

On some Species of the Genus *Urophlyctis*¹.

BY

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With Plates VII and VIII.



ON March 16, 1882, at the meeting of the Botanical Section of the 'Schlesische Gesellschaft für vaterländische Cultur,' J. Schroeter described the development of the old *Physoderma pulposum*, Wallr.² He pointed out that it produces large swarm-sporangia which rest superficially upon the epidermis of species of *Chenopodium*, and send forth fascicles of rhizoids into the cells. It also develops resting-sporangia by the conjugation of two cells of similar form inside the living tissue of the host. One of these cells empties its contents into the other, which then grows into the resting-sporangium. Upon these characters he based the genus *Urophlyctis* in the 'Kryptogamen-Flora von Schlesien,' v. III. part I, p. 196 (1886). There he also added a second species under the name of *U. major* (*U. majus* in the text) which does not form swarm-sporangia.

In 1888 I described³ a third species, parasitic on *Carum Carvi*, which I named *Urophlyctis Kriegeriana*. It is con-

¹ Read before Section K of the British Association, Liverpool, 1896.

² Botanisches Centralblatt, 1882, Vol. xi, pp. 219-221.

³ Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin, p. 100.

fined to the epidermal cells, which, owing to their being attacked in this way, swell out, together with the adjacent cells, into a pearl-shaped gall, having a depressed umbo at the apex. The apical orifice leads into the much-enlarged epidermal cell which contains the Fungus. This species of *Urophlyctis*, which does not extend beyond the epidermal cell, forms resting-sporangia by the conjugation of two cells derived from different mycelial threads. This I described in the paper cited.

In the second edition of Rabenhorst's 'Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz,' vol. II. Pilze, Part IV, Phycomyceten, p. 131, Alfred Fischer unites the genera *Cladochytrium* Nowak., *Physoderma* Wallr., and *Urophlyctis* Schroet., into one genus *Cladochytrium*, and in it he places the three above-mentioned species. As to the formation of the resting-spores in this enlarged genus *Cladochytrium* he says (p. 132): 'Die Dauersporen entstehen entweder an Stelle der Sporangien aus der inhaltsreichen Zelle der zweizelligen Anschwellungen und tragen dann ebenfalls eine kleinere, leere Anhangszelle; oder terminal an kurzen, von den Sammelzellen ausgehenden unverzweigten Fäden, deren Enden anschwellen und, ohne sich wieder zu theilen, zur Dauerspore werden.' Fischer does not therefore admit the process of conjugation from which the resting-spores of *Urophlyctis* originate, but considers the antheridium to be that cell of the two-celled swellings which is less rich in protoplasm.

Without any mention of Fischer's opinion, however, Schroeter retains the genera *Physoderma*, *Cladochytrium*, and *Urophlyctis* in Engler and Prantl's 'Natürlichen Pflanzenfamilien,' I. Theil, 1. Abtheilung, pp. 81 and 86, and refers the last-named genus to his tribe Oochytriaceae. Possibly at the time when Schroeter wrote, Fischer's paper had not yet been published, and nevertheless he quotes Fischer's 'Phycomycetes'¹ amongst the more important literature on the Chytridiaceae. It may

¹ In Rabenhorst's Krypt.-Fl. Deut., I. Bd., iv^{te} Abtheil. Leipzig, 1892. Lieferungen 45-47.

be that the last number was issued during the revision of the proofs.

I can confirm Schroeter's statements concerning the formation of the resting-spores of the oosporangia, having repeatedly examined *Urophlyctis Kriegeriana*, *U. pulposa*, and also a third species belonging to this genus.

As mentioned above, *U. Kriegeriana* presents the appearance of pearl-like galls on the surface of the stems, leaves, and floral parts of *Carum Carvi*. Neighbouring galls often fuse more or less completely, thereby forming smaller or larger hyaline punctate crusts, especially on the surface of the stems (Fig. 1). Every gall has externally at its apex a more or less depressed umbo (Figs. 1 and 2), which leads into a very large cell occupying the centre of the gall. *U. Kriegeriana* occurs only within this cavity. The inner membrane of this enlarged central cell always reaches the base of the umbo, and is at that point exposed; but with that exception the cavity is surrounded on all sides by a wall consisting of many layers of cells. The membrane at the free apex is traversed by a mycelial thread which dilates immediately below into a vesicle, from which, in young galls, hyphae originate (Figs. 3-5 and 9). These hyphae form swellings which grow into conjugating cells (Figs. 6-7), and hyphae of the same kind are attached to many points of the cell-wall. They either immediately produce the conjugating cells or, more rarely, they first form a swelling from which delicate hyphae arise (Fig. 6), and these form the conjugating cells. Conjugation takes place as described by Schroeter. The cells, which conjugate by means of a connecting channel, always originate from distinct hyphae. At first the conjugating cells differ but slightly in size; one of them, however, soon enlarges considerably, whilst the other remains small, and its contents pass through the connecting channel into the larger cell (Figs. 10, 13).

It is noteworthy that the male cells giving off their contents always spring from one distinct set of hyphae; so that we have here male plantlets developing at long intervals male

cells which conjugate with female cells originating from other hyphae (Figs. 10 and 13). The hyphae often branch, especially from the male cells (Figs. 10 and 11).

As Schroeter has already described in the case of *Urophlyctis pulposa*, the receptive and enlarging cell separates also, in the present instance, from the parent hypha. Therefore I have not been able to determine whether a single hypha produces several receptive or female cells.

The female cell enlarges, becomes filled with dense protoplasm containing oil-globules, and develops a thick brown cell-wall. On the side where conjugation with the male cell takes place it remains flat and depressed in the centre. The process of conjugation can be most clearly observed, as Schroeter has done in the case of *U. pulposa*; and I believe that Fischer was led to his conclusions rather from descriptions, and the statements made by Büsgen as to the formation of resting-sporangia in *Physoderma*, than from actual personal investigation of the subject.

From the structure of the gall, as described, it is most probable that the germs of the parasite enter an epidermal cell, which in consequence swells considerably and causes frequent divisions in the surrounding epidermal cells. The particular cell attacked by *U. Kriegeriana* becomes the central cavity of the gall, whilst the surrounding epidermal cells undergo repeated subdivision and form a wall around it consisting of several layers of cells, leaving at the apex a crater-like opening.

As before stated, *U. Kriegeriana* grows only within the enlarged cavity of the gall, and never extends beyond it. The development of the wall of the central cell corresponds with this. The wall thickens considerably, almost attaining the width of the neighbouring cell-layer of the envelope of the gall. It never exhibits the sieve-like perforations or the grating-like appearance which De Bary and Schroeter have described in *U. pulposa*. The strong imperforate membrane is not traversed by the delicate hyphae of the Fungus, and the parasite remains confined to its enlarged host-cell.

I have never observed the formation of other propagative organs, especially the development of zoosporangia, although I have often directed my attention to this point. The formation of zoosporangia seems to be wanting here, as in the case of Schroeter's *U. major*, or it may, perhaps, be restricted to the germination of the oospores.

Urophlyctis Kriegeriana is very common on *Carum Carvi* throughout Europe. Besides Saxony and Bohemia, the only habitats known to me up to 1888, it has since been found in Thuringia by F. Thomas¹, and Herr E. Ule has discovered it near Coburg, according to a specimen communicated to me. G. de Niessl has collected it near Schwarzkirchen in Moravia, and distributed it under the name of *Protomyces macrosporus*, Ung., in Rabenhorst's *Fungi Europaei*, No. 1100. Herr Friederich Stolz gathered it in the Gschnitz valley and in the Stubai valley, Tyrol; and Blytt has found it in Norway².

I am able, however, to record its occurrence not only on *Carum Carvi*, but also on *Pimpinella Saxifraga*. The Fungus which W. Voss has indicated on *Pimpinella Saxifraga* as *Synchytrium aureum*, Schroet., in the first part of his *Mycologia Carniolica* (in 'Mittheilungen des Musealvereins für Krain,' 1889), p. 17, is my *Urophlyctis Kriegeriana*, as I have proved by a specimen communicated to me by Herr W. Voss himself. Perhaps the parasite also occurs on other Umbellifers³.

Another species of *Urophlyctis* I knew to be the cause of a serious disease of the Beetroot in Algiers. L. Trabut reported⁴ on a disease observed on the thick primary roots of *Beta vulgaris*, var. *rapacea*, at Rouiba, near Algiers. It consists of thick fleshy botryoid swellings contracted at the

¹ Mittheilungen des Botanischen Vereins für Gesamtthüringen, Bd. viii, 1889.

² Bidrag til Kundskaben om Norges soparter iv, p. 25 in Christiania Videnskabs-Selskabs Forhandlingar, 1896, No. 6.

³ In a collection of Fungi made by J. Bornmuller in Persia, 1892-93, and sent to me for investigation, I found *Urophlyctis Kriegeriana* on *Carum persicum*, Boiss. from the province Kerman, on Mount Kuh-tagh-Ali, near the city of Kerman, 2,100 m. above the sea. (No. 4402 of J. Bornmuller, *Iter Persico-turcicum*, 1892-93.)

⁴ Comptes Rendus de l'Académie des Sciences de Paris, June 4, 1894.

base. Trabut proved these to be due to the presence of a Fungus which he named *Entyloma leproideum*, and described and figured it afterwards in the 'Revue Générale de Botanique,' T. vi (1894), p. 409, under the name of *Oedomyces leproides*, Saccardo having founded upon it the genus *Oedomyces*. Subsequently Saccardo and Mattiolo published an elaborate paper on the subject in *Malpighia* anno X (1895). Trabut, Saccardo and Mattiolo state that the Fungus occurs in cysts provided with a strong membrane (quasi cellulas giganteas). The cysts are scattered irregularly through the swellings, and the spores are produced from evanescent hyphae by acrogenous and intercalary abstriction. Saccardo distinguished it from *Entyloma*, mainly 'cystis vel singularibus et forma subhemisphaerica sporarum.' Trabut describes the spores thus: 'De forme sphérique déprimée avec pédicelle très court, inséré sur une éminence au centre de la face déprimée. . .'

These authors refer the Fungus to the Ustilagineae. Saccardo and Mattiolo support this view by pointing to the formation of the cysts within the tissue of the root of the host-plant, to the new growth caused by the parasite, to the acrogenous and intercalary origin of the spores, and finally to the structure and colour of the latter. Ed. Prillieux, in his work, 'Maladies des plantes agricoles et des arbres fruitiers et forestiers, causées par des parasites végétaux,' Tome I (Paris, 1895), pp. 193-197, refers to this disease and assigns the Fungus to the Ustilagineae.

Thanks to the kindness of Professor O. Mattiolo, who sent me a specimen in alcohol, I have been able to examine this Beetroot parasite. It proves to be a *Urophlyctis*, and must therefore bear the name *U. leproides* (Trab.), P. Magn. The cysts have a wall of exactly the same thickness as the central cell of the gall of *U. Kriegeriana*, and the parasite lives also exclusively within the cysts, as the authors above cited have shown. According to these authors the cysts are embedded singly in the parenchyma of the swellings, and originate from the hypertrophy of the cells attacked by the parasite. I cannot quite confirm this. I found rather that

many cysts are connected with each other by narrow tubes originating from the cysts (Fig. 17). Each cyst throws out pointed processes which penetrate the parenchyma, and then at intervals widen out again into fresh cysts ; each new cyst does the same. and so on (Figs. 17-22). It often happens that many such tubular processes spring from one cyst ; they may be short or long, wide or narrow ; and they may frequently be followed a long way through the tissue. The tubes are provided with the same kind of thick membrane as the cysts. The observation of young processes and small cysts shows that the protoplasm affected by the parasite enters them, and that this protoplasm leads the way for the *Urophlyctis* that follows at a later period. In any case I have not succeeded in tracing the hyphae of the Fungus in the protoplasm of the youngest swellings. The parasite, however, soon follows, and entering these swellings often forms new spores within their wider portions (Fig. 18).

It is only in the narrowest portions of the channels, as shown, for instance, in Figs. 22 and 23, that the formation of spores is suppressed. The majority of the cysts of one swelling are therefore connected with each other, or rather they are excrescences of a single cyst pervading the parenchyma of the swelling.

The only difference between this growth and that of the gall of *Urophlyctis Kriegeriana* is that the development of the cell attacked by the latter parasite, and consequently also that of the gall, is limited. On the other hand, in the case of *U. leproides*, the cell attacked by the Fungus grows without limit ; it pervades the parenchyma, the frequent divisions of which are the cause of the cell's growth into the new tissue, while it reacts on the parenchyma as a stimulus for still further divisions. Thus the large botryoid swellings on the upper part of the root of *Beta vulgaris*, var. *rapacea*, make the disease very conspicuous.

The wall of the infected cell is also in this case very thick, and it never possesses sieve-like perforations as in *U. pulposa* and *U. major*. The formation of spores takes place in exactly

the same manner as in *U. Kriegeriana*. In this species there are also certain hyphae which produce only male cells, and often branch from these cells (Figs. 24, 28–30). It is remarkable, as I have observed, that the male cells are sometimes divided by septa (Figs. 32, 33). They conjugate by means of a narrow connecting channel through which the protoplasm of the male cell passes into the female (Figs. 24, 28, 29). The conjugating cells are alike, or differ only slightly in size at first (Figs. 28 and 32); but the receiving-cell soon enlarges considerably and separates from the mother-thread, the remains of which are only seldom perceptible (Figs. 29 and 33 *r*). Thus it would appear that conjugation always takes place on the side opposite the stalk. This conjugating side remains also flattened and usually somewhat depressed in the centre, as the authors quoted above have described and figured, and eventually a strong brown membrane is formed. No swarm-sporangia are known: it is, however, quite possible that they exist, as so far only the cysts of the inner tissue of old galls have been examined, not the surface of young galls. The specimen I examined did not show any zoosporangia.

The case is very different in *Urophlyctis pulposa*, the development of which has already been described by Schroeter in its more essential features. The parenchymatous cells infected by the parasite enlarge considerably, but at the same time the wall is perforated, owing to the action of the parasite, by local gelatinization, whereby their protoplasm, together with that of the parasite living in it, passes into the surrounding cells (Figs. 14–16), causing in this case also considerable enlargement (Fig. 14). Thus the parasite wanders through the perforations of the wall caused by local gelatinization of the membrane from one cell to another, and all the infected parenchymatous cells of an infected area represent a continuous system of cavities pervaded by the parasite, and often intermixed with unchanged small parenchymatous cells (Fig. 14).

Schroeter, in Engler and Prantl, *Natürl. Pflanz.*, I. Theil, 1. Abtheil., p. 86, also refers his *Physoderma Butomi* to the

genus *Urophlyctis* without giving any reasons for so doing. Should it actually belong to this genus, and form resting-sporangia—in contradiction to the statements by Büsgen—by conjugation, then it would represent a *Urophlyctis* which wanders from cell to cell by means of its mycelium, and does not cause the host-cells to increase in size. In future years I hope to extend my investigations to such species of *Physoderma*.

In every case it is of great interest to discover the different ways in which the various species of *Urophlyctis* affect the host-cell, and the tissue of the plants on which they are parasitic.

The figures which accompany this paper have been drawn from nature by Dr. Paul Roeseler in my presence. To Dr. Stapf I am much indebted for his kind assistance in translating this paper.

EXPLANATION OF FIGURES IN PLATES VII AND VIII.

Illustrating Professor Magnus's paper on *Urophlyctis*.

Figs. 1-13. *Urophlyctis Kriegeriana*, Magnus, on *Carum Carvi* from Prossen in Saxony.

Fig. 1. Transverse section of the stem with several confluent galls. $\times 15$. The galls are cut in the tangential or median planes; only the latter show the umbo (*u*). $\times 15$.

Fig. 2. Transverse section of the stem with a single gall cut through the apex (*u*). $\times 106$.

Figs. 3-5. Longitudinal sections of the apex (*u*) of the galls. The short mycelial threads that have penetrated the membrane of the infected cell are shown enlarging into vesicles from which originate long mycelial threads. $\times 390$.

Fig. 6. A single mycelial thread attached to the cell-wall. It shows a vesicular enlargement from which spring hyphae that give rise to conjugating cells.

Fig. 7. Mycelial threads attached to the cell-wall. These have formed conjugating cells. $\times 390$.

Fig. 8. Mycelial threads attached to the cell-wall. $\times 390$.

Fig. 9. Apex of the host-cell (*u*) showing the vesicle from which originate the mycelial threads. One mycelial thread is shown attached to the cell-wall.

Figs. 10-13. Conjugating cells. The male conjugating cells are modified from special mycelial threads with long internodes, which frequently branch out from the male cells. They conjugate with the female cells through narrow fertilization-channels. $\times 390$.

Figs. 14-16. *Urophlyctis pulposa* (Wallr.), Schroet., on *Chenopodium*.

Fig. 14. Large parenchymatous cells of *Chenopodium rubrum* (Karlsbad, Bohemia) in which the parasite grows; next to unchanged parenchymatous cells which remain small. The walls of the neighbouring infected cells are pierced in a sieve-like manner, and the mycelial threads may be seen passing through the pores from one cell to the other. At *a* a young parenchymatous cell is shown, into which, in the young state, the mycelial threads of *Urophlyctis pulposa* have entered through the pores in the cell-wall. The cell is beginning to swell; the mycelial threads have as yet formed no conjugating cells. $\times 420$.

Figs. 15-16. Cells in which *Urophlyctis pulposa* has developed, showing the sieve-like perforated walls. $\times 207$.

Figs. 17-31. *Urophlyctis leproides* (Trab.) P. Magn., on *Beta vulgaris*, var. *rapacea*, from Rouiba in Algiers.

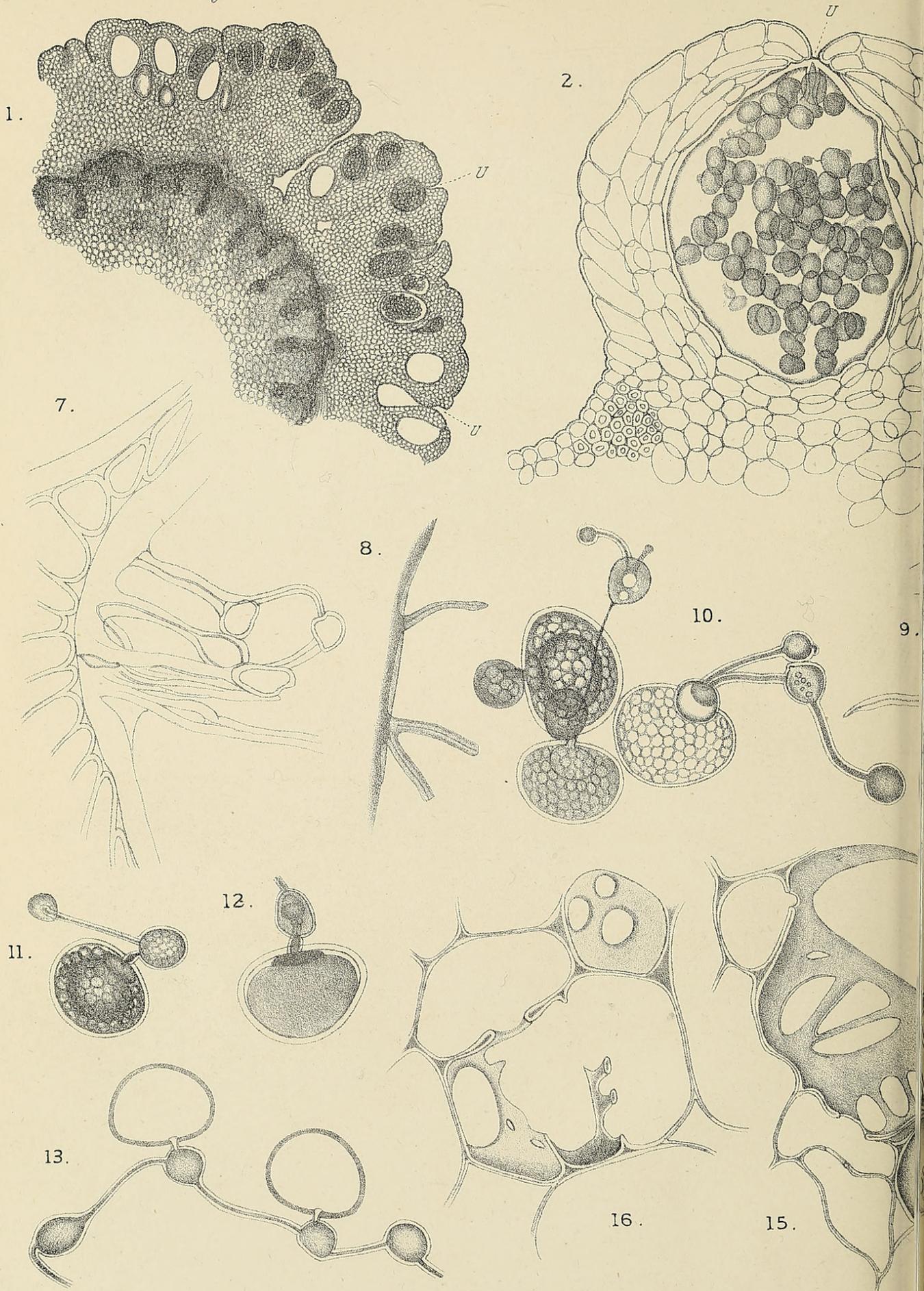
Figs. 17-23. Transverse sections of the galls showing the cysts.

Fig. 17 shows several cysts connected together by channels which arise from the cysts. The latter are shown also in Figs. 19-21. Figs. 22 and 23 exhibit the separate long connecting channels of the cysts of the galls. Fig. 18 shows these in part cut in transverse section. (Figs. 17-20, $\times 111$; Figs. 18, 19, and 22, $\times 162$; Figs. 21-23, $\times 420$.)

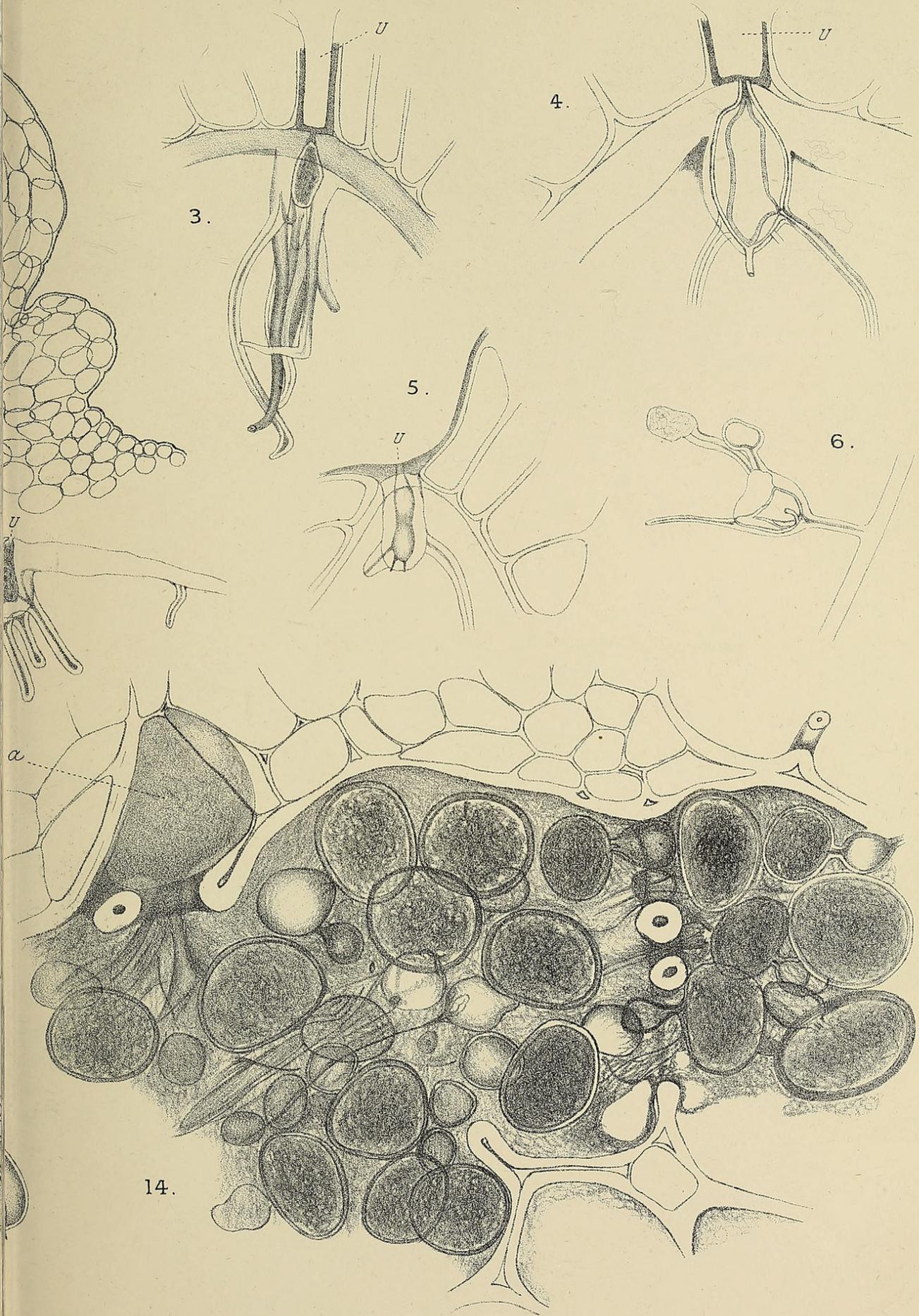
Figs. 24-32. Conjugating cells formed from mycelial threads.

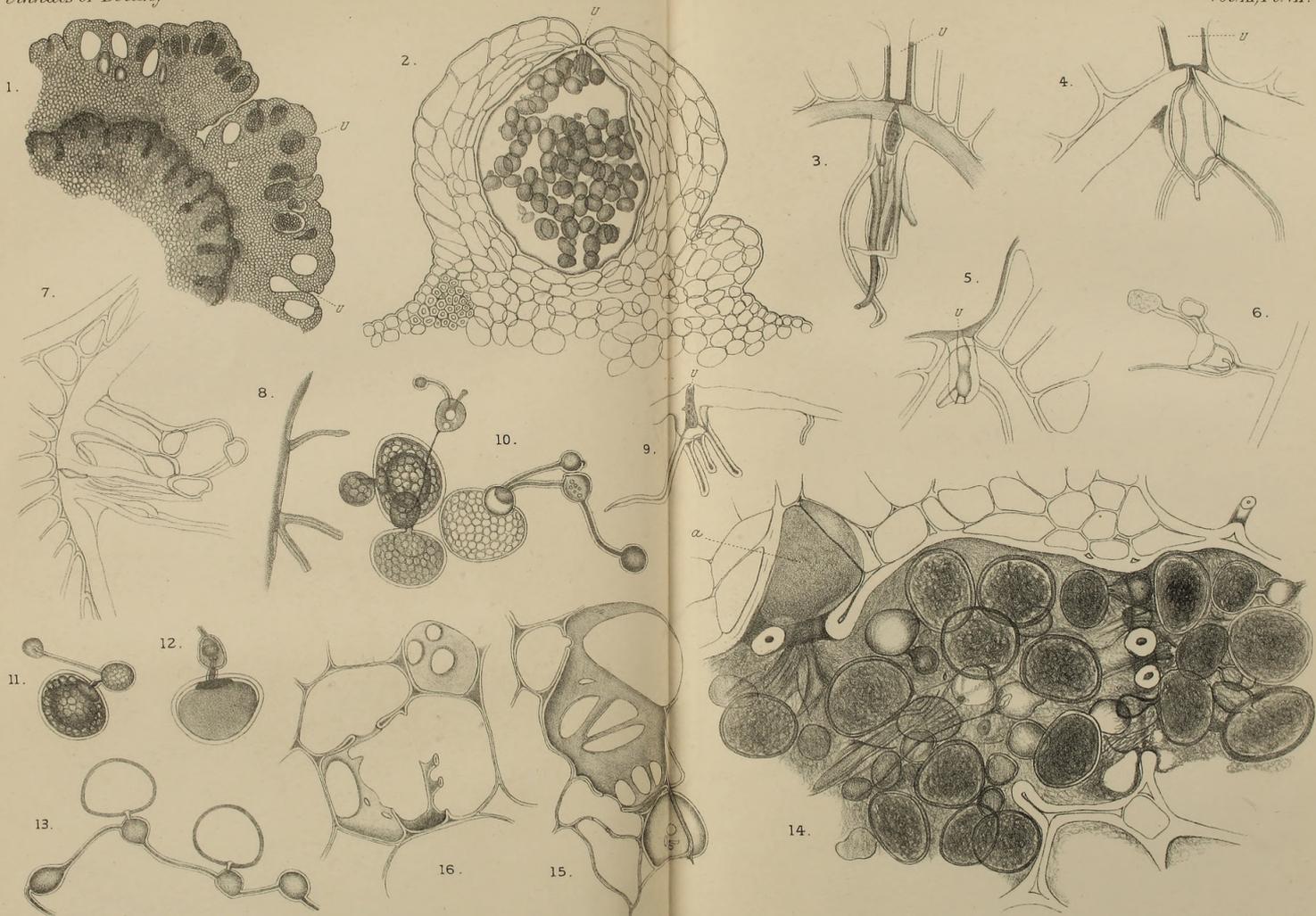
In Figs. 24, 28, and 29 are shown the threads which give rise only to male fertilizing cells with long intermediately segmented cells, which branch out from the fertilizing cells. Figs. 25-27 show the fertilization-channels. Figs. 29 and 33 show at *r* the remains of the carrying threads of the female receptive cells.

In Figs. 32 and 33 the male cells have become divided. $\times 420$.



P. Röseler del.

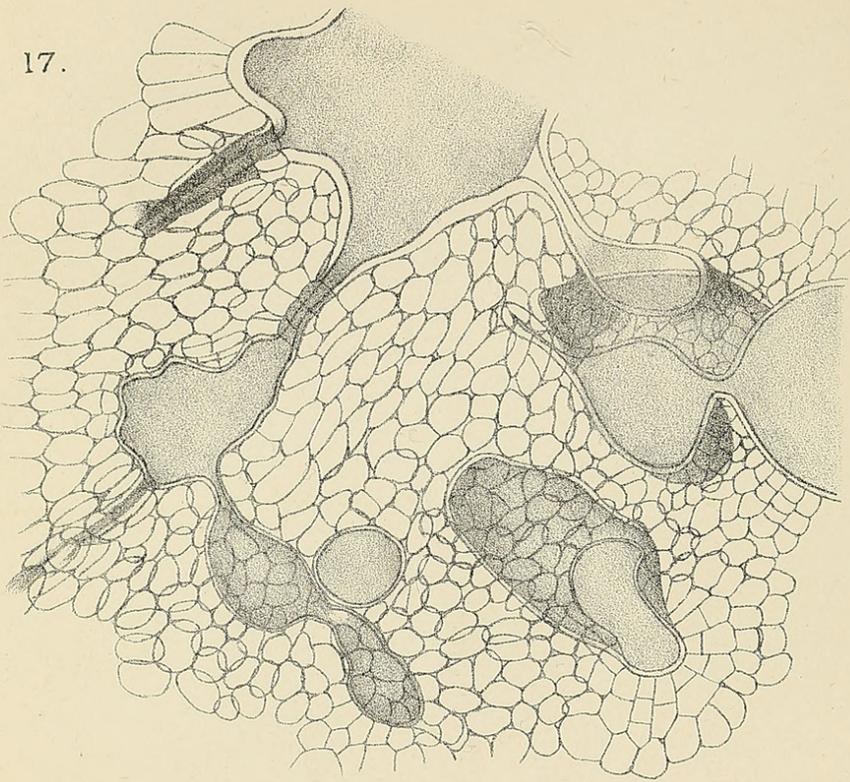




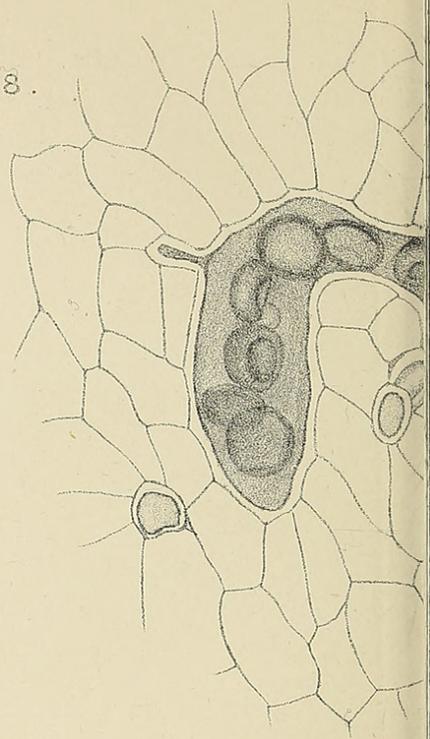
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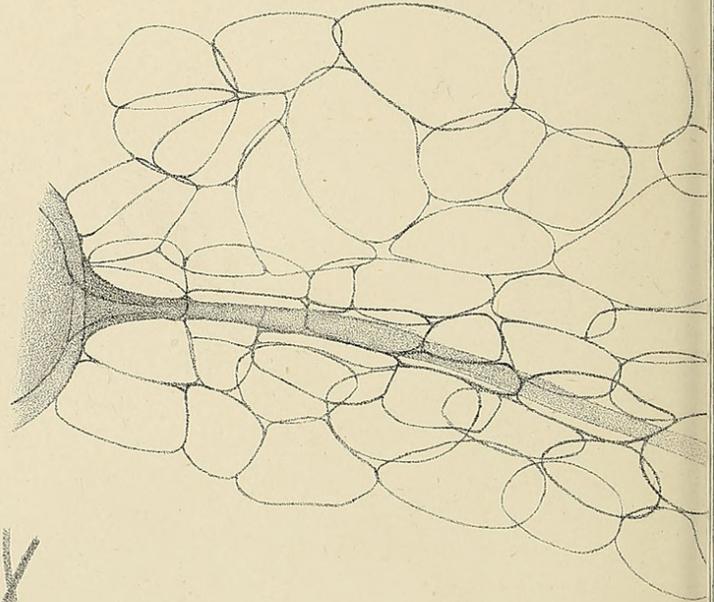
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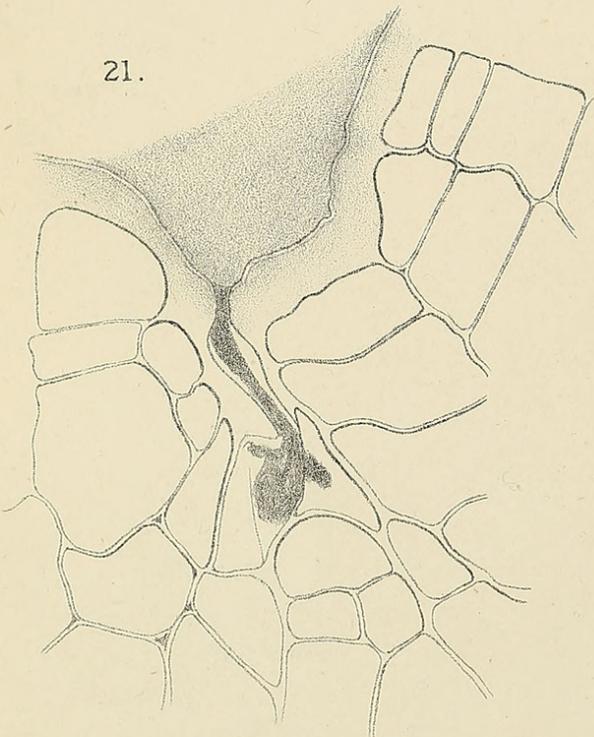
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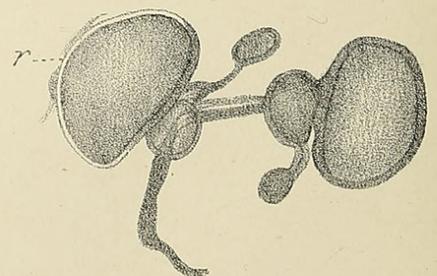
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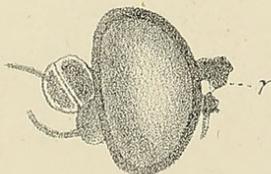
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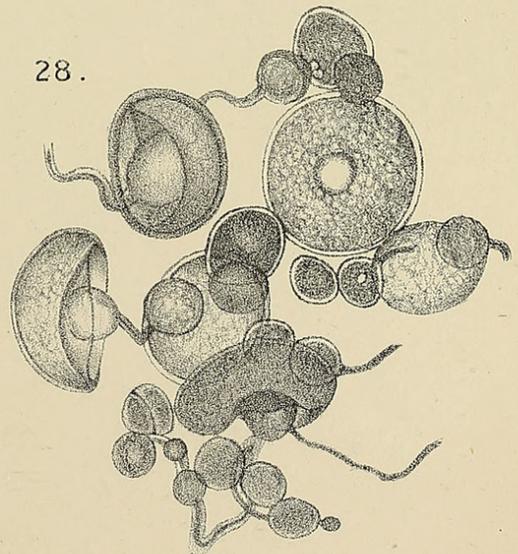
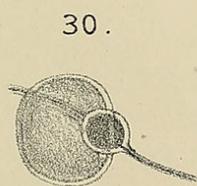
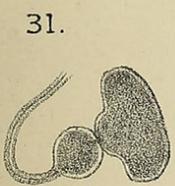
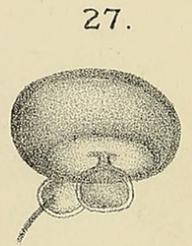
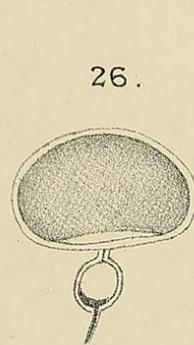
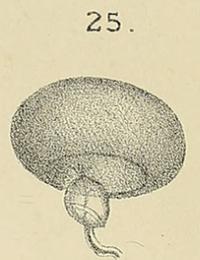
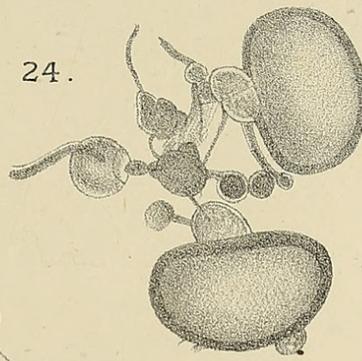
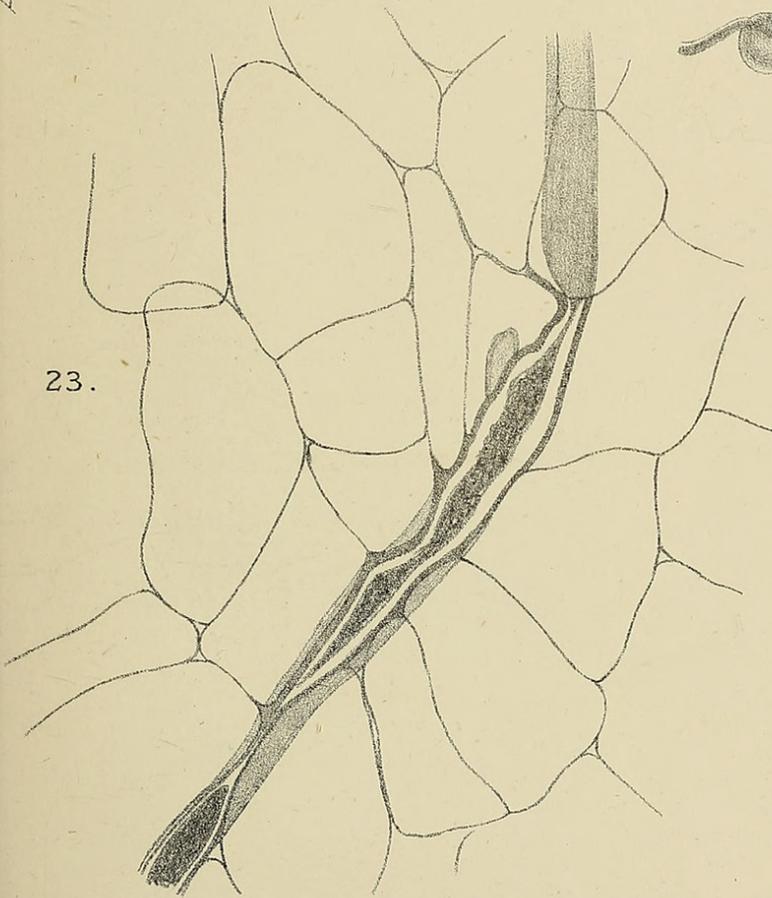
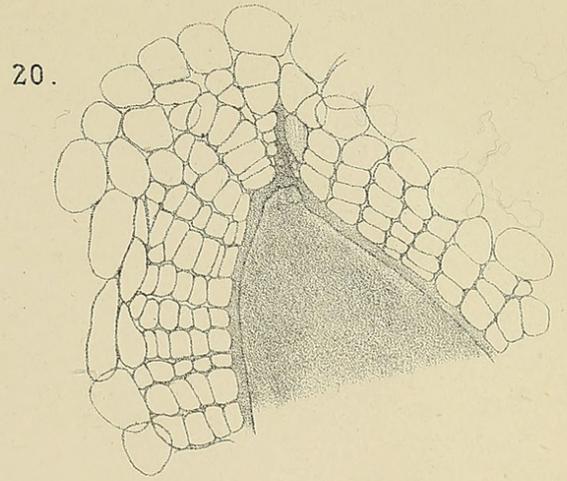
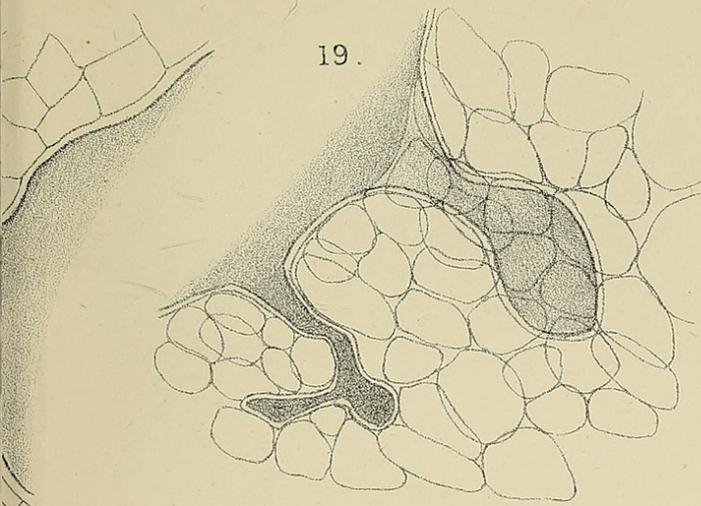
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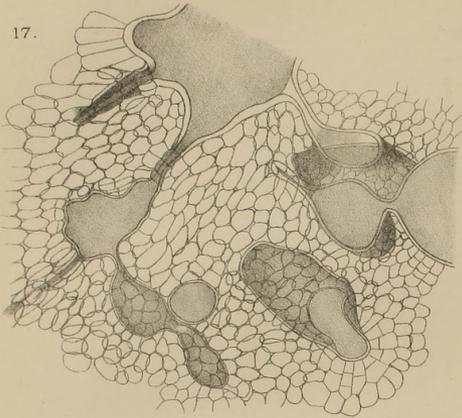
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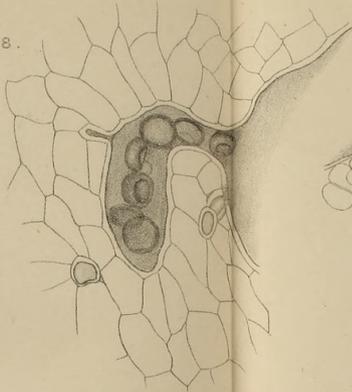
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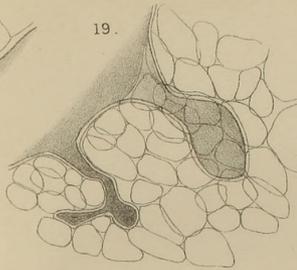
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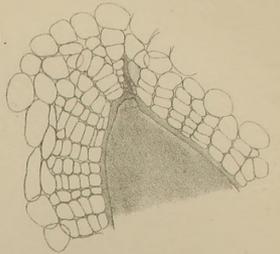
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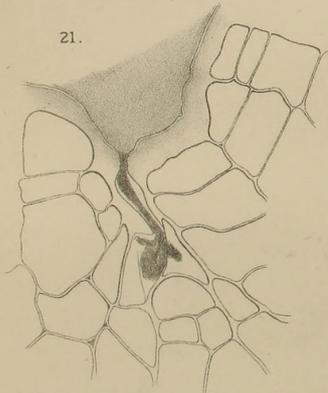
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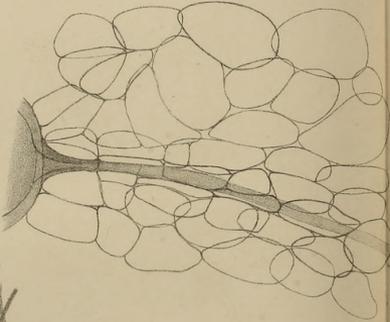
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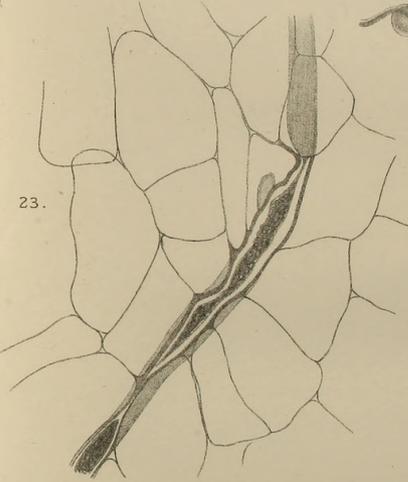
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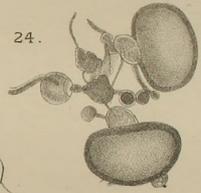
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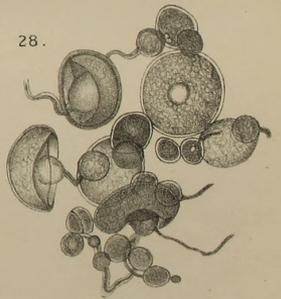
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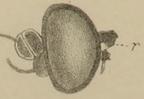
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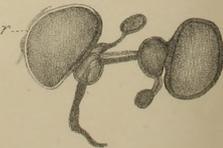
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Magnus, P. 1897. "On some species of the genus *Urophlyctis*." *Annals of botany* 11, 87–96. <https://doi.org/10.1093/oxfordjournals.aob.a088645>.

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