THE CLASSIFICATION OF GYMNOSPERMOUS PLANTS

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ABSTRACT

Various systems of classification of the gymnospermous plants are briefly reviewed. Arnold's classification (*Bot. Gaz.*, 1948) is tentatively modified as follows:

Division: *Cycadophyta* — Class 1. Pteridospermopsida, Orders: 1. Lyginopteridales, 2. Medullosales, 3. Glossopteridales, 4. Peltaspermales, 5. Corystospermales, 6. Caytoniales; Class 2. Cycadopsida, Order: 7. Cycadales; Class 3. Pentoxylopsida, Order: 8. Pentoxylales; Class 4. Cycadeoideopsida, Order 9. Cycadeoideales.

Division: *Chlamydospermophyta* — Class Gnetopsida, Orders: 1. Gnetales (restricted to *Gnetum*), 2. Welwitschiales.

Division: *Coniferophyta* — Class 1. Coniferopsida, Orders: 1. Cordaitales, 2. Ginkgoales; 3. Coniferales; Class 2. Ephedropsida, 4. Ephedrales; Class 3. Czekanowskiopsida, Order: 5. Czekanowskiales; Class 4. Taxopsida, Order: 6. Taxales.

The position of the Pentoxylales, Ephedrales, Glossopteridales and Czekanowskiales is discussed in the light of recent research.

INTRODUCTION

The history of gymnosperm classification begins with the year 1827 when Robert Brown recognized the naked seed of the Cycads and the Conifers, and called them Gymnosperms. Later, Endlicher (1836-1840) gave them the same rank as the three divisions of Dicotyledons under his Acramphibrya, Adolphe Brongniart (1843) actually included them in the Dicotyledons and Bentham & Hooker (1862-1883) placed them between the Dicotyledons and the Monocotyledons. Ultimately, Hoffmeister's epoch-making work (1851) on the development and embryology of diverse plants led Van Tieghem (1898) to remove them from this intermediate position and he installed them as one of the two primary divisions of the Spermatophyta[1].

Bentham & Hooker (1862-1883) recognized only three orders of the living Gymnospermae, viz. Gnetaceae, Coniferae and Cycadaceae. The genus *Ginkgo* was in those days traditionally included in the Coniferae, e.g. it was included by Eichler (1889) in Taxeae along with *Taxus*, *Torreya* and *Cephalotaxus*. But soon after the discovery of motile sperms in this genus (HIRASE, 1896), Engler (1897) created a special class, the Ginkgoales for *Ginkgo* and its fossil representatives. By the beginning of the present century the knowledge of three more types of fossil gymnospermous plants had also become sufficiently clear and had led to the establishment of three more classes, the Cordaitales, the Pteridosperms and the Bennettitales. Engler (1897), Coulter & Chamberlain (1917), Engler & Prantl (1926), Rendle (1930) and others all recognize the Gymnosperms as primary division of the Spermatophyta-Phanerogamia or Embryophyta - Siphonogama. They then directly divide the group into classes or orders of co-ordinate rank, viz. (1) Pteridospermae (or Cycadofilicales), (2) Cycadales, (3) Bennettitales, (4) Cordaitales, (5) Ginkgoales, (6) Coniferales, and (7) Gnetales.

In contrast, Berry (1917) divides the gymnospermous plants into the Pteridospermophyta, Cycadophyta and Coniferophyta without classing them as Gymnosperms.

DEVELOPMENT OF PHYLOGENETIC SYSTEMS

In 1919, Sahni (1920) for the first time clearly recognized two main phyletic lines in the orders of the Gymnosperms: (1) the Phyllosperms consisting of (a) the Pteridospermae, (b) the Cycadales and probably (c) the Bennettitales, and (2) the Stachyosperms consisting of (a) the Cordaitales, (b) the Ginkgoales, (c) the Coniferales, and (d) the Taxales (separated from the Coniferales and including *Taxus*, *Torreya* and *Cephalotaxus*). As their names indicate, the ovules of the Phyllosperms are borne on leaves or regarded to be so, while those of the Stachyosperms are believed to be stem-borne[2]. Besides the differences in the nature of the ovule-bearing organs, Sahni

1. The term Spermaphyta which is sometimes used is etymologically incorrect.

2. This difference between the morphological nature of the ovule-bearing organs of Cycads and Conifers was first pointed out by Strasburger (1879).

also pointed out the differences between the generally large and much-divided leaves of the former and the simple leaves of the latter. Subsequently, Margaret Benson (1921) suggested that Sahni's two main lines may have been totally distinct and she associated the Stachyosperms with the Sphenopsida and the Phyllosperms with the ferns.

Almost simultaneously with Sahni, Chamberlain (1920, 1935) also recognized two main groups among the Gymnosperms and called them by the old names Cycadophyta and Coniferophyta. Although the composition of Chamberlain's Cycadophyta is the same as that of Sahni's Phyllosperms and that of his Coniferophyta essentially similar to Sahni's Stachyosperms (except that Chamberlain also includes the Gnetales in the Coniferophyta), yet the emphasis on the primary characteristics in the two classifications is different.

The main basis of Sahni's classification is the morphological nature of the ovule-bearing organs. As Scott (1923) pointed out soon after Sahni proposed his scheme, it was mainly a theoretical distinction for some of the groups, e.g. the Cordaitales, Bennettitales, and Conifers. Schoute (1925), who first showed that the ovule in *Cordaianthus* was attached on a lateral appendage, pointed out that this did not support Sahni's division of the Gymnosperms into the Stachyosperms and the Phyllosperms. Since then Florin's extensive work (1938-45, 1951) on the strobili of both Cordaitales and Conifers has made it abundantly clear that the ovule in both these groups is borne on the lateral appendage of a short axis. Florin does not precisely state the nature of the ovulate organ, but the fact that he often refers to it as a megasporophyll suggests that he regards it as a foliar structure. No doubt he compares it with a telome, but even foliar structures are fundamentally telomes. Eames (1952) has already pointed out that the stachyospermous character of the Cordaitales and the Conifers cannot stand.

Chamberlain (1920, 1935), on the contrary, emphasizes mainly the factual details of the differences in habit, stem anatomy and leaves of the two groups. The names chosen by Chamberlain are also non-committal. Accordingly, despite the slight priority of the names proposed by Sahni some recent authors, e.g. Arnold (1948), Engler, Melchior & Werdermann (1954), have preferred Chamberlain's names[3]. The acceptance of Chamberlain's nomenclature for the two classes of Gymnosperms is, however, not against Sahni's recognition of the two main phyletic lines in this group, only the basis of their distinction is different.

Another feature of Sahni's classification which seems to have come to stay is the separation of *Taxus* and its allied forms from the Coniferales and their inclusion in a new order, the Taxales. Florin (1948) has subsequently upheld Sahni's separation of the Taxales as an order of co-ordinate rank with the Cordaitales, Ginkgoales and Coniferales (restricted), but he includes only *Taxus*, *Torreya* and three other newly discovered genera (*Nothotaxus*, *Amentotaxus* and *Austrotaxus*) in the group retaining *Cephalotaxus* within the Coniferales.

The enigmatic Gnetales have been left out in a doubtful position by Sahni while Chamberlain includes them in the Coniferophyta but without connecting them to the other coniferophytes (*see* CHAMBERLAIN, 1935, p. 4, FIG. 2). Pulle (1938) included them in a separate class, the Chlamydospermae, which is made co-ordinate with his other classes of seed plants, viz. Pteridospermae, Gymnospermae and Angiospermae. The customary inclusion of the three genera *Ephedra*, *Welwitschia* and *Gnetum* in the single order Gnetales has also become questionable in view of the contributions of Pearson (1929), Florin (1931, 1933, 1934), Eames (1952) and others. Arnold (1948) proposed the separation of *Ephedra* in a separate order, the Ephedrales. Eames (1952) goes further and suggests that the Ephedrales are nearest to the Cordaitales and the Coniferales and rather widely separated from *Gnetum* and *Welwitschia*. He also suggests the creation of two separate orders, Gnetales restricted to *Gnetum* and Welwitschiales for *Welwitschia*.

In a new classification of the Gymnosperms, Arnold (1948) suggested that the terms Spermatophyta and Gymnospermae could not indicate natural relationships mainly because they are based on single characters. He emphasized the differences between the Cycadophyta, Coniferophyta and Chlamydospermophyta (Pulle's Chlamydospermae) and in his classification raised them to the

3. Takhtajan (1953), however, retains Sahni's nomenclature and Lam (1950) extends the distinction even into the Angiosperms.

status of classes equal in rank with his Pteridophyta (ferns only) and Angiospermophyta under the division Pteropsida. In addition to the separation of the Ephedrales (*see* above) under his Chlamydospermophyta he accepted the separation of the Taxales under the Coniferophyta. He rejected the names Spermatophyta and Gymnospermae as terms which had " outlived their usefulness ".

EMBERGER'S PREPHANEROGAMS AND PHANEROGAMS

In the meantime, the use of the term Phanerogams (and its counterpart Cryptogams) had automatically fallen in disuse, mainly because it was a misnomer. Coulter & Chamberlain (1903) are against the use of the term because it artificially combines the Gymnosperms with the Angiosperms although actually they are somewhat more closely comparable with the Pteridophytes from which it separates them. However, Emberger (1944) recently reintroduces the term Phanerogamae along with a new name Prephanerogamae to include the Pteridospermae and Cordaitales which have no embryos in their seeds at the time of shedding. According to Emberger, the Prephanerogamae shed only megasporangia wrapped in integuments and not true seeds which, according to this author, should also have embryos at that time. Favre-Duchartre (1943) and Chaudefaud (1944) and others have pointed out that *Ginkgo* and the Cycadales should also be included in the Prephanerogamae because in their seeds too embryos are absent at the time of shedding (this was known long before, e.g. SCHNARF, 1937). Emberger's classification, which is based on a single character, is unnatural because it introduces such anomalies as the separation of Pteridosperms and Cordaitales from the related Cycadophytes and Coniferophytes respectively. It also groups together such dissimilar plants as the Cordaitales and the Pteridosperms. The absence of embryos in the seeds of the two groups merely indicates that their seeds are in the same stage of evolution.

ENGLER, MELCHIOR AND WERDERMANN'S SYSTEM

Engler, Melchior & Werdermann (1954) have suggested yet another classification. They have incorporated some of the features of Arnold's classification, but have introduced the following changes:

1. The name Gymnospermae is reincorporated as a division of the plant kingdom co-ordinate with the Bryophyta, Pteridophyta, Angiospermae and others.
2. Two class names have been changed to Cycadopsida and Coniferopsida, and a new class Taxopsida has been introduced to include the order Taxales.
3. The class name Chlamydospermophyta is changed to Chlamydospermae and instead of dividing it into two orders all the three genera are included in the single order Gnetales as in older classifications.
4. The Caytoniales have been separated from the Pteridospermae and the Nilssoniales from the Cycadales and introduced as distinct orders in the class Cycadopsida.
5. A new order Pentoxylales, including the Pentoxyleae (SRIVASTAVA, 1946; SAHNI, 1948), is incorporated in the Cycadopsida.
6. The Ginkgoales have been shifted from the Coniferopsida and included under Cycadopsida.

While some of the changes, introduced by these authors, may appear justifiable, there are others, e.g. the inclusion of the Ginkgoales under the Cycadopsida, the grouping together of *Ephedra*, *Welwitschia* and *Gnetum* in the order Gnetales and a different ending for the class name Chlamydospermae, which are difficult to understand. Clearly Arnold's classification, though earlier, is more systematic.

A NEW PHYLOGENETIC SCHEME

A modified form of Arnold's classification is, therefore, suggested below. The main changes proposed here are:

1. The names Cycadophyta, Chlamydospermophyta and Coniferophyta are raised to the divisional rank.
2. The endings of the class and order names have been changed to conform with the recommendations of the latest International Code of Botanical Nomenclature, Utrecht (1956).
3. The order Ephedrales has been transferred to the Coniferophyta under Coniferopsida in view of the recent contributions of Florin (1931, 1934) and Eames (1952).
4. A new class Czekanowskiopsida with an order Czekanowskiales is formed for *Czekanowskia* and its nearest allies (HARRIS,

1951b). *Leptostrobus* is indeed very different from any other known Ginkgoalean fructification and together with its deciduous short shoots and forked linear leaves it presents such a unique combination of reproductive and vegetative characters that it would in any case appear preferable to class it separately.

5. The class Chlamydospermophyta including the Gnetales and the Welwitschiales has been placed between the Cycadophyta and Coniferophyta to bring it nearest to the Cycadeoideopsida which the two genera of this class resemble in their syndetocheilic stomata (FLORIN, 1931, 1934) and, if Pearson (1909 & 1929, p. 185) is right, in the character of their "tropophytes".

6. The Pentoxyleae are included under a class Pentoxylopsida under the Cycadophyta. They can for the time being consistently fit in with the present definition of Cycadophyta. Their liana-like polystelic stem structure has been compared with that of *Medullosa* by Stewart & Delevoryas (1956). The form and anatomy of their leaves are typically like those of the Cycadophyta. They also show some apparent resemblances to the male and female fructifications of the Cycadeoideales (MITTRE, 1954).

A brief synopsis of the scheme proposed here is given below:

Division — Cycadophyta
- Class 1 — Pteridospermopsida
  - Order 1 — Lyginopteridales
  - Order 2 — Medullosales
  - Order 3 — Glossopteridales
  - Order 4 — Peltaspermales
  - Order 5 — Corystospermales
  - Order 6 — Caytoniales
- Class 2 — Cycadopsida
  - Order 7 — Cycadales
- Class 3 — Pentoxylopsida
  - Order 8 — Pentoxylales
- Class 4 — Cycadeoideopsida (Bennettitopsida)
  - Order 9 — Cycadeoideales (Bennettitales)

Division — Chlamydospermophyta
- Class 1 — Gnetopsida
  - Order 1 — Gnetales
  - Order 2 — Welwitschiales

Division — Coniferophyta
- Class 1 — Coniferopsida
  - Order 1 — Cordaitales
  - Order 2 — Ginkgoales
- Class 2 — Ephedropsida
  - Order 3 — Coniferales
  - Order 4 — Ephedrales
- Class 3 — Czekanowskiopsida
  - Order 5 — Czekanowskiales
- Class 4 — Taxopsida
  - Order 6 — Taxales

It will be noticed that in the above scheme the Caytoniales are retained within the Pteridospermopsida. Harris (1940, 1951a) has already pointed out that our knowledge of the Caytoniales is far from being complete and all we know about them makes them quite respectable Pteridosperms. Separating them from the other Pteridosperm as done by Engler, Melchior & Werdermann (1954) but retaining the Corystospermaceae (THOMAS, 1933) and forms like *Gnetopsis* and *Calathospermum* (WALTON, 1949) within that group would require a change in our conception of a Pteridosperm itself. It is, however, possible that we have to regroup the Pteridospermopsida and the Cycadopsida at a later date when more is known about them.

The position of *Glossopteris* and *Gangamopteris* (along with some possible allied forms, e.g. *Palaeovittaria* and *Rhabdotaenia*) is at present uncertain. Plumstead (1957) includes them in a new class Glossopteridae and places them between the Angiosperms and the Gymnosperms. Lam (1957) includes them in the Glossopteridales which is made co-ordinate with the Pteridospermales and placed next to them. The leaf-attached fructifications recently described by Plumstead (1952, 1956, 1957) undoubtedly constitute remarkable finds, but none of them so far shows any carbonized incrustation. That they are fructifications of some kind is quite certain, but their interpretation as female, bisexual (or male ?) fructifications, as the discussions at the end of Mrs. Plumstead's papers also show, is largely a matter of conjecture. The nature of the fructifications in the new fertile *Glossopteris*, named *Lidgettonia* by Thomas (1958), is likewise unknown. Fructifications, borne on a slender stalk arising from the rachis (midrib), are already known to occur in the Pteridosperms, e.g. *Diplopteridium teilianum* (WALTON, 1931). Zeiller's *Ottokaria* (ZEILLER, 1902) (with its stalk appearing connected to the midrib of a *Glossopteris* leaf) which assumes additional significance in view of Plumstead's publications also looks like some laterally flattened male fructifications of the Pteridosperms. The microsporangiate discs described by Pant (1957), if they have any connection

with *Glossopteris*, could also be compared with some male fructifications of the Medullosae, e.g. *Potoniea*. The epidermal structure of at least some species of *Glossopteris* (PANT, 1957) has Gymnosperm type of lignine lamellae. These occur in association with gymnosperm-like sporangia containing two-winged pollen grains and seeds containing similar two-winged pollen grains inside their micropyles. Similar-looking sporangia or seeds are found in association with *Glossopteris* in widely separated parts of the Gondwanaland, e.g. Africa, India, Australia and South America. It is, therefore, possible that they belong to *Glossopteris*. The secondary wood and solid-rayed stele of *Vertebraria* (WALTON & WILSON, 1932; PANT, 1956) which is reported to bear *Glossopteris* leaves (ZEILLER, 1896; OLDHAM, 1897) could also suggest a Pteridosperm. Such a *Glossopteris* would resemble the Caytoniales in the venation of its leaves, their general cuticular structure, seeds, two-winged pollen grains and in having bud scales. The mode of attachment of the structures regarded as micro- and mega-sporophylls of the Caytoniales is, however, not known. Moreover, association is weak evidence and it is also possible that these sporangia and seeds belong to some unknown plants whose other parts were not preserved. A number of fructifications have been attributed to *Glossopteris* from time to time on the evidence of association and it could even be that the form genus *Glossopteris* may include leaves of diverse plants. Till recently, out of the only two known cuticles of *Glossopteris*, the cuticle of the African leaf assigned to *G. indica* by Zeiller (1896) with its thick straight-walled cells appeared markedly different from that of the Indian leaf attributed to *G. angustifolia* by Sahni (1923). The author's study of some African leaves, however, suggests that thick-walled cells and stomata like those of Zeiller's *G. indica* can occur, e.g. over the midrib of *G. fibrosa* whose stomata and epidermal cells over the lamina are somewhat comparable to those of Sahni's *G. angustifolia*. The work of Srivastava (1956) and Surange & Srivastava (1956), no doubt, suggests generic differences within the leaf forms *Glossopteris* and *Gangamopteris* but they suggest that such genera must have been closely related.

Therefore, until more favourable attached fructifications are found, it would involve fewer difficulties if we retained the Glossopteridae or Glossopteridales in the Pteridospermopsida instead of putting them in the spectacular position between the Gymnosperms and the Angiosperms.

Even otherwise the classification suggested above, as all classifications must be, is a tentative one. It will have to be modified as our knowledge of the Gymnosperms progresses. It does not assign any position to the more incompletely known fossil form genera attributed to the Gymnosperms. For these a *status quo* can be maintained until we know more about them. And finally the name "Gymnosperms", although ousted from its traditional position in a natural classification, will, however, continue to be used as a common designation for all naked-seeded plants. Even phylogenetically the name can serve to indicate the naked-seeded level in the evolution of the higher plants.

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