On *Notheia anomala*, Harv. et Bail. By ETHEL SABEL BARTON.
(Communicated by GEORGE MURRAY, Esq., F.R.S., F.L.S.)

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(PLATES 12-14.)

THE Fucaceous genus *Notheia* was founded by Harvey and Bailey on the species *N. anomala*, and published in the United States Exploring Expedition (Capt. Wilkes), vol. xvii. Botany, 1862, p. 157. The authors describe it as parasitic on *Hormosira Sieberi*, and remark on the unusual mode of growth, in which "each branch rises as it were viviparously from the scaphidium of a previous branch." They doubt here whether it may not be some spurious production of the host-plant, but in a note added later, *loc. cit.*, Dr. Harvey expresses himself as satisfied that "*Notheia* is really a parasitic alga and not a metamorphic state of *Hormosira*." Four figures are given of *Notheia*, among which is one of "a perispore with paranemata." This evidently represents an antheridium, for it contains a large number of regularly arranged cells, and the text describes the fruit as consisting of "spores in very narrow, almost linear, slightly obovate, almost parietal perispores."

The next records are in Hooker's 'Flora of New Zealand,' vol. ii. 1855, p. 215, and Hooker's 'Handbook of the New Zealand Flora,' 1864, p. 653, which, however, add nothing to the description of Harvey and Bailey. In "Observations on the Fucoideæ of Banks Peninsula" (Transactions of the New Zealand Institute, vol. xviii. 1885, p. 308), Mr. Laing gives a short account of *Notheia*. He quotes Hooker's description in the 'Handbook' (*l. c.*), and for the first time records the oogonia, which he also figures. He says, however, that from lack of good material he could not verify the number of oospheres in each oogonium.

This point is decided by Miss Mitchell in a note on *N. anomala* (Murray's 'Phycological Memoirs,' pt. ii. p. 36, 1893). She finds eight oospheres in each oogonium, though their arrangement, as figured by her, does not agree with the result of my investigations, to be described later. She gives good figures, natural size, of *Notheia* growing on its two hosts, *Hormosira* and *Xiphophora*.

Kjellman (Engler and Prantl's *Natürl. Pflanzenfam.* i. Abt. II. p. 280, 1891) and De Toni (*Sylloge Algarum*, vol. iii. *Fucoid.* p. 224) summarize the previous knowledge of *N. anomala*, but do not add to it.

In the 'Bibliotheca Botanica' a paper, "Ueber Aufbau und Entwicklung einiger Fucaceen," by Dr. Eduard Gruber, contains a short account of *Notheia*. He deals mainly with the growing-point and the development of the conceptacles, describing also the growth of the young branch. He mentions the oogonia only, and regards the plant as probably dioecious. The parasitism of *Notheia* is passed over, and no account is given of the early stages inside the host-plant.

This paper of Dr. Gruber was brought to my notice after my own investigation had been completed, and was therefore the more interesting as affording an opportunity of comparing results in the few points where our work had overlapped. I venture to differ from Dr. Gruber in a few details, but in the matter of the growing-point he was right and I wrong. These differences will be dealt with as they arise.

Notheia anomala is recorded from Australia, Tasmania, and New Zealand as parasitic on *Hormosira* and *Xiphophora*; and specimens from these localities are preserved in the British Museum, collected by Dr. Harvey, Mr. Bracebridge Wilson, and Mr. Laing. The last-named collector tells me in a letter that he has never found *N. anomala* parasitic on any other alga than *Hormosira*, though he has seen large quantities of *Xiphophora* in a living state.

The material on which this investigation was made was in part collected by Mr. Bracebridge Wilson at Geelong, Australia, and in part by Mr. W. R. Laing, of Christchurch, New Zealand, who has most kindly sent me supplies of material preserved according to various methods. He has also given me the benefit of his own observations made on living material, for which I here offer him my grateful thanks; but especially am I indebted to him for his generosity in sending me the material for a research which could have been so ably carried out by himself.

Notheia anomala is a slender, branched alga from 5-8 cm. high, though, according to De Toni, sometimes attaining a height of 15 cm. The largest plants I have seen do not exceed 12 cm., and in general they do not by any means reach this height. The mature stem is about $1\frac{1}{2}$ mm. in diameter and is branched

at intervals in no particular order, each branch again throwing out smaller branchlets. These taper considerably both at their apex and at their point of connection with the stem, giving the whole plant a rather fragile appearance (Pl. 12. fig. 1).

The thallus of *N. anomala* consists of three layers of tissue, as in *Turbinaria* and other members of Fucaceæ. The centre is occupied by the usual strand of elongated cells having very thin transverse and thick longitudinal walls. The breadth of this strand increases with the age of the plant, and in the oldest portions of the thallus the thick walls become much pitted, while other filaments arising from them intertwine irregularly among them (Pl. 12. figs. 2 & 3). These filaments, or "hyphæ" as Prof. Oltmanns calls them, have been described and figured by him for *Ascophyllum nodosum* ("Beitr. z. Kenntn. der Fucaceen," Bibl. Bot., Heft 14, 1889, pl. x. fig. 1). The layer immediately surrounding the central strand consists in the young plant of roundish cells with pits in their walls, and as the thallus increases in age the cells become longer and the walls thicker, thereby showing up in marked contrast the thin places in the cell-walls (Pl. 12. fig. 2 b). The cortical layer shows the usual narrow, radially elongated cells.

The growing-point of *N. anomala* does not lie at the base of a depression as in many of the Fucaceæ, but forms the topmost point of the thallus. It consists of three apical cells, as has been shown by Dr. Gruber (*l. c.*), who figures the growing-point both in transverse and longitudinal section, and compares it with that of *Hormosira*, which has three or, more often, four apical cells. My own conclusions with regard to the apex of *Notheia* were, as stated above, different from those of Dr. Gruber, since I believed that there was but one apical cell; but after reading his paper and re-examining the series of sections, there is no doubt as to the correctness of his decision. The division of these apical cells takes place, according to Dr. Gruber, by the cutting off of cells at the periphery, and these then divide by radial and basal walls to form the various layers of tissue.

Immediately below the apex of *N. anomala* may be seen the first appearance of young cryptostomata, also described by Dr. Gruber. They arise in the usual way by the arrested growth of one of the epidermal cells, which at once produces a hair with a large basal cell (Pl. 13. fig. 4). The depression enlarges by longitudinal division and subdivision of this arrested epidermal

cell, thus forming a layer which lines the cavity. Each of these cells produces a hair in the young cryptostoma, thus forming a thick tuft of long hairs which protrude through the mouth and are plainly visible to the naked eye in the young branches of the plant (Pl. 12. fig. 5).

In some of the cryptostomata, however, a cell which lies at the base of the depression, instead of producing a hair, grows up into a small round protuberance, and after division proceeds to cut off from the apex successive cells to form a young branch (Pl. 13. fig. 6). These apical cells are exactly similar to those of the primary thallus, as would be expected. As growth in length takes place, the lower cells begin to divide up to form the various layers of tissue, and this transverse division keeps pace with a corresponding division of the cryptostoma-cell, which originally gave rise to the branch. So that before the young branch is sufficiently advanced to protrude through the opening of the cryptostoma its base has become quite broad, and gives the appearance of having originated from a group of cells rather than from a single cell (Pl. 13. fig. 7). The remaining cells of the cryptostoma continue to produce hairs as usual.

In Dr. Gruber's description of the young cryptostoma and the origin of the branch he says that when the hairs fall off a flask-shaped cell is left at the base, which probably gives rise to the young branch. But the hairs do not fall off in the very early stages of the cryptostoma, and it is in these stages that the first sign of the branch is seen. There seems to me no doubt that the branch arises direct from one of the cells of the lining layer.

Since the branching takes place in this way from the cryptostomata, it follows that branches arise from all sides of the thallus irregularly; indeed I have seen in one section three cryptostomata with a branch growing out of each. In one instance of an old cryptostoma I have seen the centre occupied by the base of a thick branch and at the side there was beginning to shoot up another small branch, showing that one cryptostoma can produce more than one branch, and that these need not necessarily spring from the centre. I have failed, however, to find a case in which two branches have succeeded in growing to maturity from the same cryptostoma.

All this time the cells lining the cavity of the cryptostoma have continued to divide, as well as the thallus-cells surrounding

it. The large area of lining-cells thus produced shows of course very few hairs, for many of these have fallen off and the remainder have become separated from each other by the formation of the new cells. From these there now push up small outgrowths which develop into antheridia, oogonia, and unbranched paraphyses (Pl. 13. fig. 8).

Dr. Gruber describes the growth in size of the cryptostoma (or, as he calls it throughout, the conceptacle) as taking place through separation from each other of the cells surrounding the initial cell. My observations lead me rather to the conclusion that repeated cell-division of the lining layer and, later on, a growth in size of the individual cells take place, thus accounting for the appearance of new hairs, and later on of reproductive organs, from all parts of the cavity. In mature conceptacles the walls of the lining-cells are still connected with each other at their base, while the upper part becomes free by pushing up into the open space of the cavity. By this means the actual surface area of each such lining-cell is enlarged, and one cell can thus bear an oogonium and one or even two paraphyses.

As I have pointed out above, the bodies which we now know to be antheridia were probably first noted by Harvey and Bailey, since the figure (*l. c.*) evidently refers to these bodies under the name of sporangia. They arise direct from the lining-cell of the cryptostoma, or conceptacle as it has now become, and contain numerous antherozoids (Pl. 13. fig. 9). They are about 55μ long and 15μ broad, resembling entirely the antheridia of *Hormosira* and other Fucaceæ. They grow in the same conceptacles as the oogonia, but are not so plentiful. This is, so far as I know, the only recorded case of antheridia growing directly from the walls of the conceptacle in the same manner as oogonia; and it was not until after an examination of a large number of conceptacles that I felt justified in regarding these bodies as antheridia and not as oogonia, of which the cell-contents had been in some way disorganized. But the regularity of the antherozoids, and the final confirmation of their existence in fresh material by Mr. Laing, placed the question beyond doubt.

The general rule as to the position of the reproductive organs in Fucaceæ, *i. e.*, that the antheridia arise on branched hairs and the oogonia from the walls of the conceptacle, is now shown to have exceptions in both cases. *Notheia* has antheridia arising like oogonia, while *Sarcophycus* (Miss F. G. Whitting, in

Murray's Phycol. Mem. p. 39, pl. 12. fig. 3) and *Durvillaea* (Laing, in Trans. N. Z. Inst. xviii. (1885) p. 308) have oogonia on branched hairs like antheridia.

The oogonia of *Notheia* are rather larger than the antheridia and measure $75\ \mu$ by $20\ \mu$. They contain 8 oospheres, one at each end, and, between these, three groups of two each, the oospheres of the two outermost groups corresponding in position, while in the middle group the oospheres lie crossways. Thus if the two outermost groups show both oospheres side by side, the middle group shows only one, the second oosphere being hidden behind it (Pl. 13. fig. 10).

The unbranched paraphyses are of the usual size and kind found in female conceptacles, and frequently grow from the same cell which bears the antheridium or oogonium, as mentioned above.

One or two of the long cryptostoma-hairs sometimes persist during the time of fructification and may be seen among the ripe fruits (Pl. 13. fig. 8).

The history of cryptostomata has aroused a certain amount of discussion and speculation; and there is still much to learn about their origin and function from the more or less open pits of *Enceliaceæ* to the flask-shaped cavities of *Fucaceæ*—all with their typical cryptostoma-hairs. But till now I believe it has not been found that all the cryptostomata of any *Fucaceous* alga gradually lose most of their hairs and come to bear reproductive organs and paraphyses—become, in fact, fertile conceptacles. Miss Strudwick, who examined *Hormosira* at my request with regard to this point, tells me it is true also of that genus. This has been seen in *Splachnidium* (Murray's Phycol. Mem. pt. i. 1892, p. 5), but in that case the reproductive organs are sporangia, and the genus is therefore excluded from *Fucaceæ*. Of the three views concerning the origin of cryptostomata quoted by Mr. Murray ("On the Cryptostomata of *Adenocystis*, *Alaria*, and *Saccorhiza*," Phyc. Mem. 1893, p. 59), my own, as to the phylogenetic independence of cryptostoma and conceptacle, must, I fear, fall to the ground before this new light thrown on the subject by *Notheia*.

Prof. Oltmanns's view "that the fertile conceptacles are cryptostomata which have in time come to bear organs of reproduction," seems to meet the case more satisfactorily, especially if we remember how the sporangia of *Adenocystis*, *Soranthera*, *Colpomenia*,

Chnoospora, &c. cluster round the mouth of the cryptostomata. It only needs a step for the fruits to drop into the cavity in their midst, and thus convert the cryptostoma into a fertile conceptacle. This view, on the other hand, does not account for the cryptostomata of *Fucus*, *Turbinaria*, &c., which might be claimed by Prof. Bower in support of his theory that cryptostomata are incomplete sexual conceptacles.

That these hairs are of importance to many members of the Phaeophyceæ is evident by the careful protection they receive; but the manner in which they serve the plant has yet to be discovered. The subject of cryptostomata and their hairs is, however, dangerous ground for speculation, but it is hoped that new facts concerning these bodies may eventually throw a clearer light on their origin and function.

Notheia anomala has long been known as the only recorded parasite among the Fucaceæ, but details of this parasitism have been wanting. Hooker (Handbook N. Z. Flora, *l. c.*) says it grows from the conceptacles of its host *Hormosira*; but after examining a large number of instances of the junction between host and parasite, I find this statement incorrect. The point of entry is in most cases quite close to the mouth of a cryptostoma or conceptacle of *Hormosira*, but in no case have I seen any part of *Notheia* penetrate into the conceptacle itself of the host-plant. In the earliest stages, the spore apparently divides on the surface of the host and throws out a delicate septate filament, which penetrates between the host-cells and branches in every direction; thus forming a sort of loose network, without, however, actually penetrating into the host-cell. By means of offshoots running up to the surface of the host, from one of the filaments of *Notheia*, the gelatinous cuticular layer of the host-plant is thrown off and room is made for the parasite to develop. Meanwhile several of the filaments inside the host have formed together a sort of small cushion (Pl. 13. fig. 11) from which the young shoot grows up, forcing its way through the loose tissue which surrounds it (Pl. 14. fig. 12). Other cells of the cushion grow out into hairs, and the whole has very much the appearance of an irregular cryptostoma, producing a young branch as described above. As this shoot grows out from the host-thallus, the surrounding host-cells divide actively and swell up around the base of the young plant (Pl. 13. fig. 13). Rhizoids are given off from the base of the pseudo-cryptostoma which penetrate between

the cells of the host, forming knots of irregularly shaped cells, with long thin prolongations running in all directions. In early stages these rhizoids are seen only at the base immediately below the young shoot, but later many of the cells which lie along the sides of the pseudo-cryptostoma give off rhizoids in the form of thin prolongations (Pl. 14. fig. 14). It is only by following carefully the various stages of the junction of *Hormosira* and *Notheia* that it is possible to detect the line of demarcation between the two in a mature stage. The shoot of *Notheia* has widened exceedingly at the base, and the host has grown in proportion round it. In most cases the host-cells immediately adjoining *Notheia* have lost their colour, and it has generally been supposed that the line of demarcation corresponded with the change of colour. But this is not the case, for though the tissues of both plants are very much alike, it is possible to see, among the colourless cells, a slight irregularity which marks the line of contact of *Notheia* and its host (Pl. 14. figs. 15 & 16). It has not been possible to determine whether the contents of the *Hormosira*-cells, immediately adjoining the *Notheia*-shoot, have lost their colour through the action of the rhizoids which have passed down between them; but the fact that age increases both the length of the rhizoids and the depth of the colourless layer of *Hormosira*-cells leads one to suspect some connection between the two. I have never seen a genuine instance of the penetration of a *Notheia*-rhizoid into one of the host-cells, though many preparations have led me to think this not improbable. It is, however, a point which can only be worked out with satisfaction on fresh material.

The early stages in the life-history of *N. anomala* bring to mind the figure and description of young adventitious branches from the basal disc of *Fucus vesiculosus*, as described and figured by Prof. Oltmanns (in Bibl. Bot., Heft 14, p. 73, tab. 13. figs. 10-13). Here, of course, there is nothing of a parasitic nature to be considered as in *Notheia*, but there is a certain similarity in the process of the actual growth. As the result of an injury to the thallus, a few cells within the tissue begin to divide and shortly form a small protuberance. This grows up in a radial direction through the surrounding tissue, the apical cell sinks into a depression, and the branch continues to grow in the normal fashion.

ESB & PH dal Highley lith

Hanhart imp

NOTHEIA ANOMALA, Harv. & Bail.

E.S.B. & P.H. del. Highley lith.

Hanhart imp.

NOTHEIA ANOMALA, Harv. & Bail.

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ESB & P.H. del. Highley lith.

Hanhart imp

NOTHEIA ANOMALA, Harv & Bail.

Finally, I would express my gratitude to the officials of the Botanical Department of the British Museum for their never-failing kindness and interest.

EXPLANATION OF THE PLATES.

PLATE 12.

- Fig. 1. *Notheia anomala*, Harv. et Bail., growing on *Hormosira*. Nat. size.
 2 *a*. General view of thallus. Long. sect. $\times 60$.
 2 *b*. Longit. section of mature thallus, showing part of central strand and intermediate layer. $\times 140$.
 3 *a*. Transverse section of mature thallus. $\times 60$.
 3 *b*. Cells from centre of same. $\times 365$.
 5. Cryptostoma still more advanced. $\times 365$.

PLATE 13.

- Fig. 4. Cryptostoma rather older. $\times 365$.
 6. Very early stage of young branch arising from the base of a cryptostoma. $\times 365$.
 7. Branch more advanced. $\times 365$.
 8. Mature conceptacle, with oogonia and antheridia. $\times 140$.
 9. Antheridium. $\times 365$.
 10. Oogonium. $\times 365$.
 11. Penetrating filaments of *Notheia* pushing up cuticle of *Hormosira* and forming cushion. $\times 365$.
 13. Various stages of young plant. $\times 25$.
 a. Hairs arising from cushion of *Notheia* inside host-plant.
 b. Young shoot which has reached the surface of the host.
 c. Still later stage.

The light-coloured tissue surrounding the young shoot of *Notheia* is disorganized host-tissue.

PLATE 14.

- Fig. 12. Young shoot of *Notheia* issuing from host-plant. $\times 365$.
 14. Cells giving off rhizoids along the sides of the pseudo-cryptostoma. $\times 400$.
 15. Junction of *Hormosira* and *Notheia*. Mature. $\times 65$.
 16. Rhizoids of mature plant. $\times 400$.
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