

A REVIEW AND EXTENSION OF OUR KNOWLEDGE OF CALYPTOSPORA GOEPPERTIANA KUEHN

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OUR KNOWLEDGE of the haploid phase of *Calyptospora Goeppertiana* on *Abies* dates from 1805 and of the diploid phase on *Vaccinium* from 1869. That the latter was not recognized earlier is readily understood because there are no uredia, and because the teliospores are intraepidermal with no suggestive external indications of their presence. In 1880, Robert Hartig (13) announced that he had proved the connection of the two phases by means of culture experiments. His findings have been confirmed repeatedly.

Calyptospora Goeppertiana is of special interest not only for its lack of uredia but also for its reduced spermogonia. Indeed, the latter were long supposed to be absent. They do occur, however, and often in considerable numbers. But they are aborted to a greater or less extent and, so far as Hunter (15) could determine from a thorough study of the rust on *Abies balsamea*, they do not form spermatia nor do they rupture. On the other hand, Weir (21) reported normal spermogonia and spermatia for *C. Goeppertiana* on *A. lasiocarpa*. If that occurrence is representative for the rust in western North America, then it differs from what is known of it in Europe and eastern North America. Before re-defining the species, however, Weir's observations should be checked against those made on unquestionably authentic *C. Goeppertiana*, preferably from cultures on *A. lasiocarpa* in which telial material from Europe or eastern North America would be used as inoculum.

Another feature of interest concerning *C. Goeppertiana* is its phylogeny. Plainly, as has been maintained by Faull (9) and others, the characteristics of its spermogonia, aecia and teliospores suggest a close relation to *Pucciniastrum*. From a comparative investigation of the ontogeny of the teliospores in the various genera of the Pucciniastreae, Pady (19), while recognizing the resemblance of *Calyptospora* to *Pucciniastrum*, inclines to the view that they may be analogous genera in parallel evolutions. He concludes — "These results agree in a very general way with the phylogenetic tree that Faull has constructed for the *Pucciniastreae*, except for the possibility that the two lines of development indicated above might represent two phylogenetic series. In that case,

the phylogenetic tree would possess two main branches, the one leading through the intra-epidermal forms, *Milesia*, *Hyalopsora*, *Thecopsora* and *Calyptospora*, and the other passing through the subepidermal genera *Pucciniastrum* and *Melampsoridium*, to such forms as *Melampsora*. Many more data would be necessary, however, before this series could be postulated as a phylogenetic one."

Economically, *C. Goeppertiana* is probably not of great importance. Yet I have found it on seedlings of *Abies balsamea* in the forest in such abundance as to indicate some effect on the natural reproduction of that species. Weir (21) also reports that in the western United States it is injurious to various species of *Vaccinium*. But so far no exact investigation seems to have been made on that aspect of the rust.

This paper deals with four topics relative to *C. Goeppertiana*, namely, (1) nomenclature and taxonomy, (2) life history studies, (3) hosts, (4) specimens examined.

NOMENCLATURE AND TAXONOMY

***Calyptospora Goeppertiana* Kühn in Hedw. 8: 81 (1869). (III).**

Aecidium columnare Albertini & Schwein. Consp. Fung. Lusat. 121 (1805). (I).

Peridermium columnare Kze. & Schm. Deutschl. Schwämme no. 10 (1815). (I).

Caeoma columneum Link in W. Spec. Pl. 6, 2: 66 (1825). (I).

Uredo columnaris Spreng. Syst. Veg. 4, 1: 570 (1827). (I).

Melampsora Goeppertiana Wint. in Rabenhorst, Krypt.-Fl. ed. 2. 1: 245 (1884).

Melampsora columnaris Wettst. in Verhandl. Zool.-Bot. Ges. Wien, 35: 551 (1885).

Calyptospora columnaris Kühn in Rabenh.-Wint. Fung. Eur. no. 3521 (1886).

Pucciniastrum Goeppertianum Kleb. Wirtswechs. Rostpilze, 391 (1904).

Thecopsora Goeppertiana Hiratsuka in Jour. Soc. Agric. Forestr. Sapporo, 19: 167 (1927).

After it was experimentally demonstrated that *Aecidium columnare* A. & S. on *Abies* and *Calyptospora Goeppertiana* Kühn on various species of *Vaccinium* are the haploid and the diploid phases, respectively, of the same species, the nomenclatural history of this rust has mainly revolved around the proper choice of the specific and the generic names. The authoritative specific name was settled eventually by Article 49 *bis* of the rules adopted by the International Botanical Congress of 1910. The choice of generic name is still subject to differences of opinion.

Just what generic name should be adopted depends on breadth of interpretation and on the measure of regard for long established usage.

Three names are involved, namely, *Calyptospora*, *Pucciniastrum*, *Thecopsora*. Morphologically, the rusts variously referred to these genera are similar with respect to their aecia and teliospores. This fact has been deemed sufficient by some systematists to warrant the inclusion of all of them under *Pucciniastrum*, a name which has priority over the other two. Another view is held to the effect that a separation of these rusts should be made according to whether their teliospores are subepidermal or intraepidermal. Under that disposition they are distributed between the respective genera *Pucciniastrum* and *Thecopsora*. But many uredinologists prefer to retain *C. Goeppertiana* under the generic name *Calyptospora*, partly because of long established usage, as so frankly admitted by Sydow (20), and partly because *C. Goeppertiana* is characterized by such important distinctive features as more or less aborted, apparently non-functional spermogonia, lack of uredia, cauline teliospores and indeterminate telia which occupy the entire epidermides of "broomed" stems.

Up to this point the synonymy involved centers on what is universally regarded as the same fungus. Quite recently, however, Arthur (2) has added two synonyms concerning which there may be some question of fungus identity, namely, *Peridermium ornamentale* Arthur (in Bull. Torr. Bot. Club, 28: 665. 1901) and *P. Holwayi* Sydow (in Ann. Mycol. 1: 19. 1903). The former was collected Sept. 4, 1900 on Mt. Padow, Washington at an elevation of about 6000 feet on first year needles of *Abies lasiocarpa*. The latter was described from material collected Aug. 11, 1901 at Glacier, B. C., on second year needles of *A. lasiocarpa*. After careful study of the types, I am convinced that neither is *Calyptospora Goeppertiana*, and that both are probably specifically distinct from each other. Table 1 presents the data on which these conclusions are based.

In this connection it should be noted that the usual practice in herbaria nowadays is to label specimens of these rusts from the western United States and western Canada with the name *Peridermium ornamentale*, regardless of whether the peridermia are on first or second year needles. No recognition is being given to *P. Holwayi* other than to regard it as a synonym. According to the present state of our knowledge, this procedure is without warrant. In short, I tentatively agree with the opinion expressed by Boyce (6) that *P. ornamentale*, as now generally interpreted, "is undoubtedly a composite species, because Peridermia with aecia on the current season's needles and others with aecia on the one-year-old needles are so named."

Just what the diploid phases of *Peridermium ornamentale* and *P.*

TABLE 1

COMPARISON OF CALYPTOSPORA GOEPPERTIANA, PERIDERMIMUM ORNAMENTALE AND P. HOLWAYI

	<i>Calyptospora</i> <i>Goeppertiana</i> on <i>Abies balsamea</i> (Culture)	<i>Peridermium</i> <i>ornamentale</i> on <i>Abies lasiocarpa</i> (Type)	<i>Peridermium</i> <i>Holwayi</i> on <i>Abies lasiocarpa</i> (Type)
Position of spermogonia	Hypophyllous	Amphigenous, but mostly hypophyl- lous	Amphigenous; abun- dant on both sur- faces
Condition of spermogonia	More or less aborted and apparently not functional	Not aborted and ap- parently functional	Not aborted and ap- parently functional
Limits of size of spermogonia	13-30 × 42-137μ	32-54 × 81-175μ	27-54 × 68-138μ
Average size of sper- mogonia	21 × 73μ	40 × 126μ	35 × 98μ
Occurrence of peridermia	1st year needles Hypophyllous	1st year needles Hypophyllous	2nd year needles Hypophyllous
Seasonal oc- currence of peridermia	Early summer of first year	Late summer or early autumn of first year	Summer or late spring of second year
Shape and size of peridermia	Slender, terete	Robust, cylindrical to compressed cylindrical	Robust, compressed cylindrical
Average size of aeciospores	16 × 20μ	14 × 20μ	18 × 23μ

Notes:

- (1) Spermogonia of all three are flattened convex, subcuticular.
- (2) The occurrence of the spermogonia as hypophyllous or amphigenous might possibly vary according to the host species, just as was found by Faull (10) to be true of *Milesia fructuosa*.
- (3) The average size of the spermogonia might possibly vary within fairly wide limits. This could be determined only by the examination of many collections of authentically named specimens.
- (4) The robustness and the shape of the peridermia might possibly vary according to the host species or according to nutritional and environmental factors.
- (5) Whether or not a rust might form its peridermia in the latter part of the first year or the early part of the second year, depending on seasonal or other factors, is unknown. But so far this has never been demonstrated for any species. If it be true of *P. ornamentale* or *P. Holwayi*, then one important reason would be removed for regarding them as distinct species.

Holwayi may be, remains for cultural determination. Their characteristics, however, indicate a *Pucciniastrum* relationship. Such, too, is Boyce's view (5), although his surmise, based on field associations of the rusts, that *Pucciniastrum Myrtilli* on *Vaccinium* is the diploid phase of *Peridermium ornamentale* is quite improbable. *Pucciniastrum Myrtilli* is known to have *Tsuga* as its alternate host, and all attempts so far to culture it on *Abies* have failed. If *Peridermium ornamentale* does infect *Vaccinium*, then the resulting diploid phase might resemble that of *Pucciniastrum Myrtilli*; but with at least equal likelihood it might resemble that of *Calyptospora Goeppertiana*. The same applies to *Peridermium Holwayi*. That there may be a second species of *Calyptospora*, as yet unnamed, in western North America has already been suggested by Weir (21) in his comparative study of what he took to be *Calyptospora Goeppertiana*. His conclusion was influenced solely by differences in the shape and the robustness of the peridermia characteristic of *C. Goeppertiana* and *P. ornamentale*. He expressed himself as follows — "It is here proposed to reverse an earlier view on the identity of the aecial form on *Abies* with large cylindrical or flattened peridia and suggest the probability of there being another species of *Calyptospora* with telia on *Vaccinium*. This suggestion is based purely on field observations. All collections of the large aecial form so far made by the writer have been in close association with the typically appearing telial stage on *Vaccinium*. Wherever the large aecial form has been collected the form with small cylindrical peridia has been absent, with the reverse as true." He adds, — "Another view," apparently not his own, "would be that the size of the aecia is influenced by the vigor of the host and that the two forms are identical." Incidentally it should be remarked that if there be a second species of *Calyptospora* on *Vaccinium* in western North America, then the collections labelled *C. Goeppertiana* from that part of the world are subject to revision.

Here, then, is a simple, well defined problem in western North America that can be solved by making suitable cultures — the problem of adequately defining the rusts included under the names *Calyptospora Goeppertiana*, *Peridermium ornamentale* and *Peridermium Holwayi*.

LIFE HISTORY STUDIES

Several successful life history studies have been made of *Calyptospora Goeppertiana*. Robert Hartig (13, 14) cultured it from *Vaccinium Vitis-idaea* on *Abies alba*, and then in the reverse direction. He made no mention of spermogonia. Kühn (16, 17, 18) then cultured it from *V. Vitis-idaea* on *Abies alba*, *A. balsamea*, *A. cephalonica*, *A. cilicica*,

A. concolor, *A. Fraseri*, *A. magnifica*, *A. nobilis*, *A. Nordmanniana*, *A. Pinsapo*, *A. sibirica* and *A. Veitchii*. He also made no mention of spermogonia. Bubák (7, 8) cultured it from *V. Vitis-idaea* on *A. alba*. No spermogonia were recognized. Arthur (1) cultured it from *V. pennsylvanicum* on *A. Fraseri*. He remarked, "pycnia rarely if ever found." Fraser (11, 12) cultured it from *V. pennsylvanicum* on *A. balsamea*. No spermogonia were recognized. He also inoculated *Tsuga canadensis* with telial material, but the results were negative. Weir (21)* cultured a rust, which he took to be *C. Goepfertiana*, from *A. lasiocarpa* on *V. membranaceum*. In other experiments he cultured the rust from brooms of *V. membranaceum* on *A. lasiocarpa*, and also carried it forward from *Vaccinium* to *Vaccinium* by making infected tissue plantings. Finally, I have made many cultures on *A. balsamea*, using as inoculum telial material from *V. pennsylvanicum* and *V. canadense*. Summaries of my experiments are recorded in Tables 2 and 3 of this paper.

TABLE 2

CULTURES OF CALYPTOSPORA GOEPPERTIANA
FROM VACCINIUM PENNSYLVANICUM TO ABIES BALSAMEA

1. Forty-five inoculation experiments were made; all gave positive results.
2. The dates of inoculation ranged from June 8 to June 20.
3. Yellowing of the needles appeared 12 to 17 days after inoculation. The average was 14 days.
4. Spermogonia were first observed 13 to 19 days after inoculation. The average was 16 days.
5. The peridermia were first observed 17 to 24 days after inoculation. The average was 21 days.
6. The peridermia began to rupture one to five days following their first appearance.
7. The production of peridermia was practically completed within 32 days after inoculation. The average was about 29 days.

*Through the courtesy of the United States Bureau of Plant Industry I have had the opportunity of examining an unused part of Weir's aecial inoculum from *Abies lasiocarpa*, and also meager infections on *A. lasiocarpa* that resulted from his inoculations with telial material of *Vaccinium membranaceum* origin. I would be hesitant, however, to unreservedly pronounce either as *Calyptospora Goepfertiana*. Spermogonia do occur on both of them, though with comparative scantiness. No distinctly aborted spermogonia were found; but I could not determine whether or not spermatia were produced. Certainly the peridermia are more robust than those characteristic of *C. Goepfertiana* on *Abies balsamea* and not less so than some of *Peridermium ornamentale*. Moreover, the first material referred to above was collected after the middle of September, which suggests a long developmental period as compared with the few weeks required for the development of *C. Goepfertiana* on *A. balsamea*.

8. The number of infected needles with peridermia varied from 6 to 203. *The average was 70.*
9. The number of peridermia per needle varied from 22 to 41. *The average was 27.*
10. J. H. Faull Herbarium nos. 7269–7279, 7403 and 8116–8132.

TABLE 3

CULTURES OF CALYPTOSPORA GOEPPERTIANA
FROM VACCINIUM CANADENSE TO ABIES BALSAMEA

1. *Three inoculation experiments were made; all gave positive results.*
2. The date of inoculation was June 22.
3. Yellowing of the needles appeared 11 to 13 days after inoculation. *The average was 12 days.*
4. The spermogonia were first observed 13 to 15 days after inoculation. *The average was 14 days.*
5. The peridermia were first observed 21 days after inoculation.
6. The peridermia began to rupture two days following their first appearance.
7. The production of peridermia was practically completed within 25 days after inoculation.
8. The number of infected needles with peridermia varied from 75 to 108. *The average was 90.*
9. The number of peridermia per needle varied from 27 to 41. *The average was 33.*
10. J. H. Faull Herbarium nos. 8133–8135.

HOSTS

The haploid phase of *Calyptospora Goeppertiana* has been shown by cultures to have as hosts the following species of *Abies* — 1. *Abies alba* Mill. 2. *A. balsamea* (L.) Mill. 3. *A. cephalonica* Loud. 4. *A. cilicica* Carr. 5. *A. concolor* Lindl. & Gord. 6. *A. Fraseri* (Pursh) Lindl. 7. *A. lasiocarpa* Nutt. 8. *A. magnifica* A. Murr. 9. *A. nobilis* Lindl. 10. *A. Nordmanniana* Spach. 11. *A. Pinsapo* Boiss. 12. *A. sibirica* Ledeb. 13. *A. Veitchii* Lindl. Other species of *Abies* have been recorded as hosts but they have not been confirmed by cultures. It would seem probable, however, from this list that most, if not all, species of *Abies* are susceptible to *C. Goeppertiana*.

The diploid phase of *C. Goeppertiana* occurs on the following species of *Vaccinium* — 1. *Vaccinium canadense* Kalm. 2. *V. corymbosum* L. 3. *V. Myrtillus* L. 4. *V. pennsylvanicum* Lam. 5. *V. vacillans* Kalm. 6. *V. Vitis-idaea* L. 7. *V. Vitis-idaea* var. *minus* Lodd.

Many species from western North America are also recorded as hosts of *C. Goepfertiana*. But, for reasons already expressed, the determinations may be subject to revision. Nevertheless it is probable that they, too, may serve as hosts for this rust. The list is as follows — *Vaccinium caespitosum* Michx., *V. Chandleri* Jepson, *V. erythrococcum* Rydb., *V. membranaceum* Dougl., *V. microphyllum* Rydb., *V. oreophilum* Rydb., *V. ovalifolium* Sm., *V. ovatum* Pursh, *V. parvifolium* Sm., *V. scoparium* Leib.

SPECIMENS EXAMINED

O and I. On *Abies alba*.

GERMANY: München, July 1910, J. H. Faull.

O and I. On *Abies balsamea*.

NOVA SCOTIA: Card Lake, July 21, 1929, J. H. Faull. — Mahone, July 22, 1929, J. H. Faull. — Liscomb Park, July 30, 1929, J. H. Faull.

ONTARIO: Timagami, July 4, 16, 25, 1919, J. H. Faull. — Timagami, July 10–16, 1924; CULTURES from *Vaccinium pennsylvanicum* by J. H. Faull and W. G. Watson. — Timagami, July 11, 1925; CULTURES from *V. pennsylvanicum* by E. H. Moss. — Timagami, July 16–19, 1926; CULTURES from *V. pennsylvanicum* by J. H. Faull and G. D. Darker. — Timagami, July 17–18, 1926; CULTURES from *V. canadense* by J. H. Faull and G. D. Darker. — Timagami, July 12, 1927, G. D. Darker 2041.

III. On *Vaccinium canadense*.

MAINE: Eustis, Oct. 23, 1931, J. H. Faull.

ONTARIO: Timagami, Aug. 19, 1921, J. H. Faull. — Timagami, May 12, 1924, J. H. Faull.

QUEBEC: Mt. Albert, Gaspé Co., Aug. 21, 1933, J. H. Faull.

III. On *Vaccinium pennsylvanicum*.

MAINE: Eustis, Oct. 23, 1931, J. H. Faull. — Solon, Aug. 27, 1935, J. H. Faull.

NEW HAMPSHIRE: Mt. Jefferson, Aug. 31, 1932, J. H. Faull.

NOVA SCOTIA: Card Lake, July 21, 1929, J. H. Faull. — Liscomb Park, July 30, 1929, J. H. Faull.

ONTARIO: Timagami, July 5, 16, 29, 1919, J. H. Faull. — Timagami, June 18, 1923, J. H. Faull. — Timagami, July 8, 1924, J. H. Faull. — Timagami, May 31, 1925, J. H. Faull.

III. On *Vaccinium Vitis-idaea*.

ALBERTA: Mercoal, Aug. 8, 1925, W. R. Watson.

JAPAN: Mt. Oakan, Prov. Kushiro, Aug. 21, 1926, N. Hiratsuka 546.

III. On *Vaccinium Vitis-idaea* var. *minus*.

NEW HAMPSHIRE: Mt. Jefferson, Aug. 31, 1932, J. H. Faull.

SUMMARY

1. A review of the literature indicates that thirteen species of *Abies* have been proved by experiments to be susceptible to *Calyptospora Goepfertiana* Kühn. None are known to be immune.

Likewise, many species of *Vaccinium* have been recorded as hosts of *C. Goeppertiana*. A few of them have been used in making life history studies of the rust, namely, *V. Vitis-idaea*, *V. pennsylvanicum* and possibly *V. membranaceum* by previous investigators, and *V. pennsylvanicum* and *V. canadense* by the writer.

2. Life history studies made by the writer are summarized in Tables 2 and 3 of this paper. In these, *C. Goeppertiana* was successfully passed from *Vaccinium pennsylvanicum* and *V. canadense* to *Abies balsamea*.

3. *Peridermium ornamentale* Arthur and *P. Holwayi* Sydow, more recently held to be synonymous with *C. Goeppertiana* Kühn, are compared (Table 1) with one another and with the haploid phase of *C. Goeppertiana*. The disagreements noted lead to the conclusion that they are probably distinct forms and that neither is *C. Goeppertiana*. The diploid phases of *P. ornamentale* and *P. Holwayi*, interpreting these forms from their type specimens, have not yet been demonstrated.

4. So far, one species only of *Calyptospora* has been described. If, however, *P. ornamentale* and *P. Holwayi* should prove to be as yet unnamed species of *Calyptospora*, then the identification of collections from western North America, now passing under the name *C. Goeppertiana*, is subject to revision. The answer awaits culture experimentation.

5. The record of specimens studied in connection with the preparation of this paper extends our knowledge of the geographical distribution of *C. Goeppertiana* and gives recognition to *V. Vitis-idaea* var. *minus* Lodd. as a host of that rust.

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