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COMMENTS ON TWO CHARTS RELATIVE TO THE PHYLOGENY OF THE CORMOPHYTA, WITH SOME REMARKS OF A GENERAL NATURE

BY

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> ... l'Amphioxus, les Annélides, et même les Eponges, aident à comprendre les Vertébrés (Chadefaud, 1952, p. 10).

CONTENTS

1. INTRODUCTION

Occupied as I still am by the Phylogeny of the Cormophyta I have, in various consecutive publications drafted my diagrams in different forms. Aware of the fact that particularly the older ones are no longer conformable in every respect with our present knowledge, I deemed it desirable to redraft the oldest one and add another, either of which is completing the other.

Fig. 1 is a modernised version of the chart I published in 1948 which was generally based on data taken from Zimmermann. It has now been checked with data given by Arnold and others. The relative times have been brought into accordance with the estimated time scale of modern literature and some more attention has been given to the relative diversity (number of species) of recent groups. Supposed relationships have been shown by thin broken lines instead of dotted ones.

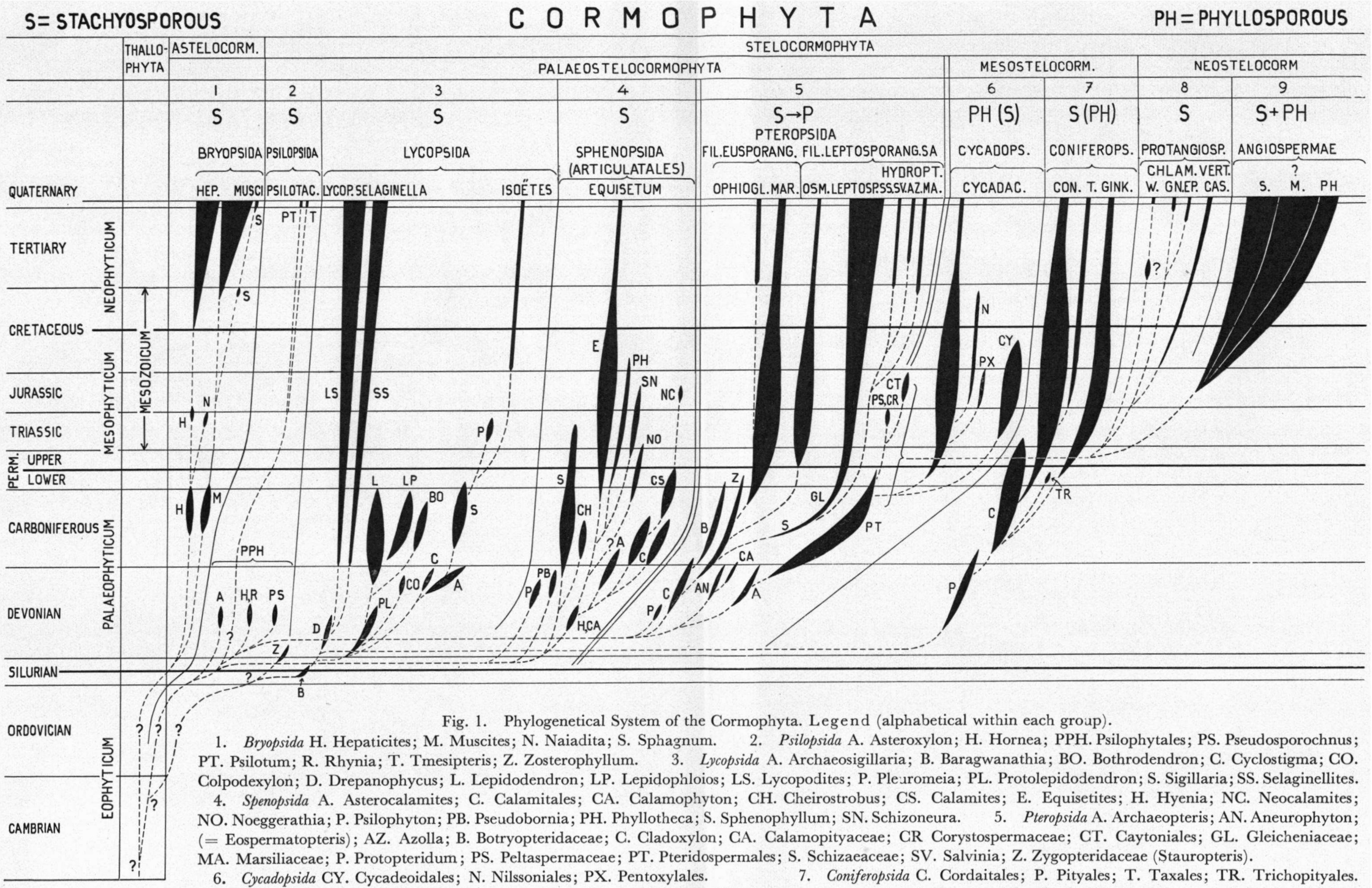

Fig. 1. Phylogenetical System of the Cormophyta. Legend (alphabetical within each group).

1. *Bryopsida* H. Hepaticites; M. Muscites; N. Naiadita; S. Sphagnum. 2. *Psilopsida* A. Asteroxylon; H. Hornea; PPH. Psilophytales; PS. Pseudosporochnus; PT. Psilotum; R. Rhynia; T. Tmesipteris; Z. Zosterophyllum. 3. *Lycopsida* A. Archaeosigillaria; B. Baragwanathia; BO. Bothrodendron; C. Cyclostigma; CO. Colpodexylon; D. Drepanophycus; L. Lepidodendron; LP. Lepidophloios; LS. Lycopodites; P. Pleuromeia; PL. Protolepidodendron; S. Sigillaria; SS. Selaginellites. 4. *Spenopsida* A. Asterocalamites; C. Calamitales; CA. Calamophyton; CH. Cheirostrobus; CS. Calamites; E. Equisetites; H. Hyenia; NC. Neocalamites; NO. Noeggerathia; P. Psilophyton; PB. Pseudobornia; PH. Phyllotheca; S. Sphenophyllum; SN. Schizoneura. 5. *Pteropsida* A. Archaeopteris; AN. Aneurophyton; (= Eospermatopteris); AZ. Azolla; B. Botryopteridaceae; C. Cladoxylon; CA. Calamopityaceae; CR Corystospermaceae; CT. Caytoniales; GL. Gleicheniaceae; MA. Marsiliaceae; P. Protopteridum; PS. Peltaspermaceae; PT. Pteridospermales; S. Schizaeaceae; SV. Salvinia; Z. Zygopteridaceae (Stauropteris). 6. *Cycadopsida* CY. Cycadeoidales; N. Nilssoniales; PX. Pentoxylales. 7. *Coniferopsida* C. Cordaitales; P. Pityales; T. Taxales; TR. Trichopityales. 8. *Protangiospermae* CAS. Casuarina; EP. Ephedra; GN. Gnetum; W. Welwitschia. 9. *Angiospermae* M. Mixed; PH. Phyllosporous; S. Stachyosporous.

2. NAMES OF MAIN GROUPS; BRYOPSIDA

Although the name *Cormophyta* does not cover etymologically all subaltern groups I have maintained it because of its traditional standing (not 'long-discarded' and 'surely antiquated' (cf. EAMES, l.c., p. 20), at least not in Europe).

It is my opinion that the vesselless *Bryopsida* are through their gametophyte characters (*i.c.* the gametangia), distinctly linked with the Tracheophytes or true vascular plants. A corroborative point is that their sporophyte, at any rate in the *Bryales*, *Sphagnales* and *Anthocerotales*, can be more readily understood in terms of the telome theory than in comparison with that of any thallophytic group (cf CHADEFAUD, 1949, p. 95 and 1952, p. 20–23). On the other hand CHRISTENSEN (1954, p. 57) goes so far as to say that 'the evolutionary connexion from the Archegoniatae back to green algae' would naturally imply 'an inclusion of Bryophyta and vascular plants among the Chlorophyta'.

Etymologically, the name *Tracheophyta* is not satisfactory: true vessels (or tracheae) only develop in the highest groups. The proper name should therefore be *Tracheidophyta*, but this is a rather long name and not very euphonious[1].

Since according to the International Code of Botanical Nomenclature the names of taxa above the rank of Order are not subject to the rule of priority, everybody is entitled to propose new names for such taxa, if he feels they are more appropriate than others.

Now, so as to avoid both the etymologically incorrect name Tracheophyta and the undesirable one Tracheidophyta, I here propose to refer to the vascular plants as *Stelophyta*, since they all possess some sort of a *stele* and the name is short enough to allow compounds. As a subaltern taxon of Cormophyta they should therefore be called *Stelocormophyta*, against the *Astelocormophyta* (the *Bryopsida*).

I was inspired to this choice by a paper by MAEKAWA (1952), which contains several ideas concurrent with mine. In his subdivision of the '*Tracheophyta*' primarily on the basis of leaf types, he proposes two classes: *Stelopsida* and *Phyllopsida*, which partly cover what I call Stachyosporae and Phyllosporae, and equally more as levels or phases than as taxa.

My system now reads (cf. Table at the end of this paragr., and Fig. 1).

I may here add the following remarks:

The prefixes *Eo-*, *Palaeo-*, *Meso-* and *Neo-* to *Cormophyta* referred to the 'four main era's of palaeobotany' (cf. LAM, 1948, Fig. 19, letterpress), in which these groups dominated or still dominate: they are not considered systematic taxa. EAMES (1951) who misinterpreted my first paper in almost every detail, misunderstood this intention as well (p. 20), though it was clearly indicated.

In the mean time on the next page of his paper he correctly states that *Bryopsida* and *Psilopsida* should not be put together in one group even if this is only a chronological one. This remark has been one of the stimuli to establish the above scheme.

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[1] A similar case is *Pteropsida* which should rather be called *Pteridopsida*.

Now that Devonian land plants are getting quite numerous, however, I think we had better drop the Eocormophyta altogether since so far the Mid-Silurian seems to remain the period in which the land plants started to develop. It therefore seems the appropriate period to ring in a new era, so that the Eophyticum may, for the time being, be reserved for the Thallophytes.

Cormophyta	Entirely or mainly	
	Stachyosporous	Phyllosporous
A. Astelocormophyta	1. Bryopsida	
B. Stelocormophyta I. Palaeostelocormophyta	2. Psilopsida 3. Lycopsida 4. Sphenopsida ←——	5. Pteropsida
II. Mesostelocormophyta	♀←—— 7. Coniferopsida ——→♂	6. Cycadopsida
III. Neostelocormophyta	8. Protangiospermae 9. Angiospermae ——?—— (cf § 15)	Angiospermae

Note: The arrows indicate some degree of transgression into the other type.

3. BRYOPSIDA AND PSILOPSIDA

Both in the *Bryopsida* and the *Psilopsida* fossil links of recent taxa with ancestral groups are either few or none (cf. Fig. 2). That the recent *Psilotales* have yet been tentatively inserted in the *Psilopsida* together with the remote *Psilophytales* is merely because there is no other group known with which they can reasonably be linked.

If the Cormophyta as understood by me, are to be considered monorheithric (= mono'phyletic' below the rank of phyla) the *Bryopsida* must have left the main trunk at a very early date. There is, however, no evidence for such a monorheithry (nor of a bi- or polyrheithry). Perhaps a closer study of the higher *Algae* (cf. CHADEFAUD, 1952) as well as more fossil material will bring us closer to filling the gap. For the rest, mono- and polyrheithry will always remain relative concepts with all imaginable gradations between the extremes (cf. § 14, where the same is stated regarding homology and analogy).

Speculations on the ancestry of the mosses are numerous. One of the most recent authors on the subject, T. CHRISTENSEN, states 'three major possibilities', *viz.* 1) derivation from 'Pteridophytes' with leaves on both sporophyte and gametophyte; 2) derivation from such leafless 'Pteridophytes' as the *Rhyniaceae*; 3) a polyphyletic combination of the two first possibilities. Christensen shows no preference for any of the three possibilities given, perhaps because he has, apparently, not thought of a fourth possibility, as has been expressed in my charts: all major groups recognisable as such are specialisations, their connections lie deeply hidden in the past in the potentialities incorporated in the polymorphous, unspecialised common ancestors (cf. § 16).

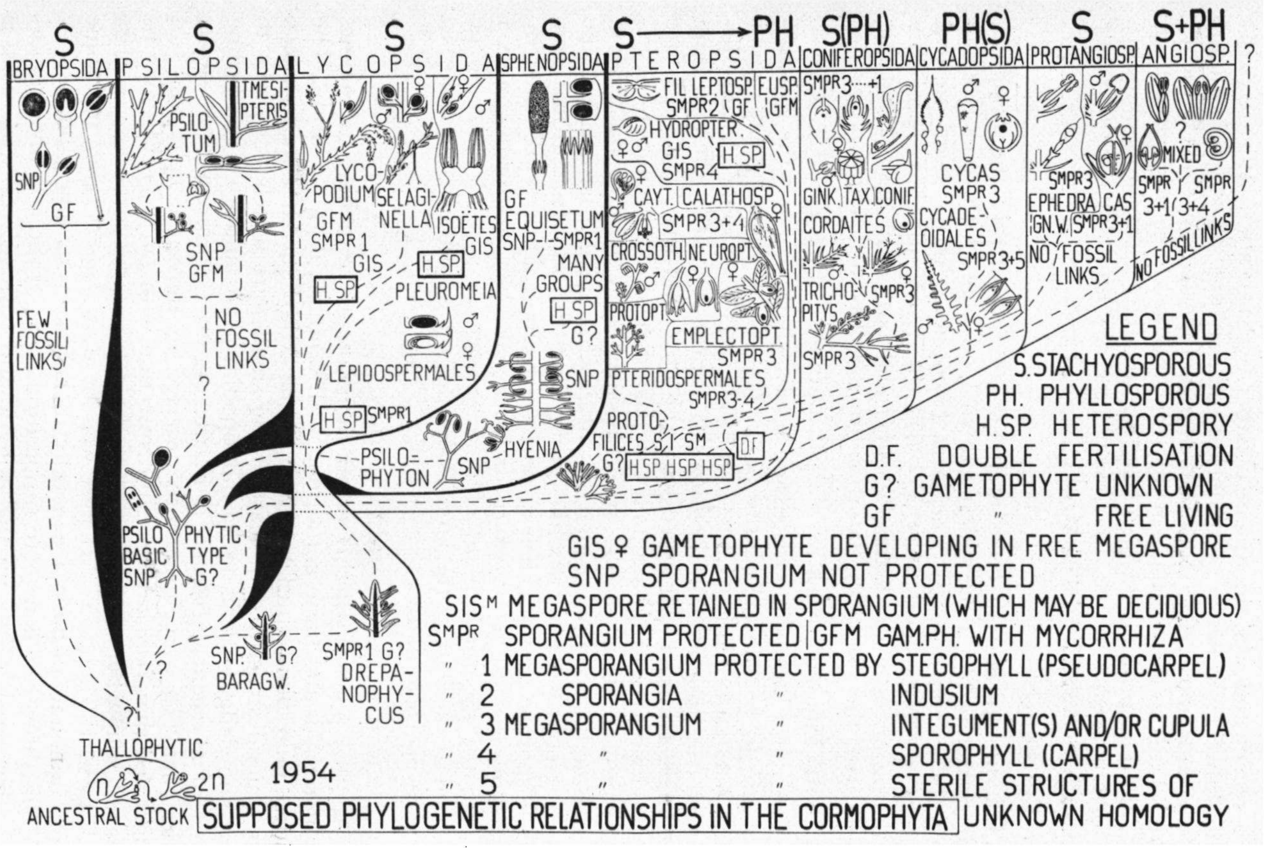

Fig. 2. Semophyletic chart showing the supposed evolution of some sporophyte characters.

The last-named possibility, of course, refers to the hypothetical ancestral forms, accepted by several authors. Some of these are quoted in a recent and well-documented paper by STEINBÖCK (1954, p. 118) who, however, is not an adherent of this way out. Mostly on account of the enormous palaeobotanical gap in time, he develops a theory which leads to the assumption that the *Bryopsida* have originated from ancient fern prothallia which have not altogether lost the potentiality of forming a sporophyte. He does not see any fundamental difference between mosses and ferns at all.

4. LYCOPSIDA

The next group to have branched of is probably the *Lycopsida*, *Baragwanathia* being the oldest known land plant with some, though doubtful connection with the later Lycopsida. As has been pointed out by me elsewhere (1954, p. 357) the Lycopsida have probably common ancestors with the *Psilopsida* and both may have something to do with the rise of the later *Coniferopsida* (see also Fig. 2).

5. THE PSILOPHYTALES AS A BASIC GROUP

There has been some discussion lately whether or not the *Psilophytales* are to be considered the basic stock of all more recent groups (DE WILDEMAN, 1943; LECLERCQ, 1952, 1954). Having already discarded the *Bryopsida* and the *Lycopsida* as probably older effluents from the main trunk, I can agree with the idea that the *Psilophytales* are generally representing a bunch of separate dead-ending lines of development. CHADEFAUD (1952, p. 22) is of the same opinion. But I deem it reasonable to suppose that the *Sphenopsida* have arisen from some stachyosporous *Psilophyton*-like group and the *Pteropsida* from some phyllosporous group of a less specialised type than is represented by *Pseudosporochnus*, *Protopteridium*, or *Cladoxylon*. As a matter of course, I except the diverging point of both *Sphenopsida* and *Pteropsida* to be located at the base of the later *Psilophytales*, e.g. in the Upper Silurian or Lower Devonian.

6. DICHOTOMY AS A BASIC CONDITION

Another point is whether or not dichotomous branching (of telomes or nerves) is the basic condition of all land plant ramification. The oldest land plant thusfar known is the Mid-Silurian *Baragwanathia*. Its general structure—at least of the small part which has come to our knowledge—seems to be monopodial (as would a corresponding part of a recent *Lycopodium*). Fertile organs (sporangia) and sterile ones ('leaves') were apparently inserted in the same helix and this suggested that *Baragwanathia* in connection with *Drepanophycus* may be placed somewhere at the base cf the *Lycopsida* and the *Coniferopsida* (cf. LAM, 1954, p. 357). It may well be that *Baragwanathia* will some time be found to have a generally dichotomous ramification.

This, however, is a mere supposition. One of the few investigators who has tried to link up thallophytic and cormophytic structures, is CHADEFAUD (1952). First of all he showed the courage to declare that, in his opinion, gametophyte and sporophyte, which are both determined by the same genome, cannot be of a fundamentally different structure (cf. also CHRISTENSEN, 1954, p. 55, 57). He has arrived at this conclusion by his study of higher *Algae*, in which the evolution of gametophytes and sporophytes is supposed to be identical or at least to have run along parallel lines. It is his conviction that the same is true for the Cormophyta, even if gametophyte and sporophyte may differ considerably and he bases this opinion on the existence of leaves in *Musci*, on the similarity of stomata and on the vascularisation of the *Psilotum* gametophyte. He sees no reason why Zimmermann's telome concept should not be applicable to the higher *Algae* as well and he is even inclined to speak of an homology (CHADEFAUD 1952, p. 25).

I have long fostered similar ideas, and I am inclined to agree even though it would imply the necessity of bringing the leaves of the *Bryopsida* in line with the telome theory.

However, our present knowledge does not allow us to go any farther than this. Only by considering the entirety of algal potentialities can we arrive at an hypothetical reconstruction of cormophytic ancestors, since no fossil evidence is available.

There is, indeed, still very much of a mystery around the most ancient land plants. CHADEFAUD (1952, p. 22) is of the opinion that the dichotomy of the Rhyniaceae with their '*structure fucoïde*' is a secondary phenomenon and that these plants have lost their leaves; they are overevolved (*surévolué*). Yet for the other Cormophyta he thinks of two possibilities: *a*) they are to be derived from bryophytic ancestors ('*d'allure rhodoméloïde*'), which would only later on have acquired the 'fucoid structure'; or *b*) they are to be derived from originally dichotomous ancestors ('*d'allure fucoïde*'), a view which automatically leads up to Zimmermann's telome theory.

Chadefaud admits that the last-named possibility is actually favoured by the majority of phylogeneticists. The other one, however, undoubtedly deserves full attention. It may perhaps even lead to an acceptable interpretation of the 'enation leaf' (*Musci*, *Asteroxylon*, *Lycopsida*, fern ramenta).

No fossil evidence, however, is available just now to make a sensible choice and so many questions remaining unanswered, I think we have to give the telome theory some more rope either to hang itself or to show its general applicability.

One thing, however, is fully supported by fossil evidence and that is that dichotomous ramification has played so overwhelming a part in the older—though perhaps not in the very oldest—land plants, that it enables us to follow up its traces through all groups up to the Angiosperms.

The paper by De Wildeman has no real bearing on the problem, since it only deals with ontological facts. It is characteristical for the still large category of investigators who seem to think that phylogenetical problems can be solved (or theories refuted) solely on evidence taken from living plants. I do not deny the importance of such evidence, but though it can sometimes support an hypothesis, it is rarely or never able to refute it, since structures of living plants can almost always be interpreted in different—and sometimes controversial—ways. To my mind all nerves are homologous with ramifications and all splittings of nerves are dichotomies (what else can they be in a phylogenetical sense?).

In fact, so long as there is no indubitable fossil evidence that other than dichotomical ramification has been inherited by the Cormophyta from their thallophytic ancestors, I am inclined to state that all ramifications in the group are to be derived from dichotomy and (eventually) subsequent shifting (growth differences with selective value). This would make the whole problem futile.

7. NOEGGERATHIALES

In accordance with recent views, the *Noeggerathiales* have been placed near the *Sphenopsida* rather than among the *Pteropsida.* The group remains, however, still of uncertain alliance and it seems even doubtful whether *Noeggerathia* and *Tingia* really belong to the same group.

8. HYDROPTERIDALES

Regarding the *Hydropteridales* I have formerly made the mistake to link them up with the Pteridospermales in the vicinity of the *Caytoniales.* Both Bower and C. Christensen bring them (at least *Marsilia*) in connection with the *Schizaeaceae* and EAMES (l.c., p. 21) has correctly pointed out that they are leptosporangiate. Their relationship has now be corrected accordingly, but fossil links are unfortunately still wanting.

Quite recently REED (1954) has published a list of all species described, both living and fossil, from which has been taken that *Marsilia* and *Salvinia* are known since the Cretaceous and *Azolla* since the Tertiary (Intertrappean beds of India).

9 RANGE OF PTERIDOSPERMALES

Among the Pteropsida, the Corystospermaceae, Peltaspermaceae and Caytoniales have now been considered mesophytic remnants of the Pteridospermales.

10. THE PTERIDOSPERMALES, ANCESTRAL TO CYCADOPSIDA AND NEOSTELOCORMOPHYTA

The only gymnosperm group which has probably a very old origin is the *Coniferopsida* which, as I have argued above, may contain some lycopsid potentialities.

For all other mesophytic and neophytic groups the origin can, for the time being at least, hardly be looked for elsewhere but in the *Pteridospermales.* However, despite the enormous mass of vegetative and 'seed' material, the fossil links are still very obscure. It is a great drawback that, as ARNOLD (1947, p. 245) states, probably less than a dozen Pteridospermales are more or less completely known, i.e. with the sporangia, and particularly the ovules, associated with the fronds. Even among these there seems to be quite some difference as to the position of the sporangia: in some cases they are inserted directly on the frond, in others they seem to occupy a more isolated position.

There is, however, some reason to believe that this range is much more considerable than appears from the material now available. That reason is that, if all younger groups are to be derived from the Pteridospermales, the latter, covering a period from the Devonian to the Jurassic, must have contained both stachyosporous and phyllosporous elements and many intermediary types between the extremes, simply because the younger groups show an enormous range in this respect, the extreme being here the *Cycadopsida* on the phyllosporous side, and the *Neostelocormophyta* on the stachyosporous one. This supposition implies that the Pteridospermales will probably have to be split up in several more orders as more material becomes available.

11. CYCADOPSIDA; THE CONCEPT OF REDUCTION

Vegetatively speaking the *Cycadales* (including the *Nilssoniales*), *Pentoxylales* and *Cycadeoidales* are generally considered closely akin. Regarding the sporangia-bearing structures, however, there is a very considerable difference which, I think, has not got the attention it deserves.

In the *Cycadales* the sporangia of both sexes are found inserted on what can safely be interpreted as sporophylls. The same can be said of the structures, however different, of the male sporangiophores of the *Cycadeoidales*.

The ovules of the last-named group, however, are (or seem) essentially different. They are either sessile or stalked, atropous, surrounded by sterile organs of unknown homology, and invariably inserted on a more or less cylindrical or convex axis.

These structures have been the subjects of various very different interpretations. The older authors spoke of 'reduced sporophylls' (an expression open to controversial interpretation itself). GAUSSEN (1946, p. 28) derived both the cycad and the cycadeoid series from a Pteridosperm like *Sphenospermatopteris* and considers the ovules of the latter the result of an extreme reduction of a multi-ovulate frond, the 'interseminal scales' being their sterile homologa.

I am afraid that the term 'reduction' has all too often been used rather loosely. I suppose most authors who apply it, mean to say that a certain structure which has actually existed gets, in the course of time, less and less complicated, it looses more and more parts and the ultimate result is an organ of so simple a shape that some people are convinced it is originally simple ('primitive').

I will not deny that processes like this may have occurred in the course of evolution but I believe that in the majority of cases it may be nearer the truth to assume that from an initial multipotential group specialised groups have emerged, among which both the simplest and various more complicated versions of the character in question are to be found. For it is our general impression that in all groups primitive conditions have been maintained next to various advanced ones; in fact, this is the very principle upon which our 'geneological tree' has been based (cf. § 16).

Applying this idea to the group under discussion I would rather presume that the ancient *Cycadopsida* originated from some pteridosperm stock of mixed stachyosporous and phyllosporous potentialities, in which however, the latter predominated. From the purely phyllosporous group emanated the later *Cycadales*; the *Cycadeoidales* originated from a group, in which, though closely related in vegetative respect, the microsporophylls were entirely different from those of the Cycads (with sori at the abaxial leaf side) as well as from those of any known Pteridosperm. Some of them (*Cycadeoidea*) remind us of pinnate fern sporophylls but they are eusporangiate and the general trend seems to be that the sporangia are placed on the adaxial rather than the abaxial leaf surface and the same holds for the simpler forms in *Williamsonia* and *Williamsoniella.*

The female organs, however, have, I think, never reached the state of phyllospory, partly perhaps on account of their being well protected at an early stage. Rather than interpreting them as somehow 'reduced' I would point at a structure like that of the pteridospermous *Calathospermum scoticum* (cf. WALTON, 1940, p. 133) in which the ovula, supported by stalks (or funiculi) of various length, were inserted in a concave receptaculum (a sort of supercupula), not fundamentally different, it would seem, from the type of *Cycadeoidea wielandii.*

I have still to mention an attempt by CHADEFAUD (1947) to save the well-known *euanthium*-theory of Arber and Parkin regarding the cycadeoid ancestry of the Angiosperms. His reconstruction, though probably too complicated to be true, is highly interesting nonetheless and worthwhile to be seriously considered.

His starting point is the curious 'flower' of *Williamsonia gigas* (cf. also GAUSSEN, Ch. IV, p. 17, fig. 108^2), in which the whorl of microsporophylls is crowning the floral axis above the part on which the ovules are inserted. His main idea is that each microsporophyll together with the ovula-bearing portion of the axis underneath it, represents a bisexual sporophyll (with the ovules on the abaxial side), all of these bisexual sporophylls being adnate to the axis but for their (male) apices.

From this type Chadefaud derives both the Cycad type and the Angiosperm type of sporophylls by alternatively dropping either the lower or the upper half of the bisexual sporophyll.

This theory necessitates the acceptance that the primitive Cycads possessed bisexual sporophylls with a staminate petiole and a pistillate blade, and that the Cycadeoids showed the reverse condition (proximal part female, distal part male).

So as to arrive at the Angiosperm sporophylls there are two possibilities. If the Cycad type is accepted as the ancestral one, the stamens would have evolved from the proximal part of the bisexual sporophyll (the distal female part being reduced), and the carpels would have been formed by infolding of the distal female part (the proximal male one being reduced). If, however, the Cycadeoid type is taken as a starting point it is inevitable to assume a change of sex of the distal (male) part (the stamens would have been evolved from the distal part with reduction of the proximal female part) into an ovule-bearing leaf.

Despite the fact that this theory would enable us to consider all *Cycadopsida* fully phyllosporous, and despite the fact that sporangia of the two sexes are always to be considered homologous and therefore, under certain circumstances (witness the teratisms) interchangeable, I do not think this theory, as it stands, is very likely to be correct. It is rather too complicated and as far as I know, there is not the slightest palaeobotanical evidence to support it. In addition, the Angiosperms are too much diversified so as to allow an explanation of their ancestry on so narrow a basis.

Nevertheless, it may contain a part of the truth, as did, one time, Thomas's idea of the *Caytoniales* as ancestors-elect of the Angiosperms (cf. GAUSSEN, l.c. Chap. IV, p. 28, Chap. V, p. 7, 18–19, with figures).

A much simpler interpretation of the 'flower' of *Williamsonia gigas* (implying that of all *Cycadeoidales*) seems to me to accept that the floral axis may either bear naked ovules, or microsporophylls, or both, in the two most likely combinations.

As to the *Pentoxylales*, I ventured to predict elsewhere (1952, p. 75) that they will ultimately show to be phyllosporous in the male organs. In addition, I am inclined to believe, that the female sporangiophores so far only known in the seed stage, will appear to possess some sort of 'perianth' (and perhaps a whorl of microsporophylls).

12. CONIFEROPSIDA

In accordance with recent views (FLORIN, 1951) the *Coniferales* and *Taxales* have been considered separate orders. The Lower Permian *Trichopitys* is chronologically at the bottom of both *Coniferales* and *Ginkyoales*, and younger than the oldest *Cordaitales*. The Coniferales seem to be the direct descendants of the Cordaitales and Trichopitys combines the dichotomous leaves of ancient Ginkyo's with the anatropous ovules of both Cordaitales and Coniferales (cf. FLORIN, fig. 8, p. 297). In view of these conditions it seems appropriate to consider *Trichopitys*, for the time being, the representative of a separate order, *Trichopityales*.

13. PROTANGIOSPERMAE

In the Protangiospermae, *Sarcopus* has been dropped, since it is obvious that this is probably some member of the Santalales.

In view of the alleged discovery of *Welwitschia*-pollen (CHIGURYAYEVA, 1953) in the Eocene of Central Asia, the fossil line of this genus has been extended down to the Lower Tertiary. The question mark points to the grave doubt expressed by Bullock and Erdtman regarding the trustworthiness of this find. GAMS (1952), who entered it on his map of the distribution of the three Chlamydosperm genera, presumes that *Welwitschia* and *Ephedra* formed part of a cretaceous Tethysflora. Even if the Asian *Welwitschia*-pollen should ultimately appear rather to belong to *Ephedra*, the find is interesting. Gams adds that some *Casuarina* fossils had perhaps better be attributed to *Ephedra*. The former genus EMBERGER (1944, p. 421) states to be known with certainty from the Lower Cretaceous of North America. ARNOLD (1947, p. 386) only mentions the Oligocene of that Continent. So far as I know, *Ephedra* has not been reported from the present centre of the *Casuarina* area, Australia, either fossil or recent. Its locality nearest (through Antarctica) to the area of *Casuarina* (extending to Fiji, New Caledonia and Tasmania, one species widely dispersed by ocean currents) is southern Argentina.

14. HETEROSPORY AND 'SEEDS'; PRAEPHANEROGAMAE; HOMOLOGIES AND ANALOGIES

Before we come to speak of the Angiosperms, I wish to say a few words on heterospory and EMBERGER's Praephanerogams (1952). It is my conviction that heterospory, i.e. the 'regression' of sex differentiation from the gametangia through the gametophyte to the sporangia and, ultimately, the sporophyte, has been achieved largely independently in different groups. This conviction has found expression in Fig. 2 by the circumlined symbol H.SP.

Exactly the same is true, I think, for the increasingly more perfect protection of the megasporangium, in every separate case according to the morphogenetical possibilities of the group, or the stage of phyletic development of each. Again, this has been summarised in a simplified manner in Fig. 2.

Thirdly the same independent development must be accepted for the 'seed'. All three phenomena are undoubtedly closely connected. They all form part of one of those 'tendencies' which seem to be rooted in 'the genome' and seem to develop with imperturbable finality under the impact of a mysterious inner directive 'pressure' which leads to the various manifestations alluded to above, every group after its own possibilities.

In evolutionary developments like these there is always the question of a choice between what is to be considered analogy and what homology. In extreme cases there is little or no difference of opinion, yet, of course, there is no such condition as a 100 % analogy or a 100 % homology, for the obvious reason that all organisms always borrow their shape (and functions) from the combined action of genome and environment. It is one of my hobbies to say that analogy is but an unknown homology. This is, of course, an aphorism rather than an exact statement, and its purpose is to point out the gradual nature of the difference between the two extremes.

The more we are considering the 'middle portions' of the scale, the more it is a matter of taste whether we should speak of an analogy or of an homology. The latter is based on the more rigid part of the genome (Plate's 'Erbstock'), the former on the more plastic skin which more or less rapidly and less or more lastingly responds to environmental stimuli. Whereas homologies refer to the development—more or less independent, it would seem, from environment—analogies reach their mutual resemblance through the influence of the environment, reshaping the genomatically determined forms as far as the latter allow.

Now it is the task of phylogeny to reduce analogies as far as possible to the fundamental homologies. To speak metaphorically, phylogeny is trying to discover the vertical (or almost vertical) lines (lineage, fr. lignée) which form the genealogical tree, among the more or less horizontal lines which connect the analogies.

In many cases the choice is extremely difficult, if not impossible; and it is only comprehensible that in dubious cases controversial opinions have been expressed. To my mind Emberger's Praephanerogams, however important to enlighten our views on the gradual process of increasing independence of the embryo, are not the manifestation of a phylogenetical (vertical) line: they rather comprise a number of groups, belonging to different lines which, in the course of their development, reached similar or comparable stages in the abovementioned process. Both in the *Cycadopsida* and in the *Coniferopsida* perfectly naturally linked groups are severed, *viz.* in the former the *Cycadeoidales* from both (the prephanerogamic) *Cycadales* and *Pteridospermales*, and in the latter the *Coniferales* from (the prephanerogamic) *Cordaitales* and *Ginkyoales*. The Praephanerogams have been characterised as oviparous, the Phanerogams as viviparous.

However, there seems to be some terminological misunderstanding. Emberger calls the 'grandes divisions systématiques' 'coupures horizontales'. Yes, one can arrange them *e.g.* chronologically, so that they can be separated by horizontal lines. Nonetheless in the modern genealogical tree the vertical lines (lignées) are preponderant and the main divisions are arranged in such a way that their dividing lines are running more or less vertical.

Emberger refers to his Praephanerogams as an 'embranchement' and his definition of this term is clearly what we would call a 'stage' or a 'phase' or a 'level': 'l'embranchement est une unité qui groupe les lignées d'un même stade phylogénétique, lesquelles sont donc comparables à des lignées "cousines" de la société humaine; ces lignées sont donc apparentées, mais moins directement qu'avec leur ascendance ou leur descendance'.

It seems to me that the misunderstanding referred to above roots in a different appreciation of analogies and homologies and I leave it to the reader to decide which vision is the most correct one; it is a choice between the 'lignée' and the 'embranchement' as the most fundamental unit in phylogeny.

From the above it is obvious that my preference is the 'lignée', the vertical line of homologies. In glancing through the 'semophyletic' literature one repeatedly comes across similar cases. Laying too much stress on what are apparently or probably analogies rather than homologies has all too often led to rather fantastic semophyleses.

15. ANGIOSPERMAE

The Angiosperms have, from the beginning, been the weakest spot in my theory, for the obvious reason that the structure of their flowers has never been thoroughly checked with the principles of the telome theory. The splendour of the 'old' morphology has been so dazzling as to make its admirers insensible to a supposition of a possible deficiency.

This attitude, however, is beginning to fade and the possibility that the Angiosperm flowers are not necessarily all of one and the same type seems to dawn in the minds of those interested in problems of phylogeny.

A well-known authority in the field of plant anatomy like I. W. Bailey (1954, p. 134, footnote) admits 'the danger of interpreting phylogeny solely upon the basis of ontogenetic sequences' (quoted from a paper in Am. J. Bot. 31, 1944, 421–428).

The number of papers devoted to the vascular supply of flowers is legion, but in practically all cases their phylogenetical conclusions are based on the preconception that there is only one type of carpel, *viz.* the infolded leaf with marginal placentation. Almost without exception the ovular strand is interpreted—without the slightest criticism—as having originated from the 'ventral median bundle' of the carpels. Eames's school shows abundant examples of this onesidedness. Even an authority like Eckardt who investigated some *Phytolaccaceae* (a family supposed by me to be stachyosporous) with the special purpose of checking my views (and with the best of intentions, too) concludes (l.c., p. 119) that 'auch aus der Leitbündelanatomie kein Anhaltspunkt für eine Stachyosporie der Samenanlagen gewonnen werden kann.' The so-called carpel (in my opinion a pseudocarpel) has one dorsal median bundle (l.c., fig. 2 a, d) and two lateral ones.

I quote: 'Das zunächst einheitliche für ein Karpell bestimmte Bündel wird in drei aufgeteilt, in einen Dorsalmedianus und in zwei lateral-marginale Bündel. Die beiden lateral-marginalen Bündel vereinigen sich sofort wieder, um einen Ventramedianus zu bilden, der nunmehr mit seinem Xylem gegen das des Dorsalmedianus gewandt ist. Damit ist das Placentarbündel, das die Samenanlage versorgt, entstanden'. (cf Fig. 3).

My remarks to this are the following:

(a) Eckardt's 'lateral-marginale' are lateral, not marginal; in this connection I wish to refer to Bailey's opinion (l.c., p. 166–173, from a paper with Swamy in Am. J. Bot. 38, 1951, 373–379) that 'the classical concept of an involute carpel with marginal placentation . . . . . will have to be modified'. His idea of a primitive carpel is a conduplicate sporophyll with a 'modified laminal' placentation, of which the margins have ultimately been reduced, resulting in a condition with (pseudo)marginal placentation. In the Phytolaccaceae studied by Eckardt the 'carpels' are not fully closed. There is a ventral transverse slit ('Querzone') marked x in Fig. 3.

(b) the orientation of the various bundles has got an interpretation ('Deutung') which is preoccupied. My interpretation is equally preoccupied but it has never been given a chance to show whether or not it would, in certain (allegedly stachyosporous) cases at least, present a more sensible interpretation than the classical one. I think it deserves that chance and I mean to let it have it.

(c) my interpretation is that the ovules are situated terminally on lateral axes in the axils of pseudocarpels. It seems unlikely that lateral leaf-bundles (Fig. 3a) should emerge and reunite at so low a level without showing any relation to the leaf-margin. But even if they are to be interpreted as leaf-bundles, we cannot be sure that they are not really bundles of an axillary axis which is adnate to the subtending leaf, a condition which is far from unusual in plants. This would logically account for ECKARDT's statement (1954, p. 120) that 'das Placentarbündel nicht selbständig und isoliert aus der Achsenstele kommt, sondern zusammen mit dem Dorsalmedianus'. The evolutionary history of Angiosperm flowers is undoubtedly a very long one and many changes, contractions, displacements, etc. may have occurred in so intricate and compressed a structure as a flower. Eckardt admits that the vascular supply is very variable. Maybe the 'loop' in vm is a reminiscence of a formerly ramified axillary axis. The orientation of the placentar bundle cannot give rise to any objection: it is exactly like that of so many axillary structures, e.g. the ovuliferous scales in Conifers.

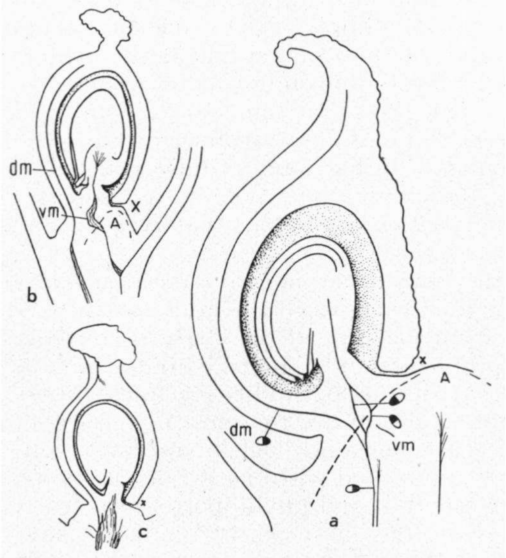

Fig. 3. Longitudinal sections of the ovaria of some *Phytolaccaceae*: a. *Phytolacca acinosa*, one of the many carpels; b. *Hilleria latifolia* and c. *Rivina humilis* with solitary carpel — A. apex of flower axis; X. transversal slit; dm. dorsal median bundle of the pseudocarpel; vm. supposed ventral median bundle of same — figures taken from ECKARDT.

(d) *Hilleria* (Fig. 3b) has a solitary pseudocarpel which has overtopped the apex (A) of the main axis, like the solitary carpel in Leguminosae. On account of this condition . . . .' steht die Achsenstele nicht nur, wie bei *Phytolacca*, mit einem schmalen Sektor für die Versorgung der Placenta zur Verfügung, sondern fast mit ihrem gesamten Umfang' (l.c., p. 123). The conclusion from this functional assumption is remarkable and characteristic: 'Dementsprechend baut sich das Placentarbündel aus zwei mächtigen, lateral-marginalen (!) Bündeln auf, die sich bald zu einem vm (why vm?) vereinigen . . . .'. It must be emphasised that Eckardt's figures (7 b, d) picture this 'vm' as almost proto- (or actino-) stelic, a condition which may be expected in funiculi as well as in (stachyosporous) filaments.

(e) ECKARDT (1954, p. 124) himself states that it is impossible 'mit Hilfe der Leitbündelanatomie eine Achsenbürtigkeit der Samenanlage rechtfertigen zu wollen'. Exactly! But what makes him suppose that the 'classical interpretation' can be found justified on these grounds, if the 'neo-morphological' one cannot?

(f) another characteristical statement by Eckardt refers to the condition found in *Trichostigma peruvianum* and *Rivina humilis*, in which the gynaeceum is restricted to one pseudoterminal pseudocarpel. Admittedly the vascular supply of the ovule consists of bundles originating from all sides of the axis-stele. Eckardt apparently sensed the allurement of a stachyosporous interpretation; accordingly he hastens to add (l.c., p. 124–125) that 'eine nach dem äusseren Anschein urteilende isolierte Betrachtungsweise für eine Stachyosporie plädieren konnte'. This sounds a bit like Eames, and it seems not to have occurred to Eckardt that the classical viewpoint is as 'isoliert' (read: partial) as mine. For the rest Eckardt admits that even he could not discover his 'vm' in *Rivina*.

Thus, Eckardt's paper has not convinced me in the least. It is characteristic of that category of investigators who seem unable to free themselves from the spell of the classical concepts, thinking that phylogenetical problems can be solved by ontogenetical or anatomical evidence alone. With the possibility of stachyospory in mind his beautiful microphotographs are the most perfect examples of what I think is, in this case, the only logical interpretation.

For we are still confronted with the major questions: where are the two types, stachyosporous and phyllosporous, so clearly discernible in all lower groups, in the most recent one, the Angiosperms; and, accepting the inevitable conclusion that they must be hidden somewhere, what is their relation, if any, with the two (at least) incompatible flower types in the group?

So far, however, we have hardly proceeded beyond the stage of guess-work and speculation on ideas, some of which are, in the mean time, by no means without foundations. As I have already stated in my first paper of 1948, the angiosperms are almost entirely unknown in this respect. An enormous task lies ahead of us to review known facts and discover new ones. The field is immense; it has to cover morphology and anatomy, embryology and teratology and probably even genetics and experimental morphology.

An interesting method is that introduced by Blakeslee and his school (Miss Satina, Avery). The object was periclinal chimeras of *Datura stramonium* and the importance of the method for the problem in question is that it shows which layers of the growing point in the flower contribute to the formation of the consecutive floral parts; three independent germ layers can, namely, be distinguished by the different chromosome numbers in the nuclei of their cells, obtained by colchicine treatment (induced polyploidy). As early as in 1940 it was concluded that the leaf primordia are made up from layers (I and) II, but that stamens and carpels depend primarily on layer III (I is the dermatogen, II the periblem, and III the plerome). 'This difference suggests that sepals and petals are homologous but that stamens and pistils may have a different phylogenetical origin' (1940). In 1941 (l.c., p. 871) SATINA and BLAKESLEE add: 'The early stages of development suggest that the stamen is not a modified leaf, but rather a reduced axis'.

In 1943 the same authors investigated the development of the pistil. They found that 'the carpel primordia arise as lateral outgrowths from opposite sides of the floral apex . . . .'; cells from layer III 'continue to predominate in the formation of the placenta and of the lower portions of the carpel wall and septa'. Their conclusion is that these conditions suggest that carpel wall, septa and placentae 'are axial and not foliar in origin'.

In the (apparently) last paper of the series Miss Satina discussed the ovule and arrived at the conclusion that the ovule is initiated from the innermost layer L III, ... the nucellus develops from the median layer L II, ... the integument . . . . develops from the outermost layer L I.

These results obtained from an entirely impartial quarter, would suggest that *Datura* is stachyosporous. More or less obscure points are, however, that the 'axial 'stamens are alternipetalous and therefore not axillary to an (existing) phyllome, and that not only the placenta, but the lower parts of the (pseudo)carpel should be of axial origin though it is stated that 'in later stages cells from L II contribute to the growth of the carpel wall and septa in their upper parts where they become connected'.

In spite of these uncertainties, the method seems promising to our purpose and we are looking forward to the next developments. It has increasingly been my impression that the majority of the Angiosperms is stachyosporous and that perhaps only the '*Polycarpicae*' and the *Liliiflorae* with their derivatives are answering the classical concept and are therefore phyllosporous.

But whatever method is applied all results gained in every field of botany, pertaining to the problem under discussion, have to be interpreted in a phylogenetical, dynamic sense. I fully agree with BAILEY and SWAMY (1951, p. 173) when they say: 'There is a similar danger at present in inferring an independent stachyosporous ancestry for selected genera . . . . without comprehensive ontogenetic and phylogenetic evidence'. . . . . 'Only by . . . . extensive and laborious methods will it be possible to determine ultimately whether all angiospermic carpels have been derived by successive modifications of conduplicate phyllosporous ones'.

Apparently Bailey and Swamy are still inclined to answer this question in the affirmative. I am of a different opinion but I heartily welcome their plea for a thorough open-minded investigation.

16. The modern 'phylogenetical tree'

Surveying the 'phylogenetical tree' in its modern shape, construed on the principles that the time factor is put along the ordinate and character or group development (i.e. mutations, by whatever cause) along the abscissa, the most striking feature is the sloping basic line. Its regularity (as pictured here) may be delusive: the relative time scale is a comparatively safe factor, but the relative rate of evolution is uncertain. Yet the fact remains that the slope never turns downward: 'les choses se présentent comme si les lignées maîtresses des plantes vasculaires avaient subi un cours distinct depuis les temps les plus anciens' (Leclercq, 1952, p. 96).

The second striking point is the steeply ascending branches. Although, again, the relative rate of evolution remains unknown, the general picture will certainly not be affected. It symbolises the general impression that some unknown power (internal or external or probably both in close interrelationship) pushes the main stem in a genetically more or less fixed direction. This main stem would then consist of a series of polymorphous, multipotential, non-specialised groups from which the more specialised branches with restricted potentiality and, it would seem, a slower rate of development, deviate. The latter all seem to be condemned to die out sooner or later, possibly by an ever increasing loss of potentiality. The everlasting, ever-modifying life is incorporated in the trunk from its dawn to its dusk.

If this picture is generally correct, the implication is that only the Angiosperms can give rise to the next group which will dominate the flora of the future. Most likely the living Angiosperms contain the ancestors of that future group but it is impossible to say where we have to look for them no more than it is possible to predict what they will look like, 'lignée' or 'embranchement', cf. § 14.

Axelrod (1952, p. 50–51) estimates that the average time elapsed between the first appearance of a major group and the beginning of its dominance is of the order of 30 or 40 million years. This would mean that if the ancestors of the next dominating group are among the now living flora, they must have started their career somewhere in the Lower Tertiary. Evolutionary processes can, to a certain extent, be understood and reconstructed in the past, prediction of what will follow, even in the nearest future, lies beyond our reach.

The relationship of the 'main trunk' and the 'branches' is still much of a mystery. The connecting points between the two are the weak spots of the system. The striking rarity of so-called intermediate forms or 'missing links' has given rise to much speculation and several ideas have been brought forward to explain it: changing rates of evolution, small and large mutations, rapid changes in environmental conditions. All this may be applicable to certain cases; to my mind, an often neglected explanation may be that we use to store away as many fossils as possible in one of the standard groups recognized by us. The result is that only a few remain which resist such attempts. Striking examples of this thesis are the mesophytic *Czekanowskia* and *Leptostrobus* which, according to Harris (1951, p. 503) are 'unclassifiable in any existing family'. Another example of this category is the Lower Permian *Trichopitys*: is it a primitive conifer or a primitive *Ginkyo*, or is it at the base of both (cf § 12)? We should remember that the main groups grow closer and closer as we dig deeper and it is therefore only logical that dividing lines get less and less distinct. Ancestral groups are probably generally only vaguely delimited.

POSTSCRIPT

After the above had already been printed and the proofs were about to be sent to me for correction, three papers have been published which have a direct bearing upon the problems under discussion.

The first of these papers, a 'plan for a simpler gynoecium' by J. PARKIN (1955), touches the subject of placentation and briefly discusses the concepts of phyllospory and stachyospory (with stegophylls) as far as the Angiosperms are concerned. As to the latter point he accepts Eames's verdict of 1951 by which he seems to be convinced that the said 'terms can be dismissed as unnecessary in angiospermous morphology'. For the rest, it must be pointed out, that I have never considered the two types in Angiosperms 'widely separated'; on the contrary I have repeatedly emphasised that they are not always sharply delimited even in lower Cormophyta and that in the Angiosperms they are possibly even mixed up. Regarding placentation, Parkin, who is an adherent of the classical carpel interpretation, confesses that he is distinctly puzzled by the so-called laminal placentation. Parkin thinks of 'an induced multiplication' of ovules (with marginal placentation as a starting point?). The reader may remember that I have originally pondered a similar idea but that my ultimate interpretation (LAM, 1952, p. C. 81–81, fig. 15) was that, in some cases at least, a fertile sporogenic axis has got adnate to its subtending bract.

The second paper is a publication by ECKARDT (1955). It is a continuation of his paper of 1954, discussed above (par. 15) and deals with certain families of Centrosperms, notably *Basellaceae*, *Portulacaceae*, some *Caryophyllaceae* with solitary ovules, and *Chenopodiaceae*.

In some cases the results are admittedly not final; neither did all of them seem to me convincing. This is particularly the case regarding the *Basellaceae*. Eckardt's descriptions do not exclude the possibility of an axis-borne funiculus. The carpels may well have subsequently enclosed the axial protrusion and their bases may have ultimately formed the floor of the ovary. Nothing is known about the vascular supply of the ovule.

Neither has it been proved in this case, that the fixed position of the solitary ovule opposite the adaxial carpel, means that its placentation was originally marginal. There is, as far as I can see, no objection to an interpretation as a fertile axis, axillary to the carpel. It would, in the meantime, be worthwhile to investigate the very youngest stages of development in order to find out in what sequence and from what places the various parts originate.

As to the other cases, however, at least that of *Claytonia* seems to be endangering the interpretation of stachyospory, since the insertion of the ovules seems to be actually marginal, as is obviously the case in some Caryophyllaceae.

However, even if it would seem that some Centrosperms are phyllosporous in the female sex—and typology should decide in how far this would hold for the whole order—we have to wait for further investigations, also in other fields. For also in placentation analogies may be expected, even most fallacious ones. In the meantime, Eckardt promises to continue this work, and cooperation of others should be very welcome. In fact, I am grateful for the attention given to the subject and I have repeatedly expressed the hope that my publications should entail such.

Again, even if it should ultimately seem that all Angiosperms are phyllosporous in the female sex—which I, again on typological grounds, still deem extremely improbable—it remains open to serious doubt whether the same holds for the male one.

The third paper bears upon the above paragraph 16. It is a paper by DÄNIKER (1955) on evolution and epharmosis. In his Taf. I he has pictured the genealogical tree of the Stelocormophyta in three dimensions instead of two, on six consecutive

Though I have some time indulged in similar schemes myself, I do not think, after all, that the third dimension clarifies much in representing a multidimensional system in which every single factor (character) would require another dimension. Diagrams like these necessarily remain highly subjective.

It must be recalled here that the two dimensions of my scheme are differentiation and time. From Däniker's expositions, however, it would appear that his two main dimensions are two types of differentiation, and that the third is time; again an attitude characteristic for a mind which starts from the static point of geological levels (why not seven, including the present and best known one?). view. So far as I can see, the arrangement of the groups in Däniker's levels seems rather arbitrary except from left to right.

It may furthermore be asked, why some groups seem to end abruptly in a flat disk, and why some others (Gymnosperms) are constricted above a certain level, to widen again higher up. Is it likely that the same group would show more than one period of great diversity ('Mannigfaltichkeitsebene')?

These remarks, however, are tokens of appreciation rather than of serious criticism; generally speaking, the scheme is instructive indeed.

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