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For Submission to "Nature"

THE STRUCTURE AND SYSTEMATIC POSITION OF THE AUSTRALASIAN BROWN ALGA, NOTHEIA ANOMALA.

Notheia anomala Harvey and Bailey[1] 1851 was first collected by the United States Exploring Expedition at the Bay of Islands, New Zealand. It grows exclusively on Hormosira banksii f. sieberi at a low littoral level and in low rock pools on rough coasts along southern Australia and in New Zealand. Previous studies of Notheia have been made by Mitchell[3], Gruber,[4] Barton[2] and Williams,[5].

The specific name is most applicable to this alga, which has previously always been classed in the Fucales, usually in a family with Hormosira. Notheia shows a group of 3 apical cells (which protrude at the branch apex and are not sunk in a depression as in the Fucales), conceptacles scattered over the thallus, and the supposed formation of oogonia with 8 eggs, and according to Barton[2], of antheridia with numerous sperms. The branches, which issue from the conceptacles, are a further anomalous feature.

The discovery, while examining living material, that the "eggs" are motile zooids, made a thorough investigation of Notheia necessary. This account gives preliminary results, which, while not complete, do clarify many features and show

that Notheia is not a member of the Fucales but is a distinctive type of the Heterogeneratae. The structure and reproduction will be discussed briefly below.

Each of 3 protruding apical cells segments latero-posteriorly, and the tissues derived from each apical cell can be recognised in both transverse and longitudinal sections for some distance from the apex due to extensive mucilage development between the 3 sectors. Some 15 or 20 cells from the apex this distinction is lost. Derivatives of the apical cells segment periclinally to form rows of cells which develop three tissues — medulla, cortex and peripheral layer which remains meristematic. The development of the cells is largely filamentous and not parenchymatous, but in older medullary tissue divisions in different planes may occur giving a truly parenchymatous tissue. Increase in thickness of the thallus is largely due to the meristematic peripheral layer, the cells of which divide first by a longitudinal - oblique wall (not reaching the base of the cell), followed by a periclinal division near the base of the larger cell. This results in dichotomous branching, the cells remaining connected by large pit connections, similar to those of the Florideae. This dichotomous branching is readily visible throughout the cortex in hand sections, but thin microtome sections obscure it.

Branching occurs largely but not entirely from within the conceptacles, resulting in a profusely and irregularly branched plant up to 12 cm. high. The plants originate from within or near the osteole of Hormosira plants. The branches are constricted within and immediately outside the conceptacles, but broaden considerably 1-2 mm. outside; here the cortex is fully developed. Occasionally however true branches, up to 3 per plant, occur; here the thallus divides into two with no decrease in thickness or association with a conceptacle. The common branches may be referred to as "conceptacular branches" and reasons will be advanced later for suggesting that these are new plants and not real branches.

Conceptacles occur profusely scattered over the thallus. They originate by enlargement and transverse division of a peripheral cell; the upper cell divides to form a hair and the lower divides longitudinally and is overgrown by surrounding cells to form the conceptacle. Most of the lining cells of the conceptacle produce paraphyses which protrude through the osteole as a dense tuft.

Sessile reproductive organs occur on the wall of the conceptacles. Most common are those containing 8 zooids, while slightly smaller ones with 64 zooids vary from plentiful to absent in some conceptacles. The larger organs measure 48-78 μ by 12 - 30 μ and are not oogonia but are macrozoosporangia,

liberating 8 pyriform macrozoospores through basal, or occasionally lateral or terminal pores. The macrozoospores are first extruded in a gelatinous envelope, and when they escape are sluggishly motile by means of a long anterior flagellum and somewhat shorter posterior one, the attachment being lateral but close to the pointed apex. Macrozoospores contain 2 to 4 chromatophores, a single eye-spot and measure 12-27 μ by 5-12 μ.

The 64 zooids, formed in organs slightly smaller than the macrozoosporangia, are actively motile, almost colourless (with one pale chromatophore), with an eye-spot and two unequal flagellae attached near the apex. They measure 6-10 μ by 4-6 μ. These bodies settle after one half to several hours but have never been observed to develop further and their nature is still unknown.

During repeated observations no fusion between the large and small zooids has been observed, although they were moving close together.

The macrozoospores germinate in culture into branched, filamentous gametophytes, with erect colourless hairs. The cells of the prostrate parts measure about 12 μ in thickness, are 2-4 times as long as broad and contain several brown chromatophores. Uniseriate, erect reproductive bodies are produced on older filaments, each cell producing a single

zooid which is liberated apically through the series of fertile cells. These zooids are pyriform, about 8 μ by 6μ and biflagellate with lateral, unequal flagellae, similar to the macrozoospores. These gametophytes and reproductive cells are very similar to the gametophytes and uniseriate gametangia of Spermatochnus paradoxus[6].

Branched, filamentous growths such as those found in culture occur frequently within the conceptacles of Notheia as was observed by Barton[2]. These filamentous growths are usually entirely within the conceptacle, ramifying amongst the paraphyses and lining cells, but with their colourless hairs sometimes protruding from the ostiole. Occasional empty uniseriate reproductive cells have been seen on them.

Satisfactory chromosome counts have not yet been obtained, but some 26-30 chromosomes have been observed in vegetative cells, about 20-24 in paraphyses and 12-15 in later divisions in the macrozoosporangium. The thallus of Notheia is probably diploid and the macrozoospores and macrogametophyte haploid.

Until the nature of the microzooids and the zooids from the uniseriate gametophytic reproductive organs is known the full life cycle of Notheia will remain uncertain. It seems likely that the macrogametophytes bear uniseriate gametangia producing a single gamete per cell. The behaviour of the microzooids towards these gametes has not yet been observed.

From the known facts, it appears likely that the macrozoospores germinate into macrogametophytes largely within the conceptacles, and possibly fertilisation also occurs within the conceptacles, giving rise to a zygote which grows from the wall of the conceptacle. If macrogametophytes develop outside the conceptacles and fertilisation occurs externally, the zygote probably is unable to develop without being associated with Notheia or Hormosira.

This speculation agrees with the development of new conceptacular branches. Commonly one, sometimes 2 or 3, branches emerge from a conceptacle, and young stages have been observed by us and by previous authors,[2,4] growing from the cells lining wall cells of the conceptacle. This would mean that the gametophytic stage of Notheia is entirely endophytic within the conceptacles, and that Notheia is essentially a simple or occasionally truly branched plant; the normal Notheia plant is actually a compound plant consisting of numerous individuals of possibly several successive generations. Occasional establishment of new Notheia plants from Hormosira conceptacles might occur by macrozoospores escaping from Notheia conceptacles and developing near or inside adjacent Hormosira conceptacles, with subsequent fertilisation (?) and development of the zygote within the Hormosira. The one record[6] of Notheia

on Xiphophora may be a rare chance occurrence.

Notheia is clearly to be classed in the Heterogeneratae group of the brown algae, having differing sporophytic and gametophytic generations. The development of the thallus is essentially filamentous, but probably with some true parenchymatous cell formation at older stages. It shows some relationship with certain members of the Chordariales, such as Spermatochnus paradoxus[6] (which has somewhat similar apical cells and gametophyte), but the only member of this group showing conceptacle formation is the southern hemisphere Splachnidium rugosum (which has only one type of sporangium with numerous spores).

Notheia differs from all Chordariales, and in fact from all brown algae, in forming two types of zoospores (if the microzooids are in fact zoospores). Other distinctive features are the 3 apical cells, the cortex of dichotomous chains of cells with prominent pit connections, the conceptacles and the endophytic gametophytes and development of new branches. The systematic position of Notheia must await knowledge of the full life history but it certainly forms a distinctive family (Notheiaceae Kuckuck ex Schmidt), which may come within the Chordariales or may justify an order of its own.

Brown algae forming zoosporangia normally produce

numerous zoospores. The reduction to 8 macrozoospores is noteworthy, as well as the production of two morphologically distinct zoospores. Notheiamay well indicate the possible origin of the Fucales, since were the macro- and microzooids to function as gametes (gametophytes being eliminated) and the apical cells become sunk in a depression, the resultant alga would undoubtedly agree well with the Fucales. It is quite possible that the microgametophyte has been eliminated already, and the microzoids function as male gametes; this, however, is still speculation and awaits further examination.

1. Harvey, W.H., and Bailey, J.W. Proc. Boston Soc. Nat. Hist. 3: 370-373 (1851).

2. Barton, E.S. J. Linn. Soc. Lond. (Bot.) 34: 417-425 (1899).

3. Mitchell, M.D. Phycol. Mem. 2: 36-37. (1893).

4. Gruber, E. Bibl. Bot. 38: 1-32 (1896).

5. Williams, M.M. Proc. Linn. Soc. N.S.W. 47: 634-646 (1923)

6. Papenfuss, G.F. K. Fysiogr. Sallsk. Luhd Forhandl. 5 (20): 1-4 (1935).

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