

Ululania stellata gen. et sp. nov. (Rhodomelaceae), a new genus and species of parasitic red algae from Hawaii

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KIRK E. APT AND KRISTEN E. SCHLECH. 1998. *Ululania stellata* gen. et sp. nov. (Rhodomelaceae), a new genus and species of parasitic red algae from Hawaii. *Phycologia* 37: 157–161.

Ululania stellata Apt et Schleich gen. et sp. nov. infects two species of *Acanthophora* (Rhodomelaceae, Ceramiales) in Hawaii. Thalli are minute (to 3 mm in diameter), colorless pustules consisting of a central, relatively undifferentiated mass of radially elongated cells that bears numerous short (to 1 mm in length), radiating, unbranched fertile axes. Trichoblasts occur on dioecious male and female gametophytes, but not on tetrasporophytes. Procarps develop on the suprabasal cells of trichoblasts and consist of a four-celled carpogonial branch and a single-celled sterile lateral borne on the supporting cell. Trichoblasts on male gametophytes form shallowly lobed to obcordate leaflets on which the surface and most marginal cells bear spermatangia, a consolidated margin of sterile cells being absent. Tetrahedrally divided tetrasporangia occur in whorls of up to seven per tier of pericentral cells within stichidioid branchlets. Features of the vegetative axes, procarp, spermatangial trichoblasts, and tetrasporangial stichidia show the new genus to be an adelphoparasite belonging to the Chondrieae.

INTRODUCTION

There are approximately 4100 species of red algae (Kraft & Woelkerling 1990); just over 100 of these are parasitic on free-living red algal hosts (reviewed in Goff 1982). Red algal parasites are characterized by little or no pigmentation, relatively diminutive size, and the establishment of secondary pit connections between penetrating parasite cells and medullary cells of the host (Setchell 1918).

Almost 95% of parasitic Rhodophyta are termed 'adelphoparasites', meaning that they are so closely related to the hosts as to be members of the same family or, in the case of the large family Rhodomelaceae (Ceramiales), the same tribe. The greatest concentration of parasites is found in the Rhodomelaceae, where c. 30 species in 18 genera have been described (Goff 1982).

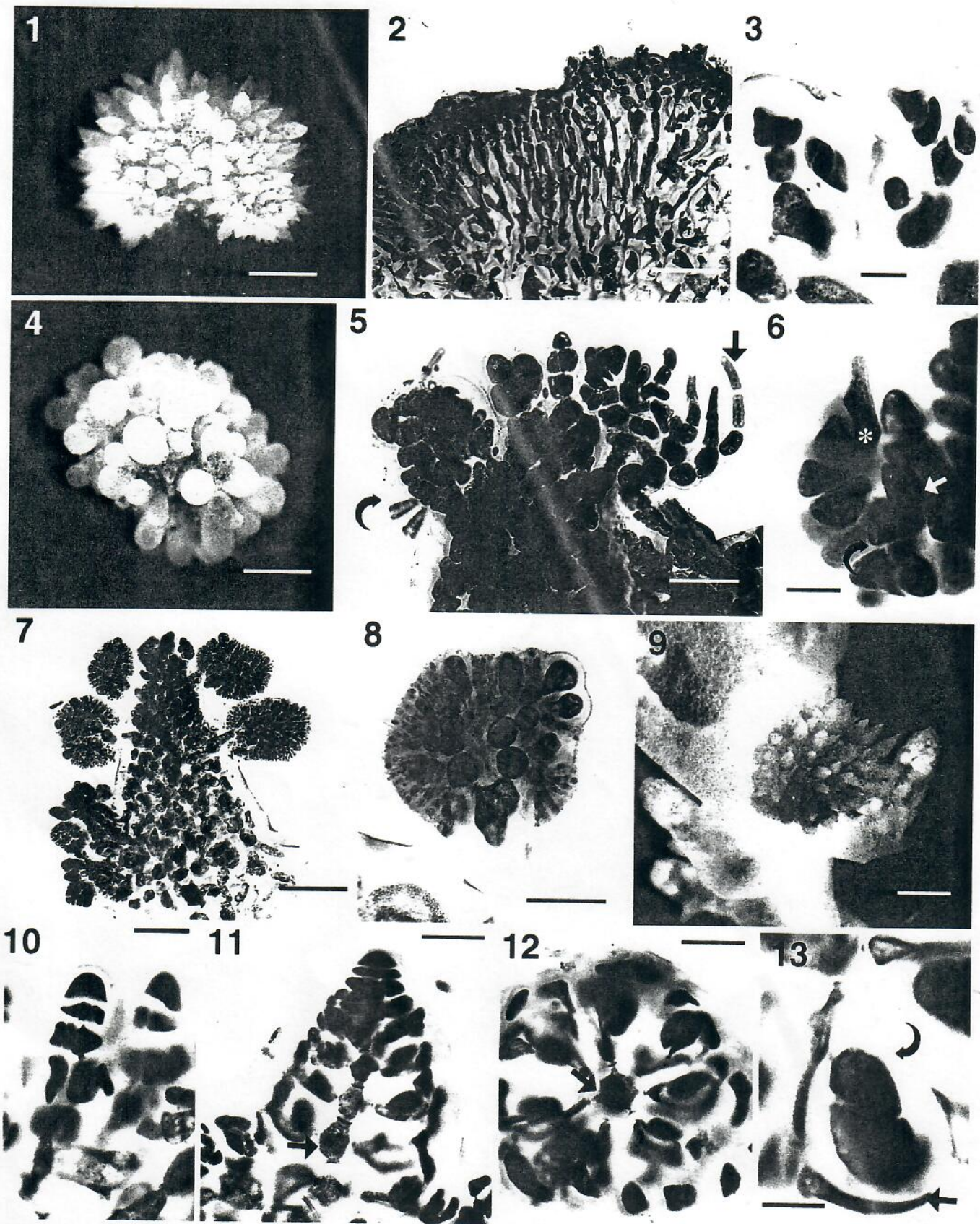
The Rhodomelaceae is subdivided into 16 tribes (Kraft & Woelkerling 1990), with most of its parasites belonging to the tribes Polysiphonieae and Laurencieae. Among the most distinctive of the tribes hosting parasites is the Chondrieae, which is defined primarily by the five periaxial cells of the vegetative axes, the common presence of 'lenticular' thickenings within the periaxial and surrounding inner cortical cells, and the distinctive, foliar spermatangial trichoblasts (Gordon-Mills & Womersley 1987). Until now, the only parasites known to occur on members of the Chondrieae were those of the obscure genus *Jantinea* (Morrill 1976b), which consists of a single species on *Chondria* from southern California; the even more obscure *Benzaitenia*, with a single species on *Chondria* from Japan (Morrill 1976a); and species of the largest parasite genus, *Janczewskia*, which, although usually occurring on *Laurencia*, are also recorded from species of *Chondria* in California (Apt 1987). *Chondria* is the most widely distributed member of the tribe Chondrieae, having at

least some representatives in most tropical to cool-temperate seas (Gordon-Mills & Womersley 1987). Other members of the tribe Chondrieae include the pantropical to subtropical genus *Acanthophora*, the New Zealand genus *Cladhymenia*, and the southern Australian *Husseyella* (Gordon-Mills & Womersley 1984). *Cladurus* and *Coeloclonium* are members with more restricted distributions and no parasites have been recorded.

At least three red algal parasites have been reported from the flora of the Hawaiian Islands. These include *Janczewskia hawaiiiana* Apt, found on *Laurencia nidifica* J. Agardh (Apt 1987); *Gelidiocolax mammillata* K.C. Fan et Papenfuss, found on *Pterocladia* sp. (Fan & Papenfuss 1959); and *Hypneocolax stellaris* Børgesen (Fan 1961), which occurs at times on *Hypnea cervicornis* J. Agardh and *H. chordacea* Kützinger, and in large numbers on the introduced *H. musciformis* (Wulfen) J.V. Lamouroux (Apt 1984).

Introduced algae are particularly significant components of the marine flora in Hawaii, because several have displaced native species over wide expanses of intertidal to shallow subtidal reefs and can be fairly accurately dated from the time of their introduction (Russell 1980). One such alga, which has come to dominate large reef areas since its first recorded appearance in 1952, is *Acanthophora spicifera* (Vahl) Børgesen, which Doty (1961) hypothesized may have entered the local waters on a heavily fouled barge towed from Guam in early 1950. Populations of this alga have been regularly monitored in the intervening years and have figured prominently in quantitative standing-crop surveys on the island of Oahu (Russell 1980). In March 1980, drift specimens of *A. spicifera* at Ewa Beach, Oahu, were discovered by K.E.S. and Gerald and Carolyn Kraft. These specimens hosted large numbers of what appeared to be a new taxon of diminutive red algal parasites. The subsequent consistent presence of such a distinctive entity on what is clearly an introduced host species prompted this

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Figs 1–13. *Ululania stellata* gen. et sp. nov.

Fig. 1. Habit of a tetrasporophyte (holotype, APT 1438) on *Acanthophora spicifera*. Scale bar = 1 mm.

Fig. 2. Cross-section of host showing the radially elongate internal cells of the erumpent parasite pustule and the early development of surface papillae. Scale bar = 100 μ m.

investigation and has led to the recognition that the alga constitutes both a new genus and species of adelphoparasite.

DIAGNOSIS AND OBSERVATIONS

Ululania Apt et Schleich gen. nov.

DIAGNOSIS: Thallus ex filamentis endophyticis per medullam hospitis ramificatis, cellulis conjunctiones secundarias ad cellulas hospitis formantibus, et pustula erumpenti sine ordinatione internali notata constans. Pustulae ex papillis superficialibus axes radiantes et determinatos et breves (ad 1 mm) multitudine portatae. Rami laterales uniaxiales, ex filamentis axialibus 5 cellulis periaxialibus et strato corticali exteriori constantes. Gametophyti masculini trichoblastos fertiles portati, his folioliformibus marginem steriles carentibus. Gametophyti feminini procarpia in cellulis suprabasalibus trichoblastorum ramosorum portati, procarpiis ex ramo carpogoniali 4-cellulato in cellula sustentanti cum 1 cellula laterali sterili constantibus. Tetrasporangia in verticillis in stichidiis producta, cum 6 vel 7 sporangiis in segmento axiale.

Thallus consisting of endophytic filaments ramifying through the host medulla, the cells forming secondary pit connections to cells of the host, and an erumpent, pustular body of tissue without distinctive internal organization. Pustules bearing large numbers of determinate, short (to 1 mm), radiating axes arising from papillar surface outgrowths. Lateral branches uniaxial, composed of a central axial filament surrounded by five periaxial cells and outer cortical layers. Male gametophytes bearing fertile trichoblasts in the form of foliar leaflets lacking a margin of sterile cells. Female gametophytes producing procarps on the suprabasal cells of branched trichoblasts, the procarps consisting of four-celled carpogonial branches borne on supporting cells that also bear a single-celled sterile lateral. Tetrasporangia produced in stichidia, in whorls of six or seven per tier of periaxial cells.

ETYMOLOGY: Named in honor of the late Carolyn Ululani Kraft, a Hawaiian who contributed significantly and enthusiastically to collections and studies of local and western Pacific marine algae.

TYPE SPECIES: *Ululania stellata* sp. nov.

Ululania stellata Apt et Schleich sp. nov.

Figs 1-13

DIAGNOSIS: Plantae in *Acanthophora spicifera* et *A. pacifica* loci dicti 'Hawaii' parasiticae. Thalli 1-4 mm in diametro, axibus stellatis ad 1 mm longis, dioecii, lamellis spermatangialibus ad 150 μ m latis.

Plants parasitic on the two Hawaiian species of *Acanthophora*, *A. spicifera* and *A. pacifica* (Setchell) Kraft. Thalli 1-4 mm in diameter, with stellate axes to 1 mm in length, dioecious; spermatangial plates to 150 μ m broad.

ETYMOLOGY: The specific epithet 'stellata' refers to the star-like appearance of the external portions of the parasite.

HOLOTYPE: APT 1438, tetrasporangial thallus (Fig. 1) on *Acanthophora spicifera*, low intertidal, rocky bench, Kapoho Pt., north side of Kawaiunui Canal, Kailua Bay, Oahu I., Hawaii, 10 May 1982; leg. K.E. Apt. Deposited as liquid-preserved specimen at Herbarium Pacificum, Bishop Museum, Honolulu, Hawaii (BISH).

ADDITIONAL SPECIMENS COLLECTED: On *A. spicifera*, front of bath house, Sandy Beach, Oahu I.: APT 1636, 12 June 1983; APT 1632, 6 July 1983. On *A. spicifera*, Ewa Beach, Oahu I.: APT 1637, 10 June 1983. On *A. spicifera*, Kapoho Pt., Kailua Bay, Oahu I.: APT 1565, 14 December 1982; APT 2592, 14 May 1990; APT 2593, 15 May 1990; APT 2594, 17 May 1990. On *A. pacifica*, front of bath house, Sandy Beach, Oahu I.: APT 1638, 12 June 1983. Deposited as pressed or liquid-preserved specimens at Herbarium Pacificum, Bishop Museum, Honolulu, Hawaii (BISH).

OTHER SPECIMENS EXAMINED: All on *A. spicifera*: BISH 517162, Barbers Pt., Oahu I., 11 November 1972, M. Doty; BISH 530542, Kaneohe Bay, Oahu I., 3 February 1972, G.A. Santos; BISH 519042, Diamond Head, Oahu I., 23 February 1974, H.J. Fortner; BISH 519043, Paiko Lagoon, Mauna Lua Bay, Honolulu, Oahu I., 10 March 1974, H.J. Fortner.

DISTRIBUTION: Although the primary host is pantropical, the parasite is known only from the island of Oahu.

HABITAT: *Acanthophora spicifera* is locally abundant in a wide variety of habitats. The parasites seem to occur primarily on low intertidal and shallow subtidal reef flats where water quality is good, as indicated by moderate to rapid water motion and a high degree of clarity. The parasites were not observed on *A. spicifera* thalli in areas of low water motion and moderate to high siltation. Infestations can be heavy (up to 50 individual parasites on single hosts 15-20 cm in length), but no apparent deleterious effects were evident. All sexual stages were found continuously in the field and no apparent seasonality was observed.

VEGETATIVE STRUCTURE: Plants form colorless protuberances 1-3 mm in diameter on the lower portions of both host species (Figs 1, 4, 9). Short, densely aggregated branches to 1 mm

Fig. 3. Detail of surface papillae. Scale bar = 10 μ m.

Fig. 4. Habit of female gametophyte on *Acanthophora spicifera*. Scale bar = 1 mm.

Fig. 5. Apex of a determinate lateral on a female gametophyte showing trichoblasts (straight arrow) and a pre-fertilization procarp surrounded by pericarp (curved arrow). Scale bar = 30 μ m.

Fig. 6. Supporting cell (curved black arrow) in a young procarp subtending a four-celled carpogonial branch terminated by a carpogonium (white asterisk) and a single sterile cell (white arrow). Scale bar = 10 μ m.

Fig. 7. A determinate axis bearing several spermatangial plates. Scale bar = 100 μ m.

Fig. 8. Mature spermatangial plate showing the internal skeleton composed of the dichotomizing trichoblast axes, the obovate terminal cells, and the surface layer of spermatangia borne on the interior and marginal cells. Scale bar = 40 μ m.

Fig. 9. Habit of tetrasporophyte on *Acanthophora pacifica*; formalin-preserved specimen. *Ululania stellata* has turned brown and *A. pacifica* is bleached. Scale bar = 1 mm.

Fig. 10. Early development of tetrasporangial stichidia from surface papillae. Scale bar = 20 μ m.

Fig. 11. Longitudinal section through a stichidial axis. Scale bar = 30 μ m.

Fig. 12. Cross section of tetrasporangial stichidia in which the central axial cell (arrow) is surrounded by seven periaxial cells. Scale bar = 30 μ m.

Fig. 13. Position of a tetrasporangium (curved arrow) on a periaxial cell arising from a central axial cell and enclosed by one of the two presporangial cover cells (straight arrow). Scale bar = 10 μ m.

long radiate in all directions from a central cushion of undifferentiated, radially elongated cells (Fig. 2) bound by a surface layer of papilliform excrescences (Figs 2, 3). Although lenticular thickenings are common in the hosts (Kraft 1979) and the host tribe (Gordon-Mills & Womersley 1987), they are not present in cells of the parasite. Determinate, unbranched laterals develop from the surface papillae and consist initially of a central axial filament surrounded by five periaxial cells. With distance from the apex, several layers of cortication develop external to the periaxial cells. The cortical cells, like the cells of the central cushion, also lack lenticular thickenings.

The internal portion of the parasite consists of ramifying filaments that grow between the pseudoparenchymatous inner cortical cells of the host and establish numerous secondary pit connections with them.

PROCARPS AND CYSTOCARP DEVELOPMENT: Female gametophytes produce dense aggregations of determinate laterals bearing cystocarps in various stages of development (Fig. 4). Trichoblasts are produced in a counterclockwise spiral and are short (to 200 μm in length) and sparingly dichotomous (Fig. 5). The suprabasal cell of the trichoblast cuts off five periaxial cells, the last-formed being adaxial and serving as the supporting cell. The supporting cell bears a four-celled carpogonial branch and an initially single-celled sterile lateral (Fig. 6). This lateral sterile cell was not observed to divide in any pre- or postfertilization stages. A well-formed pericarp is present prior to fertilization (Fig. 6), but the sequence of postfertilization stages was not observed. Mature cystocarps are obovate and reach 400 μm in diameter.

SPERMATANGIAL DEVELOPMENT: Densely aggregated determinate axes bearing large numbers of fertile trichoblasts (Fig. 7) are produced by male gametophytes. Spermatangial trichoblasts branch four or five times and are very condensed, each interior cell being the base of a dichotomy (Fig. 8). Cells of the trichoblast axes give rise to one or two layers of lateral cells that consolidate to form an irregularly contoured to obcordate plate (Fig. 8) and that in turn cut off spermatangial mother cells bearing one or two spherical to ovoid spermatangia 3–5 μm in diameter. Spermatangia form across the whole of the flattened surfaces of the fertile trichoblasts, as well as marginally, there being no consolidated border of sterile cells surrounding the fertile region as occurs on the spermatangial plates of the hosts (Børgesen 1918; Kraft 1979). Terminal cells of the trichoblast dichotomies are large and obovate; along with the pedicel cell, they are the only cells not dividing to form spermatangial mother cells (Fig. 8).

TETRASPORANGIAL DEVELOPMENT: The radiating determinate axes of tetrasporophytes (Fig. 9) differentiate from surface papillae (Fig. 10) and are more bilanceolate than those of gametophytes. At maturity the laterals are composed of 10–20 axial cells (Fig. 11), each bearing six or seven periaxial cells from which tetrasporangial mother cells differentiate (Fig. 12) in whorls of up to seven per tier. Tetrasporangia reach 50 μm in diameter and are enclosed by two presporangial cover cells (Fig. 13).

DISCUSSION

Features of the periaxial cell formation, procarp, and particularly, the spermatangial trichoblasts clearly ally *Ululania* with the Chondrieae of the Rhodomelaceae.

Three parasitic genera, *Jantinella*, *Benzaitenia*, and *Janczewskia*, occur on hosts belonging to the Chondrieae. All differ from *Ululania* and the remainder of the tribe by lacking plate-like spermatangial axes. *Jantinella*, from southern California, USA, and Baja California, Mexico, additionally differs in having five to seven pericentral cells, each dividing transversely once or twice (Abbott & Hollenberg 1976). Morrill (1976b) nevertheless allies *Jantinella* to the Chondrieae, primarily because of similar sterile groups in the procarp and the occasional coalescing of the highly branched spermatangial axes into a somewhat flattened structure.

Benzaitenia, a little-known parasite of *Chondria* and *Laurencia* from Japan, forms four to six periaxial cells that also transversely divide. In addition, it lacks both vegetative and fertile trichoblasts. Morrill (1976a) put it into the Bostrychieae, closely related to *Bostrychia* itself.

Janczewskia, which mostly occurs on species of *Laurencia*, is similar to its usual host in structural and reproductive features and is universally considered a member of the tribe Laurencieae (Apt 1987).

Like the occasionally flattened spermatangial axes of *Jantinella*, the spermatangial plates of *Ululania* lack a border of sterile cells, such as generally characterizes the genera of the Chondrieae (Kraft 1979). Gordon-Mills & Womersley (1987, fig. 19D), however, describe a species of *Chondria* (*C. angustissima* Gordon-Mills et Womersley) in which marginal cells of spermatangial plates are mostly fertile, indicating variation of this feature in what is considered by Morrill (1976b) to be the most advanced of the tribe. Morrill speculates that the fertile marginal cells of spermatangial trichoblasts in *Jantinella* represent a primitive character maintained in a highly reduced and probably derived genus, *Ululania*, with a pericentral number (five) typical of free-living Chondrieae and spermatangial plates characteristic of the tribe, would represent in Morrill's scenario a more advanced and independently reduced line within the Chondrieae. Additional evidence for separate lines of evolution within the tribe is furnished by the number of sterile groups formed in the procarps. Morrill (1976b) identifies two sterile groups as typical of the Chondrieae, as shown by *Jantinella* and *Chondria*. Gordon-Mills (1987) and Gordon-Mills & Womersley (1987) confirm the presence of both a basal and lateral sterile group in the European and southern Australian species of *Chondria* that were studied, although Dawson & Tozun (1964) reported a single sterile group for *C. nidifica*, and Kraft (1979) indicates a single sterile group for *Acanthophora pacifica*. These anomalous reports require confirmation, but in all cases the single sterile group is depicted as a pseudodichotomously branched chain of cells rather than the single cell present in *U. stellata*.

The geographic origins of the new genus are unclear. Although the primary host, *A. spicifera*, has been collected for many years in Hawaii since its introduction (Doty 1961), the parasite was not recognized until the 1980s. It is possible that *U. stellata* has simply been overlooked, although the lack of reports of any parasites on *A. spicifera* throughout its broad Indian Ocean/western Pacific range casts doubt on the likelihood that the parasite was introduced along with its host. The second host species, *A. pacifica*, is apparently native to the Hawaiian Islands, being otherwise recorded only from Tahiti and the Philippines (Kraft 1979). It may be that the parasite has been associated with *A. pacifica* all along but has gone

unnoticed because of the relative infrequency with which that host is encountered and collected. The parasite may have been transited from an uncommon host to one that was recently introduced and now is a very common component of Hawaiian reefs.

ACKNOWLEDGMENTS

The authors are very grateful for the suggestions and comments of Drs. G. Kraft and I.A. Abbott. Dr. R. Moe generously provided the Latin diagnoses and important nomenclatural advice. Portions of this work were conducted while K.E.A. was at the Carnegie Institution of Washington, Department of Plant Biology. This article represents CIW-DPB publication 1306.

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Accepted 8 February 1998