Notes RBG Edinb. 44(3):421–426 (1987)

THE ROSACEAE AND THEIR RUST FUNGI:
Some aspects of their coevolution

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ABSTRACT. The Rosaceae is one of the richest families for the number of rust genera harboured. The study of the coevolution of the rusts and their rosaceous hosts provides valuable insights into the taxonomy of both groups. The relations with some other families of the Rosidae, between the different subfamilies, and within the tribe Rosoideae are examined with some examples.

INTRODUCTION

The rust fungi (Uredinales) are parasites with a generally high level of host specificity, resulting in a long evolutionary process followed in common by the plants and their parasites. Thus, knowing the biological spectrum of a rust may provide us with taxonomic and phylogenetic information of great interest. This has been shown for parasitism in general by several syntheses or symposia (Hedberg, 1979; Savile, 1979). However, despite the amount of data already gathered on this topic very few plant taxonomists think to make use of characters of this kind (Cronquist, 1981; Dahlgren *et al.*, 1985).

It should be pointed out that information provided by parasites is not so reliable as that given by morphology or biochemistry. Firstly, it is more difficult to get a complete screening of the whole set of parasites living on a taxonomic group of hosts than to study their morphology from herbarium specimens. Secondly, it may happen, for example, that one of two related taxa does not host a parasite known on the other—it having been lost or not acquired for some unknown reason. It may also happen, because of a wide jump in the evolutionary sequence of related fungi, that they have settled on a distant host, as did some *Melampsora* (Durrieu, 1980).

Information provided by rust fungi cannot be used alone to form taxonomic conclusions. However, such information deserves to be compared with data obtained from other characters, and it is possible to gain complementary evidence regarding taxonomic or phylogenetic hypotheses.

SOME VIEWS ON THE SYSTEMATICS OF THE ROSACEAE

The Rosaceae is a very suitable example to test the taxonomic significance of mycoparasitism, because it hosts, after the Leguminosae, the greatest number of rust genera, sixteen at least (Table 1).

There is also some dispute as to the taxonomic status of certain tribes and phylogenetic sequences. Darlington (1963) stated that the most primitive Rosoid-like ancestor had x = 7 and the higher chromosome numbers arose by additions in the Prunoideae (x = 8) and Spiraeoideae (x = 9), and unequal duplication in Maloideae which originated from

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TABLE 1

The rust families and genera on Rosaceae

Pucciniastraceae	*Pucciniastrum* Otth (includ. *Thekopsora* Magn.)
Chaconiaceae	*Ochropsora* Diet.
Uropyxidaceae	*Sorataea* Sydow (=*Leucotelium* Tranz.) *Tranzschelia* Arth.
Phragmidiaceae	*Arthuriomyces* Cumm. & Y. Hirats. (=*Gymnoconia* Lagerh.) *Frommeella* Cumm. & Y. Hirats. (=*Frommea* Arth.) *Gerwasia* Racib. (=*Mainsia* Jack.) *Hamaspora* Koern. *Joerstadia* Gjaerum & Cumm. *Kuehneola* Magn. *Phragmidium* Link *Trachyspora* Lagh. *Xenodochus* Schlecht.
Sphaerophragmiaceae	*Triphragmium* Link
Pucciniaceae	*Gymnosporangium* Hedw.f. (includ. *Coleopuccinia* Pat.) *Puccinia* Pers.

Nomenclature after Cummins & Hiratsuka (1983).

hybrid polyploids between ancestors of Spiraeoideae and Prunoideae. On the other hand, most taxonomists now consider that the Spiraeoideae are the most primitive of the living Rosaceae, and the Prunoideae and Rosoideae are specialized derivatives. Possible links are known, such as: *Quillajeae* with n = 14, 15 or 17, between the Spiraeoideae and Maloideae; *Exochorda* (n = 8) could be a relict of a Spiroid ancestor of the Prunoideae; and the *Kerriae* (n = 9) are Rosoideae with the same basic number as in the Spiraeoideae.

From the results of a chemotaxonomic survey, Challice (1974) supports the hypothesis that the subfamily Spiraeoideae is the one most related to the ancestral group from which derived the Prunoideae and, directly or by allopolyploid crossing with a Prunoid ancestor, the Pomoideae. These three subfamilies share close chemical affinities, while the Rosoideae were derived from an ancestral Spiroid by a different route.

PARASITIC APPROACH TO TAXONOMY

Can parasitic fungi give complementary information to support one or other of the different hypotheses?

Mapping host distribution of rust genera on the whole family is very instructive (Fig. 1). It is clear that there are two major groups of hosts whose parasites are quite different. It appears that the Rosoideae are set well apart from the other subfamilies. Indeed the species of *Pucciniastrum* found on *Prunus* belong to the subgenus *Thekopsora,* while those on Rosoideae are *Pucciniastrum* sensu stricto. Moreover, *Pucciniastrum* is known on a wide range of host families in Fagales, Urticales, Ericales,

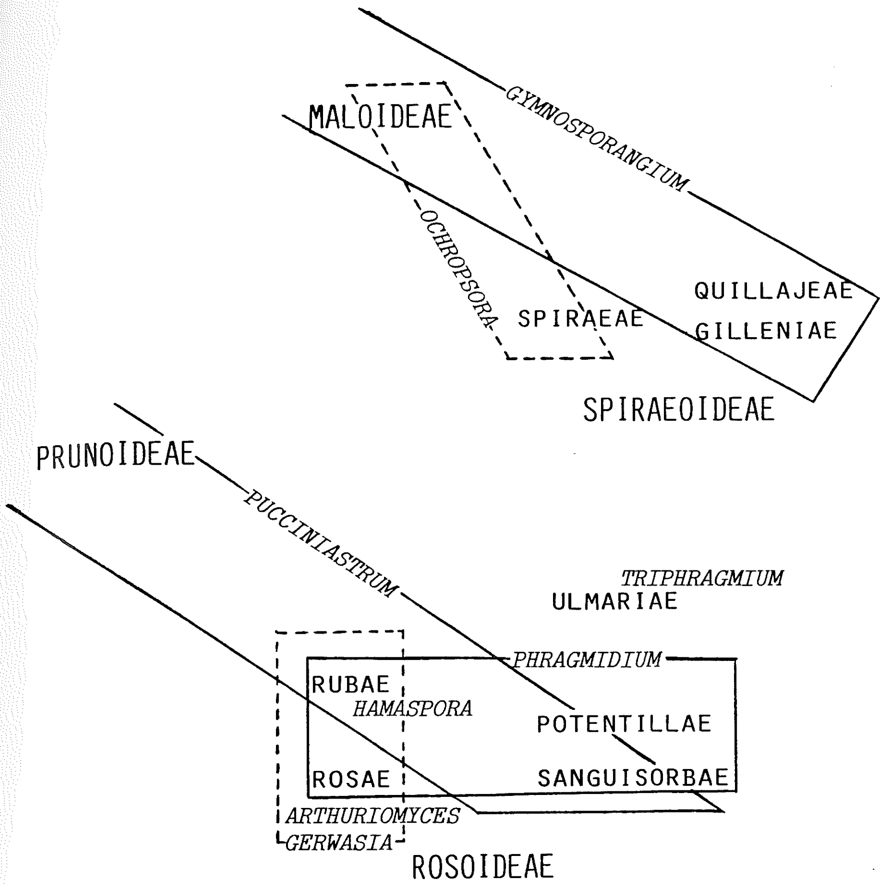

FIG. 1. Distribution of some rust genera in subfamilies and tribes of Rosaceae.

Rubiales, Orchidaceae . . . and its presence seems likely to be of little taxonomic value.

The Rosoideae is the only subfamily hosting the different genera of the rust family Phragmidiaceae which are almost exclusive on it. Clearly the Rosoideae and Phragmidiaceae are a noteworthy example of coevolution. The wide gap between the subfamilies of the Rosaceae confirms the views of taxonomists who consider that the Rosoideae had evolved through a very different pathway from that giving rise to Prunoideae and Maloideae.

The rust genus *Gymnosporangium* indicates a relationship between the Maloideae, its main source of hosts, with the Spiraeoideae by its two species attacking *Vauquelinia* of the tribe *Quillajeae* and *Porteranthus* of the tribe *Gilleniae*. The exact position of these two tribes is disputed, but the parasitism of *Gymnosporangium* suggests a close relationship with the Maloideae. Similarly, the two species parasitizing *Philadelphus* and

Fendlera indicate possible affinities of those genera of the family Hydrangeaceae to the Maloideae.

Ochropsora is a small rust genus of three species not specific to the Rosaceae, but *O. ariae* is hosted by plants belonging to the two subfamilies Spiraeoideae and Maloideae, thus reinforcing the relationships indicated by *Gymnosporangium*.

Finally the Prunoideae, on the basis of its rust flora, stays apart from the three other subfamilies. We have seen that the presence of *Pucciniastrum* (subgen. *Thekopsora*) is probably of little significance. However, the hosting of two other rust genera, *Tranzschelia* and *Leucotelium*, is much more interesting. The first is composed of a few heteroecious species with their dikaryotic stages on *Prunus* and of some derived autoecious species on *Anemone*, which is the host of the monokaryotic stages of the heteroecious rusts. The second is either treated as an isolated genus, *Leucotelium*, specific to *Prunus*, or is included in *Sorataea* the other species of which live on legumes. Both *Tranzschelia* and *Sorataea* are closely related; Cummins & Hiratsuka (1983) placed them in the family Uropyxidaceae which is segregated from the larger family Raveneliaceae (hosts mainly Leguminosae) as defined by Savile (1976).

This peculiar place of Prunoideae and their rusts deserves a more detailed study. It should be noted that the Prunoideae with *Sorataea* on one hand, and Spiraeoideae and Maloideae with *Ochropsora* on the other, harbour rust genera living also on Fabaceae. Can it be supposed that they represent 'souvenirs' of rusts which parasitized the very ancient ancestors (middle Cretaceous) of these two close, and often united, orders Rosales and Fabales?

From the point of view of phylogeny within the Rosaceae, these facts do not support Stebbins's (1974) idea of a hybrid origin of the Maloideae from the Spiraeoideae and Prunoideae.

Another problem is to establish the hitherto disputed position of the tribe *Ulmariae* with its sole genus *Filipendula* and its rust *Triphragmium*. Considered firstly in Spiraeoideae, it was later transferred to the Rosoideae, but Juel (1918) considered it to be transitional between these two subfamilies. Baker & Baker (1967) argued that the chromosome number supported its position in the Rosoideae, while Sterling (1966), after a study of the carpels, maintained it in the Spiraeoideae. According to Savile (1968) the presence of *Triphragmium* on this host supports the inclusion of *Filipendula* in the Rosoideae as he placed the rust genus in the Phragmidiaeceae, the other members of which are restricted to the Rosoideae. However, Cummins & Hiratsuka (1983) placed *Triphragmium* in their new family Sphaerophragmiaceae; if this treatment is confirmed, then Savile's supposition carries less weight. Moreover, it should be noted that *Triphragmium* and *Nyssopsora* (Henderson, 1973; Monoson, 1974) seem closely related and differ from other Phragmidiaceae by the fact that they attack hosts in several plant families, while all the Phragmidiaceae, except *Kuehneola*, live solely on the Rosaceae. Alternatively, they could suggest relationships at a higher taxonomic level: they are restricted to some orders of the subclass Rosidae, and when located on the evolutionary diagram given by Cronquist (1981) their place cannot appear as a pure coincidence (Fig. 2).

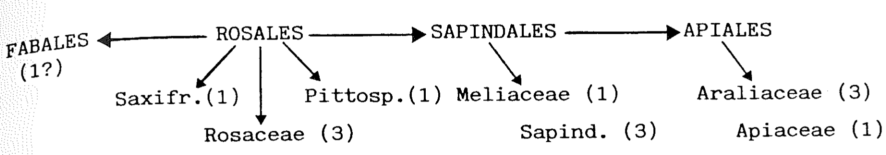

FIG. 2. Phylogenetic relationships in Rosidae (after Cronquist, 1981) and distribution of species of *Triphragmium* and *Nyssopsora.*

At a lower taxonomic level, a good example of co-evolution is shown by *Phragmidium* and its hosts, which all belong to the subfamily Rosoideae. It is generally accepted that the Rosoideae derived from woody ancestors, and that herbaceous forms are advanced, thus implying that *Rosa* and *Rubus* are closer to these ancestors than most of the other genera.

As for *Phragmidium,* this rust genus is divided into three subgenera mainly based on the structure of the teliospore pedicel. The subgenera *Phragmidium* and *Earlea* are characterized by dormant teliospores, the first with a hygroscopic swelling of the pedicel base, the second with a non-hygroscopic cylindrical pedicel. The subgenus *Phragmotelium* possesses thin-walled, non-dormant teliospores with a bicellular pedicel; its species are mainly tropical and subtropical from East Asia and the Pacific, as are those of the related genus *Hamaspora.*

Phragmidium and *Phragmotelium* are mainly confined to *Rosa* and *Rubus,* while *Earlea* is found only on the plant genera *Potentilla, Duchesnea, Geum, Poterium* . . . that are all herbaceous, and considered as more advanced. *Phragmidium andersonii* on *Potentilla fruticosa* could be deemed an exception as it belongs to subgen. *Phragmidium.* However, *P. fruticosa* is very likely a primitive species of woody habit, and hence still near the ancestral stock of the Rosoideae. So, we may trace out a coevolution scheme in which ancestral Phragmidiaceae, occurring on tropical shrubs ancestral to *Rubus* and *Rosa,* have given rise to diverse rusts with immediately germinating teliospores (as in *Kuehneola, Hamaspora* or *Phragmotelium*). These latter, evolved on temperate host species (giving rise to *Phragmidium* sensu stricto), from which they progressed to primitive woody *Potentilla,* and while following these in their evolutionary pathway, lost their hygroscopic pedicel because it was possibly of less adaptive value on their herbaceous hosts.

Savile (1979) gives further examples of the taxonomic implications of host-parasite relationships in the Rosoideae and Phragmidiaceae. These, together with the examples discussed here, clearly indicate how useful the simultaneous consideration of hosts and parasites can be in defining a tentative phylogenetic taxonomy.

ACKNOWLEDGEMENTS

I wish to thank Dr B. J. Coppins and Mr A. P. Bennell for their valuable help in correcting the English text.

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