COMMENTS ON GREGUSS'S PHYLOGENETICAL TREE OF PLANTS

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Recently (1955) I have published a new version of a phylogenetical tree of the *Cormophyta,* based on morphology, mainly ramification, leaf types, and sporangia. The concept is monophyletic but its basis is strewn with so many queries that the way is open to a number of different opinions. I add a corrected copy of my chart at the end of the present paper (fig. 2), so as to enable the reader to compare my views with those of Greguss (fig. 1).

The difficulty lies of course in our still extremely scanty knowledge of the very oldest land plants and of whether one or several — eventually more or less closely related — algal groups have succeeded in conquering dry land and converting themselves into true land plants in which the greater part of the sporophyte developed into aerial shoots. As a matter of course the fact whether a progeny should be considered to have originated mono- or polyphyletically merely depends on the degree of relatedness of the ancestral group(s). Mono- and polyphyly may seem controversial when extreme cases are compared; actually they are connected by a series of gradual differences just like mono- and polytopy, analogy and homology, and the like, whose criteria may be found in the fields of time, space and/or genealogical relationship.

Meanwhile, despite our scanty knowledge, the first steps have already been taken on the slippery ground of the possible connections between *Algae* and *Cormophyta,* viz. by Chadefaud (1952). As I have pointed out in my paper they mainly refer to structure and ramification rather than to reproductory parts. Chadefaud distinguishes two main types, the rhodomeloid and the fucoid one, and the latter which may have something to do with what in the Cormophyta is generally referred to as dichotomy, may, in different groups, be either a primary or a secondarily acquired character. At least in the first-named case may one recognise the condition which enabled Zimmermann and his adherents to apply the telome theory.

Now quite recently another attempt has been made to bridge the gap between *Cormophyta* on the one hand, and the *Thallophyta* on the other. It has been made on the basis of general morphology but the point of issue was an extensive study of the wood-anatomy — or, as the author, P. Greguss (1955) terms it, xylotomy — of living Gymnosperms. The results, however unexpected and outside the proper subject and — it would seem — the proper experience of the author, are remarkable enough to consider and briefly comment on.

The extensive large-size work consists of three main parts:

I. a short technical introduction;
II. an essay on the phylogeny of the Gymnosperms in the light of xylotomy, with a distributional map, a tabulated statement of the sharing and participation of anatomical characters in the different groups, and a phylogenetical chart of the plant kingdom from the *Algae* upwards;
III. the bulk of the work, being detailed descriptions of the wood-anatomy, with keys, and illustrated by a great number of photomicrographs and line drawings of sections.

It cannot be my task to comment upon the anatomical part of the work; I will have to leave that to experts. But as a phylogeneticist, I cannot forbear from mentioning some of Greguss's phylogenetical ideas, were it only to see where a scheme based upon an entirely different basis (vegetative instead of reproductory) may lead us. Greguss's scheme rests on a very simple, not to say simplistic basis: there are three main types of issue, differing in their mode of ramification, viz. monopodial (*Chlorophyceae*), dichotomous (*Phaeophyceae*), and verticillate (*Characeae, Rhodophyceae*).

This starting consideration seems to be rather superficial as it seems questionable typologically whether the algal groups mentioned can really be characterised as belonging to the ramification types connected with them (it is true, with some question marks).

Greguss claims that, starting with the oldest land plants the three ramification types can be recognised up to the Angiosperms inclusive. This is of course undeniable but the question is whether they have the same genetical value and are based upon homologies as we use to claim for reproductory organs. Since, however, we do not really know what a semophylesis is based upon, it may be worth while to consider the ideas of a man with another "*idée préconçue*" and see where it leads to.

According to Greguss the silurian and devonian *Psilophyta* are less homogeneous than they are often considered to be. This, of course, is correct. In *Rhynia, Horneophyton,* and *Asteroxylon* he speaks of "Mikrophyllen aus epidermalen Emergenzen hervorgegangen", i. e. enation leaves. But *Protopteridium, Taeniocrada,* and *Zosterophyllum* are "von makrophyller Struktur", whereas *Hyenia* and *Calamophyton* are "annäherend Vertizillat".

In the Carboniferous the same or a very similar distinction can be made. *Protolepidodendron, Lepidodendron, Bothrodendron,* and *Ulodendron* are considered microphyllous and pseudodichotomous ("scheingabelig"), i. e. actually monopodial. (I am afraid not many botanists will be inclined to agree here.) On the other hand *Aneurophyton, Archaeopteris* and *Sigillaria* (!) are considered macrophyllous (*Sigillaria* because of the two nerves in the base of the leaf). Verticillate are the well-known carboniferous *Sphenopsida* (the type is continued up to the present time).

The reader may have noticed that the original three ramification types are gradually being replaced — at least partially — by leaf types.

The next period leads up to seed plants. The reader of my previous papers may remember what I think of the "*Spermatophyta*" and the acquisition of the "seed", the ideas of Emberger and Martens on the Prephanerogams, and were to draw a line between the latter and the true Phanerogams on account of the condition of the ovule on being shed, whether or not containing an embryo (initial or full-grown) or merely a gametophyte. Greguss seems to belong to that category of botanists who consider the acquisition of a "seed" (of some description) in whatever group sufficient to base a homologous line (fr. "lignée"; genoreithrum of me) upon (cf Lam 1955, p. 420—421). He says to possess evidence, contributed by M. Jeliasevics that "seeds" have been found in *Sphenopsida* (in which occasional heterospory has been known for some time, cf Emberger, Plantes fossiles ...., 1944, p. 177, *Sphenophyllum*; Arnold, Introd. to Paleobot., 1947, p. 138, *Bowmanites*), and claims that if Jeliasevics's finds are confirmed this would mean one of the most important discoveries in phylogeny.

Greguss considers Gymnosperms only *Cycadopsida, Ginkyo,* and *Coniferopsida.* Whereas the lower groups have apparently been judged on account of their external morphological characters only, his aim regarding the Gymnosperms is to investigate whether his three fundamental groups can be traced among this class chiefly though not exclusively on xylotomical grounds. Again, however, the distinction is to leaf type rather than to ramification. From his exposition of xylotomical observations he claims the following relationships:

A. Macrophyllous group (derived from *Pteropsida*)

1.	*Pleuromeia* *Sigillaria* *Cycadofilices* *Cordaitales*	**Cycadales**	*Araucaria* — *Welwitschia* — *Bennettitales*		*Palmae* *Dracaena* etc.
2.		**Ginkyo**	*Araucaria* *Podocarpaceae*		
3.	*Cordaitales* —	**Araucaria**	*Ginkyo* *Podocarp.*	*Welwitschia*	

4. *Caytoniales* *Cordaitales*	**Podocarpus** — *Araucaria*		
5. *Ginkyo*	**Taxales** (incl. *Cephalotax.*) *Podocarp.* (incl. *Austrotax.*)	*Araucaria*	

B. Microphyllous group.

6. *Phyllotheca* *Calamites*	**Cupressaceae**	*Ephedra* *Casuarina*	— ? *Sympetalae* (on account of often decussate phyllotaxis)

(derived from *Sphenopsida*)

7. *Lycopsida*	**Pinaceae** **Taxodiaceae**

(derived from *Lycopsida*).

Greguss therefore assumes three different series ("Folgen") proceeding from primitive to advanced (mainly on account of medullary rays), connecting

I. *Cycadales, Ginkyo, Araucaria, Podocarpus,* and perhaps *Taxaceae* with the *Pteropsida*;
II. *Cypressaceae* with the *Sphenopsida*;
III. *Taxodiaceae* and *Pinaceae* with the *Lycopsida.*

The (recent) geographical correlations mentioned by Greguss seem rather inaccurate and insufficiently founded. Only in his phylogenetical chart do the original three ramification groups reappear. From this the following relationships may be quoted:

A. Monopodial.

? *Chlorophyceae-Musci*	*Rhynia* *Hornea* *Asteroxylon* *Protolepido-dendron*	most *Lycopsida*, except *Sigillaria*, *Pleuromeia*, and *Isoëtes*	*Pinaceae* *Taxodiaceae* *Voltzia*	— *Gnetum* ?	*Monochlamydeae* *Dialypetaleae* (*e.g. Degeneria*)

B. Dichotomous.

? *Phaeophyceae-Hepaticae* —	*Zosterophyllum* *Cladoxylon* *Pseudosporochnus* *Protopteridium* *Psilotales*	*Sigillaria* *Pleuromeia* *Isoëtes*	*Pterido-spermae* *Filicales*	*Cycadopsida* *Ginkyoales* *Cordaitales* *Taxales* *Podocarpac.* *Araucariac.*	*Welwitschia*	*Palmae* *Dracaena* *Cyperales*

C. Verticillate.

? *Characeae* ? *Rhodophyceae*	— *Sphenopsida* — ?	*Cupressaceae* *Ephedra* *Casuarina*

Greguss terminates with a tabulated scheme of the system of all plants in which he tries to keep up his tripartition from the "*Algophyta*" upward.

It is a sort of recapitulation of his phylogenetical chart and makes the impression of a scheme in which the tripartition is raised to a dogma which should be followed at all cost. The three subdivisions would be here:

Algophyta	*Chlorophyta* (?)	*Phaeophyta* (?)	*Rhodophyta* (?)
Bryophyta	*Musci*	*Hepaticae*	
Psilophyta	*Prolycopsida*	*Propteropsida*	*Prosphenopsida*
Pteridophyta	*Lycopsida*	*Pteropsida*	*Sphenopsida*
Pteridospermae	*Lepidospermae*	*Pterispermae*	*Calamitospermae*
Gymnospermae	*Isospermae*	*Homospermae*	*Cupressospermae*
Chlamydospermae	*Gnetales*	*Welwitschiales*	*Ephedrales*
Angiospermae	*Dicotyledones* a. *Dialypetaleae* etc. b. *Monochlamydeae*, etc.	*Monocotyledones* a. *Liliiflorae* etc. b. *Palmae*, etc.	*Verticillatae*

The subdivision does not exactly tally with that used in the phylogenetical chart; some of the new terms, like *Isospermia, Homospermia,* and *Euspermia* are not explained.

Apart from xylotomical evidence (on which I have no founded opinion), Greguss's knowledge of the morphology of living and fossil *Cormophyta* seems rather insufficient to inspire much confidence in his results, and I am afraid the author has overshot his aim in a rather unfortunate way.

My principal objection, both to Greguss's tripartite system as discussed above, and to Emberger's "Prephanerogams" is, that they both tear apart what are generally — and I think, on good grounds — considered really natural groups.

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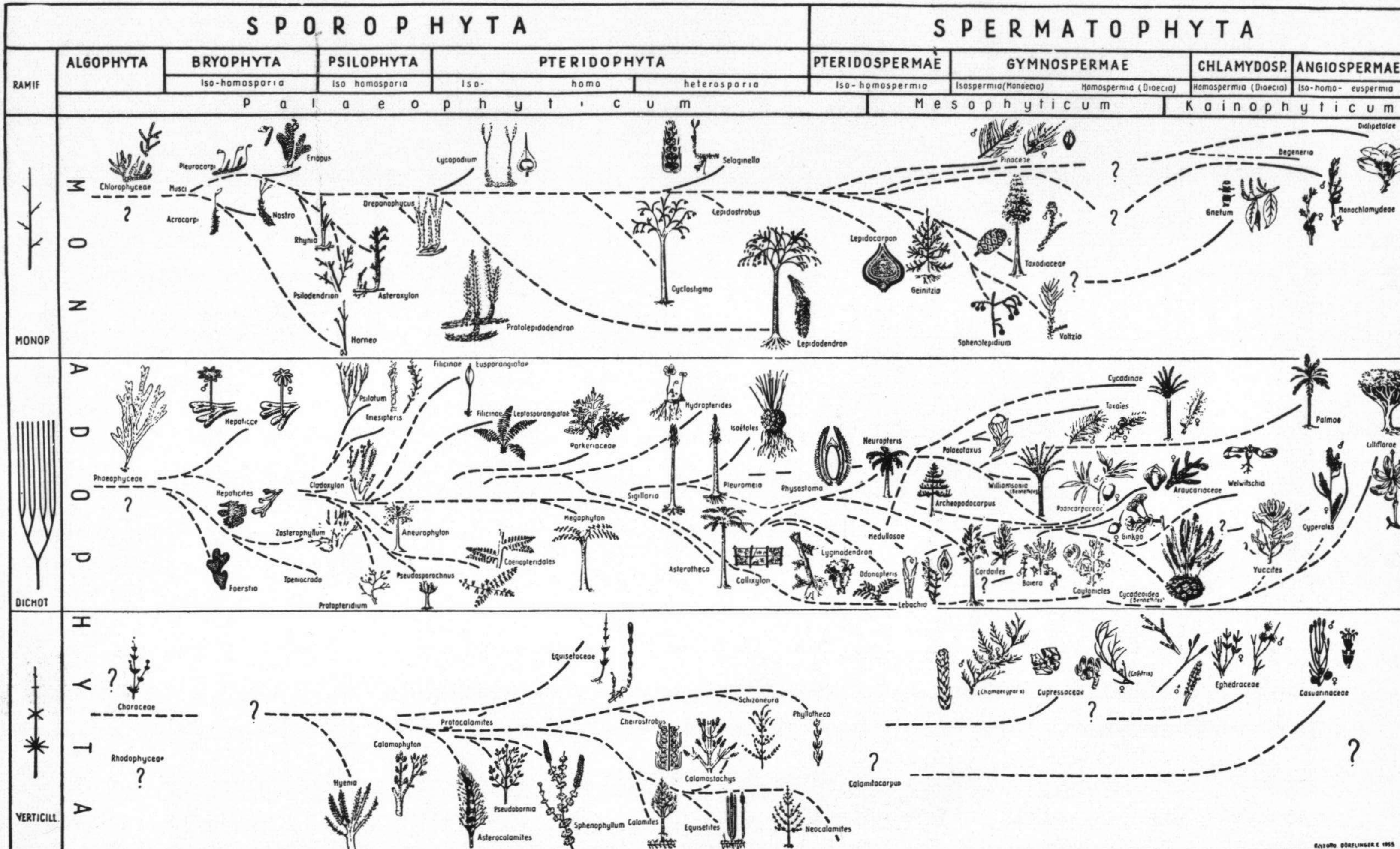

Fig. 1. Greguss's Phylogenetical Chart

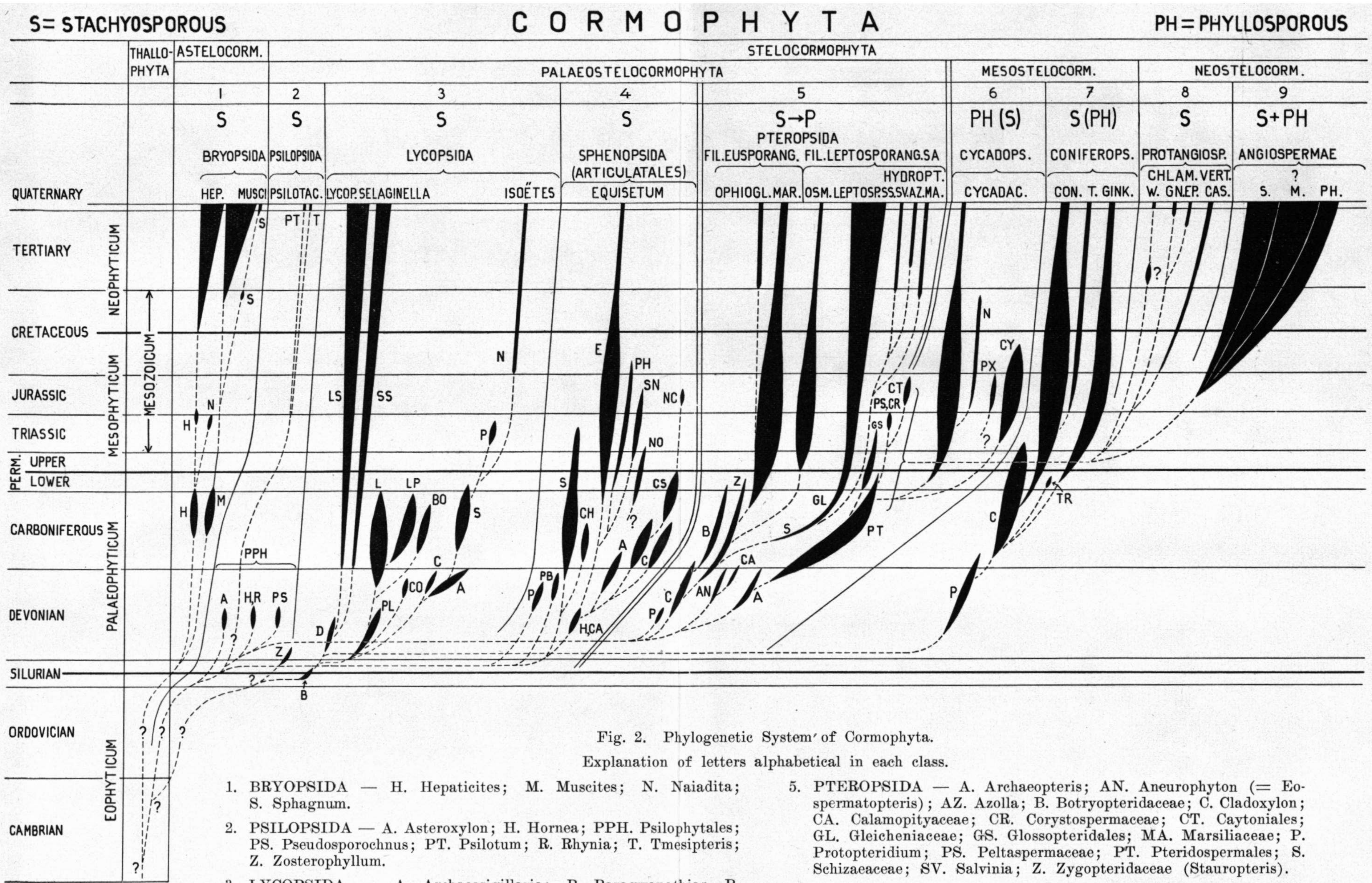

Fig. 2. Phylogenetic System of Cormophyta.

Explanation of letters alphabetical in each class.

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; B. Bothrodendron; C. Cyclostigma; CO. Colpodexylon; D. Drepanophycus; L. Lepidodendron; LP. Lepidophloios; LS. Lycopodites; N. Nathorstiana; P. Pleuromeia; PL. Protolepidodendron; S. Sigillaria; SS. Selaginellites.
4. SPHENOPSIDA — A. Asterocalamites; C. Calamitales; CA. Calamophyton; CH. Cheirostrobus; CS. Calamites; E. Equisetites; H. Hyenia; NC. Neocalamites; NO. Noeggerathiales (?); 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; GS. Glossopteridales; MA. Marsiliaceae; P. Protopteridium; 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.