Aspects of the morphology, ultrastructure and distribution of the two species of Yamadaea SEGAWA (Rhodophyta, Corallinaceae)

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Examination of the morphology and ultrastructure (with the scanning electron microscope) of Yamadaea melobesioides Segawa and Y. americana DAWSON et STEELE provides additional criteria for distinguishing them. Differences include colour, frond size, shape and density, number of intergenicula per frond, and the size and position of conceptacle ostioles. In Y. americana epithallial cells are larger and have less pronounced cell walls. Trichocytes are reported for the first time in Yamadaea, although they were found only in Y. melobesioides. The distributions of the two species are revised, with Y. melobesioides known only from Japan and Y. americana known only in North America from the Queen Charlotte Islands, British Columbia to Monterey, California.

Key Index Words: Algal distribution; Corallinaceae; scanning electron microscopy; Yamadaea.

In the Corallinaceae (Rhodophyta), Yamadaea is unusual in appearance. A thallus is comprised of an extensive epilithic crustose base from which arise erect, articulated fronds (Segawa, 1955). However, unlike other articulated coralline algae, the fronds are limited to one or sometimes two intergenicula and attain a maximum height of about 2 mm (SEGAWA, 1955; DAWSON and STEELE, 1964). Anatomically and reproductively, the fronds of Yamadaea are similar to those of Corallina (SEGAWA, 1955; JOHANSEN, 1969).

Yamadaea is presently known only from the north Pacific. Originally described from Japan, the type species, Y. melobesioides SEGAWA (1955), was later reported from California (HOLLENBERG and ABBOTT, 1966). A second species, Y. americana DAWSON et STEELE (1964), was first described from the San Juan Islands, Washington, but now this species is known as far north as the Queen

Charlotte Islands (HAWKES et al., 1978). Other than papers in which the two species are described, references in the literature are limited to range extensions. The present study was initiated to consider in detail the morphology of these species and to re-examine the application of the name Y. melobesioides to coralline algae in the eastern Pacific. This work is part of a larger study in which surface structures (as seen with the scanning electron microscope-SEM) provide additional characteristics for specific and generic delimitation in the Corallinaceae (see GARBARY, 1978; GARBARY and SCAGEL, 1979; GARBARY and VELTKAMP, 1980; and GARBARY and JOHANSEN, 1980 and in prep. for other contributions).

Materials and Methods

Specimens of *Yamadaea americana* examined were from the following herbaria: University of British Columbia (UBC); University of California, Berkeley (UC); Allan Hancock Foundation Herbarium, Los Angeles (AHFA); and the G.M. Smith Herbarium, Monterey, California (GMS). Material of Y. melobesioides was collected by H.W.J. and Dr. T. MASAKI, and fragments of these plants are deposited in UBC. Few specimens of Yamadaea have been collected, hence this report is based on three collections of Y. melobesioides and 10 of Y. americana.

Scanning electron microscopy was carried out as follows: fragments of herbarium specimens were rinsed in tap water, air dried, mounted on stubs with a silver conducting paint and coated with gold. Specimens were examined in a Cambridge Stereoscan Mark 2A at 20 kv. During specimen preparation the cell protoplasts disintegrate, leaving only the calcite cell walls and cellular debris (see also GARBARY, 1978, and GARBARY and VELTKAMP, 1980).

Results and Discussion

Our observations support the proposal of

DAWSON and STEELE (1964) that Yamadaea americana is distinct from Y. melobesioides and provide additional characteristics that strengthen this distinction (see Table 1). DAWSON and STEELE (1964) noted that the erect fronds of Y. americana were 2-3 Y. melobesioides. times as tall as in Hollenberg and Abbott (1966)and ABBOTT and HOLLENBERG (1976) inferred that size could not distinguish these taxa because supposed material of Y. melobesioides was similar in size to Y. americana. We have examined several collections of Yamadaea from the Queen Charlotte Islands to Monterey, California. Based on the criteria proposed by DAWSON and STEELE (1964), all North American plants can be accommodated in Y. americana. Our observations, however, extend the range of several morphological characteristics. Thus, in the type description of Y. americana, intergenicular diameter was given as up to 610-650 μ m. Our studies show greater variation, with measurements of 590-1020 μ m in mature plants. This contrasts with the range of 290-600 μ m for Y. melobesioides. Despite the overlap in

Table 1. A comparison of some morphological features of Yamadaea melobesioides and Y. americana.

Characteristics	Species	
	Y. melobesioides	Y. americana
Number and arrangement of fronds	abundant and tightly clustered	few and usually scattered
Thallus colour	dull purple-pink	rose-pink
Number of intergenicula/frond	1	1-2
Frond height	450-650 μm	1000-2000 μm
Frond diameter	350-550 μm	700-1000 μm
Frond shape	obovate	clavate
Ostiole position	strictly apical	apical to eccentric
Diameter of ostioles	30-40 µm	60-80 µm
Trichocytes	common to absent	absent
Surface structure	walls and concavities well developed	walls and concavities poorly developed
Size of concavities $(\pm s.d.)$	6.0±0.9 μ m	12.1 \pm 1.3 μ m
Cell wall thickness (\pm s.d.)	$1.8\pm0.7~\mu\mathrm{m}$	$1.4 \pm 0.4 \ \mu m$
% of thallus in concavities	40-55%	69-75%

measurements, all populations easily fit into one size category or the other.

Several aspects of gross morphology either not commented upon or not emphasized in earlier studies readily distinguish the two species. (1) Yamadaea melobesioides is dull purple-pink or vinaceous to almost grey, whereas Y. americana is generally rose-pink in colour. (2) The fronds of Y. melobesioides are more densely aggregated than in Y. americana, where usually no more than 2-3 are found in close proximity (compare Figs. 1, 3 with Fig. 7). (3) The height: diameter ratio of mature fronds of Y. melobesioides is approximately 1.25, whereas in Y. americana it is 1.5-1.9, resulting in frond outlines that are obovate for Y. melobesioides and more clavate for Y. americana. (4) In Y. melobesioides the conceptacle ostioles are smaller; 30-40 μ m in diameter versus 55-80 μ m in Y. americana. DAWSON and STEELE (1964) refer to even larger ostioles 125-130 μ m in diameter for Y. americana, but we have not found any this size. An additional ostiole character distinguishing the two species is the usually slightly eccentric ostiole of Y. americana (they are strictly apical in Y. melobesioides) (Figs. 9-10). DAWSON and STEELE (1964) did not notice this although they commented that the conceptacles in all reproductive types are often rostrate or beaked.

The surfaces of intergenicula and basal crusts as observed with the SEM provide features that clearly distinguish the two species of Yamadaea. The surfaces of Y. melobesioides are similar to those in many other members of the Corallinoideae. Thus there are well-developed concavities in the sites previously occupied by epithallial cells (these disintegrate during specimen preparation) and relatively prominent cell walls (Figs. 2, 4-6) separating the epithallial concavities. On the other hand, lateral walls of epithallial cells in Y. americana are little developed, and the basal pit-connections (their remains, the plugs being destroyed during tissue preparation) are more prominent when viewed by SEM (Figs. 11-12).

The concavities and walls of Y. melobesioides are round to slightly irregular whereas those of Y. americana are more angular and polygonal (compare Figs. 2, 5-6 with Figs. 8, 11). In the type description of Y. americana, DAWSON and STEELE (1964) referred to a "faintly tessellate" surface, and this is reflected in the ultrastructural views. The surfaces of Y, americana are very different from other members of the Corallinaceae examined to date, and, with the SEM, it should be possible to identify crusts of Y. americana which are devoid of erect or fertile branches. Within each species there are no differences in surface morphology between the prostrate and erect parts of the thallus.

In addition to the general appearance of the plant surfaces, several aspects of surface morphology can be expressed in numerical terms. GARBARY (1978) measured three features and showed that they were useful in characterizing species: diameter of epithallial concavities, thickness of cell walls, and the proportion of thallus surface taken up with concavities. These characteristics also provide criteria for distinguishing Yamadaea americana and Y. melobesioides. Thus Y. americana has greater concavity diameters, slightly thinner cell walls, and a higher proportion of the surface is comprised of concavities (see Table 1 for results of measurements). The differences between these taxa are very pronounced with the values for Y. americana for concavity diameter and the proportion of the surface taken up with concavities at or near the extremes of recorded values in the Corallinaceae (GARBARY, 1978).

In this study, trichocytes are reported from Yamadaea for the first time. Trichocytes are present in one of the two collections of Y. melobesioides examined with the SEM, where they appeared as small concavities raised above the thallus surface (Figs. 4, 6). In this collection the trichocytes are common in both the erect and basal parts. Despite the sporadic occurrence of the trichocytes, this feature might pro-



Figs. 1-6. Yamadaea melobesioides. Figs. 2-6 are from the SEM. 1. Light micrograph of plants with clustered fronds (scale: 2 mm). 2. General view of crust surface (scale: $10 \ \mu\text{m}$). 3. Apex of intergenicula with central ostioles (scale: $200 \ \mu\text{m}$). 4. General view of surface on erect branch with scattered trichocytes (scale: $35 \ \mu\text{m}$). 5. Detail of surface on non-fertile frond (scale: $10 \ \mu\text{m}$). 6. Detail of trichocytes and surrounding cells (scale: $10 \ \mu\text{m}$).



Figs. 7-12. Yamadaea americana. Figs. 8-12 are from the SEM. 7. Light micrograph of plants with scattered fronds (scale: 2 mm). 8. General view of crust surface with accumulated debris (scale: $60 \ \mu$ m). 9. Whole intergeniculum with eccentric ostiole (scale: $150 \ \mu$ m). 10. Apex of fertile intergeniculum with detail of cells around ostiole (scale: $150 \ \mu$ m). 11. General view of cells on surface of frond (scale: $10 \ \mu$ m). 12. Detail of frond surface with outlines of pit connections (scale: $5 \ \mu$ m).

vide an additional characteristic distinguishing the two species of Yamadaea, since trichocytes were not found in any of the six collections of Y. americana examined with the SEM. What is important is the potential ability of the species to produce trichocytes rather than their presence or absence in a particular plant. The trichocytes of Y. melobesioides are similar to those of Corallina officinalis L. both in morphology and occurrence, and in the latter species trichocytes are present or absent in plants from different collections from the same site (GARBARY and JOHANSEN, unpublished data).

The reported distributions of the species of Yamadaea are as follows: Y. americana was known from Washington to northern British Columbia, whereas Y. melobesioides was recorded from Japan (the type locality) and California. Our examinations of collections supposed Y. melobesioides California from reveal that thev are similar to Y. americana, both in terms of gross morphology and the ultrastructure of plant surfaces. That the material from California originally determined as Y. melobesioides should, in fact, be Y. americana is not surprising, since the descriptions of these plants (HOLLENBERG and ABBOTT. 1966; ABBOTT and HOLLENBERG, 1976) are much closer to Y. americana than to the Japanese species, in terms of frond size and frond distribution on the crust. Thus all material of Yamadaea from the eastern Pacific can be ascribed to Y. americana for which the known distribution is extended from northern Washington to the Monterey Peninsula. This solves the previous biogeographic problem of explaining why Y. melobesioides should be present at the extremes of the distribution range with the second species having an intermediate range. Further floristic studies of the intervening regions (Alaska, the Aleutian and Kurile Islands) would be of interest in determining the geographic limits of the two taxa, and whether or not they are completely allopatric. At present, the occurrence of Y. melobesioides in North America can be discounted, but since both species are relatively rare and inconspicuous, the possibility that Y. melobesioides occurs in North America cannot be discarded.

Of the 12 genera currently placed in the subfamily Corallinoideae (JOHANSEN, 1976), nine have been examined with the SEM (all genera except Alatocladia, Marginosporum and Serraticardia) (GARBARY, unpublished data). Two main types of surface structure differentiate JANIA and Haliptilon from the remaining genera. The two surface morphologies were designated the Corallina-type and the Jania-type, and the taxonomic implications are dealt with separately (GARBARY and JOHANSEN, 1980, and in prep.). Within plants showing the Corallina-type surface, there is little morphological diversification that can be used to characterize particular genera. It is therefore of interest that the two species of Yamadaea portray more variation than exists among six other genera of the subfamily Corallinoideae with a Corallina-type surface. This morphological divergence within Yamadaea and the apparent uniformity within much of the Corallinoideae supports the contention of JOHANSEN (1969) that Yamadaea is primitive in the subfamily.

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D.J. ガーバリー・H.W. ヨハンゼン・R.F. スケージェル: サビモドキ属 Yamadaea の2種の形態と分布

サンゴモ科, サビモドキ属の2種 Yamadaea melobesioides SEGAWA (サビモドキ) と Y. americana DAWSON et STEELE の走査型電子顕微鏡による,形態及び超微構造の観察の結果,これら2種を区別する際の付加的な分類 形質をいくつか得ることができた。藻体の色・大きさ,藻体当りの節間部 intergeniculum の数・形・密集度,生殖巣 孔の大きさ・位置において2種間に差異がみられる。これら2種を比較すると,Y. americana では,表皮細胞 は大きく,細胞壁はあまり厚くならない。サビモドキ属では初めて,毛細胞 trichocyte の存在が明らかになった。 ただしこの細胞は Y. melobesioides だけに見られた。これら2種の分布域を次のように改めた。Y. melobesioides は日本にだけ分布する種である。Y. americana は北米にだけ知られており, $ク_{4} - \cdots + \cdots + \cdots$ 計畫。(ブリ テッシュ・コロンビア州) からモントレー (カリフォルニア州) にかけて分布している。

井上 勲: 微細藻類ノート (2). 培養の海産微細藻類 フロラ研究への応用 Isao INOUYE: Notes on microalgae in Japan (2). Employment of labolatory culture to floristic studies of marine microalge

先に述べた方法(本誌,井上,1980)は1)予備培 養で10%以上に増殖した藻のみを分離する,2)10% 以下の優先度の藻については,大まかな稀釈をくりか えすことで優先順位をあげる。3)小容量の容器を用 いることで培養期間を短縮し,分離の効率をあげる という点に特徴があった。この方法は技術的に容易 で,場所をとらず,しかも試料水によって,増殖して くる種は,採集場所や時期により異るので,この予備 培養と稀釈法を組みあわせた方法で以下にあげるよう にかなりの数の藻を分離することができる。分離され る徴細藻類の大部分は,天然の試料では個体数が少な く確認が困難なものであり、また固定すると変形ある いは破裂などの変化をおこし同定が不可能になるもの が多い。わが国で従来行われてきた海産微細藻類の研 究が、比較的個体数が多く、しかも固定試料を用い得 る珪藻類や有殻の渦鞭毛藻を主な対象としてきたこと は明らかであり、その他の微細藻類が取り扱われるこ とが少なかったのは上記のような理由によるものと思 われる。従って、補助的な手段として培養技術を導入 することによって、従来の微細藻類フロラの研究では 見過されがちだった藻群をとり扱うことが可能になる と思われる。

先に報告した方法を用いて筆者が確認した微細藻類 のリストを以下にあげる。単藻培養にまで至らなかっ たが、出現を確認できたものも含めた。また種名の決 定ができていないものは除いた。 Cryptophyceae クリプト藻網