A NEW SYSTEM OF THE CORMOPHYTA

by

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> The gaps in the fossil record are many, but there is optimistic hope for the future.
> (W. C. Darrah, 1939).

Some time ago I proposed elsewhere (1) a new system of the *Cormophyta*. Since the periodical, whose hospitality was my privilege, may not reach many taxonomists who still may be expected to be interested in the proposal, I deem it justified to briefly review the results at which I arrived in the present journal; and this will give me an opportunity to explain one or two points of a nomenclatural nature which, it seems to me, were perhaps somewhat insufficiently elucidated in the paper quoted. As a matter of course, for details as well as for the full argumentation of my views I have to refer to that publication.

The (here slightly emendated) system proposed is the following (anatomical characters omitted):

CORMOPHYTA.

Ground-plan — green plants with alternation of thallose, probably dichotomous generations, at least sporophyte with aerial sporangia in the ultimate lobes, isosporous.

Tendencies — strong reduction of gametophyte; development of aerial independent sporophyte in which the dichotomous ramification is gradually replaced by other branching types; development of vascular tissue (stele), of photosynthetic surface increase (enation leaves, telome leaves), of improved sporangium protection (sporangial connections), of heterospory and of woody, leafy stems (cormus), in which gradually connections are developed between branching and phyllotaxy (vegetative connections).

I. EOCORMOPHYTA — stachyosporous, without leaves or microphyllous, vegetative connections none; sporangia terminal and orthotropous or with primitive axillary connection; isosporous (or incidentically heterosporous?).

A. E. gametophytea — gametophyte dominating, with or without leaves; sporophyte (hemi)parasitic on gametophyte, not branched, leafless, isosporous. **1. Bryopsida**

a. *Hepaticae*; b. *Musci*.

B. E. sporophytea — sporophyte dominating and physiologically independent (always?), branching primarily dichotomous, persistent even in main branches or at least in younger ones; no leaves or microphyllous (enation leaves?); sporangial connections in c only; isosporous (incidentical heterospory in b?). **2. Psilopsida**

a. *Nematophytales?*; b. *Psilophytales*; c. *Psilotales*.

II. PALAEOCORMOPHYTA — stachyosporous or phyllosporous; sporophyte dominating, physiologically independent, as is gametophyte except if seeds are developed, in which case gametophyte is parasitic on sporophyte; vegetative connections none or interfoliar or ± axillary.

A. P. microphylla — stachyosporous and microphyllous; sporangia free or with various connections with sterile organs.

1. branching primarily dichotomous, often persistent even in main branches; no vegetative connections except by (? pseudo)angular leaves; enation leaves?; ligule incidentally extant (not in a, c and d); sporangia single, fundamentally ana(epi)tropous?; sporangial connections axillary (stegophylls); isosporous or heterosporous, some with seeds (Lepidospermales). . **3. Lycopsida**.
a. *Protolycopsida*; b. *Lepidophytales* and *Lepidospermales*; c. *Pleuromeiales*; d. *Lycopodiales*; e. *Selaginellales*; f. *Isoëtales*.

2. branching in older groups still dichotomous but main branching very soon of the monopodial type, the lateral organs in whorls inducing an early and pronounced articulation; telome leaves relatively small and soon tending to strong reduction, ultimately to monotelomic microphylls; vegetative connections none or, in the most recent group (f), interfoliar; sporangia anatropous, mostly in dichotomous groups (epi- and apotropous), more rarely single and then mostly epitropous, rarely apotropous; sporangial connections, if any, axillary (stegophylls), mostly to next lower leaf whorl and then sporangia epitropous, rarely to next upper one and then sporangia apotropous; isosporous, rarely heterosporous. . . . . **4. Sphenopsida**
a. *Protosphenopsida*; b. *Pseudoborniales*; c. *Sphenophyllales*; d. *Cheirostrobales*; e. *Tristachyales*; f. *Equisetales*.

B. P. macrophylla — originally stachyosporous, but very soon phyllosporous by excessive aggregation of sterile telomes into telome leaves; dichotomous branching persistent, particularly in the younger branchings (venation), eventually blurred by younger processes (anastomosing), main one mostly sympodial or monopodial; vegetative connections by angular leaves at dichotomies, gradually developing into an axillary connection; megaphyllous, reductions slight or none; sporangia originally terminal but soon marginal and ultimately laminal (upper or lower side of leaf), fundamentally orthotropous, in sori, often protected by indusia, synangial aggregation (Fil. eusp.) or infolding of leaf parts (b ♂ and ♀; d ♀); isosporous or heterosporous, some with seeds in which special protective organs (integument, cupula) develop; eusporophylls (all?). **5. Pteropsida**
a. *Filicales*: Protofilices (= Primofilices: Cladoxylales, Coenopteridales, Fil. eusporangiatae, Fil. protoleptosporangiatae, Fil. leptosporangiatae; b. *Hydropteridales*; c. *Noeggerathiales*; d. *Caytoniales* (stachyosporous?; megasporangia "angiospermous"); e. *Pteridospermales*.

III. MESOCORMOPHYTA — sporophyte dominating, wood with tracheids only; gametophyte parasitic; vegetative connection approaching a strictly axillary stage; heterosporous megasporangia in integument(s), otherwise naked, forming seeds, orthotropous or slightly anatropous.

A. M. macrophylla — mainly phyllosporous, megaphyllous; sporangia of the Pteropsida type. . . . . **6. Cycadopsida**
a. *Cycadales*; b. *Nilssoniales?*; c. *Bennettitales* (♀ stachyosporous).

B. M. microphylla — mainly stachyosporous, tending to leaf reduction and microphylly or with cladosporophylls; sporangial connections none or axillary (stegophylls); microsporangia anatropous. . . . . . . **7. Coniferopsida**
a. *Ginkgoales*; b. *Cordaitales*; c. *Coniferales* (♂ phyllosporous exc. *Taxus?*; ♀ Pinaceae and Araucariaceae secondarily phyllosporous; Cheirolepidaceae ditto, with "angiospermous" megasporangia).

IV. NEOCORMOPHYTA — sporophyte dominating, gametophyte parasitic; wood with tracheids or wood vessels or both; vegetative connections strictly axillary; heterosporous; megasporangia tending to acquire additional protection (angiospermy); seeds; growing tendency to develop flowers (synstegophylls).

A. Stachyosporous; wood with tracheids or wood vessels or both; megasporangia in integuments, otherwise naked or, if covered by sterile organs then the plants microphyllous and with decussate or whorled phyllotaxy; sporangia orthotropous. **8. Protangiospermae**

a. *Chlamydospermales* (*Gnetales*); b. *Verticillatae* (*Casuarina*).

B. Stachyosporous or phyllosporous; wood vessels prevailing, tracheids only rare; megasporangium in integument(s) and, in addition, more or less perfectly covered by or enclosed in sterile organs (angiospermy); sporangia ortho- or anatropous. . . . . **9. Angiospermae**

a. A. stachyosporae — stachyosporous; megasporangia protected by sterile organs (*e.g.* sterilised microsporangiophores; pseudocarpels); traces of ancient dichotomies mainly in (♂) reproductive parts; ± *Monochlamydeae*, perhaps also some Monocotyledons and Sympetalae.

b. A. phyllosporae — phyllosporous; megasporangia enclosed in infolded leaves (eucarpels); traces of ancient dichotomies mainly in vegetative parts (venation); ± *Polycarpicae* and derivatives.

For a preliminary understanding of this system, a brief explanation of certain terms will be indispensable to those who are not able to consult my earlier paper.

Stachyospory I call the condition in plants, in which the sporangia, whether iso- or micro- and megasporangia, are essentially terminal on entirely (or prevailingly) fertile telomes; the latter being the endings of a branch-system, which was dichotomous (isotomous) originally but which subsequently developed into sympodial and monopodial systems in their older parts; thence in many but the most primitive types these sporangiophores were inserted on a (relative) main axis (in the most primitive groups, like the *Psilophytales*, they are [relative] main axes).

In stachyosporous groups traces of ancient dichotomies are particularly found in (♂) sporangiophores (stamens).

There seems to be a general tendency, even in the vegetative parts to reduce the leaf surface (microphylly).

Sporangia are, therefore, in this type of plants, not borne on leaves so that there are no sporophylls, but they may, particularly in the ♀ sex, and in various ways and degrees, find protection not only from integuments, etc. but from sterile organs (stegophylls) which may subtend them, to which they may become more or less closely (axillarily) connected or which may cover them in some way (e. g. in the Angiosperms as pseudocarpels). In a few cases (certain Conifers such as *Podocarpus* and the *Pinaceae* and *Araucariaceae*) the megasporangia are inserted on a secondary leaf structure or phyllocladium (cladosporophyll).

Stachyosporous are the *Bryopsida*, the *Psilopsida*, the *Lycopsida*, the *Sphenopsida*, the ♀ *Bennettitales*, the *Coniferopsida* (except the secondary phyllospory in the cladosporophylls and except the ♂ Conifers which are mainly phyllosporous), the *Protangiospermae* and the *Angiospermae stachyosporae* (perhaps ♂ sometimes phyllosporous?).

Phyllospory I have proposed to call the condition in which sporangia are essentially 'drowned' in an excess of sterile telomes, i. e. on a leaf (eusporophyll).

In phyllosporous groups traces of ancient dichotomies are particularly found in the vegetative parts (venation).

There is a general tendency to develop large leaves (megaphylly).

Protection of sporangia is procured by leaf structures (e. g. the fern indusium), of megasporangia by various structures such as teguments, cupulae, etc., and additionally by infolding of the leaf or of parts thereof (*Hydropterides, Caytoniales, Angiospermae phyllosporae* with eucarpels).

Phyllosporous are the *Pteropsida* (except the *Caytoniales*?), the *Cycadopsida* (except the ♀ *Bennettitales*), the ♂ *Coniferae* (except *Taxus*) and the *Angiospermae phyllosporae.*

There seems to be some preference for the development of phyllospory in the male sex (*Bennettitales, Coniferae, Cordaitales*?). Whether this applies also to the Angiosperms is still unknown.

The main point in this system is that the class of the Angiosperms has lost its position as a starting point for morphological interpretations of all other *Cormophyta.* At the beginning of the present century Angiosperm morphology grew more and more — sit venia verbo — constipated, and the mild laxative, gently administered by palaeobotany, has now led to a condition in which everything is loosened and, at a still increasing rate, on the move again, presumably for a long period of interesting investigation in a hitherto well-nigh unexplored domain.

In order to facilitate a survey of the principal alterations which seemed an imperative consequence of our changed morphological viewpoint, the following statement may serve as an introduction to some conclusive remarks. For comparison I chose Wettstein's system of 1935 (see page 286):

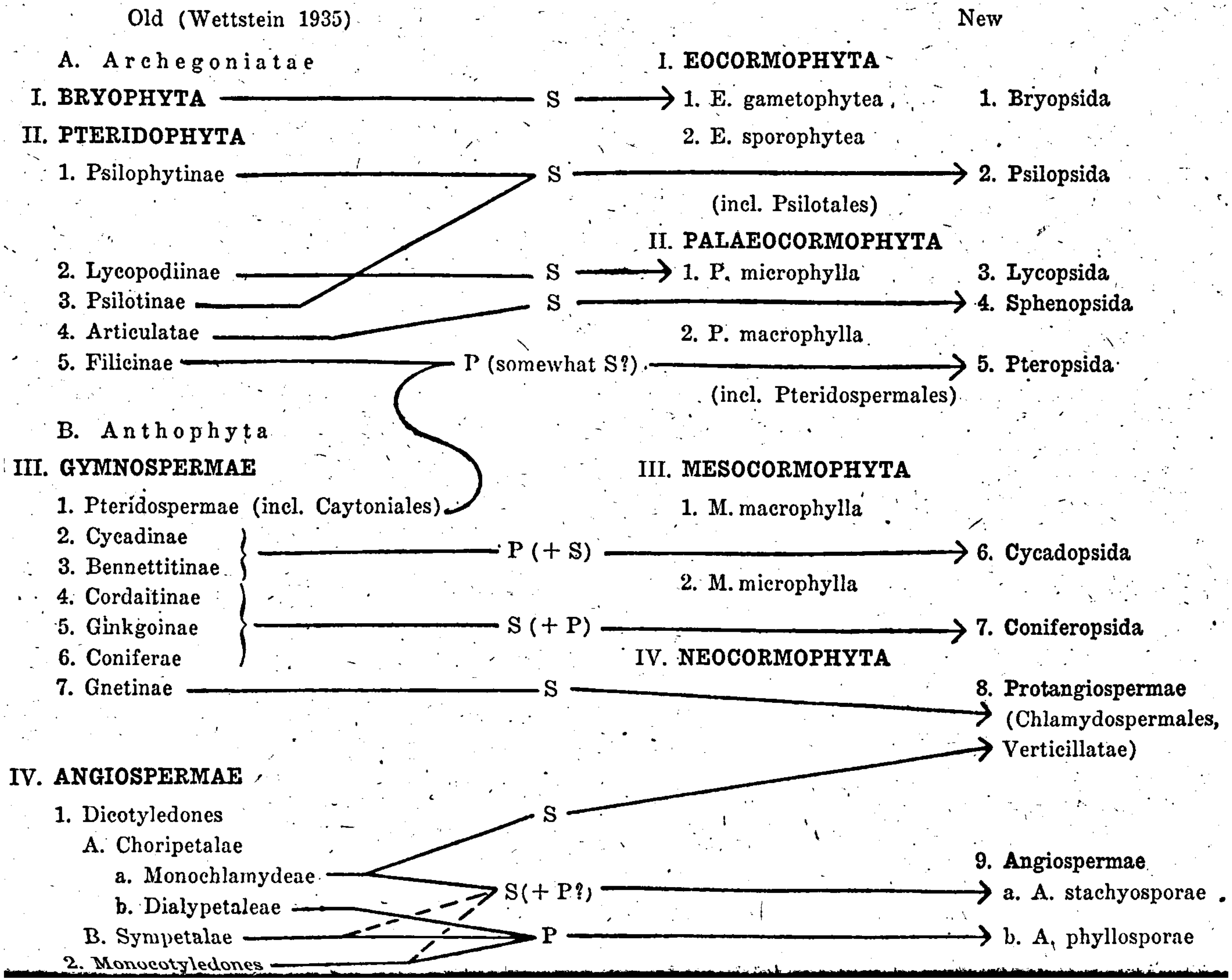
The new system is little else than a rearrangement of the well-known natural groups, of which only a few have been subject to slight but essential modifications. As appears from the above statement the groups 1, 3, 4, 6 and 7 have remained unaltered.

Altered are the groups:

2. *Psilopsida,* in as far the *Psilotales* are considered the recent plants which seem nearest to the ancient *Psilophytales*; unfortunately there are no fossil connections known thusfar.

5. *Pteropsida,* in which the Pteridosperms have been inserted. Typologically speaking, the latter clearly belong to the former (which I take in the limited sense as comprising the ferns and their near allies only; not, as was done by Jeffrey, Zimmermann and Eames, comprising all Cormophyta from the ferns upwards). That the Pteridosperms have sometimes been included in the '*Gymnospermae*' is merely a consequence of the old Angiosperm-centred morphology which convulsively clung to the concept of a 'sporophyll' in all groups; it was also a consequence of the fact that the Pteridosperms developed seeds and wood; this, however, was also the case in the *Lepidospermales* and seeds possibly also in the *Psilophytales.*

8. *Protangiospermae,* a group created by Engler for any hypothetical Angiosperm ancestors but taken over by me without any phylogenetical meaning to comprise some groups of plants which in some way seem to be intermediate between the *Mesocormophyta* and the *Angiospermae.* In this group I have placed the *Chlamydospermae (Gnetales, Gnetinae)* and *Casuarina (Verticillatae)*, both of which have always been groups of obscure relationships to other plants whilst showing indubitable traces of interrelationship, i. e. between *Ephedra* and *Casuarina* (decussate phyllo-


Old (Wettstein 1935)
New
A. Archegoniatae
I. BRYOPHYTA
II. PTERIDOPHYTA
1. Psilophytinae
2. Lycopodiinae
3. Psilotinae
4. Articulatae
5. Filicinae
B. Anthophyta
III. GYMNOSPERMAE
1. Pteridospermae (incl. Caytoniales)
2. Cycadinae
3. Bennettitinae
4. Cordaitinae
5. Ginkgoinae
6. Coniferae
7. Gnetinae
IV. ANGIOSPERMAE
1. Dicotyledones
A. Choripetalae
a. Monochlamydeae
b. Dialypetaleae
B. Sympetalae
2. Monocotyledones
S
S
S
S
P (somewhat S?)
P (+ S)
S (+ P)
S
S
S(+ P?)
P
I. EOCORMOPHYTA
1. E. gametophytea
2. E. sporophytea
(incl. Psilotales)
II. PALAEOCORMOPHYTA
1. P. microphylla
2. P. macrophylla
(incl. Pteridospermales)
III. MESOCORMOPHYTA
1. M. macrophylla
2. M. microphylla
IV. NEOCORMOPHYTA
1. Bryopsida
2. Psilopsida
3. Lycopsida
4. Sphenopsida
5. Pteropsida
6. Cycadopsida
7. Coniferopsida
8. Protangiospermae
(Chlamydospermales,
Verticillatae)
9. Angiospermae
a. A. stachyosporae
b. A. phyllosporae

taxy, microphylly, double fertilisation). In fact, *Casuarina* seems, typologically speaking, more closely connected to *Ephedra* than to any living monochlamydeous plant, though the decussate 'perianth' of the Chlamydosperms may bear some relation to the two pseudocarpels of many of the more primitive *Monochlamydeae*.

I originally added the '*Exocarpales*', but the insertion of that group is still so much uncertain that we should rather wait for the further development of this interesting case (2).

9. *Angiospermae*, which have kept their old delimitation except insofar as *Casuarina* (and perhaps *Exocarpus*) are concerned.

The main subdivision is both chronological, insofar as the four main groups correspond to the four main palaeobotanical era's (*Eophyticum* having been added by me to indicate the period of the monocracy of the Thallophytes; it ended at the rise of the — probably still unknown — oldest land plants); and evolutionary in that the sequence refers to an increasing differentiation in the sense of the telome theory. Important factors are furthermore micro- and megaphylly and particularly, stachyo- and phyllospory, which have been explained above.

As to the nomenclature I may add the following remarks to those mentioned in my earlier paper.

Obsolete are a. o. the names:

a. *Gymnospermae* — which does not cover a typologically natural group, not only because it comprises various basic types (groundplans) but since the concept of the sporophyll has fundamentally altered and, moreover, since the boundary towards the Angiosperms has grown more and more vague. In several *Monochlamydeae* (*Myrica*, etc.) the ovary is hardly closed, particularly in a young state. On the other hand "angiospermy", i. e. the state of coveredness (in some way or other) of the 'ovulum' (megasporangium), is found in the coniferous *Cheirolepidaceae*, in the *Caytoniales*, in the *Hydropteridales* and even more or less in the *Lepidospermales*. Even within the Angiosperms there are two fundamentally different types of angiospermy: the infolding of the leaf in the *Phyllosporae*; and the covering by stegophylls in the *Stachyosporae*.

b. *Spermatophyta* — which does not cover a natural group since seeds are developed in various non-related groups.

c. *Anthophyta* — which alludes to a structure, the flower, of which nobody will be able to give a more or less satisfactory definition, even if we agree to restrict this term to fertile shoots with "synstegophylls" [1]) (perianth) which are, perhaps, found in a primitive state in the Protangiosperms and which, obviously, only reach their full development in the Angiosperms. As a matter of course, the organogenetic (evolutionary) development of the flower has been a very gradual one and even if we were able, at present, to describe its rise, nobody would be in a position to mark any particular stage at which the concept would start to be applicable.

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[1]) This process is repeated "on a higher level" in the flower-imitating inflorescences of *Compositae, Umbelliferae, Euphorbia, Craterogyne*, etc.

d. *Pteridophyta* — which, in Wettstein's delimitation, does not cover a natural group. In addition to this, the following considerations seem to deserve some attention. The reason why the suffix *-opsida* has been chosen for seven out of the nine natural groups, is that I agree with Wettstein to retain the suffix *-phyta* for the main phyla, of which the whole of the *Cormophyta* constitutes a single one. The consequence was that no group of lower rank could be maintained with the same ending. Therefore, beside *Spermatophyta* and *Antophyta* which had become useless on other grounds, *Pteridophyta* had to be abandoned. Now Jeffrey in 1899 (3) introduced the terms *Lycopsida* and *Pteropsida* though both in a delimitation somewhat different from ours. In 1909 Scott (4) followed with the *Sphenopsida* and in 1936 Eames (5) with the *Psilopsida.* I deemed it only logical to complete the series, as far as this seemed desirable, and this is why I proposed the names *Bryopsida, Cycadopsida* and *Coniferopsida.*

Psilophyta which, accordingly, had to be dropped as well, could easily and logically be changed into *Psilophytales*, as the name of an order. *Thallophyta* has already to be abandoned as not being a phylum at all.

In *Eocormophyta gametophytea* and *E. sporophytea*, the second names are taken from Lignier (1908) who introduced them to cover the *Bryopsida* and the *Lycopsida* respectively (6).

I have to add here, that Mr W. H. Camp of the New York Botanical Garden in a recent letter kindly pointed out that the name '*Psilopsida*' was not coined — as I presumed in my previous paper — by Darrah but by Eames[1]), on his instigation. The name was privately used since 1933 and was first published in Eames (5, pp. 114, 330, 401 ss.). In this book, which unfortunately escaped my attention, much the same main classification of the lower Cormophytes was proposed as that used by me, with the exception that the *Bryopsida* are excluded from the '*Tracheophyta*' or vascular plants and that the *Pteropsida* comprise all groups from the Ferns onward. Gymnosperms and Angiosperms are not considered in it.

Another paper previously unknown to me, to which my attention was kindly drawn by Dr J. G. B. Beumée of the Wageningen Agricultural College, is a detailed study by H. Hallier (8), preceded by a short preliminary note (7) in the same year (1902), containing the conclusions of the larger paper. Though, naturally, bearing numerous traces of the Haeckelian way of reasoning — Hallier was one of Haeckel's devoted pupils and this paper is gratefully dedicated to the Master — it contains some remarkable conclusions. Though sometimes inclined to allow his imagination to run away with him, Hallier would, on the basis of his intimate knowledge of higher plants, occasionally arrive at clever concepts. The above-mentioned paper certainly comprises a number of conclusions which seem either too far-fetched or old-fashioned and untenable in the light of our present knowledge. But it is certainly memorable what an author of 1902, though admittedly under the influence of Potonié's public-

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[1]) Newman already mentioned this correctly, but unfortunately this was overlooked by me.

ations, said about leaf and axis of the higher Cormophytes (Conclusions 11 and 12):

"11. Das Laubblatt der höheren Achsenpflanzen ist ein Kurztrieb, ein Parasynthallium, d.h. ein durch Uebergipfelung eines Gabelastes durch seinen Schwesterast zur Seite geworfenes und abgegliedertes, flächenförmiges, dem Synklonium von Florideen vergleichbares System kongenital mit einander verschmolzener Zweige des dichotomen Marchantiaceenthallus. Auch das kleinste Aederchen entspricht dem Mittelnerven eines Abschittes des Hymenophyllaceen-wedels und des Marchantiaceen-thallus.

12. Auch die Achse der höheren Achsenpflanzen ist ein derartiges Synthallium......" (the rest is irrelevant in this connection, as it deals with the now abandoned pericaulome-theory).

In these lines Hallier — for the first time I think — stipulates that Potonié's concept which had always been rather vague about the Angiosperms, is applicable to that group as well. Both Potonié and Hallier, however, are spell-bound by the pericaulome-theory.

Another point which struck me was that (Concl. 17) the *Gnetales* were considered related to the (*Loranthaceae* and the) *Santalaceae* and *Ephedra* to the 'Hamamelidaceengattungen[1]' *Casuarina* (and *Myrothamnus*).

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[1] On p. 10 he speaks of "Amentaceengattungen".