

Anatomy of *Apophlaea sinclairii*—An enigmatic red alga endemic to New Zealand

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Apophlaea sinclairii is a curious rhodophyte endemic to the North I. of New Zealand where it forms thick, tar-like crusts on rocks in the upper intertidal zone. These crusts usually produce terete, branched upright thalli. The crust consists of a basal layer of short, parallel filaments which merge with an anastomosing meshwork of thick-walled filaments that become closely appressed and parallel to each other in the upper region of the crust. No basal rhizoids are present. Many secondary pit connections are formed. The anatomy of the upright thalli is similar, consisting of a central core of interconnected cells and a cortical layer of thick-walled, parallel filaments. Colourless hyphae of the systemic Ascomycetes fungus *Mycosphaerella apophlaeae* occur between the algal filaments throughout the thallus. Tetrasporangial conceptacles are present in both crusts and uprights and contain zonately divided tetrasporangia throughout the year. Black ascocarps and spermogonia of *Mycosphaerella* are often present, embedded just below the thallus surface. No evidence of a heteromorphic sexual life history for *Apophlaea sinclairii* was obtained. In the absence of female reproductive structures the systematic position of *A. sinclairii* remains uncertain.

Key Words: *Apophlaea sinclairii*; *benthic algae*; *Hildenbrandiaceae*; *marine fungi*; *mycophycobiosis*; *Mycosphaerella*; *New Zealand*; *Rhodophyta*; *Taxonomy*.

Apophlaea sinclairii HARVEY in HOOKER and HARVEY (1845 p. 550), the type species of the genus, is endemic to the North I. of New Zealand (MOORE 1961). The thick, crustose thallus typically bears short, erect, terete branches and forms a conspicuous zone in the upper intertidal on sheltered rocky shores.

It is apparent from the original description that HARVEY had seen dried specimens of only the erect branches (HOOKER and HARVEY 1845); however, this oversight was remedied in BAILEY and HARVEY (1862) where both an encrusting and upright thallus was described and illustrated (pl. II, fig. 1).

The systematic position of *Apophlaea* has

been uncertain from the first due to the absence of sexual reproductive structures. On the basis of conceptacles containing zonate tetrasporangia HARVEY assigned his new taxon to the Cryptonemiales (as Cryptonemeeae). When *Apophlaea lyallii* HOOKER et HARVEY in HOOKER (1855 p. 244), the only other species in the genus, was described it was placed in the Chaetangiaceae (as Chaetangieae) as was *A. sinclairii*. Subsequent workers have either made no mention of the systematic position of *Apophlaea* (BAILEY and HARVEY 1862, HOOKER 1867) or treated it as uncertain (SCHMITZ 1889, DETONI 1897, LAING 1926 1939, KYLIN 1956) or provisionally assigned it variously to the Chaetangiaceae (AGARDH 1851, as Chaetangieae), Hypneaceae (PAPENFUSS 1953, with uncertainty), Apophloeaceae *nom. illeg.* (NAYLOR 1954, no

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diagnosis of the family given), Phacelocarpaceae (ADAMS 1972), and Hildenbrandiaceae (DENIZOT 1968, ADAMS *et al.* 1974, CHAPMAN and PARKINSON 1974). Placement in the Hildenbrandiaceae was based on the encrusting habit and the occurrence of zonate tetrasporangia in uniporate conceptacles. These are superficial similarities and there have been no detailed anatomical studies of *Apophlaea* to provide further characters for comparison.

Vegetative anatomy of the crusts and uprights and reproductive anatomy of the tetrasporangial conceptacles of *Apophlaea sinclairii* were studied to more thoroughly characterize this enigmatic taxon.

Materials and Methods

Crustose and upright plants examined in this study were collected at Tawharanui Peninsula near Takatu Pt., North I., New Zealand, 36°22.4'S, 174°51.8'E, and at 'Pumphouse Reef', Leigh Marine Reserve, North I., New Zealand, 36°16.2'S, 174°47.8'E, both located on the northeastern coast of New Zealand.

Freshly collected, unfixed thalli were sectioned by hand or with a freezing microtome. For more critical light microscope observations samples were fixed in the field in 1% paraformaldehyde/2% glutaraldehyde mixture in seawater for 3-5 hr. Dehydration was done in a graded ethanol series, followed by infiltration with glycol methacrylate (Polysciences JB-4; O'BRIEN and MCCULLY 1981). Three micrometer (μm) sections were cut on glass knives using a Sorval JB-4 microtome. For light microscopic observations a Wild M-8 or Reichert Zetopan photomicroscope were used. For transmission electron microscopy specimens were fixed as described above, then post-fixed in 1% OsO_4 in phosphate or Dalton's buffer for 3 hr, dehydrated in ethanol followed by propylene oxide, infiltrated with Spurr's resin for up to 1 week, and sectioned on a Sorval Porter-Blum ultramicrotome. Sections were stained for 1 hr in uranyl acetate in 50% ethanol (DAWES 1971)

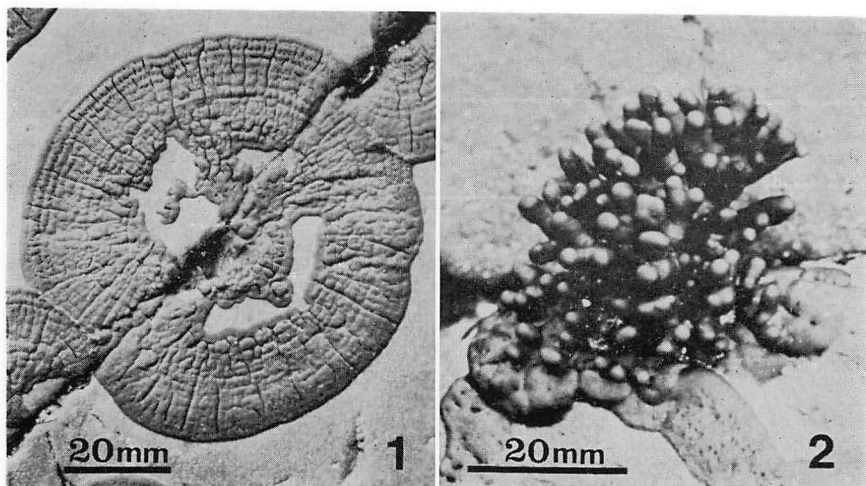
and 10-20 min in lead citrate (VENABLE and COGGESHALL 1965) and examined with either a Phillips 200 or Zeiss EM-10. Following post-fixation samples for scanning electron microscopy were freeze-fractured in isopentane cooled with liquid nitrogen, dried with an Edwards EPD5 freeze dryer, mounted on stubs, gold-coated and examined with a Cambridge Stereoscan 250.

Representative specimens from this study have been deposited in the phycological herbaria of D. S. I. R. Botany Division, Christchurch (CHR) and the University of British Columbia (UBC).

Results

Habit and habitat: *Apophlaea sinclairii* inhabits rock substrata in the upper intertidal zone where it is frequently the dominant alga. On smooth, hard substratum with adequate space *A. sinclairii* forms circular crusts (up to 2 mm thick and 100 mm in diam.) (Fig. 1) which are firmly attached to the substratum and have concentric growth lines. Under conditions of crowding or uneven substratum crusts become irregular and/or reduced in size. In the southern part of the North I. only crustose thalli are encountered (ADAMS 1972), however; along more northerly coasts crusts produce erect, terete, and irregularly to dichotomously branched growths 2-3 mm in diam. and up to 30 mm tall (Fig. 2). Both crusts and uprights have a firm, tough consistency and are red-brown when wet becoming extremely hard and black on drying.

Vegetative anatomy: The crustose thallus is composed of a basal layer of closely adhering filaments oriented anticlinally to the substratum (Figs. 3, 4). No basal rhizoids are formed. Above this basal layer is a region of an anastomosing meshwork of filaments which gradually become anticlinal and parallel to each other (Figs. 3, 4). Secondary pit connections are of frequent occurrence (Fig. 5), but are less common near the surface of the thallus (Fig. 6). Their mode of formation appears to be via an outgrowth



Figs. 1-2. Habit of *Apophlaea sinclairii*. 1. A particularly well-developed crustose thallus growing on smooth greywacke rock in the upper intertidal zone. Note concentric growth rings; 2. Upright and encrusting thallus in habitat.

making contact with a neighbouring filament (as in the Corallinaceae).

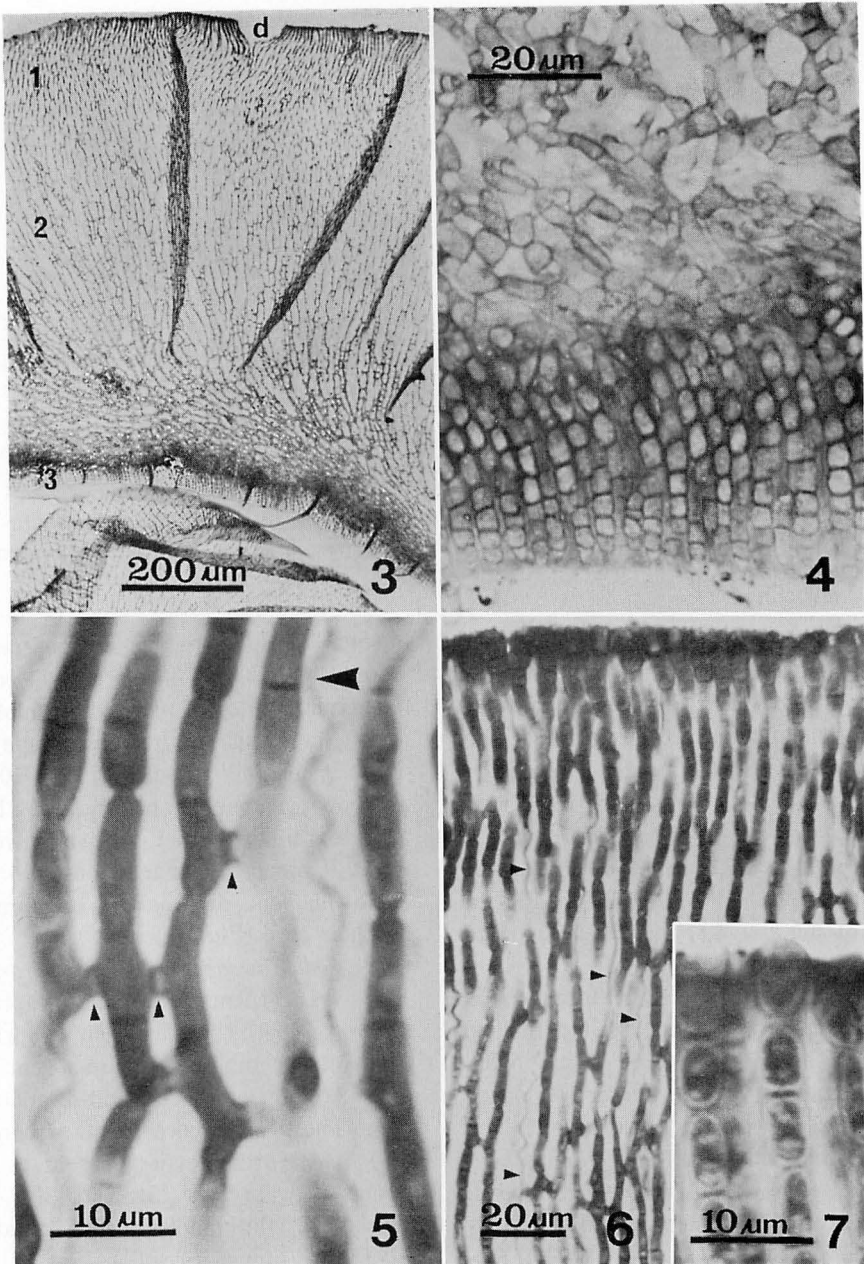
Cells of the filaments are small ($5-6\ \mu\text{m}$ wide \times $8-12\ \mu\text{m}$ long near the surface of the crust becoming more elongate towards the interior) and have a very thick cell wall (Figs. 7-9). Hyphae of the systemic fungus *Mycosphaerella apophlaeae* KOHLMAYER in KOHLMAYER and DEMOULIN (1981 p. 13) can be seen growing amongst the algal filaments (Figs. 5, 6, 8).

The anatomy of the upright branches is similar to that of the encrusting thallus, consisting of a central core of highly anastomosed filaments and an outer region of closely appressed parallel filaments. The interior of the thallus contains globular deposits of an unknown material which appears chalky white in samples embedded in methacrylate (the surface layers of parallel filaments appear clear).

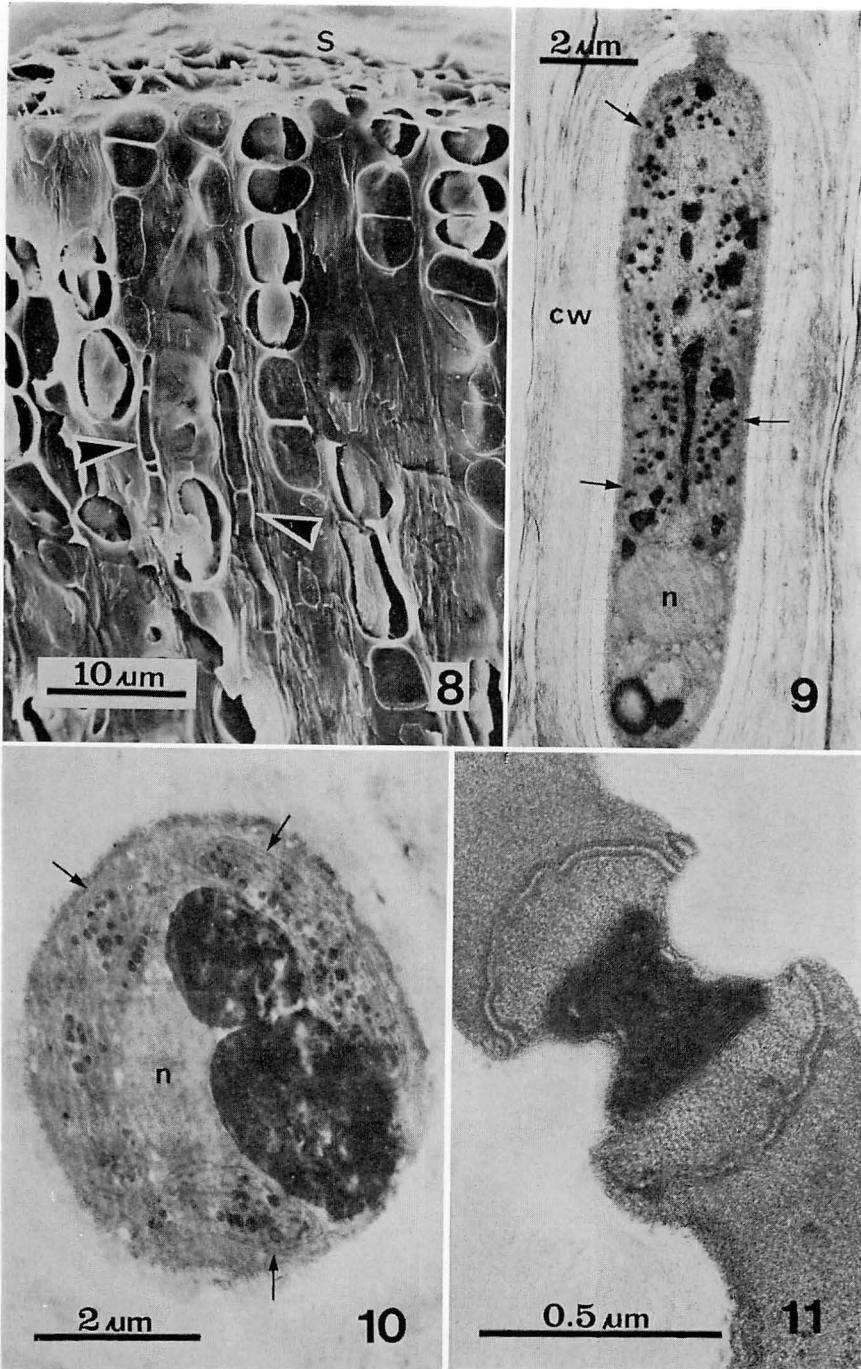
Because of the extremely slow growth rate of *Apophlaea sinclairii* it was not possible to observe many important developmental features such as whether the thallus is uni- or multi-axial and details of tetrasporangial conceptacle initiation and development. Specimens are extremely difficult to fix and embed properly for electron microscopy possibly because of the thick cell wall of the fila-

ments. Despite the poor preservation of detail in Figs. 9, 10 chloroplasts containing numerous plastoglobuli are discernible. Most cells (including the tetrasporangia) contain large osmiophilic bodies (Figs. 10, 18) of unknown composition or function. Floridean starch grains were not observed in vegetative cells. Primary pit connections join the cells of a filament and have a membrane swirl in their core (Fig. 11).

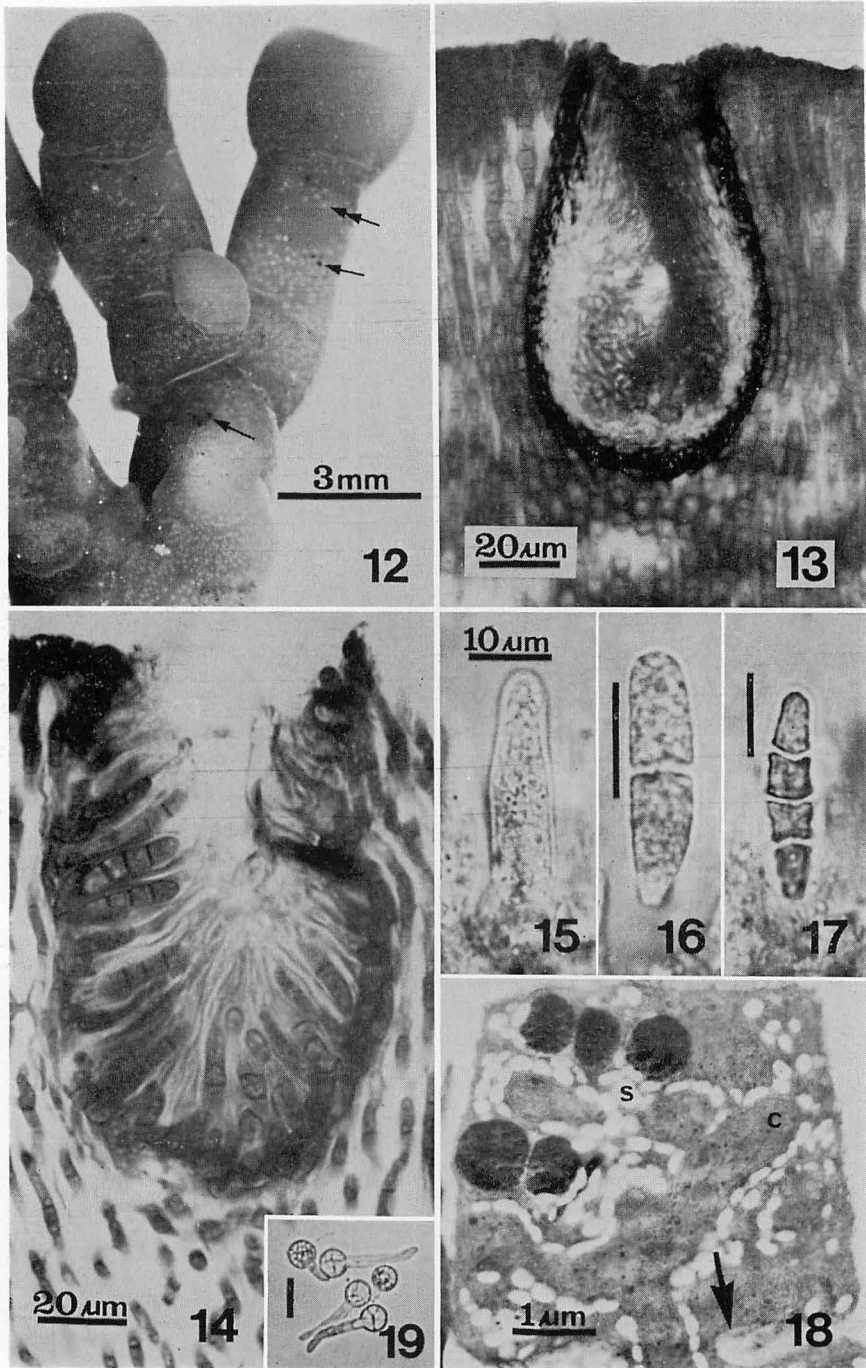
Reproductive anatomy-Tetrasporangial conceptacles: Tetrasporangial conceptacles are present in both the crustose and upright portions of the thallus, but are absent from the apical region of the upright branches (Fig. 12). The black ascocarps of *Mycosphaerella apophlaeae* are likewise present in both the crusts and uprights (Figs. 12, 13). A section through a conceptacle reveals zonate tetrasporangia lining its walls (Fig. 14) and the cavity of the conceptacle contains numerous colourless fungal hyphae. A tetrasporangial initial undergoes division in half followed by two further parallel divisions to form the mature zonate tetrasporangium (Figs. 15-17). Examination at the ultrastructural level suggests that although these divisions are initiated successively they are actually completed simultaneously (Fig. 18). Maturing tetrasporangia contain chloroplasts, abundant



Figs. 3-7. *Apophlaea sinclairii*—vegetative anatomy. Transverse sections, light microscopy, 3. The encrusting thallus. d=dorsal surface, 1=region shown in Fig. 6, 2=region shown in Fig. 5, 3=region shown in Fig. 4; 4. The basal layer (see Fig. 3, #3) of the encrusting thallus is composed of closely appressed anticlinal filaments; 5. Secondary pit connections (small arrowheads) between the parallel filaments in region 2 (see Fig. 3) of the thallus. Hypha (large arrowhead) of the systemic fungus *Mycosphaerella apophlaeae*; 6. Fungal hyphae (small arrowheads) growing between the parallel algal filaments near the surface of the crust (region #1 in Fig. 3); 7. Morphology of the cells in the surface layer of the encrusting thallus.



Figs. 8-11. Vegetative anatomy of *Apophlaea sinclairii*. Electron microscopy. 8. Scanning electron micrograph of a freeze-fractured surface of the upright thallus. s=outer surface of the thallus. Note the thick cell wall of the algal filaments and the fungal hyphae (large arrowheads) growing between them; 9. Longitudinal section of a cell in a filament 15-20 cells from the thallus surface. Despite the poor preservation of cell contents, chloroplasts (arrows) containing numerous plastoglobuli are visible; n=suspected nucleus; cw=cell wall; 10. Transverse section of a cell in the upright thallus. Arrows=chloroplasts; n=suspected nucleus. Note the large dark-staining inclusion; 11. Primary pit connection with dark-staining membrane swirl in its core.



Figs. 12-19. Reproductive anatomy of *Apophlaea sinclairii*. 12. Portion of an upright thallus with tetrasporangial conceptacles (white dots, double-headed arrow, see Fig. 14) and fungal ascocarps and spermogonia (black dots, single-headed arrow, see Fig. 13). Note that no conceptacles are present at the apices of the erect branches; 13. Transverse section through an immature ascocarp embedded in the algal thallus; 14. Longitudinal section through conceptacle showing zonately divided tetrasporangia; 15. Undivided tetrasporangial initial; 16, 17. Division sequence to form a mature tetrasporangium; 18. Longitudinal section of a maturing tetraspore. c=chloroplast, s=starch grains. Note osmiophilic inclusions similar to those observed in vegetative cells (Fig. 10). Note also the incomplete cleavage furrow (arrow) which presumably will complete division simultaneously with the two other cleavage furrows of the tetrasporocyte; 19. Germination of tetraspores in culture.

starch grains and osmiophilic inclusions (Fig. 18).

Released tetraspores are small (5 μm diam.) and pale in colour. In laboratory culture they germinated to form short filaments but did not develop further (Fig. 19).

Discussion

The presence of a systemic fungus in *Apophlaea sinclairii* was first reported by HAWKES (1981). KOHLMAYER and HAWKES (1983) subsequently described the fungal component of this mycophycobiosis more thoroughly and showed that it was referable to *Mycosphaerella apophlaeae* a species which was originally described from material of *Apophlaea lyallii*. Such a mycophycobiosis may also occur in some *Hildenbrandia* species, for example GARDNER (1917), BAARDSETH (1941), ARDRÉ (1959) and PUESCHEL (1982a, b) have all reported fungal hyphae in the conceptacles of *Hildenbrandia* spp.

It is not known what is controlling the initiation and development of upright growths from the crustose thalli of *Apophlaea sinclairii*. Grazers, availability of substratum, and seasonal scouring by sand and gravel may be important factors. Both crusts and uprights are extremely slow-growing (HAWKES, unpublished observations) making study of the developmental morphology and anatomy difficult.

Despite the new anatomical information for *Apophlaea sinclairii* presented in this paper the systematic position of *Apophlaea* remains uncertain.

In habit and anatomy *Apophlaea sinclairii* is more complex than species of *Hildenbrandia* which never form upright branched axes. The anatomy of the basal region of the crusts and core of the uprights of *A. sinclairii* is more elaborate than the simple parallel arrangement of filaments occurring in *Hildenbrandia*.

Placement of *Apophlaea sinclairii* in the Hildenbrandiaceae (DENIZOT 1968, CHAPMAN and PARKINSON 1974) was on the basis of similarities in the following characters: non-

calcareous crustose habit, small zonate tetrasporangia borne in conceptacles, small vegetative cell size, and the lack of basal rhizoids. DENIZOT (1968) reported that neither lateral cell fusions nor secondary pit connections formed in *Hildenbrandia*, however; recent ultrastructural studies of this genus have demonstrated the presence of secondary pits (CABIOCH and GIRAUD 1980 1982, PUESCHEL 1982b) which look similar to those found in *Apophlaea*. CABIOCH and GIRAUD (1982) reported that the secondary pits in *Hildenbrandia* seem to form as in the Corallinaceae (i.e. without the formation of a conjuctor cell). This seems to be the mode of pit formation in *Apophlaea* too. Another ultrastructural similarity between the two genera are the large osmiophilic inclusions present in most vegetative cells. The presence of these inclusions and absence of starch in vegetative cells of *Apophlaea* is unusual as is the abundance of plastoglobuli in the chloroplasts. AHMADJIAN (1982) reported that electron dense, lipid containing globules were common in lichen phycobionts growing under conditions of environmental stress. The lipid nature of these inclusions in *A. sinclairii* requires investigation to determine if *Apophlaea* is putting its fixed carbon into lipid rather than starch.

Recently PUESCHEL (1982a, b) reported on tetrasporogenesis in *Hildenbrandia*. He found that tetrasporocytes formed from transformed vegetative cells and that while no regenerative stalk cells were present tetrasporangia were successively initiated by subtending vegetative cells. This erosive mode of development was responsible for formation of the pit-like conceptacles. Such a mode of conceptacle development appears to be operating in *Apophlaea*, but this was difficult to follow in detail. Cleavage of the tetrasporocyte in *Apophlaea sinclairii* appears to be initiated successively and completed simultaneously as reported by PUESCHEL (1982b) for *Hildenbrandia* and other reds.

Rhodophycean species like *Apophlaea sinclairii* which produce only tetrasporangia and apparently lack sexual phases in their life

histories have been assumed to be apomeiotic tetrasporophytes, eg. *Hildenbrandia* (UMEZAKI 1969, DECEW and WEST 1977) and *Rhodophysema* (FLETCHER 1975 1977, GANESON and WEST 1975, MASUDA and OHTA 1975). However, a recent re-investigation of *Rhodophysema* (DECEW and WEST 1982) presents good evidence that the crusts are actually gametophytes producing solitary carpogonia which divide to form tetrasporangia directly following fertilization. Tetrasporophytes are absent from the life history. An examination of sectioned conceptacles from both fresh and preserved material failed to reveal evidence of such a mode of reproduction operating in *Apophlaea sinclairii*.

Another possibility is that *Apophlaea sinclairii* has a life history like other non-calcified crustose genera which were thought to produce only tetrasporangia. These crusts have been shown to alternate with heteromorphic gametophytes eg. *Petrocelis/Gigartina* (WEST 1972, POLANSHEK and WEST 1975, POLANSHEK 1977, WEST *et al.* 1978), *Cruoriopsis/Gloiosiphonia* (EDELSTEIN 1970 1972, EDELSTEIN and MCLACHLAN 1971, DECEW *et al.* 1981), *Cruoria/Halarachnion* (BOILLOT 1965), *Cruoria/Turnerella* (SOUTH *et al.* 1972), *Haematocelis/Schizymenia* (ARDRE 1977), *Porphyrodiscus/Ahnfeltia* (FARNHAM and FLETCHER 1976, CHEN 1977), *Petrocelis-Erythrodermis/Gymnogongrus* (DECEW and WEST 1981a), *Haematocelis-Cruoriopsis/Farlowia* (DECEW and WEST 1981b). During this investigation of *Apophlaea sinclairii* no evidence of a heteromorphic life history such as those reported above was obtained, however further culture study is needed to confirm this.

Despite the similarities between *Apophlaea sinclairii* and *Hildenbrandia* spp. placement of *Apophlaea* in the Hildenbrandiaceae should still be regarded as tentative. It is not presently possible to suggest where the affinities of *Apophlaea* may lie, however; the recent utilization of pit plug ultrastructure in red algal taxonomy (PUESCHEL and COLE 1982) provides a potentially useful technique for determining phylogenetic affinities of rhodophytes which lack female reproductive struc-

tures. Further studies of the ultrastructure, life history and pigment biochemistry of *Apophlaea* are needed.

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マイケル W. ホークス*: ニュージーランド特産の奇妙な紅藻 *Apophlaea sinclairii* の解剖的構造

本種は北ニュージーランド固有の海藻で、潮間帯上部の岩盤上に厚いタール状の殻状体として生ずる、この殻状体は円柱状の分枝する直立部を生ずる、殻状部は短い細胞列からなり、上部ではそれらの網目状に拡がって伸びている。基部には仮根が形成されない。二次原形質連絡が多数形成される。直立部の解剖的構造も殻状部に類似している。葉体全体にわたって子嚢菌類の1種 *Mycosphaerella apophlaeae* の無色の菌糸がみられる。四分胞子嚢巢が殻状部にも直立部にもみられ、年間を通じて環状に分裂した四分胞子嚢をもっている *Mycosphaerella* の子嚢果と精子器がしばしばみられた。*Apophlaea sinclairii* について異型の有性の世代が見出されなかった。すなわち雌性の生殖器官がわからないのでこの種の分類学上の位置は不明である。(* Department of Botany, University of British Columbia, Vancouver, B. C., Canada V6T 2B1)