

THE DESCENT OF THE FLOWERING PLANTS IN THE LIGHT OF NEW EVIDENCE FROM PHYTOCHEMISTRY AND FROM OTHER SOURCES

II SUGGESTIONS FOR A HOLOTAXONOMIC MAJOR CLASSIFICATION

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SUMMARY

In this second and final part suggestions are made towards a holotaxonomic major classification of the Angiosperms based on a pleiophyletic origin.

4. POSSIBLE PARALLELISMS AND CONVERGENCIES

Parallelisms and convergent evolution of characters during the phylogeny of the Angiosperms may be anticipated, but there is apparently a concensus of opinion concerning a homology of occurrence of the phytochemical features mentioned sub. 2.1. Analogies among morphological characteristics are not so troublesome if considerable numbers of characters are taken into account (as in Huber's extensive compilations of the *Rosiflorae* and the *Liliiflorae*). In other instances one can not always decide one way or the other. The occurrence of obdiplostemony in several orders may be the outcome of a parallelism, but I have my own ideas concerning the origin of this condition and believe it to be more clearly indicative of taxonomic affinity between major taxa than is usually assumed. Certain morphological characters which are clearly 'adaptive', such as may peculiarities of seed and fruit (e.g., dry or fleshy, dehiscent or indehiscent, one-seeded or many-seeded fruits), methods of dispersal (associated with, e.g., the presence of edible parts of the fruit or of seed appendages), and perhaps also hypogyny, are of course suspect. The remarkable correlation between the special environment and the occurrence of trinucleate pollen grains in a number of predominantly aquatic taxa (all *Helobiae*, *Lemnaceae*, *Hippuridaceae*, *Callitrichaceae*) may be attributed to a convergence, but would, in any event, cast some doubt on the primitive status assigned to the *Helobiae* by a number of taxonomists. Some general "trends", such as the reduction of the number of stamens, zygomorphy, the complete loss of the aril (or of arilloid structures), and of course sympetaly, are more likely to have developed convergently than otherwise (zygomorphy and sympetaly occur in both Dicots and Monocots).

The characters used as taxonomic pointers in the paragraphs 5–7 are carefully chosen so as to avoid this kind of difficulty. Relationships between orders suspected by the present author, if not more or less generally accepted by phanerogamists, are based on “overall similarity” apart from the more demonstrative (*e.g.*, chemical) evidence.

5. MAJOR GROUPS AND LINEAGES

The conventional classification of the Flowering Plants in two major taxa, the Monocotyledons and the Dicotyledons, does not agree well with the natural affinities of some of their subordinate groups. Relationships between certain monocotyledonous groups and certain dicotyledonous groups may be closer than those within the various monocotyledonous or the various dicotyledonous groups, respectively. There are a number of indications of a relationship between early *Dioscoreales* (and hence: the *Liliiflorae*) and the precursors of certain (or of all) ranalean groups, whereas the *Helobiae* are very isolated even in respect of the liliiflorous orders (HUBER 1969). A dismemberment of the two major angiospermous groups is ultimately unavoidable. In a previous forecast of a system (MEEUSE 1965, Chapter XIV) a number of evolutionary lines was postulated, and there is every reason to maintain this principle. Huber’s analysis of the liliiflorous assembly did not reveal a close affinity between this large taxon and, for instance, palms. An “early” separation of a liliiflorous line from a spadiciflorous-pandanalean one, as I assumed in 1965 (*fig. 20* on p. 186) may not even be sufficiently conformable to Huber’s findings, but at least two lineages must have existed side by side for a long time.

In the Dicots the number of lineages may be even greater, but the large ranalean assembly essentially is *not* the “basic” (or at least “most primitive”) group of all dicotyledonous (or even all angiospermous) groups as is so often assumed and is clearly reflected in the majority of the current systems of classification, see, *e.g.*, TAKHTAJAN (1959, 1969), SOÓ (1967) who enumerates several other examples, CRONQUIST (1968), THORNE (1968), LANJOUW *c.s.* (1968). KUBITZKI (1969) pointed out some rather fundamental differences between the androecial morphology of *Polycarpicae* and *Dilleniales*, quoting several authorities (such as Melchior and Hegnauer) who had previously expressed similar views concerning their relationships. Kubitzki postulated their early divergence, and on the basis of mainly phytochemical evidence considered the ‘*Ranales*-branch’ to be a dead-end lineage. However, this is, I believe, not so strictly true as Kubitzki suggests. Several workers, such as HALLIER (1912) and HEGNAUER (for a discussion, see NOOTEBOOM 1966), pointed out that there are clear indications of a taxonomic affinity between *Ranunculales* and *Rutaceae*, especially the presence of certain alkaloid types being considered to be rather significant. Several workers (HUBER 1963, HEGNAUER on several occasions, *e.g.*, in HARBORNE & SWAIN 1969), have also pointed out that there are other likely relations linking the *Rutales* and the *Pittosporales* with the *Umbelliferae* and *Araliaceae*, and possibly even the *Compositae*. The overall similarities do not

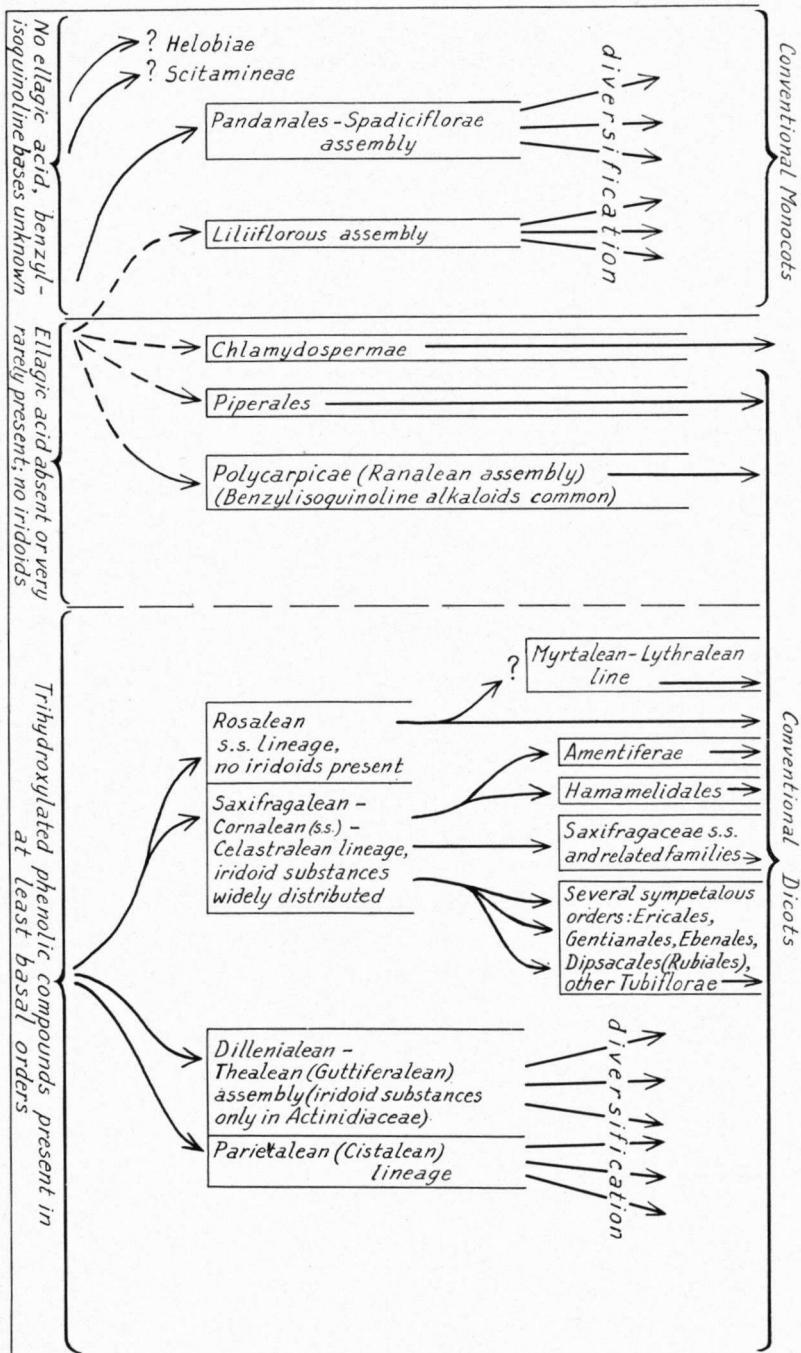


Fig. 1. Diagrammatic representation of the putative major evolutionary lines of the Angiosperms. (Centrospermae omitted).

plead against these assumptions, on the contrary: Huber's detailed analysis points quite clearly to a relation between *Araliaceae* plus *Umbelliferae* (which families are *not* associated with the iridoid-containing *Cornaceae* and other "Cornales") and the *Pittosporaceae*. The chemical similarities between these groups I regard, with Hegnauer, as highly convincing; and the "negative" pointers, *i.e.*, the absence of ellagic acid in *Rutaceae*, *Araliaceae* and *Umbelliferae* and the absence of iridoid substances, as well as some positive ones: the presence of coumarins in a number of these families including *Rutaceae* and *Compositae*, and the presence of acetylenic compounds in *Araliales* and *Asterales*, knit these taxa together (compare HEGNAUER 1964, p. 544, fig. 29, and in HARBORNE & SWAIN 1969, p. 132, fig. 2).

In several respects the *Centrospermae* are rather isolated and this is reflected in several classifications of the Angiosperms. A long independent existence of this group is postulated by, *e.g.*, MEEUSE (1965) and Kubitzki. Phytochemical pointers are the absence of ellagic acid, iridoid compounds and characteristic alkaloids.

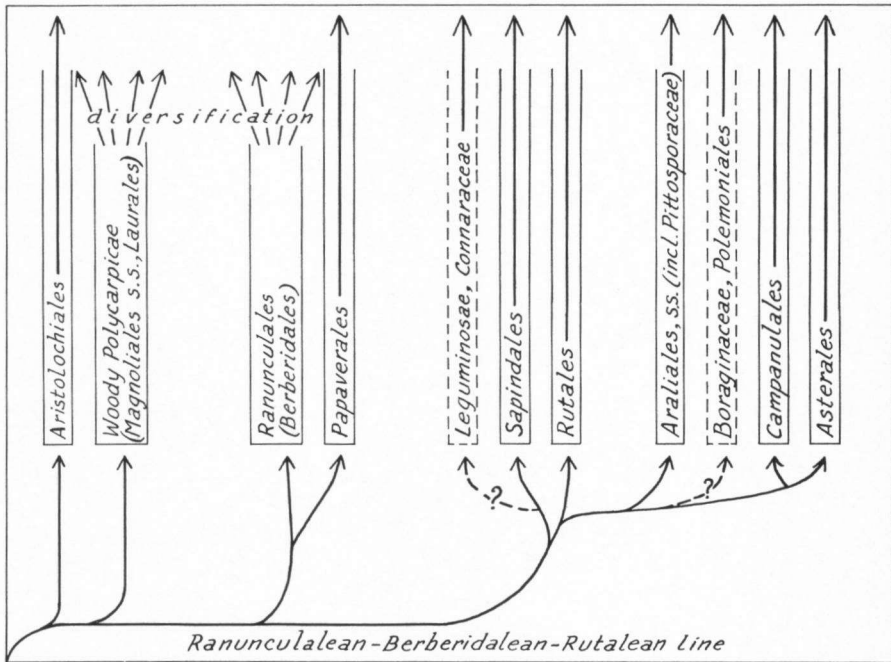


Fig. 2. Putative relationships in the *Polycarpicae* and their probable derivatives.

N.B. "Woody Polycarpicae" include *Magnoliaceae* s.l., *Winteraceae*, *Iliciaceae*, *Schizandraceae*, *Trochodendrales*, *Annonaceae*, *Myristicaceae*, *Laurales*, and a number of small associated families; "Ranunculalean-Berberidalean assembly" includes *Berberidaceae*, *Lardizabalaceae*, *Menispermaceae*, *Ranunculaceae*, *Nelumbonaceae* and a few associated taxa. — Position of *Nymphaeales* s.s. (not included) more or less dubious on account of presence of ellagitannins.

A major lineage, considered to be a kind of counterpart of the ranalean assembly and not directly derived from it, includes the rather heterogeneous *Rosiflorae*, the *Guttiferales* and the *Parietales*. Huber has pointed out that the conventional rosalean assembly includes several groups which are not necessarily closely related and the phytochemical patterns bear this out. There is one line which includes the *Cornales* in a restricted sense, with a general representation of iridoid substances and this line is believed to be close to the guttiferalean-dillenialean and to have led to a number of sympetalous orders also rich in iridoid and related constituents: *Ericales*, *Styracales* (*Ebenales*), *Gentianales*, *Rubiales*, *Dipsacales*, *Tubiflorae*, *Plantaginales*. The *Celastrales* also belong here or are at least related (Huber includes the *Aquifoliaceae*, often referred to *Celastrales*, in the *Cornales* s.s.; at least one genus of the celastralean *Icacinaceae* contains iridoids) and may have relations with the *Primulales*. The same, or more probably an early divergent, evolutionary line led to the *Hamamelidales* (phytochemically related to saxifragaceous-rosaceous groups: JAY 1968) and the *Amentiflorae*, another (or several) to noniridoid families such as *Saxifragaceae* s.s., *Rosaceae*, *Chrysobalanaceae* and perhaps the *Leguminosae*.

The remaining major branch, the dillenialean-guttiferalean-parietalean nexus, and a number of presumably derived taxa (*Myrtales*, *Malvales*, *Violales*, *Capparidales*, *Passiflorales*, etc.) must be regarded as a predominantly choripetalous assembly characterised by the almost complete absence of the iridoids and, upon the whole, general occurrence of ellagic acid. A close relation with one of the previous lines is suggested by the relation *Actinidiaceae* - *Ericales* and the occurrence of aucubin-like glycosides in *Actinidia*.

6. TAXONOMIC POSITION OF SOME SMALLER GROUPS

A number of characters render the following taxonomic conclusions highly probable:

Araliaceae and *Umbelliferae*, as previously discussed, are related to *Rutales* and belong in the *Ranales* → *Rutales* → *Araliales* → *Asterales* lineage, together with *Pittosporaceae* and *Campanulales*.

Sapindales may be associated with the *Rutales* and would, in this case, point to the possible independent origin of *Leguminosae* and *Rosaceae*. *Connaraceae* and *Sapindales* are approximate according to Huber. *Boraginaceae* may be related to *Compositae* at least according to their phytochemical patterns; if this relation is accepted the *Boraginaceae* (and possibly all the non-iridoid *Polemoniales*) developed independently of the majority of the tubiflorous *Sympetalae*.

Papaverales are close to *Ranunculales* s.s. (*Berberidales*), but the remainder of the old *Rhoeadales* (= *Capparidales sensu* Takhtajan) is allied to the *Cistales* (*Parietales*).

The order *Nymphaeales*, in the usual circumscription, is heterogeneous in that the family *Nelumbonaceae* (the genus *Nelumbo*) is rather aberrant and, if not

far removed, only distantly related to *Cabombaceae*, *Ceratophyllaceae* and *Nymphaeaceae*. *Nelumbo* deviates in morphological, palynological and chemical respects and shows affinities with the *Polycarpicae* by the presence of proaporphin- and aporphin-type isoquinoline alkaloids. BATE-SMITH (1968a) believes that the non-alkaloid and ellagic acid-containing family *Nymphaeaceae* is out of place in the order *Polycarpicae*. I dare not suggest a "better" place for the *Nymphaeales* s.s. (minus the *Nelumbonales*), but their independent origin in respect of the ranalean assembly is highly probable.

The name "*Cornales*" should henceforth be applied in a restricted sense to a group of families without the *Araiales* s.s. and according to Huber including (apart from *Cornaceae*) *Escalloniaceae*, *Philadelphaceae* (but not *Grossulariaceae* and *Saxifragaceae* s.s.!), *Styraceae*, *Symplocaceae*, *Aquifoliaceae* and *Diapensiaceae*. This is in reasonably good agreement with the chemodiagnostic characters (the presence of aucubin and related substances), but it is for this reason perhaps better to exclude the conventionally ebenaceous families (and also the presumably ericaceous *Diapensiaceae*?) and to include *Garryaceae* (aucubin present) and *Alangiaceae* (iridoid heterosides also present). The relationships with *Ericales* and (some) *Ebenales* are, in any event, quite close.

The position of the *Geraniales* is not clear, but the absence of alkaloids and the presence of trihydroxylated phenolic compounds render a direct relationship with *Ranales-Rutales* rather improbable.

7. GENERAL PICTURE AND SOME DETAILS OF THE HOLOTAXONOMIC CLASSIFICATION

The major lineages are tentatively depicted here (see *figs. 1* and *2*) as leading to Monocotyledons (at least two or three, one of them fairly close to proranalean orders), to *Piperales* and ranalean orders, and to a group of lines leading to rosalean-hamamelidalean, cornalean-saxifragalean and dillenialean-guttiferalean (clusialean, thealean) and parietalean (cistalean) assemblies. "Independent", or at least dubious, lines of descent leading to *Helobiae*, *Nymphaeales* s.s., *Centrospermae* and perhaps *Scitamineae* are disregarded here.

The relative age of origin of these lineages as independent phylogenetic sequences is of course quite conjectural and is not considered. In a diagrammatic representation we must of course place the lineages of closest affinity next to one another (see *fig. 1*). Some contrasting phytochemical characteristics are shown.

Of the individual lineages several are sufficiently shown in essential detail in *fig. 1*, but an exception must be made for the *Polycarpicae* and their putative derivatives (see *fig. 2*; this dendrogram is in so far fictitious that the "branching-off" of the various groups is mere guesswork although it is based on an assessment of their overall similarities).

The conclusions agree in several essential respects with those of Hegnauer (see under 5) and of KUBITZKI (1969, p. 366, Abb. 4) concerning the major dismemberment of the Dicots, but there are also some discrepancies, especially

with regard to the ranalean branch. Although new evidence may change the overall picture in details, the early divergence of at least three or four phylogenetic lines seems to me to be firmly established.

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