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Cytology, taxonomy, and nomenclature of autoecious pine stem rusts

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Summary

There are at least seven different species and varieties of autoecious pine stem rusts recognized in Europe, Asia, and North America. Their occurrence at high latitudes or high altitudes is consistent with a general tendency for short-cycle rusts. Two main types of germ tube morphology and cytological events are recognized. In one type, nuclear fusion occurs in the spore and subsequent meiosis occurs in the germ tube, and the resulting haploid nuclei are separated by septa. In another type, dikaryon nuclei enter the germ tube, nuclear fusion occurs in a clearly recognizable vesicle, and meiosis occurs in the vesicle or in the germ tube that grows out from the vesicle. These differences can be explained by the timing and place of nuclear fusion and meiosis in the germination process. Pine-to-pine stem rusts of both types exist in the United Kingdom in separate locations, and both types have been called *Peridermium pini* (*E. pini*), but may represent two distinct fungi. Although all autoecious species likely have been derived from parental heteroecious species and spore morphology is like the aeciospores of heteroecious species, they have endocyclic life cycles. They need to be treated as holomorphic fungi and cannot be included in the anamorphic genus *Peridermium*. The establishment of the genus *Endocronartium* is defended, and various nomenclatural options for this group of fungi are discussed.

Key words: *Endocronartium*, *Peridermium*, review, zymodeme

1 Introduction

Most of the pine stem rusts have host alternating (heteroecious) life cycles and are classified as species of the genus *Cronartium*. About 20 species of *Cronartium* are known (Peterson 1973, Cummins and Hiratsuka 1983). On the other hand, the following pine stem rusts species or forms have been recognized to have pine-to-pine (autoecious) life cycles.

1. *Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka
   - °*Peridermium harknessii* J.P. Moore
   - °*Cronartium harknessii* (J.P. Moore) Meinecke
2. *E. pini* (Pers. emend Kleb.) Y. Hiratsuka
   - °*Peridermium pini* (Pers.) Lév. emend Kleb.
3. *E. sahoanum* Imazu & Kakishima var. *sahoanum*
   - °*Peridermium sahoanum* Imazu & Kakishima
4. *E. sahoanum* var. *hokkaidoense* Imazu & Kakishima
   - °*Peridermium sahoanum* var. *hokkaidoense* Imazu & Kakishima

5. *E. yamabense* (Saho & I. Takahashi) Paclt
   °*Peridermium yamabense* Saho & I. Takahashi
6. *Peridermium filamentosum* Pk. pp.
   "Inyo *Peridermium* "
7. *Peridermium filamentosum* Pk. pp.
   "Powell *Peridermium* "
8. A blister rust on *Pinus armandii* in Central China

Several other species and forms such as *Peridermium bethelii* Hedgcock & Long, a white-spored gall rust, and a yellow-spored gall rust, which are also considered to have pine-to-pine life cycles, have been reported and considered to be distinct from other autoecious species (Vogler and Bruns 1998).

Undoubtedly, these species and forms have been derived from heteroecious parental species but their cytology, interpretation of these events, and the resulting nomenclatural treatments are still in dispute (Epstein and Buurlage 1988, Hiratsuka 1968, 1969, 1991, Vogler and Bruns 1998, Vogler *et al.* 1997). In this presentation, I will discuss their cytology, taxonomy, and nomenclature based on the recognition of endocyclic life cycles with nuclear fusions and meiotic divisions in these rusts rather than consider them as imperfect rusts having mitotic rather than meiotic nuclear divisions in germ tubes. In *E. harknessii*, we have now observed the presence of synaptonemal complexes, which indicate nuclear fusion, in the spores just before germination (Y. Hiratsuka, unpubl.). This confirmed that nuclear fusion and meiosis are occurring in the process of germination in *E. harknessii*. I will present the evidences and discuss the matter in a separate paper.

2 Distribution and origin of pine-to-pine stem rusts

It is a well-known fact that the number of rust species with shortened life cycles are more abundant at high altitudes and high latitudes. Distribution of all known species of pine-to-pine stem rusts are restricted to high latitudes or high altitudes near the edges of their pine hosts' distribution. This indicates that these species were originally derived from their heteroecious parental species. Also, when ecologically separated from their alternate hosts, instead of becoming extinct, they managed to alter their life cycles by shortening their life cycles, and they acquired the ability to re-infect their pine host without going through life cycle stages on alternate hosts.

3 Germ tube morphology and cytological events

Two main types of germ tube morphology and cytological events are recognized among known pine-to-pine stem rust species. In one type, nuclear fusion occurs in the spore, and the subsequent meiosis occurs in the germ tube (*Endocronartium harknessii* and a part of *E. pini*) (Hiratsuka *et al.* 1966, Hiratsuka 1968, Gibbs *et al.* 1988). In the other type, the subsequent dikaryon

nuclei enter the germ tube, and nuclear fusion and the subsequent meiosis occurs in a clearly recognizable vesicle; then the nuclei migrate into a germ tube growing out from the vesicle (*E. sahoanum*, *E. yamabense*, a part of *E. pini* and possibly an undescribed species on *Pinus armandii* from central China) (Gibbs *et al.* 1988, Imazu and Kakishima 1992, 1995, Imazu *et al.* 1991, Kaneko and Harada 1995). It is interesting to note that there are two different populations of "*Peridermium pini*" with different types of germ tubes corresponding to the two types. When Dr. van der Kamp as a Ph. D. student at the University of Aberdeen studied *P. pini* around 1967, he published two significant papers on this disease. However, he never published a third manuscript (van der Kamp, B.J., Cytology of *Peridermium pini* (Pers.) Lev. aeciospore germination, unpublished manuscript), that he wrote on the cytology of germinating spores, because he could not clearly explain the cytological events in the germ tubes clearly at the time. However, his figures and observation of nuclei during germination were clearly those of the second type. These differences can be explained by the timing and place of nuclear fusion and meiosis in the germination process. This may mean that the timing and place of nuclear fusion are an indication of stability of endocyclic life cycle. Possibly the first type has more and the second type a less stable endocyclic life cycle.

Vogler *et al.* (1997) found two different populations of *E. harknessii*, zymodeme I and zymodeme II, and reported that mature spores of zymodeme II had one nucleus in an average of 93% of the spores while those of zymodeme I had one nucleus in only 21 to 29% of spores. It is also interesting that the same group of researchers (Epstein and Buurlage 1988) reported only 10% of the spores having one nucleus. Although they concluded from the observations that nuclear divisions in the germ tubes were mitotic, their data clearly indicate the occurrence of nuclear fusion and meiosis. Very high proportions of monokaryotic spores in zymodeme II can only be explained as the early occurrence of nuclear fusion in the spores of this race (zymodeme II) of western gall rust. Examination of nuclear conditions of hyphae in the pine tissue and very young spores will clarify the matter.

4 Taxonomy and nomenclature

If these autoecious species and forms are recognized as endocyclic species, four options are available for nomenclature:

1. Treat as species of *Cronartium*.

Morphological and molecular studies clearly indicate that these pine-to-pine forms are short-cycle variations of parental heteroecious species of *Cronartium* (Vogler and Bruns 1998). Vogler and Bruns (1998) stated that these autoecious forms are simply all *Cronartium* despite their altered life cycle and unusual cytology. This may be an acceptable option, but this will create confusion in nomenclature because the genus would need to be defined to have two different kinds of teleomorphs. Based on the morphology of teliospores, taxa of all other life cycle variations (macrocyclic, demicyclic, microcyclic) are called by the same generic name. However, some endocyclic species cannot be placed accurately to parental genera. For example, species

of *Endophyllum* are endocyclic rusts having *Aecidium*-type sorus and spores. Many rust genera have an *Aecidium*-type of aecia such as *Puccinia, Uromyces, Cumminsiella*, and *Ochropsora*, and many times the parental genera cannot be predicted.

2. Use the anamorphic generic name *Peridermium*.
If we do not recognize these pine-to-pine forms as having an endocyclic life cycle, the use of *Peridermium* may be a reasonable solution and many researchers are using this option. However, if the group of fungi is recognized to have endocyclic life cycles, they cannot be called by the anamorphic generic name *Peridermium*. Also, by definition, use of the name *Peridermium* means that the teleomorph or telial state of the fungus is still unknown, as described in one of the tables in Vogler and Bruns (1998). However, these fungi obviously do not have a separate telial state on alternate hosts because the whole life cycle is completed on the *Pinus* host. Use of *Peridermium* does not indicate the endocyclic nature of the life cycles of the taxa, and it may be confused with anamorphic taxa in which the life cycle is still unknown.

3. Put into one of the existing endo-genera.
This option is not acceptable because all endo-genera presently recognized are based on morphological types of their aecioid telia (or aecia of parental species).

4. Create a new endo-genus specifically for this group of rusts.
The author chose this option and established a new genus *Endocronartium* (Hiratsuka 1969) because this alternative has merits over the three previously mentioned options. However, the endocyclic form is an abnormal state obviously closely related to the parental genus, *Cronartium*. Nomenclature is a tool for convenience sanctioned by the International Code of Botanical Nomenclature to facilitate everyone referring to the same taxa by the same names. We need to keep our dialog open on the subject so that all concerned will call the same fungi by the same names and avoid confusion and misunderstanding.

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