

On Two Species of *Kallymenia* (Rhodophyta: Gigartinales: Kallymeniaceae) from the Hawaiian Islands, Central Pacific¹

Isabella A. Abbott² and Karla J. McDermid³

Abstract: Two species of *Kallymenia* from the Hawaiian Islands, one rare, *K. sessilis* Okamura, and the other described here for the first time, *K. thompsonii*, n. sp., are examined, compared, and contrasted with other similar *Kallymenia* species. Both species are unusual because *Kallymenia* is generally regarded as a temperate taxon, and tropical or subtropical species are seldom encountered. The two species are alike in that they have a female reproductive apparatus that is monocarpogonial: wherein a single carpogonial filament is associated with a supporting cell also bearing an arrangement of subsidiary cells that is characteristic of some of the family Kallymeniaceae. In the genus *Kallymenia*, vegetative components shown in a cross section are a narrow outer cortex, often only three cells thick, followed inwardly by one to two layers of subcortical cells. In the two species studied here, there appears to be a constant shape and arrangement of subcortical cells in each species, whereas the number of medullary filaments and their arrangements appear to be less stable in their configuration than the subcortical cells. Branched refractive cells or stellate cells, which often occur in species of *Kallymenia*, were not seen in *K. thompsonii* and only rarely in *K. sessilis*. *Kallymenia thompsonii* commonly has perforations in the maturing blades, whereas *K. sessilis* does not.

Kallymenia sessilis OKAMURA, from central Japan, was included in the Hawaiian marine flora recently with a minimum of information because it was not known what the Japanese species looked like beyond its first description. A welcome opportunity was provided when a new species of *Kallymenia* was collected from Midway Atoll in the Northwestern Hawaiian Islands (NWHI), offering material that could be compared in detail with *K. sessilis*. The two species of *Kallymenia* reported in this paper occur in relatively deep

(6 to 10 m) to deeper (12 to 20 m) water depths. One of them, *Kallymenia sessilis* Okamura, 1934, was first reported from the Gulf of Tateyama, central Japan, and remains a rare plant in Japan (T. Yoshida, 1999, pers. comm.). It was described and illustrated by Okamura (1934:20–21, pl. 312, figs. 1–5) and was reported from the NWHI and in the main (southeastern) Hawaiian Islands by Abbott (1999). The second species, *Kallymenia thompsonii* Abbott & McDermid, n. sp., is described here.

The majority of marine algae previously reported from the NWHI, formerly known as the Leeward Hawaiian Islands, are from intertidal to snorkel depths (about 5 m) (Abbott 1989), but in recent years, dredging activities and scuba have made algae from greater depths available for study. Such current collections are obtained from depths of 10 to 100 m and have brought to light rare new records of species in the Hawaiian Islands (Abbott 1999), such as *Crouania mageshimensis* Itono, *Lejolissea pacifica* Itono (both Ceramiaceae), and *Kallymenia sessilis* Okamura from Japan, and *Malaconema minimum* Hol-

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² Correspondence: Department of Botany, University of Hawai'i at Mānoa, 3190 Maile Way, Honolulu, Hawai'i 96822 (telephone, 808-956-8073; fax, 808-956-3923; E-mail, iabbott@hawaii.edu).

³ Reprint requests: Marine Science Department, University of Hawai'i at Hilo, 200 West Kawili Street, Hilo, Hawai'i 96720 (telephone, 808-933-3906; fax 808-974-7693; E-mail, mcdermid@hawaii.edu).

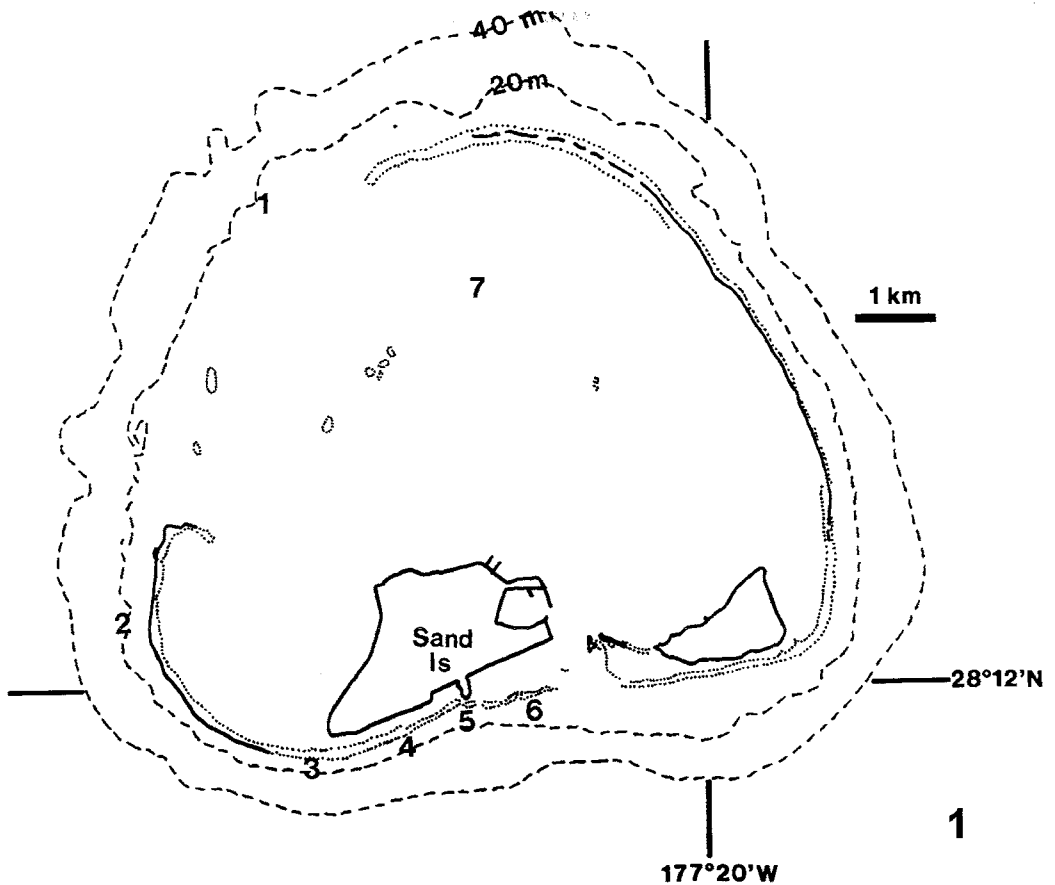


FIGURE 1. Map of Midway Atoll, Northwestern Hawaiian Islands. Collection sites of *Kallymenia thompsonii* are numbered: 1, Northwest Pass; 2, reef slope off Well's Harbor; 3, reef slope off Frigate Point; 4, reef slope between Frigate Point and "Bulky Dump"; 5, south reef slope ("Mick's Fifty"); 6, Fish Hole; 7, patch reef in north lagoon.

lenberg (Delesseriaceae) from the Marshall Islands, as well as undescribed species such as *Dudresnaya babbittiana* Abbott & McDermid (2001) from Midway, and *Kallymenia thompsonii*, n. sp., discussed in this paper.

The NWHI consist of ten major emergent islands and atolls, plus numerous shoals, pinnacles, seamounts, and reefs, of which Midway Atoll ($28^{\circ} 15' N$, $177^{\circ} 20' W$) (Figure 1) is historically, as well as phycologically, the best known. Of 205 species of marine algae reported from the entire NWHI in 1989 by Abbott, 102 were from Midway alone. The atoll consists of three small islets in a lagoon 8 km in maximum diameter. Midway Atoll is

the second most northeastern of the NWHI and was established as a National Wildlife Refuge in 1996. The U.S. Fish and Wildlife Service of the U.S. Department of the Interior is responsible for the maintenance of the atoll and has initiated a variety of studies, of which this is one, that documents the natural history of the atoll.

MATERIALS AND METHODS

Plants of *Kallymenia thompsonii*, n. sp., were collected using scuba at various sites inside and outside the lagoon at Midway Atoll from 1996 to 2001 (Figure 1). Plants were pressed

as herbarium specimens and a few portions were preserved in 5% formalin and seawater. Specimens were later sectioned and prepared for examination following the methods outlined by Tsuda and Abbott (1985), using 0.75% aniline blue, intensified with a drop of 1% HCl. Slides were mounted in a 35% glucose syrup. The type specimen will be deposited in the Herbarium of the Bishop Museum (BISH) in Honolulu (as BISH 654689), with duplicates distributed to the U.S. National Herbarium, Smithsonian Institution (us), and the University of California, Berkeley (uc). Microscope slides will be retained at BISH. Herbarium specimens of *K. sessilis* collected on Blonde Reef, Hilo Bay, Hawai'i, were sectioned and examined microscopically. Japanese specimens of *K. sessilis* loaned from the Okamura herbarium were also examined.

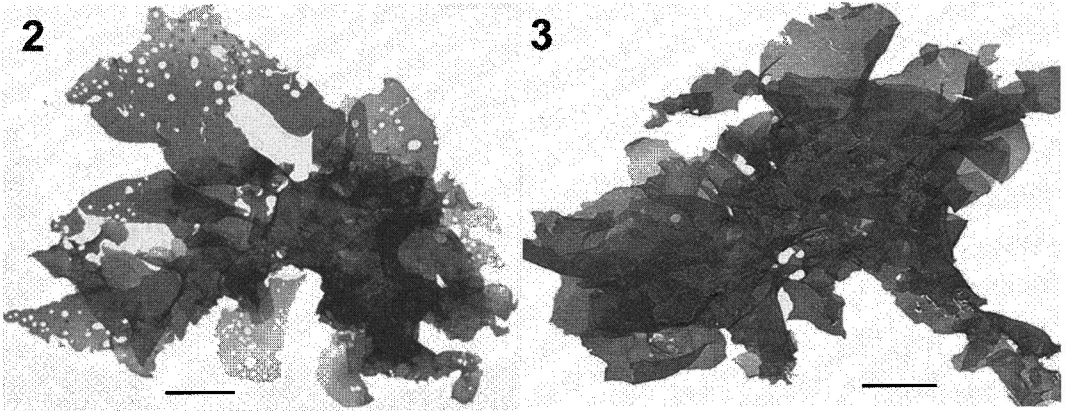
RESULTS

Kallymenia thompsonii Abbott & McDermid,
n. sp.
Figures 2–11

LATIN DIAGNOSIS: Plantae foliosae, paginis lubricis ubi vivae, compositae ex rosulis 2–3 stratorum laminarum communi haptero centrali. Lamina basalis grandissima et expansa ad 10(–18) cm diam.; laminae superae rosulae parviores, plus irregulares in circumferentia et diametro; lamina basalis ad substratum affixa per discum incrassatum vel crassitudes ventrales hic illic. Laminae atroseae ad vinaceras; ubi maturae et reproducti, laminas secundarias, ut pote laminulas secus margines distales edentes, vel marginibus erosio laceratisque librisque; aliter laminae marginibus non profunde crenatis vel late dentatis. Paginae laminarum aliquando foraminis amplitudine variabilia. In sectione transversa, laminae 140–250 μm latae, 2–3 stratis valde pigmentosarum cellularum corticalium, et 2–3 stratis grandium, irregulatim ovalium vel plerumque trapezialium cellularum subcorticalium. Omnis cellula subcorticalis ad 3–6 fila medullosa conjuncta. Cellulae externi corticis minutae, ovalis, minus quam 4 μm diam., cellulae ferenti circa 5 μm lata longaque et parum irregulari in forma. Medulla

centralis partem majorem sectionis formans, filis periclinatis et anticlinatis ad cellulas subcorticales et inter se trans medullam connexis; fila 3–13 μm lata, conspicuis plastis taeniformibus. Plantae cystocarpiferae numerosis filis periclinatis et parum paucioribus filis anticlinatis, autem plantae terasporangiferae filis anticlinatis periclinatisque similaribus numeris. Nec stellatae nec giganteo-refractivae cellulae observatae. Gametophyta et tetrasporophyta isomorpha. Tetrasporangia in cortice aggregata, numerosa; ubi matura, cruciatim divisa, 13–20 μm lata, 18–22 μm longa. Spermatangia non visa. Procarpia monocarpogonialia, uno filo carpogoniali inter 6 vel plus cellulas subsidiarias. Cystocarpia oculo nudo visibilia, circa 160–200 μm diametro, pustulas parvas manifestis carpostomatibus in pagina laminae formantes. Carposporangia sphaerica aspectu polari, 13–20 μm aspectu laterali. Fere omnes cellulae gonimoblasti in carposporangia transformantes, cellulis sterilis intermixtis.

ENGLISH TRANSLATION: Plants leafy, with slippery surfaces when fresh, consisting of rosettes of 2–3 layers of blades with a common central holdfast. The lower blade the largest and expanded, up to 10 (in one specimen 18) cm in diameter; the upper blades of the rosette smaller, more irregular in both circumference and diameter; the lowest blade attached to the substratum by a thickened disk or by ventral thickenings here and there. Blades dark rose to wine red; when mature and reproductive, putting forth secondary blades along the distal margins as bladelets, or with eroded and torn and free margins; otherwise blades with shallowly scalloped or broadly dentate margins. Surfaces of blades sometimes with variously sized perforations. In cross section, blades 140–250 μm wide, with 2, rarely 3, layers of strongly pigmented cortical cells, and 2–3 layers of large irregularly oval or commonly trapezoidal subcortical cells. Each subcortical cell connected to 3–6 medullary filaments. Outer cortical cells tiny, oval, less than 4 μm in diameter, with their bearing cell about 5 μm wide by 5 μm long and slightly irregular in shape. The central medulla forming the major part of the cross section, with periclinal and anticlin



FIGURES 2–3. *Kallymenia thompsonii* Abbott & McDermid. (2) Holotype, KM 4025a (BISH 654689), with cystocarps seen among holes in the thallus at upper left, and dark patch seen at the middle right indicating several layers of blades lying on each other, originating from a central region. The holes are not present in young and developing blades. Scale = 1.5 cm. (3) Paratype (KM 4025b) collected at the same place and date by the same collector as the holotype. Tetrasporangial. Scale = 1.5 cm.

filaments connected to subcortical cells and to each other across the medulla; filaments 3–13 μm wide, with conspicuous ribbonlike plastids. Cystocarpic plants with numerous periclinal filaments and slightly fewer anticlinal filaments, whereas tetrasporangial plants with similar numbers of anticlinal and periclinal filaments. Neither stellate nor giant refractive cells observed. Gametophytes and tetrasporophytes isomorphic. Tetrasporangia numerous, aggregated in the cortex; when mature, cruciately divided, 13–20 μm wide and 18–22 μm long. Spermatangia were not seen. Procarps monocarpogonial, with a single carpogonial filament among 6 or more subsidiary cells. Cystocarps visible with the unaided eye, about 160–200 μm in diameter, forming small pustules with obvious carpostomes on the blade's surface. Carposporangia spherical in polar view, 13–20 μm in lateral view. Nearly all gominoblast cells becoming carposporangia, intermixed with sterile cells.

TYPE MATERIAL: Holotype: KM 4025a (cystocarpic) (BISH 654689); paratype: KM 4025b (tetrasporangial) (BISH, US).

TYPE LOCALITY: At 12–19 m depths, Northwest Pass, Midway Atoll, collected by Karla J. McDermid, 19 September 1996, on coral rubble.

OTHER SPECIMENS EXAMINED: Collected at Midway Atoll (see Figure 1) by Karla J. McDermid, 28 June 1997, 13.5 to 20 m depths off Frigate Point, KM 4341; 2 August 1997, 20 m depth between Frigate Point and “Bulky Dump,” KM 4372; 2 August 1997, 20 m depth in Well's Harbor, KM 4383; 14 June 1999, 3–5 m depth in crevices of patch reef in north lagoon, KM 4673; 17 June 1999, 12 m deep at Fish Hole, KM 4697; 17 June 1999, 12 m deep on south reef slope at “Mick's Fifty,” KM 4698; 18 May 2001, 14 m deep at Fish Hole, IA 28447.

ETYMOLOGY: Named for Mark Thompson, whose vision for the opening of Midway Atoll for controlled ecotourism has made it possible for many to explore and appreciate the exciting natural resources of the Midway Atoll National Wildlife Refuge.

VEGETATIVE STRUCTURES: Plants are erect, in isolated clumps as rosettes composed of 2–3 tiers of blades (Figures 2, 3), a wine red, the largest blades 10(–18) cm in width below, with smaller-sized blades above, fastened ventrally by thickened portions of blades or a discoid holdfast. As the plants mature, the margins become torn and eroded in places so that the remaining outer blades (Figure 2) appear to be stipitate from the tat-

tered margin proximally. The lower blades are undulate along their circumferences and when dried appear folded upon themselves (Figure 3). Perforations sometimes occur on blades.

In cross sections, the blades show a two-layered (Figure 4) cortex, 13 μm tall ($n = 20$; range, 12.5–13.5 μm), in which the tiny outer cortical cells are only 3–4 μm when measured in the cross section or measured superficially. When examined from the surface, they appear to be paired above their bearing cells, never occurring in triplets. The inner subcortical cells (Figures 4–6, sub) are five or more times larger than the distally adjacent bearing cells of the outer cortex, and in this species inner subcortical cells are mostly trapezoidal (Figures 5, 6), although some cylindrical or rounded cells occur toward the central medulla (Figure 4) from which medullary filaments and individual cells are formed. The subcortical cells may be connected to one to several irregular layers of medullary filaments (Figure 6) that cross the medulla and are especially conspicuous in sections of the blade margins where the medullary filaments appear to have as many as 4–6 pit-connections with these large cells that have thickened walls (Figure 5). Irregularly shaped elongate cells with arms and highly refractive contents are not seen in this species, nor are stellate cells, which are generally star-shaped with pulled-out angular connections either to other similar cells or to filaments.

REPRODUCTIVE STRUCTURES: Tetrasporangia form small, rounded patches over the thallus (Figure 7). The tetrasporangia are nearly spherical and are slightly longer than broad. No spermatangia were observed. Carpogonial branch apparatuses and cystocarps are present in plants distinct from those that bear tetrasporangia. The carpogonial apparatus has a single 3-celled carpogonial (monocarpogonial) filament (Figures 8–10) among large, bone-shaped subsidiary cells (Figure 9, sbc). No connecting filaments were seen leaving this group of cells, nor were any subsidiary or associated cells seen with connecting filaments near them, which would be evidence of the transfer of a fertilized nucleus

from the carpogonial apparatus to an auxiliary cell. The conspicuous and deeply staining subsidiary cells belonging to the monocarpogonial apparatus were never seen at the base of a developing cystocarp, which would have perhaps indicated fusion of the carposporangium with the adjacent supporting cell.

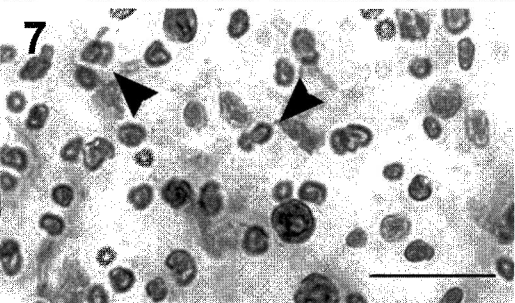
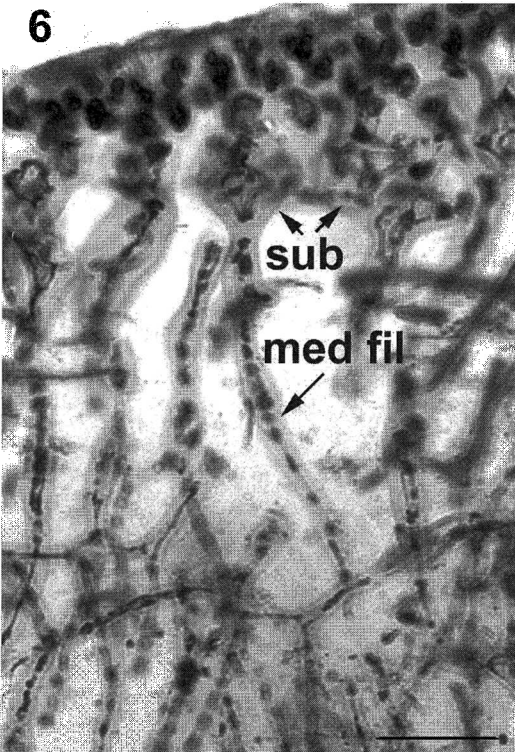
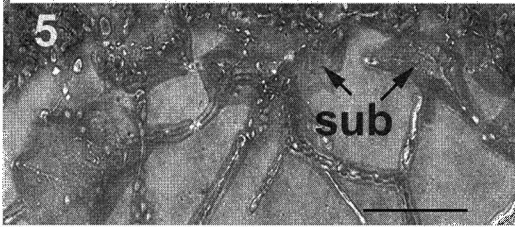
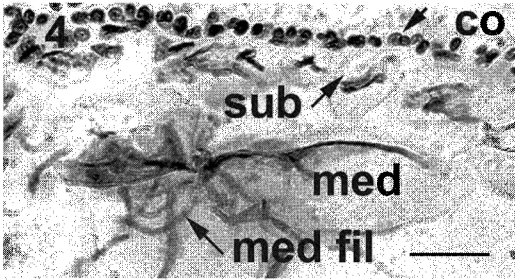
The mature cystocarp bears many small carposporangia about 10 μm in diameter (Figure 11) before release. They are borne among sterile filaments (Figure 11, sf), which is characteristic of taxa in this family. On release, they are somewhat spherical, 13 μm in diameter in polar view, and 20 μm in lateral view or longer than broad. The cystocarps make minute blisters on the surface; each has a clear carpostome.

Kallymenia sessilis Okamura

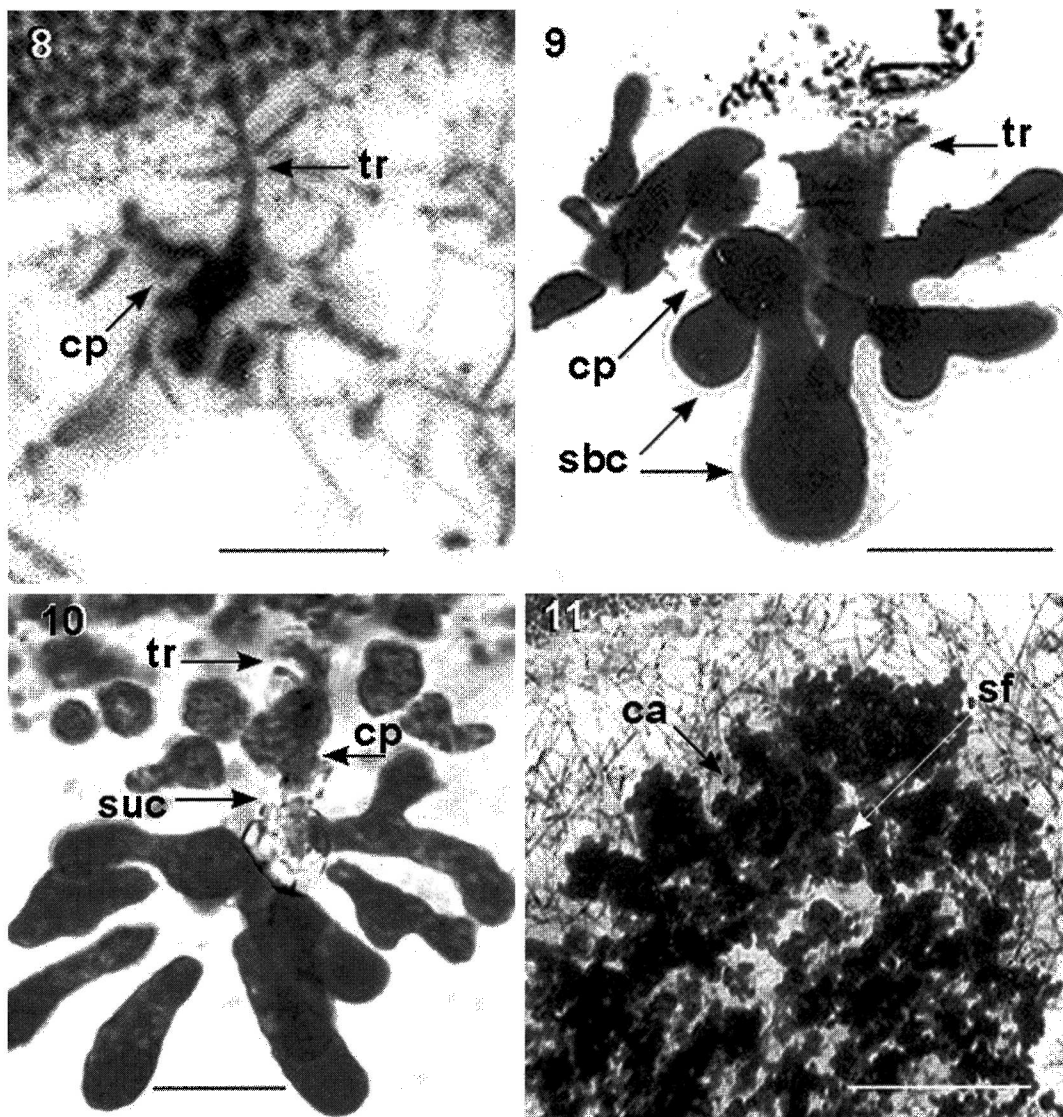
Kallymenia sessilis Okamura, 1934, *Icones of Japanese Algae*, 7 (3): 20, pl. 312.

Algae dark bluish red, or brownish red, forming flat blades in clusters, or singly, or membranous and broad, sometimes filmy, with shallow or deep lobes (Figure 12), attached by thickened portions of lower margins, or by several pegs; blades with entire margins; outer cortex 20 μm tall, the tiny outermost cells 2–3 μm in diameter, innermost (subcortical) cells 50 to 150 μm wide, rounded (Figure 13), attached by elongated pit-connections to similar adjacent cells and to medullary filaments (Figures 14, 15); medullary filaments consisting of cells 8–13 μm in diameter, of various lengths, mostly periclinally directed, not thickly dispersed, and relatively short. Refractive cells linear and very rare.

Spermatangia superficial, 2–3 attached on outer cortical cells in patches. Procarys with one carpogonial branch (monocarpogonial) and 5–6 subsidiary cells per supporting cell. Immediate postfertilization events not observed. Cystocarp (Figure 16) 150 to 200 μm in diameter, slightly elevating the cortical layers, forming carposporangia amidst sterile filaments that extend beyond the spore mass; in surface view, cystocarps each appearing like small blisters, each with a carpostome.



←
 FIGURES 4-7. *Kallymenia thompsonii*. (4) Cross section showing two-layered cortex (co) (top arrow) with large subcortical (sub) cells below, and formation of secondary filaments that will become medullary filaments (med fil). The section is from the center of the blade. med, medulla. Scale = 40 μ m. (5) Cross section to show triangular and trapezoidal subcortical cells (sub) attached to medullary filaments. Phase contrast micrograph. Scale = 40 μ m. (6) Oblique to median section showing several layers of squashed cortical cells at top, and trapezoidal subcortical layer (double arrows) beneath a cortex, with medullary filaments (med fil) (single arrow) attached to subcortical cells (sub) and to each other. Scale = 40 μ m. (7) Surface view of scattered tetrasporangia (larger dark objects) among paired cortical cells (arrowheads). Scale = 40 μ m.



FIGURES 8–11. *Kallymenia thompsonii*. (8) Portion of young monocarpogonial arrangement showing parts of young carpogonium (cp) with trichogyne (tr) reaching the cortex. Scale = 40 μ m. (9) Squashed monocarpogonial apparatus, showing trichogyne (tr) at top, part of carpogonial filament (cp) hidden by subsidiary cell, and several lobed subsidiary cells (sbc). Scale = 30 μ m. (10) Squashed subsidiary cells showing relationship to supporting cell (suc), and carpogonium (cp) with displaced trichogyne (tr). Scale = 30 μ m. (11) Portion of mature cystocarp with carposporangia (ca) mixed with sterile filaments (sf) in the medulla. Scale = 40 μ m.

Tetrasporangia (Figure 17) are in scattered patches in the cortex, nearly spherical to slightly elongated, 18–26 μ m in diameter by 26–39 μ m long.

DISTRIBUTION: Gulf of Tateyama, central Japan (type locality); Hawaiian Islands from Kure Atoll, French Frigate Shoals, and Nihoa Island (NWHI), and Kaua'i, O'ahu, Maui,

12

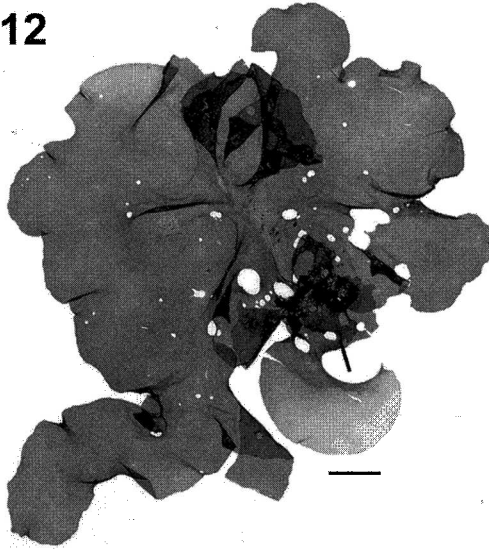


FIGURE 12. Hawaiian specimen of *Kallymenia sessilis* (KM 5050), a species from Japan, showing broadly rounded lobes, no layers of blades, and thicker blades than the thallus of *K. thompsonii*, collected at Blonde Reef, Hilo, Hawai'i Island, 6.5 m depth, 18 August 1995. Scale = 3 cm.

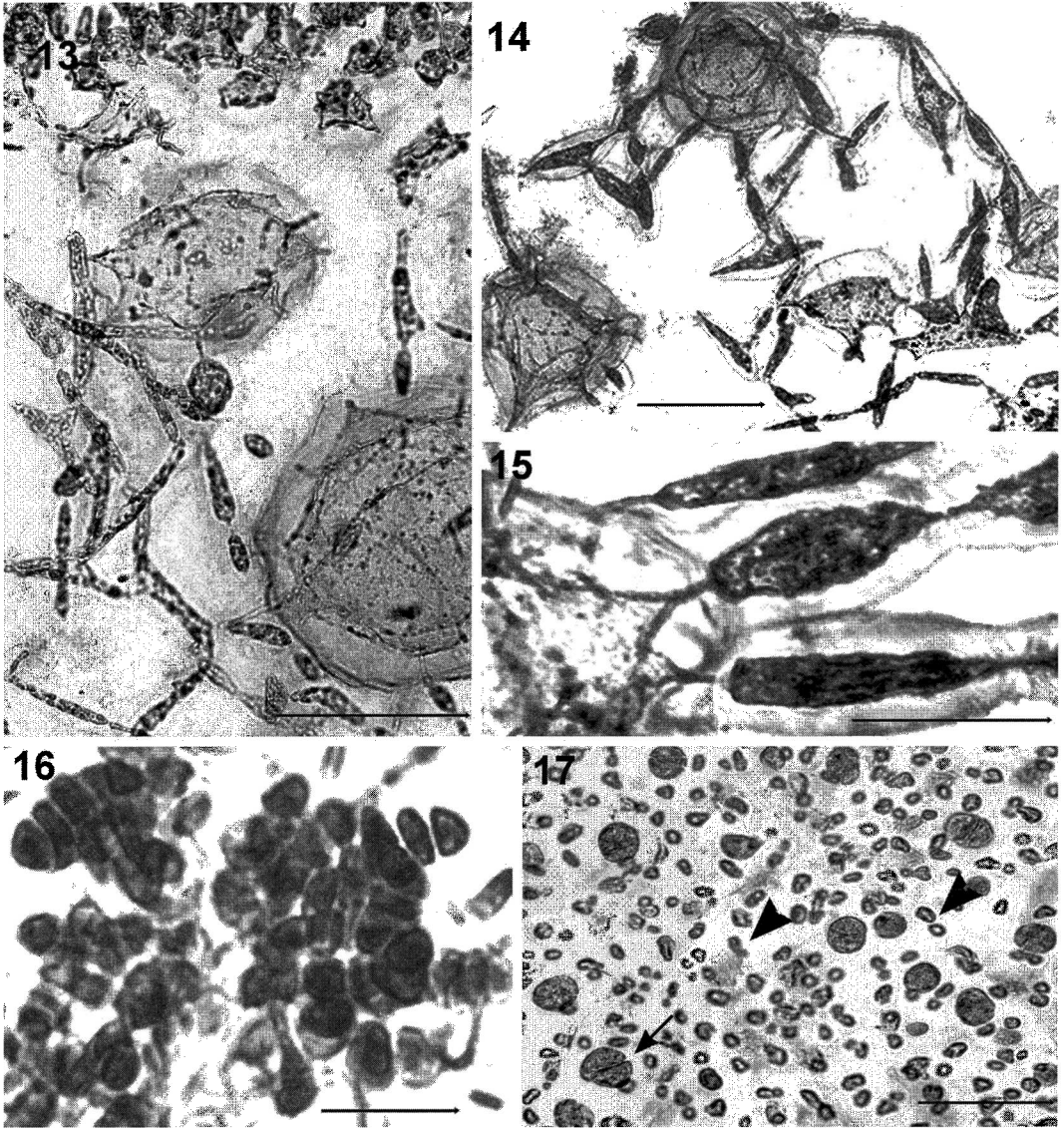
and Hawai'i Islands among the main south-eastern Hawaiian Islands. All collections were made at depths of 1 to 10 m, often growing among living coral.

This description is largely based upon that of Abbott (1999), with additional information from specimens that were collected subsequently and not included in that publication. The greatest similarity between this description and that of Okamura (1934) is in the shapes of the thick-walled, rounded subcortical cells (Figures 13–14 in this paper and Okamura's pl. 312, nos. 3, 4). Indeed, in many sections of the type specimen of *Kallymenia sessilis* from the Okamura herbarium (SAP), the only feature found that could usefully be compared with the more recently collected Hawaiian material was the round, thick-walled cells. The Japanese material had cell walls that had polymerized so much from age that they shattered, rather than yielding to a sharp razor blade, and the material "gelatinized" completely on application of water or detergent.

The greatest differences are shown in Figure 15, in which the relationship of the filamentous medullary cells to the subcortical

cells is detailed; in Okamura's plate the medullary filaments are not shown at all. In most modern studies of the Kallymeniaceae (e.g., Womersley 1994), the structure of the medulla is shown in most taxa. A further difference is the thickness of the blades of the Japanese specimens, 130–160 μm , compared with 350–400 μm widths in the Hawaiian plants.

Table 1 compares and contrasts various morphological, anatomical, and reproductive characteristics of several *Kallymenia* species. The Hawaiian species, *K. sessilis* and *K. thompsonii*, are juxtaposed with other Pacific Basin and one South African species that share similar general foliose blade morphology, including the presence of perforations. These species were also chosen for comparison because reproductive material has been described and well illustrated. This collection of taxa immediately can be divided into two groups: species with polycarpogonial carpo-gonial branch systems (*K. cribrogloea* Womersley & Norris, *K. papenfussii* Norris, *K. pertusa* Setchell & Gardner, and *K. rosea* Womersley & Norris), and species with monocarpogonial carpo-gonial branch systems (*K.*



FIGURES 13–17. *Kallymenia sessilis*. (13) Squashed, rounded subcortical cells showing attachment of several photosynthetic filament/medullary filaments from each cell. Scale = 50 μm . (14) Detail of arrangement of several medullary filaments and their connections to subcortical cells, and the thickness of the walls. Scale = 50 μm . (15) Three elongated, darkly stained medullary cells in the middle of the picture show protoplasmic (“pit”) connections from the subcortical cell on the left to other medullary cells on the right, an indication that the medulla is filamentous. Scale = 70 μm . (16) Developing carposporangia within a cystocarp. Scale = 20 μm . (17) Superficial view of a tetrasporangial patch with arrowheads showing paired tops of cortical cells. Arrow points to a tetrasporangium that has divided. Scale = 40 μm .

TABLE 1
Comparison of Perforate *Kallymenia* Species with *K. sessilis* and *K. thompsonii* from Hawai'i

Parameter	<i>K. cribrigloea</i> ^a	<i>K. cribrosa</i> ^a	<i>K. papenfussii</i> ^b	<i>K. perforata</i> ^c	<i>K. pertusa</i> ^d	<i>K. rosea</i> ^e	<i>K. sessilis</i> ^f	<i>K. thompsonii</i> ^g
Habit	Foliose, undivided or lobed, gelatinous, and firm	Foliose, undivided, margins smooth, gelatinous, and firm	Cuneate thallus, lacinate at broad end, thin	Undulato-plaited, somewhat umbilicated, waved, entire margin, lobed, strongly adherent	Irregular outline, crenate to serrate margin, thin	Foliose, lobed with leaflets on surface, soft, rubbery, thin	Clusters of large flat blades, lobed, entire margins	Rosettes, tiers of 2-3 blades, undulate margins
Color	Rose to brownish red	Rose red	Light rose red	Deep crimson lake to rose to dirty red	Rose red	Rose red	Rose red to brownish red	Dark rose or wine red
Attachment	Short stipe with discoid holdfast 1-3 mm diam.	Subsessile or short stipe with holdfast 1-3 mm	Single stipe and holdfast	Minute scutate basal disks or wherever touches	Attached to <i>Sargassum</i>	Short stipe	Thickened portions, pegs	Disk or thickened blade edges
Thallus size	50 × 50 cm	30 × 30 cm	18 × 11 cm	30-60 cm × 30-60 cm	5-35 cm length × 14 cm wide	30 × 30 cm	9-18(30) cm length	Up to 10 cm
Cross section (μm)	250-700	200-500(1,000)	122 at margins, 1,143 at base	1,140	300-370	Dried <100(150), fresh (150)250-300	350-400 ^b 130-160 ^j	140-250
No. of cortex layers	2 to 4	3 to 4	1	1 to 2	2 to 4	2 to 3	2, width = 20 μm	2, width = 13 μm
Outer cortical cells (μm)	5-9(12) angular	(3)4-6(7) rounded	— rounded	—	4-6, palisadelike	5-9, compact, round to ovoid	2-3, ovoid	3-4, rounded
Inner cortical cells (μm)	Oval to polygon	Ovoid to polygon or spherical	Angular, elongate	Roundish	Large angular	Ovoid, with large intercellular spaces	Rounded-obovate, 52 × 52 to 78-92 × 97-115, inner wall thickened	Trapezoidal 15-39 × 30-80, no thickened wall
Stellate cells	Light staining 50-100 μm with arms 1-2× as long as cell body	Light staining, (40)90-160 μm, arms rarely longer than cell body	Yes, deep staining	—	Yes, filled with dense material 30 μm diameter	Light staining, about 50 μm diameter	Refractive cells rare, linear, 5 × 130 μm	None observed

Med. filaments diam. (μm)	4–10(14) often swollen	(4)6–10	1–2.5	Laxly interwoven	3–4.0	3–8, sparse, loose, coarse	5–10	3–13
Carpogonial branch system	Polycarpogonial	Monocarpogonial	Polycarpogonial	Monocarpogonial	Polycarpogonial	Polycarpogonial	Monocarpogonial	Monocarpogonial
Auxiliary cell	8 subsidiary cells	3–5 subsidiary cells	5–8 subsidiary cells	6–11 auxiliary cells	4 subsidiary cells	5–9 subsidiary cells	—	—
Carposporangia (μm)	Subspherical, 14–30	Spherical-ovoid, (10)14–20	—	Spherical-ovoid	—	—	10 \times 10	13 \times 20
Tetrasporangia (μm)	Ovoid 22–36 \times 17–25	Ovoid, 20–28 \times 17–19	20–22 diameter	—	—	Ovoid, 14 \times 24	18 \times 20	13 \times 20
Perforations	Scattered: large (1–2 cm) and small (1–2 mm)	Scattered evenly: large (< 5 mm) and small (1–2 mm)	Irregularly scattered: circular, variable sizes	On plants of all ages, circular to oblong, up to 3 cm	Irregularly spaced, many, large, up to 40 mm	Some	Rare, without pattern, 1–5 mm	Common, irregularly spaced, 2–4 mm
Distribution	S Australia, 7–40 m deep	W and S Australia, 3–40 m deep	S Africa in drift	Japan, Ceylon, Tropics	Gulf of California, Mexico, 25 m deep	Botany Bay, NSW, 18 m deep	Central Japan, Hawaiian Islands, 1–10 m deep	Midway Atoll, 12–20 m deep

Note: Data in this table are derived from literature references, calculations based on figures and descriptions of non-Hawaiian species, and actual observations of Hawaiian specimens.

^a Womersley and Norris (1971) and Womersley (1994).

^b Norris (1964).

^c Okamura (1912) and Segawa (1965).

^d Setchell and Gardner (1924) and Norris and Norris (1973).

^e Womersley and Norris (1971) and Womersley (1973).

^f Okamura (1934), Segawa (1965), and Hawai'i specimens.

^g Hawai'i specimens.

^h Hawai'i specimens.

^j Japan specimens.

cribrosa Harvey, *K. perforata* J. Agardh, *K. sessilis* Okamura, and *K. thompsonii* Abbott & McDermid, n. sp.). The latter four monocarpogonial species are similar in the display of their subsidiary cells in the carpogonial branch system and sporangial measurements (when reported). However, these four monocarpogonial species differ among themselves in shapes and sizes of blades, attachment, blade thickness, inner cortical cell shapes, and in the position of their medullary filaments (periclinal versus anticlinal). The two Hawaiian species are similar in that they are monocarpogonial with conspicuous bonelike subsidiary cells, and they have large subcortical cells that contribute to the formation of the medullary filaments directly through numerous secondary pit-connections. However, thanks to abundant material for study, we were able to document that these two species consistently differ in other characteristics as well, including blade habit, size of cross sections, shapes of large subcortical cells, and carposporangial and tetrasporangial sizes. Of the monocarpogonial, foliose, tropical species compared in Table 1, *K. thompsonii* is the only one that forms low-growing rosettes, has the smallest blade dimensions, has the thinnest cross section, shows trapezoid-shaped inner cortical cells, lacks refractive cells, and commonly has irregularly scattered small perforations. Blade perforations are rare and randomly positioned in *K. sessilis* (Segawa 1965); large and small perforations are scattered evenly throughout the blades in *K. cribrosa* (Womersley and Norris 1971), and in *K. perforata* the large holes dominate the blade, creating an *Ulva reticulata*-like appearance (Okamura 1912, pl. 86)—all very different from *K. thompsonii*.

DISCUSSION

When faced with the identification of foliose Rhodophyta, several features can be applied generally to various species of *Halymenia* and *Cryptonemia* (Halymeniaceae) and shared with species of *Kallymenia* (Kallymeniaceae), such as attachment, size of the blade, width of the cross section, anticlinal medullary filaments, and the number of cortical layers.

Slender, elongate, highly refractive cells may be found in species of *Cryptonemia* and *Halymenia*, as well as other species of *Kallymenia* (Norris 1957, Chiang 1970), and may be abundant or few in various parts of the same thallus in *K. oblongifruca* (Setchell) Setchell (Abbott 1968), for example. The anatomy of most *Kallymenia* species seen in Norris (1964), Womersley and Norris (1971), and Womersley (1994) shares a preponderance of periclinal filaments in the medulla, whereas anticlinal filaments are common in the two Hawaiian *Kallymenia* species. Anticlinal medullary filaments are also one of the important features of *Halymenia*. The two *Kallymenia* species discussed in this paper differ from *Halymenia* in terms of the sizes and shapes of the inner cortical cells (Kraft and Abbott 1997) (in general smaller in *Halymenia*, with a few more subcortical layers). More important, members of the genus *Kallymenia* show a cystocarp in which carposporangia are developed among many sterile filaments, not true of any species of *Halymenia* or *Cryptonemia*. Among these three "red blade" genera, only *Kallymenia* shows the characteristically large subsidiary cells that are the hallmark of *Kallymenia* and other genera of the Kallymeniaceae. These last two features are therefore pivotal, and are required when identifying species within the genus and the family. We emphasize these reproductive features because the bulk of tropical red, bladelike algae are sterile when examined and not well enough known to identify in that state.

The principal reproductive difference between the two Hawaiian species and the type species of the genus, *Kallymenia reniformis* (Turner) J. Agardh (1851), as well as some morphologically similar species (see Table 1), is that the Hawaiian species have one carpogonial branch per supporting cell (monocarpogonial); whereas *K. reniformis* (Hommersand & Ott 1970), *K. cribrogloea*, *K. papenfussii*, *K. pertusa*, and *K. rosea* have two or more carpogonial branches per supporting cell (polycarpogonial). The bulk of *Kallymenia* species and genera in the Kallymeniaceae in Australia (Womersley 1994) in which the carpogonial apparatus is known show the monocarpogonial arrangement associated

with the supporting cell. Four foliose species that show a monocarpogonial carpogonial branch system and conspicuously lobed or "bone-shaped" subsidiary cells of the carpogonial branch apparatus are now reported from the Indo-Pacific Ocean: *Kallymenia cribrosa*, *K. perforata*, *K. sessilis*, and *K. thompsonii*. The monocarpogonial condition is thought to be more advanced evolutionarily than the polycarpogonial one (Norris 1957: fig. 22). Assuming that fertilization had taken place, we did not observe a connecting filament leaving the monocarpogonial apparatus and its subsidiary cells, nor did we observe a developing auxiliary cell and its subsidiary cells that might serve as the site of initiation of the gonimoblast. Should these connecting structures not be found, the implication is that in these species of *Kallymenia* it is possible that this step in development has been eliminated and the supporting cell of the single carpogonial branch is serving as the site of gonimoblast initiation, as postulated by Norris (1957) for *Euthora* and *Callocolax*.

To distinguish species in *Kallymenia* requires a shift of emphasis to vegetative structure and assessment of enough specimens to understand the variation in the selected features. In a survey of foliose, perforate species of *Kallymenia*, we found that the sizes and shapes of subcortical (inner cortical) cells varied among these species (Table 1), so that examination of many sections of each might show nearly all types of cells. However, there seemed to be a preponderance of one or another kind in each species. Together with the presence or absence of stellate cells and/or refractive cells, these cellular differences seem to contribute one of several adequate characteristics by which species may be distinguished. At least for the material we have of *K. sessilis*, the large, rounded to obovate cells of the subcortex that lie just below the cortical cells are contrasted with the numerous trapezoidal cells in a similar position in *K. thompsonii*. It is possible that more material, perhaps collected in a different season, may show that these shapes and sizes are not species-specific, but at this time we find them to be fairly constant in both reproductive and sterile specimens. The rounded subcortical

cells are found in the same specimens that bear slender, highly refractive, elongate cells among the subcortical cells in *K. sessilis*; these are lacking in *K. thompsonii*. In addition, blade perforation frequency, pattern on the blade, and size varied substantially among the species, enough to distinguish *K. thompsonii* from other monocarpogonial species. Finally, *K. thompsonii* with its tiers of blades that form rosettes is distinctive for reported species of *Kallymenia*.

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