# COLONIAL BENTHIC DIATOMS (Bacillariophyta in MAC)

#### NAVICULACEAE

Berkeleya hyalina (Round and Brooks) Cox

Chastain and Stewart 1985.

Identification and classification of diatoms traditionally depend on features of valve morphology that can be observed only after cells have been cleaned and examined with high magnification. The two colonial benthic species of *Berkeleya* included here secrete and live in tubes of mucilage that are aggregated into tufted thalli that attach to surfaces and resemble filamentous ectocarpoid algae.

B. hyalina has an easily recognizable morphology; for many years, prior to the studies that finally identified the species by frustule characteristics, I called it the "Palm" or "Broccoli" diatom, both terms descriptive of the macroscopic morphology. The species is presently known from Ensenada and Bahía de los Angeles in Baja California, southern California, and the type locality in Togo, West Africa. In San Diego County it is often abundant in mid-intertidal habitats, April-October, on rocks or mollusc shells. Thalli grow to 3 cm high, are dark olive-brown, branched as shown in Figure 2, soft and slippery to the touch.

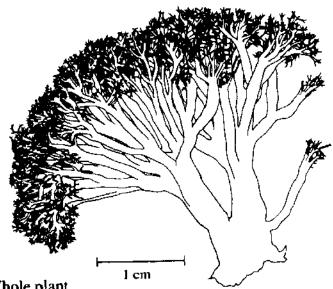


Figure 2. Berkeleya hyalina. Whole plant.

Berkeleya rutilans (Trent.) Grun.

(See comments above, for B. hyalina)

This species is cosmopolitan and on the Pacific coast has been recorded from

Baja California to the Aleutian Islands (Lobban 1985). Macroscopic colonies to 3 cm high are loosely, sparsely, and irregularly branched. In size, color, and habitat they are similar to ectocarpoid thalli, and microscopic examination may be necessary to confirm identification. The species occurs throughout the year here.

#### XANTHOPHYTA

**VAUCHERIACEAE** 

Vaucheria sp.

50

Dark green filaments, 33–60 µm diameter, without constrictions and not divided into cells (lacking septa within the long thin tubes); often found in large felt-like mats, mostly unattached, on muddy surfaces of tidal flats, or near lagoons, estuaries, or marshy areas near salt water. The genus includes freshwater, brackish water, and marine species, which are identified by microscopic reproductive features. In San Diego County *Vaucheria* is most easily observed on mud flats in the Tijuana River Estuary, at the south end of San Diego Bay, the northeastern end of Mission Bay, or in the flood control channel of San Diego River. MAC treats specimens from similar habitats in central California as *V. longicaulis*.

#### **CHLOROPHYTA**

**ULVELLACEAE** 

56-64

Marine taxa presently placed in this family have minute thalli formed of small green filaments that branch in irregular ways. Typically they are found as specks on, or in, other algae such as *Polysiphonia* and *Chondria* species, or *Pterocladia capillacea*. The filaments that compose the dark green spots can be dissected out under a microscope but field-collected epi- or endophytes are seldom identifiable. When grown in laboratory cultures, the filaments can be recognized as forms such as are attributed to this family (Chaetophoraceae in MAC).

In addition to the 4 species listed below with San Diego records, Endophyton ramosum Gard., Acrochaete geniculata (Gardn.) O'Kelly (1983) (as Pseudodictyon geniculatum in MAC), Bulbocoleon piliferum, and two additional species of Entocladia have been recorded from Los Angeles or Orange County.

\*Entocladia cingens Setch, and Gardn,

64

Endophytic in Chaetomorpha californica (type collection) and several other

algal species. Type locality, Ocean Beach in San Diego County. *Entocladia* codicola Setch. and Gardn. and E. viridis Reinke are known from Orange County.

## Pilinella californica Hollenb.

58

Light green filaments, short, unbranched or branched near base, are interspersed with longer filaments that taper to long slender hair-like tips; epiphytic on *Eisenia* stipes near Scripps Pier, La Jolla (type locality). Aguilar and Aguilar (1986) report collections from Punta Morro, Baja California, on *Egregia* stipes.

# Ulvella applanata (Setch. and Gardn.) South and Tittley South and Tittley 1986

Pseudulvella applanata Setch. and Gardn., 61

Short filaments form smooth, bright green discs to several mm broad on shells of a periwinkle, *Littorina planaxis* Nutt. Setchell and Gardner (1920) remark that the host snail is very abundant between Alaska and San Diego; although the algal species has been found only in central California, MAC suggests that it is probably coextensive with the host.

# Ulvella setchellii Dang.

**5**9

This species forms small discs, up to 2 mm broad, on the surface or within the walls of other algae. The filaments radiate in laterally adjoined, dichotomously branched rows from a central region, and remain mostly in one layer. Once this species has been recognized, it will be easily distinguished with a dissecting microscope (see Fig. 9, MAC).

In San Diego found on Amplisiphonia from the Loma Sea Cliff, 15 m, February.

## **MONOSTROMATACEAE**

[\*Monostroma oxyspermum (Kütz.) Doty

68

Traditionally, flat green blades that are only one layer of cells thick have been treated as species of *Monostroma*. *M. oxyspermum* is described as typically found in quiet brackish or fresh water "to southern California." I can find no records of specimens from San Diego County; occasionally very large specimens of *Ulva expansa* superficially resemble *Monostroma* from northern localities, but examination shows them to be two layers thick rather than one.

Dawson's Checklist includes this species (as M. quaternarium) on the basis of Setchell and Gardner's 1920 comment.]

A recent study of motile reproductive cells (O'Kelly et al., 1984), supported the transfer of this species as the type of the genus Gayralia (Vinogradova 1969); other workers reduce the genus to a subgenus of Monostroma. See discussion in Scagel et al. (1986) p. 230.

#### **ULVACEAE**

Chloropelta caespitosa Tanner

Tanner 1980

Thalli oval or rounded, a few mm to 60+ mm in diameter, peltate or split to the base, margins smooth or ruffled; distromatic, with central attachment disk. The species is separated from other small green blades (*Ulva* species) by the pattern of early development. The initial uniseriate filament becomes multiseriate and develops into a monostromatic sac, thus far resembling other Ulvaceae. Each cell then divides once so as to form a distromatic saccate germling. Rupture of the apical end and continued growth result in a peltate distromatic alga resembling *Ulva*.

The description of the genus and species was based on laboratory cultures derived from collections in Los Angeles and Orange counties. Among specimens collected from La Jolla by Dawson and originally identified as *U. californica*, Tanner recognized *Chloropelta* thalli. In 1976 he collected specimens from high intertidal rocks at Tourmaline Surfer Park, Pacific Beach and since then has found specimens at La Jolla Cove and Casa beach, in La Jolla.

# \*Enteromorpha spp.

73

Thalli pale green, sometimes yellowish, tubular, with tube walls one cell layer thick. The size and shape of the thallus varies, with more or less branching, and the thickness, shape, and proportions of the small cells that form the tube determine which of six named species can be recognized (E. clathrata, E. compressa, E. flexuosa, E. intestinalis, E. linza, E. prolifera).

Species of this genus grow from brackish water to marine habitats, are common in estuaries, tidal lagoons, sloughs, on docks and hulls of boats, or on intertidal rocks along open ocean coasts. With thorough study it perhaps would be possible to sort out distinct entities from the forms that can be collected locally, but at present, lacking adequate comparative information, I refer tubular distromatic (=two cell layers thick when the thallus is cross sectioned) green algae to *Enteromorpha* sp.

Zedler (1982) lists E. clathrata var. crinita (Roth) Hauck as one of two macroalgae associated with Batis mostly in winter—spring samples, in the Tijuana Estuary. Setchell and Gardner (1920) list E. clathrata (as E. crinita) from wood or floating in San Diego intertidal habitats. Dawson's Checklist cites the species with no collection data. Setchell and Gardner (1920) list "E. torta" in high intertidal rock pools, December, San Diego, and Dawson (1945d) repeats this information. E. torta is a name applied to specimens in Atlantic regions but is not recognized in recent studies of California collections. Setchell and Gardner (1920) include San Diego in the ranges of E. compressa and E. intestinalis ("common"). E. linza, treated by them as a species of Ulva, is also distributed from Alaska to Mexico. Dawson's Checklist repeats this information, and additionally includes E. flexuosa (as E. tubulosa) without citing collections for San Diego.

#### Ulva

Ulva thalli are bright green leafy blades, two cell layers thick, variously ruffled and clumped, and often conspicuous in intertidal habitats. There are three distinct forms in San Diego County that we treat here as U. californica, U. expansa, and U. dactylifera. The most common, at times extremely abundant over rocks on high to midtidal beaches, is a small intertidal species that we consider U. californica. U. expansa can grow to 2 m in length and nearly as broad, but usually the thalli are torn and unattached in very quiet water in San Diego Bay, Mission Bay, the San Diego River flood control channel, or intertidal creeks of the Tijuana Estuary. A third taxon grows in midsummer very low in the intertidal zone, with or near Phyllospadix. U. rigida, similar in form to U. californica, also has been identified at several locations.

# \**U. californica* Wille 78

Blades mostly less than 2 cm high, in dense clusters, oval to irregular; crisped, undulate margins; attached by slender stipe, or more broadly across the base of the blades; thin blade often appears somewhat thicker near the base. "Usually in dense, turflike stands atop rocks, occasionally epiphytic, midtidal to upper intertidal...formerly common in southern California" (MAC).

Forms that resemble this species are extremely common on all San Diego County beaches, particularly conspicuous in the late spring to early summer. Abbott currently questions the identification as U. californica of many recent collections from southern California (pers. comm.). The description of U. californica fits isolated subtidal thalli as well as dense clumps that cover intertidal rocks. Dawson's Checklist listed it as common May-July.

\*Ulva dactylifera Setch. and Gardn. [and see U. costata (Howe) Hollenb., U. taeniata (Setch.) Setch. and Gardn.] 80 [80, 87]

Blades mostly bright grass-green, simple or with several long narrow divisions from discoid base, or more commonly a short (1-2 cm), broad (3 cm) basal portion from which 1-7 cm long (to 20+ cm) narrow blades arise; blades densely ruffled with spirally twisted margins, usually more or less dentate below; blade area mostly twice as thick in the middle portion as in marginal strips.

After *U. californica* has become less conspicuous following its springtime "bloom," blades I identify as *U. dactylifera* begin to grow under other algae low on intertidal rocks. I have collected specimens up to 30 cm long late June-October, usually by searching under *Phyllospadix* leaves where it is recognized by its bright color and twisted form. Occasional individual blades resemble thalli of *U. taeniata*, stated (MAC) to occur only as far south as Ventura in California, but when they develop from a broader undivided basal blade area, the thalli conform in this and other features to the description of *U. dactylifera*. Blades of *U. costata*, another similar species, differ primarily in having a thicker median "rib"; a distinct central region can be found in some of the San Diego thalli treated here as *U. dactylifera*.

Our variable collections appear to belong to a single taxon, and the lack of clear distinctions among the three names that have been associated with long twisted thalli in California points to a need for study of this group.

\*U. expansa (Setch.) Setch. and Gardn. 80

Blades medium to pale green, elongate or more round, sometimes expanded to more than 1 m long, 0.5 to nearly 1 m wide; deeply ruffled margins, but not lobed. On rocks, or epiphytic lower intertidal to subtidal; in sheltered water, usually free-floating.

Our specimens conform to the information given in MAC. See comment above  $\approx Ulva$  species for localities.

\*Ulva rigida C. Ag. 87

Blades dark green, relatively stiff, less than 3 times as long as broad (or orbicular), deeply lobed, ruffled, with short solid stipe.

A widely distributed species with distribution records (MAC) that bracket San

Diego. Tanner has observed what he identifies as *U. rigida* at several localities in San Diego Co. "These plants are densely tufted like *U. californica* but differ in that they are larger (up to 8 cm or more), have irregularly lobed thalli instead of being cuneate, are much thicker, have several pyrenoids per cell and have dentate margins (when the margins are not eroded)" (pers. comm.).

MAC and Dawson's Checklist list *U. lactuca*, *U. lobata*, and *U. angusta* for localities both north and south of, but not within, San Diego County.

## **CLADOPHORACEAE**

\*Chaetomorpha californica Coll.

101

Setchell and Gardner (1920) quote Collins as describing this as "the most slender erect marine species (of *Chaetomorpha*), not likely to be mistaken for any other...." Filaments are less than 40  $\mu$ m in diameter, while *C. linum* is more than 40  $\mu$ m in diameter, but the two are otherwise very similar.

The type specimens were collected from sandstone rocks in shallow pools in the upper intertidal zone in La Jolla. Pools such as these along the entire coast of San Diego County often are coated in spring or early summer with Chaetomorpha thalli. Whether these represent C. californica, C. linum, (or C. aerea) or both is often uncertain.

# \*Chaetomorpha linum (Müll.) Kütz. [or C. aerea (Dill.) Kütz] 101

Unbranched green filaments, 40– $100\,\mu m$  diameter, locally mostly to 7 (25) cm long, attached at the base.

This species is seasonally abundant in the late spring to summer in shallow pools in the mid- to high intertidal zone. It also grows epiphytically as single strands in algal turf and in shallow subtidal habitats.

Plants identified as C. linum are found worldwide, often in habitats similar to those described in California, and in the past other names have been used in different parts of the range (see C. californica). Dawson's Checklist refers to C. linum (as C. aerea) without mention of San Diego localities. Blair (1983) and the Silva and Miller checklist cited in the discussion of Rhizoclonium consider that Chaetomorpha aerea and C. linum are separate species, with C. aerea generally attached and C. linum free-floating. If this opinion is correct, the plants from San Diego County represent C. aerea. MAC treats the two forms as stages of one species, C. linum.

## \*Chaetomorpha spiralis Okam.

101

Unbranched filaments, with large cells to 1 mm diameter that individually are visible without magnification; filaments firm, almost stiff, and often coiled into clumps or spirally twisted.

In quiet water the strands are less coiled, looser, and when stretched out can be up to 60 cm long. The dark blue-green color and shiny appearance often catch one's eye where the thalli grow under other algae, in dark crevices, or under overhanging rocks in the low intertidal zone, less often subtidally to 10 m. Occasionally during fall months piles of the thalli occur on the mud flats at the north end of Mission Bay or floating and semi-attached to other large algae or Zostera in the Flood Control Channel. It has been described as resembling tangled green monofilament fish line.

## \*Cladophora albida (Huds.) Kütz.

104

Small, green filamentous thalli; this species is a delicate one, much branched, with branchlets nearly the same width as the branch from which they grow.

San Diego specimens are small (to 5 mm) and found only as individual epiphytes or on rocks mixed with other algae, in mid- to low intertidal habitats on all the county beaches. Unless one deliberately looks for species of *Cladophora*, they probably will be overlooked, but the bright green color and the filamentous branched forms are conspicuous among the pale intertidal coralline forms or against the dark red-purple thalli in shaded ledges or crevices.

Specimens associated with this epithet elsewhere on both Pacific and Atlantic coasts grow in thick dense mats with a characteristic soft spongy consistency.

Dawson's Checklist (C. albida including C. delicatula) cites no San Diego County localities.

## \*Cladophora columbiana Coll.

105

Small green branched filaments, with apical cells often 90-150  $\mu m$  in diameter.

In the field, thalli appear similar to *C. albida* and occur in the same habitats. Both species are found epiphytically in algal turf as well as in more shaded habitats on sides of channels amongst other algal thalli. *C. columbiana* has

also been collected subtidally from the nest of a garibaldi fish on the Loma Sea Cliff.

MAC refers to tufts to 15 cm tall growing in dense mats on sandy horizontal rocks. Such forms are not found in San Diego County.

Dawson's Checklist (as *C. trichotoma*) cites no San Diego collections. Setchell and Gardner (1920, as *C. hemisphaerica*) mention the tufted habit associated with wave-swept rocks in central California (and lacking in San Diego habitats).

# \*Cladophora graminea Coll.

105

Thalli with bright green filaments; apical cells 4–6 times as long as wide, to 150 µm diameter, similar in size to apices of *C. columbiana*; sparsely branched until close to the tips of the axes where branches can be more regularly alternate. Cells, particularly the basal cells of axes, very long (MAC reports the length as 20–30 times the breadth). San Diego specimens to 5–6 cm high.

Several collections from subtidal (10–20 m) San Diego sites document this species locally. It is never abundant nor common, and rare in habitats where it is typically found north of San Diego. As do other *Cladophora* species, this one grows in tufts. The long narrow cells distinguish the species.

Setchell and Gardner (1920) cite San Diego collections of this as "one of coarsest of west coast species...of *Cladophora*" with "dichotomous" branching where each arm is composed of a single segment (cell). MAC records the species only south to San Pedro and describes it from mid to low intertidal habitats. K.A. Miller has collected subtidal specimens from the Channel Islands.

# $*Cladophora\ microcladioides\ Coll.$

106

Setchell and Gardner (1920) cite as San Diego records specimens from the upper subtidal zone, or (as f. stricta) the lower intertidal zone. The regular recurved branches that characterize the species are lacking in f. stricta as recognized by Setchell and Gardner (1920).

\*Cladophora sericea (Huds.) Kütz./ C. stimpsonii Harv. 108

Cladophora sp. in our collections comprises forms tentatively attributed to one

or the other of these two species, but that conform well to neither. There are many variants or ecotypes of Cladophora species in this area that are encountered both in intertidal and subtidal work, and these frequently are not easily sorted with available published information.

Setchell and Gardner (1920) refer to C. sericea from San Diego (as C. flexuosa) and to C. stimpsonii from San Pedro. As C. flexuosa, P.B.-A. 2239 and possibly 729 are cited as the basis for extending the distribution to San Diego (Dawson 1945d). No other San Diego localities or collections are noted.

# Lola lubrica (Setch. and Gardn.) Ham. and Ham.

92

Unbranched uniseriate green filaments, attached to substrate by simple unbranched rhizoids that develop from cells near the base of the thalli; cells 35-60 μm diameter, 65-180 μm long, with upper cells frequently elongate-oval and somewhat constricted.

The species has been infrequently recorded from northern Washington south to Costa Rica, typically entangled with other algae or on mud. A collection from a cable lying on the sand seaward of the Scripps Pier included some material that was identified by Hollenberg as this species. We include it here to call attention to the possibility that it may be found in overlooked habitats.

Setchell and Gardner (1920) compared this species, as Rhizoclonium, with other species of that genus, saying that L. (R.) lubrica shows fewer or no rhizoids, has thinner walls and longer cells, and in masses is slippery or

# Rhizoclonium riparium (Roth) Harv.

92

Unbranched uniseriate, dark to light-green filaments, often twisted and forming entangled masses on mud, wood, or other algae, or free-floating unattached thalli, the length/width ratio of individual cells, used in early studies to characterize species, is probably unreliable; cells mostly cylindrical, 35-50 (70) µm in diameter, 1-3 (6) times longer. Occasional cells with rhizoidal branches.

In San Diego, identified only from mud in or near the tidal creeks in Tijuana Estuary, and only occasionally present there. Growth is perhaps affected by the wide fluctuations in salinity between seasons and years. During a yearlong study in 1977, Zedler (1982) found Rhizoclonium at all times during the year, frequently in samples from the portions of the marsh dominated by Batis maritima and Monanthochloe littoralis, two vascular plants associated with intermediate and higher levels of salt marshes. In lower zones it was absent or infrequently found.

Setchell and Gardner (1920) distinguished California Rhizoclonium species from Chaetomorpha species by the characteristically cylindrical cells that are not swollen, and a tendency to form horizontal skein-like clumps. The separation of Chaetomorpha from Rhizoclonium and the usefulness of retaining Lola as a third genus on the basis of life history and vegetative morphology has been reviewed by Blair (1983) and in an update of taxonomy for California marine algae (Silva and Miller) that is in preparation. The latter workers recognize only Chaetomorpha and Rhizoclonium, "admitting that the generic boundaries are tenuous."

#### CODIOLACEAE

#### Urospora

93

The genus includes species of cooler waters that are mostly unbranched filaments with distinctive rhizoids growing only from cells near the base of plant. These rhizoidal branchlets can grow downward within or outside the extracellular wall material. The filaments appear erect, being attached at one end, in comparison with *Rhizoclonium* which occurs in the form of entangled unattached threads.

Published ranges of *U. penicilliformis* and *U. wormskioldii* extend to southern California, but we know of no San Diego County collections of either species. Setchell and Gardner (1920) treat the genus as *Hormiscia*.

#### BRYOPSIDACEAE

\*Bryopsis corticulans Setch.

111

Erect main axes sparsely branched or mostly bare below, with abundant symmetrical pinnate branches above; main axes to 1 mm diameter, ultimate branches 150-300 µm diameter, constricted at base. Older branches can develop coarse descending rhizoidal branches from their bases. Distinguished from *B. pennatula* in part by the difference in the amount of branching along the lateral branches, and in part by height. *B. corticulans* can exceed 8 cm while *B. pennatula* is described as mostly less than 4 cm high.

Numerous thalli resembling this description of B. corticulans have been collected from the docks in south San Diego Bay in March, with large speci-

mens to 7 cm high. Shevlin has examined cultured and fresh collections, and conducted crossing experiments between numerous isolates of Pacific and Atlantic Bryopsis thalli. His tentative conclusion (pers. comm. 1989) is that B. corticulans is a widespread and variable species that can resemble B. hypnoides; he questions the presence of the latter species on the coast of California. He points out that distichous branching is seen at least distally in most B. corticulans specimens and that the cultured isolates I mention as B. pennatula may also represent B. corticulans.

# \*Bryopsis hypnoides Lamour.

113

Thalli tufted, to 3 cm high, dull green and profusely radially branched.

On the open coast, specimens of *Bryopsis* species are not easily found because the typical habitat is usually inaccessible, very low in the intertidal on the vertical sides of channels, under or mixed with other algae. Many of the field-collected thalli are not clearly radially branched, and thus it is often difficult to separate the two common species in this habitat. *B. hypnoides* is described as occasional to locally abundant on sand-covered rocks British Columbia to Panama but previously has not been recorded south of Los Angeles County in California.

Distinct species as treated in MAC are often difficult to segregate from San Diego County material. Setchell and Gardner (1920) wrote that "species of *Bryopsis* present problems of determination of exceeding complexity and difficulty."

Bryopsis pennatula J. Ag. (and see B. corticulans)
113

Thalli tufted, to 3 cm high, with mostly simple erect axes with terminal branching distichous to partly radial.

This portion of the description in MAC of the species is appropriate for certain collections of San Diego plants. When such thalli were grown in culture, however, they became less tufted in the upper portions and more regularly pinnately branched as in *B. corticulans*. We find specimens intertidally and subtidally to 27 m between January and April. These collected thalli are distinctly distichous and seldom more than 3 cm high with mostly simple branchlets, and resemble *B. pennatula*, previously reported only as far south as Orange County.

Dawson's Checklist identified specimens from intertidal rocks in La Jolla as B. corticulans.

\*Derbesia marina (Lyngb.) Sol.

115

Thalli are formed from coenocytic tubular "filaments," 50–70 µm diameter, branched irregularly with no size differences between branches; no septation within the branches; under a microscope relatively large sporangia filled with multiflagellate zoospores can be seen in many collections.

In San Diego, thalli form large entangled clumps loosely attached to other algae or Zostera in the flood control channel (mouth of San Diego River), or on the jetty along the entrance channel to Mission Bay from late summer into November. In a very different habitat, Derbesia-like filaments form extensive low mats that bind sand on high intertidal rocks on Pt. Loma beaches at the same time of year. The thalli from these two very different habitats are similar.

"Derbesia" morphology occurs in algae that have been shown by laboratory studies to be alternate stages in life histories of very different gametangial morphologies (e.g., species of Bryopsis in other parts of the world, and Halicystis in California). It is quite possible that the various collections of Derbesia represent different taxa.

Dawson's Checklist recorded collections from near The Caves, La Jolla, on low intertidal rocks in June.

Halicystis ovalis (gametophytic stage of Derbesia marina)

115

Thallus a deep green coenocytic sphere, 2-10 mm in diameter, attached to coralline crusts on rocks, shallow subtidal to 25 m in or near kelp beds.

This alga, appearing as a tiny dark green globe close to the rock surface, is not often found. When it is recognized, it is very distinctive although collecting is difficult — the thallus floats away as soon as it is loosened from the substrate. Note that the habitats known for *Halicystis* and *Derbesia* in San Diego County are somewhat disparate.

#### CODIACEAE

Codium cuneatum Setch. and Gardn.

116

Thalli erect, to 35 cm high, regularly or irregularly dichotomo-flabellately branched, with more or less wedge-shaped (cuneate) flattened segments; branches 2–15 mm broad, mostly compressed throughout except for branch tips and near the base. Utricles not mucronate (i.e., without tiny spine on tip).

In San Diego County, found only at intervals of several years, in no predictable cycle, usually in late summer to fall, in quiet water in Mission Bay or the flood control channel of San Diego River. It is an easily recognized form because of its large (30–40 cm high) thalli and the broad upper segments, but the local distribution is irregular in time and restricted to a few sites. Silva (1951) described a large range of forms for this species, including some from Mission Bay collected in 1929. The species was based on a collection from Bahía de los Angeles in the upper Gulf of California and later was found on rocks intertidally to subtidally at Santa Cruz Island off the coast of California. Silva suggests that taxonomic and ecologic study is needed for this and other Codium taxa.

The statement (Dawson et al. 1960) that this species is "common 30-60 ft." in kelp beds is not presently applicable for San Diego localities. The flattened specimens discussed (Dawson 1945b) as C. simulans and compared with Setchell and Gardner's C. tomentosum and with C. cuneatum from the Gulf of California probably represent C. cuneatum.

# \*Codium fragile (Sur.) Har.

118

Thalli dark green, often appearing nearly black, to 40 cm high; one or many cylindrical branches arising from a broad basal holdfast, abundantly dichotomously branched above, clumps often appearing densely clustered. Utricles mucronate.

This is a common conspicuous larga alga on rocky beaches across the midintertidal region. New growth appears in the spring; as the thalli grow, they accumulate epiphytes. In the fall or early winter, they are often conspicuously spotted with patches of small red filaments, mostly Ceramium and Polysiphonia species in San Diego County. A blue-green alga grows just beneath the surface, entwining around the utricles that compose the Codium thallus. We have not verified the identification of the blue-green taxon associated with C. fragile here; species of Anabaena, Phormidium, and Calothrix have been isolated from Codium species elsewhere.

Silva (1951) placed most of the California specimens formerly referred to C. tomentosum in synonymy with C. fragile. The Setchell and Gardner compressed plants noted in Dawson's Checklist are not explicitly transferred by Silva; based on his opinion concerning variation in C. fragile, it is highly unlikely that they ("C. tomentosum from La Jolla") represent anything other than C. fragile.

# Codium johnstonei Silva

118

Thalli dark green, erect, consisting of a single cylindrical or slightly compressed, irregularly shaped rod, without branches, lobing or lateral protuberances; to 10 cm high and to 2 cm diameter.

MAC lists only a few records, none for San Diego County, other than the type material from Santa Cruz Island that was first described by Silva in 1951. The species is rare and always subtidal; we have found it outside the Pt. Loma kelp beds to 30 m, and near the Coronados Islands. No other subtidal organism can be confused with this alga.

Aguilar et al. (1984) recorded collections from Isla Todos Santos (Ensenada), Baja California, at 10–17 m.

# Codium setchellii Gardn./ C. hubbsii Daws.

These are two flattened, dark green (appearing nearly black underwater) species of *Codium*. Thalli of both are mostly 2–3 cm across, but occasionally to 4–5 cm, and irregular in outline. They are distinguished by examining the utricle walls with a microscope. *C. setchellii*, lacking the pits or small holes in apical portions that characterize *C. hubbsii*, is rather common in the low intertidal zone in central and northern California.

In southern California, prostrate Codium specimens are mostly subtidal and for this reason are often referred to C. hubbsii without the necessary microscopic observations. Most specimens I have examined from various subtidal habitats in San Diego County I identified as C. setchellii; for this reason, the question of the occurrence of C. hubbsii in San Diego is presently unresolved. K. A. Miller has verified specimens of C. hubbsii from subtidal sites in the Channel Islands. Silva (pers. comm.) writes that "C. hubbsii can be distinguished from C. setchellii (when the presence or absence of pitting is not obvious) by the abundance of hair scars on old utricles compared to their almost complete absence in the latter species."

Dawson et al. (1960) list both species from kelp beds, noting that C. hubbsii was common 10-25 m in northern Baja California and that the two species are macroscopically indistinguishable.

# PHAEOPHYTA ECTOCARPACEAE

(122-146)

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Included here with San Diego records are species of Hincksia (Giffordia in MAC; see Nomenclatural Note in Silva et al., 1987), Feldmannia hemispherica, and possibly Ectocarpus parvus, all representing the formerly all-inclusive genus of Ectocarpus. These are brown filamentous algae with mostly intercalary cell division, often closely branched and with neither a cushion-like amorphous basal stage nor holdfast tissue growing into a host plant. The sporangia of the three separated genera are terminal or lateral, and single rather than clustered. Ectocarpus is distinguished, in the narrow sense, by having a few band-shaped chloroplasts in each cell, a feature that is difficult to evaluate in many specimens. Hincksia and Feldmannia species have numerous discoid chloroplasts per cell, and Feldmannia thalli have distinctive zones of small dividing cells. Most collections of often very abundant filamentous brown algae have sessile lateral plurilocular sporangia and can be identified as one of several species of Hincksia. Occasionally thalli with 1- to 5-celled stalks below the sporangia have been found that may represent H. saundersii.

Populations of these various species are extremely abundant on the sides of tide pools in late summer to fall and over the sand and algae in turf mats intermittently during spring to summer months. Feldmannia hemispherica is mostly identified from Pelvetia, while several taxa grow on Zostera and algae in the quiet waters of the Mission Bay entrance and San Diego River flood control channels. Single specimens have been recorded from deep subtidal sites, including garibaldi nests. A colonial diatom, Berkeleya rutilans, forms tufted thalli that closely resemble ectocarpoid algae.

Setchell and Gardner (1925) treated 41 taxa as species or forms of *Ectocarpus* on the U.S. and Mexican Pacific coasts.

\*Ectocarpus parvus (Saund.) Hollenb. (126). This is a common epiphyte on larger brown algae along the entire Pacific coast, including southern California. Setchell and Gardner (1925) treat the taxon as E. confervoides var. parvus. The type locality cited in MAC was San Pedro, Los Angeles County, but Setchell and Gardner (1925) suggest that the "sand-covered rocks" of the original description were located in San Diego.

\*Feldmannia cylindrica (Saund.) Hollenberg and Abbott (132). MAC refers to San Diego in the distribution records. Setchell and Gardner (1925) cite a small (less than 2 mm high) form that they found on Codium fragile at La Jolla. (Ectocarpus flocculiformis of Setch. and Gardn. is now included in

- F. cylindrica.) Dawson's Checklist citation of E. cylindrica is based on the Setchell and Gardner record.
- \*Feldmannia globifera (Kütz.) Ham. (134). Also cited by Setchell and Gardner (1925) from Codium at La Jolla, and similarly, Dawson's Checklist repeats this record.
- \*Feldmannia hemispherica (Saund.) Hollenb. (134). Epiphytic brown filaments, 2–10 mm high, with basal mass of creeping filaments on or in the host alga, sparsely branched. Recorded elsewhere from several algae, but in San Diego identified only from *Pelvetia fastigiata*.
- \*Feldmannia irregularis (Kütz.) Ham. (136). The record referred to in MAC probably is based on material deposited in the herbarium at UC. [Early collections of filamentous brown algae in UC, some from southern California, are also labelled as Giffordia irregularis (Kütz.) Joly, and synonymy for this latter epithet includes Ectocarpus mucronatus, E. coniferus, E. simplicuisculus and Giffordia conifera.]
- \*Hincksia granulosa (J.E. Smith) Ham. (140), \*H. mitchelliae (Harv.) Ham. (143), and \*H. sandriana (Zan.) Ham. (145) (as Giffordia species in MAC) have been identified in our collections with reasonable certainty. H. saundersii (Setch. and Gardn.) Hollenb. and Abb. (146), "known only from Monterey County" or forms resembling this species have also been found.

\*Streblonema investiens (Coll.) Setch. and Gardn.

This species, recorded by Dawson's Checklist on the basis of an early Collins description of specimens growing on *Helminthocladia* at La Jolla, is considered by MAC to be "of questionable status."

# MYRIONEMATACEAE

157-163

Cultures that are initiated from collections of intertidal or subtidal algae often develop contaminating clumps of very small unbranched or sparsely branched golden brown filamentous algae. These thrive under laboratory conditions and probably are mostly species that are associated with the Myrionematacean genera. Reproduction is rare or absent in these cultures, and the nature of the attachment layers uncertain, and thus we hesitate to identify any of these apparently ubiquitous algae on the basis of features observed in laboratory-grown thalli. Field-collected material is inadequate for a comparative study at present. According to the distributional records cited in MAC, species of the

genus Myrionema are restricted to the colder water north of Monterey County. Three species of Compsonema are recorded only from central to northern California, and one of the two species of Hecatonema is similarly restricted. H. streblonematoides has been identified in collections from Baja California but in California is reported only from Marin County and Monterey County. Filaments, including reproductive cells, that resembled species of Hecatonema or Compsonema have been found in San Diego county habitats on subtidal sponges among sediment, debris, and other algal filaments.

Chilionema ocellatum (Kütz.) Sauv.

New, unpublished record. See citation in Parke and Dixon 1976.

George Russell, who has studied small brown filamentous algae in Europe, identified Chilionema ocellatum during a visit to La Jolla in May 1975, epiphytic on Pelvetia (voucher has been lost; basiphyte cannot be verified).

## RALFSIACEAE

163-175

The following species have ranges that include localities both north and south of San Diego County:

Diplura simulans Hollenb.

Endoplura aurea Hollenb.

\*Hapalospongidion gelatinosum Saund.

\*Hapterophycus canaliculatus Setch. and Gardn.

Pseudolithoderma nigra Hollenb.

Ralfsia confusa Hollenb.

R. integra Hollenb.

R. hesperia Setch, and Gardn.

\*R. pacifica Hollenb. (includes R. occidentalis, collected and identified 1946 by Dawson, from La Jolla, at UC)

Thin brown-black crusts adhering closely to the substrate that typically are considered as Ralfsia species are common on intertidal rocks on San Diego County beaches. Thicker, convoluted, and more loosely attached thalli of Hapterophycus canaliculatus and Petrospongium rugosum (in Leathesiaceae) are abundant in some years in the same habitats. Certain of these brown crusts have been shown to represent stages or phases in the life histories of larger erect species of brown algae in other parts of the world.

### **LEATHESIACEAE**

Leathesia difformis (L.) Aresch.

176

Thalli of the macroscopic phase hollow, globular, yellowish brown, to 12 cm in diameter to the north, smaller in San Diego County and less convoluted. When a piece of the thallus is pressed between one's fingers it separates or feels mucilaginous, in contrast with Colpomenia thalli that are similar externally.

This species is strictly seasonal, first appearing in early March, becoming abundant by April-May, and virtually absent by late May or early June. It is often much more abundant on some beaches, and in some years, than others. It attaches to bare rock, as well as to other algae, and is often epiphytic on coralline species. Internally, Leathesia consists of branched filaments, while in Colpomenia large colorless cells form a parenchyma-type medulla. This contrasting character verifies identifications.

\*Petrospongium rugosum (Okam.) Setch. and Gardn.

Cylindrocarpus rugosus Okam., 177

Macrothalli more or less prostrate, convoluted, rugose (wrinkled or ridged), and not tightly adherent to rock; golden to dark brown, often somewhat circular in outline, to 8 cm diameter. The internal anatomy, similar to Leathesia, easily distinguishes this crust from others.

Abundance and seasonality vary from year to year; thalli can be found in many habitats in and above the mid-intertidal zone.

## **CHORDARIACEAE**

\*Haplogloia andersonii (Farl.) Levr.

182

Thallus erect, gelatinous, narrow, cylindrical; branching irregular but profuse; to 40-50 cm high; most branches 2-3 mm wide; older axes often hollow; somewhat soft to the touch; the presence of numerous colored hair cells that grow out from the outer layer of cells results in a fuzzy appearance in water.

Reported as occasional to locally abundant throughout California to San Diego County, but here very rare, in pools or channels in the intertidal zone.

Setchell and Gardner (1925) (as Myriogloia) refer to variation in the size of plants from different localities and to differences in the abundance of hairs along the branches. Since Dawson's collection (1945d) of thalli on rocks near the Scripps Pier in May, there have been no other published records. We found specimens in 1968 on rocks south of La Jolla Shores beach.

Tinocladia crassa (Suring.) Kyl. 184

Thalli erect, to 15 (25) cm high, irregularly branched throughout, and soft or gelatinous; branches cylindrical, 2-3 mm diameter, with hairs.

The "La Jolla" record in MAC, as far as we can determine, is based on plants Dawson collected and identified [as Eudesme (Aegira) virescens] from midintertidal pools near the Beach and Tennis Club in La Jolla. He reported finding it in "fair abundance" in June, 1944 (1945d), and noted that vegetative growth during cool winter and spring months and seasonal occurrence would be expected for this cold-water species. Collections from Santa Catalina Island provided material for a study which placed the species in Tinocladia as T. crassa (Mower and Widdowson 1969). A single distinctive specimen that probably represents T. crassa was collected at the same time that Cutleria cylindrica (see below) recently was found.

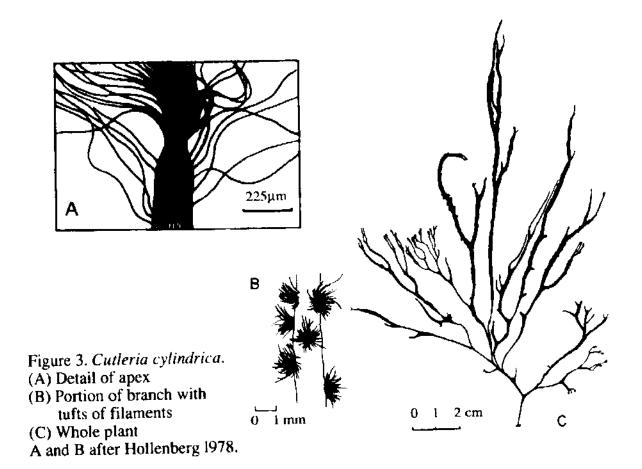
#### CUTLERIACEAE

Cutleria cylindrica Okam.

Hollenberg 1978

Axes to 23 cm high (San Diego specimens), erect from discoid holdfast; branches to 2 mm diameter, dichotomously branched with slender apices 120–200 µm in diameter; growth from meristematic activity at uniseriate base of numerous terminal, simple, colored filaments that are cylindrical, up to 1 mm long and 12–20 µm in diameter, and that quickly become multiseriate by longitudinal divisions of cells; deciduous assimilatory branchlets soon partially replaced by numerous protuberant soral tufts of unbranched fertile filaments (after Hollenberg 1978 and see for illustration of microscopic detail of thallus).

Thalli (Fig. 3C) that were conspicuously different from any previously collected species were found in Pt. Loma intertidal pools in the winters of 1984—85, 1985—86, and 1986—87, the first a year of unusually warm water and following a winter of unusually strong storms. They were absent the following winters (1987—89). Subsequent study concluded that the thalli were very similar to the alga collected at Santa Catalina Island in 1973 and identified as Cutleria cylindrica by Hollenberg (1978), a species described from Japan. He discussed the similarities of this "Cutleria" species to Myriogloia and other taxa in the family Chordariaceae (see above), and questioned its affinities with Cutleriaceae. Additional specimens were collected by Terry Klinger subtidally near San Clemente Island several times in 1986—87, and from shallow subtidal rocks off Bird Rock in La Jolla in 1986. It has not been found elsewhere in San Diego County.



## COILODESMACEAE

\*Coilodesme californica (Rupr.) Kjellm. 188

Thalli epiphytic, saccate, less compressed, and with walls thinner than C. rigida. Specimens as much as 1 m long to 12 cm broad have been found in northern California, but large specimens from San Diego are approximately 15 cm high. The color is a light olive tan that dries to almost green, an easily recognized characteristic.

The few collections from San Diego County occurred on Cystoseira osmundacea, a subtidal species.

Setchell and Gardner (1925) record it south only to San Pedro in Los Angeles County, indicating it was similarly infrequent in the southern part of the state early in the century.

\*Coilodesma rigida Setch. and Gardn.

191

Thalli are flattened brown sacs, with thick-to-thin walls, appearing as blades

attached only (?) on Halidrys dioica, and thereby restricted to the low intertidal or upper subtidal zones.

Reported as frequent at Santa Catalina Island, and in Orange and Los Angeles counties, it is not often found in San Diego. Another species is found on Cystoseira, and because of the difficulty of distinguishing young or basal vegetative parts of Cystoseira and Halidrys, the corresponding species of Coilodesme may also be confused.

Dawson (Checklist) noted it was common on Halidrys in La Jolla in June.

#### **SCYTOSIPHONACEAE**

Colpomenia peregrina (Sauv.) Ham.

204

Compared with C. sinuosa (below), thalli are thinner and smoother, but otherwise similar. Both species grow on rocks and on other algae; for San Diego County, Halidrys and Sargassum muticum are recorded as basiphytes for C. peregrina, which is probably a relatively rare alga here.

\*Colpomenia sinuosa (Roth) Derb. and Sol.

204

Thalli globular, hollow, golden to slightly darker brown, irregular in shape and size, with innumerable variations in appearance, becoming sometimes lobed or convoluted with age.

At times in the mid-intertidal region, mats of coralline algae, or rocks that have been recently rolled or broken and that therefore expose bare surfaces, will be covered with large patches of brownish blobs of algal growth that are identified as C. sinuosa. They are most abundant in late spring and early summer and can appear then disappear from large areas within several weeks. Thalli also grow in low intertidal or shallow subtidal habitats, on larger algae (e.g., Sargassum muticum) as well as on rock substrates.

Dawson's Checklist lists, as forms of C. sinuosa, several taxa now considered to be distinct species.

Colpomenia tuberculata Saund.

204

Thalli globular, irregularly shaped, with walls relatively thick, rigid, and eventually forming blunt-to-sharp projections that can give the surface a rough, "warty" appearance. This species is generally darker and heavier looking than C. sinuosa, although young small thalli of both species are similar. Thalli vary greatly in size and surface texture with habitat and age.

As thalli become older, some of the tubercles usually break away (or the walls are eaten from beneath by juvenile *Pachygrapsus* crabs?), leaving holes of various sizes and shapes. In some years, when these thalli are abundant and remain on the beaches until late in the summer-fall season, they become very perforate, superficially resembling illustrations of *Hydroclathrus*. *Colpomenia* thalli remain relatively discrete and the walls are thick and coarse while *Hydroclathrus* thalli tend to grow into large expanded mats, become "lacy" in appearance, with thinner walls, and without tubercles.

Recognition of thalli as *C. tuberculata*-with-holes depends in part on prior observation of the progression of forms, and in part on actual experience with populations of *Hydroclathrus*, a species from warm-water localities that is abundant elsewhere, but not in California. Setchell and Gardner (1925) observed that old *C. tuberculata* thalli come to resemble *Hydroclathrus*, substantiating our opinion.

# \*Endarachne binghamiae J. Ag. 200

Blades golden to dark brown (fertile portions), without midribs, several arising from small single basal discs; to 20 cm high; many clearly and conspicuously curved at the tips, scimitar-like, in some cases a useful field characteristic. The species here most often grows on otherwise nearly bare rock surfaces in the upper intertidal zone or in lower areas, mostly on tops of rocks and associated with barnacles and sparse clumps of other algae.

When thalli of Endarachne are sectioned, one sees densely intertwined branched filaments in the medulla (enda = inner; rachne = as in a spider web). When thalli of Petalonia fascia, externally similar, are sectioned, the medulla is observed to be formed from large colorless cells. There has been considerable argument about the presence or absence of one or the other of these species in localities south of Santa Barbara. Endarachne is not recorded from the coast north of Santa Barbara, while Petalonia becomes increasingly less common to the south. A representative herbarium subsample of thalli externally resembling Endarachne/Petalonia, collected from San Diego County beaches at all times of the year over a 15-year period, was examined. No Petalonia thalli were found prior to the collections of 1984 referred to below.

In a not-easily obtained Russian series (Vinogradova 1973) Endarachne binghamiae was transferred as Petalonia binghamiae (J.Ag.) Vinogradova. Until this study can be evaluated by other workers, I maintain the taxonomy of MAC. The separation of the two species from California is unambiguous and the distinction in medullary anatomy seems appropriate for generic status.

# \*Hydroclathrus clathratus (C. Ag.) Howe 206

Thalli irregularly globular when young, hollow and sessile; usually aggregated in patches; soon developing numerous perforations to 8 mm diameter; thalli later growing together to cover the rock surface; margins of perforations involute; widely distributed in tropical and subtropical seas.

In many years this alga is absent from San Diego County; the globose brown thalli with holes one sees are instead forms of Colpomenia tuberculata (see preceding). Dawson (Checklist) stated that Hydroclathrus had been found in the tide pools near the Beach and Tennis Club north of La Jolla Shores beach, and we found a few isolated thalli in the early 1960's, including a subtidal collection near the Coronados Islands. Although we have followed the development of Colpomenia thalli with this question in mind, we found no other Hydroclathrus until late fall 1984, when plants appeared south of Sunset Cliffs along the beaches of Pt. Loma. They were scattered in this area throughout winter 1984–85, following a year of warmer-than-normal water temperatures.

#### \*Petalonia fascia (Müll.) Kuntze 200

Erect olive-brown to golden-brown blades, one or more arising from small base; linear or broadly lanceolate; San Diego thalli to 15 cm high (to 35 cm in central and northern California) and mostly less than 4 cm wide, with tapering but not curved apex. Some thalli bear tufts of multicellular hairs; small surface cells enclose several layers of large colorless medullary cells.

Very rarely found in San Diego County, possibly only during or following years of "unusual" water conditions or related changes in nearshore current patterns. No known prior published records for the county or verified unpublished collections. Although Dawson collected intensively, and where it grows it is conspicuous, he cites no records specifically for San Diego County. Until 1984 every plant that was brought to us as an example of *Petalonia* proved to be *Endarachne*. For this reason we question records of *Petalonia* in San Diego localities that are based on field observation, without microscope confirmation. In 1984–87 we found dense and abundant populations scattered on rocks in shallow pools or channels in midintentidal regions during late fall to spring months. Until habitat and field appearance became familiar, we cut sections of blades collected from numerous patches for comparison with specimens of *Endarachne binghamiae* (see above). [Setchell and Gardner (1925) note that *Endarachne* resembles forms of *Ilea* (= *Petalonia*) fascia so closely in general appearance that it is necessary to examine sections to distinguish them with certainty.]

During the winter of 1984-85 we first found *Petalonia* in habitats where *Endarachne* would not be predictably found. *Petalonia* blades disappeared

from pools before *Endarachne* became common on raised rock surfaces. In the following two winters a few blades, scattered in the same area, could be found, but the species was far less conspicuous than during the first year, and it was absent from many of the pools where it grew in 1984–85. It was not found after 1987.

## Scytosiphon dotyi Wynne 198

Thalli unbranched, erect hollow cylinders that usually are (slightly) flattened; to 12 cm high, I mm diameter, tapering to rather a narrow tip and also toward base; growing in tufts of several or many tubes, sometimes twisted, greenish to dark brown; hairs in dense tufts in small depressions on surface.

MAC states that this is mostly a winter annual, restricted to vertical faces of large boulders and seawalls in the upper intertidal region. On San Diego beaches an alga that matches this description is often abundant on high intertidal rocks in summer months as well as into the winter. Many of the larger thalli of S. lomentaria that occur throughout the intertidal are not constricted; lacking this distinction, it is possible that some of the small plants may represent small or juvenile forms of S. lomentaria.

Aguilar et al. (1984) record populations of S. dotyi in five contiguous localities near Punta Cabras, Baja California, most abundantly in winter.

## \*Scytosiphon lomentaria (Lyngb.) Link. 198

Thalli unbranched, erect tube-like, cylindrical, and (ours only rarely) constricted at regular intervals; San Diego plants to 35 cm high, 3–10 mm diameter (elsewhere to 70 cm high); light to very dark brown in color. This is distinctly a late winter/early spring annual on our beaches where it can cover newly exposed rock surfaces in channels or low areas throughout the midtidal region. It also grows in quiet shallow water in Mission Bay, including the entrance channel, and in the flood control channel of San Diego River. Thalli grow rapidly, and on monitored surfaces plants can appear and grow to 16–20 cm within several weeks. Attachment to other than bare rock is very rare. In some years it is markedly more abundant than in others.

Dawson's Checklist refers to various forms, described earlier by Setchell and Gardner (1925), as occurring in La Jolla. These are differentiated primarily by width. Thalli we find are seldom constricted as shown, Figure 162, in MAC. "Ralfsia pacifica" (or another brown crust) has been shown to represent a phase in the life history of S. lomentaria, but the two forms need not alternate, each can repeat itself, and cylindrical and complanate erect forms both occur in some California localities (Littler and Littler 1983).

### DICTYOTACEAE

# \*Dictyopteris undulata Holmes

212

Thalli irregularly dichotomous, yellowish brown to olive, often with a very distinctive pale bluish iridescence when submerged; with prominent midribs, often slightly notched at the tips of blades; wavy or undulate margins.

The variability in specimens of this perennial species is extensive but probably represents changes with age and annual growth cycles in various habitats. Young, or small, plants have broad branches throughout. "Stipes" develop when lateral blade portions are lost from midribs of older thalli. Some specimens completely lack the blade areas to either side of the midrib and are so eroded as to appear to consist largely of long, to 30+ cm, dark or black cylindrical branches. Intermediates link extreme forms. The species is found in winter and spring in low intertidal pools, and to below 33 m in the La Jolla Canyon where this is one of the deepest growing species.

# \*Dictyota binghamiae J. Ag. 207

Thalli light to medium brown, darker below; flat and dichotomously divided; to 35 cm high but mostly less; occasionally with pinnate branches; axes 1-1.5 (2) cm broad, with broadly rounded tips and axils, often with marginal teeth; mostly subtidal. Regular dichotomous branching and the presence of a single relatively large apical cell distinguish this and other *Dictyota* species.

On San Diego specimens the marginal teeth are consistently observed. Subtidal specimens are often very thin and perforate.

Note: Setchell and Gardner's (1925) discussion of 'D. binghamiae' no longer is applicable due to subsequent taxonomic revisions of Dictyota species on the Pacific coast of North America.

# \*Dictyota flabellata (Coll.) Setch. and Gardn. 207

Thalli medium brown; one to several flat axes from basal disc, branching evenly and distinctly dichotomous with blunt-rounded apices, smooth surface on all parts. In cross section mostly 3 cells thick (two single-cell layers of outer cortical cells with a single layer of large colorless medullary cells). D. flabellata is distinguished from D. binghamiae by not showing a tendency to pinnate branching and by lacking marginal teeth or irregularities.

On most San Diego beaches *Dictyota* thalli grow in midtidal pools or channels where they are unlikely to be exposed to air. These grow quickly, from small

germlings to narrow plants approximately 5 cm high within several weeks, and clumps or populations appear and disappear seasonally. These usually submerged intertidal thalli are mostly light golden brown, rather thin, and seldom bear epiphytes. Margins are completely smooth, and branching is strictly and strikingly dichotomous (not as *D. binghamiae*). This small common form is presently attributed to *D. flahellata*, but in several ways it differs from deeper water forms of the species.

Among larger intertidal and subtidal dichotomous forms that lack marginal dentation, there is considerable variability in color and thickness. Some specimens show occasional adventitious branching from the sides of branches away from the growing tip (as in D. binghamiae), and others are often very dark with a leathery texture, as described for Pachydictyon coriaceum. To clarify the distinction between Dictyota and this Pachydictyon species, cross sections were cut from several different portions of each of 20 specimens selected to represent an array of forms and habitats. Most sections, from most thalli, were 3 cells thick and on this basis the plants are identified as representing Dictyota. Among the few plants where margins were more than 3 cells thick, some resembled D. binghamiae in morphology. Considering the longevity suggested by size, appearance, and epiphyte cover of some Dictyota thalli, it seems likely that in older thalli medullary cells near the margins occasionally divide to form an additional row. If this is so, the status of Pachydictyon coriaceum as a separate taxon in San Diego would be dubious. Most subtidal specimens, by morphological criteria, can be attributed to one of the two presently recognized species of Dictyota. Thalli grow from shallow to deep subtidal rocks, and in both San Diego and Mission Bay, including the Channel entrance.

# Pachydictyon coriaceum (Holmes) Okam. 209

Thallus divided into narrow dichotomous portions, with overall fan-shaped morphology; margins smooth, apices rounded; dark brown; to 30 (44) cm high, branches mostly 9–13 mm broad, often somewhat coarse or leathery appearing. Branches mostly 3 cells thick, but margins 4+ cells thick.

To distinguish thalli of this species from species of *Dictyota*, we examined cross-sections from numerous specimens of otherwise similar plants as described above. Development of additional (producing more than one layer) medullary cells near margins, considered to be diagnostic for *Pachydictyon coriaceum*, did not effectively separate our collections into two genera (see discussion for *Dictyota flabellata*). I list *P. coriaceum* as a separate species, but with a query. In San Diego County all the common subtidal dichotomously branched brown algae can probably be referred to either *D. binghamiae* or *D*.

flabellata, following the treatment for these two taxa in MAC. D. flabellata, confirmed by microscopic examinations of cross sections, includes some thalli with thick-appearing, dark-colored basal portions. Some of these specimens could be identified as P. coriaceum if sectioning located areas with two or more layers of medullary cells and if this character is considered in itself diagnostic for a separate genus.

## \*Taonia lennebackeriae J. Ag.

213

Thalli erect, golden to darker brown, to 100 cm high, variable in width, to 4-5 cm in lower third; no midrib or apparent differentiation in the blades; these often long and uniform in width, or wider away from the base, with an elongate wedge shape; occasionally with indistinct bands of dark-colored reproductive cells in a partially concentric pattern across blades.

A distinctive aspect of *Taonia* blades in the field is the torn ragged-appearing blade tip that undulates back and forth in shallow water in sand-filled channels of intertidal beaches. We have also collected subtidal thalli to 20 m offshore, as well as in quiet water sites in Mission Bay. On individual beaches the appearance and disappearance of populations seems related to sand movement, as rocks are covered and uncovered from spring through December.

This species does not occur much farther north than Los Angeles County ("California" is cited as the type locality; MAC states "probably near Santa Barbara") and presumably is more characteristic of lower latitudes where water often is warmer. Because very large (to 100 cm high) specimens have been found in deep subtidal sites (beneath summer thermocline depth), and in winter and early spring months, we hesitate to relate its distribution directly to effects of warm water.

# \*Zonaria farlowii Setch. and Gardn.

215

Profusely flabellate (fan-shaped), with frequent dichotomies in all parts of the thallus; tips of each flat branch often divided into several shallow divisions that are pale yellowish green in contrast to lower darker blade areas; no midrib or differentiation in blades; often with heavy stipe below where older blades have eroded laterally, leaving only thickened basal part; to 24 cm high; typically in aggregated clumps, attached to sand-covered rocks in the upper or midtidal region, occasionally into subtidal habitats (to 30 m).

Zonaria is often associated with the same habitats where Taonia occurs, both species being adapted to partial or complete burial by sand during part of each year. Basal thalli presumably remain viable and resume growth when

uncovered. Survival and the potential for regrowth under these conditions has been demonstrated for *Zonaria* near Santa Barbara (Dahl 1971), near the northern limit of distribution along the coast of California.

Discussed by Setchell and Gardner (1925).

## SPHACELARIACEAE

\*Sphacelaria californica (Sauv.) Setch. and Gardn.

Thalli filamentous, uniseriate only near the apices, growing in isolated discrete dark brown erect tufts, relatively stiff; all axes and branches terete, with longitudinal divisions in cells near the tips producing several elongate cells in place of the original single cell in the filament apex; to 3 cm high, more branched above than below, in irregular arrangements; the microscopic vegetative reproductive structures, characteristic of all species in this genus, are short and unbranched in *S. californica*.

This is one of two common intertidal species; the short branchlets that commonly are the only form of reproduction are not often seen. Thalli can grow directly on rocks but are often epiphytic on other algae, including algal turf on flat intertidal platforms. We have identified the species additionally from high intertidal pools. Our records suggest it may be most often found November–March.

# Sphacelaria didichotoma Saund.

218

Thalli densely tufted, filamentous; uniseriate near apices; all axes and branches terete with longitudinal divisions in cells near the tips producing several elongate cells in place of the original single cell of each filament; thalli to 4 mm high, with creeping basal axes usually epiphytic; rare. Propagula (vegetative branchlets serving reproductive function) are branched into at least two bifurcations.

This species has been recorded growing on subtidal algae along the Loma Sea Cliff and near the Coronados Islands to 17 m. When bleached formalin-preserved specimens are examined, the branching pattern and branch dimensions appear similar to Cladophora thalli that grow in the same sites. Cladophora is rarely, if ever, an epiphyte; with closer examination, the polysiphonous structure of Sphacelaria can be recognized.

Sphacelaria rigidula Kütz. Prud'homme van Reine 1982 S. furcigera Kütz., 218 Thalli often densely tufted, filamentous, uniseriate near apices, all axes and branches terete; longitudinal divisions in cells near the tips producing several elongate cells in place of the original single cell in the filament; usually 5 mm to 1 cm (or more) high, branching often distant and sparse; the slender short branchlets that function as reproductive structures are rarely seen. They consist of a narrow straight "stalk," usually with 2 or 3 narrow straight arms of equal length. In European material, apical cells of the first-developed arms can occasionally produce new arms and the process can be repeated several times. This sequence could produce thalli resembling those described for S. didichotoma in California.

In San Diego, thalli at times are very abundant and easily found where the dark stiff tufts contrast with the pale coralline thalli on intertidal horizontal rock surfaces between Ocean Beach and the tip of Pt. Loma in winter and spring months. It is one of two common intertidal species. In other parts of the world this cosmopolitan species is widely distributed. Although MAC records it as "rare" in California, it apparently becomes rather less rare in this southern part of the state.

# **DESMARESTIACEAE**

\*Desmarestia ligulata (Lightf.) Lamour.

All Desmarestia species are characterized by having large flat, dark to light brown thalli that are clearly divided into mostly round or slightly compressed axes and branches that bear broad leaf-like or more narrow blades in very symmetrical regular patterns. Tufts of hairs terminate blade apices. When blades are damaged (crushed, or exposed to air or rain) they turn greenish blue due to the release of H<sub>2</sub>SO<sub>4</sub> from cells. D. ligulata is an extremely variable and widely distributed species. In San Diego, thalli are up to 2 cm wide, more narrow toward the apex of the thallus, usually branched more oppositely than alternately. Growth follows an annual cycle. Specimens up to 2-3 m high have been collected in fall months, while very small plants are found in spring through summer months. Locally it is abundant both on sand bottom sites in La Jolla Bay and on rocky areas off Pt. Loma; always subtidal, 13-27 m, or on rocks at the lowest, rarely exposed border of the intertidal zone. Most of the variants recognized in California collections can be found in San Diego. The species fluctuates greatly in abundance from year to year.

The two species listed in Dawson's Checklist for San Diego (D. munda, D. herbacea) were included in MAC as synonyms of D. ligulata var. ligulata on the basis of vegetative characters. Comparisons based on other features, and extended to European species, suggest that nomenclatural and taxonomic changes are likely in the future.

Desmarestia ligulata var. firma (C. Ag.) J. Ag. 225

Thallus differing from the preceding forms in lacking the division into distinct axes and blades, consisting more or less of a single mostly unbranched blade. These thalli can be large (to 34 cm high and 21 cm broad) with a clearly evident midrib the entire length of the blade.

The variety thus described was formerly treated as a separate species, D. tabacoides, referring to the tobacco leaf-shaped blades. Most specimens are much less distinctive than the "typical" specimen illustrated in Figure 186 of MAC. Nakahara (1984) showed that specimens of D. tabacoides and D. ligulata from Japan differ in several attributes, including chromosome number, and therefore represent two distinctive species. Specimens resembling var. firma infrequently are found in subtidal habitats to 25 m; variants of D. ligulata var. ligulata grow in the same habitats.

### **LAMINARIACEAE**

Agarum fimbriatum Harv.

234

Thalli are single unbranched brown blades on short stipes attached by small inconspicuous haptera. A distinct broad midrib runs from the base toward the distal part of the blade, which is usually torn and ragged. The blade surface is bullate, meaning with bulging ridges and pockets, not smooth. The entire blade area is perforated by small holes that develop early in the growth of juvenile thalli.

Specimens in San Diego County sites, to 80+ cm high, can be collected during all months, 17-33 m deep on rocks in or near Pt. Loma and La Jolla kelp beds. Our records suggest that small young plants are found winter-spring and the largest thalli in August-January, perhaps representing an annual growth cycle.

The species occurs from Alaska south along the Pacific coast, and recently the range was extended from San Diego to Isla Todos Santos, Ensenada, Baja California where thalli to 90 cm high were found (Aguilar et al. 1984).

[Costaria costata, with an implied range into San Diego County (Dawson 1945d) has not been found here.]

\*Laminaria farlowii Setch.

231

Thalli consist of a single short (4-7 cm) stipe growing from a holdfast and bearing a large blade that lacks a midrib and that lies close to the substrate

rather than rising erect in the water column. The dark brown blade (to 5 m long) is covered with blister-like bulges and ridges ("bullae"), but many smaller specimens are nearly smooth.

This is one of the more conspicuous large brown subtidal plants referred to as kelps. It is common under the canopy or near the edges of *Macrocystis* beds as deep as 33 m.

# [Laminaria setchellii Silva

Druehl 1979

Laminaria dentigera Kjellm., 229

California specimens previously identified as L. setchellii were combined with L. dentigera, a more northern species, in MAC; Druehl (1979) describes differences that justify retaining L. setchellii for digitate Laminaria thalli in southern California. Aguilar et al. (1984) has found specimens on several of the points south of Ensenada where cold water upwelling is associated with marine algae otherwise found far to the north. The species has not been found in San Diego County, nor is it to be expected on the basis of ecological conditions.]

### **ALARIACEAE**

\*Egregia menziesii (Turn.) Aresch. 244

Thalli large, to 15 m long, consisting of several strap-shaped flattened branches densely covered along both edges with broad or narrow, usually somewhat linear, short blades; golden brown to dark, or almost olive brownish green; flat axes sometimes smooth to 3-4 cm wide, or covered partially or entirely with minute tubercles; lateral bladelets to 8 cm long, narrow at base, and highly variable in shape, from broad to filiform; oval pneumatocysts scattered among bladelets, and variable in size, number, and shape.

The extensive morphological variability observed in different parts of the same plant, among plants in the same area, and throughout the range of the species does not make identification difficult. No other alga has long strap-like fringed thalli; these are commonly washed up on beaches wherever there are rocks offshore for attachment. Dense beds of *Egregia* grow in the very shallow nearshore subtidal zone but specimens can be found as deep as 15 m.

242

Thalli are large, conspicuous, brown palm-like seaweeds that grow just up to the lower border of the intertidal zone on stable rock substrates and extend

<sup>\*</sup>Eisenia arborea Aresch.

subtidally to over 33 m. The heavy stipe is mostly somewhat flattened, very dark brown to nearly black, and in subtidal specimens can be more than a meter long; shallow-water thalli usually are considerably shorter; top of stipe divided into two short symmetrical portions, each of which bears a clump of long dark brown blades that hang down from the erect stipe apex. Blades strikingly dentate along margins and corrugated on surface; no pneumatocysts.

Small forms, such as grow in shallow water, superficially resemble *Postelsia* of central and northern California. At the deep limit of its subtidal range, plants may resemble *Pterygophora* when the stipe bifurcation is obscure in large thalli.

# \*Pterygophora californica Rupr.

241

Thalli perennial, with a stout branched holdfast; long unbranched erect stipe, cylindrical in basal portion, flattened above, woody, with concentric rings in cross section; single terminal blade without midrib, smooth surface; lateral blades of approximately same size and shape as terminal blade, borne on both margins of flattened upper portion of stipe; each margin with row of 5–10 specialized blades (sporophylls) that produce reproductive sori; such blades are shed each year after spores are released, with new growth following; stipes to 1.5 m high, to 4 cm broad above, terminal blade to 80 cm, 10 cm wide, with entire thallus 2–3 m high.

Extensive patches of this alga grow in many offshore kelp beds, effectively cutting off most light from the underlying substrate. The dynamic interrelationships among this and other kelp bed species off Pt. Loma are described by Dayton et al. (1984).

### LESSONIACEAE

Dictyoneuropsis reticulata (Saund.) Smith

248

Blades of perennial sporangial thalli to 95 cm tall, growing from short prostrate stipes that also bear marginal haptera; blades linear, with flattened midrib, mostly 15–25 cm broad (San Diego specimens to 10 cm), with coarse network of narrow ridges across blades lateral to midrib. Sori between reticulations, at times over midrib.

R. McPeak found a few specimens in November 1973 at 16 m depth west of La Jolla. He has also observed (pers. comm.) dense and extensive patches of the species off Pt. Fermin (at site referred to as "Horseshoe Kelp"), in Los Angeles County at a depth of about 25 m. In 1983, one specimen (of two observed) was

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collected from near Todos Santos Island, Ensenada, Baja California (Aguilar and Pacheco, 1985). These several new records extend the distribution: in MAC, reported from British Columbia to northern Channel Islands in California.

\*Macrocystis pyrifera (L.) C. Ag. 257

Macroscopic thallus with a basal branched holdfast and long, erect, cylindrical stipes that are branched near the base several times and bear blades at regular intervals in an apparent spiral arrangement; terminal blade broad and curved; the entire plant can be over 33 m long; mature lateral blades are lanceolate with an uneven surface, to 80 cm long and 40 cm broad, usually with a pneumatocyst at the base near the attachment to the stipe.

This is the common kelp that is harvested off Pt. Loma and La Jolla from kelp beds where fishing and diving boats congregate, and that washes up on the beaches in huge piles after storms or (in small pieces) after kelp cutters go through the beds. The relationships among this large dominant plant, the understory algae, and the fish and invertebrates that share this habitat have been intensively studied both because so many of the species (lobster, abalone, fish, kelp) are commercially valuable, and because of intrinsic interest in this conspicuous cohesive plant community. Macrocystis pyrifera occurs on the coasts of Chile, Argentina, and several islands in the South Atlantic, as well as along the west coast of North America. Two other species occur on the Pacific coast north of San Diego County, as well as in the southern hemisphere.

\*Pelagophycus porra (Lem.) Setch. 251

Thalli consist of a holdfast with branched haptera, a long (to 27 m) unbranched stipe bearing a single large (to 20 cm diameter) pneumatocyst from which two opposite primary branches extend laterally; each of several secondary branches ends in a single large blade; these huge blades can be to 20 m long and 1 m wide, and are covered with coarse ridges and irregular "blisters"; blade margins usually with short spine-like protuberances.

Beds of this species are often referred to, and included with *Macrocystis*, as kelp. Off San Diego County the species grows in deeper water seaward from *Macrocystis* beds, to 27–30 m. The stipes and blades hang in midwater, seldom growing to the surface. This species, the only one in the genus, is limited to waters between central California and northern Baja California, and is one of the most spectacular of the west coast kelps. We have collected very small plants both in summer and winter.

#### FUCACEAE

\*Hesperophycus californicus Silva

Silva 1990

H. harveyanus (Decne.) Setch. and Gardn., 266

This is a large and easily identified alga, superficially resembling a small Fucus. Apparently it does not now grow in San Diego County. Setchell and Gardner (1925) note that it was found between Monterey and Ensenada, and a 1902 La Jolla collection by M.S. Snyder is filed at SIO. L. Aguilar (pers. comm.) has recently collected it farther south, at Punta Baja, a cold-water locality. Dawson (1945d) reported that thalli were fairly abundant near Bird Rock, 4.8 km south of La Jolla; this is a sheltered cove within a small bay where algae more frequently associated with warm water (Spyridia, Jania) are often abundant. Since then, collectors have searched in this same site, but the species has not been found again. We have located several specimens from Islas Coronados (1897-1949) at UC.

# \*Pelvetia fastigiata (J. Ag.) DeToni 261

Thalli dichotomously branched above holdfast, all branches lying in one plane, compressed above, more terete below, tough, olive green, to 90 cm high; branching regularly dichotomous throughout, but the two branches from one dichotomy generally unequal in length; the apical portions of branches broader and rough textured when reproductive structures are developing in this part of the thallus.

The intertidal distribution in San Diego conforms to that described for the species throughout California—often abundant in patches on rocks somewhat protected from open surf, mostly on or near tops of rocks in the upper midtidal region or lower on rocks near the high intertidal. Small clumps of this species are frequently found growing on nearly vertical surfaces of seawalls associated with Endocladia muricata and Nemalion. Thalli are perennial, but new growth develops in the spring and summer, while older axes become covered with epiphytic brown filaments in the late summer and fall. Gunnill (1980) describes recruitment and mortality of this species in the Ecological Preserve just south of SIO between 1973-1977.

Setchell and Gardner (1925) write that the largest plants are found in southern California, the central portion of the range on this coast. The very distinctive form gracilis occurs on high exposed rocks in the inner bay at Ensenada, to the south of San Diego, as well as in Monterey County and the offshore California islands, but has not been found in San Diego County.

## **CYSTOSEIRACEAE**

\*Cystoseira osmundacea (Turn.) C. Ag. 269

Large brown thalli, with a perennial holdfast; in San Diego, stipe and branches mostly produced in annual cycles; blades with midrib and symmetrical lateral portions; mature branches ending in a tapering series of bead-like vesicles on short side branches; beyond these, flat branches develop with fertile structures.

Basal portions of this species are similar to basal portions of *Halidrys*. In southern California *Cystoseira* grows from shallow to deeper subtidal (13–17 m) while *Halidrys* is most abundant from shallow subtidal into low intertidal habitats. When the small strings of spherical (*Cystoseira*) or flattened (*Halidrys*) vesicles are absent from the thalli, the species cannot be confidently identified; the ecological separation is useful when positive identification is not critical.

Dawson's (1945b) reference to Cystoseira neglecta cast ashore at La Jolla might have represented a drift piece of local C. osmundacea or C. neglecta carried from Catalina Island where K.A. Miller finds this latter species to be rather common. The specimen cited (Dawson, 1945b, as Blossevillea brandegeei) as representing Stolonophora brandegeei (Setch. and Gardn.) Nizamuddin, a species known primarily from Guadalupe Island, also was likely to have been drift Cystoseira (or Halidrys).

### \*Cystoseira setchellii Gardn. 269

MAC cites "to San Diego" in the distribution record, and adds "no plants from the San Pedro region were found. . .during the years 1969-72. . .probable that this species no longer grows at the type locality." Gardner (1913) established the species for plants cast ashore at Redondo Beach and near San Pedro in Los Angeles County, citing no additional records. San Diego records include specimens dredged from the Coronados Islands in 1949 and collected from 17 m off La Jolia (by C. Limbaugh, probably about 1950) presently filed in the Herbarium at U.C. Berkeley (UC). The species is described as similar to a short form of C. osmundacea. Aguilar et al. (1984) reported finding an attached subtidal population of typical C. setchellii off Isla Todos Santos (Ensenada), Baja California.

## \*Halidrys dioica Gardn.

272

Large brown thalli, often to 2+ m or more in length, differentiated into very different-appearing basal and apical portions; the lower stipe produces alternate branches that give rise to pinnately branched long branches; in upper

portions branches bear tapering branchlets formed of flat vesicles; above these, receptacles with reproductive structures develop later in the year on closely and intricately branched frond apices.

In San Diego County, as in other parts of southern California and Baja California where this species grows, *Halidrys* is abundant in intertidal channels and on shallow subtidal rocks on exposed beaches. It is generally higher on the shore than *Cystoseira* which is restricted mostly to subtidal rocks. As noted above for *C. osmundacea*, when the chains of vesicles are present, the two species are easily distinguished; when lacking, it is essentially impossible to separate specimens into two taxa by morphology.

### SARGASSACEAE

\*Sargassum agardhianum J. Ag. 275

Thalli radially or apparently alternately branched, mostly less than 25 cm high; branching continuous and similar from base to apex, including branches that are leaf-like with midribs and toothed dentate margins; pneumatocysts solitary, spherical or slightly ellipsoid, terminal on branchlets, with a tiny spine on the side away from the short stalk; small woody holdfast with several axes usually in a single clump.

For periods of several years this species will be absent on beaches where it had been collected previously; during this time populations will be found on other beaches, so it is not clear if the growth of the species is related to large-scale environmental fluctuations. Occasionally it is found on rocks in sand or in sandy channels between platform rocks, but in other sites it can develop in the midst of algal turf; growth appears to begin in late spring to early summer. In midtidal habitats where S. muticum also grows, the two species can be distinguished by the presence (S. agardhianum) or absence (S. muticum) of a sharp point on the small pneumatocysts. S. muticum in these situations is branched similarly and the contrast between clustered vs. widely-spaced branchlets (as cited in MAC) may not prove useful for field identifications. Even large thalli of S. agardhianum (25–35 cm high) are smaller and more robust-appearing than most S. muticum. Setchell and Gardner (1925) state that form is considerably modifed by habitats, being "short and stocky" in the midtidal region, more elongated in deeper quieter water.

Type locality for S. agardhianum is San Diego.

Dawson et al. (1960) report finding it to 10 m in kelp, but this is not the typical habitat, and we have not collected it away from shallow subtidal near-shore habitats.

Sargassum muticum (Yendo) Fensh. 275

Thalli to 2 m, or more in subtidal or quiet-water situations, arising from a small thick holdfast with main branches developing close to the base of the initial stipe; repeatedly branched to form bushy thalli; leaves linear in basal portion, to 10 cm long, margins dentate; leaves in upper portions more narrow, margins toothed or almost smooth; pneumatocysts borne in clusters or single in leaf axils, smooth, without a spine from the surface; fertile branchlets also developing in leaf axils.

The introduction of this species, presumably directly or indirectly from Japan, is described in MAC. We collected it in the Flood Control Channel (mouth of San Diego River) in 1969, but it had been noticed as early as 1958–59 in Quivera Basin of Mission Bay. Seasonal reproduction and growth cycles of San Diego populations (Deysher and Norton 1982) produce fertile zygotes March—June, and juvenile plants attach on previously bare or cleared surfaces primarily during this same period.

S. muticum is conspicuous in shallow water in Mission and San Diego Bays where large plants grow near the docks and piers, and on rocks along the channel entrance to Misson Bay. On exposed beaches it grows both on intertidal and subtidal rocks.

At present its distribution extends south to Punta Abreojos in Baja California (Aguilar et al. 1984).

#### \*Sargassum palmeri Grun. 277

Thalli perennial, arising from solid, rough-surfaced holdfast; stipe terete, to 1.2 m long, bearing 2-5 terete or slightly angled alternate branches at apex, disintegrating following reproduction; primary branches producing sterile "leaves" that are alternately dissected into 15-25 slightly flattened divisions 2-3 cm long; older branches and occasionally branchlets more or less spiny; numerous lateral terete secondary branches arising in axils of "leaf"; leaves with indistinct midrib; pneumatocysts produced in blade axils, usually solitary, smooth, on ends of stalks as long or longer than the diameter of the pneumatocysts.

This species is recorded as being distributed on offshore islands south from Santa Catalina. We have found it in drift on beaches near Imperial Beach and from just north of Del Mar to Encinitas during winter and spring months. It is likely that it grows on rocks offshore on sandy beach slopes. We have not collected attached plants.

Dawson's Checklist refers to a specimen from San Diego Bay (drift?).

### RHODOPHYTA

## **PORPHYRIDIACEAE**

Chroodactylon ornatum (C.Ag.) Basson

Basson 1979

Asterocytis ramosa (Thwaites) Schmitz, 283

Microscopic filaments in gelatinous walls.

R.A. Lewin isolated and identified (as A. ornata, Lewin and Robertson 1971) the only known California collection from a seawall near an ocean-water discharge pipe. In culture the alga appeared blue-green, with sheaths 1-3 mm thick.

\*Stylonema alsidii (Zan.) Drew

Drew 1956

Goniotrichum alsidii (Zan.) Howe, 280

Thalli filamentous, to 5 mm high, often branched irregularly, with cells surrounded by colorless gelatinous sheath layer and partly appearing loose and irregularly arranged in some thalli.

Epiphytic on many different algae in various habitats. Locally we have found this species subtidally to 27 m, on Gelidium nudifrons, Sarcodiotheca gaudichaudii, Polysiphonia, unattached blades of Zostera marina var. latifolia, and other unspecified substrates. It will be recognized only when the larger thalli are examined under a microscope.

Dawson's San Diego Checklist lists this as G. elegans; in PMR 1 (Dawson 1953b) G. alsidii includes G. elegans (Chauv.) Zan.

## **ERYTHROTRICHIACEAE**

Erythrocladia subintegra Rosenv.

Thalli microscopic, epiphytic, monostromatic, with cells laterally adherent and in radiating rows from a central area. Cells at the margins often bifurcate.

A common epiphyte from low intertidal to subtidal habitats. A specimen found on Janczewskia (which was in turn growing on Chondria nidifica) establishes this species for San Diego County.

E. irregularis, differing in having the radiating filaments free near margins (not joined), is currently treated by most taxonomists as conspecific with E. subintegra.

Erythrotrichia spp.

284-289

Thalli microscopic, often epiphytic, filaments, mostly unbranched, bright pink on various substrates.

In the course of picking tiny thalli from tunicates, sponges, other algae, rocks, or shells such as abalone or scallops, *Erythrotrichia*-like filaments are frequently recognized. The basal portion is seldom intact when the thalli are collected in this way; individual filaments are less than 1 cm tall, occasionally with multiseriate portions. It is likely that all these rather numerous collections and observations refer to a single, somewhat common (although inconspicuous) alga, *E. carnea* (Dillw.) J. Ag., described as a common epiphyte with a wide geographic distribution. MAC notes that other species reported for California may represent forms of *E. carnea*.

Our records of specimens from non-algal substrates extend the known habitats. Prior to use of SCUBA to sample deeper sites, the diversity of growth on these various substrates had not been recognized.

Dawson's Checklist refers to *E. carnea* as cosmopolitan, without mention of San Diego collections, and to *E. tetraseriata* as a southern California alga.

\*Smithora naiadum (Anders.) Hollenb.

Thalli epiphytic on *Phyllospadix* and *Zostera*, with several to many monostromatic blades mostly less than 1 cm high, rising from a basal cushion on seagrass leaves; algal blades oval to irregularly round in shape, with the upper margins often torn, occasional large plants to 2 cm high. As noted (MAC) for forma *minor* in southern California, no conspicuous sori are observed in local material.

For many years Smithora was found, sometimes throughout the year, usually particularly abundant and common during winter and spring months. Between December 1982 and 1988 the species was absent or rare on beaches where formerly it had been easily collected. The first year of this interval was a period of higher average water temperatures, with seasonal warmer water occurring earlier in the year and extending later into fall months, suggesting that distribution of Smithora may involve a response to water temperature.

Dawson (1953b) recorded the species from "virtually all peninsular (Pacific Baja California) and (Mexican) island stations to as far south as Isla Magdalena, at all seasons."

### **BANGIACEAE**

Bangia vermicularis Harv.

Sheath and Cole 1984

Bangia fusco-purpurea (Dillw.) Lyngb., 294

Thalli of the macroscopic stage unbranched filaments, dark red or nearly black, to 10 cm high, usually 1-3 cm in San Diego localities; these commonly aggregated in patches on rocks in the upper intertidal zone.

The species is ubiquitous, often common, throughout its range. Extensive mats of *Bangia* grow on rocks north from central California, but are less common on San Diego County beaches where it is usually a winter—early spring annual plant. It has been reported from a site north of Ensenada in Baja California (Pacheco and Aguilar 1984). Sheath and Cole (1984) concluded that the four species earlier described on the Pacific coast of North America are variants of a single taxon.

# \*Porphyra perforata J. Ag. 299

Thalli of very thin, delicate, small blades, mostly about as broad as long, one layer of cells thick, sessile, blades deeply lobed and ruffled, greenish to purplish-brown, reproductive portions in marginal patches appear as pale borders when the cells have been discharged.

In northern California and in cold water sites of Baja California, thalli are 15–30 (110) cm high, but the largest we have found in San Diego are 11 cm, and commonly they are 1–2 cm high. The species is most abundant as a winter or early spring ephemeral, although in some years it can be found as late as November, persisting on particular rocks on La Jolla beaches through the summer.

Because the size of these southern plants differs so markedly from the large thalli familiar to workers elsewhere, many older collections were not identified as *P. perforata*. Data for numbers of spores in packets and chromosome counts (2 per nucleus) support the identification of these several populations as *P. perforata*.

## Porphyrella californica Hollenb.

305

Thalli in clusters of small (1–2 cm) blades, pale pink to light reddish-brown, oval or broader (to 2.5 cm), on very short stipes, one layer of cells thick, and very thin and delicate appearing; reproductive cells in patches along margins that leave a pale or ragged border when shed.

The species was previously reported from Laguna Beach on the California coast. In San Diego County, very small *Porphyra*-like blades are found on mussels or gooseneck barnacles at the same sites where *Porphyra perforata* grows on rocks, and at the same season. Thalli are generally less than 1 cm high, and differ in color from *P. perforata*. The epizooic plants may represent *Porphyrella californica*. When *Porphyrella gardneri* (a species that grows on the margins of large members of the Laminariales and that is absent from San Diego) was transferred to the genus *Porphyra*, Hawkes (1977) suggested that study of *Porphyrella californica* might determine that this species also is more correctly placed in *Porphyra*.

## **ACROCHAETIACEAE**

Audouinella complex (Acrochaetium/\*Rhodochorton) 308-323

Thalli microscopic, filamentous, branched; a few taxa grow on rocks, but most are on or in other algae or animals. Monosporangia common, other reproduction rarely found.

Such algae have been collected locally as subtidal epiphytes on *Pleonosporium vancouverianum*, *Gelidium robustum*, *Callithamnion* sp., *Tiffaniella snyderae*, *Sorella delicatula*, and on sponges and tunicates; intertidally, on *Pterocladia capillacea*, *Rhodymenia* sp., and *Phyllospadix scouleri*. *Rhodochorton purpureum* grows in caves in the La Jolla area, as reported by Dawson (1945d) and confirmed by recent collections.

Species belonging to this group are found in all parts of the world, but the small filamentous thalli are not easily identified either from natural habitats or from culture studies. Woelkerling (1983) writes: "The Audouinella complex contains a diverse but distinctive assemblage of marine and freshwater red algae. . . . Compared to most other Rhodophyta, acrochaetioid algae have a simple morphology, but their taxonomy is rather more complex. . . . Since 1970, at least fourteen different classification systems have been used for these algae. Moreover, species concepts and delineations generally continue to be vague and changeable; generic concepts remain unresolved."

We have not attempted to segregate our material into "species" other than recognizing Rhodochorton purpureum in its distinctive habitat. Dawson (1953b) listed 16 species from Pacific Mexico. MAC includes 15 species of Acrochaetium, several of which were cited in Dawson's Checklist as species of Rhodochorton.

\*Rhodochorton purpureum (Lightf.) Rosenv. 323

Thalli 1-1.5 cm high, filamentous, uniseriate, usually in tufts or mats, with prostrate creeping portions bearing erect sparsely branched filaments; the basal axes are intertwined in this species that grows in caves in the high intertidal or on shaded rocks. Although *Rhodochorton* species are included in the *Audouinella* complex, the specialized habitat that is apparently everywhere associated with this species singles it out as distinct. It can still be found on the upper surfaces of shallow caves against the cliffs at the south end of La Jolla Bay, as described (as *R. rothii*) in Dawson's Checklist.

#### **NEMALIACEAE**

\*Nemalion helminthoides (Vell.) Batt.

324

Thalli gelatinous, rubbery, cylindrical, 1-6 mm diameter, unbranched or with several branches often toward the tips; axes often gradually tapering to the tip; clumps of one to several thalli growing from small circular disks, with both base and axes a dark brownish-red color.

As reported for other California regions, San Diego thalli are restricted to sloping or vertical sides of rocks or concrete seawalls in the high intertidal zone, and are most abundant between April and November.

Northern specimens are reported to 135 cm long, mostly 20–45 cm, but San Diego County plants are commonly less than 10 cm, with 25 cm representing an extremely long plant.

### HELMINTHOCLADIACEAE

\*Cumagloia andersonnii (Farl.) Setch. and Gardn.

329

Thalli clumped, with several soft, rubbery, dark reddish brown strands growing from small disks on rocks; these erect axes are cylindrical, with few or no branches, but covered with small spinelike branchlets with forked tips. San Diego thalli are mostly 6–10 cm high, occasionally to 20 or 30 cm, and 3–8 mm in diameter.

Throughout California, as well as in San Diego County, this is an annual species that is here found late March through July, with greatest abundance usually in May and June. It is particularly conspicuous on high intertidal sandstone rocks in the La Jolla area in some years; everywhere absent in other years.

Dawson described specimens from northern Baja California as being relatively small forms resembling southern California specimens, but we also find very large thalli, and populations usually include a wide range of sizes.

## \*Helminthocladia australis Harv.

327

Thalli little to much branched, but only to 3-4 orders; axes cylindrical to 10 mm diameter in San Diego County, smaller to the north; thalli very slippery, rubbery; branching completely irregular, with no pattern or similarity among specimens. Pale brownish red, or tan or dull yellowish pink, and conspicuous among other algae because of size (to 10-20 cm high) and the sprawling thick strands that stand out against the background turf of small algae on intertidal rocks. On some specimens the shorter (younger?) branchlets are dark red, in contrast with the thick pale main axes.

Recorded north only to Santa Barbara, in San Diego it is more abundant in late summer, and during many years is not found at all. In recent years, with warmer water locally, it has been more often found, suggesting it is indeed associated with such conditions. Dawson did not find it on the Pacific coast of Baja California, possibly because most rocky sites where he collected were in areas of cold water upwelling. Another explanation is that the plants do not persist long in any given site and could be overlooked by sampling only at times when the species was absent. In San Diego, it has been found on intertidal rocks on various beaches

### \*Helminthora stricta Gardn.

327

Thalli dull straw-pink in color, lubricous, 1-2.5 cm high, to 1 mm diameter, irregularly branched; attached by small disc to *Phyllospadix* leaves, where plants are found in clusters.

The type collection came from a *Phyllospadix* specimen, La Jolla, in June, and is referred to in Dawson's Checklist. The second collection known for this alga consisted of plants on drift *Phyllospadix* in central California in 1949. Only a few additional specimens, none from southern California, have subsequently been identified with this species.

## Liagora californica Zeh

329

Thalli bushy, compressed below, terete above, repeatedly dichotomously branched, 6-12 (16) cm high, with bright red apices, grayish-white below where heavily calcified.

In California, "infrequent, on rocks, lower intertidal to upper subtidal, Santa Catalina I., and Pt. Loma, San Diego Co." This MAC citation for San Diego County is based on a specimen collected in 1875 by Edward Palmer, and deposited in the herbarium at University of California, Berkeley, noted by Dawson (1945c). No other specimens from the mainland of southern California are known to us.

The color and texture of this species are striking, both when growing in shallow water habitats as well as after being collected; and if the alga were present in an area, it would easily be recognized as distinctive. If the single specimen reported for Pt. Loma was found in drift material, the source could have been outside the area, accounting for its absence from collections of locally attached algae.

### **GALAXAURACEAE**

\*Scinaia confusa (Setch.) Huisman

Huisman 1985

Pseudogloiophloea confusa (Setch.) Levr., 335

Thalli axes terete, dark red or brownish in exposed intertidal habitats, 3-15 cm high, regularly dichotomously branched, often with proliferous clusters near bases of branches; apices tapering, otherwise nearly uniform diameter (1) 2-5 mm throughout.

Infrequent, over a wide range, British Columbia to Punta San Quintín, Baja California, on rocks mid- to low intertidal and subtidal.

Dawson (1945d) commented that a portion of a fertile plant was found in July on the beach near Scripps Pier, La Jolla. No recent San Diego County collections are known to us. As noted for Scinaia johnstoniae, it is necessary to compare the size and arrangement of cortical cells to distinguish these two species. Scinaia johnstoniae is found to the south of San Diego, and drift plants could presumably reach San Diego County beaches.

### \*Scinaia johnstoniae Setch.

332

Thalli axes cylindrical, 6–13 cm tall, dichotomously branched, without constrictions, broader (3.5–5 cm) above, to 1–2 mm diameter below; upper branches appearing fan-shaped, with acute apices.

Very rare in southern California, more common south and into the Gulf of California. This species is virtually identical macroscopically with S. (Pseudogloiophloea) confusa and a cross section is necessary to distinguish the two. Several specimens in herbaria (UC, HAFH) were collected from dredge or drift material off the coast of San Diego County prior to 1946.

### \*Scinaia snyderae (Setch.) Huisman

Huisman 1985

Pseudoscinaia snyderae Setch., 333

This species is included solely on the basis of Setchell's 1914 description of the San Diego County type collection ("at Pacific Beach," 1898), as cited in MAC. It has never been re-collected, and was not discussed by Dawson.

MAC notes that this species is externally very similar to Scinaia (Pseudogloiophloea) confusa. Since no collections other than the type are recognized, its status is doubtful.

### **BONNEMAISONIACEAE**

Asparagopsis taxiformis (Del.) Trev. 340

Axes cylindrical, 1.5-2 mm diameter, to 10-20 cm tall; mostly bare in lower third, densely branched above, with soft feathery appearance.

In the San Diego area, known from subtidal collections 1986–89 at the Coronados Islands. Seen frequently at San Clemente Island, 100 km west of San Diego as well as more northern Channel Islands. Common in warm seas, worldwide, including Mexican eastern Pacific islands.

### \*Bonnemaisonia hamifera Har.

338

See MAC for description and distribution information. Dawson (1945d) cites, as, an old specimen (P.B.-A. 490) from Pacific Beach as a "record" for San Diego County. No San Diego County collections are known to us.

#### **GELIDIACEAE**

\*Gelidium coulteri Harv.

344

Thalli mostly less than 10 cm high, in clumps and patches on rocks in the midintertidal region; major branches relatively few from main axes, but all branches are covered with evenly spaced short distichous branchlets that characteristically are approximately the same length along branches from base to apex of plant; fertile apices of irregular shapes, often broad, and giving the thallus a more bushy appearance.

Further north this species is common in high intertidal habitats, as well as lower, but in San Diego County it is found predominantly in positions somewhat protected from heat or desiccation, often under ledges on sides of rocks in higher zones, or on vertical surfaces that are wave-splashed even during low tides. It is not as common or abundant here as it is to the north. In late spring or early summer patches of algae that are often identified as G. pusillum are actually young, small G. coulteri, a species that grows in an annual cycle.

Gelidium thalli are highly variable in branch dimensions and branching patterns, yet these are the criteria for distinguishing species. G. coulteri is recognized in San Diego by the presence of evenly spaced, similar length lateral branchlets and by being restricted to a rather narrow region intertidally.

Dawson (1953b) wrote that the species is common in Pacific Baja California localities with lower water temperature; its southern limit apparently coincides with the southernmost area of upwelling, near Isla Magdalena.

### \*Gelidium nudifrons Gardn.

345

Thallus to 35 cm high, clumped, sparsely and irregularly branched; axes compressed to flattened, of similar dimensions from base to apex, generally less than 0.6 mm broad. The illustration (Fig. 288) in MAC gives the plant a heavier, coarser appearance than is accurate; it appears thin, slender and wiry.

Strictly a subtidal species, it grows in isolated clumps or patches in kelp beds or on open rocks to 30 m. Along La Jolla beaches thalli are often found in piles of drift algae where they are recognized by their dark, nearly black color, as well as their morphology. Individual clumps can be large and in some offshore areas are dense and abundant, and therefore the species has been considered as a possible source of agar. Tests, however, show it to be much less useful than *G. robustum* and at this time it is not harvested commercially.

The type locality is Ensenada, 150 km south of San Diego.

# \*Gelidium purpurascens Gardn. 345

Thalli mostly with rather regular distichous branching, sometimes in part polystichous, alternate, or opposite, with or without geniculate junctions between axes and branches; more or less compressed, branches sparse, or more dense, but on single thalli consistent, usually regularly spaced; ultimate branchlets mostly less than 1 mm broad, while those of G. robustum are often wider; intertidal to subtidal.

This brief description, based on the treatment in MAC, comprises the wide range of branching patterns observed in San Diego County populations. Previously there had been 6-8 distinct species described for the more conspicuous varieties, but when a large number of specimens is assembled, the gradation from one to another is continuous, and it seems more appropriate to consider them as a single entity. For practical purposes, if a large specimen from low intertidal or subtidal rocky substrate is neither sparsely branched (G. nudifrons) nor robust (G. robustum) it is probably G. purpurascens.

Dawson's Checklist included this species as G. pulchrum, formerly a name applied to the finest, most delicately branched variants.

# Gelidium pusillum (Stackh.) Le Jol.

Thalli 1–2 (5) cm high; prostrate axes terete, producing terete erect axes and/or compressed erect branches; erect parts sometimes becoming secondarily attached to substrate, with additional prostrate axes forming near the attachment point; erect branching distichous, predominantly irregular; flattened branches to 1.5 mm broad; when tetrasporangial sori and cystocarps develop on apices, these branchlets often become conspicuously broad, or densely aggregated, giving the thalli various different appearances. This species is often very abundant in high intertidal zones, but is also common in scattered habitats throughout intertidal and subtidal regions. It is found in all the oceans of the world in warm temperate to tropical regions, always with a multitude of forms.

Many of the mid-high intertidal rocks that elsewhere would be covered or spotted with low mats containing G. pusillum are in San Diego County scoured or buried with sand during parts of the year, then at other times left bare when sand is carried farther offshore. Under such conditions the dark-red fuzzy red algal turf that develops is more often a mixture of species of Polysiphonia or other filamentous Ceramialean taxa. G. pusillum is most common in habitats less affected by sand movement and accumulation, such

as on some of the higher rocks that are above the level of sand accumulation or on exposed outcroppings where surf continually removes sand. Small patches have been found subtidally. Cystocarpic specimens are necessary to identify two small rare species of *Pterocladia* that can resemble forms of *G. pusillum*.

In Dawson's Checklist most of the plants referred to G. crinale and probably many collections of G. coulteri were included in G. pusillum as presently circumscribed.

\*Gelidium robustum (Gardn.) Hollenb. and Abb. 347

Thalli to 40 cm high (to 100 cm near offshore California and Mexican islands); branches mostly compressed but often nearly cylindrical below; branching characteristically regular, distichous, often with a bend close to the junction with main axes ("geniculate," meaning bent as in a knee joint) and frequently symmetrical and pinnate at least on upper portions of axes; lower portions of axes often unbranched as a result of having lost older branches from long-lived fronds. Nearshore, along the coast of San Diego County, there are dense populations on subtidal rocks or ledges; isolated clumps occur within kelp beds, usually on rocks that rise off the bottom. This is the largest and coarsest of California gelidiaceous algae and is easily recognized along channels in the low intertidal as well as in subtidal habitats.

Type locality is near Ensenada, 150 km south of San Diego. Dawson's Checklist listed this as G. cartilagineum. In PMR 1 (1953b) he compared collections from northern Baja California and southern California and wrote that maximum development occurred in rocky coastal areas with cold upwelling water, where plants may be up to one meter high and consist of huge clumps with "hundreds of fronds."

This species has been the subject of many studies because of its economic value as the source of high quality agar. Field work has shown it to be perennial, to grow slowly, and to occur to 20 m depth primarily in areas where water currents or surge are strong, presumably continually providing nutrients. Large amounts are presently harvested.

\*Pterocladia caloglossoides (Howe) Daws. 349

Thalli mostly less than 1 (2) cm high, axes 45–570  $\mu$ m wide (subtidal specimens mostly less than 200  $\mu$ m, while intertidal thalli may grow to 750  $\mu$ m wide) and all specimens 60–120  $\mu$ m thick. Prostrate axes flattened and similar to erect axes, flattened against substrate by regularly arranged disk- or

peg-like structures with erect axes developed from the surface opposite the attachment point; erect branches pinnately branched or simple, and often secondarily attached to the substrate and thus appearing as prostrate axes; this growth pattern repeated to form a creeping system of connected erect and prostrate branches, with variable numbers of erect system branches (Figure 4). The presence of tetrasporangia in broad V-shaped rows on the tips of branches is often characteristic of this species, but the feature also is seen in other small related species of Gelidium and Pterocladia.

When MAC was prepared, few collections were available for study. Specimens of *P. parva* from the Gulf of California were compared with the few known specimens of (Gelidium) caloglossoides from central California. The type locality of *P. caloglossoides* was incorrectly given as San Felipe, which is the type locality of *P. parva*. More recently, these several taxa were reevaluated and *P. parva* is now included as a synonym of *P. caloglossoides* (Stewart and Norris 1981); the correct type locality of this latter species is "On shells, dredged in (5 m), Island of San Lorenze (Peru)."

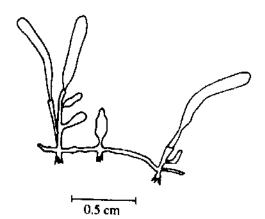


Figure 4. Pterocladia caloglossoides.

Prostrate axes with attachment structures opposite erect axes.

\*Pterocladia capillacea (Gmel.) Born. and Thur. 350

Thalli to 30 cm high, branching distichous, often with very regular and pinnate appearance, sparse to dense, uniform within single thalli, or variable in some branches; axes and branches of various widths and lengths, with the result that many morphological forms occur, some correlated with rather distinct habitats or different seasons; all branches and axes are flattened to compressed, to 2 mm broad, 0.9 mm thick below; ultimate branchlets often nearly as broad as the lower portions; the branches may be constricted where they join the parent axis, but not bent; typically one or several percurrent axes arise from a cluster of pale, cylindrical prostrate axes; branches from these are longer toward the base of the axis, shorter toward tip, giving a pyramidal outline to the frond. This symmetrical variant is common in southern California. In San Diego County, it is one of the most abundant species on midtidal to subtidal rocks (to

20 m) with consistently moderate to heavy surf. On broader, more gently sloping beaches (such as Pt. Loma) it is found only in lower zones, often near or under beds of *Phyllospadix*. This is a cosmopolitan alga of warm temperate water, found south of Santa Barbara in California and at least to the outer coast of Bahía Magdalena in Baja California.

Dawson's Checklist lists the species as Gelidium pyramidale. P. capillacea is one of the economically important red algae that provides a source of high-quality agar and is harvested off the coast of southern and Baja California. Recent studies in Hawaii suggest that this alga, in certain localities where it is abundant there, may be an important component in the diet of sea turtles.

\*Pterocladia media Daws.

351

Thalli 3–5 (8) cm high, in small clumps, simple or sparsely branched, erect percurrent axes from system of stoloniferous prostrate axes attached to rocks by short peg-like rhizoids; branching irregularly distichous, all axes and branches uniformly thin, narrow, 150–300  $\mu$ m broad, 100–200  $\mu$ m thick, compressed.

Specimens are more slender, less regularly branched than G. pusillum, which can be similar in height and grows in similar habitats. P. capillacea is usually more regularly branched and wider, flatter-appearing in all parts of the thallus. Although thalli of P. media differ markedly from other gelidiaceous algae locally, the single distinct apical cell in actively growing tips, and the presence of internal rhizoidal filaments identify specimens as a member of the family.

This species is infrequently or rarely found on rocks on sandy beaches between San Francisco and San Diego in California. Locally, when rocks with small populations of the alga are buried for many months, the following year the plants are not found on them, and therefore it is only sporadically found.

Type locality is the rocky beach just north of Wind & Sea beach in La Jolla.

Some of the collections treated as G, crinale in Dawson's Checklist represent early records of the species later treated as P, media.

### **DUMONTIACEAE**

\*Farlowia mollis (Harv. and Bail.) Farl. and Setch. 357

Thalli 10-20 cm tall, bright red to blackish red; main axis flattened, 1-3 mm wide, usually compressed; branches of higher orders frequently subcylindrical,