TROPICAL FERN HOSTS OF RUST FUNGI

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RUSTS ON FERNS are referred in current literature on mycology and plant pathology to the definitive genera *Hyalopsora*, *Milesia*, *Uredinopsis*, *Desmella* and *Puccinia* and in a few instances to the imperfect genus *Uredo*. The complete life-histories of many species of the first three have already been determined experimentally; in all cases they have proved to be heteroecious, with species of *Abies* serving exclusively as their aecial hosts. So it may quite safely be assumed that the same pattern is potentially true of all the other species of *Hyalopsora*, *Milesia* and *Uredinopsis*. Regarding *Desmella*, uredia and telia only are known; and as they are so unlike those of the three foregoing genera, the identities of hosts that can carry the aecial stages of *Desmella* rusts are not even conjectured. It is a strange genus, taxonomically standing quite apart from the other fern-restricted genera. Thus far it has been reported from the American tropics only. Among the remaining fern rusts, a single species of *Puccinia* has been described, though solely with respect to its uredia and telia. Finally, as to the *Uredo* fern rusts, they can with reasonable certainty be recognized as uredo stages of one or other of the five definitive genera. Indeed, not a few of the named species of these genera have been described from the uredo stage and without knowledge of telia. Although technically open to some objections, this practice does offer advantages if used with discretion.

With possible exceptions of Australia and Tasmania, fern rusts are world-wide in distribution. Of course, locally within any extensive region there may be limiting factors, such, for example, as continuously high day and night temperatures. Otherwise they are likely to be found wherever ferns grow and on a surprisingly large number of specific hosts. Naturally, where those that are *Abies*-infecting occur beyond the ranges of *Abies*, they can be perpetuated solely by seasonal transmission from affected ferns to plants of identical kind or of species that are likewise susceptible. Indeed, as the southern distributional limits of *Abies* are approached, this method becomes increasingly frequent, even in those rust species that lack amphispores. Of course this method is possible for amphispore-producing rusts in any latitude, but otherwise only wherever there is a sufficiently close overlapping of successive seasonal crops of fronds, that is, a succession within the vital life-span of ordinary urediospores. It may not be superfluous to recall to mind here that the most southerly ranges of existing *Abies*, though well within the tropics in the western hemisphere and reaching to the tropics in the eastern, fall far short of the equator.

TABLE I

PUBLISHED TROPICAL FERN HOSTS, THEIR RUSTS AND REGIONAL ORIGINS

Fern hosts	Rusts	Regional origins
1. *Adiantum andicola* Liebm.	*Uredinopsis investita* Faull	Guatemala†
2. *Anemia fulva* (Cav.) Sw.	*Desmella Aneimiae* (Henn.) Syd.	Brazil
3. *Anemia Phyllitidis* (L.) Sw.	*Desmella*	Brazil
4. *Anemia tomentosa* (Sav.) Sw. (*A. cheilanthoides* Kaulf.)	*Desmella Aneimiae* (Henn.) Syd.	Brazil†
5. *Antrophyum lanceolatum* (L.) Kaulf.	*Hyalopsora Polytaenii* (KCT) Cummins	Dominican Republic†; Porto Rico
6. *Blechnum occidentale* L.	*Milesia australis* Arthur	Colombia†; Costa Rica; Porto Rico
7. *Blechnum unilaterale* Sw. [*B. blechnoides* (Lagerh.) C.Chr.]	*Uredinopsis Mayoriana* Diet.	Colombia†
8. *Blechnum volubile* Kaulf.	*Desmella* (*Uredo blechnicola* Henn.)	Brazil†
9. *Cheilanthes pyramidalis* Fée	*Uredinopsis glabra* Faull	Mexico
10. *Coniogramme fraxinea* (Don) Diels	*Milesia Coniogrammes* (Hirats. f.) n. comb. (*Milesina Coniogrammes* Hirats. f.)	Formosa
11. *Cystopteris fragilis* (L.) Bernh.	*Uredinopsis glabra* Faull	Mexico†
12. *Dennstaedtia rubiginosa* (Kaulf.) Moore	*Desmella*	Porto Rico
13. *Dennstaedtia rubiginosa* (Kaulf.) Moore	*Milesia Dennstaedtiae* (Diet.) Faull	Colombia†
14. *Dryopteris* sp. [Close to *D. oligocarpa* (H. & B.) Kuntze]	*Milesia andina* Faull	Ecuador†
15. *Dryopteris Clarkei* (Bak.) Kuntze	*Milesia Miyabei* (Kamei) Faull	Formosa
16. *Dryopteris dentata* (Forsk.) C. Chr. [*D. mollis* (Jacq.) Hieron.]	*Desmella*	Porto Rico
17. *Dryopteris patens* (Sw.) Kuntze	*Milesia consimilis* Arthur	Jamaica†
18. *Dryopteris Poiteana* (Bory) Urban	*Desmella*	Porto Rico
19. *Dryopteris Poiteana* f. *prolifera*	*Desmella*	Venezuela

TABLE I (*Continued*)

Fern hosts	Rusts	Regional origins
20. *Dryopteris quadripinnata* Hayata	*Milesia carpatica* var. *erythrosora* Faull [*Milesina erythrosora* (Faull) Hirats. f.]	Formosa
21. *Dryopteris tetragona* (Sw.) Urban	*Desmella*	Porto Rico
22. *Dryopteris tetragona* var. *guadalupensis* C.Chr.	*Desmella*	Venezuela
23. *Elaphoglossum* sp.	*Hyalopsora obovata* (Arthur) Cummins	Colombia
24. *Elaphoglossum latifolium* (Sw.) J. Sm.	*Hyalopsora obovata* (Arthur) Cummins	Jamaica†
25. *Lygodium micans* Sturm (*Lygodium* sp.)	*Uredo* (*Milesina Lygodii* Syd.)	Br. Guiana
26. *Lygodium polymorphum* (Cav.) HBK	*Puccinia Lygodii* (Hariot) Arthur	Brazil†; San Salvador; Trinidad; Venezuela
27. *Lygodium volubile* Sw.	*Uredo*	Brazil
28. *Nephrolepis cordifolia* (L.) Presl	*Milesia philippinensis* (Syd.) n. comb. (*Milesia tenuis* Faull)	Philippine Islands†
29. *Nephrolepis pendula* (Raddi) J. Sm.	*Milesia columbiensis* (Diet.) Arthur	Colombia†
30. *Nephrolepis rivularis* (Vahl) Mett.	*Milesia insularis* Faull	Porto Rico†
31. *Onychium japonicum* (Thunb.) Kunze (*Cryptogramme japonica* Prantl)	*Milesia Cryptogrammes* (Diet.) n. comb. [*Milesina Cryptogrammes* (Diet.) Hirats. f.]	Philippine Islands
32. *Pellaea cardiomorpha* Weath.	*Uredinopsis glabra* Faull	Mexico
33. *Pellaea ternifolia* (Cav.) Link	*Hyalopsora Cheilanthis* (Peck) Arthur	Ecuador
34. *Pellaea viridis* (Forsk.) Prantl [*Pellaea hastata* (Thunb.) Prantl]	*Milesia nervisequa* (von Thümen) Faull	Madagascar
35. *Pityrogramma calomelanos* (L.) Link	*Desmella*	Ecuador†; Venezuela
36. "*Polypodiacea* sp."	*Desmella*	Ecuador
37. *Polypodium arisanense* Hayata	*Milesia Hashiokai* (Hirats. f.) n. comb. (*Milesina Hashiokai* Hirats. f.)	Formosa†
38. *Polystichum amabile* (Bl.) J. Sm.	*Milesia arisanensis* (Hirats. f.) n. comb. (*Milesina arisanense* Hirats. f.)	Formosa†

TABLE I (*Continued*)

Fern hosts	Rusts	Regional origins
39. *Pteridium aquilinum* (L.) Kuhn, including varieties and marginal species	*Uredinopsis macrosperma* (Cooke) Magn.	Brazil; Colombia; Cuba; Guatemala; Honduras; Jamaica; Mexico; Panama; Venezuela; Belgian Congo†
40. *Pteridium aquilinum* var. *decompositum* (Gaud.) Tryon	*Uredinopsis aspera* Faull	Hawaii
41. *Pteridium aquilinum* var. *Wightianum* (Agardh) Tryon	*Uredinopsis Hashiokai* Hirats. f.	Formosa†

†Where type was collected.

Not much collecting of fern rusts has been done in the tropics. Yet there is a considerable accumulation from mainly incidental collecting over the years. These are listed above in Table I, and it is quite an impressive compilation. But my own limited, yet intensive collectings in the tropics of North America, supplemented by occasional contributions from correspondents and a few gleanings from fern collections in the Gray Herbarium of Harvard University, are sufficient to show that the number of known fern hosts is probably a small representation of fern species that, in one region or another, carry rust fungi. Table II presents new acquisitions obtained by me in the ways indicated above. Among these are unpublished collecting records of a few species listed in Table I; they are marked with an asterisk (*).

One of the reasons for publishing these lists before detailed studies have been completed on them is to call the attention of collectors in the tropics to a seemingly passed-by group of rust hosts. They will also serve to indicate that our knowledge of fern and fir rusts is far from complete. But now at least enough materials and sources of supply are available to justify more adequate taxonomic review and a wider range of other investigations.

TABLE II

NEW RECORDS FOR TROPICAL FERN HOSTS OF RUST FUNGI

Fern hosts	Rusts	Regional origins
	A. Fam. **Ophioglossaceae**	
1. *Botrychium virginianum* (L.) Sw.	*Hyalopsora*	Guatemala
	B. Fam. **Schizaeaceae**	
2. *Anemia hirsuta* (L.) Sw.	*Desmella*	Jamaica; Mexico
3. *Anemia hirsuta* (L.) Sw.	*Milesia*	Jamaica; Mexico
4. *Lygodium heterodoxum* Kunze	*Uredo*	Guatemala
	C. Fam. **Gleicheniaceae** (?)	
5. *Gleichenia* sp. (?)	*Milesia*	New Guinea
	D. Fam. **Cyatheaceae**	
6. *Cyathea* sp.	*Hyalopsora*	New Guinea
7. *Cyathea fulva* (M. & G.) Fée	*Milesia*	Mexico
8. *Cyathea Harrisii* Underw.	*Milesia*	Jamaica
9. *Cyathea mexicana* Schl. & Cham.	*Milesia*	Guatemala
	E. Fam. **Polypodiaceae**	
10. *Adiantum Capillus-veneris* L.	*Hyalopsora*	Mexico
11. *Adiantum latifolium* Lam.	*Desmella*	Trinidad
12. *Adiantum subcordatum* Sw.	*Hyalopsora*	Brazil
13. *Anogramma chaerophylla* (Desv.) Link	*Hyalopsora*	Mexico
14. *Anogramma chaerophylla* (Desv.) Link	*Uredinopsis*	Mexico
15. *Asplenium malayo-alpinum* Holtt.	*Milesia*	New Guinea
16. *Asplenium monanthes* L.	*Hyalopsora*	Guatemala; Mexico
17. *Asplenium monanthes* var. *Galeotti* (Fée) Hieron.	*Hyalopsora*	Mexico
18. *Athyrium* sp.	*Hyalopsora*	New Guinea
19. *Athyrium Dombei* Desv.	*Uredinopsis*	Guatemala; Mexico
20. *Athyrium paucifrons* C. Chr. (?)	*Milesia*	Mexico
21. *Athyrium Skinneri* Moore	*Hyalopsora*	Mexico
22. *Blechnum* sp.	*Milesia* or *Hyalopsora*	New Guinea
23. *Blechnum fraxineum* Willd.	*Milesia*	Venezuela

TABLE II (*Continued*)

Fern hosts	Rusts	Regional origins
24. *Blechnum occidentale* L.*	*Milesia*	Cuba; Guatemala; Jamaica; Mexico; Panama; Venezuela
25. *Blechnum orientale* L.	*Hyalopsora*	Borneo
26. *Blechnum unilaterale* Sw.	*Milesia*	Mexico
27. *Cheilanthes membranacea* (Davenp.) Maxon	*Uredinopsis*	Mexico
28. *Cheilanthes microphylla* Sw.	*Milesia*	Jamaica
29. *Cheilanthes pyramidalis* Fée	*Hyalopsora*	Mexico
30. *Cheilanthes tenuifolia* (Burm.) Sw.	*Milesia*	New Guinea
31. *Coniogramme fraxinea* (Don) Diels	*Hyalopsora*	China (Lat. 25° N)
32. *Cyclopeltis semicordata* (Sw.) J. Sm.	*Desmella*	Trinidad
33. *Cystopteris fragilis* (L.) Bernh.	*Hyalopsora*	Mexico
34. *Dennstaedtia adiantoides* (H. & B.) Moore	*Milesia*	Cuba
35. *Dennstaedtia cicutaria* (Sw.) Moore	*Milesia*	Mexico
36. *Dennstaedtia dissecta* (Sw.) Moore	*Milesia*	Jamaica
37. *Dennstaedtia exaltata* (Kze.) Hieron.	*Milesia*	Mexico
38. *Dennstaedtia ordinata* (Kaulf.) Moore	*Milesia*	Jamaica
39. *Dennstaedtia rubiginosa* (Kaulf.) Moore*	*Desmella*	Jamaica
40. *Dennstaedtia rubiginosa* (Kaulf.) Moore*	*Milesia*	Guatemala; Jamaica; Panama
41. *Diplazium* sp. (?)	*Hyalopsora*	New Guinea
42. *Diplazium* sp. (?)	*Hyalopsora*	New Guinea
43. *Diplazium crenulatum* O. Liebm.	*Milesia*	Guatemala
44. *Diplazium expansum* Willd.	*Desmella*	Cuba
45. *Dryopteris* sp.	*Milesia*	New Guinea
46. *Dryopteris*, n. sp. (?) acc. to Maxon	*Milesia*	Jamaica
47. *Dryopteris boqueronensis* Hieron. (?)	*Milesia*	Ecuador

TABLE II (*Continued*)

Fern hosts	Rusts	Regional origins
48. *Dryopteris concinna* (Willd.) Kuntze	*Milesia*	Guatemala; Panama
49. *Dryopteris dentata* (Forsk.) C. Chr.	*Milesia*	Panama
50. *Dryopteris diplazioides* (Desv.) Urban	*Milesia*	Ecuador
51. *Dryopteris effusa* (Sw.) Urban	*Milesia*	Jamaica
52. *Dryopteris equestris* (Kunze) C. Chr.	*Milesia*	Guatemala
53. *Dryopteris firma* (Baker) C. Chr.	*Milesia*	Jamaica
54. *Dryopteris heteroclita* (Desv.) C. Chr.	*Milesia*	Jamaica
55. *Dryopteris melanochlaena* C. Chr.	*Milesia*	Guatemala
56. *Dryopteris navarrensis* Christ	*Milesia*	Panama
57. *Dryopteris Nockiana* (Jenm.) C. Chr.	*Milesia*	Jamaica
58. *Dryopteris oligocarpa* (H. & B.) Kuntze	*Desmella*	Jamaica
59. *Dryopteris oligocarpa* (H. & B.) Kuntze	*Milesia*	Guatemala; Jamaica; Mexico
60. *Dryopteris opposita* (Vahl) Urban (?)	*Milesia*	Panama
61. *Dryopteris paleacea* (Sw.) C. Chr.	*Milesia*	Guatemala; Mexico
62. *Dryopteris patens* (Sw.) Kuntze*	*Milesia*	Jamaica
63. *Dryopteris patula* (Sw.) Underw. var. *Rossii* C. Chr.	*Milesia*	Mexico
64. *Dryopteris pilosula* (Kl. & Karst.) Hieron. (approaches *D. navarrensis* Christ)	*Hyalopsora*	Guatemala
65. *Dryopteris resinifera* (Desv.) Weatherby	*Desmella*	Mexico
66. *Dryopteris resinifera* (Desv.) Weatherby	*Milesia*	Guatemala
67. *Dryopteris rubigena* Maxon & Morton	*Milesia*	Guatemala
68. *Dryopteris rudis* (Kze.) C. Chr. (?)	*Milesia*	Guatemala
69. *Dryopteris Sloanii* (Bak.) Kuntze (*D. oligophylla* Maxon)	*Milesia*	Jamaica

TABLE II (*Continued*)

Fern hosts	Rusts	Regional origins
70. *Dryopteris Sprengelii* (Kaulf.) Kuntze	*Milesia*	Jamaica
71. *Dryopteris tetragona* (Sw.) Urban*	*Desmella*	Jamaica
72. *Elaphoglossum lingua* (Raddi) Brack.	*Hyalopsora*	Jamaica
73. *Elaphoglossum Pringlei* (Davenp.) C. Chr.	*Milesia*	Mexico
74. *Hemionitis palmata* L.	*Milesia*	Jamaica
75. *Odontosoria Jenmanii* Maxon	*Milesia*	Jamaica
76. *Pellaea cardiomorpha* Weatherby	*Hyalopsora*	Mexico
77. *Pityrogramma sulphurea* (Sw.) Maxon	*Desmella*	Jamaica
78. *Polybotrya osmundacea* HBK	*Milesia*	Jamaica
79. *Polypodium aureum* L.	*Desmella*	Panama
80. *Polypodium ellipsoideum* Fée	*Hyalopsora*	Guatemala; Mexico
81. *Polypodium fissidens* Maxon	*Hyalopsora*	Guatemala
82. *Polypodium fissidens* Maxon	*Milesia*	Guatemala
83. *Polypodium loriceum* L.	*Desmella*	Jamaica
84. *Polypodium Martensii* Mett.	*Hyalopsora*	Guatemala; Mexico
85. *Polypodium plesiosorum* Kunze	*Uredinopsis*	Guatemala; Mexico
86. *Polypodium Veitchii* Bak. var. *glaucopsis* (Franch.) Ching	*Hyalopsora*	China (Lat. 26° N)
87. *Polystichum rachichlaena* Fée	*Milesia*	Guatemala
88. *Pteris longifolia* L.	*Milesia*	Jamaica
89. *Pteris longifolia* L.	*Desmella*	Jamaica
90. *Pteris quadriaurita* Retz.	*Milesia*	Panama
91. *Pteris quadriaurita* Retz.	*Desmella*	Jamaica
92. *Tectaria irregularis* (Pr.) Copeland (?)	*Milesia*	New Guinea
93. *Woodsia mollis* (Kaulf.) J. Sm.	*Hyalopsora*	Mexico

SUMMARY AND COMMENTS

1. Rusts are recorded for the first time as occurring in the Ophioglossaceae and Cyatheaceae. To these may possibly be added the Gleicheniaceae.

2. *Hyalopsora* rusts are recorded for the first time as occurring in the Ophioglossaceae and Cyatheaceae.

3. *Milesia* rusts are correctly recorded for the first time as occurring in the Schizaeaceae and Cyatheaceae. To these may possibly be added the Gleicheniaceae.

4. Species of the following fern genera, found growing within the tropics, are recorded in this paper as:

(a) hosts for DESMELLA rusts: **Adiantum** (1), *Anemia* (4), *Blechnum* (1), **Cyclopeltis** (1), *Dennstaedtia* (1), **Diplazium** (1), *Dryopteris* (5), *Pityrogramma* (2), "Polypodiacea" (1), **Polypodium** (2), **Pteris** (2);

(b) hosts for HYALOPSORA rusts: **Adiantum** (2), **Anogramma** (1), *Antrophyum* (1), **Asplenium** (1), **Athyrium** (2), **Blechnum** (1), **Botrychium** (1), **Cheilanthes** (1), **Coniogramme** (1), **Cyathea** (1), **Cystopteris** (1), **Diplazium** (2), **Dryopteris** (1), *Elaphoglossum* (2), *Pellaea* (2), **Polypodium** (4), **Woodsia** (1);

(c) hosts for MILESIA rusts: **Anemia** (1), **Asplenium** (1), **Athyrium** (1), *Blechnum* (4), **Cheilanthes** (2), *Coniogramme* (1), **Cyathea** (3), *Dennstaedtia* (6), **Diplazium** (1), *Dryopteris* (26), **Elaphoglossum** (1), **Gleichenia** ? (1), **Hemionitis** (1), *Nephrolepis* (3), *Onychium* (1), **Odontosoria** (1), *Pellaea* (1), **Polybotryum** (1), *Polypodium* (2), *Polystichum* (2), **Pteris** (2), **Tectaria** (1);

(d) hosts for UREDINOPSIS rusts: *Adiantum* (1), **Anogramma** (1), **Asplenium** (1), **Athyrium** (1), *Blechnum* (1), *Cheilanthes* (2), *Cystopteris* (1), *Pellaea* (1), **Polypodium** (1), *Pteridium* (including under *P. aquilinum* its varieties and marginal species).

The names in **black face** are genera within the tropics recorded for the first time as hosts for rust fungi. The numbers of species reported for each genus are indicated in parentheses.

5. *Desmella* is reported in this paper on 21 fern host species collected within the tropics, *Hyalopsora* on 24 species, *Milesia* on 63 species, *Uredinopsis* on 10 species, *Puccinia* on one species, and *Uredo* on 4 species. The paper lists a total of 109 tropical fern species (exclusive of varieties, etc.) known to be hosts of rust fungi; of these 73 are recorded for the first time.

6. I have found 25 rusted fern host species in Guatemala, 27 in Jamaica, 27 in tropical Mexico and 9 in Panama. Hashioka, in collections made both north and south of the Tropic of Cancer, reported 16 from Formosa (as published by Hiratsuka & Hashioka in their "Uredinales collected in Formosa"). Varieties are not included in any of these numbers, nor are the submarginal species of *Pteridium aquilinum*.

7. According to my experience, rusted ferns in the tropics are rarely found below an elevation of about 2000 feet above sea level. *Uredo* rust on *Lygodium* is exceptional; I collected it at sea level around Puerto Barrios in Guatemala. I could find no fern rusts on Barro Colorado Island, Panama Canal Zone; the greatest elevation on that island is said to be under 550 feet.

8. Much is to be expected from the vast mountainous regions extending eastward from Iran (Persia) to the South China Sea, from which have

come scant collections only, and these from very limited northern areas, probably in reality extratropical, such as around Kunming, Yunnan, China.

9. Comprehensive data based on old and new records embodied in fern rust collections from the tropics are summarized in Table III. This table designates all the relevant fern genera hosts, the numbers of their affected species, the involved rust genera for each fern genus, and the regions in which the collections were made.

TABLE III

FERN RUST HOST GENERA IN THE TROPICS AND THEIR DISTRIBUTION

		Desmella	*Hyalopsora*	*Milesia*	*Uredinopsis*
Adiantum	4[a]	Trinidad 1[a]	Mexico 1; Brazil 1	———	Guatemala 1
Anemia	4	Brazil 3; Jam. 1; Mex. 1	———	Jamaica 1; Mexico 1	———
Anogramma	1	———	Mexico 1	———	Mexico 1
Antrophyum	1	———	Dom. Rep. 1; Porto Rico 1	———	———
Asplenium	2	———	Guatemala 1; Mexico 1	New Guinea 1	———
Athyrium	4	———	Mexico 2; New Guinea 1	Mexico 1	Guatemala 1; Mexico 1
Blechnum	6	Brazil 1	Borneo 1	New Guinea 1[b]; Trop. Am.[c] 1, 1, 3	Colombia 1
Cheilanthes	4	———	Mexico 1	Jamaica 1; New Guinea 1	Mexico 1, 1
Coniogramme	1	———	———	Formosa 1	———
Cyathea	4	———	New Guinea 1	Guatemala 1; Jamaica 1; Mexico 1	———
Cyclopeltis	1	Trinidad 1	———	———	———
Cystopteris	1	———	Mexico 1	———	Mexico 1
Dennstaedtia	6	Jamaica 1; Porto Rico 1	———	Colombia 1; Cuba 1; Guatemala 1; Jamaica 3; Mexico 2; Panama 1	———
Diplazium	4	Cuba 1	New Guinea 2	Guatemala 1	———

[a] The numerals indicate the number of host species involved. Those in **black face** are new records.

[b] This might be a *Hyalopsora*.

[c] Colombia 2, Costa Rica 1, Cuba 1, Ecuador 1, Guatemala 1, Jamaica 1, Mexico 2, Panama 1, Porto Rico 1, Venezuela 2.