

FUNGI AS PLANT TAXONOMISTS II. AFFINITIES OF THE ROSIFLORAE

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SUMMARY

Relationships inside and outside the Rosiflorae are discussed relying upon the evidence presented by the distribution of a number of parasitic fungi. Results are compared with the system of DAHLGREN (1975, 1980). Redispositions for Vitidaceae, Chrysobalanaceae and Leguminosae are suggested.

1. INTRODUCTION

The use of host-parasite data with respect to taxonomy and evolution of higher plants we owe for the greater part to D. B. O. Savile. He published a respectable number of papers on this subject, culminating in the comprehensive treatise presented in the *Botanical Review* (SAVILE 1979).

However, when writing about coevolution of plants and parasites and its relation to phylogeny the impression is obtained, that the system is very reticulate, with rather short lines of descent connecting superorders, orders and families. In other words primary diversification was very rapid. The time required for the formation of the higher categories seems to have been much shorter than the period necessary for the evolution of the categories below the level of the family. Evolution was apparently preceded by a revolution. And, unless it might be possible to determine the exact positions of the basic orders and families, e.g. by determining enzyme amino acid sequences (BOULTER 1976), the phylogeny of higher plants will be a matter of everlasting conjecture of opinions.

Host-parasite data suggest plants with apetalous flowers to be most primitive. Hypertrophy-causing species of the genus *Taphrina*, being perhaps the oldest biotrophic parasites of Angiosperms, are reported mainly from families with apetalous (or greenish) flowers in temperate, often mountainous, regions (MIX 1949; SAVILE 1971). Hypertrophy-causing leaf parasites of the genus *Lambro* are reported from *Ulmus*, *Sterculia* and Proteaceae (MÜLLER & VON ARX 1962), all plants with an uniseriate perianth, albeit petaloid in Proteaceae and sepaloid in *Ulmus* and *Sterculia*. This genus seems to be most closely related to the monotypic genus *Bagcheea*, parasitic on *Castanopsis* species (KATUMOTO 1965), whereas the genus *Mamiania/Mamianella*, which also causes hypertrophy, infects leaves of *Alnus*, *Carpinus* and *Corylus* (MÜLLER & VON ARX 1962). It is very tempting to assume that the three fungal genera had a common ancestor infecting plants with apetalous flowers. Also SAVILE (1979) concluded, from rust data, that the petalous Hamamelidaceae are more recent than the apetalous Fagales. He

argues too that the predominantly entomophilous genus *Salix* arose from the fully anemophilous genus *Populus*. However, he was obviously reluctant to assume that plants with apetalous flowers preceded those with petalous flowers which would have been a logical and consequent conclusion.

Recently HUBER (1963), using anatomical characters, discussed the circumscription and affinities of the Rosiflorae. Concluding from the distribution of host-pathogen combinations rather close connections exist between Magnoliflorae and Rosiflorae. Remarkably enough not one species of *Taphrina* has been recorded from Magnoliflorae, thus posing the question whether or not Magnoliflorae can be regarded as the most primitive of living Angiosperms. They might have evolved later, but have retained more primitive characters due to early polyploidy, that has retarded evolution (RAVEN 1975).

Many orders e.g. Urticales, Malvales, Hamamelidales, Myrtales, Proteales could be derived from the ancestry of primitive Rosiflorae. So Rosiflorae could have a more central position than is usually accepted. Perhaps the genera *Trochodendron*, *Tetracenton*, *Cercidiphyllum* and *Euptelea* with a simple perianth, free carpels, *ab initio* cellular endosperm and simple structure of the wood (DAHLGREN 1975), usually included in Magnoliflorae, but united into the order Trochodendrales and transferred to Rosiflorae by DAHLGREN (1980), can be regarded as the most primitive of extant Angiosperms.

In many instances no complete coevolution can be accepted, but it must be assumed, that in any case a definite set of genes was present, which was not present in other groups of plants. We deal with a combination of coevolution and nearby jumps. If this was not the case we would be dealing with a character that could be blown off and on by the wind, which would lead to taxonomically meaningless conclusions.

Seimatosporium kriegerianum, for example, has been reported from Onagraceae in Europe, whereas *S. kriegerianum* together with other *Seimatosporium* species has been reported from Myrtaceae in Australia. The perfect state of *S. kriegerianum* (*Discostromopsis callistemonis* Swart) has only been reported from Australia. This strongly suggests, that *S. kriegerianum* together with related species coevolved with Myrtaceae in Australia and jumped to Onagraceae, which possessed the gene for compatibility. Numerous examples of this phenomenon exist (HIJWEGEN 1979).

It should be emphasized, that more related families may be susceptible to informative parasites than is known, because they do not harbour them due to inappropriate ecological and geographical conditions. Also numerous indicative pathogens still may have to be discovered. The ecological requirements of a host-parasite combination (a pathosystem) are usually much more delicate and the range of existence is more limited than are the ranges of plant and pathogen separately. The most meaningful correlations and also the most numerous are found between plants with apetalous flowers in temperate or subtropical regions of the Northern Hemisphere, especially in East Asia, the presumed centre of origin of the Angiosperms (TAKHTAJAN 1973). Consequently, it may be assumed that these pathosystems arose in a population of primitive plants with apetalous

flowers in mountainous regions. In the families, that migrated to more tropical climates the original pathogens evolved or more commonly disappeared and were replaced by new ones, as the conditions were not suitable enough for the survival of the original plant-pathogen combination.

In general very little can be said about families with a typical Southern distribution (e.g. Proteaceae, Melastomataceae) especially with respect to South-American members. It seems probable that many of their pathogens in any case did not coevolve with their host plants. Many of these families seem to act as "collectors", that is to say: they possess the gene for compatibility (HIJWEGEN 1979) but evolved remote from the centre of evolution and diversification of the fungi and subsequently collected members of most fungal genera, of a certain line of development, that evolved on other plant families.

2. RELATIONSHIPS

As already noticed by HUBER (1963) it is rather difficult to subdivide the Rosiflorae and the groups allied to them on the basis of morphology. The same applies to subdivisions made on the basis of host-parasite combinations. Nevertheless, this will be tried in the following.

Rosiflorae is here accepted to have the wide circumscription given by HUBER (1963). Later on this group has been distributed by DAHLGREN (1975) over four superorders: Rosiflorae, Hamamelidiflorae, Saxifragiflorae and Corniflorae (to which also Ericales were added).

Judging from host-parasite distributions the four groups are basically related, but strongly diverging and thus favouring a position of primitiveness. DAHLGREN's most recent suggestion (1980) to unite the first three groups again into Rosiflorae, under the addition of Myricales and Juglandales, and to exclude Fabiflorae seems to be the most acceptable from the viewpoint of host-parasite distribution.

Cronartium species with filiform teleutopores are reported from *Myrica*, Fagaceae and *Ribes* (ARTHUR 1934), whereas higher evolved genera of this line (Phragmidiaceae sensu SAVILE 1979) are almost confined to Rosaceae s.s. The fact, that the rusts of Rosaceae have the highest level of evolution underlines HUBER's (1963) contention, that they are very separate and diverging from other Rosiflorae.

The genus *Chrysomyxa*, related to *Cronartium* inhabits Ericaceae, Pyrolaceae, *Empetrum* and *Ilex* (Aquifoliaceae, recently placed in Cornales: DAHLGREN 1980). On the other hand leaf parasites of the genus *Protoventuria* (Syn. *Antennularia*) (South American species excluded) are reported from Ericales, Aquifoliaceae, *Rosa*, *Ribes* and, in North America, *Quercus*. (This could be a jump since the characteristic genus inhabiting *Quercus* is the related genus *Acantharia* of eastern Asia and northern America: MÜLLER & VON ARX 1962, BARR 1968.)

Other parasites, which will certainly be jumps, common to both superorders are aecidia of *Gymnosporangium* species reported from *Myrica*, Malaceae, *Fendlera* and *Philadelphus* (Hydrangeaceae) (LEPPIK 1956). The same applies to

aecidia of bamboo *Puccinia's* reported from *Deutzia* (Hydrangeaceae) (CUMMINS 1971), *Hamamelis* (SAVILE 1979) and *Corylopsis* (CUMMINS 1971) (both Hamamelidaceae) (fig. 1).

Hence, when host parasite distributions are taken into account, it can be concluded, that the two superorders are basically related (as accepted in the Engler system) but strongly diverging (as acknowledged in newer systems). Conspicuous is the rather large number of apetalous plant species in both superorders: Myricales, Fagales, Buxales, Trochodendrales in Rosiflorae and *Eucommia*, *Davidia* and *Garrya* in Corniflorae thus strengthening a basic position.

Myrtales seem to be close to Rosales: The powdery mildew species *Sphaerotheca macularis*, parasitic to many Rosaceae s.s., is reported to attack also introduced *Eucalyptus* (BLUMER 1967). *S. pannosa*, a typical rose parasite also infects *Punica granatum* in Greece (PANTIDOU 1973) whereas the related *S. epilobii* is parasitic to *Epilobium* species (Onagraceae) (BLUMER 1967).

The genus *Discostromopsis* is parasitic on Myrtaceae in Australia (SWART 1979) whereas most species of the related genus *Discostroma* are both parasites and saprobes on Rosaceae. Conspicuously *Epilobium*, of Myrtalean affinity, but geographically associated with Rosaceae is affected by the parasitic *Seimatosporium kriegermanum* (conidial state of *Discostromopsis callistemonis*) as well as by the saprophytic *Discostroma tostum* (BROCKMANN 1976). The two biotrophic species of the genus *Thrauste* are parasitic to *Pygeum* (Amygdalaceae) and *Medinilla* (Melastomaceae) (HANSFORD 1946). Moreover, there are many similarities between seed-coat structures of Hamamelidaceae, Rosaceae, Myrtaceae and Melastomaceae (CORNER 1976).

Connections between Urticales and Fagales are numerous. Thus the question arises whether Betulaceae is one of the basic families in Rosiflorae, whereas Ulmaceae could be the basic family in Urticales-Malvales. This might reconcile the controversy whether or not Urticales should be closer to Hamamelidales or to Malvales.

The powdery mildew genus *Cystotheca* has only been reported from *Celtis* and Fagaceae (HIRATA 1966). Species of the genus *Prosthegium* inhabit branches of Betulaceae, *Ulmus*, *Platanus*, *Acer* and *Populus* (WEHMEYER 1941) (fig. 2).

Platychora infects *Ulmus* (Ulmaceae) and *Alnus* (Betulaceae) (MÜLLER & VON ARX 1962). *Platychora's* nearest relative seems to be the hypertrophy-causing monotypic genus *Crotone* on *Drimys* (Winteraceae) (MÜLLER & VON ARX 1962), suggesting that the three families represent parallel evolutionary lines from very primitive Angiosperms.

Further connections with Magnoliflorae are the rust genera *Xenostele* on Lauraceae and Hamamelidaceae (SAVILE 1979), and *Melampsorium* on Magnoliaceae and Betulaceae, though the latter connection was considered to be non-indicative by SAVILE (1979).

Uncinula clintonii infects *Aphananthe*, *Celtis*, *Zelkova* (Ulmaceae), *Tilia* (Tiliaceae) and *Firmiana* (Sterculiaceae) (HIRATA 1966). *Perisporiopsis cecropiae* on *Cecropia peltata* (Moraceae) has a variety *sterculiae* on *Sterculia caribaea* (MÜL-

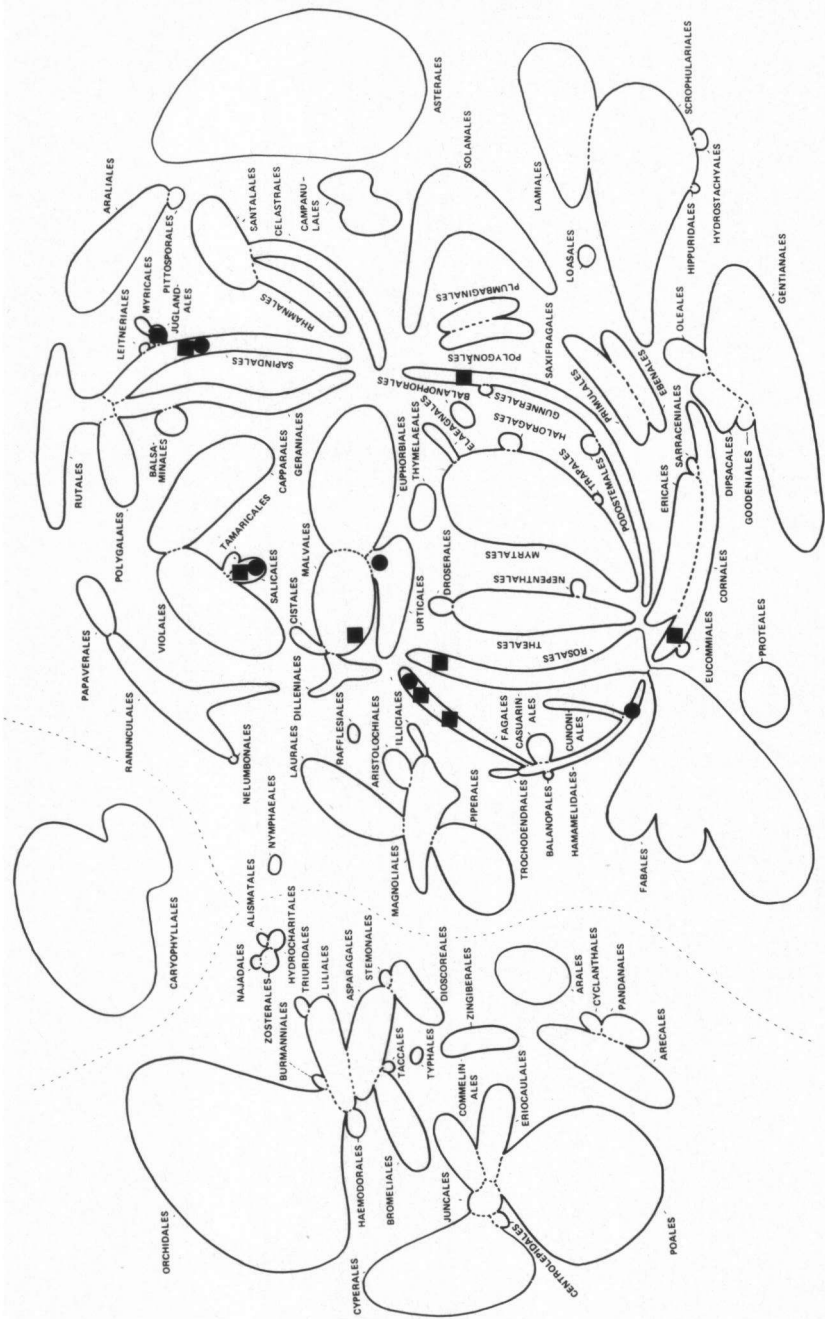


Fig. 2. Occurrence of species of *Prosthecium* ● and *Melanconis* ■ in the Plant Kingdom.

LER & VON ARX 1962), thus connecting Urticales and Malvales in accordance with DAHLGREN's positioning (1975, 1980).

Euphorbiaceae have many pathogens, it may be a "collector".

However, parasites provide very little evidence for the connection between Euphorbiales and Urticales, unless the rather polyphagous *Uncinula miyabei*, reported from Euphorbiaceae, Moraceae, Ulmaceae, Tiliaceae, but also from *Alnus* (HIRATA 1966) can be accepted as indicative. The overall distribution suggests, that they are closer to Geraniales-Rutales-Sapindales, in accordance with old Englerian concepts, than to Malvales.

The distribution of the bitypic genus *Parmulina* on Euphorbiaceae and Daphniphyllaceae is an argument in favour of placing Daphniphyllaceae close to Euphorbiaceae contrary to DAHLGREN's (1980) opinion.

Also Salicaceae seem to have a position near Urticales. The most characteristic parasites of Salicaceae are heteroecious rusts of the genus *Melampsora* (GÄUMANN 1959). These rusts have aecidial stages on Pinaceae and various Angiosperms. *M. magnusiana* (with uredia and telia on *Populus* in Europe) and *M. yezoensis* (with uredia and telia on *Salix* in Japan) produce their aecidia on *Corydalis* (Fumariaceae). *Dicentra* (Fumariaceae) harbours the aecidial stage of *Cerotelium dicentrae* with uredia and telia on *Urticastrum* (Urticaceae) (ARTHUR 1934). Most, but not all, *Cerotelium* species are parasitic to members of the Urticales and Malvales, whereas the related genus *Phakopsora* has most of its species on Euphorbiaceae. Probably, *Melampsora* and *Cerotelium* represent two parallel evolutionary lines on two related groups. It is interesting to note that one species of *Melampsora* is reported from *Idesia* (Flacourtiaceae) (HOLM 1969). BERG (1977) indeed assumes Flacourtiaceae to be not too distantly related to Urticales.

Moreover, many species of *Salix* and *Populus* are susceptible to species of the powdery mildew genus *Uncinula*, which is especially abundant on Urticales and Malvales. Most evolved species of *Uncinula* are harboured by the genus *Celtis* (Ulmaceae) (recently segregated as the genus *Pleochaeta* (KIMBROUGH & KORF 1963)) and *Acer* (genus *Sawadaea*: see BLUMER 1967).

Various other pathogens also suggest *Acer* to have a position rather close to Urticales – Malvales e.g. *Prostheccium* on *Acer*, *Ulmus*, *Populus*, *Platanus* and Betulaceae (fig. 2). This is further corroborated by similarities in cytochrome c amino acid sequences between *Acer* and Malvaceae (BOULTER 1976, BROWN & BOULTER 1974, THOMPSON et al. 1971).

Despite the numerous data "Vitidaceae, by their combination of common attributes, are difficult to place" (DAHLGREN 1980). Like many Magnoliiflorae it has P-I type sieve-element plastids (BEHNKE & DAHLGREN 1976) and very primitive seeds, resembling those of Dilleniaceae, with which it was associated by CORNER (1976). It shares species of the genus *Rhytidenglerula* (with one-celled conidia), with Dilleniaceae, Ulmaceae, Connaraceae, Euphorbiaceae and Lauraceae (MÜLLER & VON ARX 1962). It is remarkable, though possibly not significant, that *Rhytidenglerula* is reported from families from which also P-I type sieve-element plastids have been reported with two exceptions: Dilleniaceae and

Connaraceae. Perhaps this strengthens the "primitiveness" of both characters.

Vitidaceae share the rust genus *Pucciniostele* with Saxifragaceae and the rust genus *Skierka* with Sapindaceae, Rutaceae, Burseraceae and Euphorbiaceae (fig. 3). Most species of the rust genus *Physopella*, related to *Cerotelium* and *Phakopsora*, inhabit grasses and Sympetalae, but three species infect Vitidaceae, *Meliosma* and *Alchornea* (Euphorbiaceae) respectively (CUMMINS & RAMACHAR 1958). Species of the rust genus *Goplana* are harboured by *Michelia*, *Meliosma* and *Cissus* (Vitidaceae) (SAVILE 1979). BEHNKE (1977), following JOHNSTON (1974) referred Vitidaceae to Saxifragales.

The overall distribution of characters suggests a position not too far removed from Magnoliflorae, perhaps linking Saxifragales and Rutiflorae or at the basis of Sapindales, anyway separated from Rhamnaceae and Celastraceae.

The genus *Englerula* has host plants in Euphorbiaceae-Crotonoideae, Sapindaceae, Burseraceae, Anacardiaceae and occurs also on *Parinari* (Chrysobalanaceae) (MÜLLER & VON ARX 1962) (fig. 4). This raises an interesting question: Chrysobalanaceae have been shifted between Rosaceae and Leguminosae; *Krameria* was originally included in Leguminosae but in recent systems transferred to Polygalaceae. HUBER (1963) pointed out the similarities between the wood structure of Chrysobalanaceae and part of the Polygalaceae, whereas the wood structure of Leguminosae seems to have much in common with that of Sapindaceae. The bitypic genus *Phaechorella* is parasitic to Leguminosae and Chrysobalanaceae (VON ARX & MÜLLER 1954).

The Ascomycete *Asterolibertia couepiae* has been reported from *Couepia* species (Chrysobalanaceae) and a *Heteropteris* species (Malpighiaceae), whereas *A. bredemeyerae* infects *Bredemeyera* (Polygalaceae) and *Sweetia* (Leguminosae) (MÜLLER & VON ARX 1962). This suggests a position close to Rutiflorae for both Chrysobalanaceae and Leguminosae, with Leguminosae somewhere halfway between Rutiflorae and Magnoliflorae, as they have also parasites in common with Annonaceae, Berberidaceae and Menispermaceae. The other 12 species of *Asterolibertia* mentioned by MÜLLER & VON ARX (1962) are distributed as follows: Chrysobalanaceae (2), Leguminosae (1), Anacardiaceae (1), Burseraceae (1), Lauraceae (1), Rubiaceae (4), polyphagous, (among which are Chrysobalanaceae and Malpighiaceae) (2), so a bipartite distribution with most species on the "enlarged" Rutiflorae.

Two other characters also have a bipartite distribution namely

- a. acedial stages of *Puccinia andropogonis* reported from Leguminosae, Polygalaceae, Oxalidaceae and Rutaceae on the one hand and Scrophulariaceae and Santalaceae (possibly related to the Sympetalae: DAHLGREN 1980) on the other (fig. 4).
- b. Amyloids are reported from Annonaceae, Leguminosae, Oxalidaceae, Sapindaceae, Melianthaceae on the one hand and *Paeonia*, Balsaminaceae, *Tropaeolum*, Primulales, Sapotaceae and Acanthaceae (KOOIMAN 1959) on the other.

This "enlarged" Rutiflorae also include the hosts of most species of Raveneliaceae, thus giving support to the removal of Leguminosae from Rosales to a

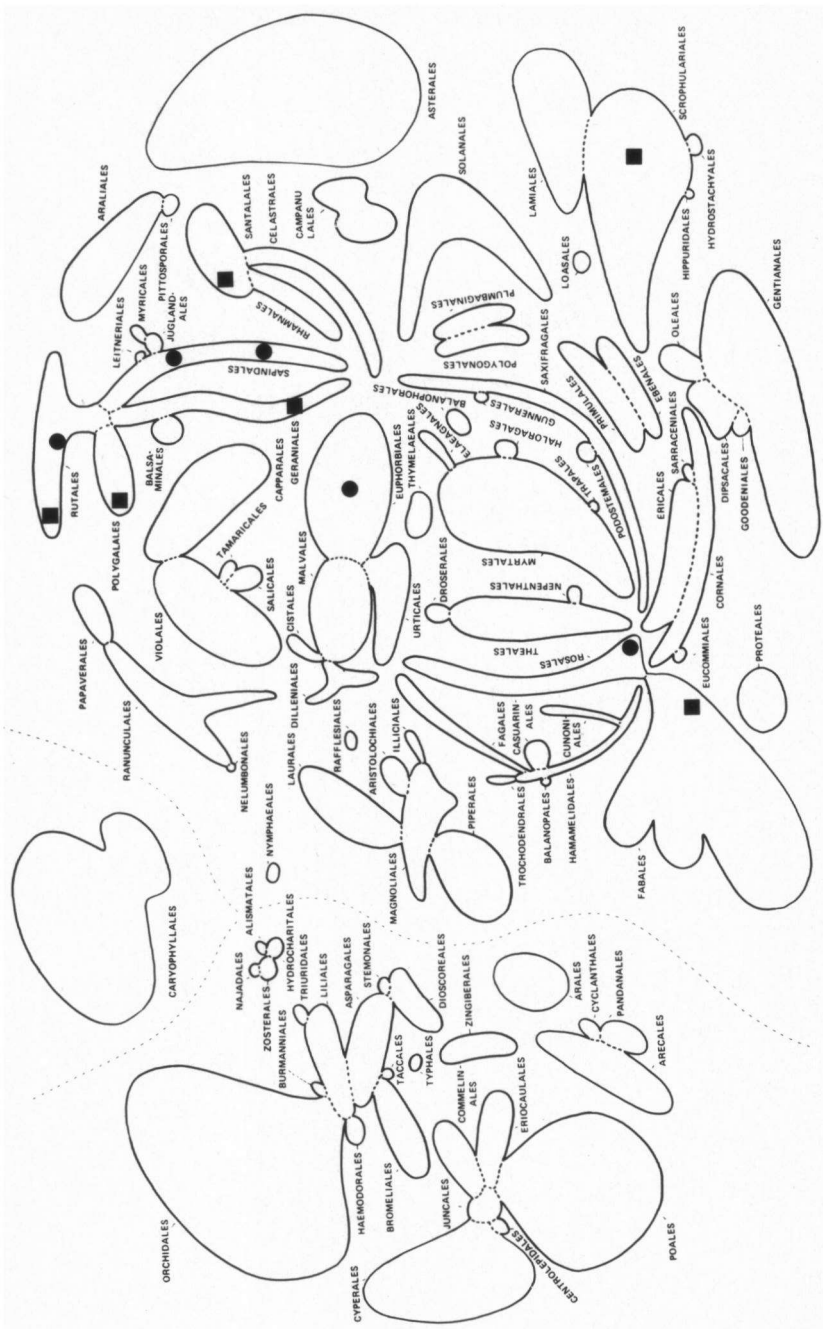


Fig. 4. Distribution of *Englerula* ● and acedial stages of *Puccinia androgonidis* ■ in the Dicotyledons.

Table 1. Distribution of some fungi on Angiospermae.

Genera (and species) of Fungi	Families of Angiospermae
<i>Asterolibertia couepiae</i>	Malpighiaceae, Chrysobalanaceae
<i>A. bredemeyerae</i>	Polygalaceae, Leguminosae
<i>Bagcheea</i>	Fagaceae
<i>Cerotelium dicentrae</i> , aecidia	Fumariaceae
<i>Chrysomyxa</i>	Ericaceae, Pyrolaceae, Empetraceae, Aquifoliaceae
<i>Cronartium</i> , pro parte	Fagaceae, Myricaceae, Ribesiaceae
<i>Crotone</i>	Winteraceae
<i>Cystotheca</i>	Fagaceae, Ulmaceae
<i>Discostroma</i>	Onagraceae, Rosaceae a.o.
<i>Discostromopsis</i>	Myrtaceae
<i>Englerula</i>	Chrysobalanaceae, Anacardiaceae, Sapindaceae, Burseraceae, Euphorbiaceae
<i>Goplana</i>	Magnoliaceae, Meliosmaceae, Vitidaceae
<i>Gymnosporangium</i> , aecidia	Myricaceae, Malaceae, Hydrangeaceae
<i>Lambro</i>	Ulmaceae, Sterculiaceae, Proteaceae
<i>Mamiania/Mamianella</i>	Betulaceae
<i>Melampsora</i> , heteroecious species	Salicaceae, Flacourtiaceae
<i>M. magnusiana</i> , aecidia	Fumariaceae
<i>Melampsorium</i>	Magnoliaceae, Betulaceae
<i>Parmulina</i>	Euphorbiaceae, Daphniphyllaceae
<i>Perisporiopsis cecropiae</i>	Moraceae, Sterculiaceae
<i>Phaeochorella</i>	Chrysobalanaceae, Leguminosae
<i>Physopella</i>	Vitidaceae, Meliosmaceae, Euphorbiaceae, Sympetalae, Poaceae
<i>Platychora</i>	Ulmaceae, Betulaceae
<i>Pleochaeta</i>	Ulmaceae
<i>Prosthegium</i>	Betulaceae, Ulmaceae, Platanaceae, Salicaceae, Aceraceae
<i>Protoventuria</i> , pro parte	Ericaceae, Aquifoliaceae, Rosaceae s.s., Ribesiaceae, Fagaceae
<i>Puccinia andropogonis</i> , aecidia	Leguminosae, Polygalaceae, Oxalidaceae, Rutaceae, Scrophulariaceae, Santalaceae
<i>P. spp.</i> of Bambuseae, aecidia	Hamamelidaceae, Hydrangeaceae
<i>Pucciniostele</i>	Vitidaceae, Saxifragaceae
<i>Rhytidenglerula</i>	Vitidaceae, Dilleniaceae, Ulmaceae, Connaraceae, Euphorbiaceae, Lauraceae
<i>Sawadaea</i>	Aceraceae
<i>Seimatosporium kriegerianum</i>	Onagraceae, Myrtaceae
<i>Skierka</i>	Rutaceae, Burseraceae, Sapindaceae, Euphorbiaceae, Vitidaceae
<i>Sphaerotheca macularis</i>	Rosaceae, Myrtaceae
<i>S. pannosa</i>	Rosaceae, Punicaceae
<i>S. epilobii</i>	Onagraceae
<i>Taphrina</i>	Salicaceae, Betulaceae, Fagaceae, Ulmaceae, Euphorbiaceae, Aceraceae, Hippocastanaceae, Anacardiaceae, Rosaceae, Saxifragaceae, Amygdalaceae, Zingiberaceae, Polypodiaceae
<i>Thrauste</i>	Amygdalaceae, Melastomaceae
<i>Uncinula clintonii</i>	Ulmaceae, Tiliaceae, Sterculiaceae
<i>U. miyabei</i>	Ulmaceae, Moraceae, Tiliaceae, Euphorbiaceae, Betulaceae
<i>Xenostele</i>	Lauraceae, Hamamelidaceae

position near Sapindales (DAHLGREN 1980).

Rosales, Myrtales, Fagales c.s. have very few indicative parasites in common with most Sympetalae (except Corniflorae). As can be seen this is not true for Rutiflorae. This feature is the more conspicuous for families like Ranunculaceae, Brassicaceae, and Tropaeolaceae. This problem will be dealt with in a separate paper.

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