The 'Endoconidia' of Thielavia basicola, Zopf.

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With Plate XXIII and one Figure in the Text.

Introduction.

THIELAVIA basicola, Zopf, is a parasitic fungus well known to plant-pathologists. The ascigerous fruit which is referred to the Perisporiaceae has only once been obtained in pure cultures of the fungus,[1] and with this exception is connected with the other spore forms only by their association on the host plant and a doubtful tracing of continuity of mycelium.

The best known condition of the fungus is the black 'torula' or chlamydospore stage, which was described by Berkeley and Broome [2] as early as 1850.

The interesting 'endospores' escaped attention until a quarter of a century later, when the fungus was very thoroughly investigated by Zopf.[3]

It is with this stage of *Thielavia* that I propose to deal in the present paper.

Zopf describes these spores as being borne on short several-celled conidiophores and formed in acropetal succession. Their lateral walls then differentiate into two layers, of which the outer forms a sheath through which the conidia successively emerge. The cause of their extrusion is presumed to be a mucilaginous middle lamella which swells on access of water and so pushes out the spore.

[1] Peglion, V.: La moria delle piantine nei semenzai. Ricerche intorno ai mezzi de difesa. Staz. Sper. Agr. Ital., vol. xxxiii, fasc. 3, 1900, pp. 221–37.

[2] Berkeley, M. J., and Broome, C. E.: Notices of British Fungi: *Torula basicola.* Ann. and Mag. Nat. Hist., ser. 2, vol. v, 1850, p. 461.

[3] Zopf, W.: *Thielavia*, gen. nov. Perisporiacearum. Verhandl. Bot. Ver. Prov. Brandenburg, j. 18. Sitzungsber. 30. Juni 1876, pp. 101–5. Die Pilze, 1890, pp. 36, 81, 96, 113, Fig. 61. Ueber die Wurzelbräune der Lupinen, eine neue Pilzkrankheit. Ztschr. f. Pflanzenkrankh., Bd. i, No. 2, 1891, pp. 72–76.

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There is some doubt whether at first, perhaps, Zopf regarded the conidia as produced endogenously; but later he discarded as superfluous the term 'Pseudosporangium' for the 'pistolenförmige Conidienbildungen', and apparently considered the peculiar formation of the spores to be correlated with a curious method of liberation.

Since this work much literature has accumulated around the subject, of which the greater part prior to 1909 is cited in the bibliography appended to Gilbert's [1] memoir.

This author, who treats of the morphology of the fungus with more than usual fullness, may be taken as representing the general opinion subsequent to Zopf's investigations. The 'endoconidiophore' consists of a tapering 'endoconidial cell' seated upon a few to several plump barrel-shaped cells. The 'endoconidia' are produced from the copious protoplasm within the terminal cell, which opens by a bursting or dissolution of the tip, and the conidia are slowly pushed out by the growth of the protoplasm in the swollen basal portion of the cell, new conidia being formed continuously in the rear of those being ejected. 'It is sometimes difficult to perceive that the conidia originate within the cell and are not formed by its direct septation.'

According to this interpretation the conidia are produced endogenously within the neck of a phial-shaped cell; and below the latest formed conidium is a naked surface of protoplasm.

Duggar [2] holds a slightly different view. The spores are formed by basipetal septation as short cylindrical cells within the branch. The tip of the latter is finally broken and the conidia are pushed out by osmotic force, the branch assuming the part of a spore-case.

Massee [3] describes the conidiophore as an upright septate branch becoming gradually narrowed above and remaining perfectly colourless. The apical portion becomes ruptured and the contents grow out through the torn apex as a chain of spores.

Professor V. H. Blackman suggested to me that this subject required a thorough investigation, and I am grateful to him for the laboratory facilities he placed at my disposal.

Method.

The differences between natural structure and artifact in fixed and stained preparations of minutiae in Fungi are frequently of so fine and nice a quality that their exact evaluation is very difficult. In the present

[1] Gilbert, W. W.: The Root-Rot of Tobacco caused by *Thielavia basicola*. U. S. Dept. Agric. Bur. Pl. Ind., 1909, Bull. No. 158.

[2] Duggar, B. M.: Fungous Diseases of Plants, 1909, p. 212, Fig. 83.

[3] Massee, G.: A Disease of Sweet Peas, Asters, and other Plants. Bull. Misc. Inform. Roy. Bot. Gard., Kew, 1912, pp. 44–52, Fig. 3. Mildews, Rusts, and Smuts. 1913, p. 50, Pl. XI.

investigation it was consequently felt very desirable to make as many observations as possible upon *Thielavia* in the living condition, and to use fixed material for confirmatory work.

Differential *intra vitam* staining by the prolonged action of very dilute aqueous solutions was largely employed. The fungus was grown principally upon banana or potato media, usually solidified by the addition of one to three per cent. agar; and that for preparation fixed *in situ* with either Bouin's fluid or weak Flemming's fluid. Alum haematoxylin with either acid fuchsin or Congo red was the stain giving the best results.

Origin and Growth of the Conidiophore.

The peculiarly shaped mother-cell or conidiophore arises from the middle region of a cell of the mycelium as a minute protrusion bounded by a very delicate and hyaline membrane. This point of origin, although perhaps not absolutely constant, contrasts sharply with that of an ordinary hyphal branch which is at the anterior end of the cell. Each cell contains a single nucleus which is minute, and appears either as an aggregation of deeply staining granules, or is well defined with granules often in immediate proximity.

An appreciable time after the inception of a conidiophore the nucleus of the parent cell divides, and one of the daughter-nuclei passes into the protrusion. The protoplasm in the latter is clear and has a higher refractive index than the vegetative cell contents. In its development it assumes a slightly curved finger-like form and soon is cut off by a transverse wall immediately above its base. The protoplasm becomes more dense, but rarely granular, and the nucleus occupies a position away from the tip of the cell.

When mature the conidiophore presents an exceedingly characteristic appearance (Pl. XXIII, Fig. 1), being slightly bulbous in its basal portion, and possessing an elongated, tapering, or almost linear apical region. The cytoplasm is often slightly alveolar or flocculent, occasionally minutely granular, and rarely slimy or homogeneous. Large vacuoles are usually present, which, particularly towards the upper region of the cell, not infrequently contain oil-globules. The nucleus lies in the basal portion of the cell.

Formation of Conidia.

The nucleus in the conidiophore apparently divides in a mitotic manner, and one daughter-nucleus remains in the original position, whilst the other passes to the apical region of the cell (Pl. XXIII, Fig. 2). Here the protoplasm shows a barely perceptible increase in density, the vacuoles contract slightly in size and frequently contain a greater number of oil-globules. This apical region containing a nucleus slung in the protoplasmic bridge between two vacuoles is now cut off from the conidiophore by a septum which grows inwards in the form of a ring or diaphragm, finally closing in the centre (Pl. XXIII, Figs. 3–4). The conidium almost invariably contains two vacuoles, thus presenting a very characteristic appearance (Pl. XXIII, Fig. 5 *a*). The oil-globules within the vacuoles may remain discrete, appearing as a cluster of grapes; or fuse to fill the entire vacuole so that it reacts as one large oil-globule; or be present as a fine emulsion within the vacuole. Rarely oil-globules may be found lying freely in the cytoplasm (Pl. XXIII, Fig. 4).

Liberation of the Conidia.

The liberation of the first conidium is brought about by a tangential splitting of its walls, which are thus differentiated into an outer closed sheath and an internal cell (Pl. XXIII, Figs. 5, 5 *a*, and 6). An exhaustive microchemical analysis of the conidiophore prior to this occurrence was carried out, but no layer corresponding to a middle lamella could be detected in the transverse wall, nor any incipient line of splitting in the lateral walls.

Almost simultaneously with its differentiation, the sheath is ruptured at or near its apex, and the enclosed conidium projected about one-quarter to one-third of its length beyond the open mouth of the sheath, appearing like a cork in a phial (Pl. XXIII, Fig. 7). Rarely the rounded tip of the sheath is torn away and may be observed fitting as a tiny cap on the end of the protruding conidium (Pl. XXIII, Fig. 7 *a*).

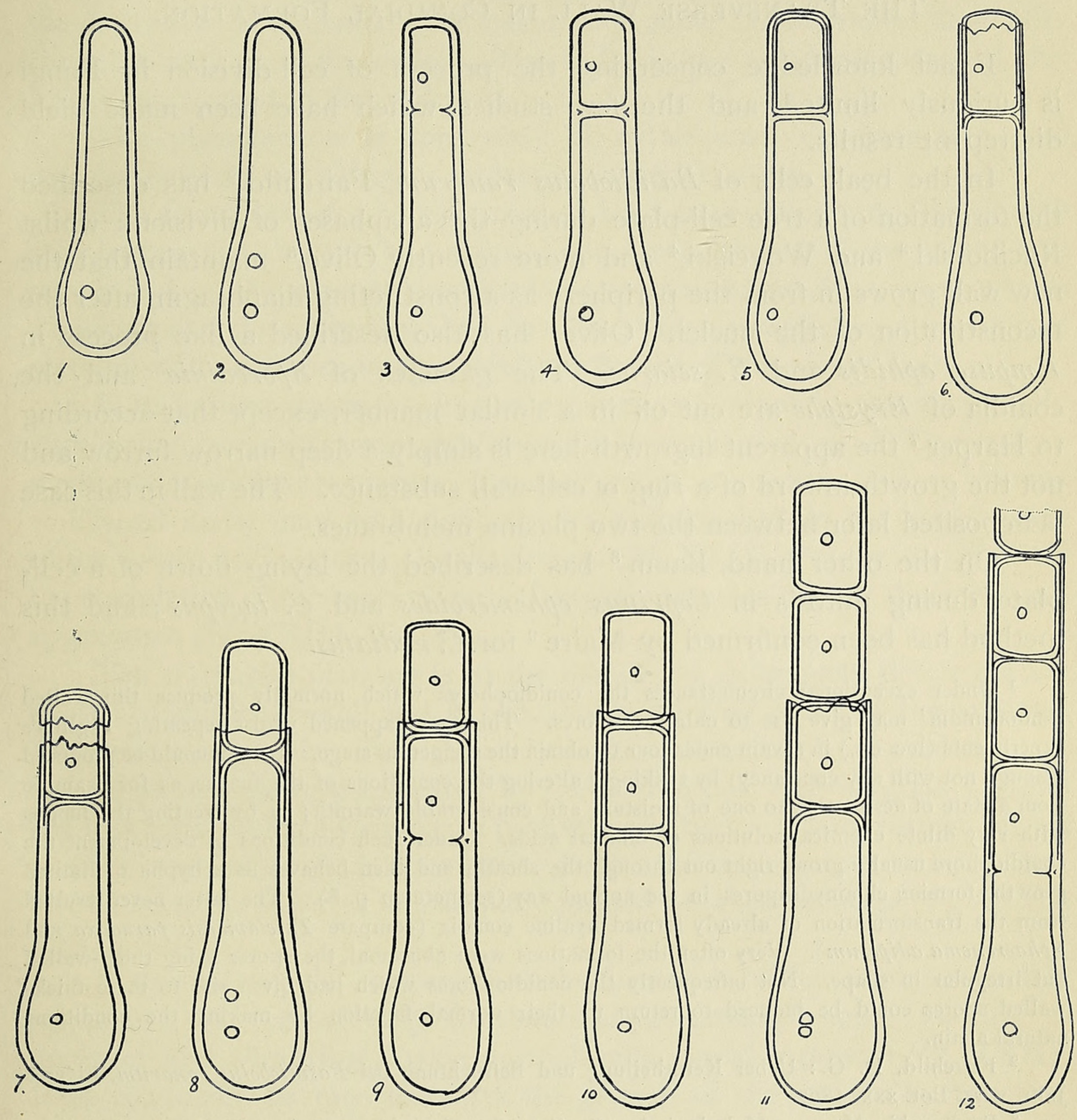
The protoplasm in the conidiophore is thus not naked at its apical surface, but bounded and separated from the sheath by a very hyaline and delicate transverse wall (Pl. XXIII, Fig. 7) whose thickness is one-half that of the normal cell membrane. This wall, which has been overlooked in all previous work, now becomes convex to the spore, and, owing to the growth of the conidiophore up through the sheath, pushes out the first conidium.

Meanwhile the nucleus in the conidiophore again divides, one daughter-nucleus passing to the apical region (Pl. XXIII, Figs. 5, 8, 9), which is then cut off as the second conidium, by a transverse wall formed in the manner already described. This wall is always immediately below the original position of the first wall, and when it is differentiated into two layers, the line of splitting being in the same tangential plane and meeting that between the conidium and the sheath, liberates the spore.

The latter is pushed out in the rear of the first by the development of the subsequent conidia, which are formed in like manner (Pl. XXIII, Figs. 5, 8, 9).

The conidia thus possess cell membranes which are only one-half the thickness of a normal cell-wall, this also being true of the sheath and elongating apical region of the conidiophore (Pl. XXIII, Fig. 7). Except in early conidial formation the latter membrane is not easy to see, owing to the browning and increasing opacity of the sheath.

It will be noted that the development of each transverse wall adds a minute fraction to the length of the sheath. In consequence early conidial



TEXT-FIG. 1. Uninucleate conidiophore. 2. The nucleus divides and one daughter-nucleus passes to the upper end of the cell. 3. A transverse wall develops as an ingrowing diaphragm cutting off the upper region of the conidiophore. 4. The first conidium is delimited. 5. The wall of the conidium differentiates into two layers. 6 and 7. Rupture of the sheath and liberation of the conidium. 8 and 9. Formation of the second conidium. 10. Liberation of the second conidium. 11. Formation of the fourth conidium. 12. Late conidial formation at base of long sheath.

formation occurs at the base of a short sheath; whilst later it appears to take place some considerable distance within the neck region of the conidiophore, in reality at the base of a long sheath (Pl. XXIII, Figs. 8, 9). The latter therefore contains several spores at once, thus giving the appearance of an active free cell formation occurring within an open tapering mother-cell or conidiophore.[1]

The process of conidial formation and liberation is diagrammatically represented in the Text-figure.

The Transverse Wall in Conidial Formation.

Exact knowledge concerning the process of cell-division in Fungi is curiously limited, and the few studies which have been made yield discrepant results.

In the beak cells of *Basidiobolus ranarum*, Fairchild [2] has described the formation of a true cell-plate during the anaphases of division ; whilst Raciborski [3] and Woycicki,[4] and more recently Olive,[5] maintain that the new wall grows in from the periphery as a constricting diaphragm, after the reconstitution of the nuclei. Olive [6] has also described a like process in *Empusa aphidis* and *E. sciarae.* The gametes of *Sporodinia* and the conidia of *Erysiphe* are cut off in a similar manner, except that according to Harper [7] the apparent ingrowth here is simply a deep narrow furrow and not the growth inward of a ring of cell-wall substance. The wall in this case is deposited later between the two plasma membranes.

On the other hand, Baum [8] has described the laying down of a cell-plate during mitosis in *Coprinus ephemeroides* and *C. lagopus* ; and this method has been confirmed by Maire [9] for *C. radiatus.*

[1] Under exceptional circumstances the conidiophores which normally produce thin-walled 'endoconidia' may give rise to chlamydospores. This first happened whilst repeating Peglion's experiments (loc. cit.) in a vain endeavour to obtain the ascigerous stage. Later it could be produced (though not with any constancy) by strikingly altering the conditions of the fungus, as for example from a state of desiccation to one of moisture and considerable warmth; or by treating the fungus with very dilute chemical solutions or mineral acids. Under such conditions of development the conidiophore usually grows right out through the sheath, and then behaves as a hypha of limited growth, forming chlamydospores in the normal way (see note on p. 8). The latter never resulted from the transformation of already formed hyaline conidia (compare *Thielaviopsis paradoxa* and *Sphaeronema adiposum*). Very often the formations were abnormal, the spores being thick-walled but irregular in shape. Not infrequently the conidiophores which had given rise to these thick-walled spores could be induced to return to their normal function by making the conditions natural again.

[2] Fairchild, D. G.: Ueber Kerntheilung und Befruchtung bei *Basidiobolus ranarum*, Eidam. Jahr. wiss. Bot. xxx 1897.

[3] Raciborski, M.: *a*. Mykologische Studien, I. Karyokinese bei *Basidiobolus ranarum*, Eidam. Bull. Internat. de l'Acad. des Sci. de Cracovie, 1896. *β*. Studya mykologiczne; Berichte der Akad. d. Wiss. zu Krakau, XIV. 2, 1899.

[4] Woycicki, Z. : Einige neue Beiträge zur Entwicklungsgeschichte von *Basidiobolus ranarum*, Eidam. Flora, 1893.

[5] Olive, E. W.: Cell and Nuclear Division in *Basidiobolus.* Ann. Mykol., vol. v, 1907.

[6] Olive, E. W. : *a*. Cytological Studies on the Entomophthoreae, I. The Morphology and Development of *Empusa.* *β*. Cytological Studies on the Entomophthoreae, II. Nuclear and Cell Division in *Empusa.* Bot. Gaz., vol. xli, 1906, I.

[7] Harper, R. A. : Cell Division in Sporangia and Asci. Ann. of Bot., vol. xiii, 1899.

[8] Baum: Über Zelltheilungen in Pilzhyphen. Inaug. Diss. d. Universität Basel, 1900.

[9] Maire, R. : Rech. cytol. sur les Basidiomycètes. Bull. Soc. Myc. de France, 1902.

Faull,[1] working on *Laboulbenia chaetophora* and *L. gyrinidarum*, figures a delicate sheet of granules appearing across the diameter of the filament after the reconstitution of the nuclei. This becomes a definite cell-wall with a middle lamella.

In the conidiophore of *Thielavia* the transverse wall is formed by the ingrowth of a constricting membrane some considerable time after the reconstitution of the nuclei. The walls in the chlamydospores of this fungus are formed in like manner.

The phenomenon is apparently of cytoplasmic determination, and merely remotely or indirectly subject to nuclear control.

The formation of a transverse wall by a constricting ring-like growth may be brought about in two ways. The inner laminae of the parent wall may infold in the manner described for certain Algae;[2] or, as occurs in *Thielavia* and the cases described by Olive,[3] by a progressive deposition of new cell-wall substance upon a localized surface of the parent wall.

In its earliest stages the septum appears as a minutely granular, barely visible ring, becoming imperceptible at its ingrowing edge. With development its peripheral margin becomes more apparent, and a minute <-shaped mark may with difficulty be distinguished in the middle line of the parent wall opposite the diaphragm (Pl. XXIII, Figs. 3, 3 *a*, 8). On the completion of the septum the wall rapidly assumes normal thickness and appearance (Pl. XXIII, Fig. 4).

The >-shaped marking is in the line of the subsequent differentiation of sheath and inner wall and is probably a splitting apart of the laminae. The most careful microchemical analysis failed to reveal it as a substance.

In certain cases investigated by Olive[4] the new wall invariably grows inwards, constricting a vacuole; a protoplasmic bridge is later thrown across, and the completion of the membrane divides the vacuole into two portions. In *Thielavia* the new wall is invariably formed between vacuoles (Pl. XXIII, Figs. 3, 3 *a*).

In normal conidial development the formation of the transverse wall is complete; but occasionally in abnormal specimens a pore varying in diameter and admitting a wide protoplasmic strand is present (Pl. XXIII, Figs. 10, 10 *a*). In rare instances the growth of the septum is such that it bears striking resemblance to the lamellose plugs of *Codium* (Pl. XXIII, Figs. 11, 11 *a*).

It is interesting to note that in the transverse walls separating the chlamydospores, a single central pit is present. This, which is figured by

[1] Faull, J. H.: The Cytology of *Laboulbenia chaetophora* and *L. gyrinidarum*. Ann. of Bot., vol. xxvii, 1912.

[2] Brand, F.: Über Membran, Scheidewände und Gelenke der Algengattung *Cladophora*. Festschr. der Deutsch. Bot. Ges., 1908, where the literature is cited.

[3] Olive, E. W.: loc. cit., 1906.

[4] Olive, E. W.: loc. cit., 1906.

Zopf but overlooked by nearly all later observers, is always closed by a middle layer of cell-wall substance.[1] Rarely a pitted transverse wall, apparently affording protoplasmic continuity, could be distinguished in the vegetative hyphae.

Discussion.

The development of 'endoconidia' is a process distributed sparingly but widely in the Fungi; and examples have been repeatedly described. In consequence the extensive literature on the subject is very scattered, and the synonymy of the forms has become greatly confused. Such species belonging to more than thirty genera are known, but it is probable that these may all be legitimately included in the following genera [2]—*Helotium*, *Sordaria*, *Phialea*, *Thielavia*, *Pyxidiophora*, *Sphaeronema*, *Thielaviopsis*, *Sporoschisma*, *Chalara*, *Cytosporella*, *Alternaria*, *Endoconidium*, *Hymenella*, *Bloxamia*.

A critical consideration and analysis of the published figures and descriptions, and in many cases of the Fungi themselves, showed an extraordinary similarity of form and, structure, size, and, where known, developmental details.

This likeness is so fundamental and complete as to nullify the discrepant accounts of the several authors, and, considering the extremely stereotyped character of the few methods of spore production known in Fungi, almost to preclude the doubt that possibly more than one process of development may be responsible.

[1] According to Zopf the chlamydospores are exogenous and their walls laid down simultaneously in the hypha (Simultane Scheidewandbildung, loc. cit., 1890): whilst Duggar states (loc. cit., p. 212) that their 'early stages of formation differ only in size from the endospores'; that is, they are endogenous and formed by basipetal septation. (Compare *Thielaviopsis paradoxa*, *Sphaeronema adiposum*.) My observations show that the spores are formed successively as thin-walled, barrel-shaped cells during the development of a hypha of strictly limited growth. They remain in this condition for some time and then gradually and simultaneously thicken their walls. It is after the walls have attained their mature thickness that the brown to black colouring matter is deposited. A slight 'lagging' in this latter process is apparent in those cells towards the apex of the chain. Frequently one to three or four cells at the base and rarely one or two at the apex remain thin-walled and colourless. Gilbert (loc. cit.) terms these the sterile segments; but I have frequently found them capable of immediate germination like the 'endoconidia'. This is interesting because the thick-walled chlamydospores will only germinate after a period of rest, in my experiments not less than ten weeks. This period may be very considerably shortened and even eliminated by subjecting the spores to a freezing process, to the action of dilute mineral acids, or of gastric juice. It is to be noted that in the case of gastric juice it is the acid and not the pepsine which renders premature development possible, the latter of itself having no effect on germination.

[2] See Additional Literature. Those Fungi which may be referred to the genera *Psiloniella*, *Glycophila*, *Sporendonema*, *Malbranchea*, and *Conioscypha* are not included in this list. In these cases what has been described as 'endoconidial formation' is better termed 'aplanospore formation', for each cell of the filament gives rise by rejuvenescence to a spore. Liberation occurs by the rupture of the mother-cells or the breaking down of the entire filament. The confusion has arisen by the frequent occurrence of this mode of spore formation in hyphae of limited growth, such that an appearance simulating an 'endoconidial cell' with a chain of spores is produced.

In only two or three cases has the mode of spore formation been developmentally observed, and then in but a cursory manner. On the other hand, in practically all, an endogenous origin of the spores by free cell-division within the 'endoconidial cell' has been assumed.

The more accurately these Fungi have been investigated the more irreconcilable are the facts with any hypothesis having a true and continuous endogeny as its basis, and the more exactly do they accord with the interpretation I have given of the process of spore formation in *Thielavia*. This latter is not one of endospory or endogeny, and the terms 'endoconidium', 'endoconidial cell', and 'endoconidiophore' are misnomers. The formation of conidia is a process of acrogenous abjunction ('acrogene Abgliederung'[1]), and it is only in the mechanism of their liberation that the peculiar character of these Fungi is seen.[2]

SUMMARY.

The conidia of *Thielavia basicola* are not endospores formed by free cell-division within an endoconidial cell. They are acrogenously abjointed from the conidiophore.

The first conidium is liberated by the differentiation of its walls into an inner wall and a sheath, and by the rupture of the latter at its apex.

The later conidia grow out through the sheath of the first, and are freed by the splitting of their basal walls.

The formation of the transverse walls is by the ingrowth of a ring of cell-wall substance which finally closes in the centre.

The process of conidial development seen in *Thielavia* is probably that of all 'endoconidia' in Fungi.

[1] de Bary, A.: Comp. Morph. and Biol. of the Fungi, &c., 1887, p. 61.

[2] It is interesting to note that neither de Bary (loc. cit.) nor Zalewski (Ueber Sporenabschnürung und Sporenabfallen bei den Pilzen, Flora, 1883) mentioned these forms, although certain of them were well known at the time.

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EXPLANATION OF PLATE XXIII.

Illustrating Mr. Brierley's paper on *Thielavia*.

The figures were drawn with the aid of a Zeiss camera lucida. A Zeiss 2 mm. apochromatic 1·4 objective was used with a × 12 compensating ocular (Fig. 7), a × 18 comps. oc. (Figs. 3*a*, 5*a*, 10*a*, 11*a*), and a × 6 comps. oc. (remaining Figures).

Abbreviations used :—*c.* = conidiophore ; *n.* = nucleus; *v.* = vacuole; *o.* = oil-globule; *p* = protoplasmic strand; *s.* = transverse wall; *sh.* = sheath ; *sc.* = sheath cap; *spl′.* = <-shaped marking outside transverse wall; *spl.* = line of differentiation of sheath and spore wall.

Figs. 1–4. Formation of the first conidium.

Fig. 1. Mature conidiophore.

Fig. 2. The nucleus divides and one daughter-nucleus (*n′.*) passes to the apex of the conidiophore. Specimen slightly plasmolysed.

Fig. 3. Formation of the transverse septum as an ingrowing ring of cell-wall substance.

Fig. 3*a*. Details of above more highly magnified.

Fig. 4. The completion of the transverse wall has cut off the first conidium.

Fig. 5. The walls of the conidium differentiate into two layers, the splitting being in the line of the <-shaped marking.

Fig. 5*a*. Details of above more highly magnified.

Fig. 6. A specimen strongly plasmolysed to show more clearly the differentiation of the walls of the conidium (reduced by one-half).

Fig. 7. The tip of the conidiophore shortly after the liberation of the first conidium.

Fig. 7*a*. The sheath, ruptured below the apex and its tip borne away on the conidium. It is interesting to note that in this case the conidiophore is the germ tube of a conidium.

Fig. 8. Late formation of conidia at the base of a long sheath.

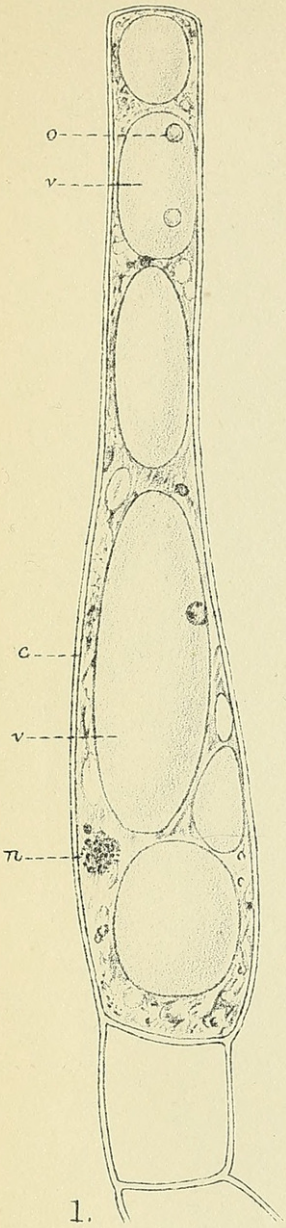
Fig. 9. A similar stage in which the conidia have been removed to show the sheath.

Fig. 10. Abnormal development of transverse wall, leaving a wide protoplasmic strand. Specimen much plasmolysed to show relations of walls.

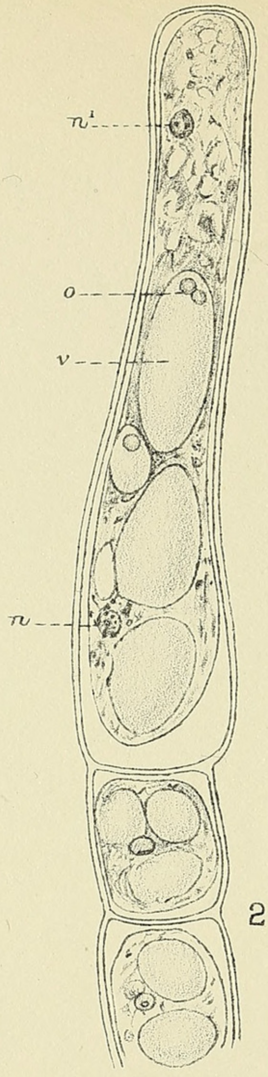
Fig. 10*a*. Details of above more highly magnified.

Fig. 11. Abnormal development of transverse wall resembling lamellose plugs of *Codium*.

Fig. 11*a*. Details of above more highly magnified.



1.



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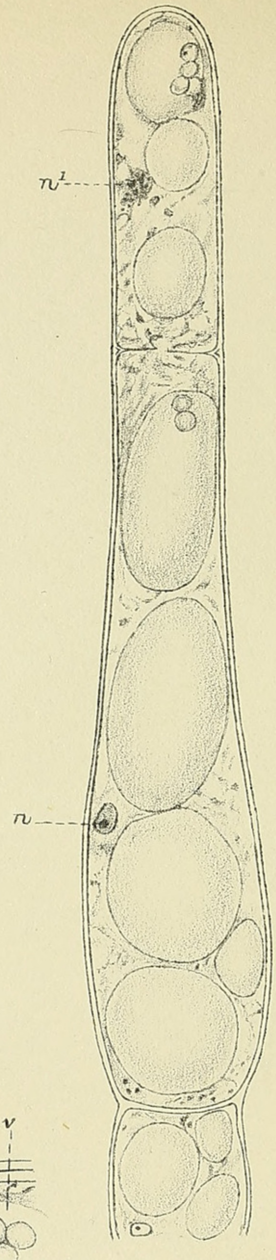

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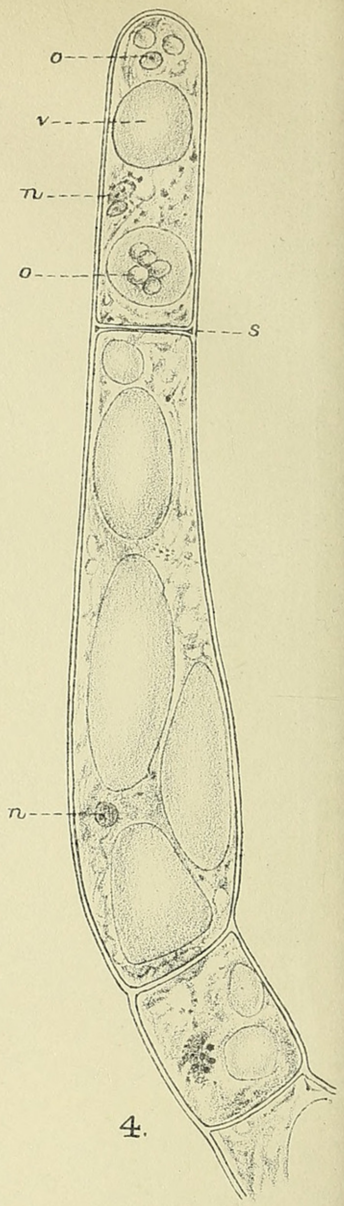

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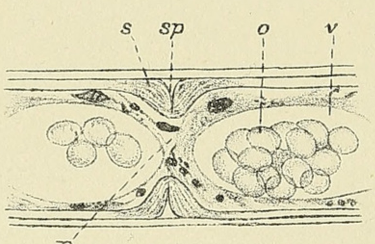
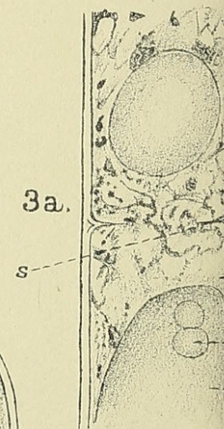
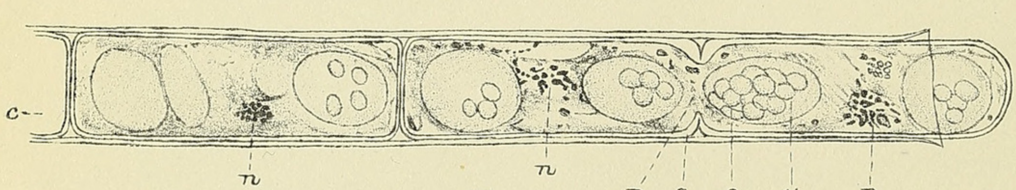


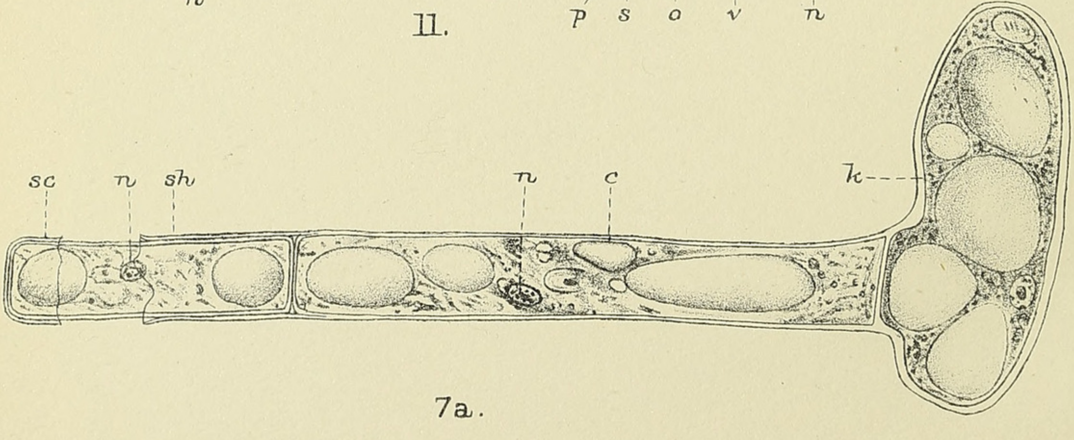
11a.



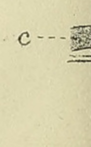
3a.



11.

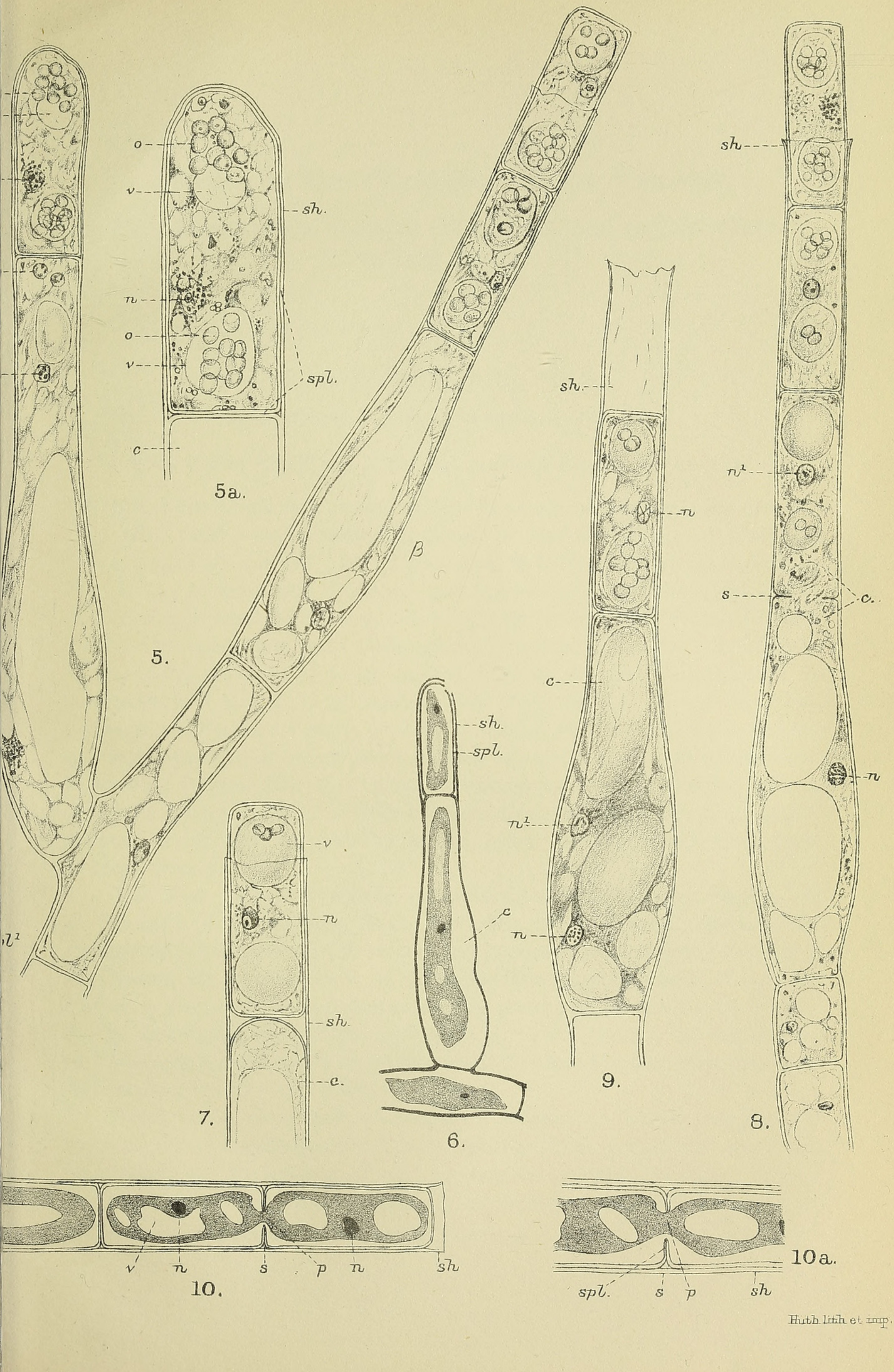


7a.

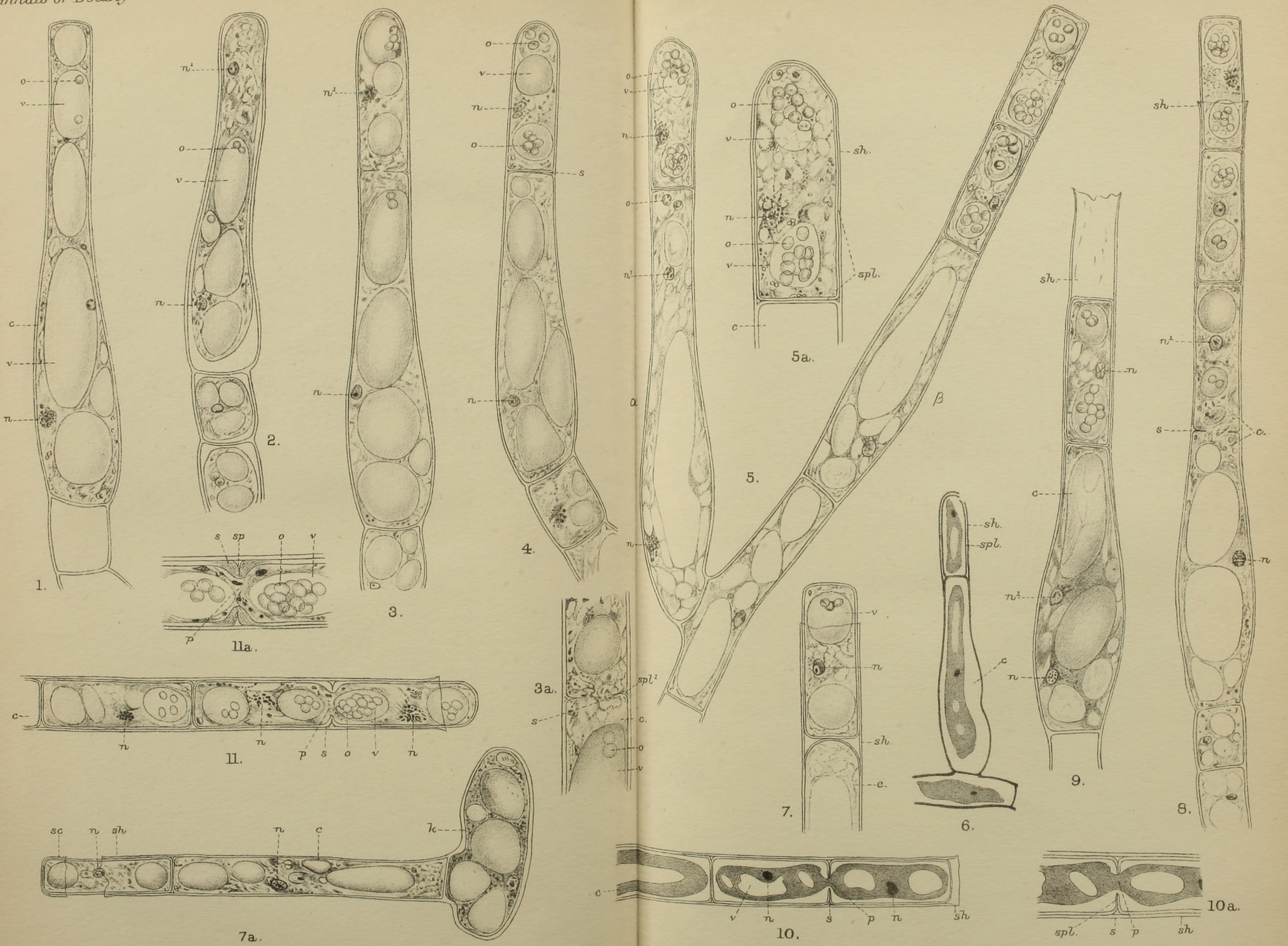


W.B.B. del.

BRIERLEY — THIELAVIA BASICOLA.



Huth lith. et imp.


1.
2.
3.
3a.
4.
5.
5a.
6.
7.
7a.
8.
9.
10.
10a.
11.
11a.