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ON THE HIGHER TAXA OF EMBRYOBIONTA

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The general system of plants and the nomenclature of higher taxa at the level of divisions and classes are now unstable and in a state of confusion. The well known schemes of classification by which all plants are grouped into only 4 or 5 divisions have been largely abandoned because they do not adequately reflect the great diversity within the plant kingdom. Phycologists have found it necessary to recognize several divisions of algae, and students of higher plants have also felt the need for a greater number of divisions. Harold C. Bold (1957) has gone so far as to recognize 24 divisions of plants.

There is now a bewildering plethora of systems and partial systems, each of which may lay some claim to being the best representation of the similarities, differences, and evolutionary relationships within all or some part of the plant kingdom. The same groups appear over and over again in many of these systems of classification, but at different taxonomic ranks and in different arrangements with respect to each other. It is forcibly brought to our attention that even when the evolutionary relationships are not in dispute, it is often possible to produce more than one system of classification which is in accord with these relationships.

Each of the authors of the present paper has published works dealing with the general system of higher plants (Zimmermann, 1959; Cronquist, 1960; Takhtajan, 1964). We have been in correspondence for several years, but our ideas have been to a large extent developed independently of each other. In August of 1965 two of the authors (Cronquist and Takhtajan) had an opportunity for extended personal consultation in Leningrad. These talks and subsequent correspondence with the third author (Zimmermann) have resulted in the production of this paper.

No person, and no group, has the authority to decide what system of classification should be adopted by all, or what parts should be taken from which system to produce a universally accepted classification. Nonetheless, it seems obvious that it would be useful if the majority of botanists were agreed on a single overall scheme. It is perhaps not difficult for professional taxonomists to remember several classifications with differing names and ranks for the generally recognized groups, but it is difficult for a student to find his way through such a jungle. We think that it might therefore be of some interest to see what sort of general system of higher plants might be mutually acceptable to three botanists from three different countries, such as ourselves. If other botanists also find this scheme acceptable, we shall be happy; if not, we have still had a profitable discussion and a pleasant pipe-dream.

Our purpose here is taxonomic rather than phylogenetic. We believe that any proper

taxonomic classification must be consistent with phylogeny, but perhaps the classification here presented may also satisfy those who reject phylogenetic considerations.

Many of the names we use here are only slightly modified from well known existing names. In order to avoid possible questions about valid publication we are listing these as nomina nova and citing previously published descriptions. Some other names which represent well known groups are here listed as new taxa in order to avoid questions as to typification. The synonymy is intended merely to validate the names used and to clarify our meaning. Many synonyms, both well-known and obscure ones, are deliberately omitted as being irrelevant to our purpose.

Zimmermann dissents from the treatment here presented on only one point: He recognizes the problems associated with the names Cormobionta and Telomobionta, but he thinks that objections may also be raised to Embryobionta. He therefore thinks it might have been wiser to adopt the name Cormobionta, based on the well known name Cormophyta Endl. 1836.

Some parts of this scheme are sufficiently well known to be self-explanatory, or at least the explanations can be found in the separate works of the three authors, (Takhtajan, 1953; Zimmermann, 1959; Cronquist, 1960) as well as in many other places. Other items may require some comment.

We have chosen the name Embryobionta for the subkingdom, in preference to Cormobionta or Telomobionta. The name Telomobionta, proposed by one of us (Takhtajan, 1964), implies the acceptance of a morphological concept which is not accepted by all botanists and whose acceptance is not necessary for recognition of the group. The name Cormobionta hardly fits the Rhyniophytes and Bryophytes, which are integral parts of the group. The most characteristic feature of the whole subkingdom is that the sporophyte begins its development as a parasite on the gametophyte (or on the adult sporophyte), and the name Embryobionta properly reflects this feature.

We have thought it advisable to extend the type concept in nomenclature to the level of division, following the suggestion of Rickett and Camp (1950). Names of divisions and lesser groups which are based on morphological characters have therefore been abandoned in favor of names based on genera. We believe that the logic which has been applied to extend the type concept in the Rules of Nomenclature from families up to orders applies equally well to classes and divisions. Now, when both the general system and the nomenclature are still fluid, is the time to introduce the necessary change.

We have not extended the type concept to the level of the subkingdom, mainly because we found it impossible to select appropriate genera to provide the names for the two subkingdoms (Thallobionta and Embryobionta) which we recognize. The Thallobionta in particular are so diverse that no genus seems to provide an appropriate base for a name.

We have adopted the standard ending -atae for classes, in accordance with the arguments presented by Nora Zabinkova (1964). Unfortunately Zabinkova's article was published too late for its nomenclatural proposals to be properly considered at the X International Botanical Congress in Edinburgh in 1964. We plan to present the same proposals for consideratin at the XI International Botanical Congress in Seattle in 1969. Reasons for not accepting the class ending -opsida, as now recommended (but not required) by the rules, may be found in Cronquist, 1960, Zabinkova, 1964 and Takhtajan, 1964.

In certain classes (Isoetatae, Polypodiatae, Pinatae) we have thought it useful to extend our consideration to the level of the subclass. In so doing, we do not intend to foreclose the possibility that subclasses may also be recognized in other classes.

We have chosen the name Rhyniophyta instead of Psilophyta for several reasons. The name Psilophyta (Zimmermann, 1930) was clearly indicated to be a descriptive

name, derived from the Greek *psilos*, naked, and *phyton*, plant. *Psilophyton* was definitely included in the group; *Psilotum* on the other hand was attached only as an Anhang, so it clearly could not provide the type for the name. Had the name been based on *Psilophyton*, it should have been Psilophytophyta, an infelicitous compound. Recent work (Hueber, 1964) suggests that Dawson's reconstruction of *Psilophyton* may have included at least two quite different plants, and there is even some question that *Psilophyton* properly belongs with the other fossils that have generally been referred to as "Psilophytes". *Rhynia*, on the other hand, is very well known and may appropriately be selected to typify the "Psilophyte" fossils.

The Bryophytes are here listed after the Rhyniophytes in the belief that the monotelomic sporophyte is reduced from that of a more rhynioid (i.e. polytelomic) ancestor. The presence of apparently functional stomata in the Anthoceratae, the occasional occurrence of forked sporophytes in various Bryophytes, and the generally admitted tendency toward reduction of the sporophyte within the Bryophyte division all combine to show that within the Embryobionta the Bryophytes are reduced and derivative rather than primitive.

Psilotum and *Tmesipteris* are here regarded as together constituting a distinct division, the Psilotophyta. We do not doubt that these two genera are fairly closely related to the fossil Rhyniophytes. The absence of roots in particular testifies to their primitiviness. On the other hand we think the differences are sufficiently formidable to warrant divisional status. The synangial, axillary or foliar sporangia and the apparently telomic leaves of *Psilotum* and especially *Tmesipteris* are wholly out of harmony with Rhyniophyte structure.

The name Equisetophyta is substituted for the names Calomophyta and Sphenophyta in the belief that it is preferable to draw group names from living members instead of fossils when it can reasonable be done.

We have retained the traditional gymnosperms as a single division (Pinophyta), even though one of us (Cronquist, 1960) has previously recognized two divisions for this group. Recent studies, especially by Beck (1962), tend to support the concept that both the Pinicae (Coniferophyta) and Cycadicae (Cycadophyta) had a common origin in the primitive seed ferns, or at least originated from a closely knit group of pregymnosperms. Simpson (1945) has set forth the principle that the characters which mark a natural taxonomic group may evolve in parallel fashion from a set of ancestors which do not themselves belong to that group, and Cronquist (1963, 1965), has noted that this sort of parallelism from similar ancestors is a common phenomenon. Zimmermann (1959) independently applied this same concept in maintaining the gymnosperms as a proper taxonomic group in spite of the possibility that the most recent common ancestor of the Pinicae and the Cycadicae did not itself have seeds. *Lepidocarpon*, in the Lycopodiophyta, does or does not have seeds, according to whether one takes as the essential criterion the parasitism and the enclosure of the female gametophyte, or the presence of an apparently syntelomic integument. According to Andrews (1961), the "integument" of *Lepidocarpon* is an almost closed sporophyll, not homologous with the integument of seed plants. Zimmermann (1959) had earlier expressed a similar opinion. Thus, the "seeds" of *Lepidocarpon* and related organ genera are not homologous with the seeds of the Pinophyta and Magnoliophyta.

We deliberately retain the Gneticae as a subdivision co-ordinate with the Cycadicae and Pinicae. The relationships of the Gneticae within the division are still controversial. Takhtajan favors a relationship to the Cycadicae, and Cronquist to the Pinicae; for Zimmermann the question of relationship is open. In any case the Gneticae are so distinctive that they can well stand as a group coordinate with the conifers and cycads. The taxonomic treatment here proposed is compatible with either of the two concepts of evolutionary relationship.

Our decision to treat the angiosperms as a distinct division, rather than subordinating them to a larger group embracing both gymnosperms and angiosperms, is purely subjective and depends on personal weighting of the characters. It would be equally in accord with probable phyletic affinities to include all seed plants (defined so as to exclude Lepidocarpaceae and Miadesmiaceae) in a single division, or even to treat all vascular plants as a single division. The question is which of these three equally phylogenetic treatments best reflects the totality of similarities and differences, so that the mind can effectively grasp and retain the system.

We adopt *Magnolia* as the type genus of the dicotyledons and of the angiosperms as a whole, and *Lilium* as the type genus of the monocotyledons, following the reasonable suggestions of Rickett and Camp (1950).

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Conspectus systematis Embryobiontorum

Subregnum Embryobionta nom. nov. (regio Cormophyta Endl. 1836, Gen. pl.: 42)

1. *Divisio* Rhyniophyta div. nov. (classis Psilophytinae Fitting et al. 1928, in Strasb. Lehrb. d. Bot. ed. 17. 403; divisio Psilophyta W. Zimm. 1930, Die Phylog. d. Pflanzen: 103, max. pars).
Typus: *Rhynia* Kidston et Lang 1917.

Classis Rhyniatae classis nov. (classis Psilophytinae Fitting et al. 1928, in Strasb. Lehrb. d. Bot. ed. 17: 403).
Typus *Rhynia* Kidston et Lang 1917.

2. *Divisio* Bryophyta A. Br. 1864.
Typus: *Bryum* Hedw. 1801.

Classis Anthoceratae stat. nov. (tribus Anthoceroteae Nees 1838, Leberm. 4: 319).
Typus: *Anthoceros* L. 1753.

Classis Marchantiatae classis nov. (ordo Hepaticae Juss. 1789, Gen. pl. 7, p.p.; classis

Hepaticopsida Rothm. 1951, in Feddes Repert. 54: 261).
Typus: *Marchantia* L. 1753.

Classis Bryatae classis nov. (Musci Hedw. 1782, Fund. Hist. Nat. Musc. Frond.; Ordo Musci Juss. 1789, Gen. pl. 10, p.p.; classis Musci Endl. 1836, Gen. pl. 46).
Typus: *Bryum* Hedw. 1801.

3. *Divisio* Psilotophyta stat. nov. (ordo Psilotales Wettst. 1903, Handb. d. Syst. Bot. 2: 91).
Typus: *Psilotum* Swartz 1806.

Classis Psilotatae stat. nov. (ordo Psilotales Wettst. 1903, Handb. d. Syst. Bot. 2: 91).
Typus: *Psilotum* Swartz 1806.

4. *Divisio* Lycopodiophyta nom. nov. (Lycopsida Jeffrey 1899, in Trans. Canad. Inst. 6: 632, p.p.; phylum Lycopsida Jeffrey 1908, in Bot. Gaz. 46: 257 p.p.; divisio Lycophyta Boivin 1956, in Bull. Soc. Bot. France 103: 492).
Typus: *Lycopodium* L. 1753.

Classis Lycopodiatae nom. nov. (classis Lycopodinae Prantl 1874, Lehrb. d. Bot.: 123).
Typus: *Lycopodium* L. 1753.

Classis Isoetatae classis nov. (classis Selagines Endl. 1836, Gen. pl. 68; classis Isoetopsida Rothm. 1951, in Feddes Repert. 54: 262, nomen subnudum).
Typus: *Isoetes* L. 1753.

5. *Divisio* Equisetophyta nom. nov. (phylum Calamophyta Bessey 1907, in Univ. Nebr. Stud. 7: 45; divisio Equisophyta Boivin 1956, in Bull. Soc. Bot. France 103: 493).
Typus: *Equisetum* L. 1753.

Classis Hyeniatae stat. nov. (subclassis Hyeniidae Pichi-Sermolli 1958, in Uppsala Univ. Årsskr. 6: 76).
Typus: *Hyenia* Nathorst 1915.

Classis Sphenophyllatae nom. nov. (classis Sphenophyllales Engl. 1892, Syllabus 58).
Typus: *Sphenophyllum* Koenig 1825.

Classis Equisetatae nom. nov. (classis Equiseta Endl. 1836, Gen. pl. 58).
Typus: *Equisetum* L. 1753.

6. *Divisio* Polypodiophyta div. nov. (classis Filices Endl. 1836; Gen. pl. 58).
Typus: *Polypodium* L. 1753.

Classis Polypodiatae classis nov. (classis Filices Endl. 1836, Gen. pl. 58).
Typus: *Polypodium* L. 1753.

Subclassis Protopteridiidae subclassis nov. (Primofilices Arber 1906, in Ann. Bot., Lond., 20: 215; subclassis Primofilicidae Pichi-Sermolli 1958, in Uppsala Univ. Årsskr. 6: 80).
Typus: *Protopteridium* Krejci 1880.

Subclassis Archaeopteridiidae stat. nov. (ordo Archaeopteridales F. Nemejc 1950, in Acta Musei nat. Pragae 6(3): 80).
Typus: *Archaeopteris* Dawson 1871.

Subclassis Ophioglossidae Takht. 1956, nomen subnudum, Telomophyta 1: 168 (ordo Ophioglossales Engl. 1898, Syllabus ed 2: 63).
Typus: *Ophioglossum* L. 1753.

Subclassis Noeggerathiidae Takht. 1956, Telomophyta 1: 77.
Typus: *Noeggerathia* Sternb. 1822.

Subclassis Marattiidae stat. nov. (ordo Marattiaceae Kaulfuss 1824, Enum. 31).
Typus: *Marattia* Swartz 1788.

Subclassis Polypodiidae stat. nov. (fam. Polypodiaceae R. Brown 1810, Prodromus 145; subclassis Filicidae Rothm. p.p. 1951, in Feddes Repert. 54: 262; subclassis Filicidae Pichi-Sermolli 1958, in Uppsala Univ. Årsskr. 6: 83).
Typus: *Polypodium* L. 1753.

Subclassis Marsileidae Pichi-Sermolli 1958, Uppsala Univ. Årsskr. 6: 83, nomen subnudum (ordo Marsileaceae R. Brown 1810, Prodromus: 166).
Typus: *Marsilea* L. 1753.

Subclassis SALVINIIDAE Pichi-Sermolli 1958, Uppsala Univ. Årsskr. 6: 83, nomen subnudum (fam. Salviniaceae Dumort. 1829, Anal. Fam.: 27).
Typus: *Salvinia* Adans. 1763.

7. *Divisio* PINOPHYTA div. nov. (classis Gymnospermae Lindl. 1830, Intr. Nat. Syst. Bot.: 245; divisio Gymnospermae Prantl 1874, Lehrb. d. Bot. 131).
Typus: *Pinus* L. 1753.

A. *Subdivisio* CYCADICAE nom. nov. (phylum Cycadophyta Bessey 1907, in Univ. Nebr. Stud. 7: 47; subdivisio Cycadophytina W. Zimm. 1959, Die Phylog. d. Pfl. ed. 2: 325. p.p., nomen subnudum).
Typus: *Cycas* L. 1753.

Classis LYGINOPTERIDATAE nom. nov. (divisio Cycadofilices Potonié 1899, Lehrb. d. Pflanzenpaleont. 160; classis Pteridospermeae F. W. Oliver et D. H. Scott 1904, Phil. Trans. Roy. Soc. Lond. B, 197: 239).
Typus: *Lyginopteris* Potonié 1899.

Classis CYCADATAE classis nov. (classis Zamiae Endl. 1836, Gen. pl. 70).
Typus: *Cycas* L. 1753.

Classis BENNETTITATAE nom. nov. (classis Bennettitales Engl. 1892, Syllabus 61).
Typus: *Bennettites* Carruthers 1870 (*Cycadeoidea* Buckland 1828, a taxonomic synonym, but not a nomenclatural synonym).

B. *Subdivisio* PINICAE subd. nov. (phylum Strobilophyta Bessey 1907, in Univ. Nebr. Stud. 7: 49; subdivisio Coniferophytina W. Zimm. 1959, Die Phylog. d. Pfl. ed. 2: 325, nomen subnudum).
Typus: *Pinus* L. 1753.

Classis GINKGOATAE nom. nov. (classis Ginkgoales Engl. 1897, Engler und Prantl, Die natürl. Pflanzenfam., Nachtr. 341).
Typus: *Ginkgo* L. 1753.

Classis PINATAE nom. nov. (classis Pinoideae Bessey 1907, in Univ. Nebr. Stud. 7: 50).
Typus: *Pinus* L. 1753.

Subclassis CORDAITIDAE nom. nov. (classis Cordaitales Engl. 1892, Syllabus 60).
Typus: *Cordaites* Unger 1850.

Subclassis PINIDAE subcl. nov. (ordo Coniferae Juss. 1789, Gen. pl.: 411, p.p.; ordo Coniferae Prantl 1874, Lehrb. d. Bot. 134; classis Coniferae Engl. 1892, Syllabus 61).

C. *Subdivisio* GNETICAE subd. nov. (classis Gnetales Engl. 1887, in Engler und Prantl, Die natürl. Pflanzenfam. II. 1: 2).
Typus: *Gnetum* L.

Classis GNETATAE nom. nov. (classis Gnetales Engl. 1887, in Engler und Prantl, Die natürl. Pflanzenfam. II. 1: 2).
Typus: *Gnetum* L. 1767.

Subclassis EPHEDRIDAE subcl. nov. (fam. Ephedraceae Dumortier 1829, Anal. Fam. pl.: 11).
Typus: *Ephedra* L. 1753.

Subclassis WELWITSCHIIDAE subcl. nov. (fam. Tumboaceae Wettst., 1903, Handl. d. syst. Bot. 158; Welwitschiaceae Lotsy 1911, Bot. Stammesgesch. 3: 310).
Typus: *Welwitschia* Hook. f. 862.

Subclassis GNETIDAE subcl. nov. (fam. Gnetaceae Lindl. 1834, Bot. Reg. 1686).
Typus: *Gnetum* L. 1767.

8. *Divisio* MAGNOLIOPHYTA div. nov. (divisio Angiospermae A. Br. et Doell 1857, ex Doell, Fl. Baden. 1: 104).
Typus: *Magnolia* L. 1753.

Classis MAGNOLIATAE classis nov. (classis Dicotyledoneae DC. 1818, Syst. 1: 123).
Typus: *Magnolia* 1753.

Classis LILIATAE classis nov. (classis Monocotyledoneae DC 1818, Syst. 1: 122).
Typus: *Lilium* L. 1753.