THE BEAUTY AND MYSTERY OF SPECIFICITY

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Let me first say how happy I am to be in this University set in sylvan surroundings in the beautiful Western Ghats. I recall my visit many years ago as a student to Agumbe and Jog Falls, not far from here, to collect plants where I first saw Podostemaceae, the royal fern *Osmunda regalis*, and the fragile but beautiful *Dictyophora*, a Gasteromycete.

Being with you here today also reminds me of my long and close association with the Indian Botanical Society (IBS) of which I became a member in 1945. My first research paper appeared in the JIBS in the following year. Indeed, much of my important work appeared in the JIBS in later years. Naturally, I am beholden to the Society and my friends for their kind thoughts in honouring me with an award which makes me proud of my association with the Society. May the IBS grow from strength to strength and ever keep in tune with the motto, "Mehr Licht"!

On this occasion, with reverence I pay homage to my parents, and to my parents' parents, and my gurus and my gurus' gurus, but for whom I would not be here talking to you. I pay homage to the founders of the Society and the stalwarts who nourished it. I have also a word of appreciation for my wife Lakshmi and my two sons for their tolerance of an over-busy husband and father.

I have chosen to speak to you today about specificity. Specificity is an unsolved problem in biology. It has intrigued me for a long time, and continues to intrigue me. When I began my research well over sixty years ago, I was asked to work on "Soil Conditions and Fusarium Wilt of Cotton". Fusariose wilt in cotton, first discovered in Alabama in the USA by G F Atkinson,(the first President of the Botanical Society of America) in 1898, occurs in many countries including Egypt and India where cotton is a major crop. S L Ajrekar, J F Dastur, G S Kulkarni and B B Mundkur pioneered studies on this disease in India. Mundkur then made the significant observation that the Indian strain of the pathogen caused wilt only on Indian cottons, but not American cotton. The American strain of the fungus caused wilt only on American cotton, but not Indian cotton. Thus, the Indian and American strains of the pathogen, though morphologically similar, showed specificity. In other words, each showed preference to a particular host cultivar. It is Mundkur's discovery that focused my attention on specificity. Both as a student and as a teacher I wondered at, and pondered over, specificity and so, thought it fit to share with you my thoughts on specificity on this occasion. Specificity is the prime mover in coevolution and it is fitting to talk about it in this bicentennial year of Charles Darwin's birth.

In the time before us I shall examine examples of specificity from the plant, fungus, and animal kingdoms in an effort to focus on the beauty and mystery of specificity.

THE VASCULAR WILT FUSARIA

First, I shall talk about vascular wilt Fusaria on which I began my work in 1944. The members of the anamorphic genus *Fusarium* that cause vascular wilts in a range of crops, are ubiquitous, typically soil-borne, and are currently considered formae speciales of *Fusarium oxysporum*. They are distinguished primarily from their choice of host. Originally, some of these *formae speciales* enjoyed the status of species with their own specific epithets, despite the fact that they are indistinguishable morphologically. *Formae speciales* denote specificity. Nearly eighty *formae speciales* of *Fusarium oxysporum* are currently recognized. The sexual state of this species is not known and it is the only species in Section Elegans of the genus.

Fusarium udum Butler (Section Lateritium) causes a severe wilt of arhar (pigeon pea, *Cajanus cajan*) and *Crotalaria juncea* [both Leguminosae] in India and the tropics. The two are considered *formae speciales cajani* and *crotalariae* of *Fusarium udum*. *Fusarium xylarioides* Steyaert (also Section Lateritium) causes tracheomycosis in Cacao (*Theobroma cacao* [Sterculiaceae]). Both are known to have a *Gibberella* teleomorph. As far as known, both these vascular wilt Fusaria seem to have a clearly circumscribed host specificity.

As Mundkur (1936) noted, the Indian and American strains of *Fusarium oxysporum* f. sp. *vasinfectum* which causes wilt in cotton have each their own preferred host species/cultivar. Currently, six Races of the cotton wilt *Fusarium* are known: Races 1 and 2 from the USA, Race 3 from Egypt, Race 4 from India, Race 5 from Sudan, and Race 6 from Brazil (Armstrong and Armstrong 1981). Races 1 and 2 cause disease only in American cotton (*Gossypium barbadense*) but not in Indian cotton (*G. arboreum*). Race 3 from Egypt causes disease in *G. arboreum* but not in *G. barbadense*. Race 4 from India attacks *G. arboreum* but not *G. barbadense* or *G. hirsutum*. Race 5 from Sudan infects both *G. arboreum* and *G. barbadense*, but not *G. hirsutum*. However, further and more intensive study of a large number of *formae speciales* on a range of hosts has shown that host specificity on which the *formae speciales* concept is built is not invariable. Though f.sp. *lini* is restricted to flax [*Linum usitatissimum* (Linaceae)], f.sp. *lycopersici* to *Lycopersicum esculentum* (Solanaceae), and f.sp. *conglutinans* to Cruciferae, f. sp. *vasinfectum* on cotton infected not only cotton (*Gossypium*) and *Hibiscus* (Malvaceae), but *Cajanus*, *Glycine*, *Medicago* and *Vigna* (Leguminosae), *Hevea* and *Ricinus* (Euphorbiaceae), *Coffea* (Rubiaceae), and *Solanum* (Solanaceae). The nature and extent of specificity in vascular wilt fusaria is now known to be so variable as to make it a really complex phenomenon. The use of specificity in the taxonomy of these Fusaria is also complicated. Further, the cotton wilt fungus has the ability to infect root systems of several weeds without causing any visible symptoms or wilt. Host plants so infected become symptomless carriers. In the case of the cotton wilt pathogen there are races with narrowly circumscribed specificity alongside extended host range outside *Gossypium* and Malvaceae. How can we explain this?

BLACK RUST OF WHEAT AND OTHER RUST PATHOGENS

From ancient times to the present, black or stem rust (*Puccinia graminis* var. *tritici*) on wheat has been a major threat and killer of wheat crops throughout the world. The stem rust pathogen completes its life cycle on two unrelated hosts, the telial host being a cereal (or grass) and the aecial host *Berberis* or *Mahonia* of the Berberidaceae. The six varieties of this species, *tritici*, *secalis*, *avenae*, *phleipratensis*, *agrostidis*, and *poae* , as the names suggest, have specific host preferences. There are also

intravarietal preferences to specific host cultivars. The 1930s saw serious and untold losses to wheat crops in the North American belt leading to urgent initiatives in studying resistance of crop cultivars and virulence and specificity of races of the pathogen. Based on the reactions of a given set of host cultivars (the so-called 'differentials') to a known set of lines of the pathogen, races were distinguished and named. The plasticity and adaptability of races and the range of variation in the response of the host cultivars to the pathogen contribute to the difficulties in identification of races. Races are known to acquire virulence to cultivars known to be resistant. The virulence-resistance equation between pathogen and host is important in specificity. For every gene that can mutate to confer resistance in the host, there is a gene in the pathogen that can mutate to confer virulence to overcome resistance. This, in fact, is Flor's (1956) hypothesis of genetics of resistance in plants. There is a view that black rust originally colonized wild grasses and, with domestication of wheat, moved on to wheat as the primary host. The pattern of race populations may change in space and time depending on the cultivars grown, the extant race populations and environmental factors. Thus, the emergence and development of races is a complex phenomenon. The pioneering work of E C Stakman on the identification of races and resistance/susceptibility of wheat cultivars paved the way for understanding genetics of rust-resistance and rust epidemiology.

The stem rust pathogen, as we have noted, completes its life cycle on two unrelated hosts, producing uredinia and telia on the primary host (wheat or other cereal or grass), and pycnia and aecia on the alternate host (*Berberis* or *Mahonia*). The importance of the alternate host becomes evident from the fact that eradication of the alternate host led to a reduction in disease incidence on wheat crops in the United States where wild populations of barberry existed. The widespread occurrence of an alternate host facilitates emergence of new races by hybridization and heterocaryosis. Thus the number of races of stem rust of wheat in the United States far exceeds the number of races of this pathogen in India where barberry occurs only in the hills, but not the plains.

The post-Stakman era of monitoring rust race populations and building up rust-resistance in wheat and other cereal crops remained rosy for a time, but suddenly all changed and there was this new race of the wheat rust pathogen, ug99, emanating in Uganda in Africa and within a decade spreading far and wide to devastate wheat crops worldwide to catastrophic levels. Known norms of specificity no longer hold. There is change. Change is perpetual.

Breeding programmes, therefore, can never be time-bound. They are perpetual. We look and hunt for new sources of resistance in the wild. There is so much to tap from the wild. And it is all about specificity.

The discovery of heteroecism in stem rust of wheat is epochal. The heteroecious condition is considered to be the primitive and the autoecious one is believed to have been derived, by reduction. (Baum and Savile, 1985). Many rusts are heteroecious. The rust on pearl millet[*Pennisetum typhoides* (bajra or cumbu)], *Puccinia substriata* Ell. & Barth. var. *indica* Ramachar and Cummins (1965) [= *Puccinia penniseti* Zimm.] bears telia on *Pennisetum*. An aecial host was not known until Ramakrishnan and Soumini (1948) found aecia of a rust occurring on *Solanum melongena* (brinjal) in the vicinity of bajra crops in Coimbatore in southern India and by experiment confirmed their suspicion that the aecia belonged to *Puccinia penniseti*. In further studies, Ramakrishnan and Sundaram (1956) noted the natural occurrence of pycnia and aecia on brinjal crops in the vicinity of rust-infected bajra crops in a number of locations in southern India. Among other *Solanum* species studied, they found aecia on *Solanum*

pubescens Willd. *S. torvum* Sw., *S. xanthocarpum* Schrad. & Wendl., but not on *S. trilobatum* L. In experiments, aeciospores from each host infected *Pennisetum typhoides*.

In experiments on seven species of *Pennisetum*, it was seen that *P. purpureum* Schum.(elephant grass) was immnune, and *P. alopecuros* Steud., *P. clandestinum* Hochst., and *P. rupellii* Steud. were resistant, whereas *P. orientale* Rich. and *P. polystachion* Sch. showed 5% infection. Two species of *Cenchrus* (Gramineae), *C. ciliaris* L. and *C. setigerus* Vahl. proved resistant. Such studies on life cycles of rusts and host range are important as they throw light not only on specificity but on life cycle and epidemiology of the pathogen.

Several *Pennisetum typhoideum* x *P. purpureum* hybrids (autotetraploids, amphidiploids) showed varying degrees of susceptibility suggesting that susceptibility came from the *P. typhoideum* genome.

It is known that another grass rust, *Puccinia paspalicola* (Pat. & Gaill.) Arthur infects *Solanum melongena*, but *P.penniseti* does not infect its host, *Paspalum scrobiculatum* L.

To add further to the confused picture of specificity of this tropical rust, new data on specificity came from a study of 31 accessions of *Solanum melongena* and 27 other species (Wilson *et al.* 1996). In the US no infection was observed on *Solanum dulcamara, S. nigrum, S. sisymbrifolium, S. carolinense, S. floridanum* and *S. perplexum*. On the other hand, several were now identified as aecial hosts: *S. anguivi, S. ferox, S. gilo, S. incanum, S. linaeanum, S. nodiflorum*, and *S. rostratum*. All other species tested were resistant, including two weed species, *S. americanum* and *S.aciculare*. The response of the Indian accessions included in the study is informative: *S. anguivi* Lam., *S. incanum* L. and *S. xanthocarpum* Schrader & Wendl. showed 100% infection; *S. capsicoides* Guatteri ex All. and *S. khasianum* C B Clarke

showed no infection.

Reports of natural hybridization between *Solanum* species in the wild (Viswanathan 1975) would contribute to diversity of *Solanums* and their response to the rust pathogen.

It is in this scenario that we need to consider the discovery of another unrelated aecial host for this cereal rust pathogen: *Euphorbia pulcherrima* Willd. [Euphorbiaceae] (Rao *et al.*1986). It is not uncommon to find several aecial hosts belonging to different genera and families for a given grass rust. For example, the telial host of *Puccinia andropogonis* is *Andropogon* (Poaceae). There are several varieties within this species with aecia on Oxalidaceae, Polygalaceae, Rutaceae, Leguminosae, Santalaceae and Scrophulariaceae, a situation known as "biogenic radiation" (Leppik 1967). We must presume the rust recognized and jumped to the new hosts in the course of evolution.

Narasimhan (1964) reviewed studies of heteroecious life cycles of rusts in India. The following connections he mentioned are noteworthy:

Puccinia caricis var. *himalayensis* : aecial host *Urtica parviflora* (Barclay 1887); *Puccinia coronata* : aecial hosts *Rhamnus purpureus* and *R.procumbens* in the Himalayas (Barclay 1891a); *Puccinia chrysopogonis*: aecial host *Jasminum humile* (Barclay1891b); *Gymnosporangium cunnighamianus* on *Cupressus torulosa:* aecial host *Pyrus pashia* (Barclay 1890); *Dasturella divina* the giant bamboo rust: aecial host *Randia dumettorum* (Thirumalachar *et al.* 1947).

Another rust pathogen I want to talk about is *Hemileia vastatrix*, the coffee rust fungus. A long-felt need for a monograph on *Hemileia* has recently been fulfilled (Ritschel 2005). Coffee rust possibly arose in southern Abyssinia in Africa in the 1850s or earlier, and is now a problem wherever coffee is grown, except on *Coffea* in Hawaii. What could be the

reason for its absence on *Coffea* in Hawaii? Species of *Hemileia* preferentially infect only plants belonging to the Rubiaceae and Apocynaceae, but not plants of any other family, reflecting their specificity. They are all hemiforms of which, curiously, the pycnial and aecial states are unknown. Coffee rust, in fact, is an enigma. Narasimhan (1964) lamented that decades of his efforts to find an aecial host in Balehonnur and other nearby areas planted to coffee were unsuccessful. While there are rust-resistant coffee (*Coffea arabica*) cultivars, there are none resistant to all strains (races) of the pathogen. Thus, all coffee genotypes are susceptible. Moreover, the pathogen can infect other plants in the Rubiaceae. At least nine genes for resistance have been identified, chiefly from *Coffea canephora* and *C. liberica*. Coffee rust co-evolved with coffee plants in the wild and in pre-Colonial times coffee was harvested in the wild. Diversification following domestication seemingly led to adaptation of the pathogen to the host and diversification of the pathogen. At least forty races of the pathogen have been identified, reflecting its high genetic variability. New races continue to emerge capable of infecting resistant hybrids. Incorporation of resistant genes from more than one source and putting out a composite cultivar with multiple resistance genes is currently being tried. In all this, the dramatic loss to genetic diversity of wild *Coffea* species in tropical forests in south-western Ethiopia where coffee evolved is a serious threat. From reactions of thousands of *Coffea* seedlings of different species and origins, twenty-four different physiological groups of coffee have been sorted out at the Coffee Rust Research Centre of the IICT. Thus, though we do not have to contend with an alternate host, the paucity of resistant host genomes and the diversity of pathogen genomes are enough to complicate the pattern of specificity.

And we do not know enough about the how of all this diversification. We know little about the life cycle of this rust. Though teliospores and basidiospores are found occasionally under cool, dry conditions, as we have noted, no alternate host is known. Though basidiospores may germinate in vitro, they do not infect coffee leaves. It might be that races arise by mutation. High genetic differentiation occurs in asexually propagated populations. Considerably more genetic variation is seen in African and Asian populations than in South American populations. African and Asian populations are, of course, older than the South American ones.

Other striking examples of specificity in the rust fungi are: the many species of the genus *Phragmidium* solely on Rosaceae, the species of *Ravenelia* on Leguminosae, and species of *Sphaerophragmium* mostly on Leguminosae.

COELOMOMYCES, MOSQUITOES AND COPEPODS

Coelomomyces is a genus of lowly chytrids, in the Blastocladiales (Blastocla-diomycota), alongside *Allomyces*.

Coelomomyces was established by Keilin (1921) for a fungus within the coelome of its insect host collected in Malaysia. M O T Iyengar, the brother of the botanist, M O P Iyengar, described two species from India on mosquito larvae. Currently, about forty species are known, of world-wide distribution in the tropics. They are primarily pathogens of mosquito larvae belonging to all the major taxa, but especially *Anopheles* and *Aedes*, vectors of malaria in the tropics. *Coelomomyces indicus* infects *Anopheles gambiae* which transmits malaria in many parts of Africa. For over five decades after the genus was established we knew little about the life cycle of this fungus, but Howard Whisler (1974), working on *Coelomomyces psorophorae*, on larvae of *Culiseta inornata* came up with the startling discovery that the fungus completes its life cycle on *Cyclops vernalis*, a copepod.

Planospores from the resistant sporangia produced within the mosquito larvae infect the copepod within which a wall-less thallus develops from within which posterirly uniflagellate spores emerge. These planospores are + and gametes that fuse to produce a zygote which then infects the mosquito larva within which resistant sporangia are produced, completing the cycle. Thus, the life cycle of *Coelomomyces* was shown to be in line with that of *Allomyces arbuscula* (Emerson 1940) in having an alternation of a gametophyte and a sporophyte . Also, it turns out that, aside from the rust fungi, *Coelomomyces* is the sole example of a fungus completing its life cycle on two unrelated hosts.

Since this breakthrough in unravelling the mystery of the life cycle of this lowly fungus, besides *Cyclops vernalis*, several other copepods have been shown to be alternate hosts of *Coelomomyces*. Also, an ostracod, *Potamocypris smaragdina,* has been shown to be the alternate host of *Coelomomyces utahensis* .which occurs on *Aedes atropalpus epactius*, *Culex tarsalis*, and *Culiseta inornata*. Attempts at infection of this new species on to *Cyclops vernalis* and other copepods have failed. *Coelomomyces chironomi* on *Chironomus plumosus* has as its alternate host the ostracod, *Heterocypris incongruens*. What determines specificity in this and other examples before us? Originally, it was thought that *Coelomomyces* embraces species with unique specificity. However, detailed studies have shown that *Coelomomyces* (for example, *C. utahensis*) can infect more than one, and sometimes several, species of mosquitoes. Study of heteroecism in *Coelomomyces* has only begun and I expect further interesting discoveries and information on the diversity, specificity and biogeography of these entomogenous pathogens. What determines the choice of primary and alternate hosts by these fungi?

PHYTOPHTHORA

Phytophthora conjures up in our minds a lot of history, politics, and science. *Phytophthora infestans* has claims to being the first ever 'fungus' to be experimentally shown to be the cause of disease in plants. The pioneers placed this lowly organism in the Oomycetes within the 'Phycomycetes' signifying its affinity to the algae, an assignment remarkable for its intuitive insight as now confirmed by an array of sophisticated techniques. After all, *Phytophthora* is not a fungus at all: it is now accommodated in the Straminiphila in the Chromista along with the downy mildews.

Phytophthora infestans causes the late blight of potato and was the cause of the famous Irish famine in 1843 (Large 1940). Its primary host is the potato (*Solanum tuberosum*) and other species of *Solanum*, besides the tomato (*Lycopericon esculentum*), also of the Solanaceae. It has also been reported on 15 other genera belonging to 10 families (Erwin and Ribeiro1996). Even within this circumscribed host range, *Phytophthora infestans* has continued to dominate as a pathogen all along. In the fight against plant disease, eleven genes for resistance to blight (R1-R11) have been identified and recognized in the potato. These eleven genes imply eleven corresponding virulence or avirulence factors in *Phytophthora infestans*. In its power to overcome resistance in its favoured host, the pathogen has shown remarkable ability as evident from the forty or more races of the pathogen that have emerged over a period of time. The race between host and pathogen for supremacy fuels the emergence of new races of the pathogen as much as the emergence of resistance genes in the host. The resulting shifts in pathogen-host interactions only add to the haziness of the picture of specificity.

The central highlands of Mexico are known to be the centre of origin and

biodiversity for potato and other tuber-bearing Solanums as much as for *Phytophthora infestans*. The Mexican *Solanum* species which co-evolved with *Phytophthora infestans* were the original source of the R-genes. It is now known that they are also a source of quantitative rate-reducing resistance that is very stable, durable and effective. Further, the central Mexican highlands are also the centre of origin of other species of *Phytophthora* such as *P. mirabilis*, *P. ipomoeae* and, possibly, *P.phaseoli*. It has been hypothesized that these species evolved sympatrically from one ancestral host through adaptive radiation onto their respective host families. Quite often, specificity and speciation are interlinked. Evolution of a pathogen population is reflected in its population genetic structure. Populations with a high evolutionary potential obviously would be able to overcome resistance better than those with low evolutionary potential.

There are about forty species of *Phytophthora*, many of which parasitize specific hosts. Of these, *Phytophthora ramorum,* is a unique pathogen with a remarkably wide host range, with the host-range list continuing to increase. In the United States, the important hosts include *Rhododendron, Pieris* (Ericaceae), *Viburnum* (Caprifoliaceae), *Syringa* (Oleaceae) and *Camellia* (Theaeceae), all of which are ornamental.

It will be instructive to consider yet another *Phytophthora*, *P. megasperma* in which, as in the case of *Fusarium oxysporum*, a system of *formae speciales* developed. Thus, *P. megasperma* f.sp. *glycinae*, f.sp. *medicaginis* and f.sp. *trifolii* came to be recognized. Eventually, host preferences which seemed simple turned out to be not so simple when the general population of the pathogen from diverse hosts came to be studied, just as in the case of *Fusarium oxysporum*. Specificity is important to the plant pathologist who aims at building resistance in preferred cultivars and

eradicate collateral hosts. The *Phytophthora megasperma* complex when classified on the basis of host preference, karyotype, and protein profile presents a picture in which there is correlation between morphology and protein profile. And there is uniformity of protein pattern worldwide. But that is not the case with karyotype groups and host groups where questions of ploidy, reproductive isolation, etc. would arise. Differences in host specificity and karyotype seem to be the *modus operandi* for the isolation between populations required for speciation (Hansen 1987). *Phytophthora megasperma* is thus an example of a plant pathogen that is evolving dynamically encountering new host species and new host cultivars, the specificity profile changing in space and time.

THE SMUTS AND RELATED FUNGI

There are about a thousand species of smut fungi known to infect about seventy-five families of flowering plants. The curious fact is: the host range of all species is restricted to not more than one flowering plant family. One wonders why this is so. Outside angiosperms, a few species occur on pteridophytes (*Selaginella, Osmunda*) and conifers (*Araucaria*). The following partial list is illustrative:

PTERIDOPHYTES

On Selaginella : *Melaniella*
On Osmunda : *Exoteliospora* Gymnosperms-Conifers
On Araucaria : *Uleiella*
Monocotyledons
On Gramineae (mostly) : *Ustilago*, *Tilletia*, *Neovossia*, *Jamesdicksonia*
On Cyperaceae : *Anthracoidea Cintractiella*, *Farysia, Planetella*,
Schizonella, Zundelula
On Cyperaceae and Juncaceae: *Entorrhiza*
On Alismataceae : *Narasimhania*
On Lemnaceae: *Tracya*

DICOTYLEDONS

On Araliaceae: *Mundkurella*
On Caryophyllaceae: *Microbotryum*
On Convolvulaceae: *Georgefischeria**
On Scrophulariaceae: *Schroeteria*
On Solanaceae: *Polysaccopsis*
On Vitaceae: *Mycosyrinx*

*Note: The two original species of *Georgefischeria*, including the type species, were on Convolvulaceae. However, several other species on hosts of other families have been added.

There are also genera in the Exobasidiales that are characterized by similar host specificity such as, for example:

MONOCOTYLEDONS

On Commelinaceae: *Kordyana*
On Palmae: *Brachybasidium, Graphiola*
On Heliconiaceae (*Heliconia*): *Proliferobasidium*

DICOTYLEDONS

On Ericaceae, Theaceae, Lauraceae, Epacridaceae, Empetraceae, Symplocaceae: *Exobasidium*
On Ulmaceae (Celtis), Anacardiaceae (Rhus): *Muribasidiospora*
On Bombaceae (*Bombax*): *Ceraceosorus*
On Lauraceae: *Cryptobasidium*

Hutchinson (1948) visualized the origin of Ericaceae from Theaceae. A close affinity between Ericaceae and Epacridaceae, considered the Australian counterpart of Ericaceae, has also been suggested from a comparison of the organography and vascular anatomy of the flower (Paterson 1961). From a chemical angle, Theaceae, Ericaceae and Empetraceae are all known to produce tannins and catechols, a feature not shared by the other families. Specialized pathogens could well be attracted by similarity in physiology and metabolism of host families. It is logical to visualize groups of related species infecting groups of related host species.

Sundstrom (1964) studied 72 strains of *Exobasidium* belonging to nine species representing 16 host-races. Specificity of host-races was confirmed. *Exobasdium vexans*, the tea (*Camellia sinensis*) blister blight pathogen was considered only distantly related to other *Exobasidium* spp.

Current interest in the smut genus *Entyloma* encourages me to highlight recent work on this genus. There are over 400 names in the genus *Entyloma*, leaf parasites mostly named on their host-occurrence. Most other foliicolous pathogens such as *Cercospora* have also in the past been christened from their host of choice. Thus, there could be as many species names as there are different hosts. In so far as host specificity is stable, such naming of species might be in order. But in most cases there is no experimental or even field observational proof. And yet, the genus *Entyloma* with more than 400 names, for example, is in the melting pot. In the result, about thirty species in *Entyloma* and related complexes have been reclassified into nine or ten new genera during the past two decades or so, as shown below:

MONOCOTYLEDONS

On Gramineae: *Ustilentyloma* Savile, *Eballistra* Bauer et al.
On Sparganiaceae (*Sparganium*): *Nannfeldtiomyces* Vanky
On Restionaceae: *Websdanea* Vanky. *Restiosporium* Vanky
On Liliaceae: *Gjaerumia* Bauer et al.
On Araceae: *Entylomaster* Vanky & R G Shivas

DICOTYLEDONS

On Nymphaeaceae: *Rhamphospora* D D Cunn.
On Ranunculaceae, Lythraceae, Primulaceae, Callitrichaceae, Acanthaceae: *Heterodoassansia* Vanky
On Sterculiaceae: *Geminago* Vanky & R Bauer

On Callitrichaceae: *Doassinga* Vanky

The authorities cited for the new generic names are intended to indicate that the revisions are recent. The major part of these revisions concerns those on monocots. The revisions reflect the significant diversity in host specificity in *Entyloma* and other related genera. One cannot help considering the *Entyloma* complex as a fast evolving taxon, rather a co-evolving one at that. Begerow, Lutz and Oberwinkler (2002) note that the phylogenetic picture emerging from their molecular studies suggests joint evolution with their hosts. For the genus *Entyloma*, their results point to unresolved groups on Ranunculales and a well-supported group on Asteridae.

Yes, as a group, the smuts have evolved in association with their hosts; in the case of monocots, with a distinctly higher preference to the Poaceae than the Cyperaceae, apparently the two most favoured families. We have thus interesting data on host preferences and specificity of the smuts and related fungi and also a reshuffling of species, genera, and families which emphasizes specificity and host range.

MYCORRHIZA

All plants, from bryophytes to angiosperms, harbour mycorrhizal fungi. Among mycorrhizas, vesicular arbuscular mycorrhizal (VAM) fungi are the most widespread, the most ancient and perhaps the least specialized. They have many potential hosts, bryophytes, lycopods and ferns, gymnosperms and angiosperms, although their diversity is limited to less than 200 species in about a dozen or fewer genera. Considering the vast host range and the long history of the group, one wonders why there has been little diversification. The answer could be that diversification comes from challenges. On the other hand, there could well be many biotypes

or races for each species, experimental proof for which is hard to get as VAM fungi are not known to have a saprophytic phase, cannot be brought into culture and so are not easily used in cross-inoculation tests. In plants with VAM fungi, other mycorrhizal fungi are seldom associated, though in rare cases VAM and ectomycorrhizas (ECM) may co-exist. The genus *Alnus* (Betulaceae) is unique in harbouring besides VAM and ECM, nitrogen-fixing *Frankia.*

Ectomycorrhizas (ECM) show more specificity in the choice of hosts than VAM. Possibly, they evolved with vascular plant progenitors of Pinaceae in the Jurassic. It would seem they also developed with progenitors of a dozen or so families of present day angiosperms (Halling 2001). Moyersoen (2006) calls attention to the consistent association of ECM with paleotropical Dipterocarpaceae and suggests an ancient Gondwanaland origin for the ECM habit in the family. The favoured hosts for ECM are dicotyledons, with only a single record on a monocot (Cyperaceae), and a few records on ferns (e.g. *Adiantum)*. Among dicotyledons, families in which many genera are known to be ectomycorrhizal include Betulaceae, (6), Dipterocarpaceae (9), Ericaceae (9), Fagaceae (8), Caesalpinioideae (12), Papilionatae (17), Myrtaceae (7), Rhamnaceae (5), and Rosaceae (9) [number of genera within brackets]. Among others, Bignoniaceae, Caprifoliaceae, Casuarinaceae Elaeagnaceae, Juglandaceae, Lauraceae, Mimusoideae, Nyctaginaceae, Oleaceae, Platanaceae, Polygonaceae, Rubiaceae, Salicaceae, Sterculiaceae, and Ulmaceae are important host families. Several genera of the Pinaceae, and *Gnetum* (Gnetaceae) among gymnosperms are also hosts. While several fungal species belonging to diverse genera can infect a given host species, a given fungal species can be mycorrhizal on several

unrelated hosts. Indeed, granting that the soil harbours a diversity of mycorrhizal fungi, it is not surprising that there is a succession of mycorrhizal fungi on say a given tree, depending on its age. The picture of specificity that emerges from all this is complex.

The majority of ectomycorrhizal fungi are Basidiomycetes, followed by Gastero-mycetes, and Ascomycetes. The genera *Lepiota*, *Amanita, Boletus, Suillus, Cortinarius, Hebeloma*, *Inocybe, Paxillus, Lactarius, Russula, Laccaria*, and *Cantharellus* represent a small fraction of the common ectomyco-rrhizal basidiomycetes. A similar short list in the Gasteromycetes would include *Rhizopogon, Lycoperdon, Pisolithus* and *Scleroderma*. Among Ascomycetes, several hypogeous forms are mycorrhizal such as species of *Tuber, Balsamia*, and *Elaphomyces*, besides others such as *Helvella.*

Those studying ecology of the larger fungi are familiar with the association of fruit-bodies of larger fungi with specific trees in woodlands. This gives indication of mycorrhizal associations of the fruit-bodies with a given tree species. For example, *Boletus edulis, Amanita muscaria*, and possibly *Lycoperdon umbrinum* and *Tuber rapaeodorum* have been reported to be associated with *Pinus patula* in South Africa (Mrais and Kotze1975). On the other hand, in Kodaikanal in the Pulney Hills in Southern India, *Thelephora terrestris* and *Laccaria laccata* are so-called "early stage" colonizers and *Amanita muscaria* and *Scleroderma verrucosum* are "late stage" colonizers of *Pinus patula* (Natarajan 2005).

It is noteworthy that the cosmopolitan *Pisolithus tinctorius* is not associated with *Pinus patula* in the Nilgiris. Also, *Laccaria fraterna,* which is closely associated with *Eucalyptus globulus*, is not found with *Pinus patula* in the Nilgiris. Indeed, specificity here propels co-evolution of host and symbiont.

In the Kadamakkal Reserve Forest in Karnataka, Dipterocarps predominate. Species of *Russula, Boletus* and *Amanita* are the dominant ectomycorrhizal components on Dipterocarps here. There is greater diversity of ectomycorrhizal fungi in this region than in the Nilgiris which might be a reflection of the tropical nature of the forest in the Kadamakkal area. The association of a new genus and species of the Cortinariaceae, *Anamika indica*, with *Hopea* species (Dipterocarpaceae), reported from Kerala in southern India (Thomas *et al.* 2002) indicates that there may be other new taxa specific to Dipterocarps.

The Pasoh Forest Reserve in Malaysia which is rich in diversity of flowering plants and their ECM fungi has been the focus of study by Roy Watling and his associates (Watling *et al.* 2002). Their study of species and genera of about 40 families of flowering plants showed a mycorrhizal component of species of 14 basidiomycete families. The Russulaceae, particularly the genus *Russula,* accounted for the largest number (218) of collections or basidiomes, followed by Amanitaceae (26) and Boletaceae (22), in that order. Also, *Russula* was represented by the largest number of species. The extensive data on host species and their respective symbiont fungi help us to gauge the range and character of specificity at least in outline. Such studies have relevance in afforestation and forest development.

ENDOPHYTES

That most flowering plants have endophytic fungi is now established although there is a long way to go toward understanding their biology. The Clavicipitaceous endophytes of grasses, the Balansiae of the Clavicipitaceae (*Atkinsoniella*, *Balansia, Balansiopsis, Epichloe, Myriogenospora*) are examples. These fungi are systemic and perennial within their hosts. Beginning as pathogens inducing sterility in the host, these endophytic fungi are

considered to have evolved to a mutualism in which the fungus itself has lost its fertility and is led to live a life of sterility reduced to a mycelial state, as numerous endophytes are known to be (Clay 1988). That these fungi produce secondary metabolites that serve to protect the hosts from herbivory ensures also the sustenance of the fungus by the host. This is an enticing hypothesis. And yet, we must know the mechanism and *modus operandi* of plant-fungus recognition in this case and the numerous examples of endopohyte-plant connection in the wide spectrum of dicot hosts that harbour endophytic fungi.

CYTTARIA-NOTHOFAGUS CO EVOLUTION

My talk would be incomplete without reference to the remarkable specificity between the fungus *Cyttaria* and its only host, *Nothofagus*. The genus *Cyttaria* was established by the British mycologist, the Rev. M J Berkeley for collections made by Charles Darwin in Tierra del Fuego during his Beagle voyage in 1832 which he (Berkeley) christened *C. darwinii* in 1842. There are about a dozen species of *Cyttaria* (Cyttariaceae, Cyttariales, Leotiomycetes, Ascomycota) obligately associated with species of *Nothofagus* (Fagaceae) which are seen only in parts of South America and Australasia. There are about thirty-five species of *Nothofagus* classified in four subgenera, Lophozonia, Fuscospora, Nothofagus, and Brassospora. Recent studies suggest that diversification at the subgeneric level should have occurred before the Gondwanan break-up (Setoguchi *et al.* 1997). Studies also point to dispersal of subgenera Lophozonia and Fuscospora between Australia and New Zealand The specificity of particular species of *Cyttaria* to particular species of *Nothofagus* propelled their coevolution and is reflected in their biogeography.

Apparently, evolution within the Australasian lineage, led to four species being currently found in Australasia. *Cyttaria darwinii* and six other species occur only in South America. Of the four Australasian species, *C. gunnii* is found in both Australia and New Zealand. *C.septentrionalis* occurs only in Australia, and *C. nigra* and *C.pallida* occur only in New Zealand. The only New Zealand host is *Nothofagus menziesii*. Molecular phylogenetic studies of *Cyttaria* suggest transoceanic dispersal from Australia to New Zealand followed by local species radiation.

The subgenus Brassospora comprises 19 of the 35 species of Nothofagus and occurs only in Papua New Guinea and New Caledonia. The occurrence of Brassospora in New Caledonia is considered a single colonization event from New Zealand where the subgenus later became extinct in the Pliocene (Swenson *et al.* 2001). In fact, the New Caledonian species form a derived monophyletic group. Curiously*, Cyttaria* is not known on *Nothofagus* in New Caledonia and Papua New Guinea, even though competent mycologists have looked for it in these regions. We do not know why. The fossil record of *Nothofagus* pollen shows three types, the oldest of which is presently found only in the *Nothofagus* of New Caledonia and Papua New Guinea. The *Nothofagus* species in these two islands have been called "living fossils" and represent relicts of the ancestral lineage. This would mean that the ancestor of all extant *Nothofagus* species evolved before *Cyttaria*. The *Cyttaria-Nothofagus* specificity and coevolution are fascinating and yet mysterious.

PARASITIC PLANTS

Parasitic plants are found only among dicotyledons, but not among monocotyledons, ferns or gymnosperms. We not know why this is so. There are about a dozen families of dicots that are parasitic: Viscaceae (the mistletoes, e.g. *Viscum album*), Loranthaceae (the mistletoes, e.g. *Arceuthobium, Nuytsia*),

Orobanchaceae (e.g. *Orobanche*), Santalaceae (e.g. *Santalum album*), Cuscutaceae (e.g. *Cuscuta*), Scrophulariaceae (e.g. *Striga),* Rafflesiaceae (*Rafflesia arnoldiana*), and Hydnoraceae (e.g. *Hydnora*). Among mistletoes, *Viscum album* has a wide host range. At one time, at least three biological species were recognized for *V. album*: the hardwood mistletoe (f.sp. *mali*), the fir mistletoe (f.sp. *abietis*) and the pine mistletoe (f.sp. *pini*). The hardwood mistletoe has a very wide host range. The dwarf mistletoe, *Arceuthobium douglasii* specifically infects only Douglas fir (*Pseudotsuga douglasii*). The Australian *Nuytsia floribunda* with its crimson flowers of arresting beauty parasitizes roots of various grasses and herbaceous plants in its vicinity. *Phrygilanthus acutifolius*, the Brazilian mistletoe, parasitizes roots of a range of trees, all at the same time. *Striga* species preferentially attack cereals such as sorghum and millets in the tropics. On the other hand, *Orobanche uniflora*, parasitizes a variety of plants. The tropical *Rafflesia* with its conspicuous flowers (the largest in the plant kingdom!) attacks only tropical species of the Vitaceae. The evolution of specificity in these parasitic dicot families, as in the other examples already cited, remains mysterious.

THE UBIQUITY OF SPECIFICITY

Look around, and we see specificity everywhere. The theme abounds in examples. The obligate mutualism between the fig, *Ficus sycamorus* and the fig wasp, *Ceratosolen arabicus* is a beautiful example of coevolution steered by specificity. The specificity of the relationship between *Yucca* flowers and the Yucca moth *Tegeticula yuccasella* similarly steered their coevolution. We know of numerous other examples of specificity, for example, of pollinators (insects, birds, bats) and plants.

Specificity can also be seen in the development of associations between plants and ants, for example in the association of *Acacia* species and species of *Pseudomyrmex*. In Malaysia and other tropical regions *Macaranga* (Euphorbiaceae) trees which are a major component of the ecosystem, have established a relationship with ants of the genus *Crematogaster*. The myrmecophytic system is complex in relation to life types and species diversity. In these associations, the ants act as active defenders against herbivores, provide the plants with nutrition, and disperse the seeds. In return, the ants are provided with nutrition and space to build nests.

Ants play host to a range of other arthropod species, feeding and sheltering them. The ants' hospitality is linked to the guests' ability to communicate in the same chemical and mechanical "language" of the host. The guests have acquired the ability to speak the visual, chemical and mechanical "language" of the hosts (Hoelldobler 1971).

There are many examples of associations of bacteria with animals and plants, many of which are ubiquitous. The *Rhizobium*-legume interaction is one such. One wonders at the specificity of the *Rhizobium*-legume phenomenon. The legume-*Rhizobium* association is unique, the *Rhizobium* not being able to form an association with any other family (with the exception of the tropical *Parasponia* [Ulmaceae]- but this needs further study). This might be because of the unique ability of legumes to synthesize isoflavonoids (Young and Johnston 1989). In contrast to *Rhizobium,* the closely related *Agrobacterium tumefaciens*, the crown gall pathogen, infects many species of mostly woody plants belonging to about a hundred families of dicots and gymnosperms, but not monocots. There are associations of nitrogen-fixing cyanobacteria (blue-green algae) with fungi, bryophytes such as *Anthoceros*, the water fern *Azolla*, the cycads, and *Gunnera*. There are about fifty species of *Gunnera* which carry in their secretory glands *Nostoc punctiforme*. The

Nostoc does not photosynthesize but fixes nitrogen at an extraordinary rate. Specificity is seen in all these associations. Cyanobacteria evolved very early in the life of our planet and their association with plants also seems to have evolved early.

Finally, we must note that saprotrophs also show specificity, though there are several which are omnivorous. There are many fungi of all major groups that preferentially colonize palms, or bamboos, grasses or other monocots such as the Cyperaceae. There are those that preferentially colonize dicot twigs, leaves, wood and bark. Lists of fungi recorded on palms, for example, show the diversity of fungi that colonize palms worldwide. In his work on chytrids and other lower aquatic fungi John S Karling used diverse substrates such as chitin, keratin and cellulose as baits to isolate fungi and categorized them as chitinophiloc, keratinophilic and cellulosophilic. Among soil-borne pathogens of plants, some such as *Fusarium udum* and *Gaeumannomyces graminis* survive only on tissues colonized as pathogens and do not usually colonize other substrates. As we have noted, there are also others such as *Fusarium vasinfectum* that colonize a variety of substrates saprophytically. Thus, we find a wide spectrum of specificity among saprotrophs also.

EPILOGUE

I have said enough to highlight the ubiquity of specificity seen in biotic interactions which are an integral part of life on our planet. In an overview of the examples I have given, from bacteria through the fungal, animal and plant kingdoms, many interactions between primitive organisms such as the bacteria and fumgi with, for example, plants are seen to be mutualistic. The endosymbiotic origin of chloroplasts and mitochondria in the Eucaryotes is itself an example of ancient mutualism. The emergence of many phyla of fungi, animals and plants in the eukaryote

lineage happened later. In this sequence, VAM fungi coevolved with Psilophytes in the Devonian, evidently as symbionts. Cyanobacterial endosymbionts also coevolved with hosts early in this sequence. ECM fungi seem to have coevolved with ancestral pines during the Jurassic and later with proto-Angiosperms. On the other hand, there are few parallel ancient records of interactions of plants and fungi as pathogens. Obviously, most known ancient interactions were mutualistic and marked by specificity. We do not see epidemic plant disease in a natural forest. Pathogens and disease were rare and appeared primarily only in the wake of domestication of plants and monoculture (agriculture).

Specificity involves recognition. In fact, it is grounded in recognition. One wonders how a symbiont or pathogen chooses and recognizes its host in the first instance. There are countless symbionts and pathogens and a comparable number of potential hosts and it is remarkable how, for example, almost all plants harbour a specific symbiont or endophyte, resulting in a beautiful mutualism. There is no doubt that fungi are good taxonomists. We know a great deal about the *modus operandi* of symbionts and pathogens, particularly their structure (morphology), their genetics and their chemistry, but not enough to explain specificity *per se.* For most interactions, having found the primary host, there is the option to find a secondary host or hosts. Though open, the option is used selectively and not necessarily always. But why? It might be that a given set of genes for compatibility present in the host of choice may not be present in non-hosts (Hijwegen 1988). It may also be a matter of chemistry.

In the case of heteroecious rust fungi which complete their life cycle on two unrelated hosts, again one wonders how the two hosts are chosen and recognized. Where there are collateral hosts, they are mostly, not necessarily always, of the same genus or

family, but this is not the case with alternate hosts. The many examples of pairs of unrelated (telial and aecial) hosts in the heteroecious rusts are thus not easily explained. This is also true of the uniqueness of the Blastocladialien *Coelomomyces* in which there is an alternation of a sporophyte within mosquito larvae and a gametophyte within the body of copepods. Following the discovery of alternation of generations in the closely related *Allomyces,* it was wonderful to find a similar condition in *Coelomomyces*, with the additional grandeur of completion of life cycle in two unrelated hosts, a feature known only in the rust fungi.

All interactions in nature are part of a system of nature governed by the dictum, "live and let live". It is this dictum that is the basis of coevolution. Every organism is sustained by a lifestyle that is unique in itself in a scheme that sustains biota. It has been said that endosymbiosis such as what we have considered steered evolution of plants quite early. Further, the synchrony of the rise of flowering plants and the rise of insects was of mutual advantage to flowering plants and insects where each served the other. As pollinating agents, insects facilitated cross-fertilization in plants thereby contributing to plant diversity. Saprotrophy is nature's wonderful way of disposing off wastes and recycling of essentials carbon, nitrogen, oxygen et al.- as part of its beautiful system. Water itself is a product of specificity of two elements to come together and unite. And even in the case of saprotrophs there is specificity. Thus, left to itself, nature takes care of itself. The rise of pests and diseases and our agenda in combating them ensures the appearance of more destructive pests and more aggressive pathogens and the genetic diversity of host cultivars and pathogen races. In other words, we have to contend with not just species diversity but genomic diversity. All this has blurred the picture of specificity.The rising population, the rise of technology, the denudation and destruction of forests and vegetation, the pollution of waterways and seas, all sum up to a dangerous onslaught on the system of nature that could have sustained itself to the benefit of mankind. That system is essentially built on interactions that are mutualistic. The human system is the best visible example of an integrated system of organs and metabolism homoeostasis, a wonder of wonders. I am led to believe specificity is basically the principle behind mutualism which is a major factor in speciation and evolution. The drive for specificity is intrinsic in the organism. And all interactions among the biota are built on specificity, be it the physical colonization of organisms or substrates, or the chemical armoury of enzymes, pheromones or other substances.

If the thoughts I have shared with you kindle your imagination to probe deeper into the beauty and mystery of specificity, I would feel happy. Thank you.

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