IX.—On a Species of Rhizophydium Parasitic on Species of Ectocarpus, with Notes on the Fructification of the Ectocarpi. By Edward Perceval Wright, M.A., M.D., F.L.S.; Professor of Botany in the University of Dublin; Secretary to the Royal Irish Academy. [With Plate III.]

[Read, February 12, 1877.]

The genus Chytridium was established by Alexander Braun, in his very interesting treatise on "Rejuvenescence in Nature," published about 1850, for some unicellular parasitical Algæ, found while working out the development of Hydrodictyon utriculatum. He thus describes it:* "The Chytridia form a new genus of unicellular, parasitical Algæ, or, if it be preferred, of aquatic Fungi. The entire plant is composed of a single balloon-shaped cell, which penetrates into the Alga upon which it grows by a more or less developed root-like base. The inflated portion of the cell is filled with colourless mucilage, from which are formed, not through successive division, but by a simultaneous process, very numerous small globular germ-cells, which exhibit a sharply-defined darker nucleus in their interior, and possess a single very long cilium. From their want of colour, and the activity of their motion, these gonidia resemble the most minute monads. Their extrusion occurs either through the casting off of a lid, or through the mere tearing off of a nipple-shaped point."

The first species described was found parasitic on Hydrodictyon utriculatum,

^{*}A. Braun, "Beobachtungen ueber die Verjüngung in der Natur," Freiburg, 1844; Zweiter Abdruck, Leipsig, 1850; or "The Phenomenon of Rejuvenescence in Nature, especially in the Life and Development of Plants," translated by A. Henfrey, in "Botanical and Physiological Memoirs," published by the Ray Society, 1854, p. 185.

gathered about 1846 at Freiburg; and in a memoir* on the genus, published about 1856, he described and figured some twenty-one species, the greater number of which were found in freshwater Algæ. The genus Chytridium was divided provisionally by Braun into four sub-genera—Enchytridium, Phlyctidium, Sphærostylidium, and Olpidium. As was anticipated by Braun, further research discovered many more new species, and the family Chytridiaceæ now contains a very numerous array of genera. Pfitzer† places the Ancylisteæ, Saprolegniaceæ, and Peronosporeæ, in an order called Phycomycetæ. The discovery, however, of a true conjugation in Polyphagus Euglenæ by Dr. Nowakowski, and in Zygochytrium aurantiaceum by N. Sorokin, § would seem to separate the Chytridiaceæ altogether from the oospore-producing Thallophytes, and to place them among the Zygosporeæ; that is, however, dependent upon two quite possible events—first, that this form of reproduction may not be the rule in all the genera of Chytridiaceæ; and, secondly, that forms may be met with connecting these two sections. The time has certainly not come for a classification of the genera and species.

Until very recently most of the species were found living in the cells of freshwater Algæ, or in the tissues of terrestrial plants. Professor Cohn, however, has described some species living in the cells of marine Algæ—one of which, *Chytridium Polysiphoniæ*, was found parasitic in *Polysiphonia violacea*. In describing it, Cohn calls attention to the fact that the occurrence of Chytridial forms in Algæ has often given rise to many erroneous conclusions, their parasitism not being understood, and they themselves

^{*} A. Braun, "Ueber Chytridium, eine Gattung einzelliger Schmarotzergewächse auf Algen und Infusorien." Monatsbericht der Königl. Akademie der Wissenschaften zu Berlin, Juni 1855; and Abhandlungen der Königl. Akad. der Wissenschaften zu Berlin aus dem Jahre 1855, s. 21.

[†] Ernest Pfitzer, Monatsbericht der Königl. Akad. d. Wissensch. zu Berlin, 1872, s. 398.

[‡] Leon Nowakowski, "Ucber *Polyphagus Euglenæ*;" in Cohn's Beiträge zur Biologie der Pflanzen. Bd. ii., s. 201.

[§] N. Sorokin, "Einige Neue Wasserpilze," Botanische Zeitung, No. 20, 15 Mai, 1874, s. 305.

being looked on as a part of the absolute tissue of the host-plant. Professor Cohn writes: " " Das Solier und Derbés die Zoosporen von Chytridien mit den Samenkörperchen von Florideen verwechselt haben, geht mir unzweifelhaft aus ihrer Beschreibung und Abbildung bei Aglaophyllum ocellatum hervor.† Hier wird offenbar ein auf dem Thallus des Aglaophyllum aufsitzendes Chytridium dargestellt, von kuglicher Form mit grauem feinkörnigem Inhalt (fig. 10a), der sich in 'granules animés d'un mouvement très manifest' umgestaltet. Es wird nun geschildert, wie diese Körperchen einzeln oder in Masse austreten, und sich allmählich mit Hülfe einer nachschleppenden Giessel gewaltsam, nach Art von Monaden, nach allen Richtungen zerstreuen. Nach den Figuren, Pl. XXI., 10a, und 11b, zu schliessen, scheint das auf den männlichen Exemplaren von Aglaophyllum beobachtete Chytridium mit meinem Ch. Polysiphoniæ identisch." Another species, Ch. (Phlyctidium) plumulæ (Cohn), was found in the cells of Antithamnion plumula (Thuret); and without expressing any very positive opinion on the subject, I would venture to suggest that the presence of this parasite has been the cause why Dasya spongiosa, Ag.—which, according to Kützing, "Keine Dasya ist"—has been elevated to the rank of a genus, and is called by him Phlebothamnion Faroense.;

In all probability, too, the thickened excrescences on the points of the trichomes ("an der spitze verdickten auswüchsen") in Acanthoceros Shuttleworthiana, figured by Kützing, § are also chytridial growths.

To Professor Magnus we are indebted for recently calling attention in some detail to this subject. In his "Botanische Ergebnisse der Nordseefahrt," he refers the abnormally swollen-up apical cells met with in Ceramium spiniferum (Kütz.), gathered at Naples, and figured by Cramer, to

^{*} F. Cohn, "Beiträge zur Physiologie der Florideen," Mac Schultze's Archiv für Mikroskopische Anatomie. Bd. iii., s. 41, 1867.

[†] Capt. Solier et Dr. Derbès, "Mémoire sur la Physiologie des Algues," p. 67, Pl. XXI., figs. 10-12.

[‡] Kützing, "Tabulæ Phycologicæ," vol. xiv., Tab. 83.

[§] Kützing, loc. cit., vol. xii., Tab. 96.

^{||} Magnus in Jahresbericht der Commission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel, fur die Jahre 1872–1873; Berlin, 1875.

his new species of Chytridium, Olpidium tumefaciens (Mag.). When noticing the occurrence of *Chytridium plumulæ* he points out some peculiarities in the habit and form of this species, which appeared to him to justify its being placed in a new section of Braun's genus, which he calls Cyphidium, and he calls attention to a number of cases in which Kützing figures this parasite as "intercellular spores" of various species of Callithamnion. Professor Harvey himself, according to Professor Magnus, figures identically the same species of Chytridium, as possibly the Antheridia of Callithannion dispar (Harvey);* and much more recently Grunow has evidently taken the same parasitic form for true spores, and so placed a species of Callithamnion from Gibraltar in the genus Sporocanthus. To these observations recorded by Magnus it would be easy to add; and it appears to me that the very same form given by Grunow† in his figure 3 is also to be seen in the side cells of his Polysiphonia dendritica, figures 4b and 4c; and the cells filled with spores figured Tab. iv., 3c, by the same author, may possibly, instead of being the true spore cases of *Leda capensis* (Grunow), prove to be Chytridia.

Professor Magnus refers the abortive spore-mother-cells described and figured by Nägeli (Die Neuern Algensysteme, Zurich, 1847, p. 202, Tab. vi., fig. 1, s, s: 4, s, s) in Callithannion cruciatum to the Chytridium plumulæ (Cohn); and it appears to me that it is the same parasite that is described and figured by Nägeli, some years later, in his "Researches," as occurring in the very same species of Callithannion as that examined by Cohn: "a peculiar appearance on the ramulus of Pterothannion (Call) plumula must still be mentioned; on the primary, as well as on the secondary ramuli, will be found semi-spherical cells appearing somewhat elongated when seen

^{*} On Plate CCXXVII. of Professor Harvey's "Phycologia Australica," vol. iv., 1862, the author figures (fig. 4) a ramulus of this species, which is referred to in the explanation of the Plate as bearing "Antheridia." As the figure is not at all characteristic, I have thought it well to give a drawing of a ramulus, with the parasite, from the very specimen of the Callithannion figured (Plate II., fig. 3); and I confess that I am inclined to think that the affinities of this and other parasitic forms nearly allied to it may be with Synchytrium rather than Chytridium. In another memoir I hope to recur to this subject.

[†] Grunow, Reise S. M. F. Novara um die Erde. Botanik, Th. 1. Algen., Tab. vi.

from above; these are generally colourless, and filled with a brownish protoplasm (Tab. vii., fig. 2 m). They are located towards the upper and inner side of the cell from which the twigs proceed. They invariably remain unicellular and solitary."*

As long as the Florideæ were studied only by the examination of dried, and more or less altered specimens preserved in Herbaria, it was not very surprising that such parasitic forms should now and then be described as being only forms of fructification; but the day would seem past when the Algæ can be studied otherwise than as living plants; and the researches of Thuret, Cohn, Bornet, Magnus, and others, show that there is much still left to reward the patient labour of many a student in this field.

While on a living specimen of any Red Alga the presence of a Chytridium is not easily overlooked, it is quite otherwise when these parasites occur on or in the tissue of the brown coloured Phæosporeæ. One species, Chytridium (Olpidium) Sphacelarum (Kny.), is already known as parasitic in the trichomes of species of Sphacelaria and Cladostephus; and I have here to describe another, the discovery of which will probably have some bearing on the history and classification of the species of that difficult genus, Ectocarpus; for, under certain circumstances, I feel sure that the Chytridial cells have been described as utricular fruit.

There is some little difficulty in deciding to which of the now numerous genera of the Chytridiaceæ this new species should be referred. Braun's genus Phlyctidium has been now limited to those forms in which the spores escape by a single aperture; and Schenk has established the genus Rhizophydium for those forms in which the spores escape by two or more apertures, as in Rhizophydium laterale, found on Ulothrix zonata; and here I would venture provisionally to place my new species—only provisionally however—because, though the discharge of the zoospores often does take place by means of two slightly oblong apertures, yet I have seen specimens on which the whole of the spores managed to escape

^{*} Nägeli, C. und Cramer, C.: Pflanzenphysiologische Untersuchungen. Heft 1, von Nägeli, Zurich, 1855; the chapter on the "Wachsthumsgesichte von Pterothamnion plumula und P. floccosum," s. 64, Tab. v.-vii.

through a single opening. The following may serve as a brief diagnosis of the species:—

RHIZOPHYDIUM DICKSONII (spec. nov.).

Unicellular; at first quite globular in shape; but during growth becoming very irregular in form, often assuming quite an oblong shape; living in the cells of *Ectocarpus granulosus*, and frequently distorting its filaments. The numerous zoospores make their escape through one or two apertures.

Parasitic in the cells of *Ectocarpus granulosus*, and occurring in great numbers; gathered at Howth, near Dublin, during the winters of 1876, 1877.

I have called this interesting form after my friend Alexander Dickson, M.D., the distinguished Professor of Botany in the University of Glasgow.

The specimens, when first met with in October, 1876, were numerous, but of small size, scarcely filling the cells of the Ectocarpus, and I at once concluded that I had met with the utricular form of fruit said to occur in this species. While watching the gradual development of the zoospores, I became aware that on the same filaments of the Ectocarpus certain of the cells were gradually becoming altered into the form of fruit described and figured by Thuret,* as found by him in Ectocarpus firmus, J. Ag. (E. littoralis, Harvey).

Remembering Thuret's statement about the zoospores of the two forms of fruit in the Ectocarpi, called by him Oosporangia and Trichosporangia—"Les zoospores issus de ces deux organes offrent une parfaite ressemblance. Seulement ceux qui proviennent des sporanges filamenteux sont un peu plus grands que ceux qui s'échappent des sporanges ovoides. J'ai vu d'ailleurs germer les uns et les autres, ce qui prouve suffisament leur complète identité"†—I determined in the present case to watch the development and escape of the spores. Those of the round utricle-like cells, which I took for Thuret's Oosporangia, ripened first. The colourless protoplasm, to use almost Braun's words, started not by a successive division, but by a simulta-

^{*} Thuret, "Recherches zur les zoospores des Algues," Annales des Sciences Naturelles, Troisième Sèrie. Botanique. Tome 14, 1850. Planche 24, V., figs. 5, 6.

[†] Thuret, loc. cit., p. 236.

neous process, into a great number of small globular spore-cells, which exhibited a sharply-defined dark nucleus in their interior; after a short interval the outline of the cell changed; sometimes it protruded itself into a wide funnel-shaped projection, which stood out from the edge of the filament of the Ectocarpus, and the apical portion of this neck-like process frequently divided into two circular openings—sometimes but one appeared and through these the zoospores with one long cilium escaped (Plate VI., figs. 1, 2, 3, and 4). There could no longer be any doubt but that I was wrong in taking these unicellular forms for true fruits (Oosporangia) of the Ectocarpus, and there was just as little that I had a species of Chytridium living parasitic in and on its cells. A few days later, the Trichosporangial fruits also ripened, and their spores made their exit through small openings in the upper corner of each cell-wall, the whole mass first issuing out from the cell by a process quite unaccountable; then quiescent for a second or two after its exit, the thin surrounding pellicle of protoplasm seemed to give way, and the numerous zoospores flew off quite wildly in every direction. These spores were unmistakeably the true normal biciliate spores of the fruit-cells of the Ectocarpus.

The question now naturally arose:—If these Chytridial cells were mistaken by me for Oosporangia—for of their nature, in the present instance,. I could have no doubt, though it is true that I have not seen the spores germinate—could others have equally misconceived their nature?

Of the British species of Ectocarpi enumerated by Harvey, in his "Phycologia Britannica," as possessing a fruit called by him "utricles or spores," and which have been taken to be the same as Thuret's Oosporangia, we find the four following:—

Ec. crinitus (Carm.)—"Spores (which I have only seen in a young state) globose, scattered, sessile;" but in another place he writes, "though I have repeatedly examined several parts of the very specimens collected by Captain Carmichael, I have not been able to detect the fructification described by him, save in a single instance that I chanced upon the young spore represented on Plate CCCXXX., fig. 3."

E. pusillus (Griffiths), near Ec. crinitus (Carm.)—"but differing in its

greener colour, larger size, and more especially in the form of its fruit, which is roundish, oblong, sessile, or subsessile, very elliptical, frequently opposite" (Plate CLIII., fig. 3).

E. granulosus (Ag.)—" Utricles elliptical, dark-coloured, with a narrow limbus, sessile on the upper faces of the ramuli, near to E. sphærophorus and E. brachiatus" (Plate CC.).

E. sphærophorus (Carm.)—" Spores spherical, dark olive, with a pellucid border, sessile, borne on the sides of the branches opposite to each other, or to a ramulus; each spore in fact occupying the normal position of a ramulus, and substituted for one in fertile specimens" (Plate CXXVI.).

In all these species the utricles are represented as out-growths from individual cells which form the filaments of the different species of Ectocarpus, and though nowhere called Oosporangia by Harvey, have been recognised as such. (The Parts of the "Phycologia Britannica" were nearly all issued at the time of the appearance of Thuret's Memoir.)

There are great difficulties in the way, however, of understanding what was meant by the term "utricle." So far as I can judge, Harvey believed a utricle to be a spore-case, giving rise to a single spore.

J. G. Agardh,* when describing the fructification in this genus, says: "Fructus duplex (?) 1. Sporæ (? aut sporidia) intra perisporium hyalinum sphæricum aut ovatum ad ramos sessile contentæ; 2. Sporidia, motu prædita;" and then he proceeds to describe the pod-like Propagula. Further on he defines these Sporidia as "Capsulæ sphæricæ aut ellipsoideo-ovatæ," with either a single or numerous spores. He has also seen spores emitted from many species of Ectocarpi "motu prædita;" but "ex qua vero parte frondis erupta erant, sive e propagulis, sive ex articulis ipsis frondis, detegere non potui."

Thuret writes:† "La seule fructification que l'on signale dans ces plantes [Phéosporées] consiste en sporanges ovoides (Oosporangia, Nobis), qui ont d'ailleurs été toujours décrits comme des spores simples, quoique en réalité ils soient remplis de nombreux zoospores. Cet organe est le plus

^{*} J. G. Agardh, Species, Genera, et Ordines Fucoidearum. Lundæ, 1848, p. 14. † Thuret, loc. cit., p. 235.

visible,* et c'est ce qui explique pourquoi il a surtout attiré l'attention des observateurs." He then proceeds to describe the Trichosporangia, which he figures in *Ectocarpus siliculosus* (Lyngb.); and in *E. firmus* (J. Ag.).

I am unable to understand what Thuret means by stating that the zoospores of the Trichosporangia are exactly like those from the Oosporangia; and another difficulty has evidently presented itself to Professor Areschoug, who, in a note to *Ec. firmus* (J. Ag.), while mentioning† that he finds on this plant at different seasons both the forms of fruit figure d by Thuret, adds: "Illa nobis videtur Oosporangia seriata, hee trichosporangia utraque in medio ramulo immersa." Areschoug also records both forms of fructification as met with in *E. fasciculatus*. In this same species Kützing figures (Tab. Phyc., vol. v., Plate 50, II.) unilocular forms of fruit as "spores," and multilocular forms of fruit as "spermatoidia."

Gobi‡ calls attention to the fact that in *Ec. siliculosus* the Trichosporangia are sometimes branched; and he figures both Oosporangia and Trichosporangia in *Ec. approximatus*, var. balticus (Kütz.).

Reverting for a moment to the British species:—I have had abundant opportunities of examining over and over again living examples of *E. granulosus* and *E. sphærophorus*; and I have also had the benefit of being able to examine a type specimen, preserved in fluid, of *E. crinitus* (Carm.).

Of *E. pusillus* I know nothing, except what I have learnt from dried specimens and figures, of which latter, I would call special attention to Kützing's figure (Tab. Phyc., vol. v., Plate 48, II.).

In Ec. granulosus I have found, and watched through all its stages, save that of germination, the new Chytridial form above described,

^{*} As contrasting with this remark, and possibly not without some further significance, I may quote the following:—"Of the two kinds of fruit [met with in Ectocarpus], Trichosporangia, or multilocular sporangia, and Oosporangia, or unilocular sporangia, only the former have been observed in this country. Harvey's *E. oviger*, from California, is very problematical." W. G. Farlow, List of the Marine Algæ of the United States, in the Proceedings of the American Academy of Arts and Sciences, vol. x., Second Series, p. 351, 1875.

[†] J. E. Areschoug, Algæ Scandinavicæ exsiccatæ, Seriei novæ, Feb. 4, 1862, Specimen 173.

[‡] C. Gobi, "Die Brauntange des Finnischen Mecrbusens," in Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, Sept Série; tome xxi., No. 9, 1874.

which I suggest has been mistaken for an oosporangial fruit (Plate VI., figs. 1-5).

In *Ec. sphærophorus* I cannot feel equally sure that the oval cells are foreign bodies; but I can assert that they occur, not as described by Carmichael, invariably occupying the place of a ramulus, but that they sprout out from, at times, even the very cells of a ramulus, and that they are most suspiciously like some Chytridial growth.

In *Ec. crinitus* I have absolutely found the new form above described; and, to put this beyond doubt, have figured two specimens from a twig on the type specimen sent to Dr. Harvey, and now in the Herbarium of Trinity College, Dublin. It would appear to be the only "fruit" known on this species (Plate VI., fig. 6).

As to *Ec. pusillus*, a glance at Kützing's figure (Tab. Phyc., vol. v., Plate 48) will show that his spermatoidia to the left, marked "d," is a fruit very like a chytridial growth.

From these facts, I venture to suggest that it is probable—Firstly, that any one or more of the cells composing the filaments of any species of Ectocarpus may from their protoplasm develop the biciliate form of zoospore, so characteristic of the Phæosporeæ: in some cases but one cell of a filament, as may be from time to time seen in Ec. firmus, may thus act as a sporangium; in others, two or more, as in Ec. mertensii, where there are occasionally four cells in a row to be met with developing spores, thus doing away with the necessity for the genus Trichopteris (vide Plate V., fig. 4a). Often there will be quite a string of these spore-cells, not quite terminating a filament, and with each cell dehiscing laterally, and the cells, though swollen, not much altered in form. At other times, these cells will be much broader than long, and will be placed nearly at the ends of the filaments, presenting the appearance of a chambered pod, and dehiscing either at the apex of the series of cells or laterally. The escape of the zoospores from the apex of the series of cells, as figured by Thuret (loc. cit., Plate 24, fig. 2), I have never seen; but I have frequently witnessed the escape of zoospores from the sides of such pod-like structures, and I have always been able to detect, in quite recent and uninjured specimens, two or more sterile cells at the apex of such a fruit, making it differ but little from the more bead-like form. I have also now and then seen a single solitary cell in *Ec. siliculosus* giving origin to zoospores.

Secondly, that some of the "utricular" fruits of Harvey, and the spores of Kützing, may be in the Ectocarpi parasitic Chytridia. It is of importance to remember that I make this suggestion only for the true Ectocarpi. These are plants of purely confervoid growth, consisting simply of strings of cells, often irregularly branching. If a branch was limited in its growth to a single cell, and this to give origin to a flock of zoospores, such a fruit would differ only in degree from one in which, as so often seen in *Ec. mertensii*, the filament develops two or more such, and then continues growing; but it would altogether differ from the fruits met with, say in Cladostephus, where there is a much higher differentiation of tissue than is to be met with in Ectocarpus. This is scarcely the place to remark on the affinities shown by *Ec. mertensii* to some species of Sphacelaria.

Thirdly, that in addition to the variously-shaped and variously-placed sporangia giving origin to motile zoospores, there are in the Ectocarpi the so-called spermatoidia of Kützing; the propagula of Agardh; the multi-locular fruits of some authors; these being metamorphosed ramuli, or parts of ramuli (Plate 2, fig. 46), sometimes sessile, sometimes stalked, indehiscent, varying very much in outline; nearly spherical in *Ec. pusillus*; pod-shaped in *Ec. fasciculatus*; and the contents of which, *motu prædita*, are destitute of cilia, and to be compared rather to the tetraspores of the Florideæ than to antherozoids or zoospores.

Further research into the exact nature in the Ectocarpi of these multilocular fruits will alone settle these questions.

[Only since this Paper was printed have I seen Professor Pringsheim's important Memoir on Sphacelaria.*]

^{*} Pringsheim "Ueber den Gang der Morphologischen Differenzirung in der Sphacelarien-Reihe." Abhandlungen der K. Akad. d. Wissen. zu Berlin, 1873, s. 137.

EXPLANATION OF THE PLATES.

PLATE IV.

- Fig. 1. Chlorochytrium Cohnii (spec. nov.) in frond of Schizonema Dillwynii × 50.
- Fig. 2. Same \times 200.
- Fig. 3. Same in fronds of a Colletonema × 200. Very crowded.
- Fig. 4. Showing large (a) and small (b) spores \times 400.
- Fig. 5. Showing the formation of Chlorophyll (a), and Spores, large (b), small (c).

PLATE V.

- Fig. 1. Ch. Cohnii in Polysiphonia urceolata, and in Vaginicola urceolata × 200.
- Fig. 2. Bryopsis plumosa × 15. By an accident this figure of Bryopsis plumosa appears on Plate II. It formed a series of drawings to illustrate some varieties of cell-growth in this pretty unicellular Alga. Although Kützing figures several species of this genus, showing rhizomes growing from the pinnæ of the frond (e. g. Tab. Phyc., vol. vi., Tab. 72. B. ramulosa, and B. rosea, Tab. 84), yet I am not aware that this method of bud-like reproduction has been noticed or figured in our common form. This condition (a and b) seemed to occur quite commonly in spring, and the little detached plantlets were on close investigation to be found nestling on tufts of Corallina. Bryopsis seems very rarely to produce its zoospores; but this is quite as effectual a method of propagation, though probably it is more likely to limit the geographical area of the species.
- Fig. 3. Callithannion dispar (Har.), with a Chytridial (?) growth × 250.
- Fig. 4. *Ectocarpus Mertensii* (Agardh), (a) with four unilocular fruits, (b) with a multilocular fruit × 120.

Figs. 3 and 4 drawn from remoistened type specimens.

PLATE VI.

- Figs. 1 to 5. Rhizophydium Dicksonii (spec. nov.), variously magnified, parasitic in filaments of Ectocarpus granulosus.
- Fig. 6. Same in *Ectocarpus crinitus* (Carm.) from type specimen preserved in fluid in the Herbarium of Trinity College, Dublin, × 200.

