Rusts

Rust fungi belong to the Uredinales, a highly specialized order of the Basidiomycetes. In common with mushrooms they have spores of the sexual stage borne in fours on a club-shaped hypha known as a basidium, but apart from this they differ very decidedly from woody and fleshy Basidiomycetes. The term rust is applied both to the pathogen and to the disease it inflicts. There are more than 4000 species of rusts, all obligate parasites on ferns or seed plants. Many are heteroecious, completing their life cycle on two different kinds of plants; but some are autoecious (monoecious), having all spore forms on a single host species. There are only two families, Melampsoraceae and Pucciniaceae.

Many rusts show physiological specialization, the existence within a species of numerous strains or races that look alike but attack different varieties of crop plants, thus greatly complicating the problem of breeding for rust resistance. Rusts with a complete life cycle have five different spore forms, numbered 0 to IV.

0. *Pycniospores* (spermatia) formed in *pycnia* (spermagonia). The pycnia resemble pycnidia of Ascomycetes, are usually on upperside of leaves. They discharge one-celled pycniospores with drops of nectar, and these, usually distributed by insects attracted to the sweet secretion, function in fertilization.

I. *Aeciospores* (aecidiospores), one-celled, orange or yellow, formed, often in chains, in a cuplike sorus or *aecium*, which has a peridium (wall) opening at or beyond the surface of the host.

II. *Urediospores* (uredospores, summer spores, red rust spores), one-celled, walls spiny or warty, reddish brown, on stalks or in chains in a *uredium* (uredinium or uredosorus), over which the epidermis of the host is broken to free the spores. Resting II spores, formed by some rusts, have thicker and darker walls.

III. *Teliospores* (teleutospores, winter spores, black rust spores), one or more cells, in *telia* (teleuto sori), either on stalks, as in the family Pucciniaceae, or sessile, in crusts or cushions as in the Melampsoraceae.

IV. *Basidiospores* (sporidia) on a basidium or promycelium formed by the germinating teliospore. Basidium is usually divided transversely into four cells, with one sporidium formed from each cell at the tip of a sterigma.

In heteroecious rusts spore stages 0 and I are formed on one host and II and III on another, and are so indicated in the information given with each species. Stage IV always follows III on germination. Although most autoecious rusts have all spore forms, on one host, there are a few short-cycle (microcylic) rusts with some spore stages dropped out. For a detailed life history of a heteroecious rust, ▶*Puccinia graminis*.

Gardeners frequently mistake a reddish discoloration of a leaf, perhaps due to spray injury or weather or a leaf-spot fungus, for rust. True rust is identified by the presence of rust-colored spores in powdery pustules or perhaps gelatinous horns. With rusts, the discoloration of tissue is yellowish, not red, and it is due to increased evaporation from the broken epidermis. Plants are often stunted.

R.K. Horst, *Westcott's Plant Disease Handbook*, DOI 10.1007/978-94-007-2141-8_42,

Losses in food crops due to rust have been enormous since the beginning of history. The Romans had a festival to propitiate the rust gods. Now we try to do it by removing the alternate host, barberry to save wheat, black currants to save white pine; or by developing more and more resistant varieties for the ever increasing rust strains; or by the use of fungicides, classically sulfur, latterly some of the carbamates, and, in a few cases, antibiotics.

Achrotelium

Melampsoraceae. Telia on underside of leaves; spores one-celled at first, four-celled on germination, stalked.
Achrotelium lucumae II, III on lucuma and egg fruit, Florida.

Aecidium

This is a form genus, a name applied to the aecial stage where the full cycle is unknown and 0 and I are the only spores. Aecia have a peridium and catenulate spores. There are many species.
Aecidium avocense On poppy-mallow, probably aecial stage of *Puccinia avocensis*.
Aecidium conspersum On houstonia and galium, Wisconsin.
Aecidium rubromaculans On viburnum, Florida.

Angiospora

►*Physopella*.

Aplopsora

Melampsoraceae. Teliospores sessile, hyaline, one-celled, in a single layer; aecia unknown.
Aplopsora nyssae On tupelo, II, III.

Baeodromus

Pucciniaceae. Spores one-celled; telia pulvinate, erumpent; short chains of spores.
Baeodromus californicus On senecio, III.
Baeodromus eupatorii (see ►*Coleosporium steviae*). On eupatorium.
Coleosporium steviae (formerly *Baeodromus eupatorii*). On eupatorium.

Bubakia (Phakopsora)

Melampsoraceae. Telia indehiscent, lenticular, spores formed in irregular succession, one-celled. Uredia without peridium or paraphyses.
Bubakia erythroxylonis On erythroxylon.

Caeoma

Form genus. Aecia with catenulate spores but no peridium.
Caeoma faulliana (see ►*Melampsora medusae*). Needle Rust on alpine fir. Aecia orange-yellow, on needles of current year.
Caeoma torreyae On torreya, California.
Melampsora medusae (formerly *Caeoma faulliana*). Needle Rust on alpine fir. Aecia orange-yellow, on needles of current year.

Cerotelium

Pucciniaceae. Spores one-celled; teliospores in a many-layered mass; hyaline, not exserted through stomata; aecia with peridium; uredia with paraphyses; spores borne singly.
Cerotelium dicentrae 0, I on bleeding heart; II, III on *Urticastrum*.
Cerotelium fici (*Physopella fici*). Fig Rust, II, III on common fig, Florida strangler fig and osage-orange, Alabama, Florida, Louisiana, Minnesota, South Carolina, Texas.

Chrysomyxa

Melampsoraceae. Teliospores in cylindrical or branching chains; promycelium exserted; urediospores typically in short chains; uredia without peridium.

Chrysomyxa arctostaphyli On bearberry, III.

Chrysomyxa chiogenis II, III on creeping snowberry; 0, I on spruce.

Chrysomyxa empetri II, III on crowberry; 0, I on red and white spruce. Aecia on upper and lower surfaces of needles.

Chrysomyxa ilicina II, III on American holly.

Chrysomyxa ledi 0, I, on black, red and Norway spruce; II, III on underside of leaves of *Ledum* spp.

Chrysomyxa ledi var. **cassandrae** Spruce Needle Rust. 0, I on black, red, blue and Engelmann spruce; II, III on bog rosemary (*Chamaedaphne*). May become epidemic on spruce, causing considerable defoliation.

Chrysomyxa ledi var. **groenlandici** On Labrador-tea, Michigan, New Hampshire.

Chrysomyxa ledi var. **rhododendri** II, III on rhododendron, Washington. A European rust first noted on Pacific Coast in 1954, apparently entering despite quarantine on nursery stock. Yellow uredia on leaves.

Chrysomyxa ledicola 0, I on white, black red, blue, Engelmann, and Sitka spruce; II, III on upperside of leaves of *Ledum* spp. Spruce needles may be so discolored that trees appear yellow.

Chrysomyxa moneses On Sitka spruce and moneses.

Chrysomyxa piperiana 0, I on Sitka spruce; II, III on underside leaves of *Rhododendron californicum*, California, Oregon, Washington.

Chrysomyxa pirolata (*C. pyrolae*). 0, I on cones of black, blue, Engelmann, Norway, red and white spruce; II, III on pyrola. Aecia are on upperside of cone scales; infected cones turn yellow, produce no seed.

Chrysomyxa weirii Spruce Needle Rust. III on Engelmann and red spruce. Waxy orange to orange-brown elongate or elliptical telia occur on 1-year needles. This is the only spore stage known; teliospores can reinfect spruce.

Coleosporium

Melampsoraceae. Pycnia and aecia are on pines; uredia and telia on dicotyledons. Pycnia subepidermal or subcortical, flattish, linear, dehiscent by a slit; aecia on needles, erumpent, with prominent peridium, spores ellipsoid or globular; uredia erumpent, powdery without peridia; urediospores globose or oblong, catenulate, with verrucose (warty) walls; telia indehiscent, waxy, gelatinous on germination; spores sessile or obscurely catenulate, one-celled, smooth but with thick and gelatinous walls.

Coleosporium apocyanaceum 0, I on loblolly, longleaf, and slash pines; II, III on *Amsonia* spp. in the Southeast.

Coleosporium asterum (*C. solidaginis*). Needle Blister Rust of pine. 0, I on all two-and three-needle pines in eastern United States; II, III on aster and goldenrod, on China aster (except far South), on golden aster (*Chrysopsis*), erigeron, grindelia, seriocarpus, and other composites. This blister rust on pine needles has pustules higher than they are long, in clusters or short rows. The rust is fairly common on ornamental pines in gardens, wintering on aster and related composites. Older needles of young pines may be severely infected, with white aecia conspicuous in spring and early summer. Aster leaves have bright orange-yellow spore pustules on undersurface. Destroy goldenrod near pines.

Coleosporium crowellii III only stage known; on needles of pinon and limber pines, Arizona, Colorado, New Mexico, Utah, Nevada, and California.

Coleosporium delicatulum Pine Needle Rust. 0, I on two-and three-needle pines; II, III on goldenrod and euthamia.

Coleosporium helianthi 0, I on two-and three-needle pines, especially in the Southeast; II, III on silphium and parthenium.

Coleosporium helianthi Sunflower Rust. 0, I on pitch and short-needle pines; II, III on wild and cultivated sunflower, Jerusalem artichoke and heliopsis. Sunflower leaves, with brown rust pustules, dry up and drop. Control is not easy.

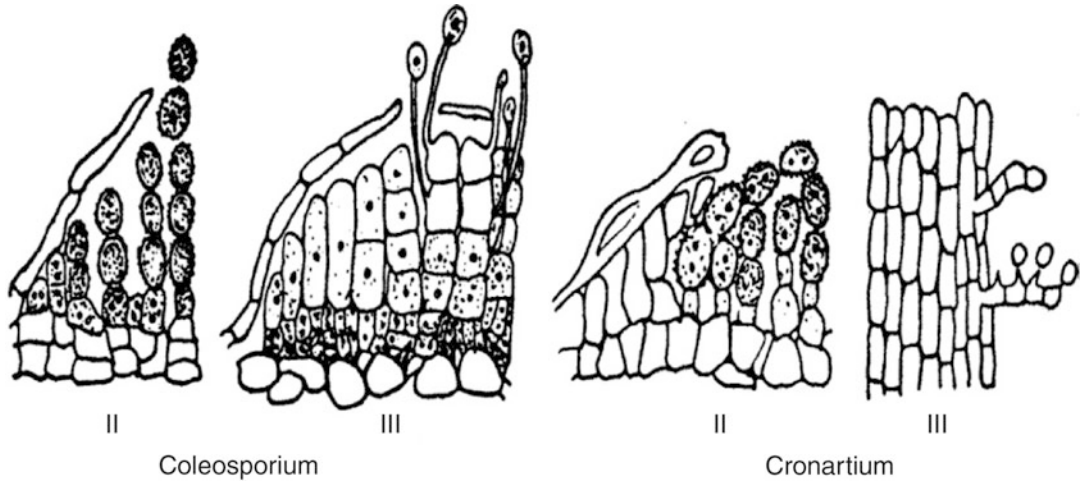

Fig. 1 Pine Rusts. *Coleosporium asterum*, uredial (II) and telial (III) stages on aster, teliospores germinating *in situ*. *Cronartium ribicola*, II and III stages on currant

Coleosporium ipomoeae 0, I on southern and Chihuahua pines; II, III on moonflower, morning-glory, sweet potato, jacquemontia, and quamoclit; most abundant in warmer regions. The uredia are orange-yellow, telia deep reddish orange on sweet potato.
Coleosporium jonesii 0, I on pinon pine; II, III on flowering currant and gooseberry.
Coleosporium lacinariae 0, I on loblolly, longleaf, and pitch pines; II, III on liatris.
Coleosporium mentzeliae On mentzelia.
Coleosporium minutum 0, I on loblolly and spruce pines; II, III on forestiera.
Coleosporium pacificum 0, I on Monterey, Coulter, and Jeffrey pines; II, III on marigold, sunflower, tarweed, and other composites.
Coleosporium pinicola III on Virginia or scrub pine.
Coleosporium tussilaginis 0, I on pitch, red, and Virginia pines; II, III on campanula, lysimachia, and specularia, Underside of bluebell leaves are covered with orange to reddish brown pustules. Leaves dry; plants are stunted.
Coleosporium tussilaginis 0, I on Scotch pine; II, III on sow-thistle.
Coleosporium tussilaginis 0, I, unknown; II, III on senecio.
Coleosporium vernoniae 0, I on two-and three-needle pines in South; II, III on elephantopus.
Coleosporium vernoniae 0, I on various two- and three-needle pines; II, III on ironweed.
Coleosporium viburni 0, I, unknown; II, III on *Viburnum* spp.

Cronartium (Causing Blister Rusts)

Melampsoraceae. Heteroecious; pycnia and aecia on trunk and branches of pine; uredia, telia on herbaceous or woody dicotyledons.

Pycnia on stems, caeomoid, forming blisters beneath host cortical layer; dehiscent by longitudinal slits in bark; aecia on trunks, erumpent, with peridium sometimes dehiscent at apex, more often splitting irregularly or circularly at side; aeciospores ellipsoid with coarsely warted walls, sometimes with smooth spot on one side. Uredia on underside of leaves or on stems of herbaceous hosts; delicate peridium, dehiscent at first by a central pore; urediospores borne singly on pedicels, ellipsoidal with spiny walls; telia erumpent, often coming from uredia; catenulate, one-celled teliospores often form a extended cylindrical or filiform column, horny when dry (see Fig. 1).

Blister rusts are characterized by swellings that are globose, subglobose, or fusiform, depending on species. A rust on a pine stem is

invariably a *Cronartium*, although this stage has often gone under the name of *Peridermium*.

Cronartium appalachianum (*Peridermium appalachianum*). I on Virginia pine, North Carolina, Tennessee, Virginia, West Virginia. Girdling bark lesions with columnar aecia.

Cronartium coleosporioides Ponderosa Pine Rust, widespread in Rocky Mountains; II, III on Indian paintbrush.

Cronartium coleosporioides (*C. filamentosum*). Western Gall Rust, Paintbrush Blister Rust. 0, I on lodgepole, ponderosa and Jeffrey pines, in West; II, III on Indian paintbrush, birds-beak, owls-clover and wood-betony. Slight swellings are formed on twigs, trunks, and branches; many lodgepole pine seedlings are killed.

Cronartium comandrae Comandra Blister Rust. 0, I on ponderosa, Arizona, and lodgepole pines in West and pitch, mountain, jack, loblolly, Austrian, Scotch, and maritime pines in the East; II, III on bastard toadflax (*Comandra* spp.). Destructive effect is limited to distribution of toadflax, which is widespread but locally restricted to small areas. Ponderosa pine suffers most severely, with many seedlings and saplings destroyed; occasionally a large tree is attacked.

Cronartium comptoniae Sweet-Fern Blister Rust.0, I on two-and three-needle pines; II, III on sweet-fern and sweet gale in northern pine regions and south to North Carolina, and on Pacific wax-myrtle on Pacific Coast. Young pines may be girdled and killed, but are fairly safe after attaining a trunk diameter of 3 inches. Losses in nurseries and plantations are high, especially among lodgepole and ponderosa pines. Affected stems swell slightly near the base with long fusiform swellings or depressed streaks on eastern hard pine; pitch oozes out from insect wounds in these areas. Killing of main stem often results in multiple-stemmed shrublike trees. Orange aecia appear on 3-year seedlings, preceded by pycnia the year before; spores are wind-borne many miles to herbaceous hosts.

Control Remove *Myrica* species for several hundred yards around nurseries or pine plantations, and allow no large groups within a mile.

Cronartium conigenum Pine Cone Rust. 0, I on cones of Chihuahua pine; II, III on oaks in Southwest. Cones develop in large galls producing aecia with distinct, erumpent peridium 2 or 3 years after infection.

Cronartium harknessii (see ►*Endocronartium harknessii*). Western Gall Rust. 0, I on Jeffrey, ponderosa, lodgepole, and digger pines; II, III on Indian paintbrush, lousewort, owls-clover, or omitted, with direct infection from pine to pine.

Cronartium occidentale Pinon Blister Rust. 0, I in pinon and Mexican pinon; II, III on currant, gooseberry and flowering currant. This rust cannot be told from whitepine blister rust on *Ribes* hosts, but is differentiated by the type of pine attacked. Aecia on Mexican or single leaf pinon are distinct sori; on pinon they form broad layers under bark.

Cronartium quercuum f. sp. **fusiforme** Rust on pine.

Cronartium quercuum f. sp. **fusiforme** - Southern Fusiform Rust, 0, I on hard pines in southern states, especially loblolly, slash, and pitch pine; II, III on evergreen oaks on underside of leaves. Pine stems have pronounced spindle-shaped swellings, sometimes with witches' broom. Branch infections that do not reach the main trunk are not serious, but those that go on to the trunk may kill the tree. Longleaf pines are rather resistant, and shortleaf *P. echinata* almost immune. Pines well spaced in good locations grow more rapidly and may have more rust than those in poor sites. It has also been reported on oaks.

Control Prune branches yearly before swellings reach main stem.

Cronartium quercuum (*C. cerebrum*) Eastern Gall Rust. 0, I on pines, especially scrub and shortleaf in the South; II, III on chestnut, tanbark and oak. Globose to subglobose galls are formed on pine stems; in spring aecia break through the bark in more or less cerebroid (brainlike) arrangement.

Cronartium ribicola White Pine Blister Rust. 0, I on eastern white pine from Maine to Virginia and Minnesota, on western white pine in the Pacific Northwest, on sugar pine in California; II, III on currant, flowering currant and

gooseberry. Occurs also on limber pine in Northcentral and Southeastern Wyoming.

This dread disease is supposed to have originated in Asia, whence it spread to Europe, where the eastern white pine introduced from America was very susceptible. White pine blister rust was found in Russia in 1854, and by 1900 had spread over most of Europe. It was recorded on *Ribes* at Geneva, New York, in 1906, but probably was there some years previously. In 1909 it was found on pine, at which time it was learned that infected pines from a German nursery had been widely planted throughout the Northeast. The next year the disease reached Vancouver, British Columbia, in a shipment from a French nursery, whence it spread to Washington, Oregon, Northern California, Idaho, and western Montana. Thus from cheap stock brought in for forest planting has come one of our greatest forest hazards. Our present quarantine laws are designed to prevent such introductions.

The western white sugar and whitebark pines are even more susceptible to blister rust than eastern white pine; but in either case robust, dominant trees are more severely attacked, with frail individuals lightly infected. This however, is partly explained by more vigorous trees having more needles to receive spores. Of the *Ribes* species, black currant is most susceptible and dangerous. Cultivated red currants are somewhat resistant, causing a minimum of pine infection; Viking and Red Dutch varieties are practically immune. Wild gooseberries and skunk currant are highly susceptible in the Northeast, as are western black currant, stink currant, and red flowering currant. The greater the susceptibility of the *Ribes* species, the more spores are produced to inoculate pines, with proportionate damage.

Symptoms and Life History When a spore arrives on a pine needle from a currant, the first sign of infection is a small golden yellow to reddish brown spot. The next season, or possibly in two years, the bark looks yellowish, often with an orange tinge to the margin of the discolored area, and there may be a spindle-shaped swelling. If such symptoms appear early in the season, pycnia are formed in bark by July or August; but if discoloration is delayed until midsummer, they appear the next year. The male fruiting bodies are small, honey yellow to brown patches, swelling to shallow blisters and rupturing to discharge drops of a yellowish, sweet liquid. After this is eaten by insects or washed away by rain, the lesions turn dark. The next spring or summer aecia push through the bark in the same region. These are white blisters, rupturing to free orange-yellow aeciospores, which are carried away by wind. The bark then dries out and cracks, with death of cambium and underlying wood. The disease has taken 3 to 6 years to reach this stage.

Production of aecia continues yearly until stem is killed beyond the lesion. Dead foliage assumes a conspicuous red-brown color. This "flag" of brown on a green background is the most conspicuous symptom of blister rust before death of the pine. Infection progresses downward from small to larger branches and into trunk. Swellings are not apparent on stems much over 2 inches in diameter on eastern white pine, but in the West they sometimes show up in stems 5 inches through. Larger limbs and trunks sometimes show constriction in the girdled area.

The aeciospores, large, ellipsoidal, with thick, warty walls, are carried by wind great distances to *Ribes* species (they cannot reinfect pine). They send their germ tubes into a currant or gooseberry leaf through stomata, and within 1 to 3 weeks pinhead-size blisters appear in clusters on yellowed leaf tissue. These uredia rupture to release large, ellipsoidal, yellow urediospores with thick, colorless walls and short, sharp but sparse spines. The spores are somewhat moist and sticky, and are windborne short distances to other *Ribes* bushes nearby. There may be up to seven generations in a summer, or the spores may remain viable over winter in uredia; this stage can infect only currant.

In late summer telia follow uredia in the same or new leaf lesions, appearing as short brown bristles on underside of leaves or looking like a coarse felt. Each felty bristle is composed of vertical rows of broad, spindle-shaped spores, which germinate *in situ* to a five-celled promycelium with each of the four upper cells bearing at the point of a sterigma a small,

thin-walled, round basidiospore. This cannot reinfect currant and soon dies from exposure to the sun unless the wind blows it immediately to a pine needle. The effective range is around 300 feet except for spores from black currants, which can be carried a mile. The spores from pine to currant can be carried many miles, up to 300. Blister rust is more important at elevations of 1000 feet or over, where it is increased by lower temperatures and more rainfall.

Control Eradication of the *Ribes* host is definitely effective in controlling white pine blister rust. This means complete removal of black currants and local removal of cultivated red and wild currants and gooseberries within 300 or 900 feet of pines, according to state regulations, taking care to get all the root system capable of resprouting.

Blister rust is seldom found on ornamental pines in cities; the smoke and fumes are unfavorable to the fungus. Elsewhere valuable ornamentals can be saved by cutting off infected branches and cleaning out trunk infection, stripping off diseased bark and a 2-inch side margin, 4-inch margin at top and bottom, of healthy bark. If the cankers are nearer to the trunk than 6 inches, the bark should be excised around the branch stub. The red currant Viking is immune to blister rust, and a couple of black currant hybrids are resistant. Some white pines are exhibiting resistance.

Cronartium stalactiforme (see ►*Peridermium stalactiforme*). 0, I on lodgepole pines in Rocky Mountain regions; II, III on Indian paintbrush.

Cronartium strobilinum Pine Cone Rust. 0, I on cones of longleaf and slash pines; II, III on evergreen oak. Cones are swollen, reddish; 25 to 90 % drop.

Endocronartium harknessii (formerly *Cronartium harknessii*). Western Gall Rust. 0, I on Jeffrey, ponderosa, lodgepole, and digger pines; II, III on Indian paintbrush, lousewort, owls-clover, or omitted, with direct infection from pine to pine. Galls are globose, with large, confluent aecia; bark sloughs off in large scales; witches' broom are formed. A variety of this species, alternate stage unknown, occurs on Monterey and knobcone pines in California.

Control Remove trees with galls for a distance of 300 yards around nurseries. Do not ship infected trees from nurseries.

Peridermium stalactiforme (formerly *Cronartium stalactiforme*). 0, I on lodgepole pines in Rocky Mountain regions; II, III on Indian paintbrush. The rust enters pine trunks through small twigs, producing diamond-shaped lesions that elongate an average of 7 inches a year, but grow laterally less than 1/2 inch. Removal of diseased trees is the only known control.

Cumminsiella

Pucciniaceae. Autoecious; teliospores two-celled; pycnia and other sori subepidermal; aecia cupulate.

Cumminsiella mirabilissima 0, I, II, III on barberry and mahonia in the West, Arizona, California, Colorado, Idaho, Montana, Nebraska, New Mexico.

Cumminsiella texana On barberry, Texas.

Desmella

Pucciniaceae. Uredia and telia subepidermal, protruding in tufts; uredia without peridium or paraphyses. Spores globoid, on pedicels, two-celled.

Desmella aneimiae On Boston fern, Florida.

Endocronartium

Badisiomycete, Uredinales, Pucciniaceae

Endocronartium harknessii Western Gall Rust or Pine-Pine Gall Rust on pine.

Endophyllum

Pucciniaceae. Teliospores in form of aeciospores; telia with cupulate peridium.

Endophyllum sempervivi III on houseleek and hen-and-chickens. Succulent leaves may be covered with reddish pustules. This is not common, but may be serious. Clean out infected parts.
Endophyllum tuberculatum III on hollyhock and checkermallow.

Frommeella

Pucciniaceae. Teliospores two-to many-septate; aecia and uredia erumpent.
Frommeella duchesneae II, III on mock-strawberry, false strawberry, or Aztec Indian berry.

Arthuriomyces (Gymnoconia)

Pucciniaceae. Uredia lacking; aecia present but without peridium; teliospores two-celled, one pore in each cell.
Arthuriomyces peckianus (formerly *Gymnoconia peckiana* (*G. interstitialis*). Orange Rust of blackberry. 0, I, III on blackberry, dewberry and black raspberry, first described from eastern United States in 1822, present from Canada to Florida and from Alaska to southern California. Very bright orange spores cover underside of leaves in spring. The mycelium is perennial in the bush, living throughout the year between cells of the stem, crown, and roots, each season invading new tissue as new growth begins. Shoots may be bunched, often with a witches' broom effect; plants are dwarfed. Spraying is useless; infected plants never recover. Plant only healthy stock, obtained from a nursery where the disease is unknown. Remove infected plants showing upright habit of growth, yellow color, and glistening yellowish dots of pycnia before the orange spore stage appears. Blackberry varieties Eldorado, Orange Evergreen, Russell, Snyder, Ebony King, dewberry *Leucretia*, and boysenberries are quite resistant.
Gymnoconia peckiana (**G. interstitialis**) (see ►*Arthuriomyces peckianus*). Orange Rust of blackberry. 0, I, III on blackberry, dewberry and black raspberry, first described from eastern United States in 1822, present from Canada to Florida and from Alaska to southern California.

Gymnosporangium

Pucciniaceae. All but one species heteroecious. Picnia and aecia usually on trees and shrubs of the apple family; telia confined to cedars and junipers except for one species on cypress; uredia wanting. Teliospores thick-or thin-walled, various in form but mostly flat, tongue-shaped, expanding greatly when moistened, usually with two cells; walls smooth, one to several pores in each cell; pedicel colorless, usually with outer portion swelling and becoming jellylike when moistened. Aecia are highly differentiated and conspicuous, with catenulate aeciospores, deeply colored with verrucose walls (see Fig. 2).

The life cycle is similar in all juniper leaf rusts. In early summer, small, slightly swollen spots appear on leaves of the pomaceous host, then small raised specks in this area on the upper surface, openings of flask-shaped pycnia embedded in leaf tissue. After exuding an orange liquid containing pycniospores, the specks are black. Later, aecia push out on the underside of the same spots as dingy white columns, rostelia, with the outer coating rupturing to release a powdery mass of yellow to brown aeciospores. The ruptured segments sometimes make the open aecium look star-shaped, but in the common cedar-apple rust aecia are cup-shaped. Aecia are also formed on fruit and tender green stems. Aeciospores released during summer are windborne to junipers. Mycelium winters in the juniper needle or stem, and in spring galls are started that take a year or more to produce teliospores in cushions or horns.
Gymnosporangium bermudianum 0, I, III on stems of eastern and southern red-cedar in the Gulf states. No alternate host; aecia precede telia on small galls.
Gymnosporangium bethelii III on Rocky Mountain juniper; 0, I on fruits of hawthorn.
Gymnosporangium bethelii III on stems of prostrate and Rocky Mountain junipers; 0, I on

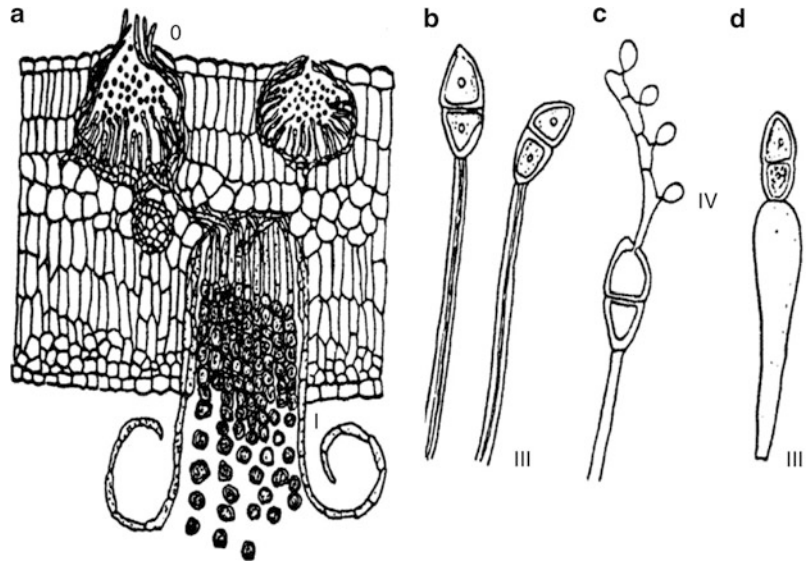

Fig. 2 Cedar-Apple Rust. *Gymnosporangium juniperi-virginianae*. **a** section through crabapple leaf with pycnidia (*0*) on upper surface and aecium (*I*) with prominent peridium and aeciospores in chains on undersurface; **b** two-celled teliospores on gelatinous stalks, which help form the jellylike telial horns on cedar galls; **c**, teliospores germinating with a promycelium and basidiospores; **d** teliospore of *G. clavipes*, the quince rust

leaves, fruit of hawthorn. Telia are 3 to 4 mm high on irregular galls on cedar twigs and branches.

Gymnosporangium biseptatum III on stems of *Chamaecyparis thyoides*; 0, I on amelanchier. Spindle-shaped swelling in stem; trees may die.

Gymnosporangium clavariiforme III on common and Mountain juniper; 0, I on chokeberry, amelanchier, pear and quince. Slender telia 5 to 10 mm high produced on long fusiform swellings on branches.

Gymnosporangium clavipes Quince Rust. III on eastern red-cedar, dwarf, mountain, and prostrate junipers; 0, I on fruits and young stems of amelanchier, apple, chokeberry, crabapple, hawthorn, mountain-ash, quince, Japanese quince and pear. Short slight swellings, somewhat spindle-shaped, occur in cedar twigs and branches, many of which die. On the main trunk, infected areas are black rough patches or rings around the bark. Mycelium is perennial, confined to the outer layer of living bark; it can sometimes be scraped out by scraping the bark. On pomaceous hosts, the disease is most frequent on fruits, often causing distortion. Rust sometimes affects twig and buds but seldom leaves. Aecia are particularly prominent on hips of English hawthorn, with long whitish perithecium around orange spores.

Control Some apple varieties susceptible to apple rust are rather resistant to quince rust, including Jonathan, Rome, Ben, Davis, and Wealthy. Red Delicious is quite susceptible. Destroy cedars in neighborhood of orchards; spray as for apple rust.

Gymnosporangium confusum III on Savin Juniper; 0, I on hawthorn.

Gymnosporangium cornutum (*G. auriantiacum*). Juniper Gall Rust. III on leaves and stems of common juniper; 0, I on mountain-ash.

Gymnosporangium cunninghamianum III on Arizona cypress; 0, I on amelanchier.

Gymnosporangium davisii III on mountain and common juniper; 0, I on leaves of red and black chokecherry. Telia are usually on upper surface of needles, sometimes at base of stems.

Gymnosporangium effusum III on eastern red-cedar; 0, I on chokeberry. Fusiform swellings on cedar trunk and branches.

Gymnosporangium ellisii Witches' Broom Rust. III on southern white cedar (*Chamaecyparis*); 0, I on sweet-fern, gale, bayberry, wax-myrtle leaves, fruits and young stems. Aecia are cluster cups; telia are cylindrical, filiform, 3 to 6 mm high, appearing on leaf blade or axil the first season after infection, thereafter only on stems, invading inner bark and wood. Witches' broom are abundant; even large trees die if heavily broomed.

Gymnosporangium exiguum III on leaves of alligator and Mexican junipers, eastern red-cedar; 0, I on leaves, fruits of hawthorn.

Gymnosporangium exterum III on stems of eastern red-cedar; 0, I on gillenia. Flattened telia anastomose over short fusiform swellings with roughened bark on cedars. Also galls on stems of juniper.

Gymnosporangium floriforme III on red-cedar; 0, I on leaves of hawthorn. Cedar galls are small.

Gymnosporangium fraternum (*G. transformans*). III gall on *Chamaecyparis thyoides*; 0, I on chokeberry.

Gymnosporangium globosum Hawthorn Rust, III general on eastern red-cedar, also on dwarf, prostrate, and Rocky Mountain junipers; 0, I mostly on hawthorn, also on apple, crabapple, pear and mountain-ash. Leaf galls on cedar are very similar to those of common cedar-apple rust, but are smaller, seldom over 1/2 inch, nearer mahogany red in color, and not perennial, producing telial horns one season only. Apple and pear foliage may be slightly affected but not the fruit; aecia are common on hawthorn pips.

Gymnosporangium gracile III Witches' Broom on juniper; 0, I on hawthorn, quince, and shadbush.

Gymnosporangium asiaticum III on leaves of Chinese juniper; 0, I on Chinese flowering quince and pear.

Gymnosporangium harknessianum III on western juniper; 0, I on amelanchier, chiefly on fruits, sometimes stems. Papery margins of aecia are usually long.

Gymnosporangium hyalinum III on southern white-cedar; 0, I on hawthorn and pear leaves. Slight swellings are formed on small twigs and branches of white-cedar.

Gymnosporangium inconspicuum III on Utah juniper; 0, I on fruits, mostly of amelanchier and squaw-apple. Juniper leaves turn yellow; rarely telia appear on branches.

Gymnosporangium japonicum (*G. photiniae*). III gall on stems of Chinese juniper; 0, I on photinia.

Gymnosporangium juniperi-virginianae Cedar-Apple Rust. III general on red cedar, eastern and southern, on prostrate and Rocky Mountain junipers; 0, I general on apple and crabapple east of Great Plains. The fungus is a native of North America and does not occur elsewhere. It is more important commercially in the apple-growing regions of the Virginias and Carolinas and certain states in the Mississippi Valley. It is important in many areas on ornamental crabapples in home plantings.

The cedar "apples" or galls vary from 1/16 inch to over 2 inches across. Leaves are infected during the summer, and by the next June a small, greenish brown swelling appears on upper or inner leaf surface. This enlarges until by autumn the leaf has turned into a chocolate brown, somewhat kidney-shaped gall covered with small circular depressions. The next spring in moist weather orange telial horns are put forth from the pocketlike depressions. The teliospores are enveloped in a gelatinous material that swells vastly, a gall covered with horns sometimes reaching the size of a small orange. They germinate in place to produce the basidiospores, which are carried by wind to infect apple or other deciduous host.

By midsummer, apple leaves show yellow areas with amber pustules on upper surface; but after pycnia have exuded drops of sticky liquid, they appear as black dots in a rather reddish circle. On the undersurface of these spots small cups are formed, with recurved fimbriate margins. These aecia may also appear near stem end of apples and are common on swollen twigs of crabapple. Spores from these cups are blown back to the cedar in late summer, the entire cycle thus taking 2 years, 18 to 20 months on the cedar, 4 to 6 on the apple host.

Chief injury is to the apple host, the rust causing premature defoliation, dwarfing and poor-quality fruit. On very susceptible crabapples, such as Bechtel's crab, repeated infection may cause death of the branches or of the entire tree. All our native crabapples are susceptible; most Asiatic varieties are resistant.

Control Care in planning is most important. Don't let your landscape architect or gardener put cedars and native crabapples or hawthorns close together. Keep them separated as far as

possible with a windbreak in between of some tall nonsusceptible host. Some states have laws prohibiting red-cedars within a mile of commercial apple orchards, but for practical garden purposes a few hundred yards is sufficient, the danger markedly decreasing with distance, especially with a house or hedge as a windbreak.

If junipers are already planted, it is possible in late winter to go over small specimens and remove galls before spore horns are formed. Spraying in spring inhibits telial development and germination of teliospores. Spray red-cedars in August to prevent infection from crabapples.

Fairly resistant apple varieties are Baldwin, Delicious, Rhode Island and North-western Greening, Franklin, Melrose, Red Astrachan, Stayman, and Transparent. Avoid susceptible Jonathan, Rome, Wealthy, and York Imperial. Most junipers susceptible to apple rusts are cultivars of *Juniperus virginiana* and *J. scopulorum*. Many cultivars of *J. chinensis* and *J. horizontalis* are resistant, and there are even some resistant forms of *J. virginiana*.

Gymnosporangium kernianum III on alligator, Utah, and western junipers; 0, I on amelanchier and pear. Telia arise between leaves on green twigs, but mycelium is perennial in stems, causing dense witches' broom 6 to 18 inches in diameter.

Gymnosporangium libocedri III on incense cedar; 0, I on leaves, fruits, of amelanchier and hawthorn, also apple, crabapple, pear, quince, Japanese quince and mountain-ash. Aecium is a cluster cup on foliage; telia are always on leaves; witches' broom and swellings are produced on branches, rarely on trunks. The fungus is said to persist in the mycelial stage up to 200 years.

Gymnosporangium multiporum III on stems of western, one -seed, and Utah juniper between leaves; 0, I unknown.

Gymnosporangium nelsonii III on juniper and red-cedar; 0, I on leaves of amelanchier.

Gymnosporangium nelsonii III on one-seed, prostrate, Rocky Mountain, Utah, and western junipers; 0, I on hawthorn, quince, Oregon crab, pear, squaw-apple and Pacific mountain-ash. Galls are firm, woody, round, up to 2 inches in diameter.

Gymnosporangium nidus-avis Witches' Broom Rust. III on eastern and southern red-cedars, on prostrate and Rocky Mountain junipers; 0, I on fruit, young stems, leaves of apple, hawthorn, mountain-ash, quince, Japanese quince, amelanchier or serviceberry. Trunks and branches of large trees have witches' broom and long spindle-shaped swellings. Aecia are on both leaf surfaces.

Gymnosporangium nootkatense Gall Rust. II, III on Alaska cedar; 0, I on mountain-ash, and Oregon crabapple. This is the only *Gymnosporangium* species with uredial stage. Uredia are bright orange fading to pale yellow; teliospores appear later in the same pustules. Aecia are cluster cups.

Gymnosporangium speciosum III on alligator, one-seed, and Utah junipers; 0, I on leaves of syringa (*Philadelphus*) and fendlera. Telia are in longitudinal rows on long fusiform swellings on juniper branches, which are girdled and die. In severe infections the whole tree dies.

Gymnosporangium trachysorum III on stem of eastern red-cedar; 0, I on hawthorn leaves. Swellings on cedar are abruptly fusiform to globoid with prominent telia 6 to 10 mm high.

Gymnosporangium tremelloides (*G. juniperinum*). III, stem gall on mountain juniper; 0, 1 on Pacific mountain-ash. On smaller branches swellings are subglobose galls up to 3/4 inch in diameter; hemispherical swellings on larger branches are covered with flattened telia.

Gymnosporangium vauqueliniae Witches' Broom Rust. III on one-seed juniper; 0, I on *Vauquelinia californica*. This rust is the only *Gymnosporangium* causing witches' broom on the aecial host.

Hyalopsora

Melampsoraceae. Telia on ferns, teliospores several-celled, in epidermis; urediospores of two kinds, with pores.

Hyalopsora aspidiotus Fir-Fern Rust. 0, I on balsam fir; II, III on oak fern (*Phegopteris dryopteris*). Pycnia are slightly raised orange-yellow spots on needles; aecia are yellow to white, columnar, on 2-year needles.

Hyalopsora cheilanthis Fir-Fern Rust. 0, I on balsam fir; II, III on rock brake, parsley fern, and cliff brake.
Hyalopsora polypodii Fir-Fern Rust. General in northern and western states on polypody fern and woodsia.

Kuehneola

Puciniaceae. Teliospores two-to many-celled; wall faintly colored or colorless.
Kuehneola malvicola II, III on hibiscus and malvaviscus.
Kuehneola uredinis Yellow Rust, Cane Rust. 0, I, II, III on blackberry, dewberry, and raspberry. The disease appears to be increasingly prevalent, especially on leaves, but there is a great difference in varietal susceptibility. Eldorado, Foster, Jumbo, Lawton blackberries are highly susceptible; Nantichoke, Austin Thornless, Boysen Brainerd, Burbank Thornless, Jersey Black are resistant. European varieties are generally resistant.

Kunkelia

Pucciniaceae. Pycnia subcuticular; telia subepidemal, caeomoid; teliospores catenulate, one-celled.
Gymnoconia nitens (formerly *Kunkelia nitens*). Short-Cycle Orange Rust of blackberry. I, general on blackberry but more common in the South and West, also on dewberry and black, but not red raspberry. This is a perennial rust, a systemic disease with only the aecial stage present. Underside of leaves may be covered with quantities of orange-yellow spores. Remove infected bushes.
Kunkelia nitens (see ▶*Gymnoconia nitens*). Short-Cycle Orange Rust of blackberry.

Melampsora

Melampsoraceae. Telia more or less indefinite; teliospores sessile, subcuticular or subepidermal, forming crusts of a single layer; aecia when present with rudimentary peridium; uredia erumpent, pulverulent; spores globoid or ellipsoid, single on pedicels.

Species heteroecious when telia are on woody plants; autoecious if telia are on herbaceous plants (Fig. 3).
Malampsora abieti-capraearum Fir-Willow Rust. 0, I on balsam, white, and alpine firs; II, III on willows, widespread. Yellow spots on willow leaves in early summer are followed by dark pustules when the telial stage is produced. There may be some defoliation.
Melampsora abietis-canadensis Hemlock-Poplar Rust. 0, I on eastern hemlock; II, III on various poplars. Cones have golden powdery masses of spores over the surface; later shrivel, turn black, and hang as mummies; no viable seed produced. Uredia are golden powdery pustules on undersurface of poplar leaves; in late summer telia are formed in orange-yellow crusts that change to black; in spring basidiospores reinfect hemlock.
Melampsora arctica 0, I on saxifrage; II, III on willow.
Melampsora farlowii Needle And Cone Rust of hemlock. 0, I unknown; III on hemlock. Reddish slightly raised telia are on undersurface of needles, shoots of the current year, and on cones. Young shoots may be twisted and killed. Injury may occur in nurseries and in ornamental hedges.
Melampsora hypericorum (*Mesopsora hypericorum*). On St. Johnswort, Montana.
Melampsora larici-populina Rust;0, I, on pine and larch; II, III, on poplar.
Melampsora medusae Douglas-Fir Needle Rust. 0, I on Douglas-fir, big-cone spruce; II, III on native poplars. Pycnia are on upper surface of current-year needles; aecia, of the caeoma type, are orange-yellow on the undersurface. The rust is often epidemic on young trees but with little permanent ill effect.
Melampsora medusae Larch Needle Rust. 0, I on larch in northeastern states; II, III on native and introduced poplars except in far South.
Melampsora medusae f. sp. **deltoidae** Rust; 0, I on Douglas fir, pine and larch; II, III, on poplar.
Melampsora occidentalis Poplar Rust. 0, I unknown; II, III on native poplars in the West.

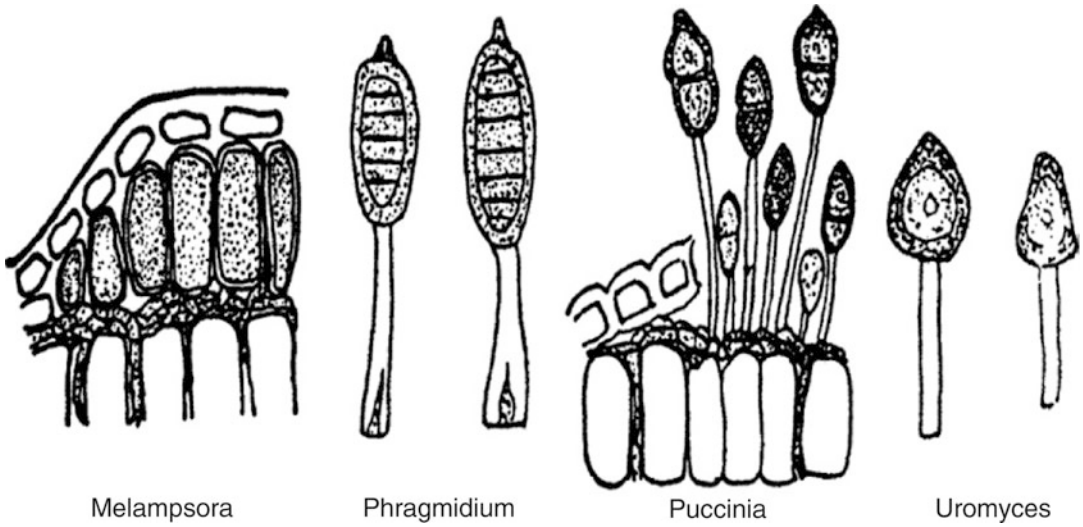

Fig. 3 Teliospores. *Melampsora*, sessile in crust under host epidermis; *Phragmidium*, stalked, with several cells; *Puccinia*, stalked, two-celled; *Uromyces*, stalked, one-celled

Melampsora paradoxa (*M. bigelowii*). Larch-Willow Rust.0, I on larch; II, III on many species of willow. The damage to larch is insignificant. The fungus winters on willow as mycelium in catkins, terminal buds, and young stems and can maintain itself on willow in the uredial stage without larches.

Melampsora ribesii-purpureae 0, I on currant, flowering currant and gooseberry; II, III on willow species.

Melampsorella

Melampsoraceae. Heteroecious on fir, spruce, and dicotyledons; pycnia subcuticular, aecia and uredia subepidermal, telia in epidermal cells. Only one species in United States.

Melampsorella caryophyllacearum (*M. cerastii*). Yellow Witches' Broom Rust. 0, I on many firs; II, III on chickweed. Infected evergreen branches develop numerous upright lateral shoots from one point, forming a compact witches' broom; twigs are dwarfed, and needles turn yellow and drop, leaving broom bare. The fungus is perennial in stems, and shoots develop with yellow leaves. Pycnia appear in raised orange spots on both surfaces of dwarfed leaves in spring; aecia form in summer on underside, in two rows of orange blisters. The disease is seldom serious enough for control measures. In forest practice remove trees with main stem infections early in life of the stand.

Melampsoridium

Melampsoraceae. Heteroecious, on larch and dicotyledonous shrubs and trees; pycnia subcuticular; other sori subepidermal; teliospores sessile, one-celled.

Melampsoridium betulinum Birch Leaf Rust. 0, I on larch; II, III on birches. Uredia on underside of birch leaves are small reddish yellow powdery pustules, followed later in summer by telia, first waxy yellow, then dark brown to nearly black.

Milesina

Melampsoraceae. Heteroecious on firs and ferns. All spores are colorless; urediospores obovate or laceolate; teliospores in epidermal cells.

Milesina fructuosa 0, I on balsam fir; II, III on *Dryopteris* spp. Aecia are white on current needles, maturing by midsummer.

Milesina laeviuscula Needle Rust. 0, I on grand fir; II, III on licorice fern, in West.
Milesina marginalis 0, I on balsam fir; II, III on *Dryopteris marginalis*. Pycnia are on both sides of needles, aecia of needles of current year, maturing by midsummer.
Milesina pycnograndis (*M. polypodophila*). 0, I on balsam fir; II, III on *Polypodium virginianum*. Hyphae are perennial in needles and small stems of balsam fir; aecia on needles 3 to 9 years old.

Nyssopsora

Puccinaceae. Autoecious; teliospore with three cells.
Nyssopsora clavellosa III on *Aralia hispida*.

Peridermium

A form genus with 0, I, on Gymnosperms. Aecia have peridia and are cylindrical, tonguelike or bullate.
Peridermium bethelii On dwarf mistletoe.
Peridermium ornamentale 0, I on white, alpine, and noble firs.
Peridermium rugosum 0, I on Pacific silver and lowland white firs.

Phakopsora

Melampsoraceae. Telia indehiscent, lenticular; spores formed in irregular succession, not in chains.
Phakopsora cherimoliae On cherimoya.
Phakopsora jatrophicola On cassava.
Phakopsora pachyrhizi On soybean.
Phakopsora zizyphi-vulgaris On *Zizyphus jujuba*, Florida.

Phragmidium

Pucciniaceae. Autoecious. Pycnia subcuticular, other sori subepidermal; aecia caeomoid; teliospores large, conspicuous, of one to ten or more cells, each with two or three lateral pores; walls somewhat layered, inner layer colored, outer nearly colorless, smooth or verrucose; pedicel colorless except near spore; often swelling in lower portion (see Fig. 3). Aecia with catenulate globoid or ellipsoid verrucose spores; uredia when present circled with paraphyses; urediospores single on pedicels, walls verrucose or echinulate with indistinct scattered pores.
Phragmidium americanum 0, I, II, III on leaves of native and cultivated roses. Teliospores with eight to eleven cells.
Phragmidium fusiforme (*P. rosae-acicularis*). 0, I, II, III on several hosts species. Teliospores with five to eleven cells, walls chocolate brown, verrucose.
Phragmidium montivagum 0, I, II, III on many species of roses. Teliospores with six to nine cells.
Phragmidium mucronatum (*P. disciflorum*). Leaf Rust of Rose. 0, Ion leaves and stems; II, III on leaves of cultivated roses, eastern states to the Rocky Mountains and on the Pacific Coast. This is the common rust of hybrid teas and other roses with large, firm leaflets. It is not much of a problem in the East, although sometimes found in New York and New England gardens, but it is a serious menace along the Pacific Coast. Aecia appear on leaves as small, roughly circular spots, 1/25 inch across, bright orange on the underside of leaf, from the spore masses, light yellow on the upper surface, sometimes bordered with a narrow green zone. Leaf lesions may be slightly cup-shaped viewed from the upper surface. Stem lesions are long and narrow. The summer uredial stage has reddish orange spores in very small spots, 1/50-inch, over underside of leaves. This stage may repeat every 10 to 14 days in favorable weather, with wilting and defoliation. In mild climates the uredial stage continues; in cooler areas the telial stage is formed toward autumn –black pustules of stalked dark spores, rough, with a point, five to nine cells.

The leaf surface must be continuously wet for 4 h for rust spores to germinate and enter the leaf; this means liquid water and not high humidity as with mildews. High summer temperatures adversely affect infection, summer spores

retaining viability for only a week at 80 °F. In southern California temperatures are uniformly favorable for rose rust, and from October to April there is sufficient rainfall. In drier months fog may provide requisite moisture.
Control Removing infected leaves during the season and all old leaves left at the time of winter or early spring pruning may be somewhat helpful.
Phragmidium rosae-arkansanae 0, I, II, III on *Rosa arkansana* and *R. suffulta*. Teliospores with five to eight cells.
Phragmidium rosae-californicae 0, I, II, III on many rose species. Teliospores with eight to eleven cells.
Phragmidium rosicola III on *Rosa engelmanii* and *R. suffulta*. Teliospores one-celled, nearly round.
Phragmidium rubi-idaei Leaf and Cane Rust of raspberry; Western Yellow Rust, general but important only in the Pacific Northwest. 0, I, II, III on red rasberries, sometimes black but not on blackberries. Small, light yellow spore pustules appear in young leaves, with black teliospores following in the same spots later in the season. Deep, cankerous lesions are formed on canes in the fruiting year, Cuthbert variety being particularly susceptible. Spring infection probably comes from sporidia formed in telia on fallen leaves. A dormant spray may be helpful, along with cleaning out infected canes at winter pruning.
Phragmidium speciosum 0, I on stems and leaves, III on stems of cultivated and native roses, throughout United States except far South.
Phragmidium subcorticium Obsolete name. Some specimens formerly recorded as this species belong to *P. mucronatum*, others to *P. rosaepimpinellifoliae*.
Phragmidium tuberculatum On *Rosa* sp. Connecticut and Alaska.

Phragmopyxis

Pucciniaceae. Teliospores colored, two-to many-septate; wall three-layered, the middle layer swelling in water; aecia, uredia, and telia with a border of paraphyses.

Phragmopyxis acuminata 0, III on *Coursetia*.

Physopella (Angiopsora)

Pucciniaceae. Only uredia and telia known. Telia indehiscent, lenticular; teliospores in chains.
Physopella ampelopsidis (*Phakopsora vitis*). On ampelopsis and grape, Florida.
Physopella compressa On paspalum, southern ornamental grass.

Pileolaria

Pucciniaceae. Autoecious, on members of family Anacardiaceae. Teliospores stipitate, dark, with pores, one-celled; pycnia subcuticular; uredia present.
Pileolaria cotini-coggyriae On smoke tree.
Pileolaria patzcuarensis 0, I, II, III on sumac.

Prospodium

Pucciniaceae. Autoecious on Bignoniaceae and Verbenaceae in warm climates.
Prospodium appendiculatum On tecoma, Florida, Texas.
Prospodium lippiae On lippiae, Arizona.
Prospodium plagiopus On tabebuia, Florida.
Prospodium transformans On tecoma, Florida.

Puccinia

Pucciniaceae. A very large genus, comprising nearly half of all known rusts; autoecious and heteroecious. Teliospores smooth, two-celled with apical pores, firm pedicels, colored; aecia cluster cups with peridium (see Fig. 3). The species listed here are a small selection of those on garden plants; others are listed in host section.
Puccinia acroptili Rust on *Centaurea*.
Puccinia allii (*P. porri*). Autoecious on onion, garlic and shallot, but 0, I stages rare. Occasional on cultivated onion, more common on garlic,

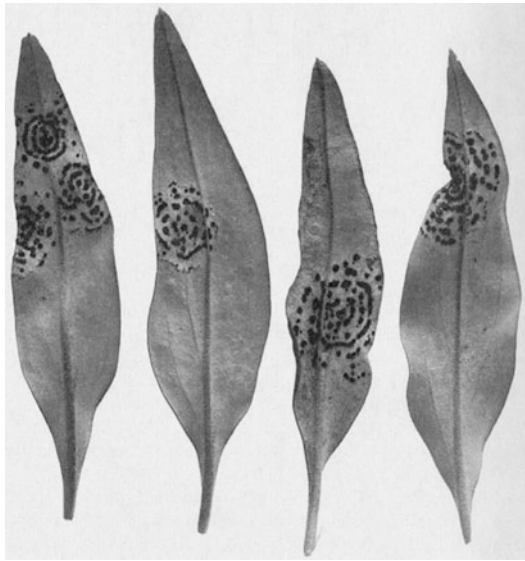

Fig. 4 Rust on Snapdragon

wild garlic, and wild onion. Uredia are yellowish, telia black.

Puccinia amphigena (*Aecidium yuccae*). On yucca.

Puccinia andropogonis, with various strains. 0, I on lupine, Indian paintbrush and turtlehead; II, III on and ropogon.

Puccinia antirrhini Snapdragon Rust. II, III general on snapdragon, also on linaria, corydylanthus; 0, I unknown. Pustules of spores on underside of leaves are chocolate brown, often in concentric circles (see Fig. 4). The area over the pustule is pale or yellow on upper surface. Spores also appear on stems; there is a drying and stunting of whole plant. The rust is spread by wind-blown spores and on cuttings. For infection, plants need to be wet with rain or dew 6 to 8 h with day temperatures around 70° to 75 °F. Spores are killed above 94 °F. There are at least two races.

Control Purchase only rust-resistant variety. Bordeaux mixture controls secondary fungi following rust but not the rust itself. Sulfur dust is still useful, or a spray made by adding 1 ounce rosin soap to a gallon of water and then adding 1 ounce dry lime sulfur.

Puccinia arachidis Peanut Rust, occasional in Alabama, Florida, Texas.

Puccinia aristidae and varieties II, III on wild grasses, *Aristides* and *Distichlis*; 0, I on eriogonum, greasewood, beet, spinach, western wallflower, garden cress, radish, California bluebell, heliotrope, cleome, primrose, sand-verbena, and others.

Puccinia asparagi Asparagus Rust. II, III general on susceptible varieties; 0, I not reported in natural infections. Also on onion. Asparagus rust reached America in 1896 from Europe and spread with devastating suddenness from Boston and New Jersey to California, reaching there by 1912, one of the fastest cases of disease spread in our history. If tops are attacked several years in succession, the root system is so weakened that shoots fail to appear in spring or are culls.

The first symptom is a browning or reddening of smaller twigs and needles, with the discolored area spreading rapidly until the whole planting looks as if it had ripened prematurely. The reddish color is due to numerous small pustules of urediospores that give off a dusty cloud when touched. These appear in successive generations until autumn, or a spell of drought, when they are replaced by black teliospores, either in the same or a new fruiting body. They remain on old stems until spring, germinating then to infect new shoots as they emerge from the ground.

Control For a long time resistant varieties Mary Washington and Martha Washington were the answer to the rust problem, but the fungus has developed resistant strains. Waltham Washington, Seneca Washington, and California 500 have some resistance. Clean up volunteer or wild asparagus around beds. A parasitic fungus, *Darluca filum*, helps keep rust in check.

Puccinia brachypodii var. **poae-nemoralis** (formerly *Puccinia poaenemoralis* (Syn. *P. poae-sudeticae*)). Bluegrass Leaf Rust, Yellow Leaf Rust. II, III on turf grasses, mostly Canada and Kentucky bluegrass; 0, I, unknown; general east of the Rocky Mountains. The uredia are orange-yellow with numerous peripheral paraphyses. Telia are covered rather permanently with epidermis; spores are dark brown with short pedicels. The wheat stem rust is more important on Merion bluegrass.

Puccinia calcitrapae var. **centaureae** (formerly *Puccinia carthami*). Widely distributed on safflower in Great Plains and California. Spores carried on seed or persisting in soil infect seedlings, which often die.

Puccinia canaliculata Rust on purple nutsedge and yellow nutsedge.

Puccinia carduorum Rust on *Carduss tenniflorus* and *Carduss thoermeri*.

Puccinia caricina (*P. caricis* var. *grossulariata, P. pringsheimia*). 0, I on currant, flowering currant, gooseberry; II, III on *Carex* spp. Common only on wild species or in neglected gardens. Leaves are thickened, sometimes curled in reddish cluster cup areas; there are enlargements on stems and petioles, red spots on berries. Control by eliminating the sedge host.

Puccinia carthami (see ►*Puccinia calcitrapae* var. *centaureae*). Widely distributed on safflower in Great Plains and California.

Puccinia claytoniicola On claytonia, Wyoming.

Puccinia conoclinii On ageratum, Ohio.

Puccinia coronata Crown Rust of oats; Orange Leaf Rust of Oats. 0, I on buckthorn and rattan vine; II, III on oats and grasses. There are several varieties and many physiological races of this rust, which is as destructive to oats as leaf rust is to wheat. Redtop, meadow fescue, ryegrass, and bluegrass are among the lawn grasses that may show orange or black pustules on leaves.

Puccinia crandallii 0, I on snowberry, wolfberry, coralberry; II, III on grasses, fescues, bluegrass.

Puccinia cynodontis On Bermuda grass, New Mexico.

Puccinia cypripedii On orchids.

Puccinia dioicae (*P. extensicola*) in many varieties. 0, I on aster, goldenrod, erigeron, senecio, lettuce, oenothera, rudbeckia, and helenium; II, III on *Carex* spp.

Puccinia dracunculi (see ►*Puccinia tanaceti* var. *dracunculina*). On artemisia, Wisconsin to the Pacific Coast.

Puccinia flaveriae (see ►*Puccinia melampodii*). On *Calendula*.

Puccinia graminis Stem Rust of grains and grasses. 0, I on barberry and mahonia, especially in north central and northeastern states; II, III on wheat and other cereals and wild and cultivated grasses.

This is the classic example of rust, the one used in school textbooks and known through the ages as the major limiting factor of wheat production. Proof of the connection between barberry and wheat in the life cycle was not made until 1864, but long before that farmers had noticed that wheat suffered when barberry plants were near. France in 1660, Connecticut in 1726, and Massachusetts in 1755 enacted laws requiring the destruction of barberry near grain fields.

There are six commonly recognized varieties of stem rust: *Puccinia graminis* f. sp. *avenae*–on oats, sweet vernal grass, brome grasses, some fescues.

P. graminis f. sp. *agrostidis*–on redtop and other *Agrostis* spp.

P. graminis f. sp. *graminicola*—on St. Augustine grass.

P. graminis f. sp. *phlei-pratensis*–on timothy and some related grasses.

P. graminis f. sp. *poae*–on Kentucky and other bluegrasses.

P. graminis f. sp. *secalis*–on rye, some wheat, and barley grasses.

P. graminis f. sp. *tritici*, wheat rust – on wheat, barley, rye, and many grasses.

Stem rust occurs wherever wheat is grown, but is most serious in northern states. It is dependent on weather conditions, with epidemics and disastrous losses in certain seasons. The amount depends on the maturity of the crop when rust strikes, but losses may run 25 % of expected yield for the nation and much higher for individual states. There are a great many physiological races.

On grains and grasses the first rust appears as long, narrow streaks on stems, leaf sheaths, leaf bases, and distal portions of blades. These streaks are uredial sori, the epidermis being torn back to form a white collar around a dark red powdery mass of one-celled urediospores. Later the same sori turn black as dark, two-celled teliospores replace summer urediospores. Stems may be broken at this stage.

The summer spores appear about 10 days after infection. This stage can be repeated, the spores reinfecting wheat, and, since they are carried by wind from one plant to another, one state to another, even to hundreds of miles, they account for large outbreaks of disease. In Mexico and southern Texas this II stage continues through the winter and causes spring infection without the intervention of barberry. Waves of urediospores coming up from the South may start northern infection.

Normally in the North, spring infection starts on barberry from sporidia (basidiospores) produced on a promycelium put forth by a teliospore wintered on a wheat stem. Two sexes occur in this rust, designated + and – rather than male and female. A young teliospore contains two nuclei, one + and the other –; as the spore matures, these fuse to a single nucleus, which divides twice in the production of the four-celled basidium (promycelium). Each cell produces a sporidium; two of these are + and two –. A sporidium falling on a barberry leaf germinates, sends in an infection thread, and develops a mononucleate (haploid) feeding mycelium and finally a flask-shaped pycnium containing pycniospores, which correspond to the sex of the sporidium starting infection. The pycnia are in reddish lesions on the upper leaf surface. Hyphal threads, receptive hyphae, extend through the mouth of the pycnium. Aided by insects, which are attracted by a sweet nectar, pycniospores (spermatia) of one sex are brought into contact with receptive hyphae of the opposite sex, and sexual union takes place, without which there is no further development of the rust.

The dicaryotic or binucleate mycelium formed from the fertilized hypha grows through the cells of the barberry leaf and masses together on the underside to produce aecia filled with a yellowish waxy layer of aeciospores in cluster-cup formation. These spores, unable to reinfect barberry or mahonia are wind-borne to the cereal or grass host, the subsequent mycelium continuing binucleate until the fusion in the teliospore. New crops of urediospores can be produced every 10 to 14 days.

Control Resistant varieties are of primary importance, but they are difficult to maintain because the sexual process in rusts allows the continuous development of new strains. More than 200 strains are known, but only a dozen or so are important in any one year. Race 15B is prevalent most years and can attack all varieties of wheat grown in this country. Eradication of the barberry eliminates the alternate host and also the breeding place of new rust varieties. Most barberry and mahonia species are under quarantine, but some have been designated rust-resistant by the U.S. Department of Agriculture and may be shipped interstate under permit.

Puccinia helianthi Sunflower Rust. 0, I, II, III general on sunflower, Jerusalem artichoke, and heliopsis. Numerous brownish pustules in which repeating spores are formed develop on underside of leaves, which may dry and drop.

Puccinia heterospora III on abutilon, hollyhock, mallow, and malvaviscus.

Puccinia heucherae III on coral bells, woodland star, saxifrage, bishops-cap, and foamflower.

Puccinia hieracii 0, I, II, III widespread on endive and hawksbeard. Endive leaves are spotted and blighted with dusty spore pustules. The crop is occasionally lost, but no control has seemed practical.

Puccinia horiana White Rust. III, IV on chrysanthemum; no alternate host known. First reported in England in 1964; became widespread there in 1976. Found in amateur chrysanthemum plantings in New Jersey and Pennsylvania in 1977.

Puccinia iridis Iris Rust. 0, I, II, III on bulbous iris, serious in the Southeast, uncommon in Northwest. Small, oblong to oval, red or dark brown powdery spots, often surrounded by a yellow margin, are present on leaves and stems, which may die prematurely. In inoculation tests with Dutch iris, varieties Early Blue, Gold and Silver, Golden West, Imperator, Lemon Queen, and Texas Gold were resistant.

Puccinia jaceae var. **diffusa** Rust on *Centaurea*.

Puccinia lagenophorae On English daisy.

Puccinia malvacearum Hollyhock Rust. III general on hollyhock, also on mallow, and lavatera. This rust is so common and destructive it limits the use of hollyhocks as ornamentals. Stems, leaves, bracts may be attacked. There are yellow areas on the upper surface of leaves, orange-red spore pustules on the underside, and elongated lesions on stems. Spore pustules are sometimes grayish from formation of sporidia, but the alternate host is unknown. In severe infections leaves dry and hang down along the stem. The fungus winters in pustules in basal leaves and in old stems.

Control Cleaning up all infected plant parts in fall and again very early in spring is most important; infection starts early in the season, and once it is under way, it is very difficult to curb with a fungicide.

Puccinia melampodii (formerly *Puccinia flaveriae*). On *Calendula*.

Puccinia melampodii On *Baccharis*, Texas.

Puccinia menthae Spearmint Rust. 0, I, II, III on spearmint, peppermint, oregano, also horsemint, mountain-mint, dittany, bee-balm, yerba buena, and germander; especially serious for mint farmers in Middle West and Northwest. In spring and early summer the disease appears as light yellow to brown raised spots on deformed stems and leafstalks, sometimes on main veins; golden to chocolate brown spots appear in late summer and fall. Affected leaves dry, and the yield of oil is reduced. The pathogen has at least 10 races. Dusting with sulfur and early cutting are recommended.

Puccinia nakanishikii Rust on lemon grass.

Puccinia pelargonii-zonalis Pelargonium Rust. The uredinial stage of a rust, presumably this species, was found on geranium in New York and California in 1967. It has now been reported in Pennsylvania and Florida. Brown spore pustules appear on leaves, petioles, and stems; leaves turn yellow and drop. Destroy infected plants.

Puccinia phragmitis 0, I on rhubarb; II, III on reed grass, sometimes present in California but not serious. Aecia are white, on underside of rhubarb leaves, surrounded by pycnia.

Puccinia poae-nemoralis (Syn. **P. poae-sudeticae**) (see ►*Puccinia brachypodii* var. *poae-nemoralis*). Bluegrass Leaf Rust, Yellow Leaf Rust. II, III on turf grasses, mostly Canada and Kentucky bluegrass; 0, I, unknown; general east of the Rocky Mountains.

Puccinia polygoni-amphibii Rust; II, III, on jointweed.

Puccinia polysora Southern Corn Rust. 0, I, unknown; II, III on corn and grasses. Present in the South, requiring higher temperatures than common corn rust; not very important. Urediospores are yellow to golden, teliospores chestnut brown, angular; often parasitized by *Darluca filum*.

Puccinia psidii Rust on allspice (*Pimenta dioica*) *Melaleuca quinquenervia*, and *Syzygium jambos*.

Puccinia pygmaea Rust on grasses.

Puccinia recondita (*P. rubigo-vera*). Leaf Rust of cereals and grasses, with several varieties:

P. recondita tritici (*P. triticina*). II, III on wheat (but not grasses); 0, I on meadow rue. This rust is worldwide and more serious than stem rust in the southern half of the American wheat belt, sometimes epiphytotic with losses up to 30 %. The leaf tissue is progressively destroyed through the season, resulting in a reduced number of kernels, shriveled grain, low weight and protein content. Rust pustules breaking through the epidermis greatly increase transpiration losses. Orange uredial pustules are followed later by gray telial sori, but urediospores are the effective spore form and can survive southern winters. There are many physiological races.

P. recondita agropyri. II, III on wheat grasses and wild ryegrasses; 0, I on clematis, buttercup, columbine, larkspur, and other Ranunculaceae. Common in Rocky Mountain area.

P. recondita agropyrina. Similar to the above but occurring outside mountainous areas.

P. recondita apocrypta. II, III on wheat and wild grasses; 0, I on waterleaf and mertensia.

P. recondita impatientis. II, III on redtop and related grasses; 0, I on touch-me-not.

P. recondita secalis. II, III on rye; 0, I on bugloss (*Lycopsis*).

Puccinia solheimi On dodocatheon, Wyoming.

Puccinia sorghi Corn Rust. 0, I on oxalis; II, III on corn, sweetcorn, general in northeastern and

north central states. Cinnamon brown spore pustules cover both leaf surfaces with black pustules toward autumn. The disease is not often serious enough for control measures.

Puccinia sparganioides (*P. peridermiospora*). Ash Rust.0, I, general on ash east of the Great Plains; II, III on marsh and cord grasses (*Spartina* spp.). Ash twigs and petioles are swollen and leaves distorted. Cluster cups filled with yellow powdery aeciospores are formed in the swellings. In New England, where rust is often severe, the most important infection period on ash is May 15 to June 20, with 6 to 8 hours of damp air necessary. Marsh grasses are infected and reinfected July 20 to August 20.

Puccinia stenotaphricola On St. Augustine grass, Florida.

Puccinia striiformis (*P. glumarum*). Stripe Rust of wheat. II, III on wheat, barley, rye, redtop, orchardgrass, and many other grasses. Uredial stage is yellow, and pustules are formed in streaklike clusters on leaves; telia are in black streaks.

Puccinia substriata Rust on eggplant.

Puccinia taneceti Chrysanthemum Rust. II general; III known only in Japan; 0, I unknown. Small blisters of pinhead size appear on underside of leaves and occasionally on upper surface. The spore mass is dark reddish brown and powdery. The rust is more common in greenhouses than outdoors. Optimum germination is at 60° to 70 °F; spores are killed at high temperatures.

Puccinia tanaceti var. **dracunculina** (formerly *Puccinia dracunculi*). On artemisia, Wisconsin to the Pacific Coast.

Puccinia thaliae (*P. cannae*). II, III on edible canna, garden canna, and maranta.

Pucciniastrum

Melampsoraceae. Heteroecious with perennial mycelium, pycnia and aecia on conifers: firs and spruces; pycnia subcuticular, other sori subepidermal; telia may be intraepidermal; aecia and urediospores yellow.

Pucciniastrum americanum Late Leaf Rust of raspberry. 0, I on white spruce; II, III on red raspberry, not black. This rust appears late in the season on Cuthbert and other susceptible varieties, in northern half of the country, most common east of the Mississippi. Fine light yellow powdery masses of spores appear on basal leaves, leaf petioles, shoots, and even fruit.

Pucciniastrum epilobii Fuchsia Rust, the alternate hosts are species of Abies.

Pucciniastrum goeppertianum Fir-Huckleberry Rust, Blueberry Witches' Broom. 0, I on firs; III on low and high bush blueberries. The fungus is systemic and perennial in blueberries, producing short swollen twigs in a witches' broom effect, and telia forming a polished red layer around the shoots. Destroy diseased bushes; keep blueberry plantations some distance from firs.

Pucciniastrum hydrangeae 0, I on eastern and Carolina hemlock; II, III on hydrangea.

Pucciniastrum vaccinii (*P. myrtilli*). Hemlock Rust, Leaf Rust of blueberry; widespread. 0, I on eastern hemlock; II, III on azalea, blueberry, cranberry, lyonia, menziesia, and rhododendron. This is the most common hemlock rust, but often only a single leaf or twig is infected. Aecia are formed on current-year needles. Blueberries have yellow pustules, on leaves only, with defoliation in mid-or late summer.

Ravenelia

Pucciniaceae. Autoecious, tropical with only a few species in United States. Teliospores more or less muriform, with compound stalks.

Ravenelia dysocarpae (see ►*Ravenelia fragrans* var. *evernia*). On *Mimosa*, Arizona.

Ravenelia fragrans var. **evernia** (formerly *Ravenelia dysocarpae*). On *Mimosa*, Arizona.

Ravenelia humphreyana On *Poinciana*, Florida, Texas.

Ravenelia indigoferae On *Indigofera*, Arizona.

Maravalia (Scopella)

Pucciniaceae. Tropical. Uredia and telia subepidermal. Teliospores one-celled, on pedicel.

Maravalia sapotae (formerly *Scopella sapotae*, Syn. *Uredo sapotae*). On sapodilla in Florida, infecting leaves in winter and early spring.
Scopella sapotae Syn. **Uredo sapotae** (see ►*Maravalia sapotae*). On sapodilla in Florida, infecting leaves in winter and early spring.

Sphenospora

Pucciniaceae. Tropical. Telia and peridia subepidermal, then erumpent; teliospores waxy, two-celled, on pedicel.
Sphenospora mera On bletilla, Florida.

Sphaerophragmium

Pucciniaceae. Teliospores stalked, four-to several-celled, with transverse and horizontal septa; on legumes.
Sphaerophragmium acaciae On lebbek, Florida.

Tranzschelia

Pucciniaceae. Teliospores two-celled, stalked; uredia with pseudoparaphyses; on Ranunculaceae and *Prunus*.
Tranzschelia discolor (*T. pruni-spinosae* var. *discolor*). Rust of stone fruits. Peach Rust. 0, I on *Anemone coronaria*; II, III on apricot, peach, plum, prune, almond, and cherry, in late summer. Yellow angular spots appear on leaves with powdery spore pustules on underside, reddish on peach, dark brown on almonds; sometimes with late season defoliation. Peach fruit may have round sunken green spots; twigs may have oval blisters in early spring. Urediospores wintering on sucker shoots can start spring infection without the alternate host. The Drake variety of almond is most susceptible.
Tranzschelia pruni-spinosae var. **typica** 0, I on anemone, hepatica, thalictrum, and buttercup; II, III on wild species of *Prunus*.

Triphragmium

Pucciniaceae. Teliospores stalked, with three cells forming a triangle, each with a single pore.
Triphragmium ulmariae 0, I, II, III on meadowsweet.

Uredinopsis

Melampsoraceae. Telia on ferns; teliospores scattered irregularly in mesophyll, rarely in subepidermal crust, typically several-celled; aecia white.
Uredinopsis osmundae Fir-Fern Rust. 0, I on balsam fir, widespread; II, III on *Osmunda* spp.
Uredinopsis phegopteridis Fir-Fern Rust. 0, I on balsam fir; II, III on *Phegopteris dryopteris*.
Uredinopsis pteridis (*U. macrosperma*). Fir-Fern Rust. 0, I on various firs; II, III on *Pteridium aquilinum*. Aecia are on 1-to 5-year needles of Pacific silver, white, lowland white, alpine, and noble firs.
Uredinopsis struthiopteridis Fir-Fern Rust. 0, I on balsam, lowland white, alpine, and noble firs; II, III on ostrich fern.

Uredo

Form genus; uredia with or without peridia.
Uredo artocarpi Breadfruit in Hawaii.
Uredo coccolobae On sea-grape, Florida.
Uredo ericae (*Pucciniastrum ericae*). On erica, California.
Uredo phoradendri On mistletoe.

Uromyces

Pucciniaceae. Like *Puccinia* but teliospores with one cell, yellow to dark; aecia when present with a persistent peridium (see Fig. 3).
Uromyces appendiculatus Bean Rust. 0, I rare on bean; II, III general on dry beans, widespread but infrequent on lima bean, scarlet runner bean. This is the true bean rust, an old disease reported

as far back as 1798 and quite distinct from anthracnose that is sometimes called rust. It is particularly serious and prevalent on Kentucky Wonder pole beans.

Small rust pustules are formed on leaves most frequently, sometimes on stems and pods. The reddish brown sori are most numerous on underside of leaves, with the upper surface yellowing in the same areas. There may be nearly complete defoliation. In late summer in the North, dark telia replace summer spores, but in the South, urediospores survive the winter and start early spring infection. Rust spores are spread by wind and on tools and clothing. Some even cling to supporting poles and can start a fresh outbreak of rust if poles are not disinfested before reuse.

Control No bean variety is resistant to all of the more than 30 races so far identified. Most snapbeans are highly tolerant of rust; and pole beans White Kentucky Wonder, U.S. 4 Kentucky Wonder, Potomac, and Rialto are fairly tolerant.

Uromyces appendiculatus var. **appendiculatus** (Syn. *U. phaseoli*). Rust on bean.

Uromyces ari-triphylli On jack-in-the-pulpit; Autoecious, O, I, II, III stages (entire life cycle) on one host.

Uromyces betae Beet Rust. II, III on beets, and swiss chard, in California, Oregon, occasionally Arizona and New Mexico. Reddish brown pustules may be numerous on foliage in late summer or in wet seasons. Control is seldom attempted for table beets; some sugar beet varieties are resistant. The seed-borne fungus also persists in volunteer plants and debris.

Uromyces ciceris-arietini Rust on chickpea.

Uromyces costaricensis Rust on wild bamboo.

Uromyces dianthi (*U. caryophyllinus*). Carnation Rust. 0, I on euphorbia (but not in United States); II, III general on carnation and sweet william, a serious disease under glass. Chocolate brown pustules, varying from 1/16 to 1/4 inch, break out on both sides of leaves and on buds and stems. Leaves curl up, often die; infected plants are stunted.

Control Use surface watering where possible, avoiding syringing; keep greenhouses properly ventilated; use rust-free cuttings.

Uromyces fabae Pea Rust. 0, I, II, III on pea, peavine, occasionally on broad bean; not very serious.

Uromyces galii-californici On galium, California.

Uromyces punctatus Rust on *Astragulus* in ID and OR.

Uromyces trifolii, in several varieties. 0, I, II, III on clovers. Pale brown pustules surrounded by torn epidermis, appear on underside of leaves and on petioles and stems.

Uromyces sp. Rust on birdsfoot trefoil.

Uropyxis

Pucciniaceae. Autoecious. Teliospores two-celled, on pedicels; uredia with paraphyses.

Uropyxis daleae var. **eysenhardtiae** (formerly *Uropyxis eysenhardtiae*). On *Dalea and Eysenhardtia* in Arizona.

Uropyxis eysenhardtiae (see ▶*Uropyxis daleae* var. *eysenhardtiae*). On *Dalea* and *Eysenhardtia* in Arizona.