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# Description of the Tetrasporangial Crustose and Gametangial Erect Phases of *Ahnfeltiopsis gigartinoides* (J. Ag.) Silva *et* DeCew (Rhodophyta, Phyllophoraceae) in Bahía de Banderas, Mexico

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Tetrasporophyte and upright gametophyte thalli of a species collected in the region of Bahía de Banderas, México are described. Both phases coincide with those observed in the life history of the genus *Ahnfeltiopsis* Silva *et* DeCew (Phyllophoraceae, Rhodophyceae). Crustose thalli are not identifiable as any of the red crustose noncoralline algae previously described, although they are similar to *Erythrodermis* Batters. The problems of identification of the specimens collected, which bear a resemblance to three species reported in Mexico: *Ahnfeltiopsis concinna* (J. Ag.) Silva *et* DeCew, *Ahnfeltiopsis gigartinoides* (J. Ag.) Silva *et* DeCew and *Ahnfeltia svensonii* Taylor, are discussed. It is concluded that the plants investigated should be assigned to *Ahnfeltiopsis gigartinoides* and that this is the only species of the genus present in the Mexican tropical Pacific.

## Introduction

A red alga with an inferred life history consisting of a crustose tetrasporophyte and an upright gametophyte was found at several sites in the region of Bahía de Banderas, México. At some sites, only crusts were found; at other sites upright thalli but no tetraspore-producing crusts were found; and at still other sites, both upright and tetraspore-producing crusts were found. In some specimens, crusts that bore gametophytic uprights also produced tetrasporangia. There was a contact zone between the basal portion of the upright thallus and crust, with a transitional line of demarcation. Crustose thalli had intercalary and cruciate tetrasporangia and upright thalli had internal cystocarps. Characteristics of these thalli correspond to those that occur in the life-history of the genus *Ahnfeltiopsis* Silva *et* DeCew (Phyllophoraceae, Rhodophyceae). *Ahnfeltiopsis* includes taxa previously assigned to *Ahnfeltia* and *Gymnogongrus* that produce internal cystocarps and have a life-history in which a crustose tetrasporophyte alternates with an upright gametophyte (Silva and DeCew 1992).

The upright thalli are very similar to three species previously reported in the Mexican tropical Pacific but we consider them misidentifications. In this paper we describe crusts and upright thalli and discuss their affinities to species previously reported in the region.

## Materials and Methods

### Study area

The study area consists of a large bay, Bahía de Banderas or Valle de Banderas, located between Punta de Mita (20°46' N and 105°33' W) to the north and Cabo Corrientes (20°24' N and 105°43' W) to the south. Within the bay, many types of environment are present: shallow beaches with sandy substrates and rocky areas more or less protected from the surf, as well as high cliffs, rocky points and areas with high, large, exposed rocky crags. Due to their orientation and position with respect to the coastline these areas may be exposed or completely protected from the surf (González-González 1993). In these environments there is a conspicuous algal flora on cliffs, in surge channels, on rocky/sandy platforms and in intertidal pools (Serviere 1993). Ten sites were visited covering the whole bay. *Ahnfeltiopsis* was found in only 5, always in the midlittoral zone (Fig. 1).

### Methodology

Algal material was collected during a floristic-ecological survey of the rocky shore of the region of Bahía de Banderas in October 1987 and April 1988 (Serviere 1993). Isolated patches, mosaics and fringes were sampled at each locality taking into account coloration, growth form and specific composition. Important environmental characteristics such as type of environment (cliff, surge channel, rocky-sandy platform, tidal pools), tidal level and the degree of exposure to 'irradiance' and surf were recorded for each sample. The material was collected by hand or with the help of spatula and chisel, and was preserved in 4% formaldehyde seawater (Serviere 1993).

Specimens corresponding to *Ahnfeltiopsis* were found in five sites: Playitas in Jalisco; Manzanillas, Las Cuevas, Sayulita and Isla Larga in Nayarit, (all

marked with an asterisk in Fig. 1). Both crustose and erect thalli were collected from the first three sites but only crusts from the last two.

The crustose and erect thalli were collected on cliffs, principally in the high and mid-midlittoral zone, with direct exposure to sunlight. At low water there is intense spray and frequent splashing by waves. At high water there is strong drag caused by surf. The accompanying species were *Chaetomorpha antennina* (Bory) Kütz., *Ralfsia confusa* Hollenberg, *Centroceras clavulatum* (C. Ag.) Mont., *Gelidium microdentatum* Daws. in greater abundance, and *Chondria decipiens* Kylin, *Grateloupia versicolor* (J. Ag.) J. Ag. and *Hypnea pannosa* J. Ag. in lesser abundance.

Thalli also were found in parts of the high and mid-midlittoral zone with indirect exposure to sunlight where there was frequent splashing at low water and slight drag at high water. Here they were found growing with *Hildenbrandia rubra* (Sommerfelt) Meneg. and *Pterocladia caloglossoides* (Howe) Daws., and less frequently with *Ulva lobata* (Kütz.) S. *et* G.

The material of *Ahnfeltiopsis* was separated from the other species in each sample and photographed. The specimens were detached under the dissecting microscope, taking care not to separate the upright thalli from their crustose parts. Radial vertical sections of the crusts were made, as well as transverse and longitudinal sections of the erect thalli. Both types of sections were stained with aniline blue and malachite green and mounted in glycerine jelly.

Since different authors describe the same crustose algal species using different characters (León-Alvarez and González-González 1993), we used the features employed for the segregation of species of non-coralline crustose rhodophytes by Dawson (1953), Denizot (1968), Maggs *et al.* (1989) and Maggs and Pueschel (1989). The erect thalli were described following Taylor (1945), Dawson (1961 a), Smith (1969), Magruder (1977), Maggs *et al.* (1989), Maggs and Pueschel (1989) and Anderson and Bolton (1990).

Samples, slides and photographs were deposited in the Herbarium of the Science Faculty of the National Autonomous University of Mexico (FCME) with the following numbers: PTM3316, 3318, 3319, 3320, 3336, 3342, 3359, 3360, 3361, 3526, 3527, 3528, 3529, 3532, 3533, 3553, 3597, 3534, 3636, 3645.

## Results

The following is a description of the reproductive crustose tetrasporophyte and erect gametophyte of the sample from Manzanillas (April 1988, PTM3532, slides 115, 116).

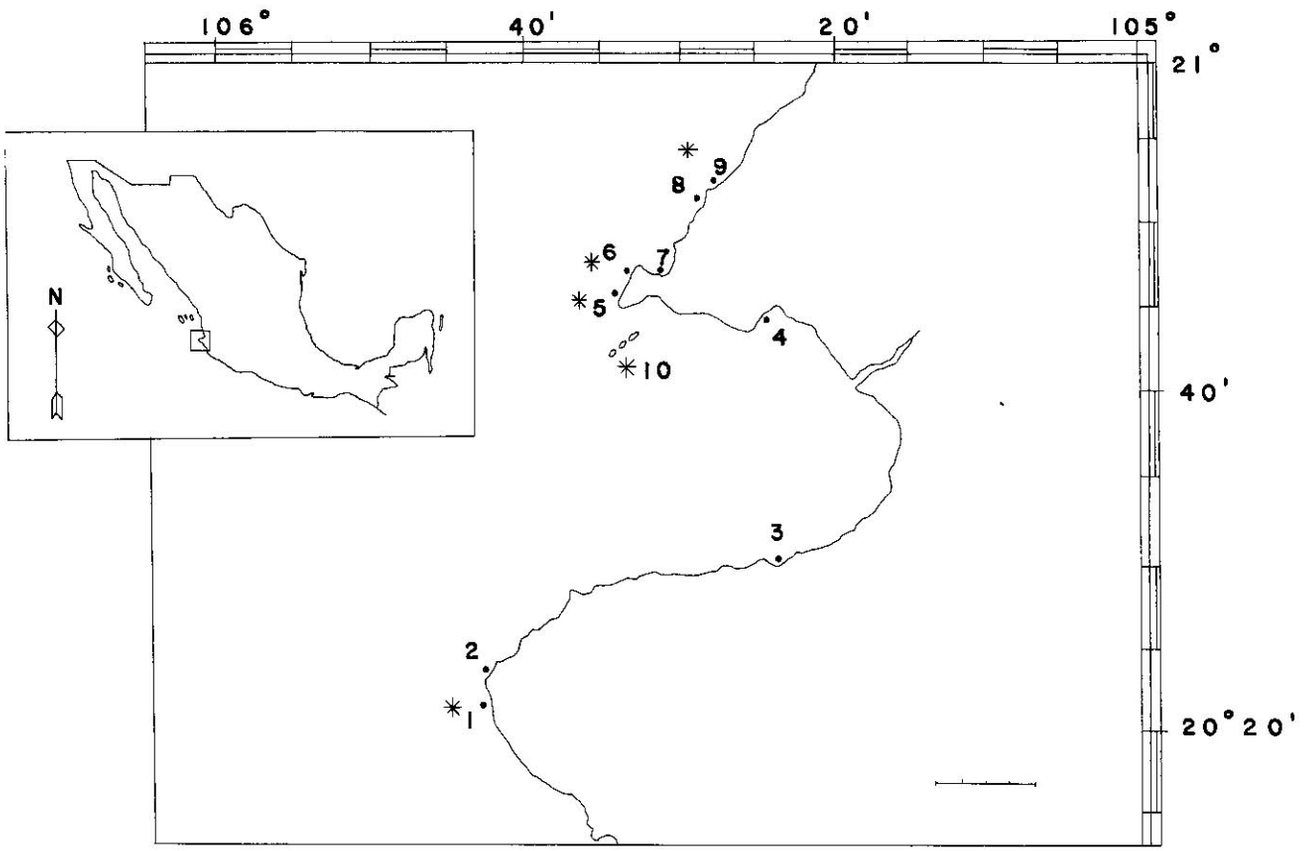



Fig. 1. Bahía de Banderas region and sites visited. 1. Playitas, 2. Corrales, 3. Colemilla, 4. El Tizate, 5. Manzanillas, 6. Las Cuevas, 7. Playa Careyeros, 8. Playa Los Muertos, 9. Sayulita, 10. Isla Larga. * = Sites where *Ahnfeltiopsis gigartinoides* was found. Scale = 10 km.

The crustose thallus, which extended greatly over the substrate, bore the erect thallus without apparent separation between them (Fig. 2). Under the microscope sections of the crustose thallus and of the basal part of the erect thallus showed a contact line between rows of cells of both thalli. This line was more evident in parts where the rows of cells of both thalli were obliquely or perpendicularly arranged (Fig. 3). The crustose thallus bore tetrasporangia and the erect thallus bore cystocarps.

### Crustose tetrasporophyte (Figs 4–9)

The crust formed isolated and irregular patches, completely and firmly attached to the rock without rhizoids. It had an indistinct margin, was smooth, uncalcified, dark brown to dark cherry-colored and was 120 to 230 μm thick.

In vertical radial section the central filaments grew towards the surface and in some parts they also grew downwards (Figs 4, 5). The part of the crust closest to the substrate consisted of one layer of diverging cellular rows, with polyhedral, ovoid or cylindrical cells 5–18 μm long × 8–10 μm in diameter. The perithallus was formed by tightly packed ascending filaments, that branched once or twice and diminished in diameter in the upper part of the thallus where the filaments were considerably thinner and more distant from each other. Secondary pit connections were abundant, fusions were absent. The basal cells of the filaments were oboboid to cylindrical and 7.5–15.0 (26.2) mm long × 5–10 mm in diameter (length/diameter ratio 0.7–2.6); in the middle portion cells were obovoid to ellipsoidal and 10–15 mm long × 3.7–11.2 mm diameter (l/d ratio 0.8–3.7); the subapical cells were elongate-ovoid and 5–10 μm length × 1.5–2.5 μm diameter (l/d ratio 2.5–4.3).

Tetrasporangia were borne among paraphyses in mucilaginous sori elevated above the vegetative surface (nemathecium) (Fig. 6). These nemathecia were 2–5 mm in diam. and 95–100 μm high. They gave the surface of the dry crust a granular aspect (seen under the dissecting microscope). Paraphyses were branched (Fig. 8), forming chains, arising independently of the tetrasporangial filaments (Figs 7, 8), with tapered basal cells oriented lengthwise, 2–3 (5) μm in diameter and ovoid to sharp-pointed terminal cells of 1.5–5 μm in diameter (Fig. 7). Tetrasporangia were seriate (Fig. 9) and intercalary, 2–3 per reproductive filament. The mature tetrasporangia were cruciately divided, elliptic to elongate biconical, 15–46 μm length × 7–13 μm diameter; the reproductive filament had 2–4 terminal cells.

### Erect gametophyte (Figs 10–11)

The thalli of reproductively mature female gametophyte were erect multiaxial fronds (Figs 10–11). The erect fronds grew from well developed basal crusts, strongly attached to the substrate. The fronds vary in size from 1.5–2.6 cm and had a stipe 8–12 mm long. The branching was generally irregular, with 2 to 4 dichotomies, at 25–35° angle. Upper branch segments (1.9 mm) were shorter than the lower ones (4.2 mm). The branch apices were apiculate (Fig. 11) and 700–1300 μm diameter. Several small erect thalli were unbranched. In transverse section a pseudoparenchymatous medulla and a cortex formed by small cells, arranged in anticlinal rows could be seen. Medullary cells were 19–30 μm in a diameter, and the peripheral ones 13–21 μm in diameter. Cortical cells were 4.5–6.0 long and 2.5–4.0 μm in diameter. In longitudinal section the central zone of the medulla had no cellular fusions. On female thalli, fertile areas were found in the upper portions. Many carposporophytes were present in the same female frond; they grew in the medulla and had a diameter of 120–180 μm (Fig. 12). The carpospores were spherical, 12–20 μm. The cystocarps had a carpostome composed of short periclinal filaments that developed from anticlinal cortical cells (Fig. 13). Males were not seen.

The range of variation of characters observed in all erect thalli are shown in Table I.

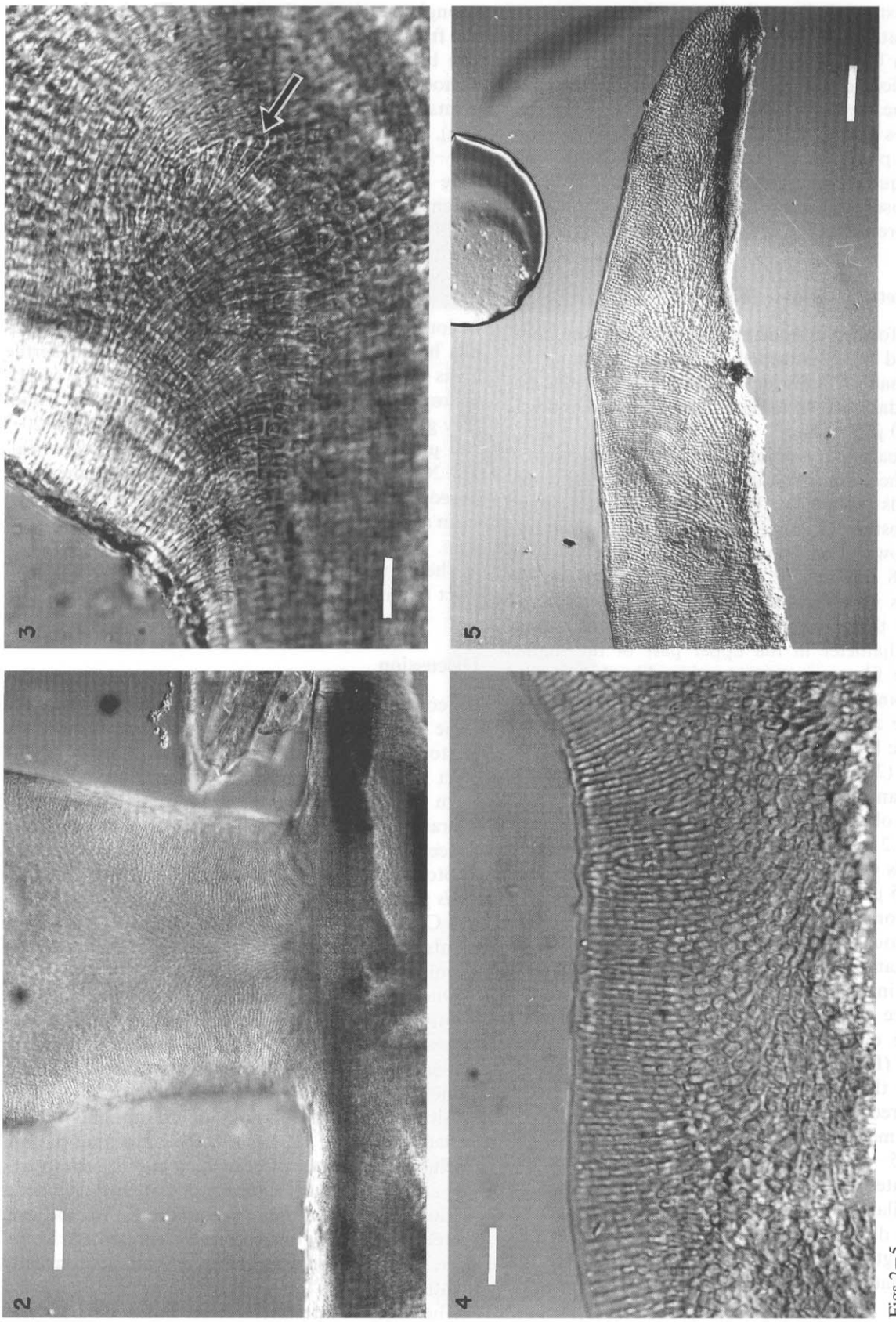
## Discussion

We consider that the crust and upright are part of the same life history because the crustose specimens are anatomically identical with the basal portion of the erect thalli. The presence of a contact zone between them suggests possible *in situ* germination of tetrasporangia. However we have no experimental evidence that the tetraspores produce these erect plants. Photos of both erect and crustose thalli of *Ahnfeltiopsis gigartinoides* sent by Thomas DeCew of Berkeley, CA. are very similar to our plants. In DeCew's plants the erect thalli were produced in culture by the germination of the tetrasporangia.

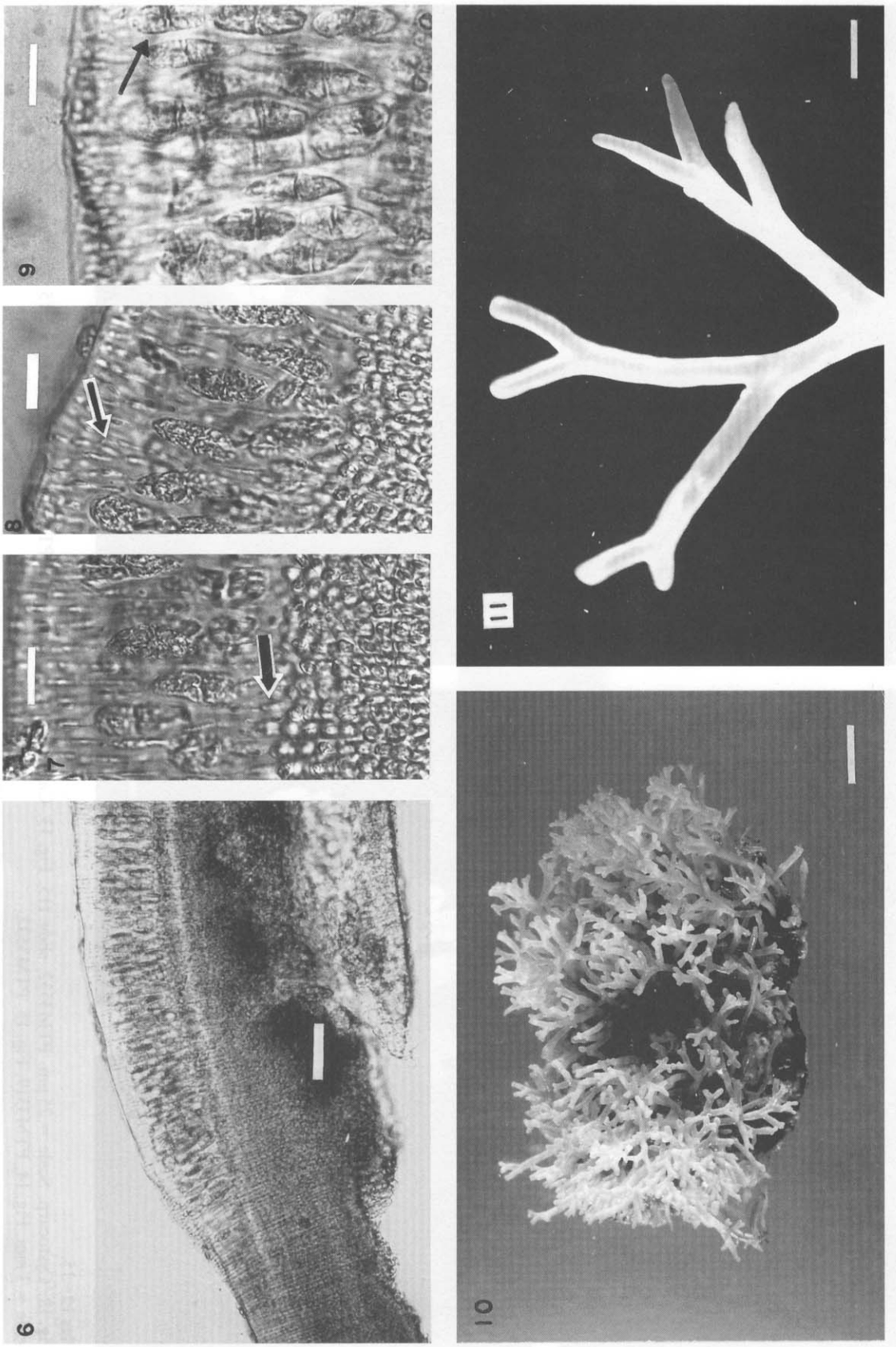
Our specimens can be assigned to the genus *Ahnfeltiopsis* because they have a crustose sporophyte with cruciately divided tetrasporangia borne in intercalary catenate series, and internal cystocarps in erect gametophytes (Silva and DeCew 1992).

Although the morphology of the uprights is very variable (Figs 10, 11, 14, 15), the branching pattern (including frequency of branching and branching angle) and branch outline (terete or flattened as seen in section) show continuous variation. We believe, therefore that only one species is represented. Moreover, the crustose specimens are all anatomically identical.

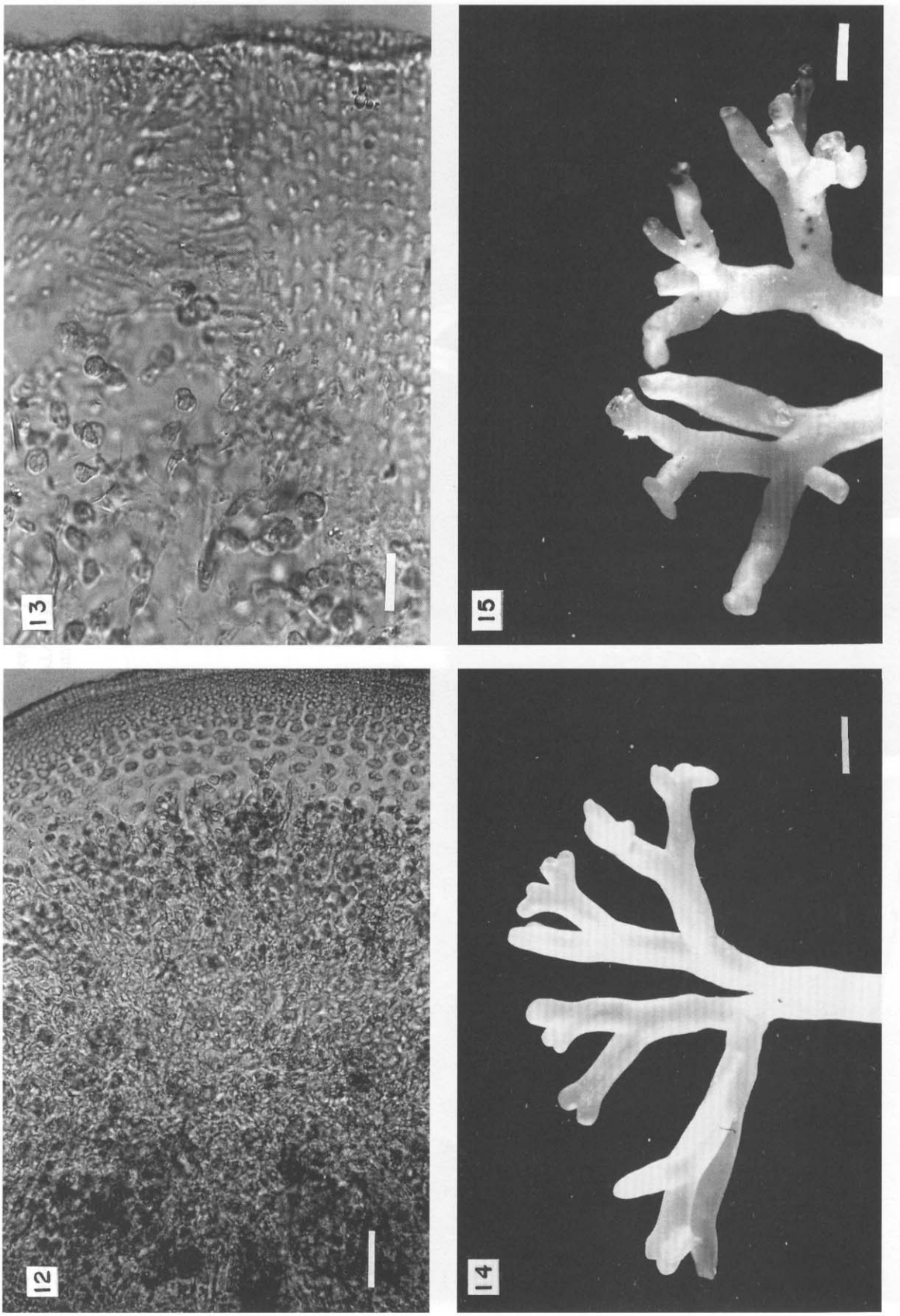
The crustose specimens from Bahía de Banderas differ from all non-coralline red crusts previously described. They resemble *Porphyrodiscus* Batters but can be distinguished from it by having multiple secondary pit connections and lacking cellular fusions and in having intercalary instead of terminal tetra-




Figs 2–5.
Fig. 2. Upright thallus with basal crust. Scale = 100 µm. PTM3532, slide 115. Fig. 3. Contact zone between erect and crustose thalli. Scale = 66 µm. PTM3532, slide 115. Fig. 4. Radial vertical section showing arrangement of the epithallial filaments. Scale = 36 µm. PTM3532, slide 115. Fig. 5. Radial vertical section of the crustose thallus showing margin. Scale = 40 µm. PTM, 3536, slide 116.




Figs 6–11.
Fig. 6. Tetrasporangial nemathecia. Scale = 45 µm. PTM3532, slide 116. Fig. 7. Tetrasporangia and paraphysis with tapered basal cell, arrow. Scale = 25 µm. PTM3532, slide 116. Fig. 8. Tetrasporangia and branched paraphysis, arrow. Scale = 25 µm. PTM3532, slide 116. Fig. 9. Tetrasporangia in series, arrow. Scale = 25 µm. PTM3532, slide 116. Fig. 10. Habit of the erect gamethophyte of *Ahnfeltiopsis gigartinoides*. Scale = 1.4 cm. PTM3319. Fig. 11. Detail of apex. Scale = 3 mm. PTM3529.




Figs 12–15.
Fig. 12. Cystocarp. Scale = 25 µm. PTM3532, slide 115. Fig. 13. Carpostome. Scale = 25 µm. PTM3532, slide 115. Fig. 14, 15. Detail of apex in different thalli. Scale = 3 mm. Fig. 14, PTM3319, Fig. 15, PTM3532.

Table I. Range of variation of erect thalli.

| | |
|---|---|
| Size | 0.6–7.4 cm |
| Branching | dichotomous to irregular and sometimes polychotomous [PTM 3318, 3319, 3320, 3342, 3359, 3534] |
| Segment shape | lower: cylindrical to flattened at the branching point<br>upper: cylindrical to compressed and occasionally with flattened point [PTM 3316, 3533] |
| Segment length | lower: 0.2–26 mm<br>upper: 0.5–29 mm [PTM 3636], mainly 1–15 |
| Segment diameter | lower: 0.5–1.2 mm<br>upper: 0.5–1.9 mm |
| Upper/lower ratio segment | upper > lower [PTM 3342, 3359, 3360, 3361, 3629, 3636]<br>upper < lower [PTM 3318, 3319, 3320, 3336, 3525, 2533, 3534] |
| Angle of branching | less than 90°, except in one specimen [PTM 3360: 60–90° (110)] |

PTM = Entry number in Herbarium of the Sciences Faculty, UNAM (FCME).

sporangia. They are also similar to *Erythrodermis* Batters but tetrasporangia in that genus are terminal according to Batter's drawing of the type species *E. alleni* Batters (1900, figs 4–5) and Hollenberg (1969). Our crusts are vegetatively similar to *E. pacifica* Hollenberg, but the latter has smaller tetrasporangia (10–14 μm long × 10–11 μm diameter) and they are more numerous (at least 6 per chain).

In general the crustose specimens also agree with the description of the crusts of *Ahnfeltiopsis concinna* (J. Agardh) Silva *et* DeCew according to Magruder (1977, as *Ahnfeltia concinna*) and with the crusts of *Ahnfeltiopsis gigartinoides* (J. Agardh) Silva *et* DeCew according to the description of Masuda *et al.* (1979, as *Ahnfeltia gigartinoides* in Table I). The crusts of both species and our specimens contain intercalary seriate cruciately divided tetrasporangia. However, the crusts of *Ahnfeltiopsis concinna* have larger tetrasporangia (30–40 μm long × 15–20 μm diameter) and the sori are not nemathecial, while the crusts of *A. gigartinoides*, which have nemathecia, have fewer tetrasporangia (1 or 2) and one or two terminal cells per reproductive filament. Our specimens resemble *A. concinna* in number of tetrasporangia per filament and number of terminal cells. They resemble *A. gigartinoides* in tetrasporangial size and in tetrasporangia location (nemathecium). Regarding erect thalli, the morphological range of variation of the specimens from Bahía de Banderas encompasses three species recorded from Pacific Mexico: *Ahnfeltiopsis concinna* (syntype locality: Hawaiian Islands), *Ahnfeltiopsis gigartinoides* (type locality: Oaxaca, México), and *Ahnfeltia svensonii* Taylor (type locality: Galápagos).

Our specimens agree with *Ahnfeltiopsis concinna* (*sensu* Dawson 1961a: 245: as *Ahnfeltia*) considering the branching angle (less than 90) and the diameter of the segments (less than 1.5 mm). Nevertheless, following these criteria, some specimens (PTM3319, PTM3360 and one from sample PTM3626) are similar also to both *Ahnfeltiopsis gigartinoides* and *Ahnfeltia svensonii* or only to the latter species (PTM3359, PTM3361, PTM3636). A specimen in one sample (PTM3528), which with respect to branch divergence angle and segment diameter could be placed in *Ahnfeltiopsis concinna*, could be assigned to *A. gigartinoides* if the shape of the frond (in one plane) were considered. Moreover, the erect thalli within one sample (PTM3526) presented features from the three species. Nevertheless, it is important to point out that the crustose thalli of all of these specimens are identical.

Dawson (1961 a: 245), following a speculation of Setchell and Gardner (1930: 152), merged *Ahnfeltia gigartinoides* with *A. concinna*, but Hollenberg and Abbott (1969) disagreed, and Silva and DeCew (1992: 577), who had access to life-history data for plants collected near the type locality of *Ahnfeltiopsis gigartinoides*, maintained both species. We concur that *A. gigartinoides* and *A. concinna* are separate species and we believe that our specimens can be identified as *A. gigartinoides* because our tetrasporophyte crustose specimens are identical to those cultured by DeCew (pers. com.) from Puerto Escondido, México (near the type locality) with elongated tetrasporangia and raised nemathecia, and the gametophytes of *A. gigartinoides* collected in same locality by DeCew are similar to some gametophytes collected in Bahía de Banderas.

We believe that previous records of *A. concinna* on the Mexican tropical Pacific coast (González-González 1992, González-González 1993, León-Tejera and González-González 1993, León-Tejera *et al.* 1993, Serviere 1993, Serviere *et al.* 1993) are misidentifications based on Dawson's papers (1953 a, b, 1954, 1961 a, b). Therefore, we consider that only *A. gigartinoides* is present in the tropical Pacific coast of Mexico. The affinities of *Ahnfeltia svensonii* cannot be determined without more study of material from the Galápagos.

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