation' theory, present author's version
(filamen- reen algae erations; st stature suberect evolution	Aquatic filamentous green algae showing a homologous alternation of generations but sporophyte developing directly from zygote and attached to gametophyte, phases of modest size; sporophyte initially submerse but developing aerial portions emerging from the water which bear the sporangia; evolution of early stages monophyletic.	Subterrestrial to terrestrial prostrate filamentous algae, with only a haploid vegetative phase which bore the sessile sporangia; the haploid plant of a modest size; early evolution presumably monophyletic.
	Gametophyte initially not very much reduced; development of large sporophytic generation after the thallus portion supporting the sporangia had emerged from the water.	No vegetative diploid phase (which developed only after the gametophyte had colonised the terrestrial habitat); reduction of gametophyte only started after a vegetative sporophyte of an appreciable size had originated.
	Only a portion emerging from the water becoming a true terrestrial organism (and later predominating).	Originating as an intercalated sporangial stalk (sporangiophore) which gradually increased in size and which was from the very beginning of its existence adapted to a life in a terrestrial environment.
	Do.	Fossils such as Sporogonites suggest an early type of prostrate terrestrial plant with solitary stalked sporangia, which renders a thalassiophytic origin most unlikely.
lgal forms branches' xual gen- (genera- postulat-	All the evidence points to small heterotrichous algal progenitors occurring in fresh water, the sporophyte developing on gametophyte after oogamy, but in recent forms no isomorphic sporophyte.	Small heterotrichous filamentous algae without a substantial asexual (diploid) generation not infrequently found in (semi-)terrestrial habitats are suggestive of putative progenitors.
resh water	Ecological requirements and other considerations render the migration and adaptation of large sea weeds altogether inconceivable.	Do., but for the same reasons migration and adaptation of large submerse fresh water sporophytes is not very probable either.
the Bryo- blind evo- their own); asexual have be- endent on	Bryophytes, but more particularly the Anthocerotales, are still rather close to early archegoniate land plants.	Do.

aerial differentiations of the gametophyte became rather elaborate structures bearing the gametangia (and subsequently the sporangia), the sporangia remaining sessile on the gametophyte, as in *Marchantiales* and several groups of the Musci (but not in the *Bryales*). The second evolutionary trend was the development of a diploid sporangial stalk which was virtually intercalated between sporangium and gameto-phyte. The most pertinent examples of such plants are the fossil taxa *Sporogonites* (as reconstructed by ANDREWS, 1960b) and *Eogaspesiea* (DABER, 1960) of Devonian age, but also the *Anthocerotales* are not far removed from this type of plant. The bryophytes with a stalked sporangium, mainly found among the *Bryales*, show both trends, *viz.*, the development of an intercalated sporangiophore and the differentiation of the gametophyte into a prostrate early phase (the protonema) and a (frequently erect) secondary phase producing the gametangia (and later bearing the sporangiophores). The position of the *Anthocerotales* is indubitably somewhere near the crossroads of the phylogenetic lines of the bryophytes and the tracheophytes, but we should not be too rash in identifying them with progenitors of the vascular plants, because the gametophyte has presumably already become reduced in size and importance in respect of its ancestral form, which we must imagine as a flat organism, either consisting of a dense meshwork of protonema-like filaments, or thallose in structure and resembling a large hornwort gametophyte, but with sessile sporangia.

4. SOME CONSEQUENCES OF AN EARLY CONQUEST OF THE TERRESTRIAL HABITAT

The most important consequence of the postulation of an early migration of the haploid generation before the intercalary development of a vegetative sporophyte between gametophyte and sporangium is that the formed sporangiophores originated *de novo*, so that one does not have to assume an "adaptation" of an originally aquatic (or even submerged!)sporophyte to a new environment. The gametophyte remained a low prostrate plant of modest size and retained some of the characteristics of an aquatic, the proximity of the substratum apparently providing sufficient moisture, but the intercalated vege-tative sporophyte developed (indeed "antithetically"!) as a terrestrial organism right from the beginning. Jeffrey's objection to a change-over from a submerse way of life (or something very similar to it in semiterrestrial habitats) to a truly subaerial existence is thus satisfactorily met with: some characteristic physiological and mor-phological features of the sporophyte originated *ab initio* and not as a secondary adaptation to a "new" habitat.

Another topic brought up by the last-mentioned author is the possible early association of the haplontic algal form or the primitive gametophyte with fungi. In this case I think not only his deductions are basically sound, but also the reconstruction of the phylogenetic history is quite plausible. In lichens the fungal component appears to be the dominant partner (being the only one capable of sexual

reproduction), but in many terrestrial orchids the mycorrhizal hyphae are virtually "milked" and there can be very little doubt about the predominance of the orchid. One can easily visualise an alternative evolution of an initial (and more or less incidental or "loose") association of fungi and, still haplontic, semiterrestrial algae, viz., the development cf a mycorrhizal relation between the two in which the algal component, though predominating, became more and more dependent on the fungal partner by the loss of its original photosynthetic capacities. The development of the mycotrophic prothalli of several pteridophytic groups can thus be satisfactorily explained, and also the fact that they became more massive and frequently subterraneous, perhaps even acquired an increased longevity. However, this was a secondary development which apparently did not occur, or had not yet initiated, in the evolutionary lines leading, eventually, to the recent bryophytes, most of the true ferns, and the water ferns. A certain amount of polyphyletic or polyrheithric evolution must have taken place which will be discussed presently. An important conclusion is that if MERKER (1958, 1959) is right in his identification of the rhyniaceous subterranean organ (the so-called "rhizome" in the previously current terminology) as the long-lived gametophytic generation, it is doubtful whether *Rhynia* and its closest allies can be regarded as representing ancestral forms of other tracheophytic groups with green, non-mycotrophic prothalli. I shall return to these points presently when various phylogenetic aspects will be considered.

. As regards the physiology of the intercalated vegetative sporophyte, there are again alternative possibilities. If one starts from the assumption that it primarily only developed as the result of selective processes favouring spore dispersal by raising the sporangium as far as possible above the frequently moist and hence unfavourable substratum, it was completely dependent on the gametophyte and presumably did not possess assimilatory plastids, but almost certainly developed a cuticle. The transport of substances supplied by, or via, the gametophyte and translocated in a watery medium (as solutes or in colloidal solution) must soon have necessitated adequate means of providing an upward flow of water, evaporation providing the translocation mechanism; in other words, stomata originated. In addition the support of the sporangia presumably induced the advent of a structural strengthening device, the central xylem strand so characteristic of the stele of early telomatic cormophytes. The other possibility is that the sporophyte became a green and partly self-supporting structure at a very early stage. Both conditions are neatly illustrated by the *Bryophyta*: in such groups as the *Bryales* the sporangiophore is completely "parasitic" on the gametophyte, whereas in the *Anthocerotales* a photosynthetic sporangiophore is found. In my opinion it is not a foregone conclusion that the sporophytes of all archegoniate plants are strictly homologous in the sense that the sporangiophore of the *Bryales* is a derivative of a partly autotrophous vegetative sporophyte of a type still found in the *Anthocerotales* (or *vice versa*).

Obviously, only a sporophyte provided with chloroplasts could eventually become the predominating phase of the two alternating generations. If the development of the large sporophytes of the pteridophytes and the spermatophytes was indeed an evolutionary process that took its origin in a vegetative diploid growth of modest size,the homology of these large sporophytes rests upon a common origin from a very simple structure, the intercalated diploid sporangiophore. Differences in the stelic structure, and in the mode of branching and the development of some characteristic morphological and anatomical features in the various pteridophytic groups need not necessarily be explained as semophyletic differentiations of the same basic structural pattern provided by a common group of isotomously bifurcating telomic progenitors resembling the sporophytes of the *Rhyniaceae*. There must have been enough room for the evolution of convergent and of parallel trends, whilst some fundamental differences persisted (compare also the arguments adduced by AXELROD, 1959). The suggested new working hypothesis concerning the origin of the sporophytes of the terrestrial plants manifestly has a considerable bearing on the inquiry into early Archegoniate evolution, and on the phylogeny of and the relationships among the Bryophyta in particular. Some of the relevant points have been tabulated in the accompanying Table I (see pages 168, 169) in which various theories are compared.

5. IMPLICATIONS OF THE MOST LIKELY SEQUENCE OF
   EVOLUTIONARY PROCESSES AND TRENDS

It appears to be reasonably well established that the migration of filamentous and oogamous green algae from the fresh water habitat to damp soils started at a very early phase in the phylogeny of algal groups. This can be visualised as a gradual change-over from a submerse life to a sessile life on periodically flooded soils, followed by a progressive adaptation to a truly "terrestrial", drier habitat. These ancestral algal forms developed a sporangium and a more massive haplontic soma. The sporangium produced soon, if not *ab initio*, cutinised spores. The more parenchymatous gametophyte may have developed from suberect aerial differentiations arising from the prostrate filaments as found in recent heterotrichous algal forms. The more massive haploid phase must have been semiprostrate in many cases, but may have been erect (as in many of the true mosses or *Musci*) or formed erect differentiations (as in *Marchantiales*), thus "raising" the sporangium into the air, the medium favouring the release and the dispersal of the dry, air-borne, and cutinised spores. It is doubtful whether in the precursors of the vascular plants the gametophytes formed erect aerial protrusions of an appreciable size, the sporangia being supported by newly intercalated sporangiophores. This may have been preceded, or followed, by an association of the gametophytic algal form with a fungus to form a mycotrophic prothallus. The sporangial stalk may or may not have been partly photo-autotrophic, but ultimately possessed a cuticle, stomata, chloroplasts, and stelic tissues. The advent of the specialised conductive tissues will be

discussed presently in connexion whit the evolution of the *Bryophyta*. The primitive vegetative sporophytes or sporangiophores were completely dependent on the gametophytes at least as far as their mineral nutrition is concerned. A fairly massive prostrate gametophyte, as found in the thallose Hepatics and *Anthocerotales*, and, like the latter, bearing a number of erect sporangiophores, may well represent the ancestral type of the tracheophytes. Such archicormophytes, accordingly, had a morphology which agrees in many respects with that of the fossil form genus *Sporogonites* and of the recent hornworts. This is a far cry from the postulation of dichotomously branched sporophytes of the *Rhynia* type as the first terrestrial plants in the Telome Theory (Zimmermann's "*Urlandpflanzen*", supposed to have inherited their extensive soma and dichotomous mode of branching from a thalassiophytic, i.e., completely submerged, diploid algal archetype). The question of a strictly monophyletic or a polyrrheitric descent of the principal groups of the Cormophytes, discussed by AXELROD (1959), among others, must be answered by assuming that their common progenitors had approximately the morphology of a *Sporogonites* and that from this archetype divergent evolutionary lines emerged. This has some far-reaching implications, in the first place with regard to the Telome Theory: not all major pteridophytic taxa went necessarily through a psilophytalean (rhyniaceous) level of organisation, so that, for instance, they need not have acquired the same morphological type of "leaf" and may have developed either "enation leaves" (Lyco-leaves) or "megaphylls". Similarly, the mode of branching, the stelar anatomy, and also the mycotrophic or autonomous gametophyte evolved independently in several parallel lineages. There may have been some "retrograde" steps in the Bryophyta, the gametophyte becoming even more important than was the case before. Upon the whole the reduction of the gametophyte advanced rapidly, but although it became reduced to modest dimensions, the early ontogenetic stages of the sporophyte are still dependent on it at least for supplying the necessary mineral nutrients (and, of course, water).

Another consequence of such a phylogenetic sequence is that there is no fundamental homology between the gametophyte, the sporangium, and the sporangiophore (a *de novo* intercalated vegetative sporophyte). These parts had an independent origin and can be considered to be *sui generis* in respect of each other. One of the arguments seemingly pleading against this antithetic nature of the originally aquatic gametophyte and the *ab initio* terrestrial sporophyte, recently mentioned again by ZIMMERMANN (1965), is the occasional occurrence of tracheids in the prothallia of *Psilotum*. This phenomenon has no demonstrative force, because there are several other examples of neotenic and proterogenic "shifts" of characteristics of post-ontogenetic developmental stages, a well-known and neatly comparable example of characters "spilling over" being the occurrence of tracheids with the characteristics of tracheary elements of the secondary xylem in the metaxylem of some dicotyledonous woody plants. The "adult" feature is "brought forward", as it were, to an earlier ontogenetic stage. This

is a matter of genetic potencies and the changed time of appearance of the phenotypic expression of the genetically determined (and initially dormant) feature. A similar explanation can be given to account for the advent of the green photo-autotrophous sporangiophore: the organism had a potential genetic constellation responsible for the synthesis of assimilatory pigments in plastids in certain cells and these determining factors only expressed themselves in the gametophyte, but not necessarily in the newly formed vegetative sporophyte. A "shift" of the expression of these potencies (latently present in the genome of the nuclei of the sporophyte as well as in the gametophyte) to the sporophyte was all that was needed to start the evolution of the large and secondarily independent (photo-autotrophic) sporophyte of all higher *Cormophyta*.

Finally, one more aspect of the suggested early evolution of the vascular plants must be considered. The advent of the sporophyte as an intercalated stalk-like structure necessitates the assumption that the dichotomously branched psilophytalean forms, which were after all the archetypes of at least some (though not necessarily of all) groups of pteridophytic and progymnospermous plants, developed out of the somewhat less complex and solitary sporangiophores. The well-known fact that the sporophytes. of all eotracheophytes bore several to numerous sporangia suggests that the dichotomously branched telomic *Urlandpflanze* of Zimmermann's Telome Theory, a plant with the morphology of a *Rhynia* or a *Horneophyton*, actually represents an aggregate of a number of stalked sporangia, an association of a number of elementary green rod-like sporophytes (sporangiophores) bearing terminal sporangia. The gametophytes of *Sporogonites*, *Anthoceros*, and several bryophytes (e.g., Bryales) each produce or produced a number of individually stalked sporangia. A reduction in size of the gametophytic soma automatically resulted in a closing of the ranks of the sporangiophores and it is feasible that they became partly fused, the coalescence phylogenetically starting at the base and proceeding acropetally. The individual sporangiophores became "tufted" or "fascicled" by apparently emerging from a common base. A more or less staggered fusion of such bunches, combined with an ontogenetic "back-shift" of the commencement of the elongation of the fused basal portions of the sporangiophores, would result in the formation of a repeated branching system and of mesomes, respectively. This stage calls to mind the Lower Devonian fossils described as *Eogaspesiea* and *Hicklingia*, whose decidedly "tufted" appearance and somewhat irregular (instead of strictly isotomous) bifurcations are, in my opinion, strongly suggestive of this mode of origin. The acropetal fusion of telomic sporangiophores must in certain cases have initiated the more complete lateral fusion of the sporangium-bearing elements which resulted in the formation of sorial and synangial complexes. This trend originated early, witness the morphology of such forms as *Hedeia*, *Yarravia*, *Zosterophyllum*, and *Horneophyton*, and soon became manifest in the *Primofilices* and *Progymnospermopsida* with soral or synangial aggreates of sporangia. However, this general trend of aggregation of

sporangiophores need not always have resulted in the morphological pattern of the psilophytic plants. It is feasible that in fundamentally the same way the verticillate mode of branching of the Sphenophyta originated and also the polysporangiate fertile axes of the *Lycophyta*. The possible connexion between the longitudinal fusion of protostelic sporangiophores and the stelar structure of the stems of *Sphenophyta* and *Lycophyta* (with several protoxylem strands) may form a future point of inquiry, even if only leading to interesting speculations. In any event one must postulate an early divergent evolution of the vascular plants starting from a primitive phylogenetic level of the sporophyte, in other words, a polyrheitric descent from ancient land plants (architracheophytes), rather than a more monophyletic development from psilophytalean prototypes as envisaged in Zimmermann's Telome Theory.

6.   The relationships and position of the Bryophyta

Although the organisation of the bryophytes did not change fundamentally from that of an earlier terrestrial precursor, the fossil remains of the first unmistakable representatives are not known from strata older than the Lower Carboniferous. This could be interpreted as indicative of a relatively late origin of this group, but there are several plausible explanations to account for their late arrival on the scene. In the homologous (transformation) theory (see, e.g., HASKELL, 1949; STEINBÖCK, 1954, 1959) the *Bryophyta* are considered to be reduced forms evolved as the result of a retrograde development of the sporophyte from an ancestral form with isomorphous generations, i.e., from a thalassiophyte or an *Urlandpflanze* in the sense of ZIMMERMANN (e.g., 1959, p. 130, fig. 6, reproduced in ZIMMERMANN 1965, p. 21, fig. 6). This has even taken the form of the postulation of a reduction of the sporophyte to the extent of an almost complete loss of the stelic structure that was supposed to be present in the progenitors; see, e.g., PROSKAUER's (1960) discussion of the occasional occurrence of columellar cells with helical cell wall thickenings among the *Anthocerotales*. This implies that the ancestral forms of the *Bryophyta* would either not be recognised as such among the fossil records or only be preserved in the form of the reduced sporophytic phase, and of sporangia (and spores), which would not unequivocally point to a bryophytic nature of these remains. In this train of thought the differentation of the originally very delicate and perhaps ephemerous gametophyte into a more massive structure took place rather late and only enabled the recognition of the fossil bryophytes a fairly long time after their evolution had begun. In the alternative intercalation theory the same arguments are relevant, but in a somewhat different context. The evolution of the group was perhaps mainly "progressive" instead of "retrograde" in that the ancestral terrestrial forms consisting of a low prostrate thallus with sessile sporangia developed into a much more massive gametophyte organism showing special adaptations and differentiations in the mosses and hepatics, with the exception of the *Anthocerotales* in which the sporophyte became relatively more impor-

tant. I am not in favour of an explanation of bryophyte evolution as a "reduction" of an anthocerotalean form for two reasons. In the first place, the sporangia are sessile in the Hepatics and in the mosses, the *Bryales* excepted, and even in the *Bryales* the vegetative sporophyte (sporangiophore) is hardly autonomous. If we admit that the sporangial stalks of the *Bryales* are not necessarily derived from those of the hornworts but may have originated as a parallelism, I believe that a more logical explanation of the early phylogeny of all bryophytes is the postulation of an ancestral form with a fairly massive prostrate gametophyte as in *Sporogonites*, but bearing sessile sporangia. The intercalation of a sporangial stalk by a diploid growth, followed by a reduction of the gametophyte resulted in a phylogenetic line leading to both *Anthocerotales* and Hemitracheophyta. The intercalation of a more or less erect outgrowth of the gametophyte (a gametangiophore) between the prostrate gametophytic soma and the sporangium may have produced a phylogenetic line culminating in the true mosses and liverworts. The *Anthocerotales* are still very close to the *Hemitracheophyta* but they did not develop much beyond the evolutionary level of the progenitors common to both. It is possible that the anthocerotalean *sporophyte* is somewhat reduced in respect of this ancestral group, if the latter already possessed differentiated stelic tissues (tracheidal elements and the like). This is of course altogether conjectural, and that is why I believe that PROSKAUER's (1960) deductions concerning the possible nature and origin of the elongated cells with helical ("spiral") cell wall thickenings which he discovered in the sporangial columella of a few representatives of the hornwort family can also be "reversed". His conclusion that the elater-like cells of the columella are modified (reduced) tracheidal elements which underwent a partial transference of function (namely from a purely water-conducting capacity in the columella and the sporophytic sporangial stalk to a partial spore-dispersing function) can equally well be reversed by assuming that, before there was any vegetative sporophytic soma, elater cells were involved in the opening mechanism of the sporangia and/or spore dispersal which had already developed a reinforced cell wall and thus acquired the capacity to accumulate, and conduct, water. The intercalation of the vegetative sporophyte favoured every evolutionary trend to shift the limits of occurrence of these water-accumulating elements towards the columella and eventually farther down into the sporangiophore. This would, among other things, be compatible with the central position of the xylem in the oldest type of stelic structure, the protostele, and with the development of conductive elements in the sporophyte alone (the exceptions, some prothalli of *Psilotum*, need not refute the general validity of this rule as we have seen). The position of the Anthocerotales, then, is most probably that of an archaic group still exhibiting features of the earliest land plants which were the common ancestors of the *Anthocerotales* and other *Bryophyta*, the *Psilophyta*, and the remaining groups of the *Cormophyta*. Similarity in morphological, anatomical and embryological features between *Anthocerotales* and,

e.g., *Bryales, Sphagnales, Andreaeales, Hepaticae* and *Psilotales*, supports the postulation of their common origin, but does not necessarily indicate a closer relationship between the hornworts and, e.g., the mosses, than exists between *Anthoceros* and *Psilotum*, or between *Musci* and *Hepaticae*.

REFERENCES

(For extensive bibliographies, see AXELROD, 1959; PROSKAUER, 1960; ZIMMERMANN, 1955, 1959, 1965)

ANDREWS, H. N. 1960a. Cold Spring Harbor Symp. Quant. Biol. **24**: 217.
————. 1960b. Palaeobotanist **7**: 85.
AXELROD, D. I. 1959. Evolution **13**: 264.
CAMPBELL, D. H. 1918. The Structure and Development of Mosses and Ferns. 3rd ed., New York.
————. 1940. The Evolution of Land Plants. Stanford (Cal.).
CHRISTENSEN, T. 1954. Bot. Tidskr. **51**: 53.
————. 1957. Bot. Tidskr. **53**: 317.
CHURCH, A. H. 1919. Thalassiophyta and the Subaerial Transmigration. Bot. Mem. no. 3. Oxford.
CORNER, E. J. H. 1964. The Life of Plants. London.
DABER, R. 1960. Z.schr. "Geologie" H. **3**: 418.
FRITSCH, F. E. 1916. New Phytol. **15**: 233.
————. 1921. New Phytol. **20**: 165.
————. 1945. Ann. Bot., N.S. **9**: 1.
HASKELL, G. 1949. Bryologist **52**: 49.
HOFMEISTER, W. 1851. Vergleichende Untersuchungen ueber Keimung, Entfaltung und Fruchtbildung bei höheren Kryptogamen. Leipzig.
————. 1868. Allgemeine Morphologie der Gewachse. Leipzig.
JEFFREY, C. 1962. Bot. Notis. **115**: 446.
MERKER, H. 1958. Bot. Notis. **111**: 608.
————. 1959. Bot. Notis. **112**: 441.
PROSKAUER, J. 1960. Phytomorphology **10**: 1.
STEINBÖCK, H. 1954. Agron. Lusit. **16**: 115.
————. 1959. Agron. Lusit. **21**: 177.
STEWART, W. N. 1964. Phytomorphology **14**: 120.
TAKHTAJAN, A. L. 1953. Bot. Rev. **19**: 1 (Transl. from the Russian version in Bot. Zur. **35**: 1950).
VISCHER, W. 1953. Ber. Schweiz. Bot. Ges. **63**: 169.
WETTSTEIN, R. VON. 1935. Handbuch der Systematischen Botanik. 4. Aufl. Leipzig & Vienna.
ZIMMERMANN, W. 1955. Feddes Repert. **58**: 283.
————. 1959. Phylogenie der Pflanzen. 2. Aufl. Stuttgart.
————. 1965. Die Telomtheorie (Band I of Fortschritte der Evolutionsforschung, G. HEBERER and F. SCHWANITZ, gen. edits.). Stuttgart.