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Pine Stem Rusts of the World-Frame Work for a Monograph

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SUMMARY: The present taxonomic status of described species of pine stem rusts belonging to *Cronartium*, *Endocronartium*, and *Peridermium* are evaluated and discussed. Sixteen species of *Cronartium* have been recognized as varid species. There are four species of *Endocronartium* and another species likely exists in central China. Within these genera, five complexes or groups of closely related species and forms can be recognized. The need for more work in central and southern China, Mexico, northern Asia, and Vietnam is discussed.

Key Words: *Cronartium, Endocronartium, Peridermium,* taxonomy, nomenclature.

INTRODUCTION

Stem rusts are probably the most important pathogens of pines in the pine-growing areas of the world. Although taxonomy and nomenclature are relatively well known in this group of rust fungi, we still need clarification of several important species complexes and separation or amalgamation of species. Also, several species with autoecious life cycle forms have been discovered in recent years and more are probably still to be found in several areas of the world. I have been preparing a taxonomic monograph of this group of fungi for some years and I am delighted to present this paper to summarize the taxonomic status of the group and point out the areas needing further work.

Pine stem rusts are classified into one of three genera: *Cronartium*, *Endocronartium* and *Peridermium*. *Cronartium* is the genus containing species of pine stem rusts with known life cycle including uredinial and telial sates on alternate hosts. *Endocronartium* species are endocyclic,repeating on pine without having alternate hosts. *Peridermium* is a form genus accomodating anamorphic states on pine. Several significant taxonomic treatments of this group of rusts by Peterson (34,35,36,37)and several others (1,2,18) exist, but no comprehensive monograph has been compiled.

DESCRIBED SPECIES OF *CRONARTIUM*

The genus *Cronartium* was describes in 1815 by Fries with the type species *Cronartium asclepiadeum* (Willd.) Fries (9,42,46). The species is now considered to be a synonym of *C. flaccidum*.

Sydow ans Sydow (46) listed 22 species of *Cronartium* in their monumental compilation of rust fungi entitled "Monographia Uredinearum". Altogether more than 60 specific names have been described in *Cronartium*. Peterson (36) recognized 36 validly described *Cronartium* species in his treatment, but 19 of them are considered to belong to other genera. These genera are *Cianothrix*, *Crossopsora, Didymopsora* and *Endophylloides* (see below). These rusts were described as species of *Cronartium* mainly because of the gross morphology of their telia, but based on types of spermogonia and other morphological characteristics, they are now not considered to be closely related to *Cronartium*. None of them have *Pinus* as aecial hosts. They are all autoecious rusts.

They are as follows:

Cronartium andina Lagh.
≡*Cionothrix andina* (Lagh.) H. & P. Syd.

Cronartium antidesmae-dioicae H. & P. Syd.
≡*Crossopsora antidesmae-dioicae* (H. & P. Syd.) Arth. & Cumm.

Cronartium byrsonimatis P. Hennings
≡*Crossopsora byrsonimatis* (P. Henn.) R. Peterson

Cronartium egenula H. & P. Syd.
≡*Cionothrix egenula* (H. & P. Syd.) H. & P. Syd.

Cronartium eupatorinum Speg.
=*Cionothrix praelonga* (Wint.) Arth.

Cronartium fici T.S. & K. Ramakrishnan
≡*Crossopsora fici* Arth. & Cumm.

Cronartium gilgiana P. Henn.
Cionothrix gilgiana (P. Henn.) H. & P. Syd.

Cronartium jacksoniae P. Henn.
≡*Cionothrix jacksoniae* (P. Henn.) H. & P. Syd.

Cronartium kemangae Rac.

≡*Crossopsora kemangae* (Rac.) H. & P. Syd.

Cronartium malloti Rac.

≡*Crossopsora malloti* (Rac.) Cumm.

Cronartium notata Arth. & Johnst.

≡*Crossopsora notata* (Arth. & Johnst.) Arth.

Cronartium paraguayense Speg.

≡*Didymopsora paraguayensis* (Speg.) J. L. Cunningham

Cronartium portoricense (Whetsel. & Olive) Sacc. & Trott.

≡*Endopylloides portoricense* Whetzel & Olive

Cronartium praelonga Wint.

≡*Cionothrix praelonga* (Wint.) Arth.

Cronartium premnae Petch.

≡*Crossopsora premnae* (Petch) H. & P. Syd.

Cronartium sawadae H. & P. Syd.

≡*Crossopsora sawadae* (H. & P. Syd.) Arth. & Cumm.

Cronartium usneoides P. Henn.

≡*Cionothrix usneoides* (P. Henn.) H. & P. Syd.

Cronartium wilsoniana Arth. & Johnst.

≡*Crossopsora wilsoniana* (Arth. & Johnst.) Arth.

Cronartium zizyphi Syd. & Butl.

≡*Crossopsora zizyphi* (Syd. & Butl.) H. & P. Syd.

About 15 species other names were either not validly published or were based on uredinial states only and therefore are considered as nomen nuda. Together with a new species, *Cronartium arizonicum* which was described by Cummins in 1984 (6), we have 16 species which are validly described and published as *Cronartium* species, as follows:

Cronartium appalachianum Hepting, Mycologia 49:898, 1957.

Cronartium arizonicum Cummins, Mycotaxon 20: 617-618, 1984.

Cronartium coleosporioides Arthur, N. Am. Flora 7: 123, 1907.

Cronartium comandrae Peck, Bot. Gaz. 4: 128, 1879.

Cronartium comptoniae Arthur, Torrey Bot. Club Bull. 33: 29, 1906.

Cronartium conigenum Hedgcock & Hunt, Phytopathology 12: 116, 1922.

Cronartium delawayi Patouillard, Rev. Mycol. 8: 80, 1886.

Cronartium flaccidum complex

Cronartium flaccidum (Alb. & Schw.) Winter, Pilze Deutschland 1: 236, 1881.

Cronartium fusiforme Cummins, Mycologia 48: 603, 1956. Recognized as a few formae speciales of *C. quercuum*

Cronartium gentianeum Thümen, Österr. Bot. Ztschr. 28: 193, 1878.

Cronartium flaccidum complex

Cronartium himalayense Bagchee, Indian Forest Rec. Bot. Ser. 18: 14, 1933.

Cronartium flaccidum complex

Cronartium kamtschaticum Jørstad, Norske Vid. Akad. Olso I. Matem.-Naturvid. Kl. Skr. 1933 (9):27, 1934.2

Cronartium occidentale Hedgcock, Betherl & Hunt, J. Agric. Res. 14:413, 1918.

Cronartium quercuum (Berk.) Miyabe ex Shirai, Bot. Mag. (Tokyo) 13:74, 1899.

Cronartium ribicola Fischer in Rabenhorst, Fungi Europaei 1595, 1872.

Cronartium strobilinum Hedgcock & Hahn, Phytopathology 12: 109, 1922.

Some species listed above may need to be combined together or divided into different species or subspecific forms according to the species concept of the treatment.

DESCRIBED SPECIES OF *ENDOCRONARTIUM*

In 1969, Hiratsuka (13), based on cytological observations of spores and germinating spores, established the genus *Endocronartium* as an endocyclic genus and included two autoecious species, *Endocronartium harknessii* from North America and *Endocronartium pini* from Europe. Since then, two new species of *Endocronartium* have been described from Japan (19,20,21,43,44), and another species may have been found in central China. Professor Jing will report on this species later in this conference (23).

The known species of *Endocronartium* are as follows:

Endocronartium harknessii (J.P. Moore) Y. Hiratsuka, Can. J. Bot. 47:1493-1495, 1969.

Cronartium harknessii (J.P. Moore) Meinecke nom. nudum

Peridermium cerebroides Meinecke

P. harknessii J.P. Moore

"Woodgate" - *Peridermium*

Endocronartium pini (Pers.) Y. Hiratsuka, Y. Hiratsuka, Can. J. Bot. 47:1493-1495, 1969.

≡*Peridermium pini* (Pers.) Lév. emend Kleb.Two forms with different germ tube morphology were discovered in the United Kingdom Gibbs et al.(10).

Endocronartium sahoanum Imazu & Kakishima,Trans. Myco. Soc. Jpn, 1989.

Endocronartium yamabense (Saho & Takahashi) Paclt, Mitt. Dtsch. Dendrol. Ges. 77: 227-234, 1987.

≡*Peridermium yamabense* Saho & Takahashi

Endocronartium sp. ? (23)

The rust is on *Pinus armandii* in central China and

germ tube morphology is similar to those of *E. yamabense* and *E. sahoanum.*

There has been considerable discussion about the true nature of these fungi, and their taxonomic and nomenclatural interpretation. Therefore, I would like to address some of the issues regarding these species.

The first point of discussion or disagreement is whether these fungi are really endocyclic forms or not, and especially whether nuclear fusion and meiosis occur upon germination of the spores (8,12,15,17,19,20,21). Another issue is nomenclatural. Laundon (27,28,29) never liked my treatment of the group and pointed out that transfer of *Peridermium pini* to *Endocronartium* is invalid because *Peridermium pini* is the type species of the genus.

Peridermium pini contains heteroecious and autoecious forms and Klebahn divided *P.pini* into *P. pini* [Pers.] Lév. emend. Kleb. for pine-to-pine form and *P. cornui* Rostr. ex Kleb. for host alternating form (13). Because of this, we cannot tell which one the type specimen belong to and there for *Peridermium pini* as such should be decleared nomen ambigum, or ambiguous name. Scince the concept of the genus *Peridermium* in the original description is to include peridermioid aecial state occur on coniferous genera not only on the genus *Pinus.* When Link (30) divided the genus *Hypodermium* Link into subgenera, his fifth subgenus *Peridermium* included "*Aecidium pini* Pers., elatinum, columnare, abietinum Albert. et Schwein", Schmidt & Kunze (45) accepted Link's concept of *Peridermium.* To preserve the concept of *Peridermium* as originally described, conservation of the name *Peridermium* with a new type species, *P. elatinum*, has been proposed and has been approved and sanctioned (16).

My main reasons for creating the genus *Endocronartium* were:

1. Autoecious nature of the life cycles.
2. Abnormal nuclear events, suggesting nuclear fusion and meiosis in early germination of spores. Two kinds of germ tube morphology ocur. One kind has straght germ tubes with septations, as in *E. harknessii* and one form of *E. pini* (10,12,17). Another kind produces distinct vesicles or bulbs, and nuclear fusion and meiosis seem to occur within the vesicle. *E. sahoanum*, *E. yamabense* and a part of *E. pini* have this type of germ tubes (10,19,20,21). I concluded that the original two species are called endocyclic forms which often occur in other rust fungi (7,12).

Several nomenclatural options were available to name and recognize these species when I judged them to have endocyclic life cycles:

1. To include endocyclic species in the parent genera, in this case *Cronartium.* Several authors such as Cunningham (5), Jørstad (5) and Laundon (28) thought that endo species should be included under their parental genera because of the apparent genetic relationships.
2. To recognize pine-to-pine endocyclic species in existing endocyclic genera such as *Endophyllum, Endoraecium, Gymnoconia*, and *Monosporium.* or
3. To establish a new genus as I proposed in 1968 (13).

The first two options are not acceptable. To call endocyclic species with the parental generic names is attractive, especially in the case of autoecious pine stem rust,s because it is obvious that these fungi have been derived from *Cronartium*, but in the whole range of rust fungi, parental genera often cannot be predicted. The second option of including endocyclic pine stem rusts in existing endocyclic genera is not desirable because all established endo genera are unrelated to pine stem rusts, making the genus very heterogeneous. Considering the above, the best solution was to establish a properly designated endo genus based on the pertinent morphological types of spore states. The new genus *Endocronartium* wss erected to include endocyclic pine stem rusts. The genus is a relatively homogeneous group restricted to species of the *Cronartium* type.

Besides the above-mentioned species of *Cronartium* and *Endocronartium*, several forms only known on pines or tentatively assigned to some *Cronartium* species need to be investigated for their morphology and life cycles. One example is a blister rust on a Mexican pine *Pinus montezuma* which has rather unique aeciospores and peridial cell morphology and is likely to be a new species. Life cycle of the fungus is not known.

DESCRIBED SPECIES OF *PERIDERMIUM* ON *PINUS*

The following species of *Peridermium* have been described on *Pinus*:

Peridermium appalachianum Hept. & Cumm.
Aecial state of *Cronartium appalachianum.*

Peridermium bethelii Hedgcock & Long
Considered to be cloesely related to *Cronartium* comandrae.

Peridermium cerebroides Meineke nomen nudum.
One race is apparently an aecial state of *Cronartium coleosporioides*, sensu lato.

Peridermium cerebrum Peck
P. giganteum (Mayr) Tub.
P. globosum Arth. & Kern

Aecial state of *Cronartium quercuum.*

Peridermium comptoniae Ort. & Adams

Aecial state of *Cronartium comptoniae.*

Peridermium conigenum (Pat.) R. Peterson

≡ *Caeoma conigenum* Pat.

Aecial state of *Cronartium conigenum* or *C. quercuum* (p.p.)

Peridermium filamentosum Peck

One race is one of the aecial states of *Cronartium coleosporioides*, sensu lato. The name, *P. filamentosum* has often been construed to include *P. stalactiforme* and occasionally *P. harknessii*; one of the forms is now described as *Cronartium arizonicum* Cumm.

Peridermium fusiforme Arth. & Kern

Aecial state of *Cronartium fusiforme* or of *C. quercuum*, pro parte.

Peridermium harknessii J. P. Moore

Now recognized as an endocyclic species, *Endocronartium harknessii* (J. P. Moore) Y. Hiratsuka.

P. cerebroides, nomen nudum. One race is apparently an aecial state of *Cronartium coleosporioides*, sensu lato.

Peridermium indicum Colley & Taylor

This is considered as aecial state of *Cronartium ribicola*, sensu lato.

Peridermium kuriense Dietel

Considered to be the aecial state of *Cronartium kamtschaticum* Jst., which is in turn, closely related to *Cronartium ribicola.*

Peridermium mexicanum Arth. & Kern

Aecial state of *Cronartium conigenum* or of *C. quercuum* (p.p.)

Peridermium occidentale Hedg., Bethel & Hunt

Aecial state of *Cronartium occidentale.*

Peridermium pini (Pers.) Lév.

In1890, Klebahn divided the species into two: *P. pini* (Pers.) Schmit. & Kunze emend Klebahn for the autoecious form and *P. cornui* Rostr. emend Klebahn for the host-alternating form (*C. flaccidum*)(13). Partly an endocyclic species *Endocronartium pini* (Pers.) Y. Hiratsuka.

Peridermium pyriforme Peck

Aecial state of *Cronartium comandrae.*

Peridermium stalactiforme Arth. & Kern

An aecial state of *Cronartium coleosporioides.*

Peridermium strobi Klebahn

An aecial state of *Cronartium ribicola.*

All species except *P. bethelii* and a part of the *P. filamentosum* complex have known teleomorph states (*Cronartium*).

MORPHOLOGICAL CRITERIA

Following is an evaluation of different morphological characteristics as taxonomic criteria.

Spermogonia and spermatia

The morphology of spermatia hss never played a big role as a taxonomic criterion, but there are distinct differences in shape and size of spermatia between some species and thus should be examined carefully. The biggest problem with use of this spore state is that most preserved specimens on pine do not have this state.

Aecia and aeciospores

Spore markings, spore shape and size are good characteristics (14,21,34).

There are three main kinds of spore markings of aeciospores (14,21).

Peridial cell markings and shape

Peridial cells and their surface markings are also distinct characteristics (Per).

Uredinia and urediniospores

Spore markings of urediniospores are remarkably similar between species, significant differences exist in sizes and shape of urediniospores.

Teila and teliospores

We have paid little attention to teliospore morphology but this may be the spore state that can distinguish different species. I have not tried it yet, but one paper described how to separate teliospores for observation (38) and this method is likely very useful.

Basidia and basidiospores

Kuhlman & Kaneko (26) showed that size and color of basidiospores can be good morphological criteria to distinguish closely related species or forms. They studied basidiospores of different forms of the *Cronartium quercuum* complex.

HOST RELATIONSHIPS

As shown in Figure 1, Scrophulariaceous plants are know to be alternate hosts of rusts that occur on both Haploxylon and Diploxylon Sections of *Pinus*. Rust species having the same II and III hosts, but parasitizing two different sections of pine need to be studied carefully. In northern Asia, blister rusts on both five-needle and two-needle pines are found in the general area where rusts on Scrophulariaceous

plants also occur.

USE OF FORMAE SPECIALES IN PINE STEM RUST TAXONOMY

In the literature, formae speciales (f. sp.) are used to distinguish and name closely related but different taxa in *Cronartium quercuum, C. ribicola* and *C. flaccidum.* Examples are:

Cronartium quercuum f.sp. *virginianae*
C. quercuum f.sp. *banksianae*
C. quercuum f.sp. *echinatae*
C. quercuum f.sp. *fusiforme*
Burdsall and Snow (3)

Cronartium ribicola f.sp. *ribicola*
C. ribicola f.sp. *pedicularis*
Yokota and Uozumi (50)

Cronartium flaccidum f. sp. *siphonostegia*
Jing and Wang (24)

I do not agree with the practice of creating and using formae speciales (f. sp.) in pine stem rust taxonomy and nomenclature.

International Code of Botanical Nomenclature (22) Article 4 (Note 3) clearly indicated that f. sp. can be used when no morphological differences exist, but host specificities are different; however naming of f.sp is outside of the provisions of the Code. In other words, f.sp. names are not governed by ICBN. In the case of *Cronartium quercuum*, Kuhlman and Kaneko (1991) have found minor morphological differences among different f.sp.; therefore they should not be called f. sp..

SPECIES COMPLEXES

Regardless of the species concepts used for pine stem rusts, the presently known species can be divided into five groups.

Cronartium ribicola complex
C. kamtschaticum
C. occidentalis
C. ribicola

C. flaccidum complex
European form (type) and Asian forms (Japan, China & Russia).

C. quercuum complex
Several North American forms (fusiforme group) and 2 or 3 asian forms exist. If they are proven to belong in more than one taxa, one matches with original type (a North American form described by Berkeley will have *C. quercuum* name and other forms need to be named differently (36). *Cronartium conigenum* Hedgcock & Hunt

C. coleosporioides complex
C. coleosporioides
Peridermium filamentosum complex
At least two , possibly three, different taxa are involved (Peterson 1967) within this species complex, including one obviously autoecious species and one or more host-alternating species. One of them was named by Cummins in 1984 (6) as *Cronartium arizonicum.* This complex, inturn is closely related to the *C. coleosporioides* complex.

C. comandrae complex
C. comandrae
P. bethelii

SPECIES OR FORMS THAT NEED TO BE INVESTIGATED

The following species or groups of species need to be studied carefully.

A blister rust on *Pinus armandii* in central China now being investigated by Professor Jing Yao and his coworkers is likely be another endocyclic species (*Endocronartium* sp.).

Blister rust(s) on *Keteleeria* spp. in Yunnan, China.
The conifer genus *Keteleeria* with several species in southern China, has a few stem and needle rusts. Two of them, *Peridermium kunmingense* Jen and *P. keteleeriae-evelynianae* Zhou et Chen, need to be examined for possible relationship to *Cronartium.* Another rust on the same host is first described as *Cronartium keteleeriae* by Tai (47), but is now considered to belong to *Chrysomyxa* (*C. keteleeriae* (Tai) Wang et Peterson).

Blister rusts on *Pinus pumila*, and *P. koraiensis* in Japan, Far East Region of Russia, northern China.
An active cooperative investigation is underway by Japanese (Katsuya, Kakishima, Ono, Imazu etc.), Canadian (Y. Hiratsuka), and Russian (Azbukina) investigators and interesting results have been obtained.

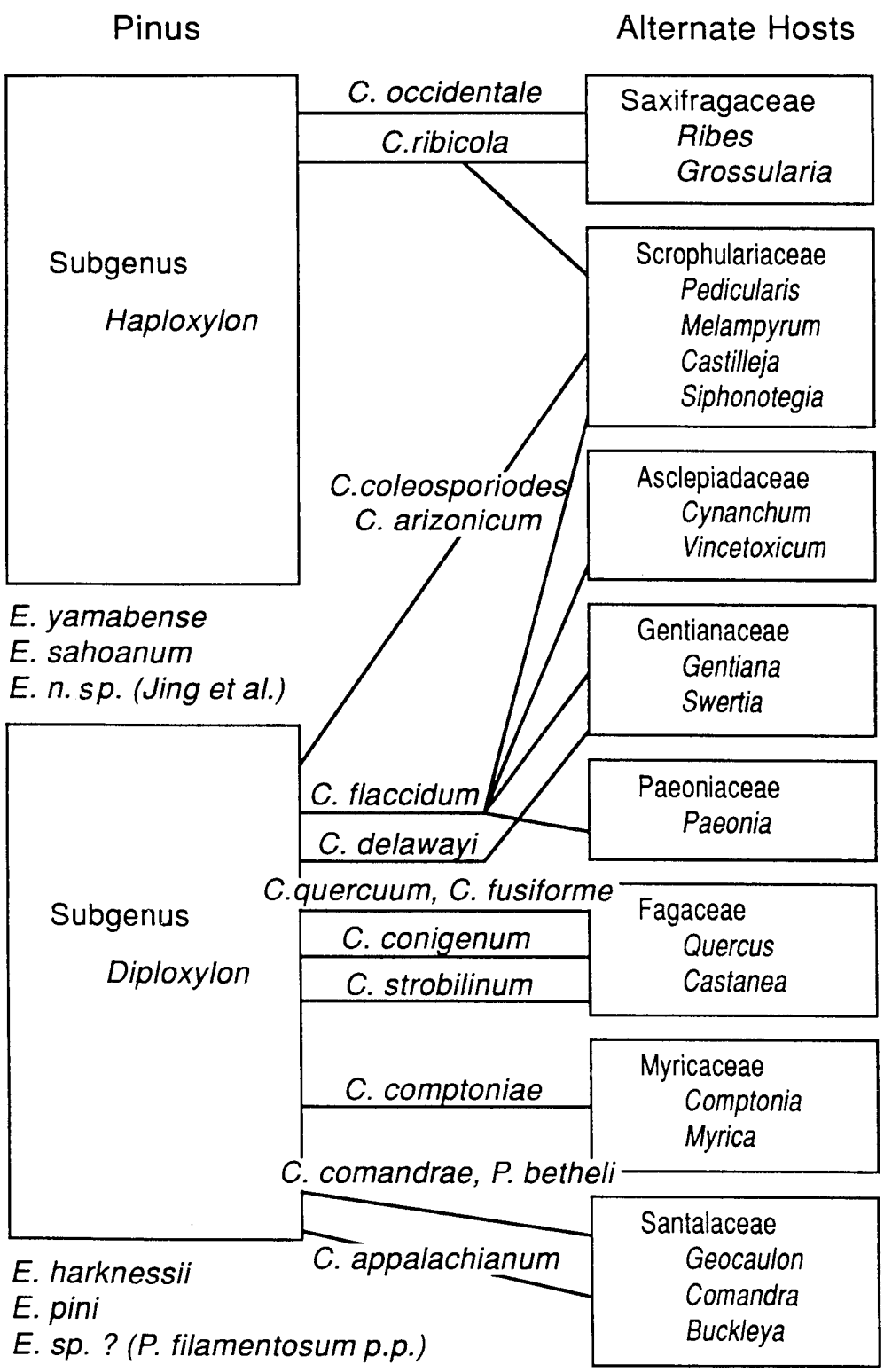

Fig. 1. Host relationships for major pine stem rusts species.

Blister rust(s) of *Pinus sibirica* in central Siberia, Russia.
Very little information is available on the blister rust(s) of this widely distributed Russian pine and investigation is needed.

Species on Mexican and central American pines
Mexico and adjacent central America have a greater number of *Pinus* species and forms (about 60, including many species occuring only in that region) than any other region of the world (4,31,33) but good stem rust information is not available. International cooperation is needed to investigate Mexican pine stem rusts.

Species on a few unique or rare pine species, including *Pinus dalatensis, P. krempifii (Ducampopinus k.), P. kesiya, P merkusi* in Vietnam and other southeast Asian countries.
No information is available regarding the stem rust(s) of these unique *Pinus* species.

CONCLUDING REMARKS

In conclusion, I think more field work is needed to collect and examine specimens in several geographical areas, especially highlands of Mexico, Central China, Far East and Siberian Regions of Russia, and central Vietnam. Also needed are more careful life cycle and cytological investigations of closely related species to complete an acceptable monograph of this group of fungi. We need to establish simple and dependable techniques to predict or confirm genetic connections between aecial and telial stages, perhaps using molecular biological methods. Relatedness information obtained from molecular work such will be presented after this by Vogler (47), and by others (40,41,49) will provide important clues for predicting the phylogenetic relationships among the pine stem rust species.

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