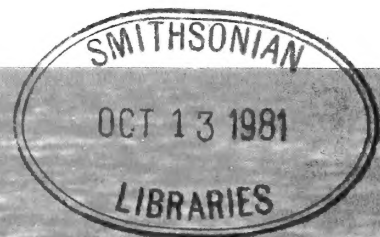


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Articulated Coralline Algae  
of the  
Gulf of California, Mexico,  
I: *Amphiroa* Lamouroux

JAMES N. NORRIS  
and  
H. WILLIAM JOHANSEN



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## ABSTRACT

Norris, James N., and H. William Johansen. Articulated Coralline Algae of the Gulf of California, Mexico, I: *Amphiroa* Lamouroux. *Smithsonian Contributions to the Marine Sciences*, number 9, 29 pages, 18 figures, 1981.—*Amphiroa* (Coralinaceae, Rhodophyta) is a tropical and subtropical genus of articulated coralline algae and is prominent in shallow waters of the Gulf of California, Mexico. Taxonomic and distributional investigations of *Amphiroa* from the Gulf have revealed the presence of seven species: *A. beauvoisii* Lamouroux, *A. brevianiceps* Dawson, *A. magdalensis* Dawson, *A. misakiensis* Yendo, *A. rigida* Lamouroux, *A. valonioides* Yendo, and *A. van-bosseae* Lemoine. Only two of these species names are among the 16 taxa of *Amphiroa* previously reported from this body of water; all other names are now considered synonyms. Of the seven species in the Gulf of California, *A. beauvoisii*, *A. misakiensis*, *A. valonioides* and *A. van-bosseae* are common, while *A. brevianiceps*, *A. magdalensis*, and *A. rigida* are rare and poorly known. None of these species is endemic to the Gulf, and four of them, *A. beauvoisii*, *A. misakiensis*, *A. valonioides*, and *A. rigida*, also occur in Japan.

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# Articulated Coralline Algae of the Gulf of California, Mexico, I: *Amphiroa* Lamouroux

*James N. Norris*  
and *H. William Johansen*

## Introduction

Species of *Amphiroa* Lamouroux (Corallinaceae; Cryptonemiales) are common in intertidal and shallow subtidal zones in tropical and subtropical areas of the world. In the Gulf of California, Mexico, they are the most prominent articulated coralline algae; two other coralline genera are found there, *Jania* Lamouroux and *Corallina* Linnaeus. The fronds of *Amphiroa* are purplish, bushy clumps 1 to 12 cm long, or turfs 1 to 2 cm thick. They grow in a variety of habitats, but usually require at least some degree of wave action.

A terminology has arisen with respect to articulated coralline algae (Johansen, 1974). The fronds are made up of numerous jointed branches consisting of calcified segments called "intergenicula." The intergenicula are separated from one another by uncalcified nodes, or "genicula" (e.g., Figures 2 and 5). Extending through a branch is a core of medullary filaments with the cells in tiers (e.g., Figure 4), which is surrounded by a cortex and epithallus.

Of the three genera in the Gulf of California, only *Corallina* Linnaeus is represented by a single

species, *C. pinnatifolia* var. *digitata* Dawson (1953), a small plant distinguished from *Amphiroa* by its percurrent axes, which are densely clothed with lateral branches. *Jania* Lamouroux, the other genus, is represented in the Gulf by four species having delicate fronds composed of branches less than 0.5 mm in diameter. These species have regular dichotomous branching and conceptacles borne in single swollen chambers at the apices of the intergenicula. Whereas, in *Amphiroa*, the fronds are coarser, branches generally over 1.0 mm in diameter (except in *A. valonioides* Yendo where they are less than 0.5 mm in diameter), and usually the dichotomous branching is irregular. Also the conceptacles of *Amphiroa* are invariably borne on intergenicular surfaces, although sometimes they may be nearly invisible, especially where branches are relatively thick.

*Amphiroa* Lamouroux (1812:187) is a member of the subfamily Amphiroideae Johansen (1969a: 47), tribe Amphiroeae Cabioch (1972:266) (see also, Johansen and Silva, 1978, and Johansen, 1981, for review of supergeneric classification). The species are distinguished from one another by the following taxonomic features: frond height, intergenicular width, intergenicular shape in cross-section, the number of medullary cell tiers in genicula and plant habit (e.g., turfey,

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recumbent, or erect and bushy). Although the branching is basically dichotomous, it is often irregular and congested, with the branches tending not to lie in one plane. As in other members of the Corallinaceae (e.g., Johansen, 1976a), the reproductive cells are produced within conceptacles which, in *Amphiroa*, are always borne on the surfaces of the intergenicula (Figure 14). Each conceptacle opens by a single pore, through which the reproductive cells exit.

The Gulf of California is a discrete body of water with unique characteristics (van Andel and Shor, 1964, for review), representing the Cortez Province of Briggs (1974) or the Gulf of California biogeographical region of W. H. Adey and R. S. Steneck (pers. comm.); yet none of the species of *Amphiroa* are now considered endemic to the Gulf. Furthermore, four of the species are present in areas other than the eastern Pacific. *Amphiroa beauvoisii* (as *A. zonata*), *A. misakiensis*, *A. rigida*, and *A. valonioides* are all present in Japan (Okamura, 1936:515-521; Chihara, 1970:71-72). It is interesting to note that Dawson (1960:97) found several non-corallinaceous species, e.g., *Pachydietyon coriaceum* (Holmes) Okamura (Dictyotales), also common to both the Gulf of California and Japan. Hommersand (1972) has also suggested a close relationship between the algae of the Gulf of California and Japan.

The first report of articulated coralline algae occurring in the Gulf of California was by Hariot (1895) who reported *Amphiroa linearis* Kützing (1858). It was more than one-half century before another account of *Amphiroa* was reported in the Gulf, with Dawson (1944:276-277) reporting three species: *Amphiroa pusilla* Yendo (1902), *A. zonata* Yendo (1902), and *A. rigida* Lamouroux (1816). Of these, the first two were originally described from Japan, and the third from the Mediterranean Sea. The bulk of information on coralline algae from the Gulf of California, and the Pacific coast of Mexico, is due to the efforts of E. Yale Dawson (1944, 1953). The first detailed treatment of these algae from the Gulf and Pacific Mexico was Dawson's (1953) report of 11 taxa of *Amphiroa* from the Gulf of California: *A. annulata*

Lemoine (1929), *A. zonata* Yendo (1902), and seven others, which were described as new, *A. annulata* var. *pinnata*, *A. taylorii*, *A. drouetii*, *A. brevianiceps*, *A. magdalenensis*, *A. subcylindrica* and *A. franciscana* var. *robusta*.

Shortly thereafter, Dawson (1959) listed the algae collected on a cruise into the southern Gulf of California, reporting several species of *Amphiroa* previously recorded for this region and described a new variety, *A. dimorpha* var. *digitiformis*. Finally, Dawson (1966b) extended the known range of *Amphiroa franciscana* Taylor (1945) var. *franciscana* into the Gulf making a total of 16 taxa of *Amphiroa* reported from this body of water. Dawson (1953:136-137) however, recognized only 13 species from the Gulf, noting that Hariot's (1895:169) report of *A. linearis* was probably *A. zonata*, included *A. rigida* in *A. subcylindrica*, and assigned specimens previously reported as *A. pusilla* (Dawson, 1944) to *A. drouetii*, *A. dimorpha*, and *A. zonata*. Later papers reporting taxa of this genus from the Gulf of California are by Dawson (1966a, 1966b) and Norris (1972).

Our study of the articulated coralline algae revealed that in the Gulf of California there are seven species of *Amphiroa* that can be separated on morphological and anatomical bases. After surveying the described taxa, we conclude that the entities of Gulf *Amphiroa* are: *A. beauvoisii* Lamouroux, *A. brevianiceps* Dawson, *A. magdalenensis* Dawson, *A. misakiensis* Yendo, *A. rigida* Lamouroux, *A. valonioides* Yendo and *A. van-bosseae* Lemoine. Four of the seven species in the Gulf, *A. beauvoisii*, *A. misakiensis*, *A. valonioides* and *A. van-bosseae*, are common and represented by many collections. The remaining three, *A. brevianiceps*, *A. magdalenensis*, and *A. rigida*, are known only from a few collections, and less confidence can be expressed in defining them.

**MATERIALS AND METHODS.**—Most of the collections studied were dried or preserved in 5 percent Formalin/seawater; individual pieces of the branches were fixed and decalcified in Susa fixative (Suneson, 1937:5). For anatomical studies, material was embedded in paraffin, sectioned (8-



10  $\mu\text{m}$ ) and stained in Delafield's haematoxylin (Humason, 1967:142).

Most of the specimens studied were collected by James N. Norris (JN), E. Y. Dawson (EYD), H. William Johansen (HWJ), Katina E. Bucher (KB), or W. R. Taylor (WRT). These specimens, as well as those collected by others, are housed in the following herbaria (abbreviations from Holmgren and Keuken, 1974):

AHFH	Allan Hancock Foundation Herbarium University of Southern California, Los Angeles
ARIZ	Algal Collection (with Dr. Robert W. Hoshaw) University of Arizona, Tucson
BM	British Museum (Natural History) London
CN	Laboratoire de Botanique Faculté des Sciences, Caen
CUW	Clark University Worcester, Massachusetts
K	Herbarium, Royal Botanical Garden Kew
L	Rijksherbarium, Leiden
LAM	Algal Collection (now at AHFH) Los Angeles County Museum Los Angeles, California
MEXU	Instituto de Biología Universidad Nacional Autónoma de México, México D.F.
MICH	University of Michigan Ann Arbor, Michigan
PC	Museum National d'Histoire Naturelle Laboratoire de Cryptogamie Paris
UC	University of California, Berkeley
US	United States National Herbarium Smithsonian Institution Washington, D.C.

In our attempts to examine type specimens of all the taxa, we were frustrated by an inability to locate those of Yendo's species (1902). It appears that Yendo's type specimens are not extant, a problem compounded by the fact that he often did not give a single type locality or ever designate type specimens for his taxa. Therefore, we have chosen herein the pertinent illustrations of Yendo's as lectotypes for his taxa (Stafleu et al., 1978, Art. 9). Only selected specimens or those of

distributional importance are cited under "Specimens Studied."

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### *Amphiroa* Lamouroux, 1812

DESCRIPTION.—*Holdfasts*: crusts, sometimes obscure or missing in plants in turfs. *Fronde*s: in clumps several centimeters high, or in turfs with sand and other algae mixed in. *Branching*: basically dichotomous, but often irregular and sometimes with branches arising from intergenicula in a seemingly random manner; branches sometimes more or less in one plane or they may form a

bushy, erect clump; the branches may be erect or recumbent to varying degrees. *Intergenicula*: flat to terete, usually 3 or more times as long as broad. *Genicula*: one or more tiers of uncalcified, deeply staining medullary cells; demarcation between intergenicula and genicula distinguished by the presence or absence of calcite in cell walls, cell tiers may be partly intergenicular and genicular; genicular cortices usually present, but often disorganized and ruptured. *Medulla*: formed by synchronous divisions of apical cells, hence resulting in arching tiers within each of which the cells are the same length, divisions such that tiers vary in height from 10–20  $\mu\text{m}$  to more than 120  $\mu\text{m}$ ; secondary pit-connections forming between the cells of a tier. *Cortex*: thick or thin, sharply demarcated from medulla, continuing to grow slowly in thickness as intergenicula age.

Data on reproductive structures are summarized from these studies: Suneson, 1937; Segawa, 1940a, 1940b; Ganesan, 1968; Johansen, 1968; and Murata and Misaki, 1978. *Conceptacles*: originating near branch apices and protrude from or are sunken into cortical tissue on surfaces of intergenicula; usually several conceptacles per intergeniculum; older conceptacles becoming buried by cortical growth in some species. *Tetrasporangial conceptacles*: originating as dome-shaped swellings on intergenicular surfaces by excessive growth of small cortical cells (the future roof of the conceptacle) over a lens of elongated cells (cavity cells, Johansen, 1968), subsequent development involving the initiation and growth of tetrasporangia, or bisporangia in some, in the periphery (and sometimes also the center) of the lens, meanwhile the cavity cells degenerating to form a chamber; also degenerating are a group of small cortical cells in the center of the roof, this space is the pore of the conceptacle; tetrasporangia 40 to 110  $\mu\text{m}$  long. *Sexual plants*: dioecious, conceptacles generally more crowded than in tetrasporangial plants. *Male conceptacles*: low profile, chambers broad and with low ceiling, fertile surface restricted to flat floor of chamber. *Female conceptacles*: roofs of conceptacles consisting of fil-

aments that have grown centripetally from tissue surrounding the fertile layer; 1 to 3, 2-celled carpogonial filaments arising from each supporting cell and constituting, along with undeveloped carpogonial systems, the fertile layer; trichogynes from the more central carpogonia projecting through pore at maturity. *Carposporangial conceptacles*: fusion cell 6–10  $\mu\text{m}$  thick and as much as 100  $\mu\text{m}$  or more in diameter, carposporangial filaments arising from margins of fusion cell and sometimes also from its upper surface near the margin, carposporangia 25 to 65  $\mu\text{m}$  in diameter.

**TYPE-SPECIES.**—*Amphiroa tribulus* (Ellis and Solander) Lamouroux, 1812:186. Basionym: *Coralina tribulus* Ellis and Solander, 1786:124.

**REMARKS.**—To distinguish among the morphologically variable species of *Amphiroa* we place

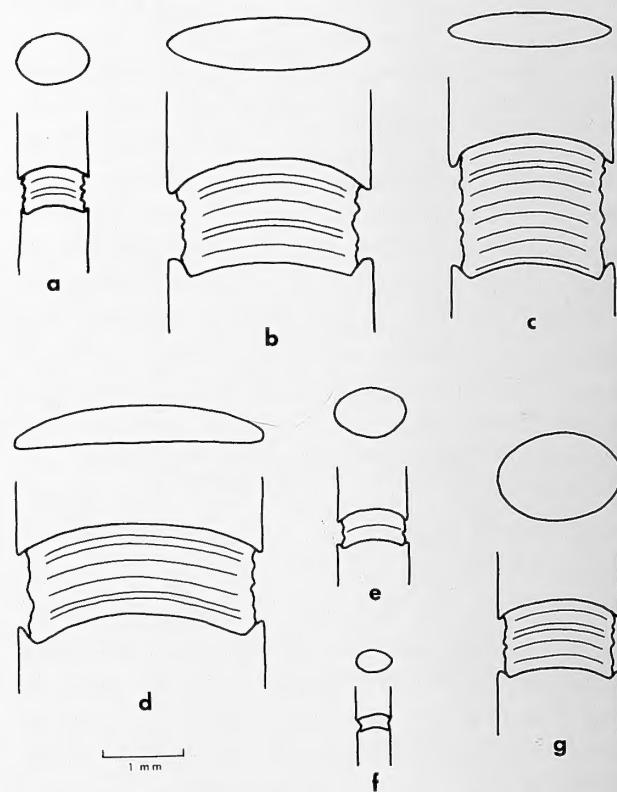


FIGURE 1.—Branch transections and genicular longitudinal sections of the Gulf of California species of *Amphiroa* (all to same scale): a, *A. beauvoisii*; b, *A. brevianiceps*; c, *A. magdalenis*; d, *A. misakiensis*; e, *A. rigida*; f, *A. valonioides*; g, *A. van-bosseae*.

TABLE 1.—Summary of the distinguishing features of the species of *Amphiroa* in the Gulf of California (rnd = round, com = compressed, ere = erect, usually as small clumps in which the branches are free from one another, rec = usually spreading or recumbent, tuf = tufts or turfs, usually compact, sand-filled)

Species	Frond		Intergenicula		Genicula
	Maximum length (cm)	Habit	Diameter or width in upper frond (mm)	Shape in cross-section	No. of tiers of medullary cells
<i>A. beauvoisii</i>	12	ere	0.5–1.0	rnd/com	3–5
<i>A. brevianceps</i>	4	ere	1.5–3.0	com	>5
<i>A. magdalensis</i>	5	ere	1.0–2.5	com	~10
<i>A. misakiensis</i>	4	rec	2.0–4.0	com	5 or more
<i>A. rigida</i>	2	ere	0.4–1.0	rnd	2
<i>A. valonioides</i>	2	tuf	<0.5	rnd/com	1
<i>A. van-bosseae</i>	10	ere	1.0–2.0	rnd	5 or more

most reliance on the internal structure of genicula and on the external form of intergenicula (Table 1, Figure 1). In the Gulf of California species there are four types of genicula: (1) a single medullary tier: *A. valonioides*; (2) two tiers of medullary cells, with oblique transverse walls between the tiers: *A. rigida*; (3) 3 to 5 tiers: *A. beauvoisii*; (4) more than 5 tiers: *A. brevianceps*, *A. magdalensis*, *A. misakiensis*, *A. van-bosseae*. In groups 1 to 3 the distinctions are clear-cut, but in the more massive genicula of the species in group 4, it has not been possible to find genicular distinctions, and reliance must be placed on intergenicular characters.

When analyzing intergenicular form, the fol-

lowing characteristics must be considered: (1) terete- or flat-shaped (circular or compressed in transection), (2) the dimensions, and (3) in flat branches, the intergenicular configuration adjacent to the genicula (Figure 1). These features are often not as taxonomically decisive as are those of genicula. Although mostly terete, intergenicula in *A. beauvoisii* and *A. valonioides* are sometimes slightly compressed. In the other species, either the terete or the flat character seems to hold (Table 1). Only intergenicula in the upper parts of the fronds can be used; basal intergenicula are usually terete, even in species where upper intergenicula are flat.

### Key to the Species of *Amphiroa*

1. Intergenicula distinctly flat; rarely cylindrical ..... 2  
    Intergenicula cylindrical or nearly so ..... 5
2. Fronds more or less erect and regularly branched; intergenicula all approximately similar in appearance ..... 3  
    Fronds spreading, recumbent and irregularly branched; intergenicula variable in appearance ..... ***A. misakiensis***
3. Intergenicula more than 1 mm wide; genicula consisting of 6 or more tiers of medullary cells ..... 4  
    Intergenicula less than 1 mm wide; genicula consisting of 3 to 5 tiers of medullary cells ..... ***A. beauvoisii***

4. Intergenicula less than 4 mm long ..... **A. brevianiceps**  
 Intergenicula more than 5 mm long ..... **A. magdalensis**
5. Intergenicula less than 1 mm in diameter; genicula consisting of 4 or fewer tiers of medullary cells ..... 6  
 Intergenicula more than 1 mm in diameter; genicula consisting of 5 or more tiers of medullary cells ..... **A. van-bosseae**
6. Intergenicula 0.5 to 1 mm in diameter; genicula consisting of 2 or more tiers of medullary cells ..... 7  
 Intergenicula less than 0.5 mm in diameter; genicula usually consisting of 1 tier of genicular cells ..... **A. valonioides**
7. Fronds less than 2 cm tall, rigidly branched in any plane; genicula consisting of 2 tiers of medullary cells ..... **A. rigida**  
 Fronds mostly 2 to 12 cm tall, more or less branched in one plane; genicula consisting of 3 to 5 tiers of medullary cells ..... **A. beauvoisii**

### ***Amphiroa beauvoisii* Lamouroux**

Figures 1a, 2, 3, 4a-c, 5, 6b, 7, 8, 14b, 15b

*Amphiroa beauvoisii* Lamouroux, 1816:299 [no illustration].

*Amphiroa linearis* Kützinger, 1858:22, pl. 46: figs. 2a-c [type locality: "Ad litora Africae occidentalis" (holotype, L 938,334 . . . 357)].

*Amphiroa zonata* Yendo, 1902:10, pl. 1: figs. 11-14, pl. 4: fig. 9 [type locality: not specified, "Misaki, Shimoda and Sunosaki" are listed (lectotype, Yendo's illustrations are herein chosen)].—Dawson, 1944:276, 1953:146; 1959:22; 1966a:18.

*Amphiroa pusilla* sensu Dawson, 1944:276 [in part] [not *Amphiroa pusilla* Yendo, 1902:13].

*Amphiroa peninsularis* Taylor, 1945:188, pl. 48: fig. 1 [type locality: South Bay, Isla Cedros, Baja California (WRT-34-646A, holotype, AHFH 90)].

*Amphiroa crosslandii* sensu Dawson, 1953:149; 1954:136 [not *Amphiroa crosslandii* Lemoine, 1929:50].

*Amphiroa drouetii* Dawson, 1953:140, pl. 27: figs. 5-6 [type locality: "Intertidal on reef at north end of Isla Turner, off Isla Tiburón, Sonora" (EYD-717-40, holotype, AHFH 1555; isotype, UC 940256)].—Dawson, 1959:21; 1966a:18.

*Amphiroa franciscana* var. *robusta* Dawson, 1953:150 [no illustration] [type locality: Acapulco, Guerrero, Mexico (EYD-3881, holotype, AHFH 55177) 1966b:59.

**Description.**—*Fronds*: up to 12 cm high, more or less erect and open, but sometimes in compact, pulvinate clumps (Figure 2). *Branching*: dichotomous, more or less in one plane, sometimes irreg-

ularly so, dichotomies sometimes separated by one or more unbranched intergenicula. *Intergenicula*: near base terete or subterete, up to 1.3 (–1.7) mm diameter and 3(–4) mm long, intergenicula in upper parts of fronds terete; subterete, or flat, especially near branch apices, becoming more terete with age because of cortical thickening, mostly 0.5–1 mm broad and 3–5 or sometimes more than 10 mm long, branching intergenicula sometimes Y-shaped (Figure 4). *Genicula*: developed by cracking and sloughing of calcified cortices overlying uncalcified tissues; fully formed genicula usually barely visible between intergenicula, consisting of 3–5 tiers of medullary cells and irregularly disposed patches of cortical cells (Figure 5). *Conceptacles*: scattered over intergenicular surfaces, protruding slightly; tetrasporangial and bisporangial conceptacles 200–250 (–300)  $\mu\text{m}$  inside diameter; sexual plants not encountered in the Gulf of California.

**TYPE LOCALITY.**—"Côtes du Portugal" (Lamouroux, 1816:299).

**HOLOTYPE.**—In Lamouroux's herbarium (CN).

**GULF OF CALIFORNIA DISTRIBUTION.**—Puerto Peñasco to La Paz (Figure 6).

**PACIFIC COAST DISTRIBUTION.**—Santa Catalina Island, off southern California (Johansen, 1976b:400, as *A. zonata*) to Ecuador (Dawson, 1953:146, as *A. zonata*); Galápagos Islands (Silva, 1966:152, as *A. zonata*).

SPECIMENS STUDIED.—*Gulf of California*. SONORA: Punta Pelicano, vicinity of Puerto Peñasco, 2 Jul

1973, JN & HWJ-73-7-3 (US, CUW); Playa Arenosa, vicinity of Puerto Peñasco, 15 Feb 1965,

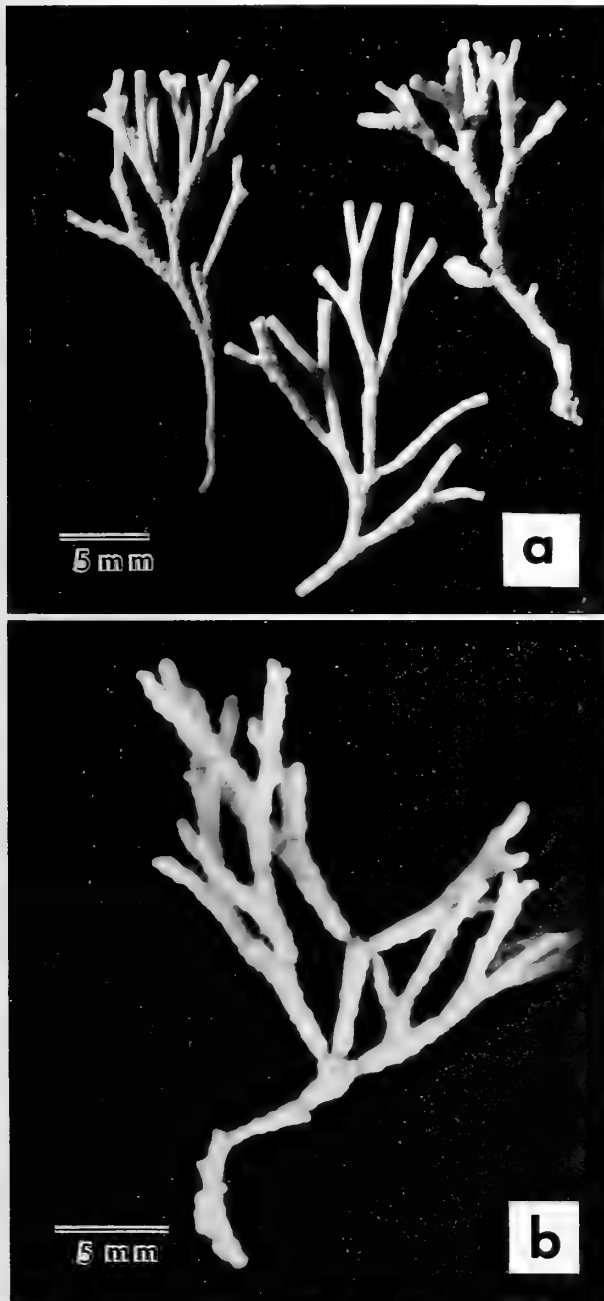


FIGURE 2.—*Amphiroa beauvoisii*: a, fronds from a single clump (JN & HWJ-73-7-3) (note variation from cylindrical to slightly compressed); b, genicula (JN-28 III 1973) (note they are more evident here than in "a," probably due to greater flexing).

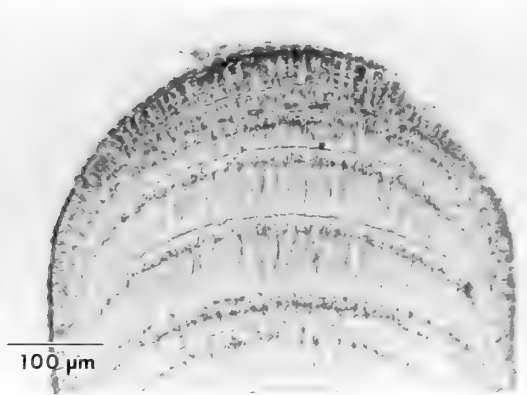


FIGURE 3.—Longitudinal sections through apex of a branch of *Amphiroa beauvoisii* (JN-4384).

A. E. Dennis D-81 and D82 (both US), 8 Apr 1966, EYD-27360 (US); Cupleaños Tide Pool, Playa Estacion, Puerto Peñasco, 4 Jul 1973, JN & HWJ-73-7-32 (CUW); Playa Estacion, in front of Laboratorio de Biología Marina, Puerto Peñasco, 27 Jul 1965, EYD-27470 (US), 7 Apr 1966, EYD-27299 (US), 8 Apr 1966, EYD-27360 (US), and 20 Oct 1972, JN-3583 (US); Isla San Jorge, 20 Feb 1946, EYD-846 (US); Puerto Lobos (Cabo Tepoca), 26 Mar 1937, Remple Sta. 724-37 (AHFH); Puerto Libertad, 19 Feb 1946, EYD-720 (US); Ensenada Bocochibampo, near Guaymas, 16 May 1946, EYD-1755 (US), 12 Feb 1946, EYD-490 (US); shallow lagoon, Guaymas Bay, 23 Jan 1940, EYD-5827 (US, UC, AHFH); Punta Colorado, near Guaymas, 15 Feb 1946, EYD-556 (AHFH); Punta San Pedro, Guaymas, 22 Dec 1939, Drouet & Richards 3386 (UC, AHFH); Ensenada de San Francisco, near Guaymas, 18 May 1946, EYD-1973 (US), 12 Jun 1958, EYD-11039 (US); Punta Prieta, Bahía Topolobampo, 10 Jun 1952, EYD-10966 (US). BAJA CALIFORNIA: Punta La Gringa, Bahía de Los Angeles, 22 May 1972, JN-3049 (US); Islas de los Gemelos, Bahía de Los Angeles, 21 May 1972, JN-3008b (US); Bahía Agua Verde, 12 Feb 1940, EYD-528-40 (AHFH), 11 Jul 1965, EYD-25852a (US); Isla

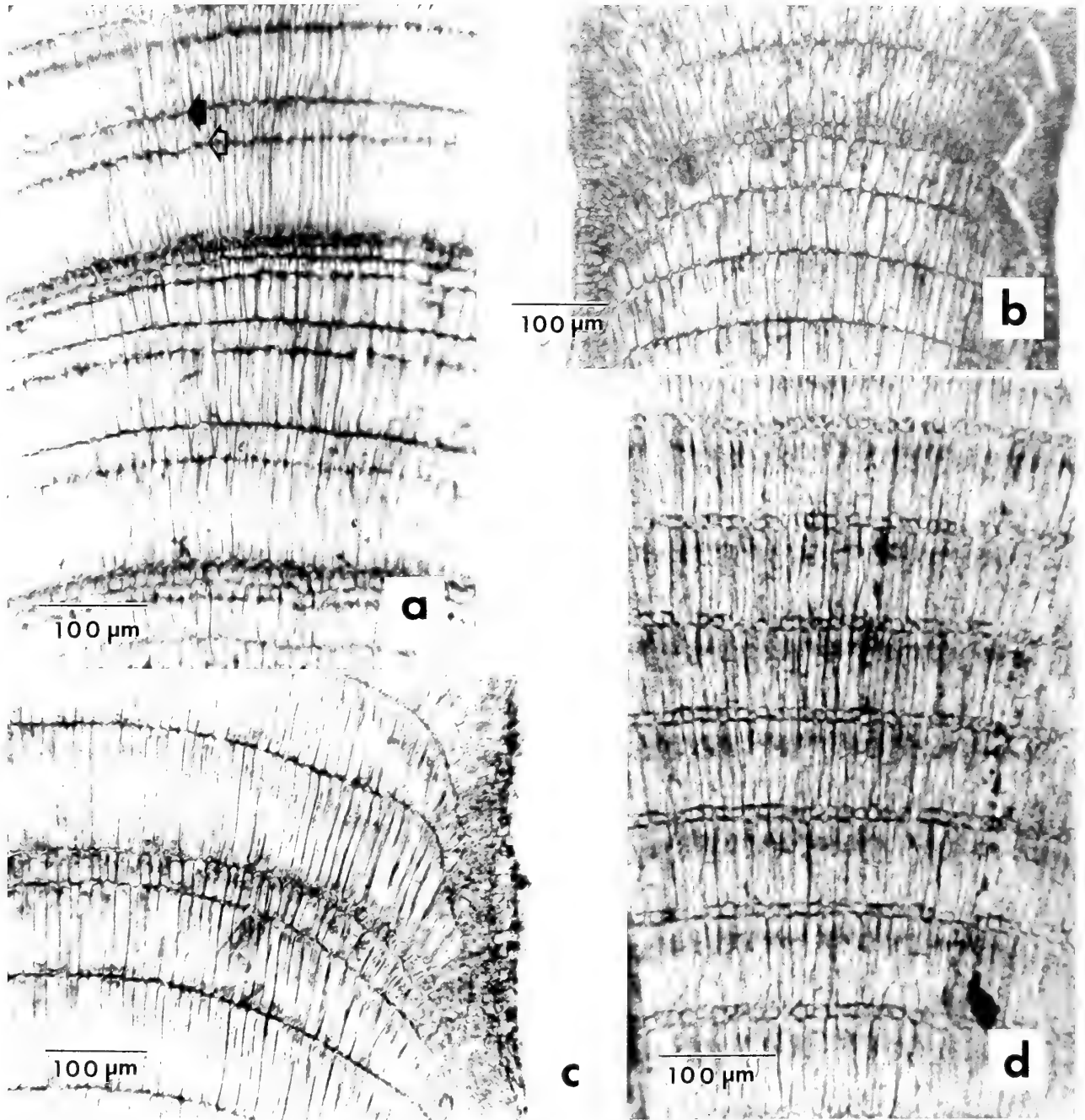


FIGURE 4.—Longitudinal sections of intergenicula: a, *Amphiroa beauvoisii* (JN & HWJ-73-7-31) (note arching lines of primary pit connections (solid arrow) and secondary pit connections (open arrow), which are about one-third below tops of cells); b, *A. beauvoisii* (JN-4384) (note thin cortex); c, *A. beauvoisii* (JN & HWJ-73-7-14) (note different heights of medullary cell tiers); d, *A. van-bossea* (JN & HWJ-73-7-31) (note unusual arrangement of alternating long and short tiers of medullary cells).

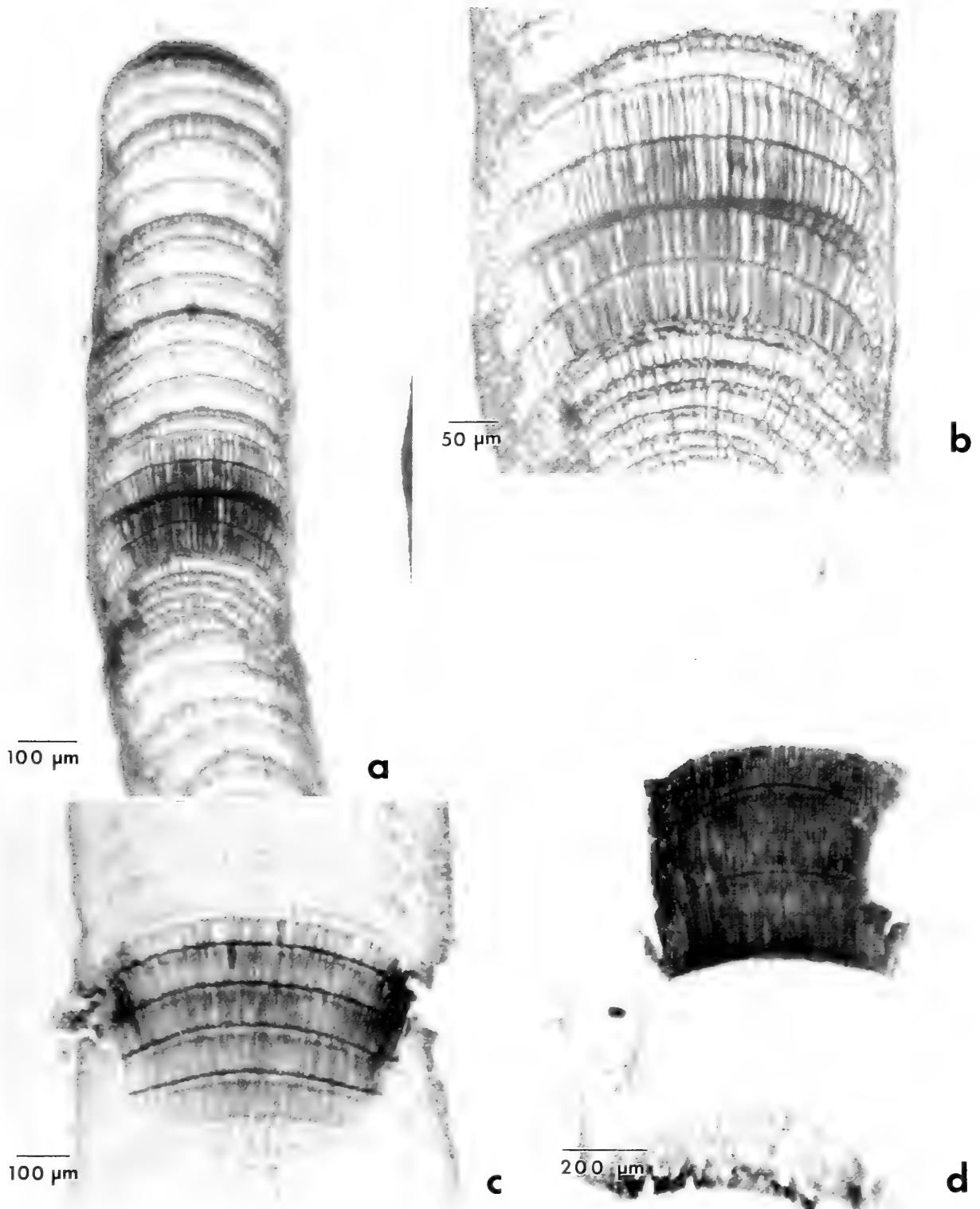


FIGURE 5.—Longitudinal sections of successively older genicula of *Amphiroa beauvoisii*: *a*, apex of branch with a young geniculum (JN-4384) (note that specimen was decalcified in preparing the slide and that the uncalcified genicular cells stain more intensely than the calcified intergenicular cells); *b*, close-up of geniculum in “*a*” (note that young genicular cortex is still intact and unruptured); *c*, older 5-tiered geniculum with ruptured genicular cortex (JN-4384); *d*, portion of branch showing geniculum and conceptacle (JN-4023).

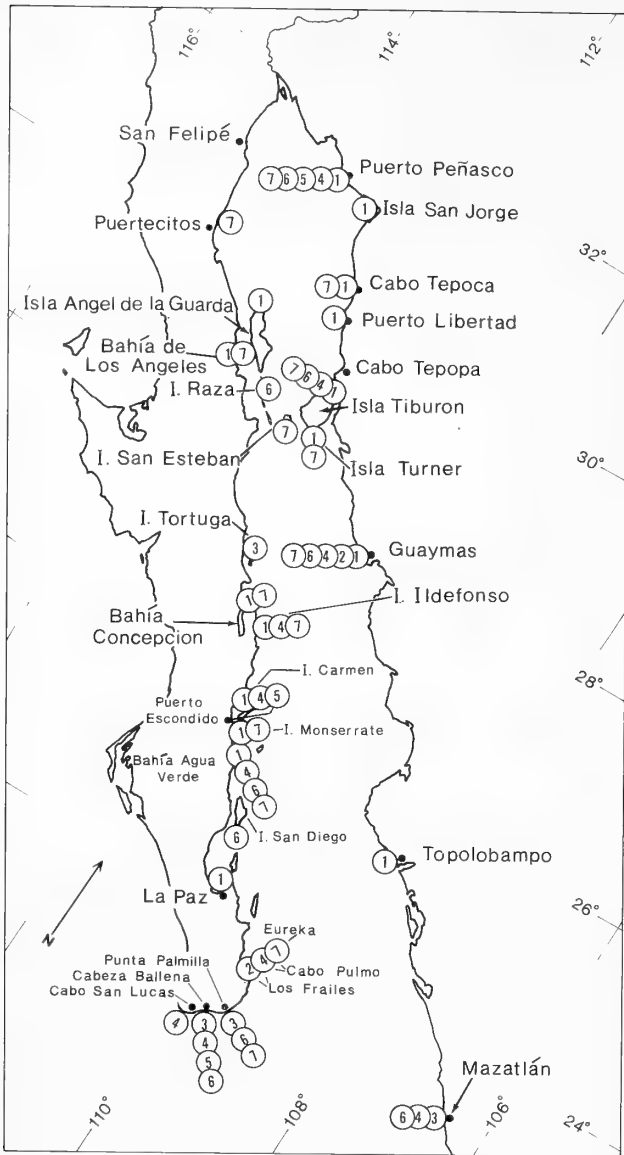


FIGURE 6.—Distribution of species of *Amphiroa* in the Gulf of California (1 = *A. beauvoisii*, 2 = *A. brevianiceps*, 3 = *A. magdalensis*, 4 = *A. misakiensis*, 5 = *A. rigida*, 6 = *A. valonioides*, 7 = *A. van-bossea*).

Ildefonso, 19 Jul 1965, EYD-25877 and EYD-25891 (both US); Isla Cholla, off Isla Carmen, 23 Apr 1958, EYD-18677 (US); Bahía Concepción, 26 Mar 1949, EYD-7112 (AHFH); Isla Monserrate, 21 Apr 1958, EYD-18795 (US); Bahía La Paz, 10 Nov 1946, EYD-3464 (AHFH). LAS ISLAS DE LA CINTURA: Puerto Refugio, Isla Angel de la Guarda, 26 Jan 1940, EYD-222 (AHFH); Isla

Patos, off Isla Tiburón, 17 Feb 1946, EYD-808 (US); Bahía Agua Dulce, Isla Tiburón, 21 Feb 1946, EYD-951 (US); Isla Turner, off Isla Tiburón, EYD-108-40 (AHFH), 18 Jul 1940, EYD-717-40 (holotype AHFH). CALIFORNIA. CHANNEL ISLANDS: Catalina Harbor, Santa Catalina Island, 14 Feb 1949, P.C. Silva-4636 (AHFH); Little Harbor, Santa Catalina Island, 8 Mar 1971, R. Setzer-5102 (AHFH); West Cove, San Clemente Island, 12 Oct 1971, R. Setzer-5803 (AHFH). ORANGE COUNTY: Corona del Mar, 21 Jan 1951, EYD-9598 (US, UC, AHFH); Laguna Beach, 8 Nov 1942, N. Cooper-151 (AHFH). SAN DIEGO COUNTY: Cardiff, 29 Jan 1949, EYD-6039 (UC, AHFH); La Jolla, 15 Jan 1946, EYD-318 (AHFH), 16 Feb 1958, EYD-18414 (AHFH), and 11 Nov 1958, EYD-19746 (AHFH). PACIFIC COAST OF MEXICO. BAJA CALIFORNIA: Isla Coronado del Sur, 20 Jun 1947, EYD-4247 (UC, AHFH) and 11 Aug 1948, C. Hubbs-48-217 (AHFH); Isla Guadalupe, 18 Dec 1949, EYD-8367 (AHFH); Punta Santa Rosallita, 10 Oct 1946, EYD-2852 (UC, AHFH); Miller's Landing, 11 Oct 1946, EYD-2946 (UC, AHFH, K); Punta Malarrimo, Bahía Sebastian Viscaíno, 17 Apr 1951, EYD-9944 (UC, AHFH); 'Campito', east of Punta San Eugenio, 31 Oct 1951, EYD-10487 (AHFH); Punta Norte, Isla Cedros, 30 Oct 1951, EYD-10582 (UC, AHFH); South Bay, Isla Cedros, 10 Mar 1934, WRT-646A (UC) and 19 Apr 1951, EYD-9864 (UC, AHFH); Punta San Eugenio, 29 Aug 1957, EYD-20841 (US); Bahía San Bartolomé (= Bahía Tortuga), 7 Nov 1949, EYD-6584 (AHFH); Punta Thurloe, 3 Apr 1955, EYD-13313 (US); Bahía Ascuncion, 28 Apr 1950, EYD-9178 (US, UC, AHFH); Isla Ascuncion, 25 Aug 1957, EYD-20379, EYD-20432a, and EYD-20439 (all US); Punta Abreojos, 30 Apr 1950, EYD-9456 (US, UC, AHFH, K) and 9 Feb 1964, EYD-26302 (US); Bahía San Hipolito, 18 Aug 1957, EYD-20336, EYD-20338, and EYD-20361 (all US); Punta Entrada, Bahía Magdalena, 2 May 1950, EYD-9296 (UC, AHFH). REVILLA GIGEDO ARCHIPELAGO: Binder's Cove, Isla Socorro, 16 Apr 1955, EYD-13602 (US). ISLAS TRES MARÍAS: Isla Maria Magdalena, 9 May 1939, WRT-



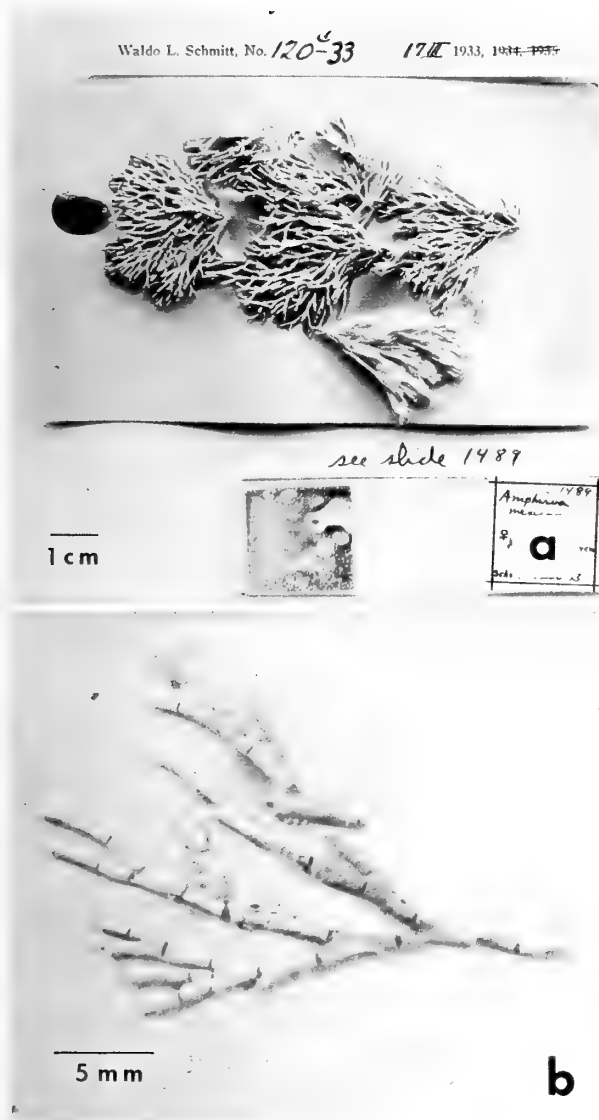


FIGURE 7.—Type specimens: a, *Amphiroa mexicana* (AHFH 91); b, *A. beauvoisii* (CN).

642A (paratypes US, UC). JALISCO: Bahía Chamelá, 14 Apr 1959, EYD-21258 (US). COLIMA: Bahía Santiago, 12 Apr 1959, EYD-21313 (US). GUERRERO: Morro de Petatlán, 17 Mar 1933, W. L. Schmitt-120C-33 (UC); Bahía Petatlán, 2–3 Mar 1934, WRT-568 (paratypes US, UC, AHFH); Puerto Guatulco, 8 Apr 1959, EYD-21440a (US); Salina Cruz, 10 Jan 1947, EYD-3826 (UC), 12 May 1952, EYD-10760 (US); Isla Grande, 10 Apr 1959, EYD-20954 (US); Aca-

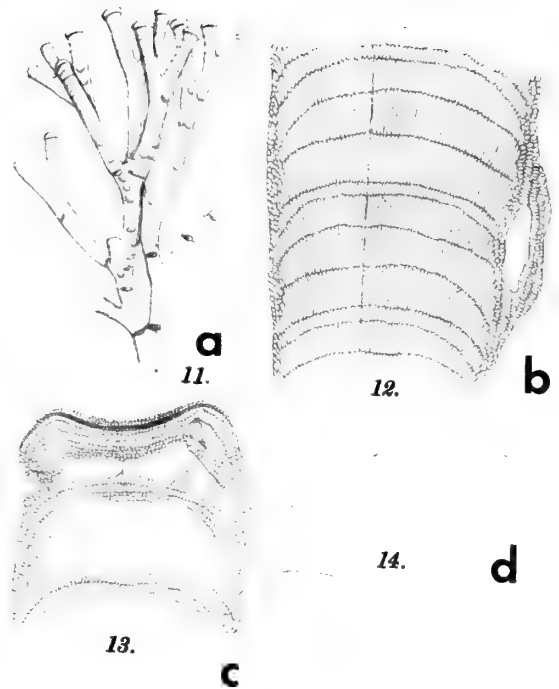


FIGURE 8.—Lectotype selected herein of *Amphiroa zonata* Yendo [= *A. beauvoisii*] (see also Figure 15b): a, habit of frond; b, longitudinal section through part of intergeniculum; c, oblique section through intergeniculum showing a young conceptacle; d, cross-section of branch. (All from Yendo, 1902, pl. 1.)

pulco, 3 Feb 1947, EYD-3881 (holotype AHFH). El Salvador. El Tunco, west of Puerto Libertad, 10 Sep 1960, EYD-21939 (US); El Cuco, 8 Sep 1960, EYD-21817 (US); Acajutla, 4 Sep 1960, EYD-21882 (US). Pacific Coast of Costa Rica. Bahía Ballena, 30 Mar 1959, EYD-21191 (US); Isla del Caño, 28 Mar 1959, EYD-21059 and EYD-21060 (both US). Pacific Coast of Panama. Isla Jicarón, 25 Mar 1959, EYD-21139 (US); Isla del Rey, Bahía San Telmo, 23 Mar 1959, EYD-21163 (US).

REMARKS.—Many specimens of *Amphiroa beauvoisii* have been collected in the Gulf of California and reported under other names. Dawson (1953: 134–135, 140–141) considered *A. zonata* and *A. drouetii* as distinct from each other on the basis of differences in the relative visibility of genicula in whole branches, in intergenicular breadth, in degree of flatness or roundness of intergenicula in

cross-sectional view, in relative lengths of intergenicula, and in the relative amounts of "forking" of intergenicula. This complex represents one widely variable species. On morphological bases, it was impossible to categorize them into the taxa that Dawson recognized in the Gulf.

We were unsuccessful in our efforts to locate type material of *A. zonata* Yendo (1902). In accordance with Article 9.3 of the *International Code of Botanical Nomenclature* (Stafleu et al., 1978), we selected the illustrations of Yendo (i.e., pl. 1: figs. 11–14; pl. 2: fig. 9) as the lectotype of *A. zonata* (Figure 8). Furthermore, the examination of this and other type specimens of *Amphiroa* shows that the earliest validly published name applicable for this morphologically variable complex is *Amphiroa beauvoisii* Lamouroux, 1816 (Figure 7b).

In all likelihood, *A. beauvoisii* is the most widespread species of *Amphiroa*, perhaps occurring in most tropical and subtropical areas where the genus may be found. Although we are as yet not prepared to consider entities other than those of the Gulf of California, it is probable that several other species described subsequent to Lamouroux (1816) may also belong to *A. beauvoisii*. For example, in the Pacific Ocean, *Amphiroa galapagensis* Taylor (1945), *A. mexicana* Taylor (1945) (Figure 6a), and *A. echigoensis* Yendo (1902) may be synonymous with *A. beauvoisii*.

*Amphiroa crosslandii* Lemoine (1929) was mentioned as occurring in the Gulf at La Paz, Baja California del Sur, by Dawson (1953:149). This is the only Gulf of California collection labeled *A. crosslandii* that we are aware of. Unfortunately, Dawson did not cite specific collections, but it is probably based on EYD-3464 (AHFH 44178, UC 974659), which we conclude represents a collection of several small aberrant plants of *A. beauvoisii*. While we have examined an isotype of *A. crosslandii* (BM) and found it to superficially resemble *A. beauvoisii*, this taxon must await further study before any conclusion can be made on its taxonomic status.

*Amphiroa linearis* was reported by Hariot (1895) from the Gulf of California. While we have not

seen the specimens on which Hariot based his record, Dawson (1953:137) noted that it was probably *Amphiroa zonata*. Further, the holotype of *A. linearis* Kützing (from Gabon, West Africa), represented by fragments in L 938, 334. . .357 is in agreement with our concept of *A. beauvoisii*. We now consider *A. linearis* as a synonym of *A. beauvoisii*.

Our study of the type specimen of *Amphiroa franciscana* var. *robusta* Dawson (AHFH) from Acapulco reveals that it too is within the morphological range we recognize for *Amphiroa beauvoisii*. When Dawson (1953:150) erected the variety, he also listed a single Gulf of California specimen (paratype, EYD-4455), which we did not study; it may also represent *A. beauvoisii*.

Unlike other species in the Gulf of California, *A. beauvoisii* is widespread in distribution in tropical and subtropical areas of the Atlantic and Indian Oceans. In the western Atlantic, it occurs from North Carolina (Schneider, 1976:138) south to Uruguay (Taylor, 1960:405–406, in part as *A. brasiliensis*). It also is reported from Portugal (type locality), the Mediterranean Sea (Hamel and Lemoine, 1953:42), and is abundant in the southwestern Indian Ocean (Johansen, unpublished data).

### *Amphiroa brevianceps* Dawson

FIGURES 1b, 6, 9

*Amphiroa brevianceps* Dawson, 1953:142, pl. 31: fig. 2.

DESCRIPTION.—*Fronde*s: in small clumps up to 4 cm high. *Branching*: somewhat regularly and densely dichotomous, in one plane. *Intergenicula*: near base subterete or flat and up to 2 mm broad, intergenicula in upper parts flat, up to 3 mm broad and short, usually less than 4 mm long, not differentiated into midrib and wings. *Genicula*: externally prominent, dark colored, bracketed by calcified extensions of the adjacent intergenicula, 6 or more tiers of cells per geniculum. *Conceptacles*: Dawson (1953:143) reported tetrasporangial and carposporangial conceptacles on both intergenicular surfaces.



FIGURE 9.—Type specimen of *Amphiroa brevianceps* (EYD-3825, AHFH).

**TYPE LOCALITY.**—"On rocky shore just east of Salina Cruz, Oaxaca, Mexico" (Dawson, 1953: 143).

**HOLOTYPE.**—EYD-3825, 10 Jan 1947 (AHFH 55180; isotype UC 925637).

**GULF OF CALIFORNIA DISTRIBUTION.**—Guaymas; Los Frailes.

**PACIFIC COAST DISTRIBUTION.**—Punta San Hipolito, Baja California (Dawson, Neushul, and Wildman, 1960b:16); Salina Cruz, Oaxaca.

**SPECIMENS STUDIED.**—*Gulf of California*. SONORA: Punta de Las Cuevas, Ensenada de San Francisco, near Guaymas, 14 Feb 1946, EYD-593 (paratype AHFH). BAJA CALIFORNIA: Punta [Los] Frailes, 13 Mar 1949, EYD-6895 (paratype

AHFH). *Pacific Coast of Mexico*. OAXACA: Salina Cruz, Oaxaca, 10 Jan 1947, EYD-3825 (holotype AHFH) and 12 May 1952, EYD-10765 (US).

**REMARKS.**—In the Gulf of California, there are three species of *Amphiroa* in which the intergenicula are flat, *A. brevianceps*, *A. magdalensis*, and *A. misakiensis*. Of these, *A. brevianceps* and *A. magdalensis* are represented by few specimens, with *A. brevianceps* the most poorly known. *Amphiroa brevianceps* is closely related to *Amphiroa anceps* (Lamarck) Decaisne, a widespread species in subtropical and tropical areas of the world (Weber-van Bosse, 1904:93, pl. 16: figs. 6–8).

Weber-van Bosse (1904) and Johansen (1969b) described the genicula of *A. anceps*; those in *A. brevianceps* are identical. The flexing of the fronds and the thickness of the intergenicular cortex results in a patch of calcified cortical tissue breaking away so that in surface view a geniculum is bracketed by calcified tissue. Dawson (1953:143) described a geniculum in *A. brevianceps* as a uncalcified "window" appearing "embraced" [by intergenicular tissue]. *Amphiroa anceps* is noted for this feature, but here the intergenicula are longer than in *A. brevianceps*. This genicular character is most evident in younger parts of the fronds before erosion and secondary growth take place. More specimens are needed so the specific relationships of these taxa can be resolved.

### *Amphiroa magdalensis* Dawson

FIGURES 1c, 6, 10b

*Amphiroa magdalensis* Dawson, 1953:143, pl. 30: fig. 2.

**DESCRIPTION.**—*Fronds*: up to 5 cm high in loose tufts. *Branching*: sparsely dichotomous or irregular. *Intergenicula*: basal intergenicula terete, others markedly flattened and 1–2.5 mm broad, 3 to 6 times as long. *Genicula*: conspicuous because of broken out pieces of adjacent intergenicula in center of branch; up to or more than 10 cellular tiers per geniculum. *Conceptacles*: tetrasporangial conceptacles scattered on intergenicular surfaces, usually more on one side than the other; sexual plants not encountered in the Gulf of California.

TYPE LOCALITY.—“Rocky shore at Punta Entrada, Isla Magdalena, Baja California, Mexico” (Dawson 1953:144).

HOLOTYPE.—EYD-6688, 8 Mar 1959 (AHFH 55165).

GULF OF CALIFORNIA DISTRIBUTION.—Isla Ildefonso (Dawson, 1959:21) to Punta Palmilla; Mazatlán.

PACIFIC COAST DISTRIBUTION.—Punta Abreojos to Bahía Magdalena, Baja California.

SPECIMENS STUDIED.—*Gulf of California*. BAJA CALIFORNIA: Isla Tortuga, 25 Apr 1958, EYD-18646 (US); Cabeza Ballena, 11 Mar 1949, EYD-6831 (AHFH); Punta Palmilla, 7 Nov 1946, EYD-3224 (AHFH). SINALOA: Mazatlán, 7 Jun 1952, EYD-10828 (US). *Pacific Coast of Mexico*: BAJA CALIFORNIA: Punta Abreojos, 9 Feb 1964, EYD-26301 (US); Punta Entrada, Bahía Magdalena, 8 Mar 1949, EYD-6688 (holotype AHFH). Punta Redondo, Isla Santa Margarita, 3 Feb 1964, EYD-26294 (US); Cabo Tosco, Isla Santa Margarita, 4 Feb 1964, EYD-26316 (US).

REMARKS.—Among the more robust species of *Amphiroa*, *A. magdalensis* may be distinguished by having flat, thin, long intergenicula (Figure 10b). The genicula have more cellular tiers than other Gulf of California species, with 10 tiers present in some specimens (Figure 1c).

Few specimens of *A. magdalensis* have been collected and the relationship of this species to other species is poorly known. Dawson labeled a Gulf specimen from near Guaymas, Sonora (EYD 650, US) as *Amphiroa foliacea* Lamouroux, probably because of the wings flanking the slightly raised midrib in some of the intergenicula, a feature ascribed to *A. foliacea* (Ganesan, 1968:16). As mentioned earlier, *A. magdalensis* and *A. brevianiceps* are similar; in the latter the intergenicula are shorter. *Amphiroa anceps*, an older species common in other subtropical areas (e.g., southeast Africa, Johansen, 1969b:120), is also related structurally to these two Gulf species. For the time being, these taxa should be considered distinct until population studies, particularly on those from type localities, and more collections have been made. It may be that they represent a single



FIGURE 10.—Type specimens: a, *Amphiroa subcylindrica* (= *A. van-bosseae*, EYD-555, AHFH); b, *A. magdalensis* (EYD-6688, AHFH).

polymorphic species. Dawson (1953:145) stated, with reference to specimens of *A. magdalensis* that “these are representative of the wide range of variation in size which may be encountered in species of *Amphiroa* and of which one must be well aware in attempting determinations of these perplexing plants.”

In addition to the Gulf, *A. magdalensis* is known from the Pacific coast of Baja California and Isla Guadalupe (Dawson, 1953:144). Hommersand (1972) suggested that this species and *Amphiroa ephedraea* (Lamarck) Decaisne (as interpreted from Japanese specimens) are closely related or possibly conspecific. In this connection, it should be noted that *A. ephedraea* as recognized in Japan (Okamura, 1936:518) is not the same species exemplified by the type of the species (PC).

***Amphiroa misakiensis* Yendo**

FIGURES 1d, 6, 11, 12a, 13a, 15c

*Amphiroa misakiensis* Yendo, 1902:14, pl. 1: figs. 24, 25; pl. 6: fig. 1.

*Amphiroa pusilla* sensu Dawson, 1944:276 [in part] [not *Amphiroa pusilla* Yendo, 1902:13].

*Amphiroa dimorpha* sensu Taylor, 1945:192, pl. 55.—Dawson, 1953: 141; 1966a:18 [not *Amphiroa dimorpha* Lemoine, 1929:76].

*Amphiroa dimorpha* var. *digitiformis* Dawson, 1959:21 [as '*digitiforme*'], fig. 4 [type locality: "... at a depth of about 5 feet, Isla Cholla, off Isla Carmen, April 23, 1958," EYD-18684 (holotype LAM now AHFH 81912; isotype AHFH)].

**DESCRIPTION.**—*Fronds*: up to 4 cm long; usually growing more or less recumbent and spreading from the substrate so that one branch surface is uppermost. *Branching*: basically dichotomous, but this pattern often obscure when one to several branches arise irregularly from intergenicula. *Intergenicula*: near base small and subterete, in upper parts of fronds flat, irregularly shaped, size varying greatly but usually up to 7 mm long and 3–4 mm broad. *Genicula*: developing by cracking and sloughing of calcified cortical tissue overlying uncalcified genicular tissue, genicula quite evident externally, comprised of 5 or more tiers of medullary cells plus patches of uncalcified cortical tissue. *Conceptacles*: several per fertile intergeniculum scattered over uppermost (or lowermost according to Dawson, 1953:142) surfaces, protruding slightly, tetrasporangial conceptacles about 200  $\mu$ m inside diameter; sexual plants not encountered in the Gulf of California.

**TYPE LOCALITY.**—"Misaki" Japan (Yendo, 1902:14).

**LECTOTYPE.**—In the absence of a known holotype, Yendo's illustrations (1902, pl. 1: figs. 24, 25, & pl. 6: fig. 1) are selected as the lectotype of *A. misakiensis* Yendo (Figure 15c).

**GULF OF CALIFORNIA DISTRIBUTION.**—Puerto Peñasco to Cabo San Lucas; Mazatlán (Figure 6).

**PACIFIC COAST DISTRIBUTION.**—Baja California to Costa Rica; Peru.

**SPECIMENS STUDIED.**—*Gulf of California*. SONORA:

Punta Pelicano, vicinity of Puerto Peñasco, 6 Apr 1966, EYD-27269 (US) and 2 Jul 1973, JN & HWJ-73-7-2 (US, CUW); Playa Arenosa, vicinity of Puerto Peñasco, 15 Feb 1965, A. E. Dennis D-72 (US), 30 June 1965, EYD-27430 (US), 5 Sep 1972, JN-3439 (CUW), and 27 Oct 1972, JN-3606 (US); Cumpleaños Tide Pool, Playa Estacion, Puerto Peñasco, 8 Sep 1972, JN-3531 (US), and 4 Jul 1973, JN & HWJ-73-7-27 (ARIZ); Playa Estacion, in front of Laboratorio de Biología Marina, Puerto Peñasco, 27 Jul 1965, EYD-27471 (US), 7 Apr 1966, EYD-27339 (US), 11 Jul 1972, JN-3146b (ARIZ), and JN-3173 (CUW), 22 Jan 1973, JN-3684 (MEXU), and 25 Nov 1972, JN-3806 (US); Guaymas, 22 Dec 1939, Drouet & Richards-3387 (AHFH); Ensenada de San Francisco, near Guaymas, 17 Apr 1946, EYD-1865 (AHFH) and 20 Nov 1946, EYD-35552 (AHFH). BAJA CALIFORNIA: Bahía Agua Verde, 20 Apr 1958, EYD-18902 (US); Isla Idefonso, 19 Jul 1965, EYD-25906 (US); Isla Cholla, off Isla Carmén, 23 Apr 1958, EYD-18684 (holotype, LAM); Punta[Los] Frailes, 13 Mar 1949, EYD-7088 (AHFH); Cabeza Ballena, 9 Nov 1946, EYD-3391 (AHFH); Cabo San Lucas, 20–23 Aug 1957, EYD-20173 (US). LAS ISLAS DE LA CINTURA: Isla Patos, off Isla Tiburon, EYD-807 (US). SINALOA: Mazatlán, 7 Dec 1946, EYD-3665 (AHFH). *Pacific Coast of Mexico*. BAJA CALIFORNIA: Chester Islets, Bahía Sebastian Viscaino, 16 Aug 1957, EYD-20493 (US); Bahía San Hipolito, 18 Aug 1957, EYD-20352 (US); Punta Abreojos, 9 Feb 1964, EYD-26303 (US); Punta Entrada, Bahía Magdalena, 19 Aug 1957, EYD-20213 (US). REVILLA GIGEDO ARCHIPELAGO: Binder's Cove, Isla Socorro, 19 Nov 1953, EYD-12139 (US); Isla San Benedicto, 17 Nov 1953, EYD-12046 (AHFH). ISLAS TRES MARIAS: Isla Maria Cleofa, 8 Feb 1954, EYD-12375 (US). NAYARIT: Mira Mar, 20 Dec 1946, EYD-3703 (AHFH). COLIMA: Bahía Carrizal, 4 Dec 1959, EYD-21008 (US). OAXACA: Puerto Gualtulo, 4 Jul 1959, EYD-21398 (US). *El Salvador*. Punta Acajutla, 4 Sep 1960, EYD-21777 (US). *Pacific Coast of Costa Rica*. Isla del Caño, 28 Mar 1959, EYD-21063 and EYD-21102 (both

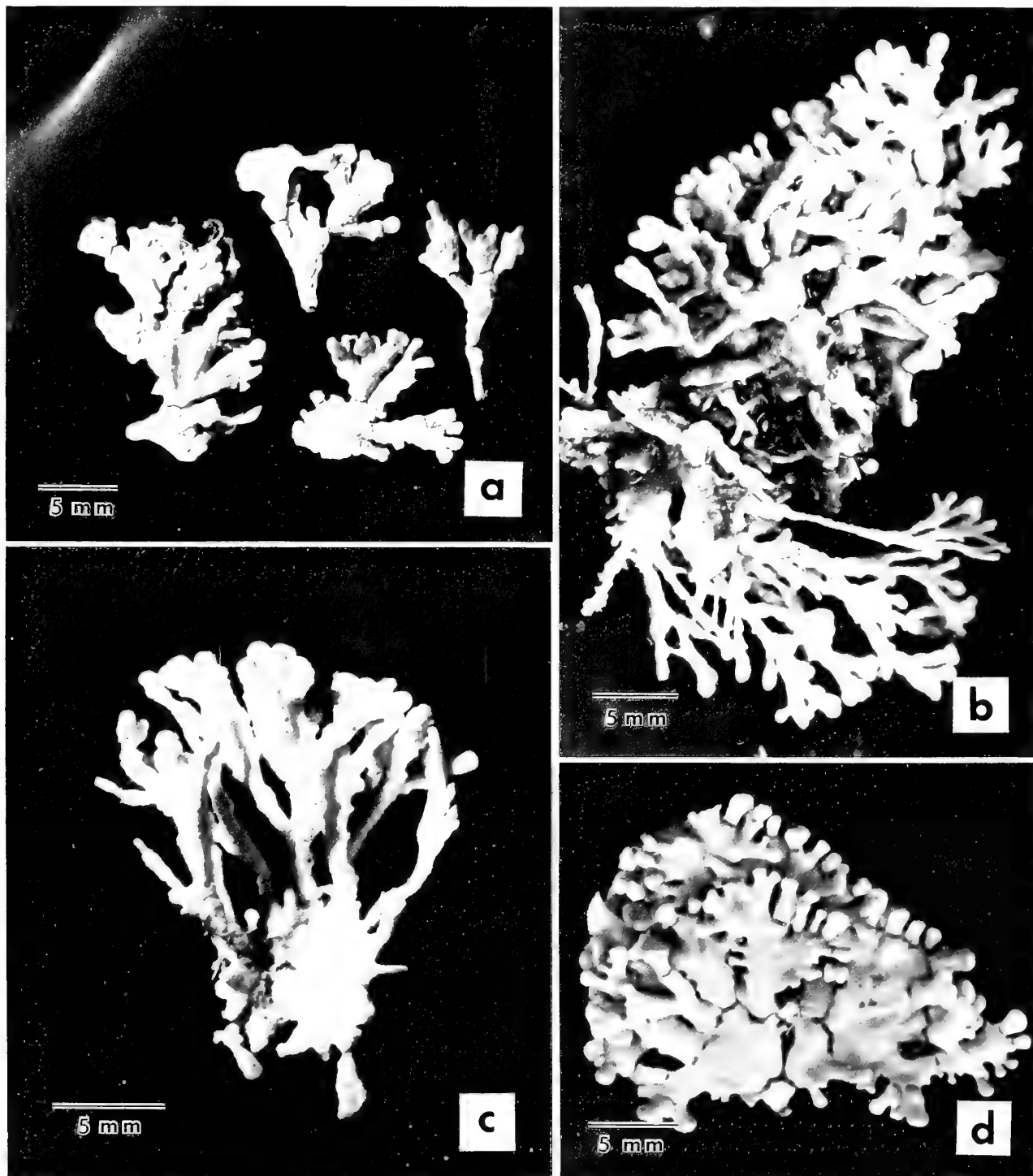


FIGURE 11.—*Amphitroa musakiensis*: a, branches and conceptacles (JN-3684) (note irregularity in branching); b, JN & HWJ-73-7-2; c, flat crust-like piece from which arises several branches (JN & HWJ-73-7-2a); d, specimen resembling Dawson's *A. dimorpha* var. *digitiformis* (JN-5102) (note numerous small branches arising from some of the large flat intergenicula).

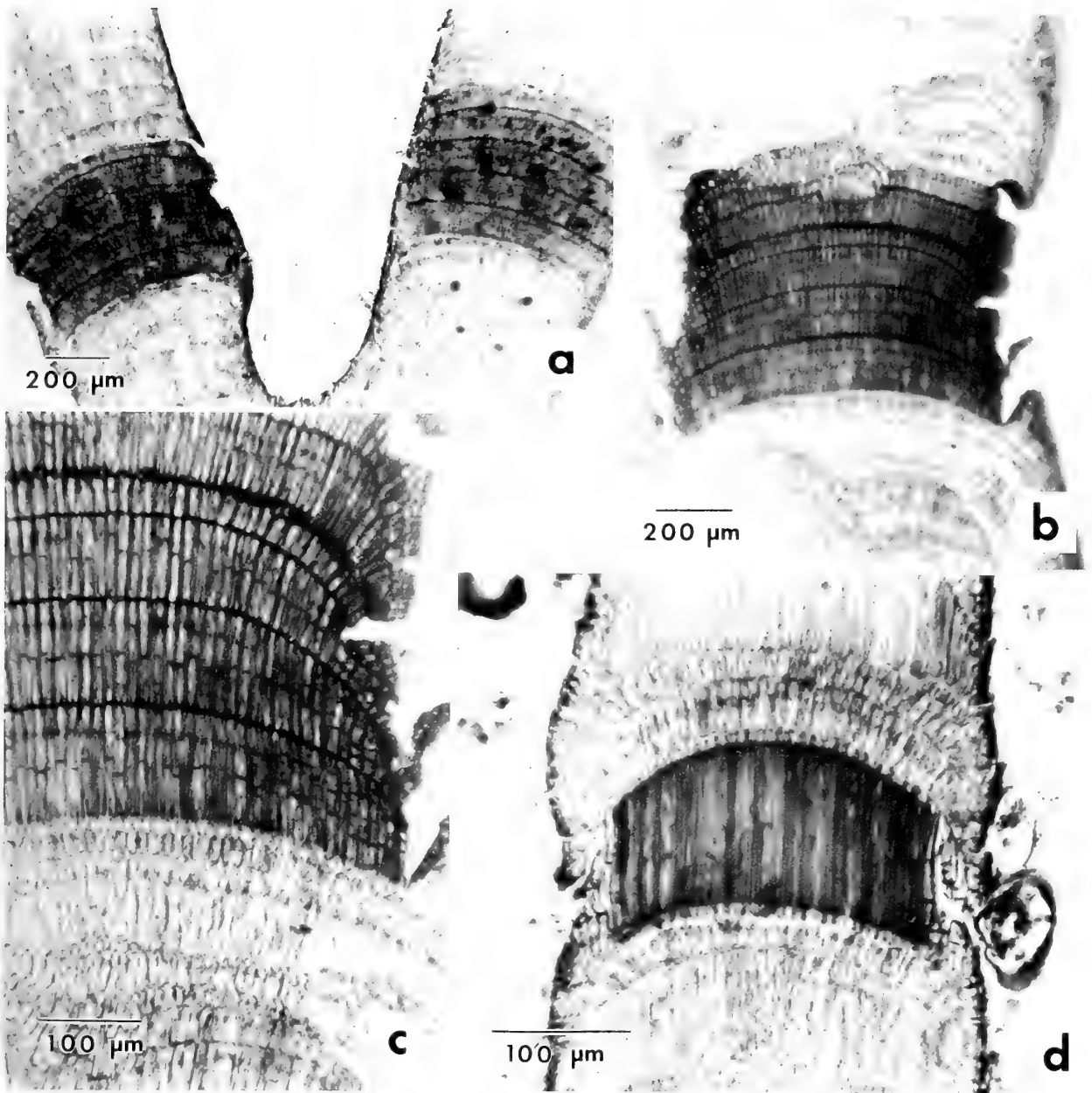


FIGURE 12.—Longitudinal sections of genicula: a, *Amphiroa misakiensis* (JN & HWJ-73-7-27) (note two branches that developed from dichotomously divided intergeniculum before the genicula formed); b, *A. van-bossea* (JN-4859) (note multi-tiered geniculum in which adjacent intergenicula are well separated by genicular tissue); c, magnified view of the geniculum shown in "b" (note remnants of genicular cortex); d, *A. valonioides* (JN & HWJ-73-7-4) (note geniculum of single-tiered cells).

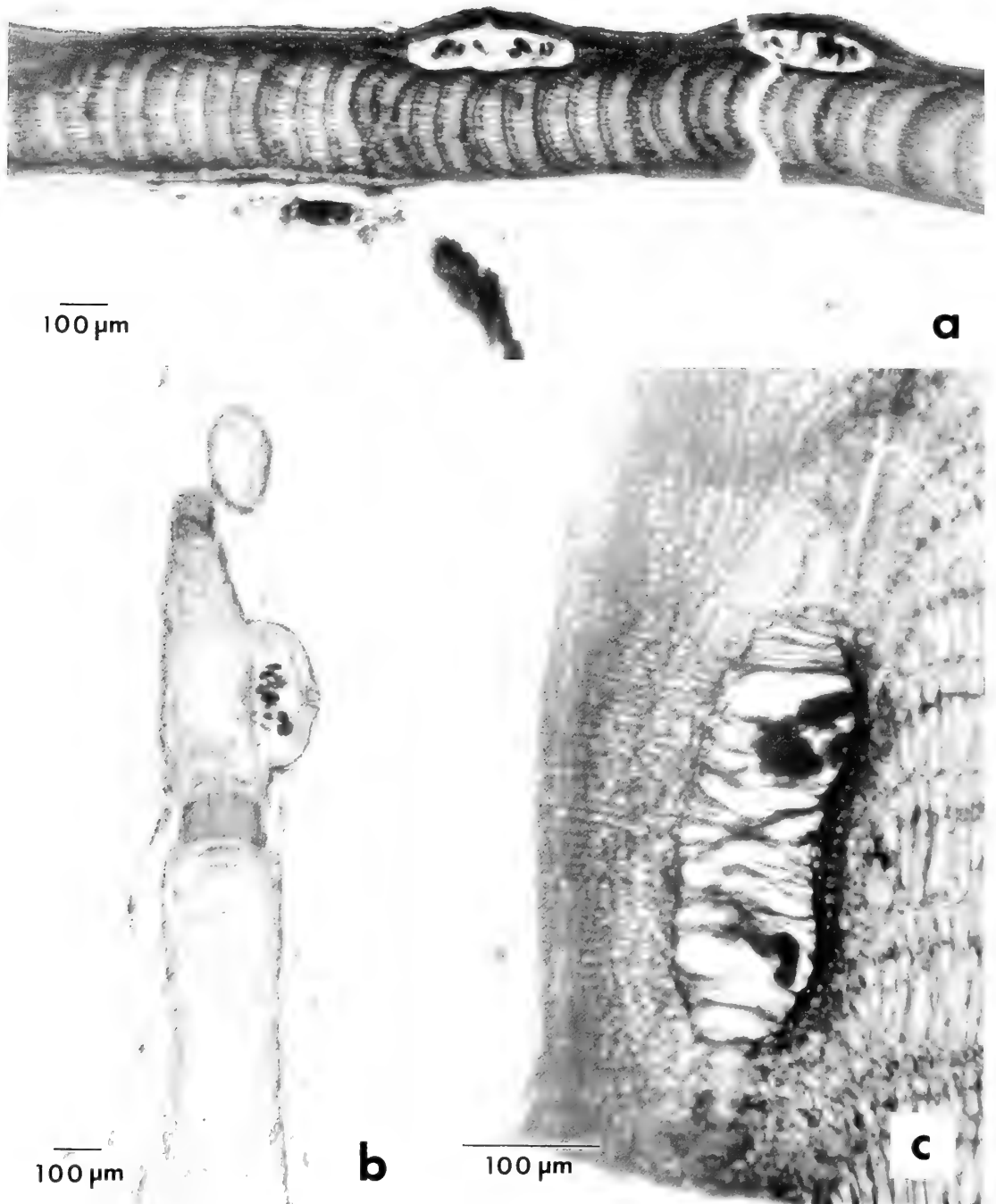


FIGURE 13.—Sections of conceptacles: *a*, two tetrasporangial conceptacles of *Amphiroa misakiensis* (JN & HWJ-73-7-2a) (note cortex is thicker on the dorsal surface); *b*, *A. valonioides* (JN-4044) (note protruding conceptacle, cf. "a"); *c*, old tetrasporangial conceptacle of *A. van-bossea* (JN-4859) (note copious cortical tissue over the conceptacle chamber).



US); Bahía Uvita, 30 Mar 1959, EYD-21092 (US).

REMARKS.—As with other taxa described by Yendo (1902), a type specimen seems not to be extant. However, Segawa (1940b) published an anatomical study of *Amphiroa misakiensis* based on specimens from Japan and, on the basis of the data he provided and Yendo's original description, illustrations and habit photograph, we refer the Gulf of California material, identified as *Amphiroa dimorpha* by Dawson (1953, 1966a), to *A. misakiensis*.

Of all the species of *Amphiroa* in the Gulf, this seems to be the most polymorphic. Generally many intergenicula are broad and flat, but occasionally small cylindrical intergenicula arise from the large flat ones, as described and figured for *Amphiroa dimorpha* var. *digitiformis* Dawson (1959), which we now consider to be a synonym of *A. misakiensis*. This species grows in tufts in which the branches are often recumbent or only partially erect (Table 1). Flat intergenicula may often have the upper surface slightly convex and the lower concave. Sometimes the edges of broad intergenicula are slightly bent toward the dorsal surface (Yendo, 1902, pl. 1: figs. 24,25). The uppermost cortices are thicker than the lower cortices (Figure 13a), a feature also seen in *Bossiella californica* ssp. *schmittii* (Manza) Johansen (1973), another species of articulated coralline in which the intergenicula are horizontally disposed.

Widely distributed in the eastern Pacific, *A. misakiensis* (as *A. dimorpha*) has been reported from Isla Cedros, off the Pacific coast of Baja California (Dawson, Neushul, and Wildman, 1960b:16) Pacific Costa Rica (Dawson, 1957:19) and from Peru (Dawson, Acleto, and Foldvik, 1964:47). Dawson, Neushul, and Wildman (1960a:44, as *A. dimorpha*) stated that in central Baja California this species is "an exclusively deepwater plant of frequent occurrence at depths of 25–65 feet [7.6–19.8m] in the southernmost kelp areas." Elsewhere, it may occur in "severely surfy habitats," such as, El Salvador (Dawson, 1961b:411, as *A. dimorpha*).

## *Amphiroa rigida* Lamouroux

FIGURES 1e, 6, 14a,c

*Amphiroa rigida* Lamouroux, 1816:297, pl. 11: fig. 1.

*Amphiroa taylorii* Dawson, 1953:138, pl. 26: fig. 1 [type locality: Bahía Braithwaite, Isla Socorro, Revilla Gigedo Archipelago, Mexico (WRT-34-27, holotype, AHFH 55156)]; 1959:22; 1966a:18.

DESCRIPTION.—*Fronds*: up to 2 cm high, isolated or sometimes in more or less erect clumps. *Branching*: irregular and usually at wide angles, branch junctions usually not coinciding with genicula. *Intergenicula*: terete, to 0.5 (–1.0) mm diameter and variable in length. *Genicula*: often nearly invisible in young parts of fronds, becoming exposed by separation of calcified cortices overlying uncalcified genicula, made up of two tiers of cells each 75–100  $\mu$ m high, end walls of cells oblique where they meet and cells appearing imbricated. *Conceptacles*: not studied in Gulf of California specimens (see Suneson, 1937, for species).

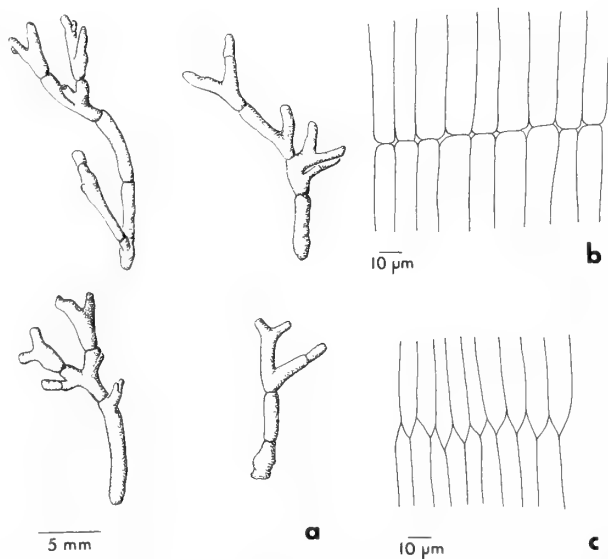


FIGURE 14.—a, Fronds of *Amphiroa rigida* from a single collection (EYD-27400) (note that genicula are seldom at the branch dichotomy); b, genicula of *A. beauvoisii* (JN & HWJ-73-7-3) (note squared-off way that cells of adjacent tiers are joined); c, genicula of holotype of *A. taylorii* (= *A. rigida*, WRT-34-27) (note unique imbrication of cell ends, a feature not found in other Gulf of California species of *Amphiroa*).

TYPE LOCALITY.—“Mediterranee” (Lamouroux, 1816:297).

HOLOTYPE.—Fragments in Lamouroux's herbarium in CN.

GULF OF CALIFORNIA DISTRIBUTION.—Puerto Peñasco; Puerto Escondido (Dawson, 1959:27); Cabeza Ballena.

PACIFIC COAST DISTRIBUTION.—Isla Socorro, Revilla Gigedo Archipelago; Isla Maria Magdalena; Costa Rica; Nicaragua (Dawson, 1962).

SPECIMENS STUDIED.—*Gulf of California*. SONORA: Playa Estacion, vicinity of Puerto Peñasco, 9 Apr 1966, EYD-27400 (US). BAJA CALIFORNIA: Cabeza Ballena, 11 Mar 1949, EYD-6833 (paratype, *A. taylorii*, AHFH). *Pacific Coast of Mexico*. REVILLA GIGEDO ARCHIPELAGO: Caleta Binmer, Isla Socorro, 19 Nov 1953, EYD-12141 (US); Bahía Braithwaite, Isla Socorro, 2 Jan 1934, WRT-34-27 (holotype, *A. taylorii*, AHFH). *Pacific Coast of Costa Rica*. Isla del Caño, 29 Mar 1959, EYD-21096a (US).

REMARKS.—The distribution of *Amphiroa rigida* is widespread, occurring in such diverse areas as the Mediterranean Sea (type locality), in Japan (Segawa, 1940a), and now the Gulf of California, Pacific Mexico, and Pacific Costa Rica. A more robust variety, *A. rigida* var. *antillana* Børgesen (1917:182), was described from the Caribbean Sea. The type specimen of *Amphiroa taylorii* (AHFH) from Isla Socorro, Revilla Gigedo Archipelago, as well as the Gulf of California specimens previously identified as *A. taylorii*, all belong to *A. rigida*. The only notable difference being that the Mexican plants are smaller than the type of *A. rigida* Lamouroux (CN).

*Amphiroa rigida* is a unique species of articulated coralline algae. Particularly characteristic are the two-tiered genicula, in which the end walls of the cells are slanted and appear to overlap (Figure 14c; Suneson, 1937:48, fig. 28A). This type of end wall has not been observed in other species of *Amphiroa*, but is clearly evident in the type specimen of *A. rigida* and in the type of *A. taylorii*. In all other species of *Amphiroa*, the end walls are transverse rather than oblique (see e.g., Figure 14b). In fact, Yendo (1904:17) in his study of

coralline genicula incorrectly considered the genicula of *A. rigida* to consist of single tiers in which each cell was “twisted” at its midpoint so as to form what appeared to be an oblique crosswall. The developmental sequence of the genicula in *A. rigida* has not been studied.

Plants of *A. rigida* in the Gulf are relatively small, inconspicuous and easily confused with *A. valonioides*. However, a character that is usually sufficient to set *A. rigida* apart is the irregularly disposed, rigid branches (Figure 14a). Rarely do the junctions of branches coincide with genicula in *A. rigida*, as they often do in other species of *Amphiroa*. This species is apparently not common in the Gulf of California. In Puerto Peñasco and possibly elsewhere, it is found growing sympatrically with *A. valonioides*.

Cabioch (1969) found that *A. rigida* from the Mediterranean Sea has a unique mode of early growth and development that results in the bases of the fronds becoming embedded in the crustose coralline *Neogoniolithon notarisii* (Dufour) Hamel and Lemoine. In this relationship the crustose plants serve as holdfasts for the articulated plants. This phenomenon has not been reported elsewhere, but Dawson (1953:138) did state that *A. taylorii* (now considered a synonym of *A. rigida*) occurs on crustose coralline algae.

It is impossible at present to give an idea of the distribution of *A. rigida* in the eastern Pacific. Some specimens that may represent this taxon are those reported as *A. rigida* var. *antillana* from Atlantic Costa Rica (Dawson, 1962:383), and *A. taylorii* from Pacific Costa Rica and Nicaragua (Dawson, 1957:19, 1962:395).

### *Amphiroa valonioides* Yendo

FIGURES 1f, 6, 12d, 13b, 15a, 16, 17

*Amphiroa valonioides* Yendo, 1902:5, pl. 1: figs. 1–3, pl. 4: fig. 1.

*Amphiroa annulata* Lemoine, 1929:78, fig. 34; pl. 4: fig. 1 [type locality: “Galapagos. Île James, James Bay, Station 2, drage a 15 brasses (27 metres)” (holotype, BM)].—Dawson, 1953:136, pl. 29: fig. 3; 1966a:18.

*Amphiroa franciscana* Taylor, 1945:187, pl. 48: fig. 2, pl. 49 [type locality: “Esmeraldas, dredged off Bahía San Fran-

cisco," Ecuador, WRT-34-484 (holotype AHFH 93, isotype MICH)].

*Amphiroa annulata* var. *pinnata* Dawson, 1953:137 [no illustration] [type locality: Cabeza Ballena, Baja California, Mexico, EYD-3374 (holotype, AHFH 55116)].

**DESCRIPTION.**—*Fronds*: up to 2 cm high, more or less erect, often in sand-filled turfs. *Branching*: dichotomous, often with lateral adventitious branches arising from sides of intergenicula, branches sometimes containing several unbranched intergenicula, especially those in turfs. *Intergenicula*: terete or rarely flat, up to 0.5 mm diameter (rarely more) and 1–3 mm long. *Genicula*: developing by cracking and sloughing of calcified cortices overlying uncalcified genicular tissues, fully formed genicula barely visible in terete branches, more easily visible in flat

branches, consisting of one tier of cells (possible 2 tiers in some instances). *Conceptacles*: often in a single row on intergenicula, protruding markedly, tetrasporangial and bisporangial conceptacles about 200  $\mu$ m inside diameter; carposporangial plants of this species (as *Amphiroa franciscana*) reported but not studied by Dawson (1953:149).

**TYPE LOCALITY.**—Not specifically given; Province of Hiuga and Misaki, Japan, listed in Yendo (1902:5).

**LECTOTYPE.**—In the absence of a known holotype specimen, we select Yendo's illustrations (1902, pl. 1: figs. 1, 3; pl. 4: fig. 1) as the lectotype (Figure 17).

**GULF OF CALIFORNIA DISTRIBUTION.**—Puerto Peñasco to Cabeza Ballena; Mazatlán.

**PACIFIC COAST DISTRIBUTION.**—Baja California to Panama; Ecuador; Galapagos Islands.

**SPECIMENS STUDIED.**—*Gulf of California*. SONORA: Punta Pelicano, vicinity of Puerto Peñasco, 6 Apr 1966, EYD-27272 (US) and 2 Jul 1973, JN & HWJ-73-7-4 (US); Playa Arenosa, vicinity of Puerto Peñasco, 8 Apr 1966, EYD-27362 (US), 5 Sep 1973, JN-3441 (US) and JN-3442 (CUW); Cumpleaños Tide Pool, Playa Estacion, Puerto Peñasco, 4 Feb 1973, JN-3772 (ARIZ), 4 Jul 1973, JN & HWJ-73-7-33 (US); Playa Estacion, in front of Laboratorio de Biología Marina, Puerto Peñasco, 29 Jun 1965, EYD-27488 (US), 11 Jul 1972, JN-3146 (MEXU), and 25 Nov 1972, JN-3675 (US); Ensenada de San Francisco, near Guaymas, 17 May 1946, EYD-1866 (US); Ensenada Bocochoibampo, near Guaymas, 16 May 1946, EYD-1780 (US). BAJA CALIFORNIA: Bahía Agua Verde, 11 Jul 1965, EYD-25852 (US); Isla San Diego, 19 Apr 1958, EYD-18919 (US); Cabeza Ballena, 11 Mar 1949, EYD-6834 (AHFH); Punta Palmilla, 7 Nov 1946, EYD-3258 (US); Cabeza Ballena, 9 Nov 1946, EYD-3374 (holotype, AHFH). SINALOA: Mazatlán, 7 Jun 1952, EYD-10824 (AHFH). LAS ISLAS DE LA CINTURA: Isla Patos, north end of Isla Tiburon, 17 Feb 1946, EYD-812 (US); Isla Raza, 21 Nov 1964, EYD-26129 (US). *Pacific Coast of Mexico*. BAJA CALIFORNIA: Isla Piedra, Laguna Ojo de Liebre (Scammon's Lagoon), 30 Apr 1946,

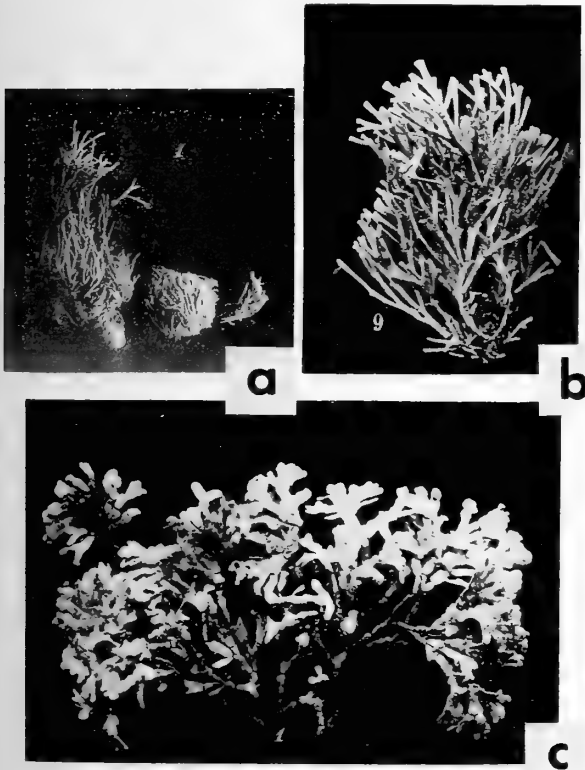


FIGURE 15.—Habit of lectotypes selected herein: a, *Amphiroa valonioides* (from Yendo, 1902, pl. 4: fig. 1; see also Figure 17a-c); b, *A. zonata* (= *A. beauvoisii*) (from Yendo, 1902, pl. 4: fig. 9; see also Figure 8a,b); c, *A. misakiensis* (from Yendo, 1902, pl. 6: fig. 1).

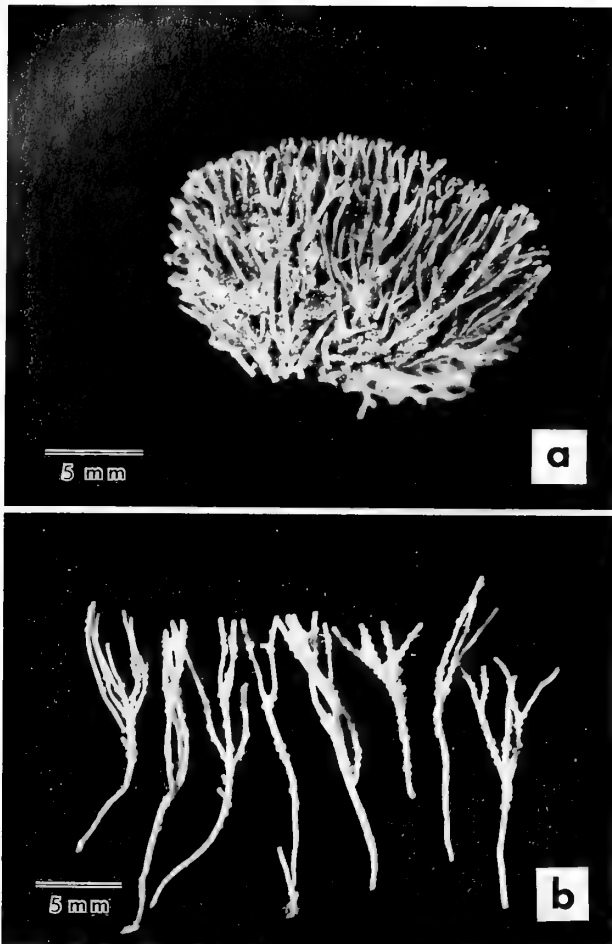


FIGURE 16.—*Amphiroa valonioides*: *a*, habit (JN-3146) (note characteristic tuft of fronds); *b*, separated branches from a tuft (JN & HWJ-73-7-33) (note protruding conceptacles).

EYD-2499 (AHFH); "Campito," east of Punta San Eugenio, 31 Oct 1951, EYD-10438 (AHFH); Punta Malarrimo, 17 Apr 1951, EYD-9951 (AHFH); Laguna San Ignacio, 11 Feb 1950, EYD-9005 (AHFH). NAYARIT: Mira Mar, 20 Dec 1946, EYD-3702 (AHFH). GUERRERO: Acapulco, 3 Feb 1947, EYD-3908 (AHFH). REVILLA GIGEDO ARCHIPELAGO: Binder's Cove, Isla Socorro, 19 Nov 1953, EYD-12144 (US) and 16 Apr 1955, EYD-13566 (US); Braithwaite Bay, Isla Socorro, 2-4 Jan 1934, WRT-27 (UC, US). LAS ISLAS TRES MARIAS: Isla Maria Magdalena, 9 May 1939, WRT-39-643A (UC). *El Salvador*. Acajutla, 4 Sep 1960, EYD-21919 (US); Isla Meanguera,

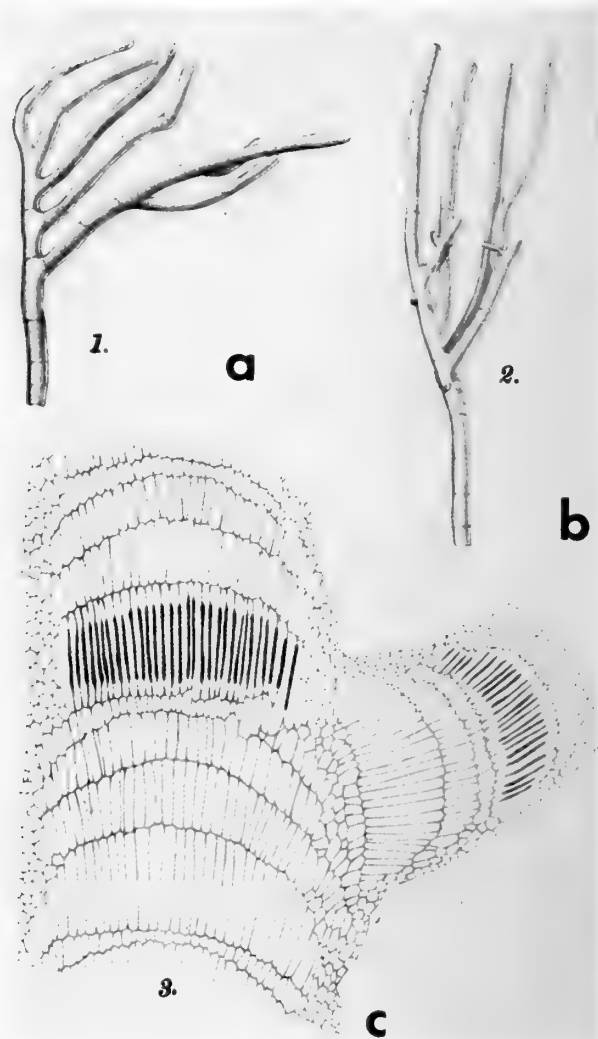


FIGURE 17.—Lectotype selected herein of *Amphiroa valonioides* (from Yendo, 1902, pl. 1; see also Figure 15*a*): *a*, part of fronds with second branching; *b*, part of frond with protruding conceptacles; *c*, longitudinal section showing genicula of single tier of cells.

Gulfo de Fonseca, 7 Sep 1960, EYD-21899 (US). *Pacific Coast of Costa Rica*. Bahía Ballena, 30 Mar 1959, EYD-21201 (US); Gulfo Dulce, 26 Mar 1939, WRT-39-112 (US) and WRT-39-116A (UC, US). *Pacific Coast of Panama*. Isla Jicaron, 25 Mar 1959, EYD-21122 (US); Isla Brincanco, Isla Contreras, 25 Mar 1959, EYD-21052 (US). *Ecuador*. Esmeraldas, Bahía San Francisco, 11 Feb 1934, WRT-34-484 (holotype

AHFH, isotype MICH). GALAPAGOS ISLANDS: Isla Santiago (=I. James), Crossland s.n. (holotype, *A. annulata*, BM). Isla Wenman, 11 Jan 1934, WRT-88a (US). Isla Fernandina, 25 Jul 1938, W. L. Schmitt-16-38 (US).

REMARKS.—Among the most diminutive plants in *Amphiroa* are those of this species, with most specimens having branches less than 400  $\mu\text{m}$  in diameter. In the field the best way to distinguish *Amphiroa valonioides* is by plant size and the frequent occurrence of markedly protruding conceptacles. The genicula are comprised of single tiers of medullary cells. The primary branching may be sparse, particularly in plants growing in compact tufts. More often fronds have secondary branches with laterals arising from the intergenicula surfaces. This latter feature led to the establishment of *Amphiroa annulata* var. *pinnata* by Dawson (1953:137), a taxon which we do not consider distinctive.

According to Dawson (1953, as *A. franciscana*, p. 149, and *A. annulata* p. 136), *A. valonioides* has a wide distribution in the eastern Pacific. From central Pacific Baja California, it occurs at least as far south as Ecuador (Taylor, 1945:187, as *A. franciscana*), and in Japan (Okamura, 1936:516). Furthermore, this species may occur in tropical Pacific islands, but verification of its presence there remains for future study.

### *Amphiroa van-bosseae* Lemoine

FIGURES 1g, 4d, 6, 10a, 12b,c, 13c, 18

*Amphiroa van-bosseae* Lemoine, 1929:73 [as '*van Bosseae*'] fig. 30, pl. 3: fig. 7.

*Amphiroa rigida* sensu Dawson, 1944:276 [in part] [not *Amphiroa rigida* Lamouroux, 1816:297].

*Amphiroa subcylindrica* Dawson, 1953:139, pl. 29: fig. 1 [type locality: Punta Colorado, near Guaymas, Sonora, Mexico, EYD-555 (holotype AHFH 4277, isotype, UC 940252)]; 1959:22; 1966a:18.

DESCRIPTION.—*Fronds*: up to 10 cm high, more or less erect, often in clumps. *Branching*: basically dichotomous, often obscure and irregular. *Intergenicula*: terete to subterete, 1–2 mm diameter and variable in length but up to or more than 1 cm

long, length difficult to discern because of genicula that are barely visible, thickening with age. *Genicula*: developing by cracking and sloughing of calcified cortical tissue overlying uncalcified genicula, fully formed genicula usually barely visible between intergenicula near branch apices, consisting of 5 (rarely 4) or more tiers of medullary cells and patches of cortical cells. *Conceptacles*: scattered over intergenicular surfaces, protruding



FIGURE 18.—Branches of *Amphiroa van-bosseae*: a, cylindrical intergenicula (JN-3050) (note they are very long and coarser than other Gulf of California *Amphiroa* species); b, intergenicula with conceptacles (JN & HWJ-73-7-1).

only slightly, becoming buried by continuing cortical growth, tetrasporangial and bisporangial conceptacles 200–300  $\mu\text{m}$  inside diameter, sexual plants not encountered in the Gulf of California.

TYPE LOCALITY.—“Galapagos. Île Charles, Post Office Bay, août 1924 (recueillie juste au-dessous de la limite de la mer)” (Lemoine, 1929: 73).

HOLOTYPE.—*St. George* South Pacific Expedition, D. C. Crossland s.n., August 1924 (BM).

GULF OF CALIFORNIA DISTRIBUTION.—Puerto Peñasco to Punta Palmilla.

PACIFIC COAST DISTRIBUTION.—Galápagos Islands.

SPECIMENS STUDIED.—*Gulf of California*. SONORA: Punta Pelicano, vicinity of Puerto Peñasco, 2 Jul 1973, JN & HWJ-73-7-1 (US); Playa Arenosa, vicinity of Puerto Peñasco, 20 Oct 1973, JN-3602 (ARIZ) and 15 Feb 1965, A. E. Dennis-D62 (US); Cumpleaños Tide Pool, Playa Estacion, Puerto Peñasco, 4 Jul 1973, JN & HWJ-73-7-28 (CUW); Playa Estacion, in front of Laboratorio de Biología Marina, Puerto Peñasco, 27 Jul 1965, EYD-27472 (US), 7 Apr 1966, EYD-27300 (US), 29 Apr 1972, JN-2957 (US), 20 Oct 1972, JN-3584 (MEXU), 25 Nov 1972, JN-3682 (US), and JN-3808 (CUW); Bahía Tepoca, 4 Feb 1940, EYD-395 (AHFH); Bahía Carrizal, near Cabo Arco, vicinity of Guaymas, 15 May 1946, EYD-1693 (AHFH); Guaymas Harbor, 9 Feb 1940, EYD-Sta. 37 (UC); Punta Colorado, near Guaymas, EYD-555 (holotype AHFH; isotype UC). BAJA CALIFORNIA: Puertecitos, 17 May 1972, JN-3296 (US); Punta La Gringa, Bahía de Los Angeles, 22 May 1972, JN-3050 (US); Punta Concepción, 15 Jul 1965, EYD-25918 (US); Isla Ildefonso, 19 Jul 1965, EYD-25890 (US); Isla Monserrate, 21 Apr 1958, EYD-18794 (US); Bahía Agua Verde, 20 Apr 1958, EYD 18885 (US); between Eureka and La Ribera, 5 Nov 1946, EYD-3179 (AHFH); Cabo Pulmo, 4 Nov 1946, EYD-3114 (AHFH); Punta Palmilla, 7 Nov 1946, EYD-3219 (AHFH). LAS ISLAS DE LA CINTURA: Isla Patos, Isla Tiburon, 17 Feb 1946, EYD-806 (US); Bahía Agua Dulce, Isla Tiburon, 21 Feb 1946, EYD-979 (AHFH); Isla San Esteban,

5 Feb 1940, EYD-460a (AHFH); Isla Turner, off Isla Tiburon, 26 Jan 1940, EYD-112a (AHFH).

REMARKS.—In accordance with Article 73.9 under examples (Stafleu et al, 1978), “a hyphen is correctly used in an epithet after a word which could stand independently. . . .” Therefore, we spell the species epithet as “*van-bosseeae*,” and do not use the original spelling of Lemoine (1929: 73), “*van Bosseeae*,” or the spelling of Dawson (e.g., 1961a:421) as “*vanbosseeae*.”

Specimens belonging to *Amphiroa van-bosseeae* may usually be recognized by the robust fronds and terete branches; it is the largest cylindrical species in the Gulf of California. Small specimens of *A. van-bosseeae* can be difficult to separate from *Amphiroa beauvoisii* based solely on gross morphology, but examination of their genicula readily allows them to be separated. In *A. van-bosseeae* the genicula are of 5, or more often, 6 to 10 cellular tiers (Figure 12b) whereas in *A. beauvoisii* there are 3 to 5 cellular tiers (Figure 5). In the Gulf only *A. van-bosseeae* combines many-tiered genicula with terete intergenicula (rarely are they compressed).

Among the species of *Amphiroa* containing large plants with mostly terete intergenicula, *A. ephedraea* (Johansen, 1968, fig. 1) is most striking in appearance and superficially resembles *A. van-bosseeae*. *Amphiroa ephedraea* occurs in the western part of the Indian Ocean (Johansen, 1968:319). The reports of this species from Japan (Okamura, 1936:518; Chihara, 1970:72) may be plants of *Amphiroa magdalensis* or possibly *Amphiroa beauvoisii*. The unique genicula in the Indian Ocean *A. ephedraea* (Johansen, 1969b:122) do not correspond to the Gulf of California species, in which development is as in *Amphiroa anceps* and as described by Johansen (1969b:120) for the Type I category of geniculum development. To the naked eye, branches of *A. ephedraea* consist of intergenicula of more or less uniform length separated by conspicuous genicula, whereas those of *A. van-bosseeae* have intergenicula of greatly varying lengths (Figure 18), and the genicula become visible only after overlying calcified tissue breaks away (Type I genicular development, Johansen, 1969b:120). In the Gulf species, genicula are most

conspicuous in older parts of the branches and may, in fact, be externally invisible where they are buried in calcified tissue near branch apices. The tendency for intergenicular cortices to continue growing is more evident in *A. van-bosseae* than in the other Gulf species. Hence, older intergenicula are greater in girth than are young intergenicula (Figure 6), and conceptacles may

become buried by cortical growth (Figure 14c), a phenomenon not occurring in the other species.

*Amphiroa van-bosseae* is plentiful in the Gulf, but the lack of published reports or specimens known to us from elsewhere suggest a limited distribution. The type locality is Post Office Bay, Isla Floreana (=Île Charles), Galápagos Islands, and more material from this area would be welcome.

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