

MORPHOLOGICAL AND CYTOLOGICAL STUDIES IN *UROMYCES HOBSONI* VIZE

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ABSTRACT

In the present study two strains of *U. hobsoni* have been distinguished: the binucleate form infecting *Jasminum grandiflorum* L. and the uninucleate form infecting *J. malabaricum* Wt. The latter has been designated as *U. hobsoni* forma *uninucleatum*. Both the strains are host specific. In the binucleate strain pycnia are regularly formed and the mode of pycniospore formation and separation has been found to be of a novel type. The structure of the telia which, in both the strains develop within old aecia, has been described in detail. The teliosporic basidia in the binucleate strain may be 2-, 3-, or 4-celled. It has been pointed out that the variability of the basidia with respect to the number of cells and nuclei in them is not an environmentally induced phenomenon. Basidiospores are bi- or quadri-nucleate. The latter are bigger in size. In the *uninucleatum* form pycnia have been found to be absent. Telioid aecia in this strain have been observed only in some collections made from stations situated at high altitudes like Purandhar and Mahabaleshwar. It has been shown that the expression of endo-condition is possibly an inherent property of some collections only and temperature variations do not play any important rôle in changing the habit of aeciospore germination. Teliosporic basidia are invariably 2-celled and the basidial variability is not as pronounced as it is in the binucleate strain found on *J. grandiflorum*. Short cycling tendencies seem to be operative in both these strains.

INTRODUCTION

Uromyces hobsoni is an "opsis" rust which has been found in India to parasitise various species of *Jasminum*, notably the following: *J. arborescens* Roxb., *J. grandiflorum* Linn., *J. malabaricum* Wt., and *J. officinale* Linn. The work of Barclay (1891) on this rust particularly with respect to life-history and aeciospore germination constitutes one of the best accounts of a tropical rust. Subsequently Ajrekar and Parandekar (1931) found that the aeciospores in the case of the rust found on *J. malabaricum* are uninucleate. Thirumalachar (1939) has worked on the cytology and life-history of *U. hobsoni* found on *J. grandiflorum*. The occurrence of nuclear migrations in the primordia of primary aecia of the rust available on *J. grandiflorum* was reported earlier by the writer (1952). Following this, an extensive study was undertaken on the mode of aeciospore germination. At the same time the observation of Ajrekar and Parandekar (1931) that the aeciospores found on *J. malabaricum* are uninucleate, was also confirmed. These studies soon indicated that occasionally the aecia are telioid, and that the aeciospores under suitable conditions of moisture and aeration germinate by producing basidiospores. This discovery of endo-condition in *U. hobsoni* has been described elsewhere (Payak, 1953). In view of such results it was thought feasible to conduct further work on the morphology and cytology of this rust. During the course of these studies it also became apparent that between the *J. grandiflorum* rust and the *J. malabaricum* rust there are not only cytological differences present but that both of them are also host specific, i.e. they are not cross inoculable. Two forms, therefore, have been distinguished: the binucleate form found on *J. grandiflorum*

and the uninucleate form found on *J. malabaricum*. The morphology and cytology of both these forms have been separately described.

MATERIALS AND METHODS

J. grandiflorum is cultivated in the gardens for its fragrant flowers while *J. malabaricum* is a wild twining bush found throughout the Western Ghat forests of India. The *grandiflorum* rust was collected locally in Poona. Studies on the *malabaricum* rust are based on material collected from Khandala, Mahabaleshwar and Purandhar Hill Fort.

Pycnial (in case of the *grandiflorum* rust) and aecial material was fixed in formol-acetic-alcohol and Flemming's weak fluid. Telial material was fixed in a stronger variant of Flemming's containing a higher percentage of osmic acid. Good fixation was also obtained in Gilson's fixative which has mercuric chloride as one of the main ingredients. Though its unsuitability for plant material was soon apparent, the fixation of the rust sori and mycelium was found to be excellent. Microtome sections were cut to a thickness of 7 - 12 μ . The sections were either stained in Heidenhain's haematoxylin or in Newton's Iodine Gentian Violet. Teliospores were germinated on slides. Basidia and basidiospores were fixed in acetic-alcohol and then stained either in aceto-carmin or in aceto-orcin.

Inoculation work was mainly conducted during the rainy season (July-September). Plants of *J. grandiflorum* were raised through "layering". The layered plants were transferred to 9" pots. As cuttings of *J. malabaricum* did not root easily, young seedlings growing under healthy bushes in the forest were brought to the laboratory and transferred to 6" pots. Majority of such seedlings survived. They were kept for observation for a week or more to check that they were free of any previous infection. These were then used for inoculation purposes. Aeciospores which had naturally fallen off from the aecial cups were used for inoculation. A spore suspension in sterile water was prepared and then sprayed on the plants. Alternatively the spores were dusted directly on the lower leaf surfaces which had been moistened before. The inoculated plants were kept in the moist chambers for at least 48 hours.

SYMPTOMS AND CULTURAL STUDIES

The symptoms of the *grandiflorum* rust have been fully described by Barclay (1891) and also by Thirumalachar (1939). The *malabaricum* rust also exhibits symptoms similar to those of the *grandiflorum* rust. The rust produces discrete or coalescent infections sometimes involving the whole length of the plant part concerned. Infections develop without any restriction on leaves, stems, and flowers. The rust incites considerable amount of hypertrophy and distortion of the affected parts. Aeciospore infections are orange-coloured which, with replacement by telia, in the dry season, turn dark brown to black.

Cultural studies were conducted to find out whether the *grandiflorum* rust can infect plants of *J. malabaricum* and vice versa. Infection studies were carried out with aeciospores. As is well known, the rust propagates itself in the favourable season through repeated generations of aeciospores. For inoculation work, aeciospores from the primary aecia associated with pycnia (in the *grandiflorum* rust) were selected. In the *malabaricum* rust it was rather difficult to select the primary aecia because so far pycnia have never been observed to occur. As controls, the aeciospores in each case were tested by inoculating them on their own hosts.

One lot of 4 potted plants of *J. grandiflorum* was inoculated on 4th September 1953. Faintly yellow spots on the leaves were discernible on 17th September

1953. Some of the aecia on these infections, when kept for long period indoors, became cylindrical and their peridia remained closed. These aecia were formed without being accompanied by pycnia. In the *malabaricum* rust also such repeating aecia alone were formed more or less within the same period. Aeciospores from *J. grandiflorum* which had been found to be viable and capable of producing infection, when cross inoculated on the *J. malabaricum* plants, gave negative results. Similarly aeciospores of the *malabaricum* rust when inoculated on the *J. grandiflorum* plants, failed to produce any infection. It thus shows that the two rusts can not be cross inoculated and there is basis to conclude that these two are separate and distinct forms of *U. hobsoni*. The rust found on *J. malabaricum* has been designated as *U. hobsoni* forma *uninucleatum*.

THE *Grandiflorum* RUST

Pycnia: Ajrekar and Parandekar (1931) were unable to observe pycnia in the material of this rust available at Poona. Thirumalachar (1939) found them to be regularly present in this rust occurring at Bangalore. The writer also has been able to observe them in the Poona material. The pycnia are quite easy to spot because, when aecia have not yet developed, the hypertrophied pustules are more reddish orange than just orange in colour. It is on such reddish infections that the pycnia develop as yellowish to orange dots. Pycnia are subepidermal globose to flask-shaped, and have numerous ostiolar periphyses (Fig. 16).

Pycniospore formation and separation: The pycniosporophores are uninucleate and so are the pycniospores. The pycniosporophore nucleus, before the formation of a pycniospore, divides (Fig. 1). The upper daughter nucleus soon begins to migrate towards the apex. Concurrently, the pycniosporophore begins to differentiate a sub-apical constriction. The degree of conspicuousness of this constriction varies from pycniosporophore to pycniosporophore. It is very narrow in Fig. 2 where the nucleus in passing has become proportionately attenuated. The nucleus after reaching the apical part assumes its rounded form (Fig. 3). The sub-apical constriction now undergoes a process of stretching and elongation (Fig. 4). It continues to elongate and become thinner and thinner (Fig. 5) until the pycniospore gradually snaps off and thus gets freed from the parent pycniosporophore. After separation, the pycniospores lose their rounded form and become elongate and bacillariform (Figs. 6 and 7).

Telia and Teliospores: The telia in *U. hobsoni* are known (Barclay, 1891 Thirumalachar, 1939) to develop within old aecia. Though the phenomenon of formation of telia in old aecia is very well known in several rusts, particularly in oopsis forms (Jackson, 1931), the morphology of such composite sori in which the two spore forms get telescoped, does not seem to have been worked out fully. Old aecia, as observed in *U. hobsoni*, have a persistent peridium and the aecial cups are either devoid of aeciospores or they may contain degenerating mass of old aeciospores which failed to get an exit from the sori. Teliospore formation is preceded by the development of numerous thick-walled hyphae. These adhere laterally and also develop one over the other in vertical chains. Ultimately the cells in mass assume an aspect of a compact cellular crust. The crust cells are at first hyaline and thin-walled but subsequently they become brown-coloured and thick-walled. A representative of such hyphae of the crust is shown in Fig. 8. Its *in situ* location is shown in Fig. 18 (arrow). Septum formation in the upper cell has not yet commenced. Curiously the lower cell is uninucleate. As can be seen in Figs. 9, 17 and 18, the uninucleate and binucleate hyphal cells of the crust occur in an intermixed condition without any order or sequence. Teliospores develop over the surface of the crust. Nuclear fusions have been observed to occur in the young teliospores regularly. Teratological teliospores like those shown in Figs. 14 and 15 occur quite commonly. In the teliospore of Fig. 14 two nuclear

spaces can be observed while in that of Fig. 15 even though the spore body has been wedged in by an invagination, only one nuclear space is present.

Nuclear fusion : In Fig. 10 two nuclei have just adressed together. In Fig. 11 a partial intermingling of the chromatin has commenced but the nucleoli have still remained unfused. In Fig. 13 the fusion nucleus shows a chromatin reticulum clearly. The nucleolus has diminished considerably in size. In Fig. 12 the chromatin threads have assumed a bipartite appearance not unlike that observed during zygotene or pachytene of meiosis. In Fig. 19 is shown a two-celled teliospore. Each cell here contains a fusion nucleus. On the whole one meets two-celled teliospores in the sori of *U. hobsoni* only occasionally.

Basidia and Basidiospores : Maximum teliospore germination can be secured when the Southwest Monsoon is about to terminate sometime in September. The teliospores at this time mature early, germinate, and the resulting basidiospore infections produce fresh pycnia and aecia on young leaves and twigs. Teliospores produced late in the season in November or December remain dormant until the onset of the next Monsoon. Collections in winter, therefore, do not show a high percentage of teliospore germination.

Owing to scarcity of good division stages meiosis has not been studied in detail. Attention has been confined to the study of the variability in the basidial cell numbers and the nuclei that they contain—a variability which has been repeatedly noted in all the material studied so far. In Fig. 20, the fusion nucleus has migrated in the middle of the basidium. The interphasic nucleus is showing a well developed chromatin reticulum along with a nucleolus. Occasionally basidia get prematurely divided into two cells without being accompanied by a nuclear division. Such a stage is shown in Fig. 21. The region below the septum is being interpreted as a cell of the basidium and not a basidial stipe. The latter, unlike the present case, is always found to be an empty space. In Fig. 22 is shown an intranuclear spindle in side view. Chromosomes are rather irregularly distributed. In Fig. 23 the nucleus is in late anaphase I while Fig. 38 represents telophase I. The spindle in the basidium of Fig. 38 owing to the typical curvature of the latter might have been pushed aside near the wall on the right. Consequently, the telophasic stage also has continued to remain in the same parietal location as the spindle.

The daughter nuclei resulting from first meiotic division undergo second division so rapidly that they have never been observed in the interphasic state. If at all they exist in interphase it must be lasting for a very brief duration indeed. In Fig. 27 the nuclei are in anaphase II. As yet even the first septum in the basidium has not developed. In Fig. 28 the nuclei are in telophase II and the first septum formation has now become apparent. The subsequent stage—a normal 4-celled basidium—is shown in Fig. 32. The development of the basidium outlined above may be considered as typical in the sense that it is the expected sequence of occurrence following teliospore germination in any rust. In more than 50 stained preparations of germinating teliospores belonging to the *grandiflorum* rust many abnormal features of the basidia have been observed. The variability of the basidia with respect to their cell numbers and nuclear distribution, following meiosis, is considerable.

In Fig. 24 the fusion nucleus has undergone both the meiotic divisions without being accompanied by septum formation in the basidium. Completion of meiosis without wall formation in the basidium has been reported by Olive (1943) to occur occasionally in *Septobasidium apiculatum* Couch and commonly in *S. grandisporum* Couch. In the latter species each basidium produces one large-sized basidiospore.

Some of the unusual variations are those shown in Figs. 40, and 41. In Fig. 40 the basidium has become forked at the mouth of the parent teliospore. The uppermost cell of the basidium has produced an apical basidiospore. In Fig. 41 a binucleate basidiospore is developing at the junction of the basidium and the teliospore; another basidiospore is forming on the second cell from below.

Two-celled basidia are depicted in Figs. 34 and 36. Both are noteworthy in that their upper cells have produced 2 basidiospores each. In Fig. 36 the nucleus of the upper cell has remained undivided. In Fig. 34 one basidiospore developing on a side-sterigmata is binucleate while the apical basidiospore shows one nucleus and two extra-nuclear stainable granules in the cytoplasm. The nucleus in the lower cell has not divided.

Three-celled basidia occur quite frequently. The various types of such basidia have been shown in Figs. 25, 26, 29 and 39. In the basidia of the type shown in Fig. 35 it is difficult to decide about the exact number of cells that they possess. The difficulty hinges on the lower region of the basidium because it can not be decisively interpreted either as a basidial cell or as a basidial stipe. In any case, it seems certain that the nucleus has undergone meiosis in the upper cell. Two daughter nuclei migrated to the basidiospore while the rest have remained in the parent cell. Majority of the 3-celled basidia are either of the type shown in Fig. 29 or of that shown in Fig. 39. More commonly the middle cell is binucleate. The basidiospores produced from such binucleate cells are quadrinucleate while the remaining uninucleate cells give rise to binucleate basidiospores. The latter are shorter in size (in stained preparations they measure $10.5-16.5 \times 4.5-6.0\mu$), while the quadrinucleate basidiospores on the same basidia are proportionately bigger in size ($18.0-22.5 \times 6.0-7.5\mu$). Another interesting occurrence in the teliosporic basidia of this rust is the absence of nuclei in certain cells. These have been shown in Figs. 26, 30, 31, 33 and 43. In Fig. 37 a quadrinucleate discharged basidiospore has been depicted. The basidium of Fig. 42 has produced 3 basidiospores. Two nuclei are apparent in each of the two lower basidiospores. In the upper one, one of the nuclei is dividing.

THE UNINUCLEATUM FORM

An endo-condition was demonstrated in a collection of this rust made from Purandhar Hill fort (Payak, 1953). Further work has shown that the aeciospores of this rust available at Mahableshwar also germinate by producing 2-celled basidia. However, in the population of the rust extant at places like Khandala, endo-condition was found to be absent. Aeciospores from such localities almost always produced 2-celled germ tubes with whip-like extensions instead of the basidiospores. Arthur (1929) has pointed out that short-cycling tendencies are more apparent at higher altitudes and deeply sheltered valleys where the atmospheric conditions are undoubtedly different from those prevailing in the plains. In order to find out whether basidiospore production is an expression of temperature response, fresh aeciospores collected from Khandala, were kept in moist chambers in a refrigerator at temperatures varying from 18°C to 25°C . Precautions were taken to see that the developing basidia from the aeciospores did not get covered up by the condensing moisture. Even in an incubation at such low temperatures basidiospores failed to develop. Aeciospores from Mahableshwar, however, regularly produced basidiospores even at room temperatures (28°C to 30°C). It thus becomes manifest that the expression of the endo-condition is possibly an inherent property of some collections only and temperature variations do not play any important rôle in changing the habit of aeciospore germination.

Telia and Teliospores: The development of telia in old aecia in the oopsis rusts is undoubtedly due to the suppression of the uredial stage. It may be

pointed out that occasionally telia in *U. hobsoni* do develop separately. Whether teliospores are formed in old aecia or in independent, telia, the sori are always deep seated in the form of globose sunken cavities. Teliospore formation in a separate telium is shown in Fig. 44. Here all the thin-walled cells of the hymenium are uninucleate.

Teliospores begin to form when the dry season is setting in. At this stage practically all the aeciospores have been shed away from the sori. By repeated divisions the hymenium forms vertical rows of 3-6 cells which adhere laterally. As the development progresses, the whole cell mass assumes an aspect of a parenchymatic crust or plate. The cells of this crust are at first thin-walled and hyaline. The cellular plate by further divisions rapidly elongates and comes to occupy more than half the space in the sorus. In some aecia, aeciospores which failed to escape now get compressed by the cellular crust and they get concentrated in the central region of the sorus (Fig. 45). This entire mass ultimately undergoes dissolution giving way to the developing teliospores.

In Fig. 46 a telium is shown which has arisen as a separate sorus. The cells of the hymenial plate are hyaline and thin-walled. In Fig. 47 the sorus, unlike that of Fig. 45, is devoid of old aeciospores. The thickening and browning commences in the intercellular hyphae which converge at the base of the sorus progressing upwards in the sorus until in the mature telium the entire cellular crust becomes hard. The thick-walled cells of the crust remain uninucleate throughout (Fig. 47). Ordinarily the cellular plate, as mentioned above, occupies about half the soral space but sometimes it assumes a domelike aspect and fills up practically the entire soral cavity (Fig. 48).

Since the crust cells are uninucleate from the beginning the resulting pedicellate teliospores also individually contain only one nucleus. One such teliospore has been shown in Fig. 49. As the binucleate condition in the constituents of young as well as mature telia is conspicuous by its absence, nuclear fusion does not occur in the teliospores of this form.

Basidia and Basidiospores: Teliospore germination, in the collections of the *uninucleatum* rust made at different places at various times, has been so erratic and in such low percentage that inoculation work with teliospores has been so far unsuccessful. However, a few stages of teliospore germination observed so far have provided some understanding of nuclear cytology of the basidium. Basidia are invariably two-celled. The nucleus from the teliospore migrates in the middle of the basidium (Fig. 50), divides (Fig. 51), and the daughter nuclei get distributed in the two cells of the basidium (Fig. 52). Occasionally the teliosporic nucleus in the basidium does not divide even though the latter becomes two-celled (Fig. 53). The nucleus in the lower cell is about to migrate in the basidiospore on the left. The occasional presence of such configurations demonstrates from a cytological point of view the truly haploid nature of this strain.

The basidia produce only two basidiospores. The nuclei after migration from the basidial cells divide once more (Figs. 55, 56 and 57). The primary basidiospores sometimes produce secondary ones (Fig. 54). The secondary basidiospores also, like the primary ones, are formed on well developed sterigmata. Thirumalachar (1939) has observed the formation of even tertiary basidiospores in the *grandiflorum* rust. A germinating basidiospore with both its nuclei intact (i.e. without degeneration) in the germ tube has been shown in Fig. 58. A comparison of aeciospore and teliospore germination within the *uninucleatum* form itself demonstrates the remarkable similarity between aeciosporic basidia and the teliosporic basidia. Both types are invariably composed of 2 uninucleate cells and both of them produce two binucleate basidiospores.

As stated above, so far pycnia have never been found to occur in this rust. Teliospore germination being very scanty, evidence through inoculation work

about the actual occurrence or nonoccurrence of pycnia, is, at present, not available. Intensive field observations, especially at the commencement of the rainy season when the rust begins to appear in the forests, have so far failed to reveal the presence of pycnia.

DISCUSSION

The mode of pycniospore formation in the rusts whose pycnia and their constituents have been rather well investigated, deserves comparison with that found in the *grandiflorum* rust. Blackman (1904) first indicated that the free ends of the pycniosporophores in *Gymnosporangium clavariaeforme*, are provided with subapical thickened rings. Presumably the separation of the newly-formed pycniospore is accomplished through this thickened ring. A somewhat similar mode of pycniospore separation has been described by the writer in *Scopella gentilis* (Payak, 1956). Olive (1944) found that in *Gymnosporangium clavipes* instead of thickened rings, pycniosporophores have open collars through which pycniospores are budded out. Colley (1819) in *Cronartium ribicola*, and Lamb (1934) in *Puccinia prostii* have shown that pycniosporophores form pycniospores through subapical constrictions. In the latter rust the pycniospore gets cut off by a cell wall. The subapical constrictions develop in the pycniosporophores of the *grandiflorum* rust also. But the separation is achieved by the gradual narrowing and attenuation of the constriction until the pycniospore frees itself from the pycniosporophore.

Jackson (1935) has reviewed the then known basidial variations in rusts and has grouped them into six types. Since then a great amount of work has been done on rusts having either an unstable life-cycle or whose basidia have a pronounced tendency to vary—both cytologically and developmentally. As Skolko (1944) has pointed out, the important consideration is whether such tendencies are fixed and typical for any given Basidiomycetous fungus, or whether they are mere fortuitous occurrences. If it is the latter then no great biological significance need be attached to them. Great as is the capability of a heterobasidiomycete basidium to vary, Rogers (1934) has emphasised the need for cautious interpretation of atypical forms in the following words: "not only is there great variation in basidial morphology from group to group and species to species, but under suboptimum conditions the heterobasidiomycete basidium is capable of any of the modifications possible to ordinary mycelium— indefinite elongation, repeated irregular septation, branching, oidium formation—and of direct germination, by hyphae instead of by basidiospores, in their occasional or regular septation and their germination by repetition or conidia as well as directly. So universal is this capacity for variation, phyletic and ontogenetic, that it may well be taken to be the surest criterion of the group; and the types of response possible must be taken into account in any attempt at interpretation of the more aberrant." In the *grandiflorum* rust, the variability with regard to the basidial cell numbers and nuclear behaviour becomes manifest in normal conditions, that is, conditions not far different from those obtaining in nature. The basidial variability here, therefore, seems to be an inherent capacity which expresses itself without regard to the environmental conditions. The variations noted in the *grandiflorum* strain of *U. hobsoni* are comparable to those found by Olive (1943) in various species of *Septobasidium*, and also in the rusts—*Sphenospora kevorkianii* (Olive, 1947), and *Gymnosporangium clavipes* (Olive, 1949).

Basidially bisporous strains have been found in many rusts particularly in the endo-forms. However, not all such rusts are uninucleate. Recently, Thirumalachar and Narasimhan (1950) and Thirumalachar and Govindu (1954) have described two new species of *Endophyllum*—*E. heliotropii* and *E. spilanthes* respectively which have two-celled basidia. In the former the mycelium is binucleate

and in the aeciospores the two nuclei do not fuse. Both the nuclei on aeciospore germination get distributed in each cell of the basidium and due to their subsequent division in the basidiospores, the latter become binucleate. In *E. spilanthus* the two nuclei from the aeciospores without fusion migrate to the basidium. These divide in the basidium itself but once and thus each basidial cell becomes binucleate. Basidiospores also are binucleate. There are, however, uninucleate strains known in the endo-forms as well as in the other rusts, like *Endophyllum euphorbiae-sylvaticae* var. *uninucleatum*, *E. centranthi-rubri*, *Gymnoconia nitens*, and *Uromyces rudbeckiae*. The *uninucleatum* form of *U. hobsoni* is not only haploid and basidially bisporous but also, what is more noteworthy, its aeciospores are telioid at least in some collections and they too like the teliospores develop only two-celled basidia. There is little doubt that short-cycling tendencies are operating not only in the *grandiflorum* strain but also in the *uninucleatum* form.

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EXPLANATION OF FIGURES

The Grandiflorum Rust

- Fig. 1, nucleus in telophase in a pycniosporophore before pycniospore formation, $\times 1,800$.
 Fig. 2, nucleus migrating through subapical constriction of a pycniosporophore, $\times 1,800$.
 Fig. 3, apical part of a pycniosporophore showing a less pronounced constriction, $\times 1,800$.
 Fig. 4, subapical constriction of pycniosporophore in a state of extension, $\times 1,800$.
 Fig. 5, later stage, $\times 1,800$.
 Fig. 6, tip of a pycniosporophore showing scar of pycniospore separation; the latter lies just above on the left, $\times 1,800$.
 Fig. 7, individual pycniospores containing elongate nuclei, $\times 1,800$.
 Fig. 8, two hyphal cells from a hymenial crust in telium (cf. Fig. 18), $\times 860$.
 Fig. 9, part of a telium showing mixture of uni- and bi-nucleate cells (cf. Fig. 17), $\times 860$.
 Fig. 10, a teliospore showing adpressed nuclei before fusion, $\times 1,800$.
 Fig. 11, later stage, $\times 1,800$.
 Fig. 12, fusion nucleus in teliospore showing bipartite appearance of chromatin threads, $\times 1,800$.
 Fig. 13, fusion nucleus in interphase in teliospore, $\times 1,800$.
 Figs. 14,15, two teratological teliospores, $\times 500$.
 Fig. 16, a mature pycnium, $\times 380$.
 Fig. 17, same as figure 9, $\times 550$.
 Fig. 18, showing *in situ* location of two hyphae (arrow) sketched in Fig. 8, $\times 740$.
 Fig. 19, a two-celled teliospore, $\times 1,790$.
 Fig. 20, interphasic fusion nucleus in middle of basidium, $\times 1,800$.
 Fig. 21, two-celled basidium; lower cell without nucleus, $\times 1,800$.
 Fig. 22, Metaphase I, $\times 1,800$.
 Fig. 23, Anaphase I, $\times 1,110$.
 Fig. 24, 4-nucleate non-septate basidium, $\times 1,110$.
 Fig. 25, 3-celled basidium, each cell uninucleate, $\times 1,800$.
 Fig. 26, 3-celled basidium, note one non-nucleate cell, $\times 1,800$.
 Fig. 27, Anaphase II, first septum not yet evident, $\times 1,110$.
 Fig. 28, Telophase II, septum evident, $\times 1,110$.
 Fig. 29, 3-celled basidium; upper cell binucleate, $\times 1,800$.
 Fig. 30, 4-celled basidium; upper cell without nucleus, $\times 1,110$.
 Fig. 31, 4-celled basidium; one cell uninucleate, lower cell binucleate, $\times 1,110$.
 Fig. 32, 4-celled basidium; each cell uninucleate, $\times 2,160$.
 Fig. 33, 3-celled basidium; middle cell without nucleus, $\times 2,160$.
 Fig. 34, 2-celled basidium; upper cell producing two basidiospores, $\times 1,330$.
 Fig. 35, most probably a 2-celled basidium; basidiospore binucleate, $\times 1,330$.
 Fig. 36, 2-celled basidium with each cell uninucleate; upper cell with two basidiospores, $\times 1,330$.
 Fig. 37, a quadrinucleate basidiospore, $\times 1,330$.
 Fig. 38, Telophase I, $\times 720$.
 Fig. 39, 3-celled basidium; note middle binucleate cell, $\times 570$.
 Fig. 40, basidium forked at teliospore mouth, $\times 1,090$.
 Fig. 41, basidiospore forming at base of basidium just above teliospore, $\times 960$.
 Fig. 42, basidium with 3 basidiospores, $\times 840$.
 Fig. 43, 4-celled basidium with two basidiospores; upper one quadrinucleate, lower one binucleate, $\times 840$.

Forma Uninucleatum

- Fig. 44, an independent telium, hymenial cells uninucleate, $\times 270$.
 Fig. 45, parenchymatous crust replacing old aeciospore mass in a young telium, $\times 200$ approx.
 Fig. 46, cells of the crust in a telium thin-walled and hyaline, $\times 200$ approx.
 Fig. 47, a telium showing uninucleate hyphal cells of the crust, $\times 270$.
 Fig. 48, telial crust occupying major part of sorus, $\times 200$ approx.
 Fig. 49, a uninucleate teliospore, $\times 2,960$.
 Fig. 50, basidium with nucleus in interphase, $\times 1,800$.
 Fig. 51, nucleus in telophase, $\times 1,800$.
 Fig. 52, 2-celled basidium; each cell uninucleate, $\times 1,800$.
 Fig. 53, 2-celled basidium; teliosporic nucleus migrating in basidiospore on left, $\times 860$.
 Fig. 54, 2-celled basidium; upper basidiospore producing secondary basidiospore, $\times 860$.
 Fig. 55, basidium with a binucleate basidiospore, $\times 860$.
 Fig. 56, 2-celled basidium with 2 binucleate basidiospores, $\times 860$.
 Fig. 57, basidium showing binucleate discharged basidiospore, $\times 1,800$.
 Fig. 58, a binucleate germinating basidiospore; nuclei in the germ tube, $\times 430$.













