THE RUST FUNGUS GENUS NYSSOPSORA AND ITS HOST RELATIONS

D. M. HENDERSON

ABSTRACT. The rust fungus genus *Nyssopsora* has extremely distinctive teliospores. The distribution on its hosts reaffirms the relation of the Araliaceae to the Umbelliferae. The occurrence on other taxonomically scattered host families may not indicate relations to the Umbellales but an evolution of the rusts from macrocyclic to microcyclic life cycles.

The host relations of rust fungi and other specialised parasites have been invoked from time to time as casting evidence on the affinities of their hosts. The subject has been treated especially by Savile (1971) in a number of papers drawing on a wide range of examples. The basic requirements on which the system rests are that the fungi have been correctly classified and that the fungi have evolved along with their hosts. The most closely related fungi occur on closely related hosts. Considerable experience shows that, carefully used, this approach can lead to useful results. This short essay probes the possibility of deriving some information on the interrelations of the Umbelliferae by considering the host relations of the rust genus *Nyssopsora.*

Nyssopsora is a small genus of nine recognised species, one on Umbelliferae, four on Araliaceae, two on Sapindaceae, one on Meliaceae and one on Pittosporaceae. In Table I their host distribution and geographical distribution is detailed. The genus is almost entirely restricted to the northern hemisphere. *Nyssopsora thwaitesii* crosses the equator, *N. citriobati* is known only from Australia; no species is known from S America.

An essential requirement for deduction of evidence from host distribution is that the classification of the fungi is correct. For the purpose of the arguments developed in this paper this requires the genus *Nyssopsora* to be monophyletic and no true species of *Nyssopsora* to be excluded. Luckily, the evidence for the cohesion of the species is very strong. The teliospores of *Nyssopsora* are very unusual (Plate 6). The spore is three-celled, each cell with two germ pores. The spore is attached to the stalk by one lower cell. The outstanding feature of the teliospores are their spines which are stout and often branched at their apices. This type of spine develops by the outgrowth of the primordial wall of the teliospore with subsequent infilling (Henderson, 1969), an uncommon mode of spine formation on rust spores. Although there is some variation in degree of branching of the spines, a feature examined in detail by Lütjeharms (1937) in his revision of the genus, examination of herbarium material confirms that the spines of other species develop by the highly characteristic method originally detected in *N. echinata.* In this feature the spines of *Nyssopsora* clearly separate it from the irregular processes on the surface of other tricellular teliospores in genera such as *Triphragmium* parasitising the Rosaceae (Henderson, unpublished electron microscope studies). The only other comparable ornamentation of uni-, bi- or multi-cellular reliospores occurs in the genus *Sphaerophragmium* whose teliospores are four- or more-celled. Although spines on the bicellular spores of species of *Puccinia* in various groups of affinity, *Puccinia prostii* (*Tulipa*), *P. coronata* (Gramineae), are undoubtedly formed by an outgrowing process, none has the apical branching of the spines of *Nyssopsora*

TABLE 1

Nyssopsora species

Species	Host genus (family)		Distribution	Uredospores
asiatica	*Aralia* *Acanthopanax*	(Araliaceae)	E Asia	—
cedrelae	*Cedrela*	(Meliaceae)	S & E Asia	+
citriobati	*Citriobatus*	(Pittosporaceae)	Australia	—
clavellosa	*Aralia*	(Araliaceae)	N America	—
echinata	*Meum* *Ligusticum* *Selinum* *Conioselinum* *Coelopleurum* *Oenanthe*	(Umbelliferae)	Europe and N America	
formosana	*Koelreuteria*	(Sapindaceae)	Formosa	—
koelreuteriae	*Koelreuteria*	(Sapindaceae)	E Asia	+
thwaitesii	*Schefflera* *Nauclea*	(Araliaceae)	SE Asia	
trevesiae	*Trevesia*	(Araliaceae)	E Indies	—

There are two main routes whereby experience of the rust fungi would suggest that their occurrence on a scattered range of angiosperm taxa could have come about, the first by colonising spread, the second by evolution of the life cycle. It is known that a rust taxon, although usually restricted to a limited host range, has some capacity for colonisation of new hosts. The new hosts, except for some unusual examples in the genus *Coleosporium*, are usually relatively closely related to the main hosts. This—limited spread amongst closely related hosts—is the basis of the idea that rust fungi may indicate host relationships. Applying this approach to the host range of *Nyssopsora* it is apparent that within the list of host families Araliaceae, Meliaceae, Pittosporaceae, Sapindaceae and Umbelliferae the first and the last are usually regarded as closely related, indeed some taxonomists would unite them. The relationship of the remaining three families, Meliaceae, Pittosporaceae and Sapindaceae, to these two and to one another are much more tenuous and no-one seems to have suggested any close linkages although the Pittosporaceae have been loosely associated with possible ancestors of the Umbellales. Within the Umbellales four species of *Nyssopsora* inhabit Araliaceae, *N. asiatica* on *Acanthopanax*, *Aralia* and *Kalopanax*, *N. clavellosa* on *Aralia* and *N. thwaitesii* on *Acanthopanax*, *Heptapleura* and *Hedera*, whereas one species, *N. echinata*, occurs on many genera of the Umbelliferae (*Meum*, *Coelopleurum*, *Conioselinum*, *Ligusticum*, *Oenanthe* and *Selinum*). All the host genera of the last species belong to the subtribe Seselinae except for *Conioselinum*. Moreover the Nyssopsoras on Araliaceae and Umbelliferae are very closely related. This seems a case of host range indicating host relationship. Within the assemblage of host genera within the Umbellales the host distribution does not give any indication of areas of relation between Araliaceae and Umbelliferae.

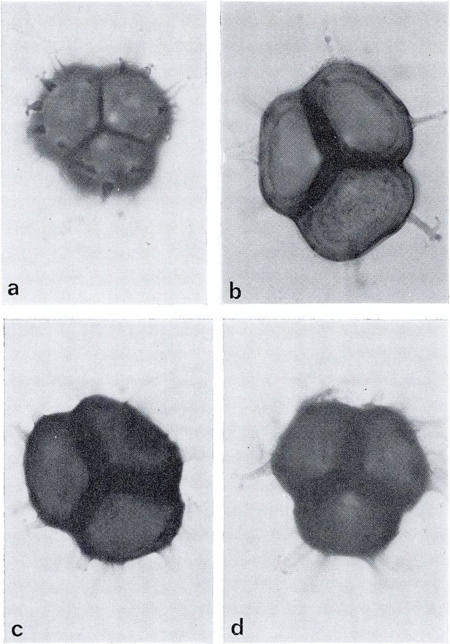

Plate 6. Teliospores of *Nyssopsora*: a, *N. koelreuteriae* (Sydow, Fungi exotici 114); b, *N. thwaitesii* (Crypt. paras. Javan, 68); c, *N. cedrelae* (Sydow, Fungi exotici 956); d, *N. asiatica* (Inonye 27). All x 1500.

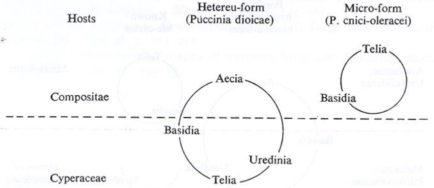

FIG. 1. Diagram to illustrate Tranzschel's Law. The life cycles of an alternating eu-form rust (*Puccinia dioicae*) and a derived micro-form (*P. cnici-oleracei*). The telia of the micro-form develop on the host group (Compositae) bearing the aecia of the hetereu-form.

The next problem concerns the life cycle of species of *Nyssopsora* so far as known and the interpretation of this information by the application of Tranzschel's Law regarding the evolution of life cycles of rust fungi. All the species of *Nyssopsora* are either microforms (teliospores only) or hemiforms (teliospores and uredospores only). No aecia are known; no species is known to alternate. Hemiforms are represented by two species, *N. cedrelae* on *Cedrela* (Meliaceae) and *N. koelreuteriae* on *Koelreuteria* (Sapindaceae). The other seven species are microforms. Tranzschel's Law, which is supported by a great number of examples throughout the rust fungi, indicates that microcyclic species whose telia closely resemble those of macrocyclic species often occur on the aecial host of the macrocyclic species. The probability is high that many microcyclic species have evolved by formation of telia instead of aecia by macrocyclic species, the life cycle is thereby reduced to one dominant spore stage—the teliospore, which may or may not be accompanied by spermogonia, and alternation of hosts becomes impossible. The accompanying Figure 1 shows life cycles of macrocyclic *Puccinia dioicae* and a presumed, derived microcyclic species *Puccinia cnici-oleracei*. *P. dioicae* forms aecia on Compositae and uredinia and telia on Cyperaceae. The microcyclic *P. dioicae* forms its only spore stage, telia, on the aecidial hosts of the macrocyclic species, various Compositae, as Tranzschel's Law demands. Returning to the problem of *Nyssopsora* there is a possibility of applying Tranzschel's Law. No aecia are known—although they may yet be discovered.

The species of *Nyssopsora* with uredinia and telia, *N. cedrelae* (Meliaceae) and *N. koelreuteriae* (Sapindaceae), could be the diplont stages of heteroecious (i.e. alternating) or indeed of autoecious (i.e. non-alternating) rusts. Their aecial stages indeed may no longer be formed. But if they are the diplont stages of heteroecious rusts then the aecial stage would occur on a host plant taxonomically remote from the diplont host (all heteroecious rusts alternate between taxonomically remote hosts). Such a host could then be a member of the Araliaceae or Umbelliferae. The possible picture of origin of *Nyssopsora* on its present host range could be as in Figure 2.

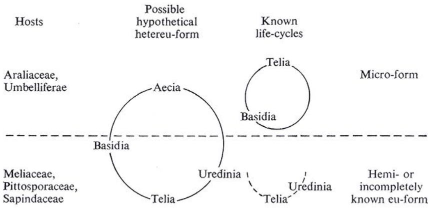

FIG. 2. Possible life cycle relations of species of *Nyssopsora*.

The occurrence on scattered families of dicotyledons represents the diplont stages of heteroecious species with aecia on Umbelliferae/Araliaceae, the microcyclic rusts at present known on Umbelliferae and Araliaceae have evolved from macrocyclic rusts with aecia on these families.

The rust on Pittosporaceae (*N. citriobati*) is indubitably a *Nyssopsora* but does not fit clearly into this pattern. Indeed it is little known and may have uredinia—an indication of a life cycle similar to the species on Meliaceae and Sapindaceae.

The relation of *Triphragmiopsis jeffersoniae* to this problem must be considered. This rust is macrocyclic and occurs on *Jeffersonia dubia* (Berberidaceae) in the USSR. Cummins (1959) includes this rust in *Nyssopsora* but remarks that it is frequently segregated in the genus *Triphragmiopsis*. There seems good reason to believe that *Triphragmiopsis* has little relation with *Nyssopsora*, the ornamentation is quite unlike *Nyssopsora*, but much closer to the typical pattern of the Phragmidiae.

The genus *Sphaerophragmium* in relation to *Nyssopsora* poses another type of problem. *Sphaerophragmium* has muriform teliospores with spines similar to those of *Nyssopsora*. The species are confined to hosts in the Leguminosae and Annonaceae—one species, *S. sorghi* Batista & Bezerna on *Sorghum* (Gramineae), certainly has little relation with *Sphaerophragmium*. It is possible that *Sphaerophragmium* is implicated in the origin of *Nyssopsora* but apart from teliospore structure there is no hint of their interrelationships. Most species of *Sphaerophragmium* have uredinia and telia, aecia are unknown. There seems no bridge between this genus on the Leguminosae and Annonaceae and *Nyssopsora* on Araliaceae, Umbelliferae, Meliaceae, Sapindaceae and Pittosporaceae. Most advance in unravelling the complexities would come from the discovery of aecia in the life cycles.

REFERENCES

CUMMINS, G. B. (1959). *Illustrated genera of rust fungi*. 131 pp. Burgess Publishing Co.

HENDERSON, D. M. (1969). Studies in the morphology of fungal spores I: The teliospores of Puccinia prostii and Nyssopsora echinata. *Notes R.B.G. Edinb*. 29: 373–375.

LÜTJEHARMS, W. J. (1937). Vermischte Mykologische Notizen I. Ueber die Gattung Nyssopsora. *Blumea*, Suppl. 1: 142–161.

SAVILE, D. B. O. (1971). Coevolution of the rust fungi and their hosts. *Quart Rev. Biol.* 46, 3: 211–218.

—— (1971). Co-ordinated studies of parasitic fungi and flowering plants. *Naturaliste Can.* 98: 535–552.