

# *Entorrhiza calospora* sp. nov., and Some Other Parasitic Fungi in *Limeum* Roots.

By

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## Summary.

A fungus, described here as *Entorrhiza calospora* sp. nov.\* and assumed to belong to the Tilletiaceae in the absence of proof by germination of the chlamydospores, is associated with large galls on the roots of *Limeum glomeratum*, *L. viscosum* and *Trianthema pentandra* in the Transvaal and on *L. viscosum* from Ficksburg, O.F.S. The galls range in diameter from less than 1 mm. to 3.5 cm. They are composed of parenchymatous cells in which the fine mycelium, often coiled, bears globose, strongly verrucose, binucleate chlamydospores 17.4–22  $\mu$  in diameter, produced singly but forming groups of up to twenty per host cell. The dry chlamydospores are lemon yellow to golden in a mass. A dusty sorus of chlamydospores is not formed; instead the spores are liberated by the gradual disintegration of the galls when the host dies in autumn. Germination of the spores and re-infection of the hosts were not observed. The parasite does not appear to harm the plant as a whole, since its aerial parts show no signs of disease nor of stimulation. *Oplidium brassicae* (Woronin) Dangeard, *Ligniera junci* (Schwartz) Maire & Tison, and an unidentified Phycomycete, were also found in the roots of a single plant of *Limeum viscosum* which bore *Entorrhiza* galls.

## Occurrence of *Entorrhiza calospora*.

In 1943, Mr. J. J. O. Pazzi collected some specimens of *Limeum glomeratum* at Brummeria, near Pretoria, and brought them to the Division of Botany and Plant Pathology. On their finer roots were many large galls whose cells contained abundant warted resting-spores which were thought at the time to belong to a Phycomycete. The following year Mr. Pazzi again sent specimens from the same area. These were referred to a student of Phycomycetes, but without a full knowledge of the life-cycle of the fungus this person rightly would not commit himself to an identification, replying that although the fungus appeared to be a Phycomycete even the youngest galls lacked stages of the fungus prior to the formation of resting-spores.

A morphologically identical fungus in similar galls on the roots of *Trianthema pentandra* was collected by Mr. B. N. Wolff near Malati in 1945. The subject was then dropped until 1953, when the writer became interested and endeavoured to locate fresh material to study, beginning his search at the Botanical Reserve, Pretoria University Farm, which is close to Brummeria. This report deals only with the galls on *Limeum viscosum* from the Botanical Reserve, and on *L. glomeratum* from Brummeria. Miss M. Henderson kindly identified the host plants.

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\* *Entorrhiza calospora* sp. nov.

Sori radicolii, tumores globosi vel elongati usque ad 3.5 cm. diam. inducentes. Hyphae intracellulae, hyalinae, 1.0–2.6  $\mu$  diam., tenuissime tunicatae, apice ramulorum lateralium chlamydosporas magnas generantes. Chlamydosporae globosae, hyalinae vel luteae, binucleatae, 17.4–22  $\mu$  diam.; episporio verrucis prominentibus, 1.3–3  $\mu$  crassis, 2–4  $\mu$  altis, exornato. Hab. in radicibus *Limeae glomerati*, *L. viscosi*, *Trianthemae pentandrae*. Typus: Herb. Pretoriae No. 33770, leg. J. J. O. Pazzi.

*Limeum viscosum* is common on the ridge included in the Botanical Reserve, and was abundant for a season on a patch of ploughed sandy soil west of the ridge. Later, veld grasses invaded the ploughed soil and ousted the *Limeum* plants. The host plant also grew along a little-used road on the south-east side of the ridge. From all these sites *Limeum* plants were dug up and a rather small proportion of them bore the galls that were being sought. The presence of the galls could not be inferred from the aboveground appearance of the plants. On the other hand most *Limeum* plants at the Reserve had insect-galls or thickenings at the collar or on the stems. Sections of these thickened tissues were free of fungus but occupied by insect larvae.

*Limeum viscosum* is an annual herb of prostrate, procumbent or decumbent habit, and favours cultivated or disturbed sandy soils. According to herbarium records, it is commonest on sandy or gravelly soils. Fungus-galls are more easily found on those plants growing in deep sand where the roots are better developed than in shallow gravelly soils.

Phillips (1951) places *Limeum* in the Phytolaccaceae and *Trianthema* in the Aizoaceae, two adjacent families in the classification he adopts. In *Limeum* he notes eight species widely distributed in South Africa, while in *Trianthema* there are four species, some of which occur in each Province.

When the writer began this work the following herbarium specimens of the fungus-galls were available in the National Herbarium: 33770, Pazzi, on *Limeum glomeratum*, Brummeria, 1943; 35291 and 35391, Pazzi, on *L. glomeratum*, Brummeria, Spring 1944; 39031, Wolff, on *Trianthema pentandra*, Mahale, P.O. Malati, 1945. In the phanerogamic section of the National Herbarium, the writer found a specimen of *Limeum glomeratum* collected by H. B. Terry, 30/1/1943, *sine loc.*, with typical galls on its roots. Finally specimens have been received from Ficksburg, O.F.S., on *L. viscosum* collected by Dr. Meredith, March, 1955.

With the preconceived idea that the fungus was a Phycomycete, the writer spent some time collecting galls of all sizes and dissecting, sectioning and examining them in an attempt to trace stages of a Phycomycete life-cycle, but only mycelium and resting-spores were found. He accumulated a good deal of information about these without coming any nearer to classifying the fungus, and all attempts at germinating the chlamydo-spores failed. Then a paper by Schwartz (1910) came to hand, and at once the imposing similarity between the *Limeum* fungus and *Entorrhiza* was evident. **Technique.**

The freshly collected galls were fixed in the field and sectioned after embedding in paraffin. The following fixatives were tried: Formol-alcohol, Carnoy, Gilson, Bouin, and Chicago Chrome-acetic-osmic acid, according to the formulae given by Chamberlain (1915). Fixation for two hours in Carnoy or twenty-four hours in Bouin gave satisfaction, the latter possibly being the better.

Paraffin sections were cut in thicknesses between 3  $\mu$  and 15  $\mu$ . Sections about 7  $\mu$  thick were generally the most useful, but those at 3  $\mu$  were necessary for seeing the contents of the chlamydo-spores. The mycelium was of course only seen in short lengths in the sections, and was best studied by teasing out coarse hand sections mounted in warmed lactic acid with cotton blue as stain, or in Cartwright's picro-aniline blue (Cartwright, 1929). The stained, teased out portions were washed and mounted in lactic acid. The cover glass was ringed with nail lacquer. In such preparations the mycelium was easily seen but its cytological details were not clear.

Fifteen common stain combinations were tested on the paraffin sections. Many gave pleasing colour combinations but insufficient cytological detail. The cytology was well shown, however, by using Heidenhain's haematoxylin with a light counterstain of Orange G, or with Giemsa stain, or with Safranin O counterstained with Delafield's haematoxylin. In the last combination it was found that after differentiating the haematoxylin in acid alcohol it was desirable to intensify the remaining coloration

with ammonia alcohol to bring out the colour in the hyphae and host nuclei satisfactorily. Used in this way, Safranin and Delafield's haematoxylin was perhaps the best of the combinations tested.

**Description of the Galls and of *E. calospora*. (Figs. 1-38).**

The galls measure less than 0.5 mm. to 3.5 cm. in diameter. The smaller galls are rounded and more or less smooth. They may be formed laterally on a rootlet, or may surround the root thus later interrupting the continuity of the conducting system. A laterally formed gall may often have only the slightest connection with the root, whose structure then remains quite unimpaired. Here one is reminded of the galls of *Sorodiscus radicolus* described by Ivimey Cook (1931) except that in the *Entorrhiza* galls the youngest stages of the fungus are not necessarily found adjacent to the root. Mycelium and young chlamydospores were present even in the smallest galls. A root may bear a linear series of galls which coalesce on further growth into an irregularly elongated mass. Some of the larger galls are obviously formed like this, but others with an irregularly globose form and a tubercular surface are apparently formed by prolonged growth of a single gall.

The galls consist of parenchyma cells and interrupted conducting tissues. The host nuclei are somewhat enlarged and clearly seen in young galls, but later disappear. The interior of an old gall is pale yellowish, marbled or granular, owing to innumerable chlamydospores occupying practically all the parenchyma cells. A dusty sorus is not produced. Scattered and displaced Xylem elements may be present depending upon the degree of root involvement, but the Xylem never contains chlamydospores or mycelium. A very thin peripheral layer of suberised tissue may surround old galls.

The galls of *E. calospora* are far larger than those of any other species of *Entorrhiza*. Descriptions of other species mention galls tending to be ovoid, cylindrical, or digitate, and none measuring more than 3 mm. wide and 10 mm. long.

The hyphae of *E. calospora* are colourless, 1.0-2.6  $\mu$  in diameter, with very thin walls. They are intracellular, but may perhaps be intercellular too, though this condition was not seen. The hyphae are often continuous with the cell walls of the host. Within the cells they are sharply and irregularly bent at intervals, or spirally coiled. Coiled hyphae are typical of those bearing chlamydospores. The coiled and contorted hyphae form unentangleable masses which commonly enmesh the host nucleus, and so close is their connection that the hyphae may appear to arise from the host nuclei. The hyphae vary very much in diameter over short distances. Their contents are difficult to observe as they resist differential staining and their alternately strongly and weakly refractile zones appear respectively under- and overstained. Minute dark-staining granules, possibly nuclear material, are scattered in the hyphal cytoplasm which is itself either dense or vacuolate. The hyphae are sparingly branched, with occasional septa, and the chlamydospores are formed singly and terminally on lateral branches, which are somewhat narrower than the purely vegetative mycelium.

The chlamydospores are pale lemon to golden in a dried mass when mature, but appear almost hyaline and strongly refractile in the microscope. Early in their development, as soon as they are recognisable as spores, they are more or less globose with a lobed outline of strongly refractile warts. The warts are scanty at first but later cover the whole surface and become very conspicuous. The mature chlamydospores are globose, 17.4-22  $\mu$  in diameter (including the warts). The warts are 2-4  $\mu$  high and 1.3-3  $\mu$  broad at the base. They are cylindrical or conical with a rounded apex which is narrower than the base. Some rather dark chlamydospores have warts which differ in being abruptly narrowed towards the apex. The wall of the chlamydospore

totals 3.3–4.7  $\mu$  in thickness and consists of three layers, the outermost warted layer and two smooth inner layers. Refractile (? oily) masses or vacuolate cytoplasm fills the chlamydospore. Two relatively large nuclei, 1.3  $\mu$  diameter, are present in the mature spores, and the vacuolate cytoplasm often carries a few small dark-staining granules. As many as twenty chlamydospores have been seen in a single host cell; the average number is 4–5 per cell. The greater numbers occur in greatly enlarged cells. It is possible that the latter are formed by the breaking down of the intervening walls of several smaller cells, but only in one instance was this clearly seen. The immature chlamydospores stain deeply with all the common stains; the mature ones are more resistant to stains but show up well on account of their refractility.

Galls appear in early spring and continue to grow, new galls also being formed, throughout the summer. In the autumn, about March, the host plants begin to die and the galls dry out and quite rapidly disintegrate into a powder composed of aggregations of chlamydospores and pieces of the softer host tissues, often stranded together by the more resistant Xylem elements of the host.

#### Germination Experiments.

In the foreword to Ainsworth & Sampson's "British Smut Fungi", 1950, the Director of the Commonwealth Mycological Institute wrote, "The compilation of this monograph focuses attention on the gaps in our knowledge of the germination of many of the species and it is hoped that its publication will stimulate interest in this group of fungi, which is of such great importance to agriculture." In the text of the book, the authors write of *Entorrhiza* (p. 88), "Spore germination is not well known . . ."

The writer has tried several times to germinate the chlamydospores of *E. calospora* using spores taken from fresh material, from newly disintegrated galls and from disintegrated galls which have been placed in a refrigerator for one month at 8° C. in an attempt to simulate overwintering. After refrigeration some of the material was also left at room temperature for the months of June–August inclusive. The refrigerated galls were divided into two batches kept respectively in dry and moist sand. Hanging drop cultures in water, acidified water, and Czapek solution were made, and chlamydospores deposited in a thin film on slides were exposed to alternately wet and dry atmospheres, but none of these methods resulted in germination after four weeks. The spores that were used appeared to be mature but this point certainly merits further investigation. Work on germination is continuing.

#### Synopsis of the genus *Entorrhiza* C. Weber.

This genus was erected by Weber (1884) to accommodate the smut described by Magnus (1878) as *Schinzia cypericola*, which causes root swellings on *Cyperus flavescens*. The genus *Schinzia* Naegeli (Naegeli, 1842) had been based on two uncertain species found in *Iris* roots, and moreover was a later homonym of *Schinzia* Dennstätt (1818). *Entorrhiza cypericola* (Magn.) Weber is thus the type species of the genus *Entorrhiza*. But in his work, Weber wrongly attributed the root swellings on *Cyperus flavescens* and *Juncus bufonius* to the single species *E. cypericola*, and his biological observations were made on the material of *Juncus bufonius*. Magnus (1888) corrected this error by showing that the smut on *C. flavescens* had finely reticulate or punctate spores, whereas that on *J. bufonius* differed in having coarsely warted spores. Still accepting the genus *Schinzia*, Magnus named the smut on *Juncus* as *Schinzia aschersoniana* Magn. In Aug. 1888 Lagerheim (1888) made the combination *Entorrhiza aschersoniana* (Magn.) Lagerh. and was followed independently in this by De Toni in Oct. 1888 (De Toni, 1888).

Nine species described or combined under *Entorrhiza* have been traced in the literature, namely:—

- E. cypericola* (Magnus) Weber in Bot. Zeit. 42 (1884) 370.  
 = *Schinzia cypericola* Magnus in Verh. bot. Vereins Brandenburg 20 (1878) 53;  
 Magnus in Ber. deutsch bot. Gesellsch. 6 (1888) 102.
- E. aschersoniana* (Magnus) Lagerheim in Hedwigia 27 (1888) 262.  
 = *Schinzia aschersoniana* Magnus in Ber. deutsch bot. Gesellsch. 6 (1888) 103.  
 = *E. cypericola* (Magnus) Weber, *pro parte*, in Bot. Zeit. 42 (1884) 370.
- E. casparyana* (Magnus) Lagerheim in Hedwigia 27 (1888) 262.  
 = *Schinzia casparyana* Magnus in Ber. deutsch bot. Gesellsch. 6 (1888) 103.
- E. digitata* Lagerheim in Hedwigia 27 (1888) 264.
- E. cellulicola* (Naegeli) De Toni in Saccardo Syll. Fung. 7 (1888) 498.  
 = *Schinzia cellulicola* Naegeli in Linnaea 16 (1842) 281.
- E. solani* Fautrey in Rev. de Myc. (1896) 11.
- E. scirpicola* (Correns) Sacc. & Syd. in Saccardo Syll. Fung. 14 (1899) 425.  
 = *Schinzia scirpicola* Correns in Hedwigia 36 (1897) 40.
- E. caricicola* Ferdinandsen & Winge in Dansk Bot. Arkiv. 11 (1914) 10.
- E. raunkiaeriana* Ferdinandsen & Winge in Dansk Bot. Arkiv. 11 (1914) 8.

Of the above, *E. cellulicola* in *Iris* roots and *E. solani* in *Solanum tuberosum* are doubtful members of the genus. Until now, all species referred with certainty to *Entorrhiza* have been found exclusively on members of the Juncaceae and Cyperaceae. *E. casparyana* with globose, strongly verrucose chlamydospores 17–22  $\mu$  diameter, is the only one sufficiently like the fungus in *Limeum* root galls to require close comparison. It is doubtful if authentic material of *E. casparyana* exists. In these circumstances, and also in view of the difference in host families, the writer was advised by Dr. M. B. Ellis of the Commonwealth Mycological Institute to describe the fungus on *Limeum* as a new species. Such treatment is in accordance with the species concept in Smut fungi recently proposed by Fischer & Shaw (1953), whose views are summarised as follows (in Rev. Appl. Myc. 33, 1954, 116): “Any two or more smuts of similar morphology and symptomatology, parasitising different species and genera of the same host family, would be regarded as belonging to one morphological species. On the other hand, smuts of comparable morphology attacking members of different host families would be deemed distinct species.” As a practical convenience this treatment has much to commend it. Nevertheless, the writer is disinclined to propose yet another new species for the *Entorrhiza* present in *Trianthema* when it is so patently indistinguishable from that in *Limeum*.

#### Other parasitic fungi of *Limeum viscosum* roots.

Some *L. viscosum* plants potted with their own soil at the Botanical Reserve were kept in the laboratory to watch the development of galls known to be on their roots. During subsequent transfer of one plant to another pot, some of its rootlets were sampled to see whether the root hairs might contain sporidia of *Entorrhiza*. These were not seen, but instead the following fungi were found: (1) a single rootlet infected with *Ligniera junci* (Schwartz) Maire & Tison; (2) abundant rootlets heavily infected with *Olpidium brassicae* (Woronin) Dang.; (3) several hypertrophied root hairs infected with an unidentified Phycomycete in the resting-sporangium stage; (4) a rootlet with a perithecium of *Chaetomium* adhering to it; (5) several roots bearing a mantle of sterile mycelia, both brown and hyaline. The sterile mycelia and the *Chaetomium* were evidently only fortuitously associated with the rootlets and were not investigated further. The first two parasitic fungi mentioned above are now described.

*Ligniera junci* (Schwartz) Maire & Tison in Comptes Rendus Acad. Sci. Paris 152 (1911) 206, Ann. Mycol. 9 (1911) 235; Ivimey Cook in Trans. Brit. Myc. Soc. 11 (1926) 196-213, Pl. 8, Archiv für Protistenkunde 80 (1933) 222-227, Pl. 11; Karling, The Plasmodiophorales (1942) 60, Pl. 11.

*Sorosphaera junci* Schwartz in Annals of Bot. 24 (1910) 512, Pl. 40. See Figs. 39-41.

A small lateral rootlet was seen with twelve cystosori in the cortical tissues. The root was not hypertrophied. The cystosori appeared solid and were globose or ellipsoidal. They were rather small, the largest measuring  $17 \times 22 \mu$ . They consisted of closely aggregated resting spores lacking a common membrane. In the smallest cystosorus ten resting spores were visible, in the largest twenty-five, but other spores were hidden behind those that could be seen. The resting spores were  $3.8-6.1 \mu$  in diameter, and varied somewhat in shape. Basically they are globose but the central ones become angled and the peripheral ones wedge-shaped by compression. Some of the peripheral spores have a slightly concave outer wall giving them a bluntly bicuspid appearance. Such spores are illustrated in figs. 14, 15, 17, 20 of Schwartz's paper (Schwartz, 1910, loc. cit.). The spore walls are smooth, very thin and hyaline. No zoosporangia or other stages in the life-cycle were seen in the very limited material available.

The form of the cystosori was not well shown in the single preparation in which this fungus was found, but there can be little doubt of its identity with *Ligniera junci*. Our knowledge of the life-cycles, host relationships and taxonomy of the species of *Ligniera* is quite fully covered in the literature cited above. Probably only two good species of *Ligniera* are known (Cook, 1933), namely *L. junci* and *L. verrucosa* Maire & Tison, the latter having verrucose resting spores. Karling (1942) however, includes a further two species, *L. pilorum* Fron & Gaillat and *L. isoetes* Palm, which he regards as possibly distinct from *L. junci*.

*L. junci* attacks many different hosts, and consequently has been described under several different names. Cook (1933, p. 227) lists the recorded hosts of *L. junci* and concludes, rather sweepingly, "From such a variety of hosts it seems probable that this fungus is able to infect any vascular plant under suitable environmental conditions."

*Olpidium brassicae* (Woronin) Dangeard in Ann. Sci. Nat. Bot. ser. vii, 4 (1886) 242-343; Sampson in Trans. Brit. Myc. Soc. 23 (1939) 199-205, figs. 1-22, Pl. 5.

*Chytridium brassicae* Woronin in Jahrb. Wiss. Bot. 11 (1878) 548-574. See figs. 42-51.

Abundant material was found consisting of solitary or aggregated zoosporangia occupying the cortical tissues of small lateral roots without causing hypertrophy. Zoosporangia globose,  $12.5-70 \mu$  diam., or elongated  $10-36 \times 32-194 \mu$ , with homogeneous or large globular contents, thinwalled or sometimes somewhat thickened. Exit tubes of the zoosporangia are  $2.9-8.0 \mu$  diameter and  $4.6-23 \mu$  long depending on the distance to the exterior of the host. Zoospores more or less globose, about  $3 \mu$  diam. (with a single flagellum up to  $17 \mu$  long fide Sampson, loc. cit.). Resting sporangia (cysts) are angular-globose,  $13.6-28.5 \mu$  diam., or sometimes elongated and then angular-ellipsoid up to  $22 \times 29 \mu$ , with an exospore which is coarsely and deeply ridged giving a stellate appearance in optical section, with 7-9 points to each star; endospore smooth, thinwalled.

Our material did not show the full life-cycle of this fungus, nor any sporangia bearing more than one exit tube. Preparations stained with Heidenhain's haematoxylin showed the ridges of the cysts very well and we were able to confirm Miss Sampson's observations on their morphology. Miss Sampson has made an excellent case for

reducing *Asterocystis radialis* De Wild., *Olpidium borzii* De Wild., *Olpidium radicum* De Wild., and *Olpidiaster radialis* (De Wild.) Pascher to synonymy with *Olpidium brassicae*. The reader is referred to her paper for an authoritative account of the life-cycle, morphology and taxonomy of *Olpidium brassicae*, and to another paper (Sampson, 1932) for differentiation of the species of *Olpidium* which have been recorded on higher plants.

As neither *Ligniera junci* nor *Olpidium brassicae* had previously been recorded in South Africa, attempts were made to secure further material by planting cauliflower seeds in the soil from which these fungi had been isolated. The seedlings were kept rather wet, which favours the development of *O. brassicae* according to Miss Sampson, but they remained uninfected.

Perhaps the greatest interest concerning this discovery of *L. junci* and *O. brassicae* lies in their association in the roots of a single plant, which also bore *Entorrhiza* galls. We believe that *L. junci* and *Entorrhiza* have not been recorded in association with one another since *L. junci* was originally described (Schwartz, 1910, as *Sorosphaera junci*), when it occurred with species of *Entorrhiza* in the roots of *Juncus bufonius*, *J. articulatus* and *J. lamprocarpus*. On the other hand, associations of *Ligniera* spp. with *Olpidium brassicae*, and of other Plasmodiophoraceae and chytrids, are well documented (Maire & Tison, 1911, b, pp. 241–242; Guyot, 1927; Ivimey Cook, 1927, 1933; Bartlett, 1928; Fitzpatrick, 1930, pp. 62–63; Karling, 1942, pp. 64–68). Often such fungi were found occupying the same tissues in a single root and not unnaturally were thought to be a single organism in various stages of development. Thus certain species and genera were proposed (e.g. *Rhizomyxa hypogaea* Borzi, *Sorolpidium betae* Némec and *Anisomyxa plantaginis* Némec) which now appear to have been based on the accidental association of two different species. The identities of some of the component fungi of such “mixed species” are still debated, but it is now generally accepted that the infection is indeed a mixture of species and not a single organism in various developmental stages. Cook (1933, p. 241), giving several examples of associated chytrids and Plasmodiophoraceae, states, “The use of *Sorolpidium betae*, *Anisomyxa plantaginis* and *Rhizomyxa hypogaea* as evidence of a relationship between Plasmodiophoraceae is unsatisfactory as these species are mixtures.” No one who has seen this phenomenon of mixed infection is likely to contest Cook’s statement.

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**Explanation of the Figures.**

Figs. 1-38: Stages in the development of *Entorrhiza calospora*.

Figs. 1, 2, 6, 11, 13, 14, 15, 17, 34, show the relationship of the host cell nucleus and the hyphae. Note that the host nucleus is often enmeshed by a tangled knot of hyphae.

Figs. 1-6, 10-12, 14-18, 25-38, show the hyphae of abruptly bent and contorted form. The characteristic spiral coiling of the hyphae is seen in figs. 16, 28, 32, 33, 38. Hyphae knotted into unentangleable masses are depicted in figs. 1, 2, 6, 11, 15, 17, 18.

Fig. 24 represents a host cell containing seventeen chlamydospores and presents the only evidence seen of fusion between adjacent cells to form larger ones containing the greatest numbers of chlamydospores.

Figs. 7-10, 13-18, 25-38, trace the development of the chlamydospores. The youngest chlamydospores, globose with an indented, sparsely verrucose outline are seen in figs. 7-10, 25-30, 33, 37, 38. Older stages with strongly verrucose exospores are also shown in some of these and in the remaining illustrations of the chlamydospores. Figs. 19-22 depict mature chlamydospores in section, showing the wall structure and contents. The binucleate condition of the chlamydospores is shown in figs. 19-20.

Figs. 39-41: Cystosori of *Ligniera junci* composed of closely aggregated resting spores.

Figs. 42-51: Stages in the life-cycle of *Olpidium brassicae*. Zoosporangia with exit tubes are shown in figs. 42-45, 47-50. Young zoosporangia without exit tubes are seen in figs. 45-46. Stellate resting sporangia (cysts) are depicted in fig. 51.









