Inland spruce cone rust, *Chrysomyxa pirolata*, in *Pyrola asarifolia* and cones of *Picea glauca*, and morphology of the spore stages

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Intact and sectioned specimens were examined by using a light and a scanning electron microscope to determine the presence and spore morphology of inland spruce cone rust, *Chrysomyxa pirolata* Wint., in *Pyrola asarifolia* Michx. plants and in white spruce, *Picea glauca* (Moench) Voss, cones. Field observations of rust development and sporulation were made throughout the year. The microscope studies confirmed that *C. pirolata* is systemic and perennial in shoots and connecting rhizomes of *P. asarifolia*, indicating that one mode of fungus spread is between plants originating from the same rhizome. Sometimes, hyphae of *C. pirolata* occurred only at the nodes along part of a rhizome connecting diseased *P. asarifolia* plants. Spring-collected buds from diseased *P. asarifolia* contained *C. pirolata* mycelium, but the fungus was not evident externally on current growth until the following spring. However, all leaves, especially those produced in the current year, on these plants were more upright and their upper surface less shiny. In some years, all *P. asarifolia* leaves in a locality bore mostly uredinia or telia; at other times about equal numbers of both were present on each leaf. About 6 weeks after telial production, spermogonia appeared on nearby spruce cones and about 4 weeks later these cones bore aeciospores on most scales of the systemically infected cones. Fruiting bodies and spores for each stage of the life cycle of the fungus are illustrated.

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À l'aide de la microscopie optique et à balayage, les auteurs ont examiné des spécimens intacts et sectionnés, pour déterminer la présence et la morphologie des spores de *Chrysomyxa pirolata* Wint., dans des plants de *Pyrola asarifolia* Michx. ainsi que dans des cônes de *Picea glauca* (Moench) Voss. Des observations ont été effectuées aux champs tout au cours d'une année. Les études microscopiques confirment que le *C. pirolata* est systémique et pérenne dans les tiges et dans les rhizomes interconnectés de *P. asarifolia*, ce qui indique qu'un des mode de propagation du champignon s'effectue entre les plants originant du même rhizome. Quelquefois, les hyphes du *C. pirolata* ne se retrouvent qu'aux noeuds le long d'un rhizome reliant des plants de *P. asarifolia* infectés. Des bourgeons infectés de *P. asarifolia* récoltés au printemps contenaient du mycélium de *C. pirolata*, mais le champignon n'est pas devenu visible extérieurement sur les pousses de l'année avant le printemps suivant. Sur ces plants cependant, toutes les feuilles, particulièrement celles produites au cours de l'année, étaient plus dressées et leur surface adaxiale moins luisantes. Certaines années, toutes les feuilles de *P. asarifolia* d'une localité portent surtout des urédies ou des télies; à d'autres moments on retrouve les deux types en quantités à peu près égales sur chaque feuille. Environ 6 semaines après la production des télies, les spermagonies apparaissent sur les cônes de *P. glauca* voisins et environ 4 semaines plus tard ces cônes montrent des éciospores sur la plupart des écailles qui sont systémiquement infestées. Des illustrations sont présentées pour chacun des stades du cycle vital.

[Traduit par le journal]

Introduction

Inland spruce cone rust (*Chrysomyxa pirolata* Wint.) is a serious disease of spruce (*Picea* spp.) cones in the boreal regions of the northern hemisphere (16,19). The fungus is heteroecious and displays the full life cycle with pycnial and aecial stages occurring on female spruce cones; the mycelium of the telial and uredinial stages is systemic and perennial in several species of *Pyrola*, *Moneses*, and *Orthillia secunda* House (14,16,19). These plants (Ericaceae: Pyroloideae) are small, perennial herbs with simple, alternate or opposite leaves (12); species differentiation within these genera is mainly based on various floral characteristics (2,8,9). The general distribution, disease symptoms, and life history of *C. pirolata* are known (19), but many aspects of the systemic nature of the fungus in the nonconifer hosts required clarification. Additional information was also needed regarding phenology and morphology of certain spore states. This study was made to improve our knowledge of *C. pirolata* as it occurs in and on *P. asarifolia* Michx. plants and on white spruce, *Picea glauca* (Moench) Voss, cones.

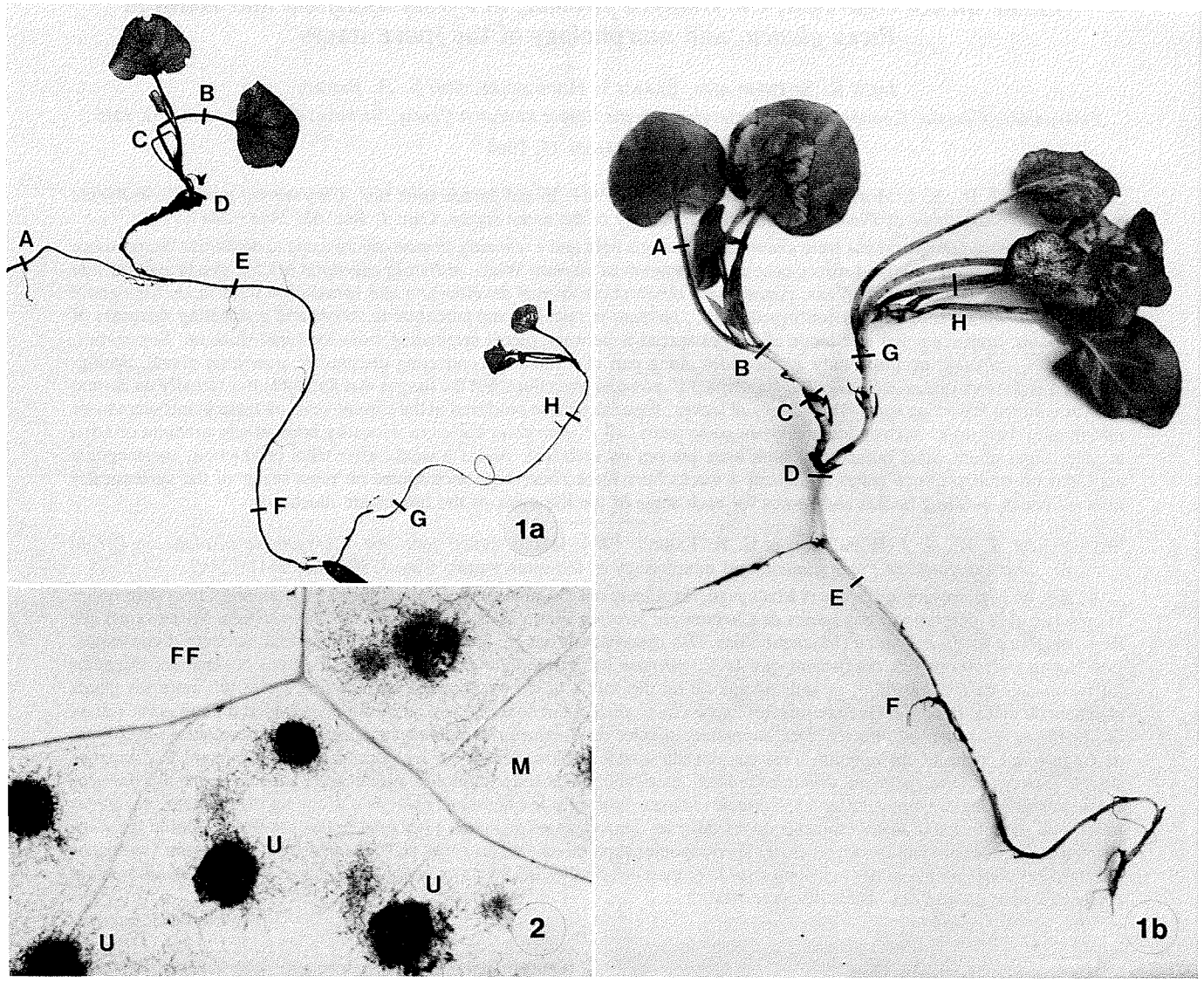
Materials and methods

Most observations were made on *P. asarifolia* plants affected and unaffected with *Chrysomyxa pirolata*. Samples (shoots plus about 1 cm of attached, belowground rhizome and connecting rhizomes) were collected from early spring through autumn, 1978 through 1983 (and especially the last 2 years), and mainly from the forest surrounding the Skimikin seed orchard near Salmon Arm (119° W longitude, 50° N latitude), British Columbia. Observations were also made of diseased and healthy cones collected from white spruce trees within and around the orchard over the same 5 years. Additional collections of *P. asarifolia* plants and spruce cones were made at Prince George, B.C. Plants and cones for sectioning were fixed in FAA (Formalin–acetic acid–alcohol), dehydrated in tertiary butyl–ethyl alcohol (10), and infiltrated and embedded in Paraplast. Cross and longitudinal sections, 10 and 12 μm thick, were stained with safranin and fast green FCF (10), periodic acid – Schiff's reagent (5), trypan blue (1), safranin and picro aniline blue (17), or modified Gram–Weigert (13). Leaves were cleared (NaOH) and stained with lactophenol – trypan blue (18). All of these specimens were examined using a light microscope. Other, intact specimens were fixed in glutaraldehyde and buffer (0.1 *M*, pH 7.2), postfixed in OsO_4 in buffer, dehydrated in an acetone series, dried under CO_2 in a critical point drier, and then coated with gold–palladium using a Hummer III sputter coater. They were examined (× 40 – 10000) using a JEOL-350 scanning electron microscope operated at 10–15 kV.

Results and discussion

Chrysomyxa pirolata *mycelium in* P. asarifolia *rhizomes and shoots*

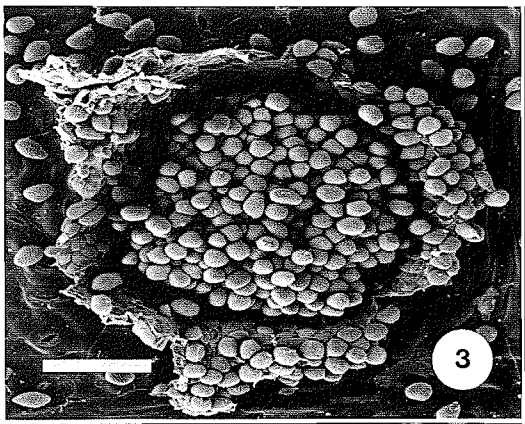
Field excavations verified earlier observations (6,14) that plants arise from and are connected by a common rhizome

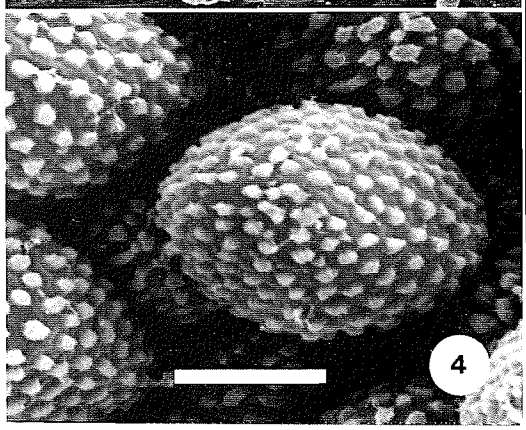


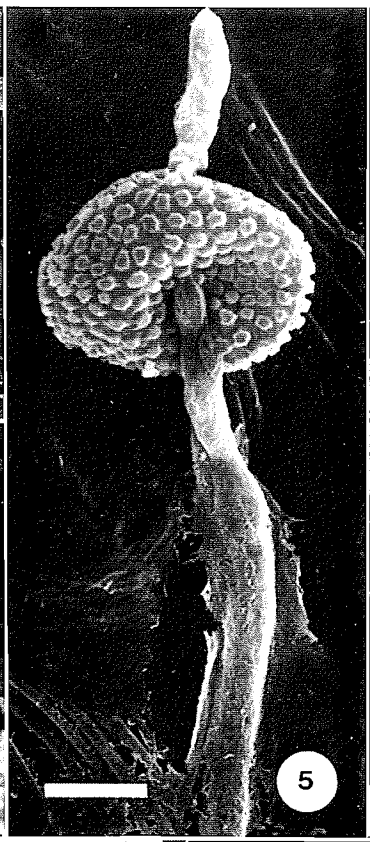
FIGS. 1 and 2. *Pyrola asarifolia* plants from which cross sections were examined with a light microscope to determine the presence and location of *C. pirolata* mycelium, and portion of diseased *P. asarifolia* leaf. Fig. 1*a*. Two rhizome-connected plants (collected September 1981), both with uredinia-bearing leaves. Letters A–I (also in Fig. 1*b*) represent points of sampling. × ca. 0.5. Fig. 1*b*. Two rhizome-connected plants (collected mid-June 1982), one (left) sorus-free and the other with all leaves except one (location H) with uredinia. × ca. 0.5. Fig. 2. Portion of a *P. asarifolia* leaf with a section where mycelium (M) and uredinia (U) are present, adjacent to a fungus-free section (FF). × ca. 100.

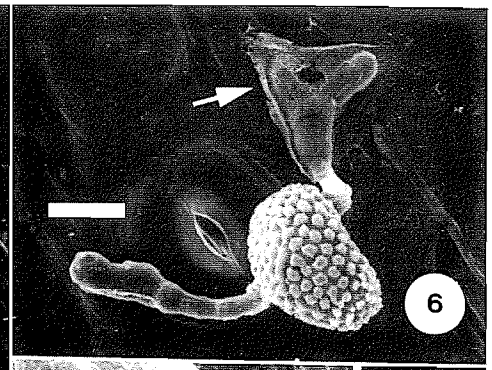
(Figs. 1*a* and 1*b*). All plants connected by a common rhizome are either healthy or diseased, i.e., a diseased and a healthy plant were never observed to be connected by the same rhizome. In a group of diseased, interconnected plants, one plant is often larger than the others (Fig. 1*a*); perhaps it is younger and has not been exposed as long to the chronic effect of the rust. Cross sections from two rhizome-connected plants (Fig. 1*a*) which bore uredinia on at least one leaf when collected in early September 1981 contained *C. pirolata* hyphae in the cortex of the petiole, stem, and bud tissues, including scales, and in those portions of the rhizome nearest to each plant (Fig. 1*a*, positions B–D and G–I). The fungus was absent except at the nodes in a section of the rhizome (Fig. 1*a*, positions A, E, and F). Mycelium of the rust was also present throughout two rhizome-connected plants (Fig. 1*b*, positions A–I), collected in mid-June 1982 (Fig. 1*b*, left), one of which was free of uredinia and telia. Although mycorrhizae are known for some Pyroloideae (e.g., 3), the mycelium that we observed in

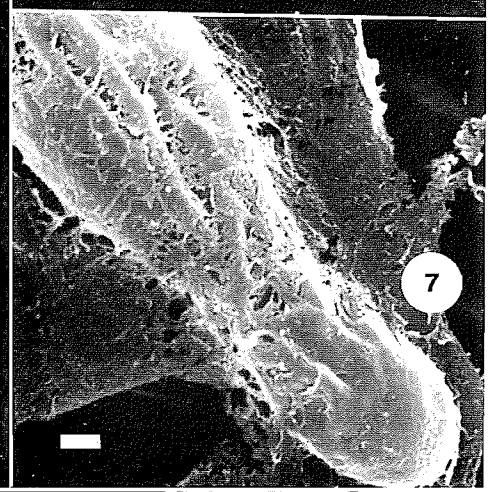
FIGS. 3–11. Sori and spores of *Chrysomyxa pirolata*. Fig. 3. Uredinium, formed subepidermally and dehisced by irregular fissures; with mature urediniospores. ×200. Bar, 100 μm. Fig. 4. Verrucose aecioid urediniospores with the warts forming a network of convex polygons. ×2000. Bar, 10 μm. Fig. 5. Two germ tubes produced by a germinating urediniospore. ×940. Bar, 10 μm. Fig. 6. Appressorium (at arrow) produced at the tip of germ tube of a urediniospore. ×1500. Bar, 10 μm. Fig. 7. Sticky matrix surrounding germ tube from urediniospore adhering to undersurface of *P. asarifolia* leaf. ×660. Bar, 1 μm. Fig. 8. Telium in cross section. ×63. Fig. 9. Germinating teliospores in surface view (urediniospores are incidental). ×200. Bar, 100 μm. Fig. 10. Metabasidium (M) and basidiospore (B). ×2000. Bar, 10 μm. Fig. 11. Spermogonia (at arrows) on cone scales. ×7.

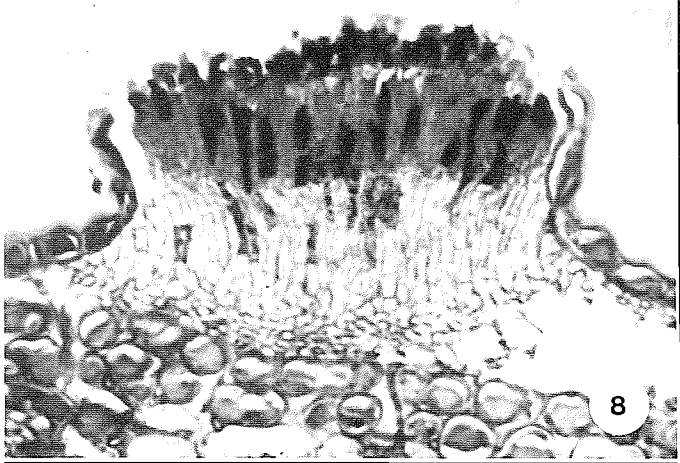


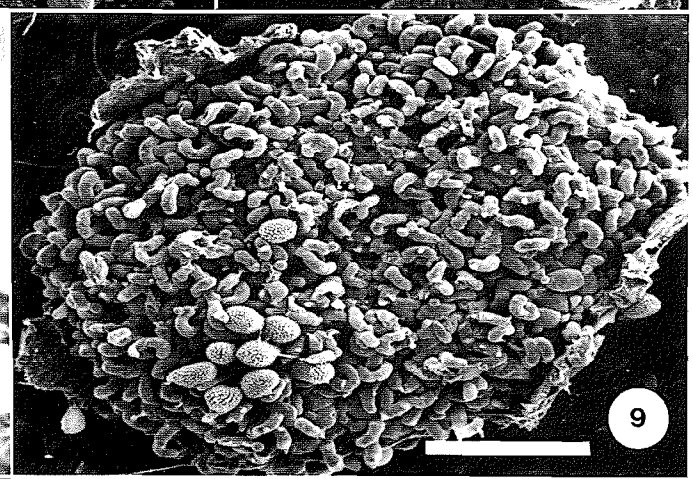


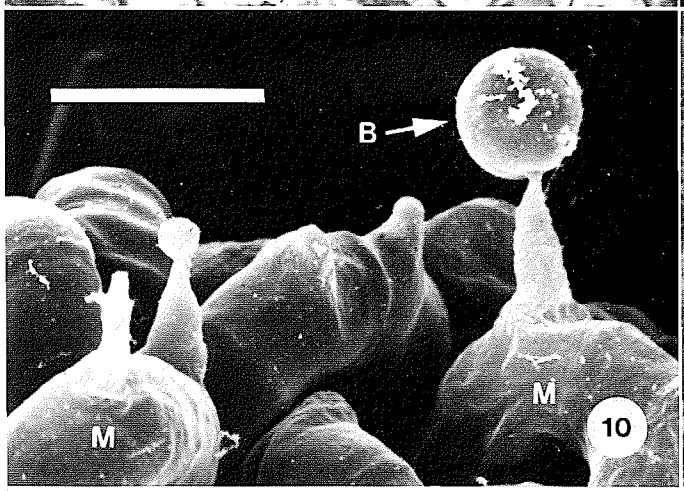


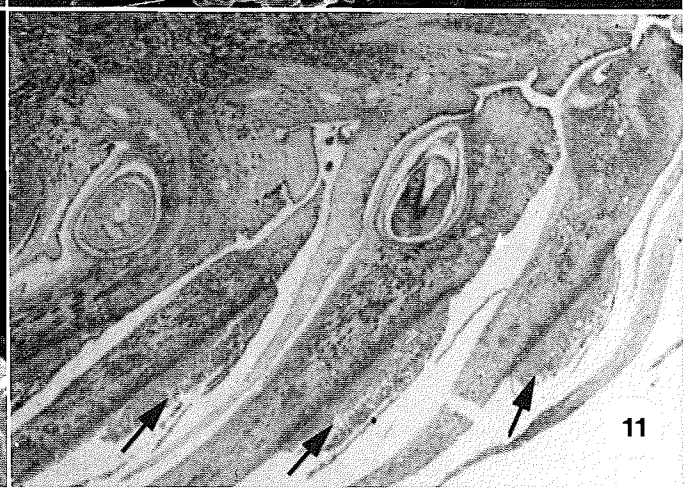












P. asarifolia rhizomes was undoubtedly that of *C. pirolata*, and not a mycorrhizal fungus, because it could be traced through serial sections from the shoot into the rhizome and it was never observed in rhizomes of healthy plants. The fungus also occurred in the petiole and blade of a sorus-free leaf from the plant with other uredinia-bearing leaves (Fig. 1*b*, right, position H). These and other observations of material from both aboveground and belowground tissues, including the presence of *C. pirolata* in the terminal bud in early spring before growth occurred, confirm the systemic and perennial nature of the fungus in *P. asarifolia* (6, 14). The nature of the relationship needs to be determined for other hosts of *C. pirolata* as apparently the fungus is confined to the leaves in *O. secunda* (R. L. M. Ross and S. H. Farris, unpublished data). Although *C. pirolata* is systemic in the vegetative tissues of *P. asarifolia*, it is not known if the fungus is in or is spread by seeds.

Uredinia and urediniospores

Examination of cleared sections of *P. asarifolia* leaves in early winter, before snow accumulation, revealed *C. pirolata* hyphae distributed throughout the leaves of diseased plants, but there was no indication of prosorus formation. However, at spring snow melt, hypophyllous subepidermal, orange–yellow prosori, which later became either uredinia or telia, were observed on old leaves, but they seldom were noted on current-year leaves. Gäumann (6) made similar observations. Since these prosori were absent in early winter (November) before snow accumulation, they obviously developed over the winter. Determining the necessity of snow cover for fungus development could be useful in predicting cone rust outbreaks. Orange–yellow, spore-producing uredinia were evident on the lower leaf surface of *P. asarifolia* by early May and, depending upon weather and longevity of the sorus-bearing leaf, urediniospores were liberated for 2–12 weeks in 1981 and 1982 (J. R. Sutherland, unpublished data). Periodicity of urediniospore production may differ on other *C. pirolata* hosts, e.g., at Skimikin sporulation on *O. secunda* can occur from late summer to snowfall.

In 1982, uredinia were distributed evenly over the leaf undersurface, or sometimes patches of the leaf area were devoid of both hyphae and uredinia (Fig. 2). Usually sori were absent from the convex surface of major leaf veins and usually hyphae did not cross over or through these veins. Uredinia formed subepidermally and dehisced by irregular fissures (Fig. 3). Also, in 1982 the diseased *P. asarifolia* leaves lived through the fall and died during the winter. In 1983, telia were more abundant on *P. asarifolia* leaves and only a few uredinia were scattered along the leaf margin. Leaf longevity also differed in the 2 years (see the subsequent section on telia).

Urediniospores are aecioid, ellipsoid to obovate (18–27 × 13–24 μm), catenuate, with intercalary cells, and verrucose. The warts are entire and crowded, with variable spacing, forming a network of convex polygons (Fig. 4) (Littlefield and Heath 15). The spore wall is apparently thinner than that of aeciospores. Urediniospores dusted onto the wet undersurface of a *P. asarifolia* leaf germinated; each spore usually produced two germ tubes (Fig. 5) that eventually branched and produced appressoria at their tips (Fig. 6). Urediniospores of other conifer rusts, e.g., *Cronartium comandrae* (11), also frequently produce more than one germ tube. A sticky matrix apparently adheres the germ tube to the host (Fig. 7). Germ tubes were not observed to have any trophism and preliminary inoculation studies indicated that appressoria were not formed over stomata.

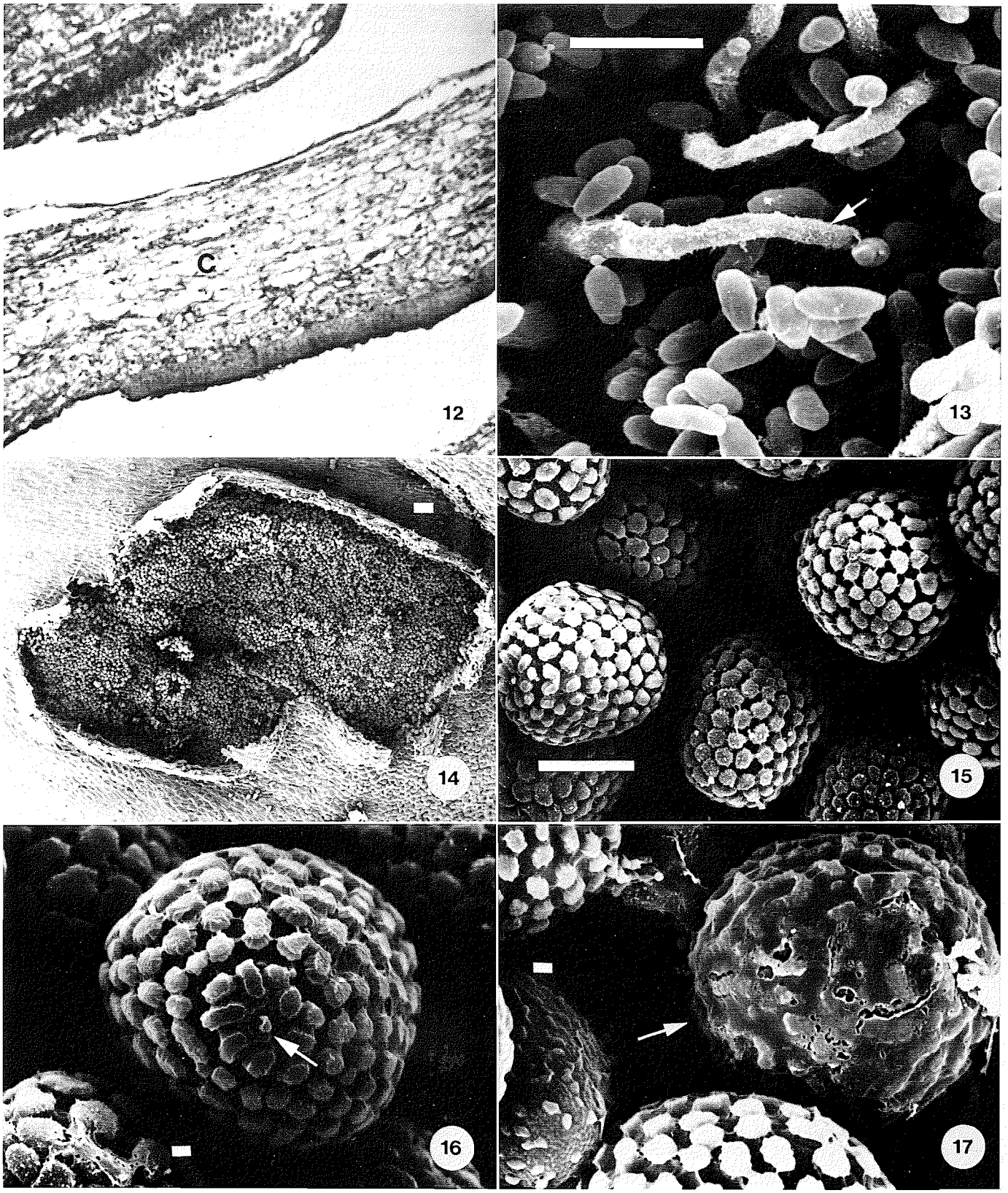
Telia, teliospores, and basidiospores

Hypophyllous telia are on *P. asarifolia* leaves for a 6-week period, starting about 2 weeks before spruce cone pollination. In 1982, the telia occurred in groups of two or three, or sometimes up to 10, scattered among the uredinia. In 1983, the leaves predominately bore telia. When both uredinia and telia were present, the latter tended to be more prevalent near the distal end of the leaf midrib. Interestingly, in 1983 when telia predominated at Skimikin and also at Prince George, the local spruce cone crop was heavy at both localities. Perhaps the same factors, probably weather conditions, predetermine both cone and telia production. In 1983 the leaves upon which sporulation occurred died soon afterwards. Maybe the drier and hotter than normal weather during sporulation or the heavy production of telia, or both, were responsible for leaf death. Nelson and Krebill (16), in Utah, noted death of *Pyrola* leaves upon which telia of *C. pirolata* sporulated. The remaining leaves on diseased plants were distinguishable throughout the rest of the growing season by their more upright habit and less shiny, dull gray appearance. In early winter leaves of both healthy and diseased plants became somewhat chlorotic and the chlorophyll appeared to be concentrated in numerous, evenly distributed patches.

Young telia are light orange (lighter than uredinia), finally becoming dry brown. Telia form subepidermally (Fig. 8) and are erumpent, pulvinate (Fig. 9), and round to oblong (400 × 250 μm). They frequently coalesce. Teliospores are one celled, irregularly oblong or ellipsoid (12–20 × 6.8–9.0 μm), catenulate (basipetal chains), and smooth walled. Germination occurs soon after teliospore formation; germinating spores appear swollen and stain darker (Fig. 8). The metabasidium is external and after it forms, the teliospore (probasidium) collapses, but the cell wall retains stain. One basidiospore is produced by each of the four linearly arranged metabasidium cells; only one or two of the four basidiospores were observed at the same time (Fig. 10); presumably the others had been released or had not yet formed (7). Basidiospores (Fig. 10) are round–globoid (5–7 μm), smooth, and thin walled with a prominent apiculus.

Spermogonia and spermatia

At Salmon Arm, spermogonia appeared in mid-June (about 6 weeks after telia appearance on *P. asarifolia*), mostly on the abaxial covered surface (beneath the overlapping scale above) of pendulant ovuliferous cone scales (Figs. 11 and 12). Less often, spermogonia were observed on either surface of bracts. The mycelium is systemic in the cone tissues and numerous monokaryotic haustoria are present. Basidiospore inoculation studies are needed to determine the exact sequence of cone invasion because the fungus is systemic in cones when spermogonia appear. Spermogonia are subepidermal, of various sizes and shapes (indeterminate), and golden; the hymenial layer is flat and irregular shaped, i.e., except for their inconsistent sizes and shapes they are typical of group I, type 2 spermogonia (4). The flexuous hyphae which are scattered throughout the spermogonia are blunt ended and have a rough surface (Fig. 13). The ostiolar trichomes which occur around the periphery of the spermogonia are longer than flexous hyphae and have tapered apical ends. Spermatia (Fig. 13) are one celled, smooth, narrowly ellipsoid with rounded ends (5–7 × 1.5–2.0 μm), and uninucleate.



FIGS. 12–17. Sori and spores of *Chrysomyxa pirolata*. Fig. 12. Spermagonium (S) on spruce cone (C). ×10. Fig. 13. Blunt-tipped, rough-surfaced flexous hypha (at arrow) on spermogonium. ×2000. Bar, 10 μm. Fig. 14. Aecium. ×40. Bar, 100 μm. Fig. 15. Aeciospores. ×2000. Bar, 10 μm. Fig. 16. Annulate knobs on aeciospore wall and small knob (at arrow) at end of spore. ×4000. Bar, 1 μm. Fig. 17. Young aeciospore (at arrow) with a membrane covering the knobs. ×4000. Bar, 1 μm.

Various wasps and flies were noted feeding on spermatia and excudates from diseased and healthy cones, suggesting that such insects play a role in spermatization. Not all cones with spermatia produced aeciospores; in 1983 only 63% of the cones on nine small seed orchard trees (averaging 83 cones each) with spermatia as of June 12 eventually produced aeciospores as of August 20. Cones with only spermatia ceased development prematurely, became desiccated, and were sometimes attacked by insects. Thus, simply counting aeciospore-bearing cones may underestimate cone rust damage.

Aecia and aeciospores

About 2 weeks after spermagonia first appear, caeomoid (15) aecia (Fig. 14) are produced, primarily on the abaxial surface of the cone scales; adaxial aecia apparently are smaller. A scale may bear both spermagonia and aecia simultaneously or just aecia. Occasionally, aecia occur on both surfaces of a cone bract. Aecia (Fig. 14) are oblong and irregular shaped, and as noted by Gäumann (6), they tend to coalesce as they develop. Dehiscence is by an irregular fissure. Paraphyses and peridium are absent. Produced in abundance, the aeciospores (Fig. 15) (19) are yellow–orange, ovoid to subglobose (25–37 × 17–35 μm), and catenuate. Annulate knobs, consisting of two cushionlike discs stacked on top of one another, cover the surface of mature aeciospores (Fig. 16) (also see Littlefield and Heath (15)). Narrow ridges interconnect the knobs. These knobs are similar in shape and distribution to those on urediniospores (Fig. 4). Sometimes two or more knobs are united. Young aeciospores are rough walled and seem to have a covering membrane (Fig. 17), which disappears as the spores mature to reveal the knobs. Each aeciospore has a small, modified knob or appendage at one or both ends (Fig. 16).

Conclusions

Cummins and Hiratsuka (4) give *Chrysomyxa* as one of several genera of rust fungi with nonresting (nonresistant) teliospores, i.e., teliospores that germinate as soon as they are fully formed. Our observations indicate that *C. pirolata* is typical of the genus. Cummins and Hiratsuka (4) also state that it is axiomatic that rust fungi lacking resistant teliospores compensate with some development elsewhere in the life cycle to permit survival in unfavorable periods. We conclude that the systemic nature of *C. pirolata* in *P. asarifolia* and especially its ability to inhabit the rhizomes of its perennial host is an important survival mechanism for this rust fungus. Besides invading new host plants that arise as the rhizome grows, *C. pirolata* apparently survives at the nodes of old rhizomes where it could invade new plants that might arise there. Others (14,19) imply that *C. pirolata* enters one or more *P. asarifolia* plants and moves via the common rhizome to other connected plants. Inoculations of *P. asarifolia* with both urediniospores and aeciospores are needed to see if this is true. Another possibility, that inoculations should help to clarify, is that all plants arising from a common rhizome are clones of susceptible *P. asarifolia* that become diseased solely from airborne inoculum. Existence of rust-susceptible clones could explain why only about 5% of *P. asarifolia* plants are diseased, particularly in areas where their leaves are often covered with a yellow dust of aeciospores.

Our conclusions regarding the morphology and phenology of *C. pirolata* fruiting bodies and spores are as follows.

Uredinia and urediniospores

On *P. asarifolia* hypophyllous, subepidermal, orange–yellow prosori form over the winter and are evident at spring snow melt, usually becoming distributed evenly over the leaf; later, uredinia dehisce by irregular fissures. Urediniospore liberation begins in early summer (early May at Salmon Arm), continuing for 2–12 weeks; aecioid urediniospores are ellipsoid to obovate (18–27 × 13–24 μm), catenuate, with intercalary cells and verrucose; warts are entire, crowded and with variable spacing, forming a network of convex polygons.

Telia, teliospores, and basidiospores

On *P. asarifolia* hypophyllous, subepidermal, orange–yellow prosori, form over the winter and are evident at spring snow melt. Young telia are erumpent, beginning to form about 2 weeks before cone pollination and persisting for about 6 weeks; they are light orange (lighter than uredinia), pulvinate, round to oblong (400 × 250 μm), either in groups of up to 10 among the uredinia or sometimes covering the entire leaf undersurface and frequently coalescing. Teliospores are one celled, irregularly oblong or ellipsoid (12–20 × 6.8–9.0 μm), catenuate (basipetal chains), and smooth walled; they germinate soon after formation; the metabasidium is external. One basidiospore is produced by each of the four linearly arranged metabasidium cells. Basidiospores are round–globoid (5–7 μm diam.), smooth, and thin walled with a prominent apiculus.

Spermogonia and spermatia

Both spermogonia and spermatia are evident on *Picea* cones about 6 weeks after telia are first noticed (on *P. asarifolia*), normally on abaxial, covered surface of scales of ovuliferous, pendulant cones. Spermognia are subepidermal, of indeterminate shape and size, and golden; the hymenial layer is flat, irregular in shape; the blunt-ended, flexuous hyphae are scattered throughout; ostiolar trichomes occur around the periphery. Spermatia are one celled, smooth, narrowly ellipsoid, with rounded ends (5–7 × 1.5–2.0 μm), and uninucleate.

Aecia and aeciospores

Both aecia and aeciospores are evident about 2 weeks after spermogonia and usually on the abaxial surface of the same spruce cone scales as the spermagonia. Aecia are oblong and irregular shaped, tending to coalesce with development; they dehisce by irregular fissures. Aeciospores are yellow–orange, ovoid to subglobose (23–37 × 17–35 μm), catenuate, with a surface covered by annulate knobs.

Acknowledgments

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