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Department of Botany

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date 25 June 1985
ABSTRACT

A cladistic analysis of the red algal family Dumontiaceae supports the hypothesis that the ancestor of the family was multiaxial, with narrow poorly differentiated axial filaments, small pit connections, narrow rhizoidal filaments, and irregularly branched assimilatory filaments of cylindrical, uninucleate cells. Secondary pit connections and a cuticle were probably lacking. The terete or slightly flattened, subtidal, ephemeral gametophyte may have alternated with a crustose tetrasporophyte with small, lateral, basally attached cruciate tetrasporangia. The long, straight carpogonial branches of slightly differentiated cells terminated in a carpogonium with a long, straight trichogyne. Spermatangia occurred in double whorls around spermatangial mother cells. Following fertilization, the carpogonium divided transversely, and the connecting filaments that developed after fusion to cells of the carpogonial branch were proximally septate but distally nonseptate. The auxiliary cell occurred proximally on a filament slightly differentiated from assimilatory filaments. The connecting filament divided adjacent to an auxiliary cell, and the distal segment continued on to contact other auxiliary cells. The proximal segment, after fusing with the auxiliary cell, cut off 2-5 gonimoblast initials that produced a compact cystocarp of many, small carposporangia. Enlargement of pit connections in the auxiliary cell branch did not exceed 5 μm, and fusions between cells of the auxiliary cell branch or between cells of the gonimoblast were lacking. Spores germinated in a diprotocellular pattern.
The hypothesized ancestral condition in the Dumontiaceae supports the origin of the family from a species in the Helminthocladiaceae sensu lato. No evidence was found that any member of the Dumontiaceae is either a direct ancestor or descendant of any other families of the Cryptonemiales or Gigartinales with the possible exception of the Peyssonneliaceae, Polyidaeaceae, and Rhizophyllidaceae.

As a result of the cladistic analysis, the tribes Farlowieae and Dumontieae are recognized as distinct lineages in the Dumontiaceae, and the genera Dudresnaya and Neodilsea are recognized to be paraphyletic. In addition, the following taxonomic changes were made: The genera Acrosymphyton and Neoabbottiiella were removed from the Dumontiaceae. Farlowia irregularis was recognized to represent a distinct genus. Neodilsea integra was reinstated in Dilsea, and N. integra var. longissima was raised to specific rank. The discovery of older specific epithets for Neodilsea americana and Weeksia fryeana necessitated new species combinations for these taxa. A new genus and species was described from Alaska. The genus Thuretellopsis was synonymized with Dudresnaya and the following synonymies were suggested: Thuretellopsis japonica with Dudresnaya minima, Farlowia compressa with F. mollis, Pikea robusta with P. californica, Weeksia digitata with W. reticulata and possibly both of these species with the species formerly known as Weeksia fryeana.
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CHAPTER I. INTRODUCTION

The Dumontiaceae currently consists of 50 species in 17 genera (Table I). Previously described species which are currently considered synonyms of recognized family members are discussed in the body of the thesis.

The family name Dumontiaceae has been attributed to two authors—Bory (Silva 1980:82) and Schmitz (Kylin 1956:142). Bory (1828:197) characterized the "Famille des Dumontiées, Dumontiae" as, roughly translated, not at all distinguished by the stem in its organization, consisting frequently of simple tubes, more or less compound, with young individuals produced by the germination of spores being taken as branches, and most individuals the color of other marine Florideae, be it purple or green. Bory attributed four species in three genera to this family, Dumontia fastigiata (Bory) Bory [=Nothogenia fastigiata (Bory) Parkinson], Asperococcus lessonii Bory [=Adenocystis utricularis (Bory) Skotts.], Asperococcus durvillaei Bory [=Utriculidium durvillaei (Bory) Skotts.], and Solenia compressa (L.) Bory [=Enteromorpha compressa (L.) Greville]. These species were collected, probably in New Zealand, by the naturalists on La Coquille.

Although Bory did not specifically mention Dumontia incrassata (Mueller) Lamouroux, the type of the genus and hence the family, he did not specifically exclude it. Therefore the International Code of Botanical Nomenclature considers it a

---

\[1\] Silva (1980:79) has discussed the use of Florideae as a subclass name (Schmitz 1892:16, nom. descript.). Since Kylin, most authors have preferred the orthographically correct name Florideophycidae. I have used whichever name the authors themselves employed.
legitimate, validly published family name; however, had Bory not included the Latin family name Dumontiae, which Schmitz (1889:453) corrected to Dumontiaceae, the family name would not have been validly published (Nicolson, pers. comm., 27 June 1983).

Different nineteenth century phycologists adopted various schemes that bear little resemblance to our currently accepted classification of the Rhodophyceae in general and the Dumontiaceae in particular. For example, J. Agardh (1851:233) included Constantinea in the Tribe Kallymenieae of the Order Gigartineae. Dumontia, ?Halisaccion [sic], Catenella, and Rhabdonia, were placed in the Tribe Dumontieae in the Order Dumontieae (1852:348). Although his suprafamilial classification varied from the one now generally followed, by 1876 J. Agardh had brought Cryptosiphonia, Pikea, ?Dasyphloea (as Nizzophloea), Dumontia, ?Halosaccion, Farlowia, and Dilsea (as Sarcophyllum) together into a single taxon, which he identified as "Ordo VI. Dumontiaceae" in "Series III. Nematospermeae, Subseries I." J. Agardh classified Dudresnaya (including D. purpurifera, now Acrosymphyton purpuriferum) in "Ordo V. Dudresnayaeae," but he maintained Constantinea together with Kallymenia in the Tribe Kallymenieae, Order Gigartineae.

Schmitz (1883, see Dallas 1884 for English translation), in his epoch-making treatise on post-fertilization development in the Florideae, included comparative observations on three species in the Dumontiaceae, Dudresnaya purpurifera, D. coccinea, and Dumontia filiformis. He described in some detail the stages from the formation of connecting filaments by the
fertilized carpogonium in conjunction with neighboring cells (at least in *D. purpuriferum*) to the fusion of the segmented connecting filament with a remote auxiliary cell and the initiation of sporangia from the remnant of the connecting filament attached to the auxiliary cell.

Subsequently, Schmitz (1889) proposed a new classification of the genera in the Florideae. Although other families experienced significant shifts, the Dumontiaceae remained unaltered from J. Agardh's classification except for the inclusion of *Dudresnaya* and *Constantinea* in the family and the removal of *Halosaccion*.

Schmitz (1889) included the Dumontiaceae in the Cryptoneminae, later changed to the Cryptonemiales (Schmitz 1892, non vidi) after the Gloiosiphoniaceae and Grateloupiaceae¹ (=Cryptonemiaceae/Halymeniaceae; see Silva 1980:82, 84) and before the Nemastomataceae (=Gymnophloeaceae, now in the Gigartinales), Rhizophyllidaceae (ascribed by Wiseman 1975, to the Gigartinales), Squamariaceae (=Peyssonneliaceae), and Corallinaceae (soon to be placed in its own order). He placed the Cryptonemiales at the end of the Florideae, after the Rhodymeniales. In his introduction, he stated that the linear arrangement of the families provided only a rough approximation of the many-faceted resemblances and relationships of these taxa.

Schmitz and Hauptfleisch (1897:515) observed the same order of families. In their narrative account of the Dumontiaceae,

¹Family names follow those of the original authors. Currently accepted or proposed-for-conservation names are indicated in parentheses after the first use of a name only.
they characterized the family by the many-celled, separate carpogonial and auxiliary cell branches scattered in large numbers through the thallus and by details of post-fertilization development already described above. To the eight genera already included in the family, they added *Andersoniella* Schmitz (=*Leptocladia* J. Ag. 1892). *Erythrophyllum* J. Ag., now considered a species of Kallymeniaceae, was included under "Gattung unsicherer Stellung."

Oltmanns (1904) moved the Cryptonemiales from its position as the last order in Schmitz's list to a position between the Nemaliales and Gigartinales.

Beginning in 1923, Kylin began publishing a series of detailed studies of reproductive structures and post-fertilization development in species of red algae (prior to this time each of his papers encompassed only a single species). He adopted Schmitz's embryological basis for classifying the Florideae and stressed as major characters carpogonial branch structure, auxiliary cell position, sporogenous filament behavior, and gonimoblast development. Kylin (1923:133) concluded that the Cryptonemiales represented a lower developmental line than the other three major diplobiontic orders because it lacked procarps.

Sjöstedt (1926), who also studied reproductive structures of a number of higher Florideae, provided another critique of their classification. He concurred with Oltmanns and Kylin that the Cryptonemiales represented the most primitive and least differentiated group among the orders under consideration. He believed that the Dumontiaceae and Gloiosiphoniaceae represented
parallel primitive groups in the Cryptonemiales and that from the Dumontiaceae were derived, in separate parallel lines, "all the other hitherto embryologically better known diplobiontic Florideae," i.e., the Rhizophyllidaceae, Squamariaceae, and Grateloupiaaceae in the Cryptonemiales, the Nemastomataceae, Rhabdoniaceae (＝Caulacanthaceae), and Rhodophyllidaceae (＝Cystocloniaceae) in the Nemastomales, the Rhodymeniales, the Sphaerococcales (including Plocamium and Sphaerococcus) and the Gigartinales (including only the Gigartinaceae in Sjöstedt's system); only the Gelidiales, the Ceramiaceae, and Gracilaria were placed elsewhere.

Kylin (1928, 1930), like Sjöstedt, viewed the Cryptonemiales in a narrow as well as a broad sense. The Cryptonemiales sensu lato encompassed not just the Cryptonemiales but also the Nemastomales (an order proposed but not validly published by Kylin in 1925 to contain the Nemastomataceae, Rhabdoniaceae, and Rhodophyllidaceae), the Rhodymeniales, and the Gigartinales. Kylin considered the Cruoriaceae to be the outgroup of this "superorder" and sequentially drew off the Nemastomales, the Rhodymeniales, the Cryptonemiales, and the Gigartinales. Within the Cryptonemiales, he showed two lines. In one line, in which the sporogenous filaments first fuse with special nutritive cells in the carpogonial branch and only then grow toward the auxiliary cell, the Dumontiaceae represented the sister group of the Rhizophyllidaceae, Squamariaceae, and Corallinaceae. He distinguished the Dumontiaceae from these other families by the fact that the carpogonial and auxiliary cell branches are
scattered throughout the thallus rather than occurring in nemathecia. In the other line, in which no cells of the carpogonial branch are contacted before the generative auxiliary cell, he included the Grateloupiaceae, Gloiosiphoniaceae, Endocladiaceae, Gigartinaceae, and Kallymeniaceae. Kylin (1932) dropped this scheme in favor of entirely separate schemes for the Cryptonemiales and Gigartinales (the latter now including the families of the Nemastomales plus the Gigartinaceae). The 1932 scheme of the Cryptonemiales was essentially that of the 1930 publication with the addition of the Tichocarpaceae and the Kallymeniaceae.

In 1930, Kylin singled out the properties of the auxiliary cell as representing the most important character in florideaen systematics, and in 1932, he outlined the characteristics of the auxiliary cell that distinguish each order of the Florideophycidae. In particular, he distinguished the Cryptonemiales from the Gigartinales on the basis of the accessory nature of the branch bearing the auxiliary cell. (The auxiliary cell is still used as a major criterion for ordinal classification.)

Fritsch (1945:656) questioned the importance of this distinction between the Cryptonemiales and the Gigartinales. He considered a definition of the Gigartinales based on an intercalary, vegetative auxiliary cell and that of the Cryptonemiales on an auxiliary cell located in a special accessory branch to be a rather "trivial feature upon which to base a major taxonomic subdivision." Nevertheless, he felt such a delineation served a useful purpose until clearer concepts of
affinities could be obtained. This distinction was also questioned by Drew (1957), who pointed out that this character does not hold in all cases. Searles (1968:1) wrote, "It is not yet clear, however, whether these orders represent natural assemblages or only convenient groupings."

Kylin's emphasis on characteristics of the auxiliary cell in florideophycidean classification influenced at least a generation of phycologists to concentrate on red algal reproductive morphology in order to refine the Kylinian system.

Papenfuss (1951) tried to clarify the distinctions between the different types of auxiliary cells. He believed the Dumontiaceae to have two kinds of auxiliary cells, nutritive and generative, and he described the Weeksiaceae (a segregate of the Dumontiaceae proposed by Abbott in a then unpublished thesis) as having nutritive auxiliary cells which have become generative auxiliary cells. (Papenfuss apparently did not realize that the gonimoblast of members of the Dumontiaceae develops not from the auxiliary cell itself but from the connecting filament following establishment of a connection with an auxiliary cell, thereby giving the Dumontiaceae two kinds of nutritive auxiliary cells.)

Drew (1954:57) distinguished four major types of carposporophytes found in the Florideophycidae: (a) carposporangia-producing gonimoblast not fusing with other cells of the gametophyte but arising directly from the carpogonium, (b) carposporangia-producing gonimoblast fusing with other cells of the gametophyte but not transferring the diploid nucleus to another cell, (c) primary gonimoblast transferring the diploid nucleus to specified cells at some distance from the carpogonium
from which arise carposporangia-producing gonimoblast, and (d) carposporangia-producing gonimoblast arising from a specified cell of the gametophyte relatively near the carpogonium and to which the diploid nucleus is transferred. Drew (p. 60) included *Acrosymphyton* in Group B ("Finally, in *Acrosymphyton*, the spore-producing laterals develop from the gonimoblast itself as in the other cases but right at the point of fusion with the cell of the gametophyte") and the rest of the Dumontiaceae in Group C ("This type, as represented by *Dudresnaya coccinea*, has been well known since the time of Oltmanns' researches...After each fusion between a gonimoblast and and auxiliary cell, a nucleus passes from the former into the latter, from each of which one or more compact spore-forming branch systems then develop...").

Drew made a number of generalizations based on what she perceived as trends in carposporophyte development. Firstly, she stated that the transfer of a diploid nucleus to a specified cell of the female gametophyte "has arisen from the condition in which specified cells of the gametophyte fuse with the carpogonium or the gonimoblast without any accompanying transfer of a nucleus." In support of this trend, she cited the species pairs *Bertholdia (=Schmitzia) - Calosiphonia* and *Acrosymphyton - Dudresnaya* in which "in the first mentioned pair the spore-producing branch arises from the primary gonimoblast, but in the second, it arises from the cell of the gametophyte, after entry of a derivative of the fusion nucleus contributed by the gonimoblast after fusion." Secondly, she stated that the specified cells of the gametophyte, with which the gonimoblast fuses, are homologous in all of these genera. [Drew, like
Papenfuss, erroneously believed most Dumontiaceae to have generative auxiliary cells.

In *Die Gattungen der Rhodophyceen*, Kylin (1956:453) distinguished the Dumontiaceae, as in his earlier papers, by the diffuse distribution of carpogonial and auxiliary cell branches in the female thallus and by the fertilized carpogonium first contacting one of the middle cells of the carpogonial branch, and this cell then forming connecting filaments which seek out auxiliary cells. Kylin also stated that one of the middle cells of the auxiliary cell branch serves as the auxiliary cell, and that after the auxiliary cell has received a diploid nucleus, it develops several short branched cell-filaments each cell of which produces a carpospore. This characterization differs to some extent from that of Schmitz, who recognized that the connecting filaments issue from the fertilized carpogonium, usually after fusion with several cells of the carpogonial branch (Schmitz and Hauptfleisch 1897:516) and that the gonimoblast filaments arise from the remnant of the connecting filament attached to an auxiliary cell (Schmitz 1883:231; Schmitz & Hauptfleisch 1897:516). In fact, Kylin is somewhat ambiguous. All subsequent phycologists appear to have interpreted "diese Zelle dann Verbindungsfäden bildet" as referring to the immediately previous "einer der mittleren Zellen des Karpogonastes" rather than to the subject of that clause, "das befruchtete Karpogon." Based on Kylin's earlier writings and particularly his figures, I believe Kylin meant "diese Zelle" to refer to "das befruchtete Karpogon." I cannot explain his interpretation of the connecting filament actually
transferring a diploid nucleus to an auxiliary cell rather than retaining it and producing the gonimoblast filaments itself while in cytoplasmic continuity with the auxiliary cell as all his illustrations show.

During the past 30 years or so, many references to the Dumontiaceae have come from phycologists studying other taxa in the Cryptonemiales or Gigartinales. Because these papers, like the earlier ones by Papenfuss and Drew, have contributed considerably to our present understanding as well as misunderstanding of the family, they are briefly summarized in the following paragraphs.

Norris (1957:306) argued that the Dumontiaceae is the most primitive family within the Cryptonemiales. He believed that all families in the Cryptonemiales, except the Dumontiaceae, "probably originated from an ancestral stock that was polycarpogonial and that produced the auxiliary cell on a branch separate from the carpogonial branch apparatus." He hypothesized that the Dumontiaceae was "possibly linked with the polycarpogonial line by such advanced forms as Cryptosiphonia, in which several subsidiary branches issue from the lowermost cells of the carpogonial- and auxiliary-cell branches."

Norris further argued for the primitive condition of the Dumontiaceae by stating, "Generally, those who have dealt with the phylogeny of the Florideophycidae agree that the most primitive members of the Cryptonemiales are those in which the carpogonia and auxiliary cells occur on branch systems that are removed from each other and consist of many cells (up to fifteen in certain Dumontiaceae, fig. 24, A). Evolution in the
Cryptonemiales seems to have resulted in a reduction in the number of cells in the carpogonial branch and, more particularly, in the auxiliary cell branch." Norris challenged Kylin's (1932) division of the Cryptonemiales into two lines on the basis of the presence or absence of procarps as, it seemed to him, procarps had arisen more than once in the Cryptonemiales.

Norris did not discuss the homology of the carpogonial and auxiliary cell branches outside the context of the Kallymeniaceae, but he believed his observations supported the conjecture "that the auxiliary-cell systems of some species of red algae are homologous to the carpogonial-branch apparatus."

Balakrishnan (1960:93) followed Norris in considering the Dumontiaceae to have the least advanced reproductive characters of any family in the Cryptonemiales.

Searles (1968:79) discussed the distinction between the purportedly accessory versus vegetative nature of auxiliary cells in the Cryptonemiales and Gigartinales, respectively. He wrote that he did not question the common origin of the auxiliary cell filaments in the Dumontiaceae, but he felt there was no basis for assuming their homology with those in many of the other families currently placed in the Cryptonemiales.

Chiang (1970:76) concurred with Norris (1957) and Balakrishnan (1960) that the families of the Cryptonemiales, except the Dumontiaceae, probably evolved from a polycarpogonial, nonprocarpic ancestor.

Dixon (1973:160) stated that the auxiliary cells of Dudresnaya and Dumontia "develop in relation to special
accessory filaments which have been shown to be equivalent to carpogonial branches." He also argued that the difference between the disposition of the auxiliary cells in Dumontia (in the Cryptonemiales) and Platoma (in the Gigartinales) appears to be trivial.

Kraft (1973:880) observed two modes of increasing complexity in post-fertilization development in members of the Cryptonemiales and Gigartinales: the tendency to go from nonprocarpic to procarpic systems and the progression from morphologically simple to complex carposporophytes. At the less derived extreme, Kraft cited families such as the Dumontiaceae, Cryptonemiaceae, Nemastomataceae, and Calosiphoniaceae, which not only produce long connecting filaments between carpogonial branches and auxiliary cells but also possess carposporophytes consisting of simply "a 'root' (auxiliary cell), a primary gonimoblast cell, and variously lobed clusters made up completely of carposporangia." At the more highly evolved extreme occur the procarpic Kallymeniaceae, Mychodeaceae, Phyllophoraceae, and Gigartinaceae in which the carposporophytes consist of "elaborate networks of intermixed sterile and sporogenous cells." However, Kraft noted that these two modes have developed independently in other lines: there are numerous procarpic families with relatively simple carposporophytes (e.g., Tichocarpaceae, Plocamiaceae, Sphaerococcaceae, etc.) and several families with nonprocarpic members with relatively complex carposporophytes (Kallymeniaceae, Cubiculosporaceae).

Kraft (1975:289), in discussing his newly created genus Adelophyton, pointed out the similarity between auxiliary cell
branches in this genus and those of members of the Cryptonemiales, although he called those of the former adventitious and those of the latter accessory. He speculated that the divergence of lower cryptonemialean algae, with their accessory auxiliary cell branches, might have taken place from simpler gigartinalean types through the modification of rhizoidal filaments, similar to those he observed in Adelophyton. He placed Adelophyton in the Nemastomataceae because of the characteristics shared with Nemastoma such as conspicuous gland cells, lack of a known isomorphic tetrasporophyte generation, initiation and development of gonimoblasts from the connecting filament near its junction with the auxiliary cell and lack of a distinct ostiole.

Lebednik (1977:395) proposed to emend the Cryptonemiales to include species "in which the auxiliary cell is located in a receptive carpogonial branch system or in a reduced carpogonial branch system [italics his]," in contrast to the Gigartinales in which the auxiliary cell is an "unmodified or specialized vegetative cell." In order to include the Dumontiaceae within this revised circumscription of the order, he argued (p. 398) that "the auxiliary and carpogonial 'branches' of the Dumontiaceae are homologous to a fertile axis (composed of several branch systems) in which cells of the first or second order of branching are homologous to carpogonial supporting cells." He felt that his argument was supported by Sjöstedt's statement (1926:17) that the ampulla of Cryptonemia is "homologous with and fully corresponds to the auxiliary branch and carpogonial branch respectively in, say, a Thuretellopsis or
a *Dudresnaya*." However, near the end of the same paragraph, Lebednik concluded, "Assignment of the Dumontiaceae and Weeksiaceae to the fertile axial line is made with some reservation."

Two families have been segregated from the Dumontiaceae in the last twenty years, but neither has received general recognition. Bert (1965:2704) established the Dilseaceae on the basis of the multiaxial habit of *Dilsea* and *Neodilsea* as compared to the ostensibly uniaxial character of the type and most other species in the family. Abbott (1968:181) trivialized the basis on which Bert separated the genera of the Dumontiaceae into two families and (p. 188) proposed a second segregate family, the Weeksiaceae, on the basis of the supposedly nonfunctional auxiliary cell and therefore procarpic nature of *Weeksia*, *Leptocladia*, and *Constantinea*. Bold & Wynne (1978:501) argued against the separation of the Weeksiaceae from an otherwise unified family by invoking the analogous argument that other families, such as the Kallymeniaceae, also have both nonprocarpic and procarpic genera which show obvious means of derivation. Kraft (1981:22) appeared to recognize the Weeksiaceae but not the Dilseaceae although he stated, of the former, that Norris (1957) had previously disputed as family criteria the features on which this family was established. Only Perestenko (1975:1686) appeared to accept the Dilseaceae by placing her newly described genus *Abbotia* (now *Neoabbottiiella*) in this family. At the same time she suggested that the family be broken into three groups, the *Dumontia* group, which she felt should include only *Dumontia*, *Hyalosiphonia*, and evidently
Dudresnaya and Dasyphloea, the Dilsea group (composed of Dilsea and Neodilsea), and the Pikea group (including Pikea, Acrosymphyton, Thuretellopsis, and Farlowia?). She noted a kinship tie of the latter group to the Gloiosiphoniaceae and concluded (in translation), "Whether it is a member of this family or should be set apart in an independent family can only be decided by monographic research."

Up to the present, studies of the Dumontiaceae have been studies of individual species, often with comparative comments on other species in the same genus or rarely on other genera in the family. Included in these studies is Abbott's (1968) monograph on the family. There have been no attempts to study the family from an evolutionary perspective to hypothesize phylogenetic relationships among the member taxa. That is what this study attempts to do.
CHAPTER II. MATERIALS, METHODS AND TERMINOLOGY

Representative specimens of each taxon examined are listed in the Appendix. Herbarium abbreviations are those of Holmgren et al. (1981). Loans or donations by the following people and/or institutions are gratefully acknowledged: Dr. C. O. Acleto (USM), Ms. N. I. Calvin and Mr. R. J. Ellis (Sitka, Alaska), Dr. M. Chihara (Tsukuba Univ.), Dr. M. Dube (Western Washington State Univ.), Dr. P. W. Gabrielson (Univ. of British Columbia), Dr. P. Gayral (CN), Dr. M. D. Guiry (University College, Galway), Dr. M. W. Hawkes (Univ. of British Columbia), Dr. M. H. Hommersand (Univ. of North Carolina, Chapel Hill), Mr. R. G. Hooper (NFLD), Dr. M. Kurogi (SAPS), Dr. Christine Maggs (The Queen's University of Belfast), Dr. T. Masaki (Hokkaido Univ., Hakodate), Dr. M. Neushul (UCSB), Dr. J. N. Norris (US), Dr. L. P. Perestenko (LE), Dr. R. B. Searles (Duke University), Dr. P. C. Silva (UC), Dr. R. T. Wilce (MASS), Dr. M. J. Wynne (MICH), AHFH, BISH, FH, LD, NY, and TNS. ABL refers to the algal collection at the National Marine Fisheries Service, Auke Bay Laboratory, Auke Bay, Alaska, PWG to Paul Gabrielson's personal collection, and SCL to my personal collection.

Both dried herbarium specimens and formalin preserved material were used. Dried material was rehydrated in 5% formalin in seawater (sometimes a small amount of powdered detergent was added). Rehydrated or liquid preserved material was stained either with aniline blue (usually a 20:1:1 solution of 30% Karo syrup: 1% aqueous aniline blue: 1 N HCl) or with Wittmann's (1965) iron haematoxylin following the procedure of Hommersand (unpublished): Briefly, specimens are placed first
in about 3:1 5% formalin in seawater: 45% acetic acid for 45 min, then in 1 N KOH for 45 min, back into 3:1 formalin:acetic acid for 15-20 min, then in the iron-haematoxylin solution for 20 min. The solution is then heated for about 20 min at 50-55 °C. The haematoxylin is discarded and the specimens are destained with 45% acetic acid and then mounted in 30% Karo. Mounting was occasionally done in Piccolyte, following dehydration with alcohol and replacement of alcohol with xylene.

Specimens of Gibsmithia, Kraftia, Dudresnaya, and Thuretellopsis were examined without further treatment. Specimens of other species were sectioned, preferrably longitudinally and usually by hand, but occasionally transversely and sometimes by using a freezing microtome.

Fast Green (0.1%) and Acid Fuchsin (1.0%), both in distilled water, were used to stain protein, and potassium iodide, to stain floridean starch.

Microscope slides were examined with an Olympus Model E microscope. Line drawings were made with the aid of a camera lucida. Micrographs were taken with a Nikon Microflex Model AFM automatic photomicrographic attachment. Habit photographs were made with a Canon FT-QL 55 mm macro lens or a Nikon FM with a 55 mm Nikkormat microlens on a Bencher copy stand.

In order to obtain an estimate of evolutionary relationships among the species and genera of the Dumontiaceae, a phylogenetic systematic approach (sensu Hennig 1979) was used. According to this approach, taxa are grouped on the basis of their shared derived character traits (synapomorphies). Two methodological considerations therefore become necessary: (1)
How are synapomorphies recognized? and (2) By what algorithm are the taxa grouped using these synapomorphies?

As Wiley (1980:199) has pointed out, character states shared by all taxa under consideration or those possessed by only a single taxon provide no relevant information on the relationships of the taxa. For characters to be useful, they must display at least two different character states in the group being investigated, and these character states must be homologous. Watrous and Wheeler have identified outgroup comparison as perhaps the strongest criterion in determining character polarity (Wheeler 1981:300). The strength of outgroup comparison lies in the fact that it does not make ad hoc assumptions about the direction or pattern of evolution of particular characters; it is based only on the assumptions that evolution has occurred and that the characters exhibited by species are a reflection of evolution.

Wiley (1980:200) has defined the outgroup criterion: "Given a pair of homologous characters [character states] found within a monophyletic group, that character [character state] found in the close relatives of the monophyletic group is plesiomorphic [i.e., primitive] while that found only within the group is apomorphic." Since one is not always sure of the monophyletic nature of the group under study and/or the relationship of the group to other groups, the use of more than one outgroup is recommended. However, a monophyletic group need not correspond to a taxonomically recognized group (Watrous and Wheeler 1981:6). It is therefore possible to find functional outgroups to smaller but monophyletic units of the study group from within...
the study group. This is necessary particularly when a multistate character occurs only within a part of the study group, being absent from the rest of the study group and from the outgroups.

Because misinterpretations of character state polarities and incorrect assessments of ingroup-outgroup relationships are revealed in later stages of the analysis by conflicts with other characters, the existing, albeit imperfect classification system is usually taken as the starting point of an analysis. [Another rationale supporting this initial step is the acknowledgment that some progress has been made in systematics in the last two centuries (Eldredge 1979:171, quoted in Watrous and Wheeler 1981).]

In this study, both functional and taxonomic outgroups were used. Because Sjöstedt, Kylin, and subsequent authors have considered the Dumontiaceae to be the most primitive family of the Cryptonemiales and the Cryptonemiales, the most primitive order of the higher Florideophycidae (i.e., those Florideophycidae possessing auxiliary cells), I sought an outgroup for the Dumontiaceae in the next most primitive order, the Nemáliales sensu lato. The Helminthocladiaceae sensu lato was selected as the taxonomic outgroup. The Dumontiaceae shares at least one synapomorphy with some members of the Helminthocladiaceae sensu lato. The relatively long carpogonial branches, of 5 or usually more cells, distinguish the members of the Dumontiaceae from most other species of higher Florideophycidae (long branches have also been recorded in Acrosymphyton and Polyides); they have also been observed in
certain Helminthocladiaceae, including Dotyophycus, Helminthocladia, Helminthora, Liagora, Nemalion, and Trichogloea. Although the apomorphic nature of other traits shared by the Dumontiaceae and the Helminthocladiaceae is arguable, the more generalized species of the Dumontiaceae resemble members of the Helminthocladiaceae in other ways—undifferentiated axiality, long, terminal trichogynes, carpogonial division following fertilization, involucral development, etc. These characters are examined in more detail in the DISCUSSION (p. 299). Functional outgroups included Gibsmithia hawaiensis, Gibsmithia sp. nov. from the Great Barrier Reef, and Kraftia dichotoma—all species that are considered to be primitive in the Dumontiaceae because of similarities to the taxonomic outgroup. These species also stand apart from the rest of the Dumontiaceae in details of both vegetative and reproductive anatomy. Hyalosiphonia caespitosa and "Farlowia" irregularis were used as the functional outgroups for the species of Dilsea and Neodilsea.

The states of each character were arranged in a transformation series (sensu Hennig 1979:89). For each character, the plesiomorphic state was coded 0 and the apomorphic state 1. If more than a single apomorphic state was present, these derived states were coded (1, 2, 3, etc.) according to what was perceived to be a progressive change in character states from the plesiomorphic condition. An apomorphic state restricted to a single species (i.e., an autapomorphy) was usually not coded as derived; such autapomorphies provide no useful information in the cladistic analysis since they do not identify groups of taxa.
but merely a single taxon.

The data matrix resulting from the coding of characters for all the taxa was analyzed using the Wagner algorithm of phylogenetic inference (Farris 1970) as implemented by PHYSYS, a computer program developed by J. S. Farris, State University of New York, Stony Brook. In essence, the Farris program arranges the taxa at the termini of a rooted, branching diagram on the basis of shared, derived character states (states determined in this study by outgroup comparison), minimizing the number of character state transitions but still accounting for all the data. The Farris algorithm was the one of choice because it assumes that the best estimate of phylogenetic relationships among the taxa of a monophyletic group requires the fewest possible character transformations (Wiley 1981:179) and hence the fewest possible ad hoc assumptions about the way evolution has proceeded.

The red algae are notorious for the web of terminology that surrounds their vegetative and reproductive features. Although the use of specialized terms is undoubtedly necessary to define clearly the attributes of the various species, their use has also served to obscure similarities. Below I define some of the terms used in this study in the context of the Dumontiaceae. Use of these terms to describe the features of the Dumontiaceae should not be taken as evidence that the structures to which they refer are homologous to similar structures described by the same labels in other families or orders. Terms are arranged alphabetically.
Auxiliary cell branch is a branched or unbranched filament that bears an auxiliary cell somewhere along its length. At least some if not all (in most species) cells of the branch are differentiated in size and shape from vegetative cells not associated with reproduction.

Capping cell is a small terminal, nondividing cell that is usually distinctly smaller than subtending cells.

Carpogonial branch is a branched or unbranched filament that terminates in a carpogonium. In most species, all cells of the branch are differentiated in size and shape from vegetative cells not associated with reproduction.

Carpogonial derivative cell refers to one or two (rarely more) products of an enlarged fertilized carpogonium that has divided. Usually a carpogonial derivative cell fuses with a cell of the carpogonial branch, thereby becoming a carpogonial fusion cell. It produces the connecting filaments.

Cells 1, 2, 3, 4... refer to cells of the carpogonial or auxiliary cell branch counting from the distal end, which is the less variable end in most species. For the carpogonial branch, the carpogonium is therefore cell 1 and cells successively more distal from the carpogonium, 2, 3, 4...

Conjunctor cell refers to a small cell that is cut off one cell and fuses with a nearby cell, thereby creating a secondary pit connection between the two larger cells.

Cystocarp refers to the cluster of carposporangia that develops from the gonimoblast filaments. No associated gametophytic
tissue is included in this usage.

Gonimoblast initiator cell is the piece of connecting filament that is cut off from the onward growing connecting filament adjacent to an auxiliary cell and that, after fusing with the auxiliary cell, produces the gonimoblast initials.

Major and minor whorl branches are terms used to refer to the branches in the plane and perpendicular to the plane of a flattened thallus, respectively.

Periaxial cell is a cell cut off an axial cell; it is the basal cell of a whorl branch.

Pit connection (pit plug to some authors) is used to denote the actual proteinaceous plug between two connected cells.

Reproductive filament refers to either a carpogonial branch or an auxiliary cell branch. During early stages of filament differentiation, the identity of the reproductive filament, whether carpogonial or auxiliary, cannot always be determined, and hence the need for the more general term.

Rhizoids (also rhizoidal filaments) are nonpigmented, often unbranched filaments of elongate cells that grow downward through the thallus, often cloaking an axial cell; they are produced after the structural plan of the thallus has been laid down.

Spermatangial mother cell is the cell that produces spermatangia.

Unisexual and bisexual refer to whether a thallus bears reproductive structures of a single sex (unisexual) or both sexes (bisexual).

Whorl branch refers to a determinate lateral branch (called
cortical fascicle by Robins and Kraft 1985) which clothes an axis; where axes are indistinct, the term assimilatory filament is an equivalent.

Some specialized terms from phylogenetic systematics are also used:

Apomorphy refers to the derived condition of a character; a synapomorphy is a shared, uniquely derived character state. Character states are the alternate forms of expression of a particular feature (character) of an individual; the feature can be morphological, physiological, biochemical, biogeographic, genetic, or whatever, and it is assumed to be homologous in the taxa being compared. A clade is a natural taxonomic grouping derived from uniting taxa on the basis of synapomorphies. Consistency index for a cladogram is equal to the number of transformations in a character matrix divided by the number of transformations in a tree derived from that matrix times 100; the closer the value is to 100, the better the fit between the character matrix and the tree. For an individual character, the consistency index equals the number of character states for that character divided by the number of character state transformations in the tree times 100.

A grade is an artificial taxonomic grouping derived from uniting taxa on the basis of symplesiomorphies. Homology refers to a uniquely derived character state (in a cladistic analysis); it represents the inheritance of a
particular trait unmodified or minimally modified from an ancestor that also possessed that trait.

Homoplasy refers to a character state that is not uniquely derived (in a cladistic analysis); such a character state can represent a parallelism (independent derivation of the same character state) or a reversal (change in a character state from an apomorphic to an earlier, plesiomorphic condition). Homoplasious characters states are nonhomologous.

Monophyly refers to a group of taxa which includes the ancestor and all descendants.

Paraphyly refers to a group of taxa which does not include all descendants of a common ancestor.

Plesiomorphic refers to the primitive condition of a character; a symplesiomorphy is a shared, primitive character state.

Polyphyly refers to a group of taxa whose most recent common ancestor is not a member of the group.

Below I consider all the species of the Dumontiaceae which have been described to date. The genera are ordered in a manner that approximates their placement on the phylogenetic cladogram presented at the end of the thesis. Within each genus, the species are discussed in the order of their dates of publication. For each species I first provide an historical introduction, which includes pertinent observations of that species by earlier authors, and then follow with descriptions of the habitat, distribution, phenology, and vegetative and reproductive morphology of the species. Comments not included in Chapter 4 (p. 296) are appended to the appropriate species.
After considering individually all the species of the Dumontiaceae, I provide a phylogenetic analysis of the family in Chapter 4 based on the characters discussed in Chapter 3.
CHAPTER III. SYSTEMATIC SURVEY

Gibsmithia hawaiiensis Doty 1963:458

INTRODUCTION

The genus Gibsmithia stands apart as the most distinct member of the Dumontiaceae. It was originally described by Doty (1963:458) and named for Gilbert M. Smith. Currently, it contains but one species from Hawaii and possibly New Caledonia (Karam-Kerimian 1976:21), but may contain additional species from Japan (Itono 1971:94) and Australia (P. W. Gabrielson, pers. comm.).

Gibsmithia is distinguished by its perennial "woody" stem and successive crops of distal club-shaped, mucilaginous tufts of branches. Doty described seirosporangia and clusters of cruciately divided, pedicillate tetrasporangia. Carpogonial branches and auxiliary cell branches occur separately as in other Dumontiaceae, but cell 3 is distinctly smaller than the other hypogynous cells. The carpogonium is relatively small and does not stain darkly with aniline blue; it is eccentrically placed at the apex of the carpogonial branch and appears to disintegrate if not fertilized. The auxiliary cell is one of several enlarged cells near the base of a distally undifferentiated branch. Doty described cystocarps as occurring in low, wartlike sori reminiscent of the Peyssonneliaceae.

Doty's material lacked stages of immediate post-fertilization development, but Karam-Kerimian (1976) observed such stages in material from New Caledonia. He described the typical Dumontiaceae pattern of an extension of the fertilized carpogonium dividing, fusing with cells 4 and 5 of the
carpogonial branch, and producing a number of connecting filaments which then contact remote auxiliary cells and from which gonimoblast filaments arise and other connecting filaments continue on. He also described and illustrated male reproductive organs on his bisexual specimens.

**OBSERVATIONS**

Assimilatory filaments that compose the club-shaped mucilaginous tufts (no main axis is evident) are irregularly branched, each cell producing usually only a single, pseudodichotomous lateral if it is branched at all. Subsequent growth of the axial cell is predominantly at the distal end so that a lateral becomes progressively displaced toward the middle of the axial cell further from the apex.

Branches terminate in bullet-shaped apical cells 3.5-7 μm in diameter by 5-8 μm long (Fig. 1b). Subapical cells are cylindrical to slightly flabellate (when branched), 3.5-11 μm wide by 7-25 μm long 10 cells from the apex. Axial cells can elongate to at least 650 μm and reach about 20 μm in diameter (including the relatively thick wall). When 2 laterals occur on the same axial cell, they are situated approximately 90° to each other. Periaxial cells are distinctly smaller than adjacent whorl branch cells. As the whorl branch matures, an additional branch is usually produced by the periaxial cell—it can be rhizoidal, assimilatory, or reproductive. A second species of Gibsmithia from the Great Barrier Reef was available for comparative observation. In habit, it is similar to *G. hawaiensis*, but the cells of the assimilatory filaments are
more cylindrical (Fig. 1a). Terminal cells are 3 \( \mu \text{m} \) in diameter by 6.5-18 \( \mu \text{m} \) long and 10 cells distant they are 3.5-5 by 25-30 \( \mu \text{m} \).

As previously described, cell fusions between medullary cells can occur by a short protrusion from one cell fusing with a nearby cell. No conjunctor cell is cut off so no secondary pit connection is formed.

Hairs are generally rare.

Refractive inclusions are uncommon. When present, they are about 5 \( \mu \text{m} \) in diameter.

Carpogonial branches and auxiliary cell branches are borne directly on axial cells or periaxial cells. I have found it impossible to determine whether these reproductive filaments should be considered accessory since the number of periaxial cells varies from none to two. However, in one instance, an axial cell was seen bearing 3 periaxial cells, one of which was a carpogonial branch, suggesting that at least carpogonial branches might be accessory (Fig. 1c).

Carpogonial branches 6-8 (-9) cells in length were seen in the Hawaiian material (Fig. 2a). Cells 2-5 (-6) are refractive. Cell 2 is somewhat cuneate and cells 3-5 are round or squarish in outline. As previously noted and illustrated, cell 3 is distinctly smaller than the other cells of the branch (this has been noted and illustrated by Doty 1963 and Karam-Kerimian 1976). Cell 6 is transitional in size and shape to the undifferentiated, cylindrical proximal cells. Cells 5-8 can bear lateral branches. I was unable to detect nuclei in most cells of the carpogonial branch in the material available. The
carpogonium is attached laterally to the side of cell 2. It is small and does not stain darkly with aniline blue. The long, usually straight trichogyne can project to the side in a manner similar to that illustrated by Littler (1978: Fig. 13) for 
Dudresnaya lubrica. The carpogonial branches of the Great Barrier Reef species are similar to those of G. hawaiiensis except that cells 4 and 5 can be somewhat more elongate (Fig. 1c).

Auxiliary cell branches 8-18 cells in length were observed in the Hawaiian material (Figs. 2a, b). The auxiliary cell was cell 4-6 (-8) from the base of the branch. As noted previously, the branches are borne directly on axial or periaxial cells. They usually take the place of a whorl branch, but occasionally they are borne abaxially on the basal cell (i.e., the periaxial cell) of a whorl branch. An auxiliary cell branch borne abaxially on the basal cell of a carpogonial branch is shown in Fig. 2a. One to five cells, including the auxiliary cell and its immediate neighbors, are highly refractive. The auxiliary cell is initially slightly larger than the other cells of the branch, but at maturity it is usually somewhat smaller than its immediate neighbors. The auxiliary cell and its neighbors are rectangular-quadrate to round (they are more elongate in the Great Barrier Reef material; Fig. 3). The distal cells of the branch resemble the distal cells of an assimilatory filament. The proximal cells of the branch are cylindrical to quadrate. Laterals begin to develop on 2-3 cells one to two cells below the auxiliary cell as the branch matures (Figs. 2a, b). At maturity, these proximal cells bear (3-) 4-5 (-6) lateral
branches that curve around the maturing carposporophyte like involucral filaments (Fig. 3).

Early post-fertilization stages were not seen. These stages have already been described and illustrated by Karam-Kerimian (1976) and referred to in the INTRODUCTION (p. 27). In the cystocarpic material from the Great Barrier Reef, few carpogonial branches were evident, and the distal cells of those present were vacuolate and appeared to be disintegrating. The remains of a single fertilized carpogonial branch were observed in this material, and there appeared to be some connecting filament segmentation upon leaving the branch. No other connecting filaments were observed. The forking of the gonimoblast initiator cell attached to the auxiliary cell suggested both incoming and outgoing connecting filaments, but direct observations are lacking. Pit connections between cells of the auxiliary cell branch can enlarge to 4 μm, as can pit connections between the gonimoblast initials and the gonimoblast initiator cell. No cell fusions were observed. The wall surrounding the differentiated cells of the branch is relatively thick, 3-5 μm (Fig. 3). Carposporangia to 15 μm in diameter were measured, but most are about 10 μm. All cells of the gonimoblast appear capable of maturing into carposporangia although some of the proximal cells were incompletely differentiated in some cystocarps. Mature cystocarps can reach at least 200 μm in diameter (Fig. 3).

One instance of in situ carpospore germination was observed. The pattern is like that of Dudresnaya.

Hawaiian plants are unisexual. Among six specimens
collected 19 Oct. 1969, two were female and two were male. In the Hawaiian plants, as in those observed by Karam-Kerimian (1976), spermatangial mother cells and spermatangia are borne on short, lateral branches up to about 7 cells long (Fig. 2c). More than a single tier of spermatangial mother cells can occur on the proximal cells of the branch.

Tetrasporangia are cruciate in both species. In G. hawaiiensis, they are pedicillate and borne in clusters, the pedicels acting as stalk cells and regenerating additional sporangia after release of early-formed ones (Fig. 1d). Sporângia are 25-30 by 39-39 μm (n=10), including the wall. In the Great Barrier Reef material, tetrasporangia are sessile near the distal end of the bearing cell, 11-15 by 20-25 μm (n=5), including the wall (Fig. 1e).

COMMENTS

Among the recognized species of the Dumontiaceae, Gibsmithia hawaiiensis appears to reflect some of the most primitive conditions in the family. Both the carpogonial branch and the auxiliary cell branch show relatively little differentiation. The thallus itself shows little differentiation between determinate and indeterminate filaments. The mucilaginous habit and sometimes bisexual thalli are other characteristics generally considered to be primitive, as is a tropical Pacific distribution. The same can be said of the Great Barrier Reef Gibsmithia.

Because of their distinctness in the family and because they appear to display many character states assumed to be
primitive in the family (either through the ontogenetic rule or through comparison with species in the Nemaliales), both species of Gibsmithia were used as outgroups in initial cladistic analyses of the entire family.

*Kraftia dichotoma* Shepley et Womersley 1983:209

**INTRODUCTION**

Another distinctive genus attributable to the Dumontiaceae was described by Shepley and Womersley (1983:209) from southern Australia (Port Denison, West Australia, to Western Port, Victoria). *Kraftia dichotoma* is distinguished by its subdichotomous, multiaxial habit, its thick-walled, terminally rounded, reflexed hairs, the distinctly enlarged cells 4 and 5 of the carpogonial branch, and an auxiliary cell branch in which the auxiliary cell is slightly laterally displaced and with all cells below and often some above it bearing short lateral branches. The 1-3 cm high, slightly compressed thalli grow around the lower stems of the seagrass *Amphibolis* in 1-11 m of water. Upright thalli arise by simultaneous elongation of a group of vertical filaments within the crust. Gametophytes are bisexual. Carpospores about 10 μm in diameter germinate in a manner similar to *Dudresnaya*. No tetrasporangia have been observed on cultured crusts. Tetrasporophytes are also unknown from nature. Shepley and Womersley recorded collections from only September to April.

**OBSERVATIONS**

Apical portions of thalli were missing in the material
available for study. Shepley and Womersley (1983:211) described the small apical cells terminating the central, longitudinal medullary filaments as "curved in towards the centre and protected by the rapidly developing cortex from slightly older and more lateral medullary cells...One or occasionally two branch systems of cortical cells arise midway along each cell of the outer medullary filaments." Cells of the filamentous medulla are "laterally connected by frequent secondary pit-connections." A compact cortex is composed of dichotomous filaments of cells 5-8 μm in diameter. Unfortunately, except for a figure of the dichotomous cortical filaments, none of these features are illustrated by Shepley and Womersley, and I have observed few of them myself.

A longitudinal section of the thallus 1-2 cm from the distal end showed moderately spaced (about 50 μm apart) medullary filaments whose cells were 130-160 μm long and about 30 μm wide (the protoplast occupied less than half this width) separated by pit connections up to 8 μm in diameter and up to 3 μm deep. Most cells branch only once, occasionally twice, near their midpoint to produce a proximally mostly unbranched rhizoid-like filament which terminates in the cortical filaments (=whorl branches). The majority of the medulla is composed of long, unbranched rhizoidal filaments which arise at various points from cells of the whorl branches. No secondary pit connections were seen between any of the cells.

Both floridean and hyaline hairs stain somewhat darkly with haematoxylin. Floridean hairs can reach lengths of at least 600 μm. A thin line of cytoplasm is evident through most of the
length of the hair, and a small nucleus is discernible in the bulge of cytoplasm at the distal end. These hairs are pit-connected to a somewhat enlarged, moderately staining subcortical cell (Fig. 4a). In contrast, hyaline hairs are relatively short (to about 75 μm long) and apparently lack both cytoplasm and a nucleus. They are pit-connected to cells of the outermost cortical layer.

All vegetative cells in which nuclei could be detected were uninucleate.

No refractive inclusions were evident.

Reproductively, Kraftia shares a number of features with other members of the Dumontiaceae. Carpogonia and auxiliary cells are borne on separate reproductive filaments of moderate lengths, 9-12 cells and 9-14 cells, respectively. Certain cells of these filaments have enlarged nuclei. The distal 3 cells of the carpogonial branch are recurved. Following fertilization, the basal part of the carpogonium expands, divides, and fuses with cells 4 and 5. Numerous connecting filaments issue from the carpogonial part of these fusion cells. The connecting filaments contact an intercalary auxiliary cell. Secondary outgoing connecting filaments and gonimoblast filaments develop from the remnant of the connecting filament attached to the auxiliary cell.

Although the preceding paragraph is the norm for the Dumontiaceae, Kraftia differs in details of its female reproductive structures from all other members of the Dumontiaceae. Like other Dumontiaceae, both types of reproductive filaments appear to arise as unbranched files of
cells, and some incompletely differentiated branches terminate in rhizoidal filaments. The distal end of the carpogonial branch becomes reflexed, usually at cell 3 (Figs. 4b-e). The pit connection between cells 3 and 4 is centripetally displaced whereas that between cells 2 and 3 is more medially situated. This disposition of pit connections suggests that the distal curvature of the branch is due to differential growth of the walls of cell 3. The carpogonium is small and nondescript, as are cells 2 and 3. Cells 4 and 5 are enlarged and can be somewhat lobed, and cells 4-9 (-10) all have enlarged nuclei. The wall around these cells can be relatively thick (to about 5 μm).

Following fertilization, the cytoplasm between the trichogyne and the base of the carpogonium separates, but the wall remains confluent. Carpogonial fusion cells produce a number of segments which can divide further to produce up to at least 17 outgoing connecting filaments per carpogonial branch (Fig. 5). As occurs in other Dumontiaceae, there is some variability in which cells of the carpogonial branch the fertilized carpogonium or its derivative cells contact.

Auxiliary cell branches are very distinct. The branch appears to reach its full length before the auxiliary cell extends laterally and other cells begin to form lateral branches. As noted by Shepley and Womersley, most cells of the branch, excluding the auxiliary cell, can produce 3-4 short-celled lateral branches. The auxiliary cell itself grows disproportionately to one side of the axis of the branch (Fig. 6a).
The auxiliary cell was (4-) 5-6 (-7) cells from the distal end of the branch in the material examined. Outgoing connecting filaments are sometimes initiated from an elongate segment cut off the gonimblast initiator cell attached to the auxiliary cell (Fig. 6b). Some gonimoblast initials also appear to arise from this elongate segment when present. Three or four gonimoblast initials are commonly produced (Fig. 6c). As the carposporophyte matures, pit connections between the cells of the auxiliary cell branch enlarge to nearly 4 μm in diameter. Shepley and Womersley recorded carposporangia 8-12 μm in diameter. They did not record the size of mature cystocarps, and I did not observe any mature cystocarps.

Neither spermatangia nor tetrasporangia were observed in the material available for study.

**Dudresnaya verticillata** (Withering) LeJolis 1863:117

**INTRODUCTION**

**Dudresnaya verticillata** was originally described by Withering (1796:127) as *Ulva verticillata* based on material sent to him by Major Velley. His description is vague: "Stem and primary branches of equal thickness, broadest at the origin of the branches: ultimate branches very numerous, of equal thickness, filled with close set whirls [sic] of fructifications." To this he added the distinctive comment: "So very slippery that when first taken up it glides through the fingers."

C. Agardh (1824:51) introduced the name *Mesogloia coccinea* followed by a short description. He attributed the name *Ulva*
coccinea to Poiret (1808) and included Ulva verticillata
Withering and Rivularia verticillata Smith as synonyms. Smith
(1813, pl. 2466) had included a brief description and habit
figures of this species in his work. C. Agardh (1824:51) also
introduced the name Mesogloia fruticulosa, another synonym of D.
verticillata (Silva 1950:260).

The Crouan brothers (1835) recognized the difference in
vegetative anatomy between Mesogloia multifida, the type of the
genus, and M. coccinea. They proposed the name Dudresnaya
coccinea for the latter species, making it the type and only
species of Dudresnaya.

Although Bonnemaison (1822) had originally introduced the
name Dudresnaya (dedicated to Colonel Dudresnay de Saint-Pol-de-
León), his concept of the genus was identical to Agardh's of
Mesogloia (1817:xxxvii, 126, non vidi), making Dudresnaya
nomenclaturally superfluous and hence illegitimate (Article 63,
International Code of Botanical Nomenclature, 1983). Because
Dudresnaya Crouan frat. is a later homonym of Dudresnaya
Bonnemaison, Silva (1950:263, 1952:283) proposed the
conservation of the former name, and it has been accepted
(1952:283) also proposed the conservation of Dudresnaya Crouan
frat. against Borrichius S. F. Gray (1821: 330), an ignored
older name based on Withering's Ulva verticillata (which Gray
had renamed Borrichius gelatinosus nom. illeg.).

DeCaisne (1842, Pl. 16, Fig. 8) was the first to illustrate
the zonate tetrasporangia of this species.

Although Kützing (1843:373) had originally referred to this
species as *Callithamnion verticillatum*, in 1849 (p. 713) he identified it as *Nemalion coccineum*. He also referred to its distribution in the Atlantic Ocean and the Adriatic and Mediterranean Seas and mentioned specimens sent to him by Meneghini and Lenormand.

Harvey (1849, pl. 244) included this "gelatinous" species in his British seaweed flora, calling it "one of the rarest of the British Algae, scarcely known except on the southern shores of England." He noted that "in young plants the branches appear moniliform like those of *Batrachospermum*; but in old plants they are cylindrical." Branching to four orders was reported. Cystocarps develop at the base of assimilatory filaments and are commonly produced in abundance. Zonately divided tetrasporangia terminate short lateral branches near the apices of assimilatory filaments; they are much rarer than cystocarps. Harvey's figures show alternate, indeterminate branches, pronouncedly verticillate determinate branches, and relatively large globose cystocarps, similar to the illustrations of Smith.

LeJolis (1863:117) recognized the priority of Withering's species and published the name *Dudresnaya verticillata* (Withering) LeJolis in his list of marine algae of Cherbourg.

Bornet and Thuret (1867) described the carpogonial and auxiliary cell branches and post-fertilization development in this species (as *D. coccinea*). Later (1876), they provided illustrations and a more detailed account based on material from Saint-Malo, France. They described carpogonial branches as being 7 or 8 cells in length (and always unbranched according to Bornet's figures), with the distal cells placed obliquely and
with a long, straight trichogyne. Spermatangia are borne on the same individuals as those having cystocarps. Following fertilization, the base of the carpogonium produces an "ampulle" which extends down the length of the branch to the 5th cell. The ampulle establishes communication with the somewhat enlarged 4th and 5th cells of the branch and divides transversely. Connecting filaments issue from both ampulles and contact one (usually the 5th or 6th cell from the base) of three enlarged cells on the 10-12 cell-long auxiliary cell branch before continuing onward to contact other cells. Three gonimoblast initials produce the cystocarp.

J. Agardh (1876:245) recognized a separate family, the Dudresnayaeae, based largely on D. verticillata (as D. coccinea), but he also recognized its reproductive similarities to the Dumontiaceae despite its vegetative similarities to Crouania and Wrangelia. He described the anatomy of the thallus and the cystocarps in some detail and in 1879 (pl. 16) provided figures of female, cystocarpic, and tetrasporic structures. Long, unbranched reproductive filaments are shown terminating vegetatively; from several middle cells carposporangia appear to be arising in some figures (2, 6, 7) and tetrasporangia in others (2, 5). Maturing cystocarps are subtended by involucral filaments (6, 7), and mature cystocarps appear to be borne near the base of the assimilatory filaments.

Ardissone (1883:189) provided records of this species in the Mediterranean.

Schmitz (1883; Dallas 1884) also described post-fertilization development in D. verticillata (as D. coccinea).
In particular, he noted the lack of mingling of the auxiliary cell nucleus and the fertilization nucleus and the origin of the gonimoblast from two gonimoblast initials which arise from the remnant of connecting filament attached to the auxiliary cell.

Berthold (1884) discussed the vegetative and reproductive structures of *Dudresnaya* (mostly *D. coccinea*) in relation to other members of the Cryptonemiales from the Gulf of Naples.

Hauck (1885:98) included *D. verticillata* (as *D. coccinea*) in the *Algae of Germany and Austria* based on Adriatic specimens. He described the axis as an initially uncorticated filament around which di- and trichotomous whorl branches eventually form a peripheral layer. Later, the central axis becomes thickened with downward-coursing rhizoids out of which also arise whorl branches.

Buffham (1888:259) mentioned that the spermatangia of *Dudresnaya verticillata* (as *D. coccinea*) are similar to those of *Helminthora divaricata* (C. Ag.) J. Ag. "but much less distinguishable." He reiterated that they are found on the same plants which bear cystocarps.

Oltmanns (1898:106) repeated many of the observations of Bornet and Thuret (1876) and Schmitz (1883). In addition, he noted that the trichogyne was slightly curved (illustrated but not described by Bornet and Thuret 1876). Oltmanns also expanded on their observations of auxiliary cell contact and gonimoblast initiation. In particular, he noted the formation of a second outgoing connecting filament from the "sporogenous" portion of the fusion cell, the position of the auxiliary cell nucleus and later the double auxiliary nuclei against the wall
opposite the connecting filament, and the development of two spores masses from gonimoblast initials on opposite flanks of the fusion cell. Connecting filaments and gonimoblast initials are both formed by the diploid nucleus moving to a particular locality along the fusion cell wall, where an appendix is initiated. Cytoplasm and eventually a daughter nucleus move into the appendix, and a transverse wall develops. Oltmanns particularly noted that the part of the fusion cell that produces spores is equivalent to the connecting filament.

De Toni (1903:1626) listed early references to this species (as *D. coccinea*). He summarized its known distribution and collectors and provided a brief description, including the fact that specimens adhere very firmly to herbarium paper.

Killian (1914:237) studied spore germination and upright initiation in *Dudresnaya verticillata*, identified by him only as *Dudresnaya*. A protrusion from the spore initiates a short filament, which soon branches to form a coherent disc. The original spore body and oldest cells of the primary filament then degenerate. Upright shoots are initiated as side branches of the original sequence of cells.

Chemin (1927:166) noted the similarity of spore germination patterns of *Dudresnaya verticillata* (as *D. coccinea*) to *Helminththora divaricata*. He indicated that the spore bodies of both species occasionally produce two short filaments, but both preserve their contents. Later (1937:356), he published figures of his observations of spore germination in *Dudresnaya*.

Kylin (1928:32) also studied post-fertilization development in *Dudresnaya verticillata* (as *D. coccinea*). His observations
were made on plants collected at Roscoff in July and closely followed the earlier reports by Bornet and Thuret (1876), Schmitz (1883), and Oltmanns (1898). His illustrations are particularly graphic, clearly showing the size and position of the nucleus in each cell. He also noted the origin of connecting filaments from carpogonial fusion cells, stating, "The haploid nuclei of the nutritive cells remain quietly lying in their original place [translation]." Kylin stated that auxiliary cell branches were homologous to carpogonial branches, and he interpreted the auxiliary cell—the middle of 3 enlarged cells—as receiving the diploid nucleus and producing the protrusion that first cuts off a secondary outgoing connecting filament and then the gonimoblast. [Kylin's figures, however, show it is the remnant of the connecting filament that produces a secondary connecting filament and the gonimoblast.] In contrast to earlier authors, Kylin stated that the species is unisexual and that the smaller, lighter red male plants are less abundant than females. He also reported that among the several hundred individuals collected in July he observed no tetrasporic thalli.

Newton (1931:276) and Irvine (1983:12) have provided descriptions and illustrations of this species in their British floras.

J. Feldmann (1939:284) recorded this species from 20-25 m, attached to pebbles or encrusting coralline algae, on the coast of Albères (Cap Béar, Cap l'Abeille), near the border between Spain and France on the Mediterranean. In June and July, most individuals are fertile, either cystocarpic or zonately
tetrasporic. This species frequently has a fungal invasion of Blastophysa rhizopus and Endoderma majus.

Sundene (1953) first recorded this species from southern Norway.

Recent Mediterranean records have been provided by Giaccone (1969, 1978:46), who recorded it in a Laminaria ochroleuca - Phyllaria purpurascens community at 50-60m and as "infralitorale" and "circalitorale" in the Adriatic Sea, and by Battiato, et al. (1979:112), who reported it from 8 to 10 m at Syracuse.

Irvine (1983:12) has provisionally accepted as lectotype an unlocalized, undated Velley specimen in BM-K. I have seen the specimen, a faded tetrasporophyte about 9 cm tall and labeled simply, "Major Velley." Zonate tetrasporangia measured 13-15 by 31-38 μm without the wall (18-20 by 35-40 μm with the wall).

Because of the similarities of D. verticillata to D. crassa and D. australis, OBSERVATIONS of it follow the INTRODUCTION to the other two species.

Dudresnaya crassa Howe 1905:563

INTRODUCTION

Dudresnaya crassa was originally described by Howe (1905:563) from material collected at Castle Harbor (type locality), 6 July 1900, and from Spanish Point, Bermuda. Howe distinguished his plants from D. verticillata (as D. coccinea) on the basis of size and habit, his plants having obtuse ultimate branches nearly the diameter of the primary axis. In D. crassa, peripheral filaments are 2-4 times as long as in D.
verticillata, and the auxiliary cell is always conspicuously smaller than the adjacent cells. In addition, Howe stated D. crassa to be unisexual in contrast to D. verticillata, which is bisexual. Howe also referred to J. Agardh's D. canescens but stated, "This, however, is a plant of entirely different habit from ours and is not a Dudresnaya, as a recent examination of the single type-specimen in hb. Agardh has shown."

Howe found the development of the gonimoblast to be much like that of D. verticillata, as described by Bornet and Thuret (1876) and others, but he emphasized that in D. crassa the auxiliary cell is a "single definite highly specialized cell lying between the two larger ones." In addition, he noted, "The content of this cell appears at first very much like that of the adjacent cells, but as it matures it undergoes a change, becoming more homogeneous and translucent; at the same time the auxiliary-cell and the two neighboring cells become enveloped in an especially thick layer of mucus which stains yellowish with safranin."

The holotype of Dudresnaya crassa is in NY. It was illustrated by Howe (1905, Plate 28).

Collins and Hervey (1917:150) included additional records from Bermuda and described spermatangia, which they always found on plants different from those bearing cystocarps. The spermatangia terminate small, densely branched ramuli borne on short, erect lateral branches near the ends of assimilatory filaments, sometimes so dense as to form a continuous mass.

Taylor (1950) made a morphological study of D. crassa. He found a large amount of variation in immediate post-
fertilization stages. The protrusion from the fertilized carpogonium can divide in two or remain undivided, and either cell 4 or 5 can be contacted first by this protrusion (rarely, a cell other than one of these is contacted--Figs. 16, 34, or only a single cell is contacted --Figs. 18, 19, 28). Taylor showed up to 5 connecting filaments per fusion cell leaving the carpogonial branch. In several instances (Figs. 16, 26, 30), he interpreted connecting filaments as arising from uncontacted carpogonial branch cells. Certainly, his Figures 26 and 30 could easily be seen as showing connecting filaments arising from carpogonial fusion cells; I am unable to interpret his Fig. 16. Taylor described gonimoblast initiation: "The cystocarp is initiated by the cutting off of a dense cell from the auxiliary obliquely opposite the oöblast connection (Fig. 48) and then, generally, a second obliquely on the other side."

In Taylor's (1960:364) Caribbean flora, *Dudresnaya crassa* was again recorded only from Bermuda.

Taylor (1961:280) reported "tetrasporangia" from one very small plant collected February 1960 in 50 m on Challenger Bank southwest of Bermuda by J. T. Frederick. The tetrasporangia are cylindrical, obtusely rounded structures, 10-15 \( \mu m \) in diameter and 30-43 \( \mu m \) long, terminating assimilatory branches. They could be displaced by young ones immediately below. Although most structures were zonate to irregularly zonate, others showed unusual patterns of division, and some appeared to show in situ germination.

Almodóvar (1970:24) recorded several collections of *D. crassa* from Puerto Rico: 3 mi. off Punta Brea, Guanica, 15-18 m,
12 Dec, 1966; 4 mi. off Media Luna Reef, La Parguera, 14-18 m, 28 Feb. 1967; Laurel Reef, La Parguera, 17 m, sand-rock bottom 12 June 1967.

Schneider and Searles (1973:203) found *D. crassa* off the coast of North Carolina on 15 July 1972 at 23 m (female) and again on 18 Sept. 1972 at 30 m (cystocarpic).

Cheney and Dyer (1974:187) recorded the occurrence of *D. crassa* in at least 25 m on the Florida Middle Ground in September.

Norris and Bucher (1982:194) collected bisexual specimens in March and April in Belize from 1 to 12 m.

**Dudresnaya australis** Setchell 1912:245

**INTRODUCTION**

The name *Dudresnaya australis* was first used by J. Agardh for plants collected at or near Port Phillip Heads and Western Port, Victoria; it was published by Wilson (1892:181), the collector, as a nomen nudum with the following entry:

"*Dudresnaya australis* J. Agardh MS, species nova 1887." Later, J. Agardh (1899:35) discussed it as distinct from the European *D. coccinea*, but he did not describe it. Setchell (1912:245) published a Latin description for this name after observing four of Wilson's specimens in the British Museum and three in Herb. J. Agardh at Lund. Both tetrasporic and cystocarpic plants of *D. australis* were represented among the specimens at LD and BM. Setchell described the tetrasporangia as zonate and the cystocarps as reniform but non-apiculate, 60-75 μm across. He found the long auxiliary cell branches, with about 15 swollen
cells in the middle, one of which is wider and flatter than the rest (the auxiliary cell), to terminate in long, 2-3 times dichotomous sterile deciduous portions. The specimens were bisexual.

Setchell compared *D. australis* to both *D. coccinea* and *D. crassa*, noting the similarity of habit to the former but the similarity of assimilatory and auxiliary cell filaments to the latter. He also noted that the auxiliary cell filaments were much longer than those of either of the other two species and that the spermantangia were similar to those of *D. coccinea* as illustrated by Bornet and Thuret (1876, Pl. 11, Fig. 2).

Setchell included a plate of the habit of one of the BM specimens. However, in choosing a lectotype, Robins and Kraft (1985) selected a Lund specimen (LD 34730).

Mitchell (1966:215) included *Dudresnaya australis* in her discussion of southern Australian Dumontiaceae. In addition to the specimens already mentioned, she noted a collection by Harvey from King George's Sound, Western Australia (AD 18555). Harvey originally identified the material as *D. coccinea*, but Mitchell noted its identity with the type of *D. australis* in Lund. She also mentioned material (MELU 5333) collected by J. B. Wilson in 1874 from Western Port, Victoria,

Mitchell described the thalli as up to 12 cm tall, 3.5 mm in diameter, irregularly radially branched to several orders. The whorled branch system on each axial cell gives younger branches an annulate appearance. Large zonate tetrasporangia (18 by 45 μm) occur terminally on cortical filaments.

Mitchell included a plate of the habit of MELU 5333, a
tetrasporic specimen.

OBSERVATIONS

Specimens of the preceding three species and *D. capricornica* Robins et Kraft (1985:23) share a number of characteristics. I will therefore discuss them together. Because of the limited amount of material available, particularly of *D. capricornica*, for which no female or male material was seen, observations on these four species are necessarily sketchy. Reference to other works has therefore been made to provide as complete a comparison as possible.

All four species have relatively modest distributions—*Dudresnaya australis* from King George’s Sound, Western Australia, to Western Port, Victoria (Robins and Kraft 1985), a distance of approximately 2800 km; *D. capricornica* from the northern Great Barrier Reef to Lord Howe Island along the eastern coast of Australia, a distance of approximately 3200 km, and from Rottnest Island, Western Australia (Robins and Kraft); *D. crassa* from Belize (Norris and Bucher 1982) to Bermuda (Howe 1905), a distance of approximately 3300 km; and *D. verticillata* from the Canary Islands (Gil-Rodriguez and Carillo 1980), the Mediterranean (from the Adriatic westward, Kützing 1849, Ardissone 1883) north to southern Norway (Sundene 1953). Based on their distributions, I would classify *D. australis* as warm temperate, *D. capricornica* and *D. crassa* as subtropical to tropical, and *D. verticillata* as cool temperate to subtropical.

Bodard (1971:18) recorded "*Dudresnaya aff. crassa*" in 10 m off Senegal. Lawson and John (1982:224) reported "a lubricous
alga having zonate tetrasporangia" off Ghana; they thought it was probably a member of the Dumontiaceae but preferred not to assign it to a genus because of lack of sexual organs. A specimen in MICH collected by D. M. John (No. 6374) in 25 m off Ghana on 20 Feb. 1970 had zonate tetrasporangia 10-20 \( \mu \text{m} \) wide by 50-60 \( \mu \text{m} \) long. This size range does not clearly fit any of the previously described species of *Dudresnaya*. The size of the cells of the assimilatory filaments is intermediate between *D. capricornica* on the one hand and *D. crassa* and *D. verticillata* on the other. Some cells have groups of refractive bodies to 6 \( \mu \text{m} \) in diameter.

All species display relatively long seasons for an otherwise ephemeral genus: October to March for *D. australis* (Robins and Kraft 1985), August to March for *D. capricornica* (Robins and Kraft), March to September for *D. crassa* (Collins and Hervey 1917; Schneider and Searles 1973), and early spring to October for *D. verticillata* (Irvine 1983).

These species also show wide vertical ranges--2 to 33 m for *D. australis* (Robins and Kraft 1985), 6 to 35 m for *D. capricornica* (Robins and Kraft), 0.2 to 50 m for *D. crassa* (Taylor 1950, 1961), and 0 to 90 m for *D. verticillata* (Funk 1927, Irvine 1983).

*Dudresnaya australis* is always epiphytic; *D. capricornica* is found on coral rubble; *D. verticillata* is epiphytic, epizoic and epilithic (Robins and Kraft 1985). Howe (1905) and Taylor (1950) found *D. crassa* to be epilithic.

As noted by Howe (1905) for the type specimen, thalli of *D. crassa* from Bermuda are frequently permeated by a species in the
Acrochaetiaceae. This species was identified as *Acrochaetium corymbiferum* (Thuret in LeJolis) Batters by Collins and Hervey (1917:150). North Carolina specimens are infested with another member of the family, *Audouinella ophioglossa* Schneider. Although *Audouinella corymbifera* (Thuret in LeJolis) Dixon in Parke and Dixon is recorded from North Carolina, it is known from only *Dasya* there.

Compared to the other species, *D. australis* appears to display a somewhat firmer texture.

All four species are terete. They range in maximal height from 11 cm in *D. capricornica* (Robins and Kraft 1985) to 25 cm in *D. crassa* and *D. verticillata* (Collins and Hervey 1917, Newton 1931). In *D. australis*, *D. crassa*, and *D. verticillata*, axes are commonly 1-3 mm in diameter. In *D. capricornica* and *D. crassa*, they can reach 10 mm in diameter. The three to four orders of slightly progressively narrower branches produce a generally pyramidal thallus. Branch tips are initially obtuse in *D. crassa* and acute in the other three species, but they can become rounded due to erosion. Annulations are frequently visible on younger branches in all but *D. capricornica*.

Indeterminate branches arise as unbranched primordia in *D. australis*. In the other species, they appear to arise by the transformation of assimilatory filaments. Although the apical cell can elongate to 10 μm, or more in all but *D. australis*, subapical cells are discoid/quadrate to at least 20 cells from the apex in *D. australis* and *D. verticillata* but to a somewhat shorter extent in *D. capricornica* and *D. crassa*. Several instances of "indeterminate" branches terminating in
assimilatory filaments have been seen in *D. capricornica* (Robins and Kraft 1985, Fig. 94), *D. crassa* (Fig. 10a), and *D. verticillata* (Fig. 7a).

The apical cell may or may not be exserted in any of the four species. Whorl branches that are cut off below the apex may curve around it and obscure it.

Axial cells enlarge to at least 150 μm in diameter in all species, and 300 μm has been recorded for *D. capricornica*. Maximum lengths are quite variable. The main difficulty in establishing ranges for these species has been the problem of recognizing axial filaments in older parts of the thallus. All species possess some fairly large axial cells with relatively low length to width ratios: 1.9 to 3.1 in *D. australis* (this study), 1.8 to 10.0 in *D. capricornica* (Robins and Kraft 1985), 1.7 to 6.7 in *D. crassa* (this study), and 0.8 to 7.0 in *D. verticillata* (Robins and Kraft). Pit connections between axial cells enlarge to a maximum diameter of 5 to 6 μm.

The number of whorl branches per axial cell is variable in most species--4 to 7 have been observed in *D. australis* (Robins and Kraft 1985), 3 to 5 in *D. capricornica* (Robins and Kraft), 4 to 6 in *D. crassa* (this study), and 4 in *D. verticillata* (Irvine 1983). Whorl branches are attached near the midpoint of the axial cells. Basal cells of whorl branches, initially cylindrical, enlarge to become somewhat cuneate to quadrate. These periaxial cells bear 2(-3) whorl branches and possibly a single rhizoidal filament in *D. australis* (limited material seen), 1 (-4) whorl branches, 1-2 rhizoids, and an occasional reproductive filament in *D. crassa*, and 1 (-4) whorl branches
and 1 rhizoid in *D. verticillata* (limited material seen). Robins and Kraft observed up to 4 rhizoids in *D. verticillata*; they also recorded the branching of rhizoidal filaments and their production by other inner whorl branch cells. They described rhizoidal cortication in *D. australis* as similar to *D. verticillata*. They observed that rhizoids can give rise to whorl branches in *D. australis* and *D. verticillata*, but in *D. capricornica*, the rhizoids that arise from cells of cortical fascicles are simple or sparsely branched and do not regularly give rise to secondary cortical laterals. In *D. crassa*, I observed that filaments of colorless cells that loosely run down the axes often have pigmented apical cells reminiscent of assimilatory filaments. Each cell of these filaments can bear a single unbranched lateral more or less perpendicularly.

Periaxial cells can bear "intermediate cells" (cells that fork to form both a whorl branch and a rhizoid) in *D. capricornica, D. crassa, and D. verticillata* (Fig. 7b). Rhizoids enlarge in diameter as the periaxial cells to which they are attached enlarge. Maximum diameters have been recorded as 120 μm in *D. australis*, 85 μm in *D. capricornica*, and 40 μm in *D. verticillata* (Robins and Kraft 1985) and as 135 μm in *D. crassa* (this study). The center of the mature thallus of *D. verticillata* is filled with numerous large colorless cells whose origins are at that stage indeterminable.

Cells of the whorl branches are cylindrical in all species. Their dimensions and degree of branching vary among the species, as can be seen in Fig. 9. *Dudresnaya crassa* and *D. verticillata* display a moderate amount of branching and most resemble each
other in cell dimensions. *Dudresnaya australis* and *D. capricornica* show little branching distally. The cells of the former possess the lowest length:width ratio whereas those of the latter, the greatest. The cells of *D. australis* are also distinguished by their thick walls.

Hairs occur on all four species.

Hexagonal crystals have been observed in specimens of all four species. They vary somewhat in size and shape among the species. These crystals fluoresce under UV light when stained with 1% aqueous aniline blue (Robins and Kraft 1985). In addition, refractive inclusions to 6-8 μm in diameter have been seen in all but *D. verticillata*.

Reproductive filaments occur in a variety of positions. In *D. capricornica*, *D. crassa*, and *D. verticillata*, they have been observed arising directly from an axial cell in place of a periaxial cell (Robins and Kraft 1985, this study). In *D. australis*, *D. crassa*, and *D. verticillata*, they commonly occur on a periaxial cell, where they tend to be abaxial, but they can also occur to at least 5 cells from a periaxial cell in *D. crassa*. Although carpogonial branches and auxiliary cell branches usually occur at some distance from one another, branches sharing at least one differentiated branch cell have been observed in *D. crassa* and *D. verticillata*.

Carpogonial branches are 6-10 cells long in *D. australis* (Shepley and Womersley 1983:207; Fig. 12a, this study), 6-30 cells long in *D. capricornica* (Robins and Kraft 1985), 5-19 cells long in *D. crassa* (Howe 1905:573; Fig. 10b, this study), and 5-14 cells long in *D. verticillata* (Eisemann and Norris
1981:188; Figs. 7c, 8a, this study). The distal end of the branch is recurved—moderately in D. australis, D. capricornica, and D. crassa but markedly in D. verticillata due to two successive oblique divisions. In contrast, D. australis and D. capricornica undergo only a single oblique division (Robins and Kraft). Dudresnaya crassa appears to be intermediate, the second division being more strongly oblique than the first. These oblique divisions seem to be marked by centripetal displacement of pit connections between cells (at least in D. crassa and D. verticillata). Although Robins and Kraft state that mature carpogonial branches of D. australis and D. verticillata differ in cell shape, I did not observe consistent differences (compare their Fig. 26 to my Fig. 7a). However, cells 4 and 5 are usually larger in D. verticillata than in the other three species. In all species, at least several proximal cells are frequently unmodified.

Trichogynes of D. crassa and D. verticillata can curve broadly as they leave the base of the carpogonium in order to reorient the trichogyne toward the exterior of the thallus. Spiralling in any of the trichogynes is lacking. Forked trichogynes have been observed in D. crassa (Taylor 1950, Fig. 47). In D. capricornica, Robins and Kraft (1985) have reported that some plants bear up to 4 carpogonia per reproductive filament, and rarely a carpogonium produces more than one trichogyne. Reversion of carpogonial branches to vegetative filaments has also been noted in this species.

Lengths of auxiliary cell branches also vary among the species. Shepley and Womersley (1983) found them to be 11-20
cells long in *D. australis* from South Australia; I found them to be 6-13 cells long (x=9.6, n=60) in the same species from Flinders, Victoria. Because ten to twelve cells are differentiated, few auxiliary cell branches in the Flinders material terminated vegetatively. However, many branches appeared to terminate in a capping cell and at least one ended in a hair. In *D. capricornica*, Robins and Kraft (1985) reported them to be 6-39 cells long, 3-18 cells of which are modified. In *D. crassa*, I observed them to be 9-22 cells long, with 7-10 cells differentiated (Taylor 1950 reported branches 9-20+ cells in length but other authors have referred only to the number of enlarged or differentiated cells in the middle of the branch). In *D. verticillata*, Robins and Kraft reported them to be 9-17 cells long with 3-14 cells modified; I found them to be 11-24 cells long (x=15.5, n=44) with 5-15 cells differentiated, and the shorter ones appeared to be elongating.

Differentiated cells of reproductive filaments in all species are round to quadrate to horizontally oblong. The auxiliary cell is usually quadrate and slightly to distinctly smaller than its neighbors (size varies within each species and may also vary with branch maturity). The difference in size between the auxiliary cell and its neighbors is greatest in *D. crassa* from Bermuda (Fig. 10c). The auxiliary cell occurs among the differentiated cells, usually near the proximal end of the filament. Its position ranged from 3 to 8 cells from the proximal end of the filament in *D. australis* (x=5.0, n=50; Fig. 12b), from 2 to 8 cells in *D. crassa* (x=4.2, n=60; Figs. 11a, b, d), and from 4 to 11 cells in *D. verticillata* (x=6.0, n=60;
Figs. 8c, d). Robins and Kraft (1985) distinguished *D. crassa* from all other species of *Dudresnaya* except *D. hawaiiensis* and *D. japonica* by a thick mucilage coat around auxiliary cell branches; such a mucilage coat was not seen in any specimens of *D. crassa* that I examined (however, see Fig. 11c).

Lateral branches may or may not be present on reproductive filaments of these species. They can occur on basal to intermediate cells of the filament, including occasionally cells distal to the auxiliary cell in *D. crassa* and *D. verticillata* (Fig. 8d). The proximal cells of the lateral branches can be differentiated in the same manner as the differentiated cells of the reproductive filaments, and they can resemble assimilatory filaments distally or throughout their length. Although Robins and Kraft (1985) reported that the reproductive filaments of *D. capricornica* can bear rhizoids, this interpretation requires confirmation since only the basal cells of such branches are illustrated by them (and I have found filaments in other species to resemble rhizoidal filaments proximally but to differentiate into assimilatory filaments distally). All laterals observed in this study or reported elsewhere have themselves been unbranched.

Post-fertilization development is similar in all four species. It has been described previously in detail for *D. verticillata* (Bornet and Thuret 1876, Schmitz 1883, Oltmanns 1898, Kylin 1928). The number of carpogonial branch cells which are contacted by the fertilized carpogonium varies from 1 to 2 cells in *D. australis* (Shepley and Womersley 1983; Robins and Kraft 1985) and *D. crassa* (Taylor 1950), from 1 to 4 cells in *D.
capricornica and from 1 to 3 cells in D. verticillata (Robins and Kraft). In all but possibly D. capricornica, the enlarged fertilized carpogonium usually divides into individual cells each of which fuses with only one cell of the carpogonial branch. Variations in the cells contacted by the fertilized carpogonium or its derivative cells occur in all species, but most commonly cells 4 and 5 are the ones contacted.

The usual or maximum number of outgoing connecting filaments from a single carpogonial fusion cell has not been documented by any of the previous workers. Taylor (1950), who provided the most abundant illustrations of any of the studies, shows a maximum of 5 from any single fusion cell in D. crassa. Robins and Kraft (1985) show up to 4 from individual fusion cells in D. australis and D. verticillata. Connecting filaments are relatively nonpersistent in all four species. They are identifiable usually only a short distance behind the growing tip. They reach a maximum diameter of 5 μm.

If not fertilized, the distal 5 cells of the carpogonial branch disintegrate in D. australis (Fig. 12a) and D. crassa. In D. verticillata, cells 1-4 were seen disintegrating after connecting filament production.

In all species, the auxiliary cell is contacted in the same manner as is typical for other Dumontiaceae. However, a varying number of secondary outgoing connecting filaments and gonimoblast initials are produced depending on the species. In D. australis, two gonimoblast initials are formed (Shepley and Womersley 1983, Robins and Kraft 1985), and a second outgoing connecting filament is sometimes observed (Robins and Kraft,
The origin of gonimoblast initials from the auxiliary cell itself in *D. australis* (Shepley and Womersley, Robins and Kraft) conflicts with my own observations and needs to be confirmed. In *D. capricornica*, the gonimoblast initiator cell cuts off either an additional connecting filament and two gonimoblast initials or just three gonimoblast initials (Robins and Kraft). In *D. crassa* and *D. verticillata*, two or three gonimoblast initials are formed, and an additional outgoing connecting filament is sometimes initiated (Taylor 1950, Robins and Kraft). As first noted by Robins and Kraft, gonimoblast initials of these species (including *D. crassa*, this study) tend to be curved and somewhat elongate (Figs. 8d, 11a, 12c). The gonimoblast initiator cell can be relatively long and forked in *D. australis*. In *D. verticillata*, it is usually shorter than in *D. australis*; in *D. crassa*, it appears to be intermediate in size and shape.

If unfertilized, the auxiliary cell may disintegrate, as was seen in one instance in *D. crassa*.

In *D. crassa*, several of the cells distal to the auxiliary cell can swell to at least 13 μm in diameter as the carposporophyte matures (Figs. 11c, d); this phenomenon has also been seen in *D. hawaiiensis* and *D. japonica*.

As the carposporophyte matures, pit connections between cells of the auxiliary cell branch enlarge, particularly those proximal to the auxiliary cell. They enlarge the most in *D. crassa* (to about 7 μm; Fig. 11d), somewhat less in *D. verticillata* (to about 3.5 μm; Fig. 8e), and least in *D. australis* (to about 1.5 μm, but this smaller size may be due to...
the younger stage of carposporophyte development in the material studied; Fig. 12d). Pit connections between the gonimoblast initiator cell and the gonimoblast initials enlarge to 1.5 \( \mu \text{m} \) in *D. australis*, to 4 \( \mu \text{m} \) in *D. crassa*, and to 2 \( \mu \text{m} \) in *D. verticillata*. No cell fusions were observed in any species. Nuclei in cells adjacent to the auxiliary cell remain large (about 3-6 \( \mu \text{m} \) in diameter) during carposporophyte maturation in *D. australis*, *D. crassa*, and *D. verticillata*.

Cystocarps reach 175 \( \mu \text{m} \) in diameter in *D. australis* (Shepley and Womersely 1983), 250 \( \mu \text{m} \) in *D. capricornica* (Robins and Kraft 1985), 240 \( \mu \text{m} \) in *D. crassa* (Howe 1905), and 170 \( \mu \text{m} \) in *D. verticillata* (Robins and Kraft). The size of the carposporangia appears to vary with their maturity. Maximum sizes of 27 and 25 \( \mu \text{m} \) in diameter have been observed in *D. australis* and *D. capricornica*, respectively (Robins and Kraft) and 18 and 25 \( \mu \text{m} \) in *D. crassa* and *D. verticillata*, respectively (this study). Carposporangia are relatively loosely aggregated in *D. australis*, *D. capricornica*, and in Florida populations of *D. crassa* and relatively compactly arranged in *D. verticillata* and North Carolina populations of *D. crassa*. However, this observation may reflect the maturity of the cystocarps, the more loosely constructed cystocarps being younger. Basal cells of the gonimoblast appear not to differentiate in specimens of *D. crassa* from Bermuda and to differentiate only partially in *D. verticillata* (although, again, this may be due to the maturity of the cystocarps).

Both bisexual and unisexual thalli have been recorded for all species but *D. capricornica*, which is bisexual. In *D.*
australis, early collections were bisexual (Setchell 1912), but more recent ones have been unisexual (Shepley and Womersley 1983, Robins and Kraft 1985). In D. crassa, specimens from Florida, North Carolina (this study), and Belize (Norris and Bucher, 1982) are bisexual, but those from Bermuda are unisexual. In D. verticillata, all British and some French material is bisexual, but Kylin's material from Roscoff, France, is unisexual.

Besides variation in uni- and bisexuality, different thalli of the same species can display different arrangements of spermatangia and spermatangial mother cells. Robins and Kraft (1985) have already pointed out the difference between their material of D. australis, in which the spermatangia "are produced terminally on fascicles of short cells that are borne on the 2-3 outermost cortical cells" and that of Shepley and Womersley "in which each fertile cortical cell appears to be surrounded by a double whorl of short spermatangial filaments." This latter pattern, also seen in D. hawaiiensis, is the only one that has been observed in D. capricornica (Robins and Kraft). Dudresnaya crassa and D. verticillata also each display two patterns although these patterns may actually represent the extremes of a continuum. In bisexual thalli, 1-4 spermatangia are cut off the distal ends of the terminal 1-3 cells (Figs. 7d, 10d). In unisexual thalli of D. crassa, 3-5 (-6?) spermatangia or spermatangial mother cells are cut off the distal ends of 5 or so branch cells (Fig. 10e). In unisexual thalli of D. verticillata, spermatangia or spermatangial mother cells are cut off the faces of cells of short, small-celled branches (Figs.
7e, f). Both of these latter patterns produce a dense, pyramidal terminal cluster of spermatangia on male thalli. As in other species, would-be spermatangia can themselves become spermatangial mother cells.

Tetrasporangia are generally common among specimens of D. australis, D. capricornica, and D. verticillata. They are zonately divided in all three species and occur terminally or laterally on assimilatory filaments. Tetrasporangia in D. crassa have been observed only once—in a very small plant from 50 m off the southwest coast of Bermuda—and these, although usually zonate, showed frequent abnormalities (Taylor 1960). However, their size, 10-15 \( \mu \text{m} \) by 30-43 \( \mu \text{m} \), was similar to that recorded for D. australis [12-20 by 25-45 (50) \( \mu \text{m} \), Robins and Kraft 1985], D. capricornica (6-18 by 15-55 \( \mu \text{m} \), Robins and Kraft), and D. verticillata (11-23 by 25-53 \( \mu \text{m} \), Irvine 1983).

Kylin (1928) noted an apparent absence of tetrasporic thalli among hundreds of gametophytes at Roscoff. Tetrasporangia and gametangia have been observed on the same thallus in several specimens of D. capricornica (Robins and Kraft). Ardissone (1881) reported a similar condition for D. verticillata.

**Dudresnaya japonica** Okamura 1908:209

INTRODUCTION

Okamura (1908:209) described *Dudresnaya japonica* from specimens collected near Nagasaki, Nagoya, and Tokyo, Japan. He found the plants to resemble closely the previously described D. verticillata and D. crassa in female reproductive morphology and post-fertilization development. His illustrations of female
reproductive structures and stages show slightly distally recurved carpogonial branches of about 10 differentiated cells (Figs. 1-4), an undivided "primary connection filament" growing down the carpogonial branch (Fig. 3), connecting filaments developing from carpogonial fusion cells (Figs. 4, 5—the precise nature of the fusion cells is obscure), contact of auxiliary cells by a connecting filament and production of a secondary connecting filament (Figs. 6, 7), gonimoblast initiation from the connecting filament attached to the auxiliary cell (Figs. 8, 9), the mature gonimoblast (Figs. 12, 13—Fig. 12 shows the gonimoblast surrounded by several presumably mucilaginous layers), and carpospore germination (Figs. 14-16). Okamura's figures do not show vegetative tips on auxiliary cell branches although he stated that they terminate in "a multiarticulate prolongation similar to that of the other peripheral filaments or often remain shorter." Okamura also showed gonimoblast developing from a segmented connecting filament several cells distant from the auxiliary cell. Figures 10 and 11 show spermatangia developing along nearly the entire length of an assimilatory filament. Further observations by Okamura are incorporated into the OBSERVATIONS below.

Umezaki (1968) studied germination of carpospores of D. japonica. He collected cystocarpic specimens at Shirahama, Wakayama Prefecture, in April. Carpospores, 15-17 μm in diameter, were cultured under 24 hours daily illumination of about 1000 lux at room temperature (degrees not specified). Umezaki observed both normal and abnormal patterns of spore germination. In both patterns, the spore initially divided
perpendicularly to the substrate. In normal development, both
cells then produced protuberances that grew to produce a highly
branched but compact prostrate thallus. In abnormal
germination, the spore divided to form a cruciate, irregularly
cruicate, zonate, or irregularly zonate pattern before
initiating lateral processes. Umezaki likened the normal
pattern of germination to that of *Halymenia*, termed
"diprotocellular type" by Inoh (1947). Erect axial filaments
developed directly from branches of the prostrate thallus; such
axial cells were 5-10 μm broad by 20-62 μm long and were loosely
surrounded by lateral branches. Umezaki was unable to produce a
pseudoparenchymatous thallus in culture or to verify the
uniaxial condition of the species. Rhizoids were not observed
in culture.

A lectotype for this species has yet to be chosen.

Because of their similarities, observations of this species
and the following are included together after the INTRODUCTION
to *D. hawaiiensis*.

*Dudresnaya hawaiiensis* R. K. S. Lee 1963:315

INTRODUCTION

Lee (1963:315) separated this species of *Dudresnaya* from
those already described by its "thick, short stipe, its closely
set main branches, and its very dense covering of slightly
flattened, obovate branchlets." This species is also distinctive
in the length to which the fertilized carpogonium must grow
before it fuses with another cell of the carpogonial branch
(always cell 4 in *D. hawaiiensis*). It is noteworthy that this
carpogonial extension, which Lee called the primary connecting filament, grows past the nutritive auxiliary cell (this is how the "generative" auxiliary cell in all Dumontiaceae is contacted) before a protrusion from the connecting filament makes contact. The primary connecting filament continues growing onward, a pit connection is formed, and it becomes what Lee called a secondary connecting filament. Further secondary connecting filaments can develop from the primary connecting filament between the carpogonium and the nutritive cell.

Siotas and Wetherbee (1982:333) observed the fine structure of the cells neighboring the auxiliary cell in *D. hawaiiensis*. They noted enlargement of pit connections, including aperture diameter and surface area, and a decrease in core staining density.

Robins and Kraft (1985) have studied *D. hawaiiensis* from the Hawaiian Islands, the Great Barrier Reef, Lord Howe Island, and Norfolk Island. Significant details from their study are incorporated in the OBSERVATIONS below.

The holotype of *D. hawaiiensis* (A. Soegiarto No. 137, Kaneohe Bay, Oahu I., Hawaii, March 1961, in BISH) is missing (Schlech, pers. comm., 21 Feb. 1984) and a lectotype has not been designated.

OBSERVATIONS

As noted by Robins and Kraft (1985), *D. hawaiiensis* and *D. japonica* share a number of features.

*Dudresnaya hawaiiensis* is the widest ranging species of the genus, having been reported from the Hawaiian Islands and from
eastern Australia and vicinity (Great Barrier Reef, Lord Howe Island, Norfolk Island). *Dudresnaya japonica* has been recorded only from Japan: from the west coast of Kyushu, the Pacific coast of Honshu west of Tokyo, and Hachijo Island, to the south.

*Dudresnaya hawaiiensis* grows on coral rubble, encrusting calcareous algae, and mollusc shells in 1.5 to 35 m (Robins and Kraft 1985). Chihara (1975:261) lists the habitat of *D. japonica* as "fairly deep water[translation]."

*Dudresnaya hawaiiensis* appears to be a relatively long-lived ephemeral, occurring from August to February south of the equator and from March to June north of the equator (Robins and Kraft 1985). *Dudresnaya japonica* has been recorded only from spring collections.

Thalli of both species can be compressed basally (Okamura 1908; Robins and Kraft 1985). In *D. japonica*, the higher orders of branches are terete, but in *D. hawaiiensis*, they are usually slightly compressed, rarely terete. *Dudresnaya japonica* is reported to reach a height of 30 cm and a breadth of 5 mm; *D. hawaiiensis* can attain a height of 18 cm and a width of 26 mm. Annulations have not been recorded for either species. *Dudresnaya hawaiiensis* has a particularly fuzzy appearance due to the long, distally mostly unbranched assimilatory filaments. The margins are irregular in *D. japonica* but not conspicuously furry. Cystocarps are visible to the unaided eye. Both species become yellowish when old (Robins and Kraft, Chihara 1975:103, habit photograph).

Axial files are recognizable in thalli of *D. hawaiiensis*, but all files that I saw terminated in assimilatory filaments.
Not until 20 to 30 cells behind the distal ends of such filaments can one clearly recognize the irregularly branched percurrent axis. Typically, an axial cell bears 1-3 laterals. Periaxial cells are relatively short and often forked, each giving rise to a single whorl branch and a rhizoid. A second rhizoid sometimes develops from such periaxial cells. I did not see any rhizoidal filament branch as has been reported by Robins and Kraft (1985), who also observed up to 4 rhizoidal filaments from a periaxial cell. Whorl branches are rarely branched except for basal rhizoidal production; cells are long and narrow (Fig. 14a) as in D. capricornica. Lateral branches are initially borne distally on such axial cells, but as the axial cells mature, they begin to elongate distally to the lateral. Eventually, lateral branches come to lie near the midpoint of the axial cell. In D. japonica (Fig. 13a), assimilatory filaments are also sparsely branched but cells are distinctly shorter and somewhat broader than in D. hawaiiensis.

Hairs were not seen on any of the material.

Groups of refractive inclusions about 2 µm in diameter are occasionally seen in cells associated with spermatangial production in D. hawaiiensis. The refractive inclusions are so numerous that they cause distension of the cells containing them.

Reproductive filaments are borne in the same position as assimilatory filaments.

Carpogonial branches 5-15 cells in length have been observed in D. hawaiiensis (Figs. 14b-d). Only the distal 5-6 cells are strongly differentiated in shape and stain darkly with
aniline blue. Unlike most other species in the Dumontiaceae, whose differentiated cells are round to elliptical to discoid, those of D. hawaiiensis and D. japonica (Fig. 13b) are more quadrate or trapezoidal to cylindrical. In both species, the base of the carpogonium is elongate (to 10-12 μm long), and the wall material surrounding the base of the trichogyne at its constriction is particularly prominent. The carpogonium does not stain with aniline blue and appears to consist of a starch-grain-like material. In D. hawaiiensis, the female nucleus was occasionally observed directly below the trichogyne while it was elongating, but in mature cells it rests at the base of the carpogonium. The trichogyne is straight in both species, but proximally it sometimes appears somewhat wavy in D. hawaiensis.

Auxiliary cell branches 9-28 cells in length were observed in D. hawaiiensis (Figs. 15a-c). Five to thirteen cells differentiate. The future auxiliary cell is recognizable in many branches before the branches are fully differentiated by its initially larger size (the largest in the branch), its approximately quadrate shape, and its dense staining.

Reproductive filaments bear frequently one or occasionally two rhizoidal filaments from their basal cell, which comes to resemble an undifferentiated periaxial cell. Auxiliary cell branches can instead bear 1 or 2 laterals of round or discoid cells near the middle of the branch.

A thick coat of mucilage was observed around reproductive filaments in material of D. hawaiiensis from Lord Howe Island but not in specimens from the Great Barrier Reef.

Because of the nearly complete lack of curvature in the
carpogonial branch of *D. hawaiiensis*, the basal outgrowth of the fertilized carpogonium must travel the greatest distance of any *Dudresnaya* species before contacting another cell of the carpogonial branch (Fig. 14c). During this process, there is a distinct hiatus between the protoplasm of the trichogyne and the base of the carpogonium. Robins and Kraft (1985) record that the fertilized carpogonium can fuse with 1-3 cells of the carpogonial branch (any of cells 2-6). In all of the examples I observed, two carpogonial fusion cells were always formed, either with cells 4 and 5 or with cells 4 and 6. Robins and Kraft showed up to 6 connecting filaments arising from any one carpogonial fusion cell, and in two cases, they observed gonimoblast production directly from one of the carpogonial fusion cells (their Fig. 74). In both *D. hawaiiensis* and *D. japonica*, there is usually some segmentation of the connecting filaments before leaving the carpogonial branch (Figs. 13c, 14d). Connecting filaments are moderately persistent and reach 8 μm in diameter in *D. hawaiiensis*.

The auxiliary cell, which is 3-10 (-13) cells from the base of the branch (x=6.1, n=60) in *D. hawaiiensis*, is contacted as in other Dumontiaceae (Fig. 15b). Usually, at least one additional connecting filament is produced before gonimoblast initiation, and up to five have been seen in *D. hawaiiensis* (Robins and Kraft, 1985, Fig. 78). The first gonimoblast initial is slightly elongate and frequently produced on the distal side of the connecting filament. Up to two additional gonimoblast initials can be produced.

The auxiliary cell is usually about the same size as its
immediate neighbors at the time of contact in D. hawaiiensis (Fig. 15b), but it can be distinctly smaller in D. japonica (Figs. 13d, e). The immediate neighbors stain intensely with aniline blue. They appear to enlarge somewhat further after the auxiliary cell is contacted in D. hawaiiensis (Figs. 15c, d) and considerably more in D. japonica, to about 20 μm in diameter (Fig. 13f), and continue to stain darkly during carposporophyte maturation. Pit connections between the auxiliary cell and its neighbors enlarge to about 2.0 μm in D. hawaiiensis (Fig. 15d). They can enlarge to nearly 7.0 μm in D. japonica (Fig. 13f), but they are usually smaller, about 3.0 μm. Pit connections between most other cells below the auxiliary cell also broaden somewhat in D. hawaiiensis. Cells above the auxiliary cell enlarge and become vacuolate in both species (Fig. 15d) although not consistently.

Gonimoblast filaments are relatively tightly appressed in D. hawaiiensis (Fig. 15c). Proximal cells frequently remain undifferentiated, and pit connections between them and the gonimoblast initiator cell enlarge only slightly in D. hawaiiensis but to at least 2 μm in some D. japonica carposporophytes. The gonimoblast initiator cell remains relatively small and slightly forked in D. hawaiiensis (Fig. 15d); in D. japonica, it enlarges somewhat as the carposporophyte matures (Fig. 13f). Although Robins and Kraft (1985) reported cystocarps to 180 μm in D. hawaiiensis, the ones I observed were smaller. Cystocarps to about 200 μm have been observed in D. japonica. Carposporangia to about 15 μm in diameter have been measured in D. hawaiiensis and to about 12 μm
in *D. japonica*. Carposporangia of both species stain lightly with aniline blue.

**Dudresnaya bermudensis** Setchell 1912:244

**INTRODUCTION**

This species was first collected by Farlow in February 1881 at Cooper's Island, Bermuda (Collins and Hervey 1917). Farlow apparently sent some of his material (#46 and #46X in part) to Bornet, who identified it as *Dudresnaya purpurifera* but wrote [in translation]:

46 and 46X. The two numbers belong to the same species. The trichophoric apparatus and the procarp are not different from those of our figures of *Dudresnaya coccinea*. However, I am not disposed to unite 46 and 46X with this species because the peripheral filaments are different. They are cylindrical in *D. coccinea*, but in the Bermudan alga they are oboval or round like those of *D. purpurifera*.

Setchell (1912:244) described the species as new. He distinguished it from other species of *Dudresnaya* by its moniliform rather than cylindrical assimilatory filaments and from *Acrosymphyton* by its *Dudresnaya*-like arppogonial and auxiliary cell branches. He likened its appearance to *D. verticillata* (as *D. coccinea*) but stated it to be more complanate and distichous. In addition to the characters already mentioned, it differed from *D. crassa* by "the absence of a single specialized (smaller) auxiliary cell in each auxiliary cell branchlet." Setchell also distinguished it from *D. japonica* and *D. australis* on the basis of vegetative and reproductive characters.

The holotype of *D. bermudensis* is housed in UC (160726). It is identical to the photograph in Setchell's paper and is
annotated in Setchell's hand, "type specimen of Dudresnaya bermudensis W A Setchell!" The sheet is also labeled "49." A second specimen on the same herbarium sheet can probably be considered an isotype even though it is labeled simply, "Cystocarps! W. A. S." Additional material of D. bermudensis labeled "49 in part" is found in FH, and these specimens should also be considered isotypes. More problematical is a specimen in NY stamped "type" and annotated "Dudresnaya bermudensis from type material." Although this specimen is indeed D. bermudensis, none of the labeling indicates that it is part of #49, and thus its position is equivocal. The remaining collections, #46 and #46X in part, can be considered syntypes since they were obviously used by Setchell in arriving at his concept of the species. Most of these specimens are labeled "Dudr. #2" in Setchell's hand. "Dudr. #1" is D. caribaea (J. Ag.) Setchell [now Acrosymphyton caribaeum (J. Ag.) Sjoestedt]; some of #46X is also this species.

Collins and Hervey (1917:150) included an additional record of this species from Bermuda: "St. George's, washed ashore, March, Hervey." However, Taylor (1952:32) pointed out that this second collection, gathered by Hervey at Buildings Bay, 2 March 1916, and distributed as P.B.-A. #2195, is Acrosymphyton caribaeum in the four sets of the P.B.-A. that he examined. To this list can be added the U.B.C. set. Howe (1920:583) included D. bermudensis in the Bahama flora, stating it to be "washed ashore, Great Bahama." I have yet to locate this collection. As far as I am aware, the only other collection of the species is one by Taylor from Buildings Bay, Bermuda, 30 March 1960, which
is deposited in MICH.

The following account of the vegetative and reproductive morphology is based on the Farlow and Taylor collections.

OBSERVATIONS

Specimens of *Dudresnaya bermudensis* are of moderate size. The largest observed was about 9 cm tall. The thallus is irregularly branched to at least 3 orders with branches of somewhat narrower diameters. Branches are usually somewhat narrower basally but not obviously constricted; they reach a maximum diameter of about 4 mm. Branch tips are acute except where eroded. Pressed specimens are straw pink in color (a faded Pompeian red in Ridgway's 1912 scheme). Although the thallus does not have a furry appearance as in some of the other species of *Dudresnaya*, the margins of distal branches appear to undulate in response to the periaxial whorls. Cystocarps are only rarely visible to the naked eye. Specimens adhere firmly to paper, but a dampened fragment can be easily removed intact.

Indeterminate branches terminate in a single dome-shaped apical cell (Fig. 16a). Whorl branches are initiated 3-4 cells from the apex, and by about cell 7 three whorl branches are usually present. Axial cells appear to bear at least three whorl branches; only occasionally four can be seen clearly. Whorl branches densely clothe the axis soon after their initiation. Behind the apex, axial cells enlarge so that cell 5 is 6-10 μm wide by 9-15 μm long, cell 10, 5-14 by 15-44 μm, and cell 20, 17-33 by 52-90 μm.

Cells of the axial filament can reach at least 750 μm in
length and 160 μm in width (including the cell wall). These cells are linked by pit connections about 5 μm in diameter. They bear their whorl branches near the midpoint of the cell. Refractive inclusions are prominent only in the isotype from the type sheet; they are round, quadrate, or an intermediate shape and attain a size of 6 μm on a side. They are particularly prominent in some cortical cells.

Rhizoids to at least 10 μm in diameter are present, but their origin could not be ascertained. Cells of whorl branches decrease in size toward the periphery. Nearly all cells of the whorl branch are di- or trichotomously branched from near their distal ends (Fig. 16b). Whereas basal cells are more or less cylindrical, more distal cells become obpyriform. Some surface cortical cells have short, narrow hair cells.

Female reproductive structures resemble those of other species of *Dudresnaya*. Carpogonial branches 7-11 cells in length were seen; only the distal 6-9 cells were differentiated (Fig. 16c). The branch is distally recurved; pit connections are somewhat centripetally displaced, but cells are only slightly wedge-shaped. The trichogyne is long but uncoiled. No fertilized carpogonia were observed.

Auxiliary cell branches to 17 cells in length were seen (Fig. 16d). As in other species of *Dudresnaya*, distal cells of the branch are not modified; basal cells can also be undifferentiated, resembling rhizoidal cells. The auxiliary cell can be 4-9 cells from the base of the branch. It is usually quadrate to discoid in shape and usually distinctly smaller than its immediate neighbors. [This size difference was
also noted by Taylor (1952:32) and is in contrast to Setchell's original characterization of the species.] The auxiliary cell appears to differentiate when first formed; in a 5-cell-long branch, the fourth cell from the base was already shaped like a future auxiliary cell.

Lateral branches are rare on both kinds of reproductive filaments.

Cystocarps to 200 μm were observed. They are only rarely visible to the naked eye. Proximal cells of the gonimoblast stain relatively darkly and appear not to differentiate. The stainability of carposporangia appears to decrease with maturity. Most carposporangia are 10-14 μm in diameter, but they can reach 18 μm in diameter.

One of the MICH specimens was male. Macroscopically, it differed from typical *D. bermudensis* by its fuzzy, distal annulations, distinctly narrower orders of branching, and overall pyramidal shape. However, microscopically it resembled this species by its obpyriform cortical cells. The catenate spermatangia are illustrated in Fig. 16e.

*Dudresnaya minima* Okamura 1932:86

**INTRODUCTION**

Okamura (1932:86) described a new species of *Dudresnaya, D. minima*, from the Inland Sea of Japan. This small (3-4 cm high, 1 mm thick), soft, gelatinous plant was originally diagnosed as "lower portion subnaked, densely branching upward in patent and irregularly dichotomo-alternate manner in an inverted triangular outline; auxiliary cell intercalary." The auxiliary cell was
identified as the second or third cell from the base of a 5-6-cell branch. Cells of assimilatory filaments were described as 2-3 times as long as broad.

A lectotype for this species has yet to be chosen.

Hasegawa (1949:52) recorded this species from Okushiri Island, a small island off the southwest coast of Hokkaido in the Sea of Japan. In addition to a description of vegetative and reproductive characters, he included several figures. His Text Fig. 2 shows a typical assimilatory filament of cylindrical cells terminating in unicellular hairs 50-60 μm in length (these can reach 220 μm). Two carpogonial branches, one 6 cells in length and one 7 were also figured; the basal cell of the latter was undifferentiated. Auxiliary cell branches 6-8 cells in length were illustrated. The auxiliary cell, the third cell from the base of the branch, was not strongly differentiated in these unbranched chains of moniliform cells. The gonimoblast developed from the remnant of the connecting filament attached to an auxiliary cell.

Kawashima (1959a:11) also observed female reproductive structures and post-fertilization development in Dudresnaya minima from northern Japan (Aomori Prefecture). He found carpogonial branches of 6-7 (-8) cells in length. Following fertilization, the carpogonium fuses with cell 4; it then cuts off a process that fuses with cell 5. Connecting filaments are cut off the carpogonial parts of the two fusion cells. Auxiliary cell branches (5-) 6-9 (-10) cells in length were observed. The auxiliary cell was usually the third cell from the base of the branch. Although Kawashima described the auxiliary cell as
producing "an uneven process, which fuses with the connecting filament," his figures clearly show what has been interpreted in other species of Dumontiaceae as remnant of connecting filament attached to the auxiliary cell, this connecting filament remnant then producing the gonimoblast. Kawashima believed that D. minima was more closely related to D. verticillata (as D. coccinea) than to D. crassa or D. japonica.

COMMENTS

Material of this species was not available during the course of this study. For further comments on this taxon, see COMMENTS under Thuretellopsis.

**Dudresnaya colombiana** Taylor 1945:162

INTRODUCTION

Cystocarpic fragments of *Dudresnaya colombiana* were first collected from Isla Gorgona, Colombia, 12 February 1934, by Taylor (1945:162). In describing the species as new, Taylor provided only a brief summary of its characteristics. The most distinctive feature appeared to be the oval, 4-7 μm diameter cells terminating the assimilatory filaments. Taylor did not include any figures with his description. The type collection includes three fragments mounted on mica. Two fragments are in the MICH type collection, and one is in the AHF type collection.

Mower and Widdowson (1969:76) identified a cystocarpic specimen from a rock outcrop in 20 feet of water at Little Harbor, Catalina Island, California, 20 November 1967 as this species. They provided the first figures of the species,
including a habit drawing. In another drawing, they illustrated an auxiliary cell as the second cell from the base of a filament of oval cells; the filament is one of 5 distally situated branches attached to the supporting cell. In a drawing of assimilatory filaments arising from an axial file, a young cystocarp is developing on a whorl branch some distance from the main axis at about the region where the vegetative cells change from cylindrical to oval.

Norris and Bucher (1976:8) attributed several specimens from the Gulf of California, Mexico, to this species. These specimens, collected at Isla Mejía, 23 April 1974, in 15-23 m and at Isla Estanque, 27 April 1974, in 9-11 m, reached a maximum height of 14 cm, a width of 3-5 (-10) mm, and sometimes exhibited four orders of branching. The translucent pink to rose thalli branched predominantly from their lower portion (also seen in Mower and Widdowson's specimen, Fig. 3a). They found axial filaments to range from (5-) 7 to 12 (-21) μm to 45-70 μm in diameter in broader, older parts. Assimilatory filaments branched dichotomously. Cystocarps were 120-180 μm in diameter, borne on an auxiliary cell usually the third cell from the base of an 8-17 cell unbranched filament of moniliform cells. Terminal spermatangial clusters were found on separate plants.

Like some of the other species of *Dudresnaya*, *D. colombiana* appears to be fairly rare. It is known from only three expeditions or collecting trips, and specimens from all three have been examined.
OBSERVATIONS

Specimens to 13 cm tall were observed. Thalli usually broaden above the base and reach a maximum width of 13 mm. Branching can occur to at least 3 orders, and each order is progressively narrower. Branches narrow slightly if at all basally. Margins are smooth. Color is a light rose pink (faded Acajou Red, Ridgway 1912).

Indeterminate branches tend to be clustered, a group of them arising in proximity to one another (Fig. 17a). This is manifested macroscopically on the thallus by its somewhat flabellate aspect and distal tufts of branches. Indeterminate branches terminate in a dome-shaped, slightly elongate (4-7 μm in diameter, 5-9 μm long, n=10) apical cell. Subapical cells are discoid and gradually enlarge away from the apex. Apical cells are exserted. Lateral branching is initiated 4-6 cells behind the apex and is frequently initially secund. Lateral (=whorl) branches can begin to branch when only two cells long, with one fork growing upward along the main axis and the other growing outward, as in Dumontia contorta. This pattern may be due in part to the closely appressed axes, whose overall aspect is reminiscent of some Delesseriaceae. This pattern may be responsible for the complanate habit of the plant. Basal cells of whorl branches are of the same shape as more distal cells of the branch but slightly larger. Cells of the branch decrease in size toward the surface of the thallus.

Axial cells to 100 μm in diameter and 700 μm long were measured. Three whorl branches are attached near the midpoint of each axial cell. Pit connections between axial cells reach 5
µm in diameter. Rhizoids to at least 5 µm in diameter were observed; they appear to develop from a dichotomous branch whose growth becomes deflected downward. One or more somewhat rhomboid refractive inclusions to 11 µm on a side can be found at times, usually near the ends of axial cells.

Assimilatory filaments are abundantly di- or trichotomously branched (Fig. 17b). Distally, cells are oblong-elliptical, sometimes hemispheric at the tip of the branch; these apical cells themselves can terminate in hair cells. The shape and size of these apical cells is about intermediate between the obpyriform type and the cylindrical type of other species of *Dudresnaya*. Proximally, cells enlarge predominantly longitudinally and develop shoulders (if dichotomous) and a neck (if trichotomous, see Fig. 17d.). Small, single, obpyriform cells can occur laterally on cells of assimilatory filaments; these cells appear to be initiating new branches.

Female reproductive structures resemble those of other species of *Dudresnaya*. Only two, moderately curved carpogonial branches were seen, and for both only the distal 5 cells were present (Fig. 17c). Carpogonial branches have not been recorded by earlier authors. It may be assumed that they disintegrate following fertilization, or lack thereof, as has been seen in other species.

 Auxiliary cell branches 10-16 cells in length were observed (Fig. 17d). The auxiliary cell is 2-8 cells from the base of the branch, usually the second cell from the base of a file of 4-5 differentiated cells. It appears not to differ in size or shape from its immediate neighbors. Auxiliary cell branches can
be borne as one branch of a trichotomy, sometimes in the center as in *D. patula*, or as one of two dichotomous branches. Basal cells of the branch can be assimilatory/rhizoidal in character; distal cells become assimilatory.

The auxiliary cell appears to be contacted as in other Dumontiaceae. Connecting filaments to 5 μm in diameter have been measured.

After fertilization, the auxiliary cell becomes lightly staining, but adjacent cells remain darkly staining. Three or four gonimoblast initials are cut off the lightly staining remnant of the connecting filament attached to the auxiliary cell (Fig. 17d). As the gonimoblast matures, proximal cells remain lightly staining; they do not necessarily differentiate into carposporangia. Mature carposporangia are lightly staining except for the nucleus; they are 5–12 μm in diameter. Pit connections between the auxiliary cell and its neighbors do not enlarge as the carposporophyte matures. Cystocarps to about 150 μm in diameter have been observed; they are not visible to the unaided eye.

Plants appear to be unisexual. Spermatangia are borne in groups of mostly 3 on small, specially-formed, mostly terminal spermatangial mother cells (Fig. e). They resemble those of *D. bermudensis* and *D. lubrica*.

**Dudresnaya lubrica** Littler 1974:149

**INTRODUCTION**

Littler (1974:149) described a new species of Hawaiian *Dudresnaya, D. lubrica*, which he distinguished by the small,
rounded terminal cells of vegetative branches. In *D. lubrica*, the carpogonial branch contains 5-6 modified cells and is distally recurved; it can bear laterals basally. Two carpogonial fusion cells are formed. Although Littler's figures show connecting filaments leaving the carpogonial fusion cells via pit connections as is typical for the family, they also show pit connections between the carpogonial derivative cells and the cells of the carpogonial branch to which they are fused; this phenomenon needs to be verified. Littler states, "Carpospores are produced directly by the fertilized branch system of *D. lubrica,*" but his discussion and illustrations portray the typical non-procarpic developmental pattern of the family.

As far as I am aware, *D. lubrica* is known only from the type collection, and the following observations are based on those specimens in BISH.

**OBSERVATIONS**

The largest specimen observed was 7 cm tall. Thalli are irregularly branched to at least 4 orders, and branches are of uniform diameter throughout, measuring 1 mm or less. Branches are not constricted basally. Branch tips are blunt, occasionally somewhat forcipate, and the margins are smooth. Color is a straw pink (a faded Acajou Red, Ridgway 1912). Cystocarps are visible to the unaided eye and are scattered in intermediate areas of the thallus.

Indeterminate axes terminate in a dome-shaped apical cell that divides transversely. Axial cells remain relatively small to at least 20 cells from the apex (Fig. 18a)—longer apical
fragments were not observed. Branching below the apical cell is moderately lax, but the few whorl branches that are cut off reach the level of the apical cell. Distal cells of whorl branches are oval to obpyriform, and proximal cells are cylindrical (Fig. 18b). The four to five (to six?) periaxial cells are relatively small and bear 1-3 assimilatory filaments and 1-3 rhizoidal filaments. They are initially ovoid to quadrate but soon elongate somewhat and can later increase in diameter. They are borne near the midpoint of the axial cells. Axial cells to about 850 μm long and 135 μm in diameter have been measured. They are linked by pit connections to 6 μm in diameter. Surface cortical cells can bear short hairs like those seen in *D. bermudensis*. Rhizoids to about 25 μm in diameter including the cell wall have been observed.

Round to quadrate refractive inclusions to 8 μm in diameter have been seen.

Female reproductive structures resemble those of other species of *Dudresnaya*. Carpogonial branches are 7-10 cells in length, but only the distal 5-6 cells are differentiated (Fig. 18c). The distal end of the branch is recurved due to cells 2 and 3, and cell 4 to a lesser extent, being wedge-shaped. Pit connections between these cells are centripetally displaced. The trichogyne is terminal to somewhat lateral on the base of the carpogonium, and it is straight. No fertilized carpogonia were observed, but Littler (1974) has already illustrated them. In Littler's figures, undifferentiated lateral branches can occur on proximal cells of these branches.

Connecting filaments measured 2-7 μm in diameter.
Auxiliary cell branches to at least 14 cells in length were observed (Fig. 18d). Although the distal ends of the branches appear to become vegetative, only rarely do they terminate in an assimilatory filament. The auxiliary cell is usually indistinguishable in size and shape from its neighbors, but it sometimes stains differently from the adjacent cells (either more lightly or more darkly). It is usually the second cell from the base of a file of differentiated cells. Subtending cells can bear up to 3 (4?) undifferentiated lateral branches. Contact of the auxiliary cell by the connecting filament and gonimoblast initiation appear to be typical of the family as illustrated by Littler (1974). Carposporangia stain relatively lightly and can reach a diameter of 30 μm. Pit connections between the auxiliary cell and its neighbors enlarge to 5 μm, but no fusions take place, and the pit connections further from the auxiliary cell enlarge proportionately less. As the gonimoblast develops, the auxiliary cell nucleus remains within the auxiliary cell, and the diploid nucleus remains in a corner of the gonimoblast initiator cell. Both of these fused cells stain relatively lightly, but the adjacent differentiated cells of the auxiliary cell branch and the basal cells of the gonimoblast filaments stain rather darkly (see Littler, Fig. 19). These basal cells appear not to differentiate into carposporangia.

Plants appear to be unisexual. Spermatangia are borne in groups of 4 or more on small, specially-formed, terminal spermatangial mother cells (Fig. 18e). As in D. bermudensis, they sometimes appear to be catenate.
**Dudresnaya patula** Eiseman et J. N. Norris 1981:188

**INTRODUCTION**

*Dudresnaya patula* was the name given by Eiseman and Norris (1981:188) to a compressed, gelatinous species from 32-58 m off the coast of Florida. This species was distinguished from others in the genus by its overall flattened aspect. Carpogonial and auxiliary cell branches were reported to be longer than those known for any other species and to be borne within the dichotomies of assimilatory filaments. Cells of both branches generally appeared moniliform. Furthermore, the carpogonial branches were described as straight; the carpogonium was said to be recurved toward the base of the branch, but cells 2 to 4 were not displaced from the branch axis. However, as in other Dumontiaceae, the five distal cells of the branch stained darkly with aniline blue, particularly cells 4 and 5, which were enlarged. Cells flanking the auxiliary cell were also enlarged and stained darkly whereas cells more distant from the auxiliary cell were less enlarged and stained less intensely.

**OBSERVATIONS**

A single herbarium specimen of *Dudresnaya patula*, the holotype (US 072305), was examined although slides of both the holotype and a paratype (US 072423) were also studied. The holotype is about 7.5 cm tall and about 15 mm wide at its broadest, with 8-10 simple or once forked branches to about 4 cm long and 5 mm across. These branches are generally not constricted basally.

Only a single indeterminate branch was seen, and this
appeared to terminate in an assimilatory filament (Fig. 19a). The filament was profusely branched throughout. Although distal cells were isodiametric-quadrate, cells soon began to lengthen and broaden. Axial cells to about 70 \( \mu \text{m} \) in diameter and 390 \( \mu \text{m} \) long were measured. Pit connections between axial cells can reach at least 4 \( \mu \text{m} \) in diameter.

Axial cells can bear up to 5 periaxial cells. These cells do not lengthen to the extent of more distal cells, but they increase more in diameter. They bear 1-3 unbranched rhizoidal filaments from their abaxial surface and a distal whorl branch. Cells of a whorl branch usually branch once, producing either a pseudodichotomous assimilatory branch or a lateral rhizoidal filament (Fig. 19b). Rhizoids can arise almost anywhere along an assimilatory filament. Occasionally, cells branch twice, but when two branches are present, at least one is rhizoidal. Cells of assimilatory filaments are initially cylindrical, but they develop arms as they mature. Apical cells of assimilatory filaments are 2-3 by 8-14 \( \mu \text{m} \).

Two very long cells were seen; one reached nearly 1650 \( \mu \text{m} \) in length but was only 90 \( \mu \text{m} \) in diameter; the other cell was slightly smaller. Both cells forked. One had three normal-sized dichotomously branched cells attached near the midpoint of the cell. I could not determine how these very long cells fit into the vegetative anatomy of the plant.

Refractive inclusions were not seen, but cells of the inner cortex themselves can become refractive. Clear vacuolar regions are sometimes present at the ends and branch points of these cells.
Reproductive filaments are borne distally on cells of assimilatory filaments between the arms or shoulders, if arms have not yet developed, of the pseudodichotomously branched cells. Usually only one reproductive filament is borne per cell, but occasionally two can be seen in the fork of a single cell. Rarely, a reproductive filament is borne as one of the dichotomies of an assimilatory filament. All cells of reproductive filaments are differentiated, usually round to elliptical to somewhat barrel-shaped. Only in one instance did I observe the apical cell of an auxiliary cell branch to resemble the apical cell of an assimilatory filament.

Occasionally, a lateral branch is associated with a carpogonial branch. In these instances, the basal cell of the filament is dichotomously branched, one dichotomy appearing rhizoidal, the other being a carpogonial branch.

Carpogonial branches 12-19 cells in length were observed (Fig. 19c). Cells 4 and 5 are particularly enlarged and darkly staining, cell 6 to a lesser extent. Cells 2 and 3 are distinctly smaller and stain less intensely. The carpogonium appears to be cut off cell 2 by a somewhat oblique wall, resulting in only a slightly recurved branch. The trichogyne is long and somewhat curved but never distinctly coiled. An elongating trichogyne that was 9 μm wide distally was seen, but most trichogynes are much narrower.

A single example of connecting filament initiation from a carpogonial branch was observed (Fig. 20a). Two enlarged carpogonial fusion cells attached to cells 4 and 5 were initiating connecting filaments. Because of the perspective, it
was not possible to see how the carpogonial fusion cells and carpogonium were connected, but the possibility of pit connections cannot be ruled out. Connecting filaments were initiated with or without pit connections. Some outgoing connecting filaments formed pit connections after a short distance; these cells then cut off at least two further connecting filaments. Connecting filaments to 8 μm in diameter were measured.

Auxiliary cell branches to 40 cells in length were observed. The auxiliary cell is the fourth to sixteenth cell from the base of the branch. Although all cells of the branch are differentiated from vegetative cells, only cells in the vicinity of the auxiliary cell are enlarged. The mature auxiliary cell itself is quadrate to slightly flattened (Fig. 20a). Cells on either side of the auxiliary cell can reach at least 25 μm in diameter. They stain darkly with aniline blue and continue to do so even as the carposporophyte matures. The cells adjacent to these neighboring cells show a rapid decrease in diameter.

A connecting filament appears to contact an auxiliary cell as in other species of *Dudresnaya*. A hint of a protrusion of an auxiliary cell toward a passing connecting filament was seen in one instance. The incoming and initial outgoing connecting filament form a distinct fork (Fig. 20b). A second outgoing connecting filament is usually formed without producing such a fork. Two or three gonimoblast initials arise from the gonimoblast initiator cell.

Mature carposporophytes can reach 285 μm in diameter; they
appear to envelop completely the auxiliary cell branch. Carposporangia can enlarge to 20-25 μm in diameter. Pit connections between the auxiliary cell and its neighboring cells can enlarge to about 2 μm, but pit connections between these neighbors and the cells beyond enlarge only slightly.

Neither spermatangia nor tetrasporangia were observed.

**Dudresnaya georgiana** Searles 1983:309

**INTRODUCTION**

Searles (1983:309) described a new species of *Dudresnaya*, *D. georgiana*, from a single collection made at Gray's Reef, Georgia, 26 July 1980, in 21.5 m. Searles distinguished his taxon from other species of *Dudresnaya* primarily on the basis of vegetative features. In particular, he noted that in most species of *Dudresnaya* assimilatory filaments are dichotomous throughout but that secondary branchlets at the base of determinate branches frequently occur in some other configuration. In *D. crassa*, the basal cell can bear more than two secondary branchlets, and in *D. georgiana*, up to 5. Searles also noted that the thallus is composed of loosely organized tufts of filaments that do not produce the cylindrical or complanate branches characteristic of other species and that large amounts of mucilage are lacking. Searles did not find any reproductive characters which distinguished his species from other species of *Dudresnaya*.

**OBSERVATIONS**

I have studied slides of the holotype and an isotype of *D.*
q. Georgiana. As noted by Searles, thalli are diminutive, 2 cm tall or less and only about 1 mm in diameter. The exserted apical cells are 4-5 μm wide by 6-7 μm long. Axial cells increase in size gradually: cell 5 was 4-6 by 4-6 μm, cell 10, 6-8 by 6-10 μm, cell 20, 8-11 by 16-20 μm, and cell 30, 9-12 by 27-36 μm. Apical cells are exserted because whorl branches also develop only gradually around the axis. Up to four whorl branches can occur on each axial cell. The first whorl branch first appears on cells 3-8, the second on cells 5-9, the third on cells 11-18, and the fourth on cells 14-36+.

Indeterminate axes are initially recognizable by the relatively small size of the cells compared to those of whorl branches and by the more abundant branching along the length of the primordium (compare Figs. 3 and 4, Searles 1983, Fig. 21a, this work).

Axial cells can reach a length of 700 μm and a diameter of 125 μm. Pit connections between axial cells attain 3-4 μm in diameter. Periaxial cells, initially quadrate to cylindrical, do not elongate as much as more distal cells. At maturity, they are irregularly quadrate (Fig. 21b). They bear up to six subsidiary filaments (Searles observed up to five). These subsidiary filaments can be rhizoids, whorl branches, or intermediate cells which themselves bear both rhizoids and whorl branches. Rhizoids are initially very slender but can increase in diameter to at least 75 μm. They envelop mature axial cells. Rhizoids occasionally bear secondary cortical laterals, which usually remain small and unbranched. Except at their origin, rhizoids do not branch to form other rhizoidal filaments.
Whorl branches can be at least 32 cells in length, but they are frequently shorter. They are relatively sparsely branched. Hairs are present, but they are not abundant. The longest hair measured about 130 µm.

Refractive inclusions are rare except in cells of branches bearing spermatangia. In these branches, refractive inclusions are round to rectangular, 5-6 µm in diameter or on a side.

Female reproductive structures resemble those of other species of *Dudresnaya*. Reproductive filaments typically occur somewhat abaxially on periaxial cells, or their basal cell can be the periaxial cell itself, but they can also occur up to at least four cells from a periaxial cell. Carpogonial branches can also develop from cells of rhizoidal filaments. Up to two reproductive filaments in any combination can occur on the same periaxial cell, and rarely a carpogonial branch and an auxiliary cell branch share the same differentiated basal cell. One or more unbranched lateral filaments can occur on the proximal cells of the reproductive filaments. In only one instance was an unbranched lateral distal to an auxiliary cell seen.

Carpogonial branches are 6-11 cells long (x=7.6, n=60; Figs. 21c-e). At maturity, the trichogyne terminates a relatively long (up to 10 µm) carpogonial base. Initiation of the trichogyne from the distal end of the carpogonium commences before cell 2 is cut off. Both cells 2 and 3 are cut off by slightly oblique angles. They are initially somewhat discoid but enlarge to become irregularly ovate-cuneate. Cell 2 enlarges more than cell 3 and in such a way that the pit connections between it and its adjacent cells, which were at
approximately 180° at initiation, approach 90°. As a result, the distal end of the branch becomes strongly recurved, and the trichogyne must consequently curve back on itself to reach outside the thallus. Cell 2 enlarges to 5-9 by 5-8 μm and cell 3 to 6-8 by 5-7 μm. Cells 4 and 5, which are nearly round, enlarge to about 8-10 μm in diameter. Cells 2 and 3 stain less intensely with aniline blue than cells 4 and 5, but their nuclei are nearly as large. Cells 6 to 9 can be round or cylindrical, but, when present, cells 10 and 11 are always cylindrical. Several examples of a trichogyne with a pit connection and a vegetative terminus were observed.

If unfertilized, the carpogonium appears to disintegrate. Connecting filaments are 3-4 (-6) μm in diameter.

Auxiliary cell branches are 7-16 cells in length (Fig. 21f). The auxiliary cell is the third or fourth cell from the base of the branch, occasionally the fifth cell. Two to four cells are differentiated; these cells are quadrate to round to discoid in shape. More distal cells are cylindrical and resemble cells of young whorl branches or indeterminate branch primordia. The auxiliary cell is not distinguishable from neighboring cells.

Contact of the auxiliary cell by a connecting filament is presumed to be as in other species of *Dudresnaya* (Fig. 21f). A second outgoing connecting filament is sometimes seen but not consistently. Two elongate, curved gonimoblast initials are formed on opposite sides of the gonimoblast initiator cell, which is relatively small and not strongly forked. Gonimoblast filaments eventually completely encircle the axis of the
auxiliary cell branch. No evidence of pit connection enlargement or lack of gonimoblast differentiation was seen. Cystocarps to 87.5 μm in diameter were observed. Carposporangia reached about 8 μm in diameter in these cystocarps, but none of the cystocarps or carposporangia appeared mature. These small cystocarps are not visible to the unaided eye.

Thalli are bisexual. Up to four spermatangia are borne on spermatangial mother cells, which are 3-6 by 5-10 μm (Fig. 21g). As previously mentioned, cells of branches bearing spermatangia frequently contain refractive inclusions. Another peculiarity of these branches is that they appear to be connected to the rest of the thallus by only wall material (i.e., no pit connection was evident), suggesting that their basal cell has disintegrated. In one instance, the subtending thallus appeared to be branching into the unoccupied space at the base of such a branch. As in other species of *Dudresnaya*, spermatangia can become spermatangial mother cells, and this phenomenon may account for the scattered occurrence of spermatangia along such branches. Spermatangia are occasionally seen on what appear to be normal branches, but these may just be at an earlier stage in the development of these distinctive branches.

No tetrasporangia were seen.

*Thuretellopsis peggiana* Kylin 1925:13

and *T. japonica* Segawa et Ichiki 1958:5

INTRODUCTION

*Thuretellopsis peggiana*, the type species, was described by Kylin (1925:13) from a cystocarpic fragment dredged at a depth
of about 10 fathoms near Friday Harbor, Washington. Kylin noted the similarity of the vegetative structure, which he described as uniaxial with verticils of densely branched filaments, to *Thuretella shousboei* (Thuret) Schmitz. However, *T. peggiana* had the female reproductive structures of a member of the Dumontiaceae: its separate carpogonial and auxiliary cell branches grow from the basal cell of the verticils; the fertilized carpogonium unites with one of the middle cells of the carpogonial branch, after which connecting filaments are formed that grow toward auxiliary cell branches; the connecting filament joins one of the middle cells of the distal, contents-rich 3-4 cells of the auxiliary cell branch, and the gonimoblast then grows from "this cell," all cells producing carpospores.

Norris and West (1966) collected cystocarpic specimens from 5-7 fathoms (9-13m) at Salmon and Hein Banks, southwest of San Juan Island, Washington, on 13 June 1964.

Dixon and Richardson (1969) successfully cultured carpospores of *T. peggiana*. Carpospores developed into a crust two cells thick in the centre and a single cell thick at the margin. Under a photoregime of 9:15 light:dark, surface cells of the crust produced cruciately divided tetrasporangia. Tetraspores germinated in a unipolar manner to give rise to upright gametophytes. Subsequently, Richardson and Dixon (1970) provided additional information on the morphology and life history of the species. They observed that each axial cell produces 4-6 pericentral cells, some of which develop into whorls of limited growth and some into the downward growing corticating (rhizoidal) filaments, which can themselves bear
whorl branches. Growth of whorl branches is limited by the conversion of their apical cells into hyaline hairs, or, in fertile material, into monosporangia or spermatangia. They observed reproductive filaments to develop from periaxial cells by either replacing a filament or, "by conversion of the apical cell of such a filament at an early stage of development." In cultured material, carpogonial and auxiliary cell branches frequently occurred on the same periaxial cell. Monosporangia to about 15 μm in diameter were reported on both the upright gametophyte and the prostrate tetrasporophyte. They produced plants of the morphology of their parents on germination.

The holotype of Thuretellopsis peggiana was collected by Kylin on 2 July 1924. It is represented in LD by a small, blackish, cystocarpic fragment. A fragment in UC (279527) is also small, blackish, and cystocarpic. The abundant hairs stand out on the mica slide, and the short, pseudodichotomous assimilatory filaments and the rhizoids cloaking the axes are also visible. This specimen is labeled co-type and appears to be part of the type collection.

Segawa and Ichiki (1958:5) described a second species of Thuretellopsis, T. japonica, from Misumi-Nishiko, Kumamoto Prefecture. They distinguished their species from the type by the "obtuse" apices of assimilatory filaments, usually lacking hairs, by the well-developed medulla of secondary descending filaments (=rhizoids), and by the subdichotomous, rather than irregular, division of the branches. They also stated that their plant was collected from a sheltered place near low-water mark in contrast to the distinctly subtidal habitat of the North
American species. Their figures show an alga remarkably similar not just to *T. peggiana* but also to *Dudresnaya minima*. Further collections and studies of this species are obviously needed.

**OBSERVATIONS**

The diminutive thalli of *Thuretellopsis peggiana* are 2 cm or less in height and less than 500 μm in diameter (Fig. 22a). They are bright rose pink when first collected. They can be abundantly branched in the primary order of branching; second-order branches are much less common.

Indeterminate axes terminate in a bullet-shaped apical cell 4-6 μm in diameter by 7-14 μm in length (Fig. 22b). This apical cell divides transversely to produce a series of approximately quadrate subapical cells that finally begin to enlarge about 12 cells from the apex. Up to five periaxial cells can be cut off, but there are usually only four. They initially densely clothe the developing axis, obscuring the apex to some extent, and they are situated distally on the elongating axial cells. Periaxial cells vary in shape from cylindrical to quadrate. Differences in size and shape may be related to the order in which they are cut off, but this hypothesis could not be verified. Periaxial cells branch pseudodi- and -trichotomously to produce relatively short (7-11-cell) whorl branches (Fig. 22c).

Periaxial cells also cut off 1-3 rhizoidal filaments which descend the axial file and can reach a diameter of at least 18 μm. As they grow, all older rhizoidal cells initiate a secondary cortical lateral that develops perpendicularly to the main axis (Fig. 22d). In the meantime, axial cells begin to
elongate more rapidly distally than proximally. Secondary cortical laterals derived from the rhizoids provide the majority of cortication in older parts of the thallus, where the axial cell can enlarge to at least 160 μm in diameter and 450 μm in length. Rhizoidal filaments rarely branch to produce secondary rhizoidal filaments. No cell of a rhizoidal filament was seen to produce more than one secondary cortical lateral. Secondary cortical laterals were generally less robust than the primary whorl branches (with smaller and fewer cells and fewer branches). In at least one instance, the basal cell of a cortical lateral was seen to be initiating a rhizoidal filament.

Indeterminate axes appear to be initiated as branched, percurrent axes of relatively small cells compared to assimilatory filaments.

Pit connections between axial cells can enlarge to about 3 μm.

No refractive inclusions were observed.

Female reproductive structures resemble those of Dudresnaya, but, like the thallus as a whole, they are diminutive. Both carpogonial and auxiliary cell branches are borne within 1 (-2) cells of a periaxial cell and can be borne on the periaxial cell itself. Occasionally, such a periaxial cell resembles a cell of the branch by its relatively small size and the small size of laterals developing from it. Reproductive filaments can also be borne on cells attached directly to a periaxial cell, either on a rhizoidal cell or a cell of an assimilatory filament. Reproductive filaments borne more than one cell from a periaxial cell are uncommon, but such filaments
may be seen in older parts of the thalli where determining the attachment of branches was sometimes impossible because of the density of the various filaments.

Carpogonial branches are 5-8 cells in length (Fig. 23a). The distal 5-6 cells are strongly differentiated whereas the proximal 0-3 cells, although smaller than nearby vegetative cells, are quadrate to cylindrical and can bear laterals. These laterals can eventually develop into normal assimilatory filaments.

The carpogonial branch is distinctly recurved due to the oblique nature of the two final divisions of the branch (Fig. 23a). Occasionally, the second oblique division does not occur—in one instance, there was only one somewhat enlarged cell between the carpogonium and "cell 4;" in another, the single cell between the carpogonium and "cell 4" had cut off a second cell on the flank directly opposite the carpogonium. The trichogyne can be variously coiled.

Following fertilization, the trichogyne is cut off the base of the carpogonium, which enlarges parallel to the carpogonial branch. The fertilized carpogonium then divides. One carpogonial derivative cell fuses with cell 5, the other with cell 4. At least one connecting filament is initiated from each carpogonial fusion cell in contact with another cell of the carpogonial branch (Fig. 23b). Usually, a pit connection is formed between the carpogonial derivative cell and the outgoing connecting filament. After one to several connecting filaments have been initiated, the distal 4-5 cells of the carpogonial branch begin to disintegrate. Remains of carpogonial fusion
cells are nearly impossible to detect in thalli with mature cystocarps.

Variations in early stages of post-fertilization development include the failure to form more than one carpogonial fusion cell because of the failure of the fertilized carpogonium to divide (Fig. 23b), and the fusion of one of the carpogonial derivative cells with cell 6 rather than cell 5.

As in other members of the Dumontiaceae, a connecting filament stains intensely only at its distal end, which contains a presumably diploid nucleus. Behind the nucleus, the filament collapses, and the remnant of wall material (and cytoplasm) is hardly visible (Fig. 23c).

Auxiliary cell branches are 4-12 cells in length (Figs. 23b, d, e, 24a-c). Such branches contain 1-5 strongly differentiated cells. The remaining cells, although smaller than normal vegetative cells, nonetheless resemble them in shape. Such undifferentiated cells proximal to the auxiliary cell frequently bear 1-2 lateral branches that can develop into assimilatory filaments (Fig. 23b). Undifferentiated cells distal to the auxiliary cell only rarely bear lateral branches and/or take on the appearance of assimilatory filaments (Fig. 23d).

The auxiliary cell is the second to fourth cell from the base of the branch. It is round, quadrate or slightly discoid. At first, it appears to be slightly larger than its neighbors (Fig. 23a), but at maturity it is usually somewhat smaller and stains somewhat more darkly with haematoxylin (Figs. 23b, d, e, 24b). Mature auxiliary cells are 8-10 μm in diameter. There is
no obvious difference in the size of the auxiliary cell nucleus and that of its immediate neighbors.

The auxiliary cell appears to be contacted as in other species of the Dumontiaceae (Fig. 24c). After contact, the auxiliary cell appears to increase slightly in diameter and becomes translucent except for its nucleus, which appresses itself to the auxiliary cell wall, often on the side opposite the gonimoblast initiator cell (Fig. 24d). The remnant of connecting filament shows only a slight forking that is lost as the gonimoblast begins to develop. I was not able to determine whether a second outgoing connecting filament is cut off the gonimoblast initiator cell prior to gonimoblast initiation. The gonimoblast initiator cell usually appears somewhat inflated from its inception. Three or four gonimoblast initials produce a tightly appressed gonimoblast. The gonimoblast initially develops to one side of the auxiliary cell branch (Fig. 24d), but at maturity it usually complete encircles the branch (Fig. 24e). Pit connections between the auxiliary cell and its neighbors enlarge only to about 1.5 μm and only slightly more between the auxiliary cell and the cell distal to it. Globose cystocarps can reach at least 175 μm in diameter; they are not visible to the unaided eye. Individual carposporangia can reach a diameter of about 20 μm at maturity; they stain darkly with aniline blue. Cystocarps vary in whether all cells mature into carposporangia or whether some of the basal cells of the gonimoblast filaments remain undifferentiated. In several instances, it appeared that some of the intermediate cells of the gonimoblast also sometimes fail to differentiate. If
unfertilized, the auxiliary cell and cells distal to it eventually disintegrate (Fig. 24b).

Thalli are bisexual. Three or four spermatangia are cut off the distal ends of spermatangial mother cells by slightly to distinctly oblique walls (Fig. 24f). Spermatangial mother cells are 4-5 µm in diameter and 7-10 µm long. They are formed on the distal cells of assimilatory filaments near the apices of indeterminate branches (Fig. 22b). As these branches mature, spermatangial mother cells can appear on more proximal cells of the whorl branches further from the apex. Branches tend to be protandrous, with spermatangia maturing distally to the developing carpogonial branches. Occasionally, two spermatangial mother cells were observed in a series, suggesting that one of the spermatangia on the more proximal mother cell had been transformed into a spermatangial mother cell itself.

Tetrasporophytes were not observed during this study.

COMMENTS

Descriptions of Dudresnaya minima, Thuretellopsis japonica, and T. peggiana suggest that these species are closely related. Since D. minima and T. japonica are found in the same geographical area, there is a higher probability that they are more closely related than either is to T. peggiana.

The cladogram in Fig. 91 shows that Thuretellopsis appears to be derived from a species of Dudresnaya and that the lineage that gave rise to it appears to be ancestral to other species of Dudresnaya. This situation makes indefensible the maintenance of Thuretellopsis as a genus distinct from Dudresnaya. I
therefore propose the following combination:

**Dudresnaya peggiana** (Kylin) comb. nov

**Basionym:** *Thuretellopsis peggiana* Kylin 1925:13, Fig. 5.

**Acrosymphyton** Sjoestedt 1926:8

The genus *Acrosymphyton* has been maintained in the Dumontiaceae since its original diagnosis by Sjöstedt (1926:8). Its position there arose in part by the inclusion of its type species, *A. purpuriferum* (J. Ag.) Sjöstedt, in the genus *Dudresnaya* when the species was first described. Its maintenance in the family probably occurred because of similarities in post-fertilization development between it and other members of the Dumontiaceae. In *Acrosymphyton*, as well as in other Dumontiaceae, other cells of the carpogonial branch are contacted by an outgrowth of the fertilized carpogonium prior to connecting filament formation, and an auxiliary cell on a separate, modified branch is contacted by a connecting filament prior to gonimoblast initiation from a remnant of the connecting filament attached to the auxiliary cell. The unique morphology of the carpogonial and auxiliary cell branches and details of post-fertilization development suggest, however, that *Acrosymphyton* may be better allied elsewhere than with the Dumontiaceae.

A review of pertinent literature revealed that the two characteristics that linked *Acrosymphyton* to the Dumontiaceae are shared with a variety of taxa in several different families and orders. An outgrowth of the carpogonium that fuses with
other cells of the carpogonial branch before initiating gonimoblast filaments directly or indirectly (i.e., not until after an auxiliary cell has been contacted) is also seen in the Dermonemataceae (Svedelius 1939), the Helminthocladiaceae, the Naccariaceae (Kylin 1928), the Calosiphoniaceae (Feldmann 1954), the Peyssonneliaceae (Nozawa 1968), and the Polyidaceae (Rao 1956, Nozawa 1963). Among these taxa, a remote auxiliary cell is contacted prior to initiation of gonimoblast filaments in species of the last three families.

These observations suggest that these two character states, like the uniaxial habit (see Hawkes 1982:453), are plesiomorphic. Since grouping taxa on the basis of plesiomorphic character states rather than apomorphic traits tends to produce grades rather than clades, the removal of Acrosymphyton from the Dumontiaceae is warranted. Its unique reproductive morphology and aspects of post-fertilization development do not allow its immediate alliance with any other genus or family. Similarities of certain character states not shared with other Dumontiaceae are seen in some families already mentioned: abundant lateral branches on cells of the carpogonial branch in Atractophora (Naccariaceae; Kylin 1928) and a basally coiled, elongate trichogyne, production of a single gonimoblast initial from an irregularly septate connecting filament in contact with a remote auxiliary cell, and development of a relatively small, compact cystocarp in Bertholdia (=Schmitzia, Calosiphoniaceae; Feldmann 1954).

_**Pikea californica** Harvey 1853:246_
INTRODUCTION

The genus *Pikea* and the type species *P. californica* were described by Harvey (1853:246) from sterile specimens collected at Golden Gate, California, and sent to him by Capt. Nicholas Pike. The genus was described as, "Frond plano-compressed, linear, cartilaginous, internally costate, distichously decompound, composed of three strata..." The three strata were: (1) the central, articulated, axial filament, (2) an intermediate layer of slender, longitudinal, densely packed, anastomosing rhizoidal filaments, and (3) the outer cortical layer of small cells. For the species diagnosis, Harvey went on to describe the manner of branching: "branches irregularly disposed, repeatedly compound, irregularly pinnate or secundly ramulose, the divisions erect-patent; sometimes opposite, frequently secund, the upper ones plano-compressed; ultimate ramuli filiform or subulate, acute, not tapering at base, very erect, unequal, long and short intermingled."

Harvey included *Pikea* in the "Genera Incertae Sedis" of his Rhodospermae because of lack of reproductive structures. Based on its vegetative characteristics, he felt it belonged to either the Ceramiaceae, near *Carpoblepharis*, or to the Sphaerococcoideae, but he recognized the vegetative structure as distinct enough to warrant a new genus.

Following the species diagnosis, Harvey included a longer description of the specimens. In addition to the characters already mentioned, he wrote that the thalli were 3-4 inches high (about 7.5 to 10.0 cm), the branches half a line to a line in breadth (about 1-2 mm), nearly flat to nearly terete, rather
naked in the lower part but closely and repeatedly divided above, the color a brown-red. He described the anatomy of both a transverse section and a longitudinal section. In particular, he noted the large central axial tube surrounded by two or more smaller tubes and a plexus of narrow "endochromatic" longitudinal filaments; a narrow rim of minute, spherical, colored cells occupied the periphery of the section.

Harvey referred to specimen 50, in part, and 78 (v.s. in Herb. T.C.D.). A request for these specimens to TCD produced two sheets. One sheet (Fig. 25a) contained a single specimen mounted separately and pinned to the herbarium sheet, labeled "50" and "C" in the upper right corner (all labeling appears to be in Harvey's hand), "Pikea californica WHH" in the upper left, "Ceramiaceae!" and "September 1851" in the lower right, and "b" and "Golden Gate, California" in the lower left. Also in the left corner of the sheet are two drawings. One drawing is a transverse section showing a central axial filament labeled "axial cell easily escapes notice unless cut through a node" surrounded by a "dense filamentous" area extending to the cortex. The other drawing shows a longitudinal section with the central axial filament surrounded by a "dense plexus" of rhizoidal filaments and a thin cortex.

The second sheet, labeled "Sheet D" in the upper right corner, has three separate sheets of specimens pinned to it (Fig. 25b). The upper sheet (Fig. 25c) is labeled "in part only," "50," and "1" in the upper right corner, ",(sent to Hooker. 1853)" and "Sept. 1851" in the lower right, and "Pikea californica WHH," "a." and "Golden Gate" in the lower left
together with a drawing of a transverse section. The drawing is labeled "upper ramulus" and shows a central axial filament and two lateral filaments amid rhizoidal filaments. The other two sheets attached to Sheet D are not *Pikea*. The middle sheet is labeled "78" in the upper right, "1851" in the lower right, and "Golden Gate" in the lower left. Near the lower right is written "Farlowia compressa W.A.S." in Setchell's hand. The third sheet is labeled "2" in the upper right and "Pikea californica WHH," "c" and "Golden Gate, California" in the lower left. Near the lower right is a drawing of a transverse section of the thallus showing a "central cell" below which is written "Ceramiaceae:". This plant was also annotated by Setchell: "Farlowia, probably F. compressa, W.A.S."

I concur with Setchell's determinations. The two *Farlowia* specimens are broader (and flatter, if one goes by the drawings) than the two *Pikea* specimens, and a midrib is discernible as a more lightly colored line running through the thallus (particularly in specimen 78).

Harvey (1858:131) amended the species description to include XLIX. B., which included sketches of two specimens and of a longitudinal and transverse section. The sketches of the two specimens do not precisely match either of the specimens present in TCD. However, I feel that they resemble 50C most closely, and I have accordingly selected that specimen as the lectotype.

J. Agardh (1876:250) placed *Pikea* in his "Ordo Dumontieae" and included it with *Cryptosiphonia* and *Nizzophlaea* (=*Dasyphloea*) in the Tribe Cryptosiphonieae. Although J. Agardh
believed *Pikea* and *Cryptosiphonia* to be very much alike, he discussed only their differences: flattened and pinnately branched versus cylindrical and radially branched; an axial siphon densely clothed in longitudinal filaments versus an axial siphon surrounded by loosely arranged branches, this distinction extending into the fertile parts of the thalli; relatively numerous, small carposporangia versus relatively few, large carposporangia.

Schmitz (1889) also apparently observed reproductive material of the species, and Schmitz and Hauptfleisch (1897:519) briefly described the female reproductive structures.

Setchell (P.B.-A. 648) described a second species, *P. pinnata*, based on specimens "growing on stones at and just below extreme low water mark at Fort Point, San Francisco, California, Feb. 18, 1898." (This site is probably only a stone's throw from the type locality of *P. californica*.) Setchell distinguished *P. pinnata* by its flexuous, decidedly flattened and usually narrow primary branches beset by regularly pinnate secondary branches. He placed his species in *Pikea* because the female specimens had cystocarps "situated in the short and much swollen tips of the branchlets, considered by Schmitz to be characteristic of the genus *Pikea*." The sterile specimens in UBC bear a marked superficial resemblance to *Bonnemaisonia nootkana*.

The type specimen of *Pikea pinnata* (Fig. 25d) is deposited in UC (UC 95041). It is one of four cystocarpic specimens on separate pieces of paper attached to a single herbarium sheet to which is affixed the P.B.-A. 648 label. All specimens include
the number 1807 in the upper right corner, and along the top of the label is written "=#1807." The upper right specimen is annotated, "type specimen W.A.S.," in Setchell's hand. It is the largest specimen, approximately 20 cm long (the basal discs are missing on all four specimens). The main axis is only about 1 mm in width and successive orders of branching are progressively narrower. A maximum of four orders of branching occurs. Cystocarps appear as swollen bumps and can occur on all but the final order of branches (Fig. 26a; the final order appears too narrow to support such structures). On the shorter branches, the cystocarps appear as a series of one or more bumps occupying the width of the branch with sterile tissue occurring both distally and proximally. On the longer (and broader) branches, the cystocarps appear as lateral warts along either or both sides of the branch.

An additional sheet of *Pikea pinnata* from the type collection (UC 95040)--this one with two apparently sterile specimens--has been annotated *Pikea californica* Harvey by Dr. I. A. Abbott.

The *Phycotheca Boreali-Americana* has, in addition to *Pikea pinnata*, specimens of *Pikea californica* (P.B.-A. 897, 1901), collected by Mrs. E. Snyder at Pacific Beach, California. The UBC specimen (Fig. 26b) is irregularly, almost secundly branched. Under the microscope, the characteristic axial structure is discernible even without sectioning or staining. In transverse section, short, sterile reproductive filaments characteristic of the family are present. No collection date is given.
DeToni (1903, 4 (Sec. III):1630) included the genus *Pikea* and the species *P. californica* in his *Sylloge Algarum*.

Okamura (1921:127, Pl. 181 Figs. 1-6) recognized *Pikea californica* as an element of the Japanese flora. His description is similar to Harvey's, but he included a somewhat sharper analysis of the vegetative anatomy:

Central axis consists of cells of larger calibe [sic], from which branches arise on all sides: of them those standing on the frank [sic] give rise to the central axis of lateral branches, while those on the surface-side remain short without developing to branches. From the cells of the axis cortical cell-filaments arise, and rhizoidal cells which fill up the inner cavity of frond are abundantly produced both from axial and infra-cortical cells. In growing apex terminal cells are horizontally articulated.

Doty (1947) included both *Pikea pinnata* and *P. californica* [as *P. nootkana* (Esper) Doty] in his *Oregon flora*. He synonymized *P. californica* with *Fucus nootkanus* on the basis of the similarity of Harvey's (1858, Pl. 49) Fig. B and Esper's (1802) Pl. 125. (Silva 1953:225 has since shown that the name *Fucus nootkanus* properly applies to a species of *Bonnemaisonia*, for which he has made the appropriate combination.) Doty discussed the fact that there are 4 quadrately disposed filaments from at least some cells of the axial filament and that the quantity of rhizoids increases and the arrangement of macroscopic branches becomes irregular with age. He further believed that *Leptocladia conferta* was a growth form of *P. californica*.

Dawson (1953:87) provided a detailed description of *Pikea californica*, which he recorded from Pacific Baja California (Punta Baja). He distinguished it from *Leptocladia binghamiae*, with which it could be confused, by its more slender
proportions, its usually denser branching, its cystocarps aggregated in the swollen ends of the narrow ultimate branches, and the presence of more than one large filament in addition to the central primary axial filament.

Abbott (1968:182) was the first to describe in detail and illustrate reproductive features for the genus. She wrote that the carpogonial and auxiliary cell branches developed "as accessory filaments of the early derivatives of the basal cell of a lateral and lie between the medullary and cortical areas." The recurved carpogonial branches contained 12-20 cells. After fertilization, "the carpogonium fused directly with the third or fourth cell behind it from which there is produced a primary connecting filament which grows toward an auxiliary cell and fuses with it." Auxiliary cell branches averaged 8 cells and could have sterile laterals at the base. The auxiliary cell was the second or third cell from the tip of the branch. Cells adjacent to the auxiliary cell participated in gonimoblast formation, and the gonimoblast, nearly all cells of which became carposporangia, produced several massive lobes which pushed up the cortex and formed "irregular, bumpy nemathecia-like areas subterminal to the tips of the thallus." Abbott also observed spermatangia which she described as "superficially produced in whitish patches at the tips of the younger parts of the thallus." Her figures show reproductive filaments developing between the cortical and medullary layers (Figs. 7, 10, 11), a carpogonial branch with two spermatia attached distally to the trichogyne and the carpogonium initiating a lateral process (Fig. 8), and the fusion of a connecting filament with an
auxiliary cell (Fig. 9; the disposition of the cells in this figure are also interpretable as a single carpogonial fusion cell initiating a solitary connecting filament).

In addition to the type species, to which Abbott attached *P. pinnata* Setchell and *P. nootkana* Doty, non *Fucus nootkanus* Esper, Abbott recognized a second species, *P. robusta*, which encompassed Smith's (1944:202) and Doty's (1947:164) *P. pinnata*. She described this species as up to 40 cm tall, main axis 1.5 to 4 mm wide, strongly flattened, pinnately branched to 3-4 orders, mature thalli pyramidal in shape, and cystocarps occurring in small wartlike nemathecia involving an entire branchlet. Abbott recorded specimens of this taxon from northern Washington to San Luis Obispo Co., California. She particularly stressed the wide, flattened main axis and the terminal wartlike cystocarps as features distinguishing her new species from *P. californica*.

I have seen the holotype of *Pikea robusta* (Fig. 26c). It is a sterile specimen collected by G. M. Smith from cast ashore material at the south end of Carmel Beach, California, 20 July 1939 (formerly GMS 4582, now US 084196). This fragment, pinnately branched to four orders, is about 14 cm tall and attains a maximum width of about 3 mm. In color, it falls between Carmine and Ox-blood red in the Pure Color category and between Acajou red and Vandyke red in the 32% Neutral Gray category (Ridgway 1912). Nothing except width distinguishes it from other specimens which Abbott has identified as *P. californica*, and I prefer to consider it only a wide variant of *P. californica*. If further studies do prove it to be a distinct species of *Pikea*, however, its pinnate habit suggests it should
be considered a synonym of *P. pinnata*.

Scott and Dixon (1971:295) cultured carpospores of *Pikea californica*. Each carpospore germinated to form a short filament. The lateral branches of these filaments aggregated to form a disc. The crusts in cold (10° C), low light (25 ft-c), and short-day conditions (8:16 light:dark) grew much more slowly than those under warmer (16° C), brighter (100 ft-c), longer-day conditions (16:8). Both cell size and number of cell divisions were inhibited by the former conditions. Crusts under low-light conditions produced numerous filamentous outgrowths, many of which terminated in callus-like clusters of cells. Monosporangia 5 μm in diameter developed from the upper cell layers of the crust or from the cells of the unbranched marginal proliferations, especially under low light and short photoperiods. Cruciate tetraspores, 16-20 μm in diameter, were induced to form terminally on cells of the callus-like clusters on plants transferred from 8:16, 10° C to 12:12 or 16:8, 16° C. Isolated tetraspores germinated in a manner similar to the carpospores and eventually gave rise to upright thalli vegetatively similar to the gametophytes of *P. californica*. Upright plants developed from tetraspores within 3-4 weeks in 16:8, 16° C, 100 ft-c, but they arose only after nearly one year in 8:16, 10° C, 25 ft-c. Scott and Dixon noted the occurrence of cystocarpic specimens only during the winter months (in this case, November through January); their specimens came from Morro Bay, San Luis Obispo Co., California.

In contrast, Chihara (1972a:314) found cystocarpic plants of *Pikea californica* on October 1 and again on May 1 in Chiba
Prefecture, Japan. His released carpospores, 11-13 μm in diameter, germinated in the same, usually unipolar manner as that observed by Scott and Dixon, but the resulting crusts produced upright thalli directly apparently without the intervention of tetrasporangia.

Collins (1913:128) reported *Pikea californica* from Ucluelet and Port Renfrew, British Columbia. Scagel (1957:143) included new records of both *P. californica* and *P. pinnata* from Washington. Garbary et al. (1980:322) found it in northern British Columbia, and Hansen et al. (1982:121) recorded it from the northern Gulf of Alaska. Along the eastern North Pacific, then, it is known to occur from Prince William Sound, Alaska, to Punta Baja, Baja California, Mexico. It occurs on rock from the extreme low intertidal into the upper subtidal zone, usually on moderately exposed shores, but populations are also known from the San Juan Islands, Washington (UBC A1796, 1797, 60395) and from Vancouver harbor (UBC A65881, 65889, 66392).

Japanese specimens are reported from the central part of the Pacific coast of Honshu (Chihara 1975:275).

Recently, Christine Maggs (19 July 1983) of University College, Galway, Ireland, communicated to me specimens of a species of *Pikea* very close if not identical to *P. californica*, which she collected in the Scilly Isles off the end of Cornwall, England, 3 July 1983 (Fig. 26d). These specimens represent the first record of the genus *Pikea* in the North Atlantic. Subsequently, Dr. M. Guiry (11 October 1983) provided me with a portion of a specimen of this taxon collected by D.E.G. Irvine at Long Point, St. Agnes, Scilly Isles, 8 Sept. 1967.
Parker and Dawson (1965:288) described a species of fossil algae, which they felt was remarkably suggestive of *Pikea pinnata* in its general size, habit, and branching. However, as they noted, the branching of *Paleopikea cranei* tended to be more alternate than opposite, and I would conclude from their figures that their species is not readily referable either to the *Pikea* lineage or to any other part of the Dumontiaceae.

**OBSERVATIONS**

*Pikea californica* is uniaxial. A dome-shaped apical cell divides transversely to produce subapical discoid cells which subsequently cut off two major and two minor whorl branches (Fig. 27a). The major whorl branches, in turn, branch abaxially, starting with cells near the middle of the branch. About 8 to 10 cells behind the apex, the cells of the axial filament begin to enlarge abruptly. (In one instance, cell 13 was 30 \( \mu \text{m} \) in diameter by 30 \( \mu \text{m} \) long and cell 14, 40 by 40 \( \mu \text{m} \); in another instance, cell 13 was 20 by 35 \( \mu \text{m} \) and cell 14, 25 by 45 \( \mu \text{m} \).) The axial cells continue to enlarge to at least 150 \( \mu \text{m} \) in diameter and 650 \( \mu \text{m} \) in length. The pit connections between axial cells enlarge to a maximum diameter of only 4 \( \mu \text{m} \).

In other genera, the growth of the major whorl branches produces a gentle upward sweep of these branches (see *Farlowia mollis* below, e.g.). In *Pikea*, the whorl branches appear nearly parallel to the main axis only one cell removed from the axial cell (Figs. 27b, 28c). This phenomenon occurs by the differential growth of the periaxial cell supporting the whorl branch. Near its point of attachment to the axial cell, the
periaxial cell elongates perpendicularly to the axis, effectively pushing the whorl branch away from the axis. The distal end of the periaxial cell elongates parallel to the main axis, thereby producing a somewhat L-shaped cell. Rhizoids develop from these periaxial cells and from other inner cortical cells and form a dense covering around the axial cell. Secondary pit connections form between the cells of a major whorl branch and those of the major whorl branch developing parallel to but just outside it (Fig. 27b). Secondary pit connections also form between branch cells and rhizoidal cells. Whorl branches become deflected somewhat outwardly as they leave the thallus in macroscopic lateral branches. The fate of minor whorl branches could not be followed. Since the pattern of macroscopic branching is distichous, it is assumed that the minor whorl branches serve only to provide cortication.

In transverse section, *Pikea* displays a broadly elliptical to nearly rhombic aspect. The axial cell is usually represented by a rather large central lacuna. Along the main axis of the ellipse, in line with the central axial lacuna, one or more smaller lacunae indicate the locations of successive major whorl branches as they course upward along the axial filament before swerving outward into their own macroscopic branches. The central region of the ellipse surrounding the lacunae is filled with rhizoids. From among the rhizoids emerge the somewhat enlarged and elongate cells of the inner cortex. These cells branch, forming a cortex of 9-10 layers of progressively smaller cells. The inner cortical cells can be multinucleate due to the formation of secondary pit connections.
One or more subquadrate refractive inclusions to about 7 μm on a side were detected in some cells.

*Pikea* exhibits two basic gross morphologies. Harvey (1853) recognized one type in his original description of the genus. Setchell recognized a second type in his description of *P. pinnata*; this type appears to be identical to Abbott's *P. robusta*. I believe these two types represent forms of one and the same taxon. The "pinnata-robusta" type appears to represent young specimens—they are usually relatively broad (to about 4 mm wide) but flat, bright rose-red, and abundantly and regularly pinnately branched. The "californica" type, in contrast, appears to represent older specimens—they are narrower and more cylindrical, nearly black in color (except at the distal, younger ends), and very irregularly branched. Since this species is believed to be perennial, a gradation in forms is expected, particularly one which goes from broad and flat to narrow and cylindrical (due to an increase in internal rhizoid production and possible erosion of the marginal alae), from bright red to dusky (due to the production of protective pigmentation), and from regularly to irregularly branched (due to erosion and grazing) as the thallus ages. Since the two forms seem to grow in the same habitat and to have the same geographic range, one can expect them to represent different stages in the development of a single thallus. However, only critical field observations or experiments can verify the identity of these two forms.

Macroscopically, *Pikea californica* can be described as initially flattened, distichously branched to five orders,
progressively narrower from a main axis ranging from less than 1 mm to about 4 mm wide. Branching is initially regularly pinnate, becoming irregular with age. A faint midrib is occasionally evident due to internal rhizoid production. Thalli can reach 25 cm in height, but thalli 5-15 cm tall are more common; they can become extremely bushy with age.

_Pikea californica_ appears to have a very restricted fertile period. A few spermatangia have been observed on plants collected in late August and early September, but females have not been detected in these collections. Fully mature males and females were present in an October 1 collection, and several specimens showed early post-fertilization stages of gonimoblast production. Mature cystocarps have been observed in plants collected from late October to mid February in the northeast Pacific. Only unisexual thalli have been observed.

Reproductive filaments develop from inner cortical cells or rhizoids. All cells of the reproductive filaments are differentiated (Figs. 29-32). In mature filaments, distal cells are enlarged and elliptical-cuneate. Filaments are 6-15 cells in length, and a few short lateral branches are typical. The basal cell of a filament occasionally bears an undifferentiated lateral the same length as the filament itself, and the lateral can itself be branched. Rarely, rhizoidal filaments extend from the basal cells of a reproductive filament (Fig. 31g). Now and then, a single-celled lateral is borne on a middle cell of a filament (Figs. 31b, c); this middle cell can be the auxiliary cell (Fig. 31e).

The carpogonium is initiated as a somewhat narrow
projection, usually before cell 2 is cut off (Figs. 29a, b). As the trichogyne elongates, the distal cells of the branch enlarge (Figs. 29c, d). If unfertilized, a mature carpogonial branch appears to disintegrate, beginning with the carpogonium, followed by cells 2 and 3, and finally by cells 4 and 5. During this process, cells 2-5 initially appear somewhat refractive (i.e., opaque, no nuclei visible), but later they become lightly granular. In other instances, a number of nearly fully differentiated carpogonial branches were observed reverting to vegetative growth (Fig. 30e). Carpogonia with forked trichogynes were also observed on occasion.

After fertilization, the trichogyne separates from the basal part of the carpogonium (Fig. 29f), and this basal part of the carpogonium enlarges and divides. One carpogonial derivative cell fuses with cell 5, to which it is adjacent (Figs. 30a, b). The other carpogonial derivative cell fuses with cell 4, and both carpogonial fusion cells begin to initiate connecting filaments (Fig. 30d). A number of carpogonia were observed which appeared, because of their characteristic staining properties, to have been fertilized, but these showed no further development. At other times unfertilized disintegrating carpogonia appeared to have expanded toward cell 5 but without dividing or making contact. Several old carpogonial fusion cells were observed. In these, a series of two or three nuclei, possibly all in one cell, were seen, and pit connections showed the sites of earlier outgoing connecting filaments (Fig. 30c).

Auxiliary cells appear not to differentiate from
neighboring cells until fertilization occurs. In the single reproductively mature specimen in which no fertilized carpogonia or carpogonial fusion cells were observed, numerous incompletely differentiated auxiliary cell branches were seen. These branches terminated in a file of small but darkly staining cells (similar to *Farlowia molliss*, shown in Fig. 35e).

The auxiliary cell can be cell 2 to cell 6 of the filament bearing it (Figs. 31a-g). It is distinctly smaller than the enlarged neighboring cells. The auxiliary cell itself occasionally bears two distal cells (see *Weeksia digitata* below), but only once did I see such an auxiliary cell that had been contacted by a connecting filament.

A degree of reproductive filament polymorphism existed among specimens of *Pikea* collected at Execucution Rock, 1 Oct. 1983. Two of the plants examined occasionally displayed a second cell attached distally to the auxiliary cell. In one of these plants, the auxiliary cell was usually the cell 2 or cell 3, rarely cell 4, and never cell 5 or cell 6. The auxiliary cell branches were 7-15 cells long, averaging 11.6 cells (n=61), and the carpogonial branches displayed a similar range in lengths. In the other four plants examined, the auxiliary cell was usually cell 3 or cell 4, occasionally cell 5, and rarely cell 2 or cell 6. Carpogonial and auxiliary cell branches were of similar lengths, 6-11 cells (13, in one of about 150 measured), and averaged 7.8 and 8.2 cells, respectively (n=60), in one of these specimens.

Cells adjacent to the auxiliary cell are the largest of the branch and possess the largest nuclei (Figs. 31, 32). Further
from the auxiliary cell, the cells of the branch and their nuclei become progressively smaller. This observation suggests that the auxiliary cell exerts a direct influence on the degree of differentiation of cells of the branch.

The auxiliary cell is contacted in a manner similar to other Dumontiaceae: as the connecting filament passes the auxiliary cell, its nucleus divides, and the connecting filament segments (Fig. 32a). One nucleus follows the onward-growing connecting filament; the other remains in the gonimoblast initiator cell, which fuses with the auxiliary cell. A second connecting filament is frequently produced (Fig. 32b) prior to production of 2-4 somewhat elongate gonimoblast initials (Fig. 32c). As the carposporophyte matures, the pit connections between the distal cells of the auxiliary cell branch can enlarge to a maximum diameter of about 3.5 μm, and some cell fusion can occur between distal cells. Distal cells can contain many small (about 2 μm in diameter), darkly staining granules in addition to their still enlarged nuclei (Fig. 32d). The pit connections between the gonimoblast cells enlarge to a maximum diameter of only about 2.5 μm. Most cells of the gonimoblast become carposporangia, but some of the proximal cells can remain undifferentiated.

No ostiole appears above the maturing cystocarps, which notably swell the branchlets bearing them. Release of the carpospores is assumed to occur by progressive erosion of the fertile branchlets.

Some auxiliary cells and cells distal to them appeared to be disintegrating, possibly indicating their fate if
unfertilized.

Abbott distinguished *Pikea robusta* from *P. californica* in part by terminal, wartlike cystocarps. I have seen no cystocarpic specimens identified as *P. robusta* by Dr. Abbott. Among the specimens she identified as this species are found several (US 085141, 085142) which have wartlike protuberances along the final orders of branching. However, these protuberances are sterile and may be a kind of gall. They appear to be fairly common among specimens from California (seen also on UBC A62019). Since carposporangia seem to be released by the erosion of the branchlets bearing the cystocarps, terminal cystocarps should be found after the tips of the branchlets bearing them have been eroded.

Spermatangia are borne, usually in pairs, on short, somewhat quadrate spermatangial mother cells 2-3 \( \mu \text{m} \) wide by 4-6 \( \mu \text{m} \) high (Fig. 27c). As in other Dumontiaceae, a spermatangial mother cell can itself produce another spermatangial mother cell. The spermatangia are 1.5 - 3.5 \( \mu \text{m} \) wide by about 5-8 \( \mu \text{m} \) long and possess a distal nucleus. Long (to 16 \( \mu \text{m} \)), sterile cells can occur among the spermatangial mother cells and spermatangia.

No other reproductive structures were observed.

**Farlowia mollis** (Harvey et Bailey)

*Farlow et Setchell 1901:898*

**INTRODUCTION**

J. Agardh described the genus *Farlowia* and distinguished two species, *F. compressa* J. Ag. (1876:262) from Monterey Bay,
California, and *F. crassa* J. Ag. (1876:262) from the coast of Oregon. He recognized these species as members of the Dumontiaceae by their characteristic short-celled and curved moniliform filaments bearing gonimoblast filaments between the inner cortex and the medulla. He distinguished *Farlowia* from most other genera of Dumontiaceae by its lack of an axial siphon. He believed the genus to be midway between *Pikea* and *Sarcophyllis* (=Dilsea).

Farlow (1877:241) included records of *F. crassa* from Santa Cruz, California, and from Oregon and of *F. compressa* from Santa Cruz, Santa Barbara, and San Diego, California.

Farlow and Setchell (P.B.-A. 898, 1901) recognized that *Gigartina mollis* Harvey et Bailey (1851:372) from Puget Sound, Washington, also represented a species of *Farlowia* and made the combination *F. mollis*.

I have observed type material of all three species. Two specimens of *Farlowia compressa* (LD 35034, LD 35035), both collected by Dr. C. L. Anderson at Santa Cruz, California, in 1873, are on a single herbarium sheet. Both specimens possess immature reproductive filaments. The specimens are about 10 cm tall and 6 mm across at their broadest point. They are irregularly distichously branched with strap-like branches terminating either acutely or with branch tips broken off. No midline or veins are evident in macroscopic view (this trait has been used by Abbott and Hollenberg 1976:357 to distinguish this species of *Farlowia*), and the thallus appears to be quite thin. Color is near Vandyke Red (Ridgway 1912).

LD 35036-35038 includes, on a single herbarium sheet, three
specimens of *Farlowia crassa* from Oregon sent to J. Agardh by Farlow. The specimens are 9-10 cm tall, 4 mm wide at their broadest but mostly narrower, irregularly distichously branched, with branch tips mostly blunt or broken off. The thickness of the specimens is evident in their nearly black color. Mature reproductive filaments and young cystocarps are evident in sectioned material.

The type specimen of *Farlowia mollis* (Fig. 33g) is deposited in TCD. The small sheet of paper to which the moderately branched (to 3 orders), 10 cm tall specimen is attached is labeled "Puget Sound" in the lower left corner and "Gigartina mollis B. and H." in the lower right in a hand other than Harvey's (Bailey's?). A small envelope to the right of the specimen, also labeled "Gigartina mollis B. and H.", contains a mica slide on which are mounted fragments of thallus. In stained sections, the cells did not pick up the acidified aniline blue very well; they seemed to be somewhat decayed. The 7-8 cortical layers gave way to a rhizoid-filled interior; no central axial filament was discernible. Immature reproductive filaments to 9 cells in length were present. A branched, probably green endophyte occurred throughout the thallus.

Although Kylin (1956) considered *F. compressa* to be the type of the genus, Abbott (1979, in Farr et al.) correctly stated it to be *F. crassa* based on Schmitz's (1889) lectotypification. Doty (1947) synonymized *F. crassa* with *F. mollis*.

*Farlowia compressa* and *F. mollis* are represented in the Phycototheca Boreali-Americana by three collections. In the UBC
set, P.B.-A. 898 (1901) consists of two cystocarpic specimens of *Farlowia mollis* collected at Dillon's Beach, California, 12 Dec. 1898; P.B.-A. 1150 (1903) is a young female specimen of *F. mollis* from Botanical Beach, British Columbia, July 1901; P.B.-A. 1349 (1907) is a male specimen of *F. compressa* from Moss Beach, California, 8 June 1906; it completely fills a sheet 21.0 by 29.5 cm.

Abbott (1962) studied the reproductive morphology of *Farlowia mollis* and *F. compressa* from California and Oregon. She noted a paucity of reproductive material among her collections. She described carpogonial branches as consisting of 10-18 cells that can bear one- or two-celled laterals on the lowermost cells. After fertilization in *F. mollis*, a proximal extension of the carpogonium fuses with the third or fourth cell below the carpogonium, and connecting filaments are produced from this extension. She observed the auxiliary cell to be two, three, or four cells from the tip of a branch 9-14 cells in length. She described the T-shaped attachment of the connecting filament to the auxiliary cell and the presence of several centers of gonimoblast initiation. Abbott illustrated these reproductive features and early stages of post-fertilization development.

DeCew and West (1982) cultured carpospores and tetraspores of *F. compressa* and *F. mollis* and found that crusts bearing irregularly cruciate to irregularly zonate tetrasporangia alternate with the upright gametophyte in both species. Although they distinguished *F. compressa* and *F. mollis* on the basis of the germination pattern of the carpospores, their results are not directly comparable since the carpospores were cultured.
under different conditions: *F. compressa* at 10 C 12:12 at 1800 lux and 15 C 8:16 at 450 lux and *F. mollis* at 15 C 16:8 at 200 lux. Tetraspores of *F. mollis* grown at 15 C 8:16 germinated in the same manner as both carpospores and tetraspores of *F. compressa*. Tetrasporangia were 11-15 by 37-45 μm in *F. compressa* and 13-15 by 35-45 μm in *F. mollis*. Tetrasporic crusts collected in the field near gametophytes of both species were of a similar thickness although the tetrasporophyte of *F. compressa* became notably thicker than that of *F. mollis* in culture. Carpospores of *F. compressa* were 9 μm in diameter; their size in *F. mollis* was not stated, but they appeared to be somewhat larger.

My observations of the type specimens and the results of studies by Abbott (1962) and DeCew and West (1982) strongly suggest that *Farlowia compressa* cannot be maintained as a species distinct from *F. mollis*.

**OBSERVATIONS**

The following observations are based on plants identified as both *Farlowia mollis* and *F. compressa*. No qualitative differences could be found to distinguish plants identified as either taxon, and quantitative characters were found to be continuous. I therefore recognize *F. compressa* as a taxonomic synonym of *F. mollis*.

Macroscopically, the thallus of *Farlowia mollis* varies from completely unbranched (Figs. 33a, b) through sparsely branched (Figs. 33c, d) to profusely branched (Figs. 33e-h). The height and width of the strap-like blades are also highly variable (see
Thalli of *Farlowia mollis* are uniaxial (Fig. 34a). A dome-shaped apical cell divides transversely to produce discoid subapical cells. Major whorl branches are initiated 2 or 3 cells below the apex by the somewhat oblique division of the axial cell to cut off two lateral cells in the plane of the thallus (Fig. 34a). After these cells have been cut off, the axial cell begins to elongate. As the axial cell elongates, the lateral cells divide obliquely. At the same time, two additional cells are cut off the axial cell to form corticating minor whorl branches. Continued oblique divisions of major whorl branches cause the branches to curve toward the apex (Fig. 34a). To fill in the thallus, all but the top 1-2 cells of each major whorl branch cut off a cell abaxially beginning with a cell 1-3 cells above the basal cell of the branch. Cells of the major whorl branch and cells of the abaxial branch derived from it both cut off corticating cells that develop into minor whorl branches. The appearance of minor whorl branches varies with their position. On the main axis, minor whorl branches become deflected to one side of the axis or the other; opposite pairs of branches are deflected in opposite directions, but this pattern does not alternate in a regular manner. Basal cells of minor whorl branches on the main axis remain relatively small as they do in other, but not all, positions in the thallus. The pattern of branching of the thallus is summarized below, and Fig. 34b shows the branching pattern of the mature thallus.

The length of axial cells increases gradually. Near the apex, axial cells elongate more rapidly proximally, but further
Main Axis
2 M
2 N

Major Whorl Branch
1 B, 2 N
2 N

Abaxial Branch
2 N (1,4 cells)

For abbreviations, see p. 379.

apex, axial cells elongate more rapidly proximally, but further from the apex they elongate more rapidly distally so that at maturity whorl branches are attached near the midpoint of the cell (Fig. 28a). Whorl branches on an axial cell 1025 μm long (the longest cell observed) were 0.56 of the distance from the distal to the proximal end of the cell. The diameter of the cell increases from about 5 μm just below the apex to a maximum of 22 μm for the cell 1025 μm long. The size of pit connections also increases, from <1 μm to about 6 μm in diameter, a size reached less than 1 mm from the apex.

Major whorl branches become indeterminate well after they have been initiated. Proximal to its point of departure from the margin of the thallus, the pattern of branching and cell elongation of an indeterminate branch is the same as that of a determinate branch. Although indeterminate branches usually develop from major whorl branches, one example was seen (Fig. 34c) in which indeterminate branches arise from three successive orders of branches (the major whorl branch, one of its abaxial branches, and a minor whorl branch arising from the abaxial branch).

Rhizoids which invest the axial filament can develop from cells of branches of all orders and types. Secondary pit connections were not seen, and all cells appear to be
**Farlowia mollis** is distinguished in transverse section by an elliptical shape. Sections vary in thickness depending on their age and reproductive condition. The thickness of the cortical layer also varies but is commonly 7-11 cells. The outer layer of small pigmented cells gradually gives way to large inner cortical cells usually filled with starch grains. A small central axial cell is sometimes evident amidst the medulla of predominantly rhizoidal filaments.

Reproductive filaments destined to bear a carpogonium or an auxiliary cell develop from inner cortical cells (Fig. 34b); however, some inner cortical cells have begun to elongate and look more like medullary cells. Carpogonial branches tend to grow downward in relation to the orientation of the upright thallus (Fig. 34b). In transverse section, these distally recurved branches extend from the inner cortex into the medulla (Fig. 35b). In the specimens examined, reproductive filaments first appear in late spring and mature through the summer. Although gonimoblast filaments were evident in some June specimens, they were more common in specimens collected in August. Mature cystocarps can occur at any time of the year (this may be related to the time involved in thallus erosion, which is necessary for spore release).

Carpogonial branches range from 6-14 cells in length \(x=10.0\), the mean of the mean of eight specimens from different collections). No seasonal or geographic trends in branch length were detectable. As in other Dumontiaceae, the distal end of the carpogonial branch becomes strongly recurved as a result of the oblique angle of the final two divisions of the branch. The
trichogyne has already begun to elongate before the final division has occurred (Figs. 35c, 36a-c). Cells of the branch enlarge (particularly the distal ones) as the branch matures (Fig. 36d). Cell 4 is always the largest, usually followed by cell 5, cell 2, and then cell 3 (Fig. 36d). Laterals (Figs. 36e, f) are rare.

Following the division between the carpogonium and cell 2, the carpogonial nucleus remains for a short time in one corner of the base of the carpogonium before moving to the base of the trichogyne (Fig. 36d), where it appears to remain while the trichogyne elongates. The carpogonial nucleus then returns to the base of the carpogonium (Fig. 36f).

Following presumed fertilization, the carpogonium enlarges distally. The fertilized carpogonium divides into two cells, the proximal one fusing with cell 4 and the distal one fusing with cell 5. Both carpogonial fusion cells enlarge and their diploid nuclei divide to produce connecting filaments (Figs. 37a, b). Several examples of mature carpogonial fusion cells each having produced 3 or 4 connecting filaments were seen (Fig. 37c).

A number of disintegrating carpogonia were observed, probably indicating their fate if unfertilized. No nucleus was visible in these carpogonia.

In specimens with carpogonial fusion cells, many reproductive filaments bearing immature carpogonia (carpogonia in which the trichogyne is still elongating) appear to be reverting to vegetative growth (Fig. 39c). This condition is first recognized by the presence of a nucleus in the trichogyne.
Next, the carpogonium divides above or below the point of origin of the trichogyne. The former trichogyne can then elongate further and divide, forming what appears to be a rhizoidal filament.

Auxiliary cell branches are immature when the carpogonia first mature (Fig. 35e) but are fully differentiated by the time connecting filaments are initiated. In the material examined, auxiliary cell branches were 4-13 cells in length, and one of cells 2-4 became the auxiliary cell (usually cell 3). This cell is distinguished by its slightly smaller size and by staining less intensely with iron haematoxylin than neighboring cells (Fig. 35f). Laterals are rare on both kinds of reproductive filaments.

A somewhat spindle-shaped nucleus is located just behind the tip of each connecting filament that grows through the thallus. Connecting filaments do not branch except in association with an auxiliary cell. The tip of a connecting filament passes an auxiliary cell. When the nucleus is opposite the auxiliary cell, it divides (Figs. 35g, 38a), and contact is made between the connecting filament and the auxiliary cell (Fig. 38b). One nucleus continues behind the growing tip of the connecting filament, and a pit connection is formed between this outgoing connecting filament and the gonimoblast initiator cell (Fig. 35h) containing the other nucleus. No pit connection is formed between the incoming connecting filament and the gonimoblast initiator cell; rather, the cytoplasmic continuity is simply broken. The gonimoblast initiator cell expands as does its point of contact with the auxiliary cell. The nucleus
of the gonimoblast initiator cell moves to one side of the cell and initiates a protrusion (Fig. 38c); the nucleus divides, and one of the daughter nuclei moves into this protrusion; a pit connection is formed, giving rise to a second outgoing connecting filament. This process is repeated 2-4 more times, but the cells cut off by these divisions become gonimoblast initials (Figs. 35i, 38d, e). The gonimoblast filaments form only a moderately compact cystocarp. All cells appear to become carposporangia. None of the cells of the gonimoblast filaments are incorporated into a gonimoblast fusion cell, and the gonimoblast initiator cell remains relatively small throughout post-fertilization development (Fig. 39b). As the gonimoblast develops, the pit connections between the auxiliary cell and its neighboring cells enlarge. The auxiliary cell nucleus maintains its integrity throughout carposporophyte maturation.

Cystocarps can reach 150 µm in diameter. They form a nearly continuous layer in the inner cortex (Fig. 35a). Carpospores are relatively small, less than 20 µm in diameter. They are thought to be released by the gradual erosion of the thallus.

Despite the apparent basipetal release of mature carpospores, the thallus does not necessarily show a consistent pattern of spore maturation. In the specimen from Davenport Landing, California (9 Aug. 1979, leg. M. H. Hommersand), macroscopic branches contained only initial stages of gonimoblast development whereas the main axis of the thallus contained immature cystocarps. However, these showed a decreasing degree of maturity toward the base of the thallus.
A degree of variability occurs in post-fertilization development in *Farlowia mollis*. In the formation of the carpogonial fusion cells, the two carpogonial derivative cells can fuse with cells 4 and 6 rather than cells 4 and 5 (not uncommon), with cells 4 and 7 (rare), or with cells 5 and 6 (rare). Also rarely the distal or proximal carpogonial derivative cell does not fuse with another cell. Which cells the carpogonial derivative cells fuse with appear to depend on topographic considerations (namely proximity). Variations in the geometry of enlargement of the fertilized carpogonium prior to dividing are reflected in the point of attachment of the remnant of the trichogyne to the carpogonial derivative cells. Most frequently, the trichogyne is attached to the distal cell (Figs. 37a, c), but it can also be attached to both the distal and proximal cells or to just the proximal cell. The nucleus in a carpogonial fusion cell can divide with one nucleus remaining behind and one becoming the nucleus of a connecting filament separated from the carpogonial fusion cell by a pit connection (Fig. 37b), or the nucleus in the carpogonial fusion cell can become the nucleus of the outgoing connecting filament, in which case no pit connection is formed (Fig. 37a). Figure 39a shows gonimoblast production from what appears to be a segmented outgoing connecting filament attached to an auxiliary cell.

In none of the instances of cell fusion (i.e., in the formation of either carpogonial or gonimoblast fusion cells) do the nuclei of the contacted cells lose their identity or disappear.

Spermatangia were found on specimens collected from June to
September, and on one specimen collected in December (UBC A28001). They are cut off by oblique walls (Figs. 39d, e) from the superficial spermatangial mother cells 1.5-3.0 μm wide by 8-12 μm long. Spermatangial mother cells can also cut off cells which themselves produce spermatangia. Reproductive filaments of various lengths (including some with carpogonia) were seen on some male specimens, and some female specimens had a few spermatangial mother cells terminating the cortical cells. Therefore, at least some Farlowia thalli appear to be bisexual but protandrous.

COMMENTS

In response to a request for female and cystocarpic specimens of Farlowia irregularis, Prof. M. Kurogi of Hokkaido University sent me two specimens collected in 1951 by H. Mikami at Horoman, Hidaka, Hokkaido, Japan; one was collected 7 Aug. (SAPS 042253; Fig. 40c) and one on 20 Oct. (SAPS 042254; Fig. 40d). At least one of the specimens, that collected 20 Oct., was used as part of the basis for Mikami's (1957) description of female reproductive structures and post-fertilization events in Farlowia irregularis. Sections of both specimens revealed that they have a vegetative structure very similar to F. mollis. A central axial filament approximately 25-35 μm (outer wall diameter) was seen in a transverse section made 1 cm from the base of the 7 Aug. plant. In the 20 Oct. plant, a longitudinal section of a branch revealed a central axial filament of cells which reached 450 μm in length and were 50-100 μm in diameter at the slightly distal branch point, with protoplasts approximately
15 μm in diameter at the ends of the cells. Axial pit connections reached a maximum diameter of about 8 μm. The cortex of 8-9 cell layers resembled that of *F. mollis*, as did the rhizoid-filled interior of the thallus. Carpogonial branches 7-13 cells in length were observed. Reproductive filaments thought to be bearing auxiliary cells showed little if any differentiation in the size and the aniline-blue staining properties of the distal cells of the branch. Post-fertilization stages were not seen in the sections examined. The basal 1-2 cells of the reproductive filaments commonly bore 1-2 short lateral branches that could become rhizoidal. As in *F. mollis*, cells appeared to be uninucleate, and secondary pit connections were absent.

*Farlowia mollis* was first recorded from the western North Pacific by Nagai (1941:159) who observed collections from Kobune, Uruppu I., Kurile Is. Although he examined only sterile specimens, Nagai described both their gross morphology and their anatomy. In particular, he noted a "medulla of abundant, very slender rhizoidal cells, arranged closely by anastomosing with each other, surrounding a comparatively large, round cell in the center, which may be a cross section of the axial cell running lengthwise in the frond."

The specimens whose female reproductive anatomy and post-fertilization development Mikami (1957:14) described under the name *Farlowia irregularis* now appear to be referable to *F. mollis*. Abbott (1962:34) recognized the similarity of Mikami's material, which she observed (but believed to be *F. irregularis*), to *F. mollis* when she wrote, "From an examination
of their internal structure and the position of their reproductive organs, it is clear that they are members of the genus *Farlowia* as presently understood. Further examination of a larger number of specimens may show them, indeed, to be conspecific with *F. mollis*.

Chihara (1972b:156) also recorded *Farlowia irregularis* from Hidaka, Hokkaido, Japan. I have studied three of his specimens deposited in TNS. They were collected 21 July 1970 at Shiraizumi. One specimen is male (TNS 24746); two are female (TNS 24759, 24760). All three appear to be referable to *F. mollis*.

Whether the western North Pacific entity is indeed *Farlowia mollis* or whether it should be described as a new species in the genus can only be determined by further collecting, comparing, and culturing. For the present, I have chosen to consider it *F. mollis*.

Therefore, *Farlowia mollis* sensu lato is distributed in northern Japan and the Kurile Is. and occurs from Prince William Sound, Alaska (Lindstrom and Calvin 1975) to Punta Cabras, Baja California (UNC, 25 Oct. 1969, leg. M. H. Hommersand, as *F. compressa*). The "*F. compressa*" reported from Coghlan Island, Alaska (Lindstrom 1977) is the *Orculifilum denticulatum* of this study.

*Farlowia conferta* (Setchell) Abbott 1968:186

**INTRODUCTION**

Setchell (1912:252) described *Leptocladia conferta* from Dillon Beach and other central California localities. The bushy
tufts of dark red thalli, 15-20 cm tall, were characterized by abundant fasciculate proliferations. They grew in the low intertidal zone. Setchell recognized the similarity of his new species to both *Leptocladia* and *Pikea*, but he preferred to place it in the former genus.

Abbott (1968:186) also studied this species from the central California coast. She observed that the female reproductive structures differed from those of *Leptocladia*. She transferred the species to *Farlowia*, noting that like *Farlowia* but unlike *Pikea* the species lacked axial lacunae, spindle-shaped branches bearing mature cystocarps, and auxiliary cell fusions during gonimoblast formation.

DeCew and West (1982) have cultured carpospores of *F. conferta*. They found crusts bearing irregularly cruciate to irregularly zonate tetrasporangia, 8-10 by 20-24 μm, to alternate with the upright gametophyte.

*Farlowia conferta* as represented by P.B.-A. 1848 (1912) is a male specimen from Dillon's Beach, California.

**OBSERVATIONS**

*Farlowia conferta* is distinguished macroscopically from *F. mollis* by its proliferous branching and nearly cylindrical habit (Figs. 40a, b). Microscopically, as in *F. mollis*, the cells of the main axis are branched near their midpoint. However, these cells tend to be somewhat broader (to 90 μm in diameter) and have somewhat larger pit connections (to about 13 μm) than the axial cells of *F. mollis*. The axial filament is also more heavily invested with rhizoids than in *F. mollis*. As in *F.*
mollis, the major whorl branches extend perpendicularly from the main axis and shortly thereafter curve upward. At least one minor whorl branch occurs on each cell of a major whorl branch.

Reproductive details were not studied in F. conferta, but the following features were noted in female specimens from Corona del Mar (10 Feb. 1979, leg. T. C. DeCew, WS in UC): cells that start out looking like basal cells of reproductive filaments can become rhizoidal after 2 or 3 cells; one cell of a reproductive filament has elongated laterally and become rhizoidal; the distal cells of carpogonial branches are frequently tightly appressed and surrounded by short-celled rhizoidal filaments, some of which pass through cells of the branch; reproductive filaments can have 1-3-celled lateral branches on one or two proximal cells of the branch; reproductive filaments are 10-12 cells long; the trichogyne can be forked; cell 2 of the carpogonial branch is often larger than cell 3; the connecting filament is relatively thick and fairly distinct; the remnant of the connecting filament attached to the auxiliary cell is relatively large; gonimoblast filaments are loosely organized.

Orculifilum denticulatum gen. et sp. nov.

DIAGNOSIS

Thalli dark red, to 20 cm tall, 1-6 (-12) mm wide, compressed, distichously and abundantly linearly branched. Uniaxial. Immature axial cells cask-shaped, elongating to at least 850 μm and broadening to about 65 μm; branches arising near the midpoint of mature axial cells but some distance from
the circumference of the cell; central axis surrounded by rhizoids; secondary pit connections lacking. Reproductive filaments typically 7-15 cells in length; distal cells, except carpogonium and auxiliary cell, enlarged and lobed; connecting filaments to 14 μm in diameter; gonimoblast fusion cell apparently lacking. Spermatangia borne on spermatangial mother cells 5 by 7 μm. Tetrasporangia unknown.

OBSERVATIONS

Orculifilum denticulatum gen. et sp. nov. is a subtidal species. It has been collected on rock and shell, occasionally on a soft bottom, from about 3 to 15 m. Plants usually occur singly but can occur in small clusters. They are rare; probably only one plant is seen in about 10 dives (N. I. Calvin, pers. comm., 13 Nov. 1984). To date, all collections have come from near Juneau, Alaska: Marmion Island, Auke Bay, Shrine Island, and Amalga Harbor.

Phenology is difficult to establish because of the paucity of specimens (fewer than 24 have been seen). Among these, plants with mature carpogonial branches and a few mature auxiliary cell branches have been collected in June, and mature carposporangia have been observed in December and January. Spermatangia were seen on specimens collected in August. No plants bearing tetrasporangia have been observed. Sterile specimens have been seen throughout the year; their status cannot be explained at the present time. Individual plants of this species are thought to persist for at least several years, producing new growth in the spring and summer.
The habit of this species is shown in Figs. 41d-f.

The uniaxial thalli are composed of compressed branches, mostly 1 - 6(-12) mm wide. The margins have spine-like projections which can expand to form new branches. Lateral branching is sparse to proliferous and can vary from region to region on the same plant. Plants to 20 cm tall have been measured. The central axis and lateral veins are frequently visible in pressed specimens due to the abundant formation of corticating rhizoids around the axial filament. Color varies among Ox-blood red, Acajou red, and Vandyke red (Ridgway 1912), sometimes approaching almost black.

A dome-shaped apical cell divides transversely to produce subapical discoid cells which begin to branch 2-3 cells behind the apex (Fig. 42). Branch cells are cut off by a somewhat oblique (out of the plane of the thallus) division of the axial cell, and they continue to divide by slightly oblique walls so that the branches curve slightly toward the apex. Corticating minor whorl branches are initiated 6-7 cells behind the apex on both the main axis and the basal cell of both major whorl branches. Further from the apex the suprabasal cells of the major whorl branches also initiate corticating minor whorl branches and the subapical cells of the major whorl branches branch abaxially. The corticating branches divide transversely once or twice before initiating a lateral to help fill in the cortical layers of the thallus.

An axial cell begins to enlarge 6-8 cells behind the apex of the branch (Fig. 42). At first it increases about equally in length and girth to form nearly quadrate cells; most of the
increase in length must occur proximally since the lateral branches become distally attached. Between 20-30 cells from the apex (Fig. 43), the cells begin to elongate (still predominantly proximally) faster than they increase their girth. The cells become rectangular to campanulate flaring at the distal end where the lateral branches are attached. About 100 cells from the apex, the cells begin to elongate distally and cease to increase in circumference. These cells are frequently somewhat barrel- or cask-shaped (hence the name *Orculifilum*). Axial cells near the base of the thallus can reach at least 850 \( \mu \text{m} \) in length; the rectangular ends of these cells are 50-65 \( \mu \text{m} \) in diameter. These axial cells swell in diameter near their midpoint where the major whorl branches attach to the relatively long lateral processes of the axial cells. The basal cells of the major whorl branches can elongate to over 1000 \( \mu \text{m} \) but their diameter increases somewhat less than the axial cells (from about 30 \( \mu \text{m} \) including the outer wall throughout most of their length to about 75 \( \mu \text{m} \), including the outer wall, near their branch point).

Rhizoids develop from the relatively small, undifferentiated corticating cells; these include the basal cell of the minor whorl branch (this cell does not enlarge appreciably after formation) and the laterals cut off by it and from the basal cells of the minor whorl branches cut off the basal (and possibly suprabasal) cell(s) of the major whorl branches. The proximal cells of rhizoids can initiate additional corticating branches.

All cells are uninucleate. Secondary pit connections are
lacking.

In transverse section one observes an outer cortex of 3-4 layers of small, pigmented elliptical to quadrate cells and an inner cortex of 3-5 layers of colorless suborbiculate cells of increasing diameter. Cells of the outer layer are 7-10 (-13, if division is impending) \( \mu \text{m} \) high by (4-) 6-10 \( \mu \text{m} \) in diameter. In the inner cortex the cells increase in size inwardly to about 70 by 90 \( \mu \text{m} \) although they are usually more modest in size. A small refractive inclusion (approximately 5 \( \mu \text{m} \) in diameter) is sometimes present in the intermediate cortical layers.

In transverse section, the central axial filament and the proximal cells of the lateral branches are embedded in a medulla of mostly unbranched rhizoidal filaments. The medulla increases in thickness toward the base of the plant, producing thalli to about 1.2 mm in total thickness.

Rhizoids are 10-12 \( \mu \text{m} \) in diameter, including the outer wall; the protoplast occupies only 3-5 \( \mu \text{m} \) of that diameter.

Orculifilum is distinguished by the great enlargement of the distal cells of both carpogonial and auxiliary cell branches (see below and under Constantinea). Like Constantinea, it is distinguished by the lobing of these cells, particularly cell 4 (Fig. 44a). Carpogonial branches are 7-14 cells in length. Not infrequently, the basal cell bears a lateral branch, which is often rhizoidal, and occasionally one or two of the middle cells of the branch bear 1-2-cell laterals. The distal cells of both carpogonial and auxiliary cell branches are usually tightly appressed. Connecting filaments to 14 \( \mu \text{m} \) were measured, but no carpogonial fusion cells were clearly observed.
Auxiliary cell branches are 7-15 (-18) cells in length, mostly unbranched and usually the second (occasionally the third) cell from the apex differentiates into the auxiliary cell (Figs. 44b, c). As in *Weeksia* and *Leptocladia*, the auxiliary cell is enlarged but not to the extent of the neighboring cells. A relatively large remnant of connecting filament becomes the gonimoblast initiator cell. It produces 1 or 2 outgoing connecting filaments and 2-3 gonimoblast initials, which branch profusely, producing a large number of relatively small (15-20 μm in diameter) carposporangia (Figs. 45a, b). As the carposporangia mature, the pit connections between the distal cells of the auxiliary cell branch can enlarge to about 7 μm. The pit connections between the gonimoblast initiator cell and the gonimoblast initials can also enlarge to 7 μm or more in diameter, but no cell fusions were observed.

A weakly developed ostiole appears above maturing cystocarps. Cystocarps can reach 350 μm or more in their longer dimension.

Outer cortical cells 16-23 μm by 3-4 μm, similar to spermatangial mother cells in some species of Dumontiaceae, were observed in an August specimen. However, these cells did not bear any spermatangia. Cells which appeared to bear 2-3 spermatangia were not differentiated from the normal vegetative surface cells of the plant and were 5 by 7 μm. This specimen also had carpogonial branches. Definitive spermatangia or spermatangial mother cells were not seen on other female thalli.

No tetrasporangia have been found on any of the specimens, and it therefore appears possible that *Orculifilum* has an
alternation of heteromorphic generations.

**Leptocladia binghamiae** J. Agardh 1892:96
and **L. peruviana** Howe 1914:176

**INTRODUCTION**

**Leptocladia binghamiae** was described by J. Agardh (1892:96) from plants collected at Santa Barbara, California, by Mrs. Bingham. J. Agardh originally placed this species in his Rhodymenieae. He described the linear, cartilaginous, serrate, pinnately branched thalli as composed of three layers: a central axial filament surrounded by many filaments, an intermediate layer of angular-orbicular cells, and an outer layer of small cells in vertical files. He also observed the cystocarps, which he described as being composed of a central placenta-like apparatus from which radiate the roundish cells of the fertile filaments.

Schmitz and Hauptfleisch (1897:520) described **Andersoniella farlowii**, which Setchell (1912) subsequently placed in synonymy with **L. binghamiae**. Setchell inferred the type of **Andersoniella** to be represented by four slides labeled **Farlowiella** in the Schmitz collection at the British Museum of Natural History (numbered 4.86). These in turn were purported to have been prepared from no. 28 of Farlow, Anderson and Eaton's *Algae Exsiccatae Americae Borealis* (P.B.-A. 700, 1900). Setchell believed this specimen to have been supplied by Anderson to Grunow, who then loaned it to Schmitz. Although labeled **Farlowia compressa**, different sets were found to contain different species, including in addition to **F. compressa**, both
L. binghamiae and F. conferta. Anderson also distributed duplicates labeled Alg. Exc. Am. Bor., another source of confusion according to Setchell.

Howe (1914:176) described a second species of Leptocladia, L. peruviana, from Peru. He felt that the form and structure of the Peruvian plant left little doubt as to its relationship to L. binghamiae, but he chose to create a new species because of its greater breadth, conspicuous marginal foliar appendages, more distinct marginal teeth and more regular arrangement of young cortical cells.

I have studied the type specimen of Leptocladia peruviana from NY. The original label indicates it was collected by Robert E. Coker, April 8, 1907, dredged in 5 fathoms (9 m) in the Bay of Sechura, Peru. It is the same specimen illustrated by Howe (Pl. 66) and by Dawson et al. (1964: Pl. 32). As described by Howe, the specimen is irregularly lacerate-pinnate and repeatedly subdichotomously branched, obscurely to distinctly costate. Although Howe indicated that plants attain a height of 25 cm and a width of 8 mm, the type specimen is just under 10 cm tall and is 8 mm wide at its broadest point. As described by Howe, the type specimen bears numerous ligulate, irregularly serrate appendages or innovations, mostly 2-10 mm long by 1-3 mm wide. These appendages appear to represent new growth by their lighter color and more delicate aspect than the thallus bearing them. The faded color of the thallus itself suggests it may have been stored in preservative for some time before being pressed. I observed the costa and wings to be thicker than the 30-130 μm and 20-50 μm, respectively, reported by Howe. In
reconstituted sections, the costa were 1100 \( \mu m \) and the wings about 400 \( \mu m \), suggesting Howe's figures may have been simply a decimal point error. Although the type specimen appears to be sterile, the irregular cortical layer in older parts of the thallus suggest it may have been spermatangial. Howe described the spermatangia as occurring in irregular, often marginal bands and patches which can become continuous, and tetrasporangia as 10-16 by 25-42 \( \mu m \), irregularly cruciate to irregularly zonate (his figures of 10 tetrasporangia show sizes from 8-14 by 23-35 \( \mu m \)).

Kylin (1944:8) wrote that the type specimen of *L. binghamiae* in J. Agardh's herbarium (No. 28231) was fairly fragmentary but two good specimens of the species (No. 34819 and 34820) could be found in his herbarium under *Pikea californica*. These were also collected by Mrs. Bingham at Santa Barbara.

Although Dawson (1952 p. 90) indicated that a search for J. Agardh's specimen No. 28231 at Lund in July 1950 failed to reveal it, I have observed the specimen on loan from LD. I have not seen LD 34819 or LD 34820.

LD 28231 consists of 2 small fragments. The fragments are both cystocarpic and appear to be derived from the same inividual. They are labeled, "inter algas ex Santa Barbara California" and "Leptocladia Binghamiae J. Ag. mscr." in J. Agardh's hand. LD 28230, also labeled "Leptocladia Binghamiae" in J. Agardh's hand, is a set of drawings of the anatomy of the species, presumably from LD 28231 fragments. A transverse section shows the elliptical shape of the thallus and the three layers of cells mentioned by J. Agardh in his original
description. Chains of small gonimoblast cells are depicted arising from a large basal cell flanked by two smaller but still enlarged cells; there is also a hint of an ostiole.

Dawson et al. (1964) noted that *L. peruviana* was known only from the type collection.

Abbott (1968) studied both *L. binghamiae* and *L. peruviana*. She included *L. binghamiae* in her newly created family Weeksiaceae based on her belief that carposporangia are produced directly from the carpogonial fusion cell, and she moved *L. peruviana* to the genus *Rhodophyllis* in the Gigartinales on the basis of the parenchymatous structure of the subcortex.

Acleto (1973) collected drift female specimens of *L. peruviana* at the type locality and at Paita, Peru. His description of the form and structure of the plants closely adheres to Howe's, and he followed Abbott in ascribing the origin of the gonimoblast filaments to the carpogonial fusion cell. However, he disagreed with her transfer of the species to *Rhodophyllis*. He stated that his plants were very similar to *L. binghamiae* in their internal organization and in the structure of the carpogonial branch, the carpogonium, and the auxiliary cell branch, and his illustrations support this statement. However, he stated that *L. peruviana* differs from *L. binghamiae* in having more globose inner cortical cells and a larger quantity of rhizoidal filaments surrounding the central axis.

Abbott (1968:195) recorded *L. binghamiae* from 8 to 30 m, and Abbott and Hollenberg (1976:365) described it as saxicolous. Taylor (1945:163) dredged specimens from 26-55 m. The specimens I observed were cast ashore.
Setchell (1912:252) recorded *L. binghamiae* along the coast of California from San Diego to Santa Cruz, but Abbott (1968) recorded it north only to Pismo Beach and Shell Beach, San Luis Obispo Co. Dawson (1954) found it along the coast of Pacific Mexico from Punta Descanso to Punta Hughes, and Taylor (1945) collected it in the Galapagos Islands.

*Leptocladia peruviana* also appears to be a subtidal species (Howe 1914). It is known only from Peru.

**OBSERVATIONS**

*Leptocladia* displays the same pattern of vegetative development as *Farlowia* and *Orculifilum*: a single dome-shaped apical cell produces subapical discoid cells which divide slightly obliquely to cut off major whorl branches which in turn branch predominantly abaxially. Both axial and major whorl branch cells cut off corticating (=minor whorl) branches whose lower cells produce rhizoids. Axial cell elongation occurs predominantly proximally. All cells are uninucleate, and secondary pit connections appear to be lacking.

As with *Orculifilum*, the difference between *Leptocladia* and *Farlowia* is cell and pit connection dimensions. Axial cells to 600 μm in length have been measured in both *L. binghamiae* and *L. peruviana*. These cells have protoplasts 30 to 50 μm in diameter in the former and are of similar dimensions in the latter, and they are connected by pit connections about 20 μm in diameter in both species. Broader cells (to 65 μm) with slightly larger pit connections (to 25 μm) have been seen in branches of *L. binghamiae* from Puerto Santo Tomás. In contrast to the other
two genera, the major whorl branches of *Leptocladia* are borne distally even on mature axial cells (Fig. 28d), and in contrast to *Orculifilum*, the pit connections occur close to the circumference of the cell.

In transverse section, the thalli are about 2 mm thick in *L. binghamiae* and about 1 mm thick in *L. peruviana*. Thalli of both species display a central rhizoidal area surrounding the axial filament. The rhizoids can also extend into the lateral regions of the section. The outer cortex is composed of 3-4 layers of pigmented cells, the inner cortex of 3-4 layers of unpigmented elliptical cells. In *L. binghamiae*, surface cells are 6-8 μm high by 4-6 μm in diameter. Cortical cells increase in size to approximately 50 by 55 μm (60 by 70 μm including the outer cell wall) in the innermost cell layer. Similar measurements were not made for *L. peruviana* because of compression and shrinkage of cells due to pressing and drying.

The cells of both species contain one or more refractive inclusions. The smaller refractive inclusions are usually round and have been measured to 8 μm in diameter in *L. peruviana*. Larger inclusions are usually rhomboid and not uncommonly reach 15 μm by 12 μm in this species. One inclusion measured 20 μm by 12 μm in *L. peruviana* (Parachique, 7 July 1977). The inclusions are generally smaller and less abundant in *L. binghamiae*, frequently reaching only 7 μm on a side, but the largest was 15 μm on a side. When present, they attain their greatest development in the inner cortical cells and are usually prominent in at least the proximal cells of reproductive filaments. They can be present in rhizoidal filaments but are
not particularly conspicuous there.

The macroscopic habits of *L. binghamiae* and *L. peruviana* can be observed in Fig. 41.

Reproductive filaments are borne, mostly abaxially, on inner cortical and outer medullary cells and on rhizoidal filaments. As illustrated by Abbott (1968 for *L. binghamiae*) and by Acleto (1973 for *L. peruviana*), the relatively long carpogonial branches in this genus can bear one or more laterals and are characterized by the enlargement of certain of the distal cells of the branch. Carpogonial branches were (8-) 12-14 (-19) cells long (n=48) in a specimen of *L. binghamiae* from Santa Cruz I., Calif., and (11-) 13-19 (-25) cells long (n=83) in one from Puerto Santo Tomás, Mexico. Initially, the trichogyne projects as a narrow extension of the carpogonium (Fig. 46a). Cell 4 enlarges the most, followed by cells 5 to 7 (Figs. 46b, c), and these are the cells that stain most intensely with aniline blue. Cell 4 has the largest nucleus followed by cell 5, cells 2, 3, and 6, cells 7 and 8, and lastly cell 9. Laterals are formed on reproductive filaments prior to maturation of the branches; they can appear moniliform or rhizoidal, and they can branch. Most laterals are borne near the base of reproductive filaments. Occasionally, two carpogonial branches are borne on reproductive filaments sharing a common differentiated basal (or near-basal) cell. Vegetative cells have been seen invading the enlarged cells of the carpogonial branch.

Formation of a carpogonial fusion cell was not observed. In one instance, an enlarged (possibly fertilized) carpogonium was
seen (Fig. 46d), and on several occasions, a connecting filament appeared to be issuing directly from the carpogonium (Fig. 46e). Connecting filaments are fairly thick, frequently 10-12 μm in diameter, and reach a maximum diameter of about 20 μm. Connecting filaments not infrequently pass close to mature carpogonia, and one example was seen in which the connecting filament appeared to be trying to fuse with a carpogonium and initiate additional outgoing connecting filaments or gonimoblast filaments.

The auxiliary cell is the second cell from the tip of an auxiliary cell branch; it is smaller than neighboring cells but larger than more proximal cells of the branch (Fig. 47a). The cell above it and one or two cells below it are greatly enlarged. The nuclei of these cells are also enlarged and can occur at a slight constriction near the middle of these cells. After passing a mature auxiliary cell, a connecting filament segments distally, and the auxiliary cell initiates a slight protrusion toward the proximal segment of the connecting filament (Fig. 47b). The connection between the auxiliary cell and the connecting filament enlarges, and the more proximal portion of the connecting filament is pinched off. Several secondary connecting filaments can then arise from the gonimoblast initiator cell prior to gonimoblast initiation (Fig. 47c).

The gonimoblast initials appear to enlarge, but the other proximal cells of gonimoblast filaments remain relatively small while the intermediate cells elongate, and only the distal cells develop into carposporangia (Fig. 49a). The proximal cells
gradually become incorporated into a gonimoblast fusion cell (Fig. 48). Little enlargement of pit connections occurs prior to such incorporation. The pit connections in the auxiliary cell branch, in contrast, enlarge to 3-6 μm throughout the length of the branch, including the connection between the branch and the vegetative cell bearing it.

An ostiole develops above the maturing cystocarps.

Male thalli of *L. binghamiae* were not seen. In *L. peruviana*, spermatangial mother cells occur in patches over the surface of the thallus, including the margin but excluding the central region. Spermatangial mother cells develop from transformed cells of the outermost cortical layer; they are 7-16 μm high by about 2 μm in diameter and cut off 1-2 spermatangia by oblique walls (Fig. 49b). Spermatangia are mostly 4-6 μm high by 2-3 μm in diameter. A spermatangial mother cell can also produce another spermatangial mother cell.

Thalli of both species appear to be unisexual.

The irregularly cruciate to irregularly zonate tetrasporangia measured 11-16 μm by 21-31 μm (n=18) in *L. binghamiae* (Santa Cruz I., 17 Aug. 1969) and 7-13 μm by 15-20 μm (n=10) in *L. peruviana* (Hassler Expedition 21207 in MICH). The tetrasporangia are attached basally and are usually borne on cells of the fourth cortical layer (Fig. 49c).

Because of the limited specimens available, phenology could not be determined. Young female structures were observed in May and June specimens of *L. binghamiae*, and mature carpogonial branches occurred in a November. Cystocarpic plants of *L. binghamiae* were present in February, June, August, September,
and November collections. Tetrasporic specimens were present only in an August collection, but old tetrasporangia were evident in February, June, and November collections.

COMMENTS

Abbott (1968:194), in her characterization of *Leptocladia*, stated that the gonimoblast arose directly from a carpogonial fusion cell in *L. binghamiae* and that the auxiliary cells were nonfunctional. Acleto (1973:35) upheld a similar view for *L. peruviana*. This study shows that functional auxiliary cells exist in both species and that these cells serve as the attachment point from which the gonimoblast originates. Neither Abbott nor Acleto apparently realized that the distal cells of the auxiliary cell branch enlarge, mimicking those of the carpogonial branch, and this oversight may have led to their interpretation of post-fertilization events in the genus. The illustrations which both Abbott and Acleto label as auxiliary cell branches represent incompletely differentiated reproductive filaments, which I would label neither carpogonial nor auxiliary cell with certainty. In contrast, the figures they describe as showing gonimoblast developing from a carpogonial fusion cell are equally convincing illustrations of gonimoblast arising from the remnant of the connecting filament (=gonimoblast initiator cell, this study) attached to an auxiliary cell.

From the specimens I have observed, thalli of *L. binghamiae* tend to be narrower and more cylindrical than those of *L. peruviana*. Typical *L. binghamiae* specimens have main axes 2-5 mm wide and reach more than 2 mm in thickness whereas specimens
of _L. peruviana_ can attain widths of 10 mm but a thickness of just over 1 mm. I was unable to verify Acleto's statement that _L. binghamiae_ has more globose inner cortical cells than _L. peruviana_. Further study is required to confirm the distinctness of these two species.

*Weeksia reticulata* Setchell 1901:128

**INTRODUCTION**

*Weeksia reticulata*, the type of the genus, was described by Setchell (1901:128) and named in honor of Mrs. Weeks, "who first detected and insisted upon the distinctness of the only species." Setchell described the blades of the species as "broadly reniform up to 30 cm in diameter, of a rose pink to dark red color, soft and fleshy, adhering well to paper when drying, with many radiating broad indistinct veins which are more plainly seen below, and which anastomose forming a distinct reticulation which becomes indistinct above and towards the margins." Setchell described the fronds of the genus as:

...orbicular to reniform, from a short stipe and discoid holdfast, proliferating from the margins and thus producing new blades similar in shape and behavior to the original, consisting of three layers: a medullary layer of coarser and finer filaments, much intertwined, and two cortical layers each consisting of large, rounded colorless cells within, and outer small colored cells arranged in short filaments vertical to the surfaces.

For both genus and species, Setchell described the cystocarps as scattered over the frond, adding, for the genus:

...immersed (lying in the medullary layer, beneath a small opening through the cortex which is not at all prominent) with the spore-mass reniform, not distinctly lobed, provided with a curved pedicel composed of several cells (on its inner side) from which arise branching filaments whose outer cells
develop into spores.

Setchell included no figures with his text.

I have seen the type of *W. reticulata* (UC 96497). The specimen, collected at Pacific Grove by Mrs. J. M. Weeks, March 28, 1896, is Vinaceous-rufous (Ridgway 1912), just under 8 cm in height, and about 13 cm in breadth (Fig. 50a). The blade is variously cleft and has conspicuous veins for much of its length. It appears to be sterile. It is designated, "Type plant!" in Setchell's hand and is indicated to be the "original of drawing by A. A. Lawson--Nov. 1899" also in Setchell's hand. (A drawing, which appears to be part of the original material used by Setchell to describe *Weeksia reticulata*, is found in FH, but it does not resemble the type specimen very well.) The UC specimen, like others collected in the same year (and deposited in FH), was initially identified as *Kallymenia reticulata* by Setchell, but the generic designation was changed to *Weeksia* when published.

Smith's (1944:206) description of *W. reticulata* generally followed Setchell's, but he reported thalli of up to 40 cm tall and included a habit figure.

Abbott's (1968:190) characterization of this species is summarized in Table II. She included a description of male and female reproductive structures. She described the distal 5-7 cells of the carpogonial branch, referring to her Fig. 12, as "highly modified by humeruslike (bone-shaped) nutritive cells or nutritive auxiliary cells." Also, apparently referring to her Fig. 23, she continued:

The relatively small carpogonium bears a massive, spirally contorted trichogyne as much as 8-12 μm wide
and 200 µm long. The carpogonium lies next to the nutritive cells and after fertilization fuses directly with one of them (usually the third or fourth behind the carpogonium) and presumably transfers the diploid nucleus. A gonimoblast is produced by 1 (Fig. 21, 23) or 2 lobes from this nutritive cell...

An alternative interpretation of these figures is presented below under COMMENTS.

In addition to noting the type in UC, Abbott mentioned a "technical (cystocarpic) type" in the Farlow Herbarium. She observed other specimens ranging from Cypress Point, California, to Punta Santo Tomás, Mexico. These collections covered a depth range of 40 to 110 feet (12 to 34 m).

I have examined the specimen Abbott refers to as the technical type of *Weeksia reticulata* (Fig. 50b). It was collected by Setchell and Saunders at Moss Beach on July 30, 1896. This plant, like the holotype, is Vinaceous-rufous in color; it is 7 cm in height and just under 8 cm in breadth. It has conspicuous veins throughout its length. It is deeply cleft at one point but otherwise only modestly lobed. Although this specimen does appear to be cystocarpic, the preservation of cellular detail is so poor that no meaningful observations could be made. Like the other plants collected that year, this specimen was initially identified as "Kalymenia [sic] reticulata." The fact that it is cystocarpic was not noted on the herbarium sheet until 1911, and it was presumably at this time that Setchell wrote, "Portion of cystocarpic type!"

Although this specimen was probably examined by Setchell in preparing the generic diagnosis, since he did describe the cystocarps of the genus in some detail, there appears to be no justification for making it the type of *Weeksia reticulata*. The
International Code of Botanical Nomenclature makes no provision for technical types, i.e., specimens that have some significant anatomical or morphological feature missing in the holotype or lectotype, and therefore, the FH specimen lacks any legitimate nomenclatural status.

Abbott distinguished *W. reticulata* from the other species in the genus by its greater thickness, presence of veins in more than the basal part of the blade, and the relatively small, reniform to rounded blades.

Reed and Foster (1984:943) noted the recruitment of *Weeksia reticulata*, a perennial species, in the fall rather than the spring when most species of fleshy red algae first appear.

Observations on *Weeksia reticulata* are included under *W. digititata*.

*Weeksia fryeana* Setchell 1912:254

**INTRODUCTION**

Setchell (1912:254) described a second species of *Weeksia*. This species was first collected by Prof. T. C. Frye and Dr. N. L. Gardner in material cast ashore or dredged ("presumably in twenty fathoms of water") off Orcas and San Juan Islands, Washington. The large fronds of *Weeksia fryeana*, as Setchell designated this taxon, were described as broadly or narrowly reniform, 30-35 cm tall, 15-30 cm broad, entire or divided into narrow lobes, rose- to purple-red, with a short stipe. The transection showed three layers: a medullary layer of thick, interwoven, colorless filaments; an inner cortical layer of large, spherical, colorless cells; and an outer cortical layer
of small, pigmented cells in a short anticlinal series. Tetrasporangia, immersed in the cortex, were described as triangularly divided. Spermatangia were believed to occur on plants separate from those bearing female reproductive structures. The distal cells of the carpogonial branch, composed of a gently curved series of cells, were said to be swollen and unilaterally elongate, and the cells of the auxiliary cell branch were described as depressed-spherical (the same as the proximal cells of the carpogonial branch).

Cystocarps, dispersed in the cortical layer, were said to be composed of pedicellate branched gonimoblast filaments radiating from a central cell and terminating in catenate sporangia with an inconspicuous, but as it seems, present carpostome ("carpostomio inconspicuo, sed, ut videtur, adente.")

I have examined the type of *Weeksia fryeana* (UC 96308; Fig. 50e). The cystocarpic portion of the blade approaches Vinaceous-rufous (Ridgway 1912) while another sector, in which cystocarps are not visible, is closer to Coral pink. The blade is approximately 15 cm tall and 25 cm broad, and there is no indication of veins anywhere on the deeply lobed, or dissected, blade. Prof. T. C. Frye collected this specimen at Deer Harbor, San Juan Islands, Washington, on July 1, 1904. It was originally identified by Setchell as "Sarcophyllis (californica?)" with the annotation, "Certainly from the cystocarps and characteristic auxiliary branchlets, one of the Dumontiaceae in Schmitz and Hauptfleisch sense!" In February 1909 Setchell added, "This seems certainly to be a Weeksia. Can it be *W. reticulata* S?" And, finally, in January 1912 Setchell
wrote, "Weeksia Fryeana Setchell, cystocarpic type!" This appears to be the only specimen designated as a type of any kind for the binomial *Weeksia fryeana*.

Kylin (1925:15) recorded this species from 10 fathoms at Canoe Pass, Washington, and included drawings of carpogonial branches in different stages of development.

Scagel (1957:145) included new collection records of this taxon from northern Washington and reported its habitat to be on rocks in the subtidal zone to a depth of about 5 fathoms (9 m).

Abbott's (1968:191) description of this species is summarized in Table II. She included records of more recent collections from the San Juan Islands. She distinguished *W. fryeana* from the other species of *Weeksia* "by a lack of veins, and from *W. reticulata* further by its larger size."

Norris (1971:205) studied the development of the foliose thallus of *Weeksia fryeana*. He discovered that the mature multiaxial blade develops from an initially uniaxial frond in which apical cells of lateral branches take over blade production when the blade is approximately 0.5 mm tall. Young thalli less than 0.5 mm usually have a single apical cell. Although Norris described this apical cell as dividing in one plane to form a linear row of cells, he showed the terminal cells of the axial file to be cut off in a zigzag pattern (somewhat reminiscent of *Cryptosiphonia*). He went on to state that the axial cells produce two opposite laterals in the plane of the thallus and that these laterals branch predominantly abaxially. Corticating cells can be produced by all branch systems. Axial cells elongate considerably during blade growth.
Although early multiaxial growth is contributed by most of the lateral branches, gradually the two uppermost branches become dominant; they and their derivatives are mainly responsible for the upward growth of the blade. The primary medullary filaments are recognizable in mature blades as long, deeply staining giant cells or filaments. Norris noted that these were also seen by Abbott in *W. reticulata* and that thalli of *W. fryeana* maintained for one and one-half years in a seawater table at Friday Harbor Laboratories developed veins similar to thalli of *Weeksia reticulata*. Norris did not mention the occurrence of secondary pit connections between inner cortical cells, but he did note the fusion of secondary medullary filaments to cells of the cortex opposite their site of formation.

Scagel (1973:144) reported specimens from Barkeley Sound, B. C. Lindstrom (1977:156) recorded specimens collected in the northern part of the Alaska Panhandle, and Hawkes et al. (1979:110) found the species scattered along the mainland shore of northern British Columbia.

Lindstrom and Foreman (1979:178) included *W. fryeana* as a constant and characteristic species of the deep water (11.9 ± 3.5 m) association in the Flat Top Islands area of the Strait of Georgia.

In attempting to determine the affinity of *Neoabbottielia araneosa* (Perestenko) Lindstrom, which I found to be a member of the Cryptonemiaceae, I requested a loan of *Halymenia coccinea* (Harvey) Abbott from TCD. This specimen (Fig. 50d) was originally designated *Schizymenia? coccinea* by Harvey (1862:174). The large fragment (30+ cm across by 21.5 cm tall--
the basal portion is missing) was dredged by David Lyall in March 1858 in Griffin Bay, San Juan Island (48°30'N, 123°W). The specimen has a distinct orangeish-pink cast (Ridgway: Dragon's blood red to Vinaceous tawny) reminiscent of certain specimens of *Weeksia fryeana*. Closer examination of the specimen revealed distinct veins radiating from the presumed basal region of the thallus (Fig. 50f). Attempted peels of the blade showed several of the giant cells Abbott has described for the genus. The thin cortex and medulla further suggested *Weeksia fryeana*, as did both the depth of occurrence and its collection site. Therefore, I must propose the following combination:

*Weeksia coccinea* (Harvey) comb. nov.


Figs. d, f (this paper).


Harvey described this species as having large, thin, reddish-scarlet, gelatinous-membranous blades, firmly adhering to paper on drying, with a lax structure and few weblike axial filaments.

The application of the name *Halymenia coccinea* to more recently collected specimens from this geographical area, specimens that are obviously not referable to *Weeksia*, will not be treated in this study.

Observations on *Weeksia coccinea* are included under *W. digitata*.

*Weeksia templetonii* Setchell et Gardner. 1937:76
INTRODUCTION

Setchell and Gardner (1937:76, Pl. 10) described specimens dredged in 120 feet off Isla Cedros, Pacific Mexico, 15 August 1932, by J. T. Howell as *Weeksia templetonii*:

Fronds attached by a small disk, mucilaginous, flaccid, orbicular in outline, 8-12 cm. high, 200-250 μ thick, with a very short slender stipe and a few faint, radiating, false veins, but no differentiation of tissues to form them; medulla composed of a network of filaments with relatively straight cells 5-7 μ diam., 8-12 times as long; cortex composed of a single layer of color-bearing cells slightly elongated radially, 7 x 10 μ; subcortex composed of mostly 2 layers of spherical or subspherical cells with few chromatophores; cystocarps numerous, very small, distributed uniformly over the surface of the frond; curved auxiliary branchlets composed of 6-8 cells mostly; cells of these branchlets approximately 7 μ diam., tetradsporangia broadly ellipsoidal to subspherical, 18-22 μ x 22-26 μ, cruciately divided; antheridia unknown.

Abbott (1967a:143) made the combination *Halymenia templetonii* (S. and G.) Abbott and included Dawson's *Halymenia megaspora* as a later synonym. She followed Setchell and Gardner's description but went on to note that the cystocarps of *H. megaspora* were scattered, embedded, and about 150 μm in diameter. She compared the cortical layer of *Weeksia templetonii*, 3-4 cells and only 20-30 μm deep, to that of *W. reticulata*, 5-8 cells and 80-100 μm thick. She further noted that the capituliform cells of the innermost cortical layer in *Weeksia* were lacking in *W. templetonii*. Although the type of *H. megaspora* was much larger than that of *W. templetonii*, Abbott felt that the similarity of texture, shape, and vegetative structure of the two taxa made combining them advisable. Abbott also noted that the specimen illustrated by Dawson (1944, Pl. 7, Fig. 1) as *W. templetonii* from Santa Cruz I., California, was
rather a specimen of *W. reticulata*.

I have borrowed the type sheet of *Weeksia templetonii* (CAS 236484 in UC) and an isotype (UC 543986). Abbott stated that *W. templetonii* is definitely known from only two specimens on the type sheet, both of which are tetrasporangial. I found the type to consist of an orbiculate, about 10 cm in diameter, tetrasporic specimen affixed to a separate sheet attached to the herbarium paper plus an envelope containing several smaller specimens or fragments affixed to paper or mica. The isotype consisted of a single cystocarpic specimen.

All of the specimens are greenish and are very thin. Faint veins are visible near the base of several specimens (Fig. 50g). One or more refractive inclusions to about 7 μm on a side are visible in some inner cortical cells. Relatively long, thick, and moderately staining (with aniline blue) medullary filaments are also visible here and there. The tetrasporic specimens bear irregularly cruciate tetrasporangia 14-19 μm wide by 17-23 μm long. The cystocarpic specimen possesses ostiolate cystocarps of small, tightly appressed carpospores. Incompletely differentiated reproductive filaments typical of the Dumontiaceae can be seen in the cystocarpic specimen. Further morphological details could not be obtained because of the poor condition of the material.

The observations outlined in the preceding paragraph support Setchell and Gardner's original attribution of this species to the genus *Weeksia*. Because of the lack of material, this species will not be described further. I will not deal at all with Dawson's *Halymenia meqaspora*. 


**Weeksia howellii** Setchell et Gardner 1937:77

**INTRODUCTION**

Setchell and Gardner (1937:77) described a second species of *Weeksia* from the Templeton-Crocker Expedition, *W. howellii*:

Frond elongate to suborbicular, attached by a small disk with stipe merging almost directly into the frond, irregularly lobed or laciniate margins, thin and flaccid, 20-30 cm. high; medulla composed of moderately straight filaments with cells 6-8 μ diam. and 8-12 times as long; cortex composed of a single layer of cells slightly elongate radially and more or less conical; subcortex composed of 2-3 layers of cells irregular in shape and size, mostly angular and densely filled with granules; cystocarps distributed over the frond, deeply embedded in the medulla; curved auxiliary branchlets composed of 7-9 cells; cells of auxiliary branchlets 10-13 μ diam.; tetrasporangia distributed evenly over the frond, not abundant, spherical to subspherical, 18-22 μ diam.; antheridia unknown.

Two specimens are illustrated in their Plate 11. They are part of the type (CAS 236496) sheet and were dredged by J. T. Howell at Natividad Island between Cedros Island and the mainland of Baja California on 17 August 1932.

Abbott's description of *W. howellii* is summarized in Table II. In addition to the type, she recorded one collection, that of Neushul (No. 1591), from Anacapa Island California, at 85' (30 m), November 1964. Abbott distinguished this species from its congeners by its fewer cortical cell layers and its shorter carpogonial and auxiliary cell branches. The reported lack of veins and reddish brown color are also distinctive.

The type sheet of *Weeksia howellii* (CAS 236496 in UC) includes both cystocarpic and tetrasporic specimens. The specimens lack discernible basal discs, although part of one specimen covers a small pebble to which it may be attached. All the specimens are somewhat wrinkled and badly cracked. The
largest is just over 28 cm tall by about 12 cm wide. The color is close to Dragon's blood red and Vinaceous-rufous (Ridgway 1912). No veins are evident on any of the specimens. Two sheets (CAS 482550 in UC, UC 543981) of isotype material are also housed in UC and are in similar condition to the type sheet.

The thin blades have an outer pigmented cortical layer of 1-2 cell rows and an inner cortical layer of somewhat enlarged cells, full of starch grains, which produce the rhizoidal filaments. Cells typically have one or more prominent, round to quadrate refractive inclusions to about 6 μm in diameter. Reproductive filaments are initiated as in other species of *Weeksia*. Connecting filaments to at least 14 μm in diameter were observed. Carposporangia are tightly appressed in the cystocarp, which appears to be surrounded by a mucilaginous sheath 20-30 μm thick. Some carpospores have been released into this sheath; they are 14-20 μm in diameter, including their outer wall. Large ostioles to at least 65 μm across were seen. The cruciately divided tetrasporangia were 15-22 μm wide by 16-24 μm long.

The condition of this material, like that of the preceding species, is rather poor. It is possible that these two species are conspecific. It is also possible, though it seems less so, that these species are conspecific with *Weeksia reticulata* and the following species. However, more collections of both *W. templetonii* and *W. howellii* are needed before such synonymies can be proposed.
*Weeksia digitata* Abbott 1968:191

**INTRODUCTION**

Abbott's (1968:191) diagnosis of *Weeksia digitata* is summarized in Table II. The type specimen (Abbott 4011 in Herb. G. M. Smith, now US 084201) was collected by W. J. North on 1 August 1964 off Mission Point, Carmel Bay, Calif., from a depth of 20-30 feet (6-9 m). Abbott stated that this species was the dominant foliose red alga at this depth. She recorded additional specimens from Moss Beach, San Mateo County, south to Mission Bay, San Diego County, California, and from depths of 10 to 100 feet (3 to 30 m). Abbott distinguished this from other species of *Weeksia* by its firm texture, cuneate to falcate segments, and reddish as opposed to bluish color.

I have examined the holotype of *Weeksia digitata* (Fig. 50c). This deeply dissected, Nopal to Pompeian red (Ridgway 1912) blade reaches a height of just over 20 cm. Veins are relatively inconspicuous and are visible only near the base of the blade. The margin is distinctly crisped. Ostioles are just beginning to appear above a few of the cystocarps composed of many small, tightly appressed carposporangia.

**OBSERVATIONS**

Many specimens of both *Weeksia reticulata* and *W. digitata*, including the types, were examined. Most of these specimens had been annotated by Dr. I. A. Abbott. Among them, I could find no consistent distinctions with regard to color, size, shape, venation, seasonality or depth of occurrence. Since specimens identified as *W. digitata* by Dr. M. Hommersand provided the best
material on which to make anatomical observations, the following description and figures are based on that material unless noted otherwise. Because I could find no definitive differences between *W. reticulata* and *W. digitata*, the following observations may be considered to apply to the former taxon as well.

Filaments to 950 μm long have been measured in distal parts of *Weeksia digitata* blades. These filaments, about 10 μm in diameter and about 30 μm across at the usually distally situated branch points, probably represent major whorl branches. Cells thought to be axial cells, observed near the base of specimens of *W. coccinea*, reached lengths of 580 μm and widths of 70 μm; branching occurred near the midpoint of these cells, and axial pit connections were 8 μm in diameter. (In contrast, more distal axial cells in *W. coccinea* blades were measured to 500 μm in length and 15 μm in diameter, 50 μm wide at branch points.) One or more refractive inclusions are present in most cells; they can reach about 7 μm on a side.

The remaining observations refer to specimens identified as *W. digitata*.

In transverse section, the thallus is composed of one or two outer cortical layers of small, pigmented cells and three to four inner cortical layers of elliptical to orbiculate cells to about 30 μm in diameter. Secondary medullary filaments can arise from the inner cortical cells and contribute to the medulla.

Specimens to about 30 cm tall by about 35 cm across were seen. Blades can be smooth or occasionally wrinkled. Veins
range from completely lacking to conspicuous. When present, they can be visible only near the base, or they can be seen through much of the length of the plant. Colors represented by the specimens included Pompeian red, Ox blood red, Dragon's blood red, and Madder brown (Ridgway 1912), Pompeian red being the most common. Carpogonial and auxiliary cell branches have been seen in May specimens, and cystocarps have been found in July, August, October and November specimens. What appeared to be old cystocarps were observed in April and May specimens. Tetrasporangia were seen in July, August, September, and December material and in one April specimen.

Reproductive filaments are borne on inner cortical or outer medullary cells; they are seldom branched. Two incompletely differentiated reproductive filaments were the only ones observed to bear a lateral branch; one bore its 4-cell branch basally, the other its 4-cell branch near the middle of the filament.

Carpogonial branches are 7-14 cells in length \( (x=10.6, n=60) \). As in *Leptocladia binghamiae*, the trichogyne is initiated as a narrow projection. As the branch matures (Figs. 51a, b), the distal cells, particularly cells 4 and 5, elongate considerably, increasing only modestly in diameter and becoming humerus-like, as described by Abbott (1968).

Following fertilization, the carpogonium can divide, and both carpogonial derivative cells can fuse with nearby cells (i.e., cells 4 and 5) of the carpogonial branch (Fig. 51c). Connecting filaments originate from the carpogonial derivative cells attached to the nutritive cells. In one instance,
abundantly segmented filaments, similar to what has been observed in *Constantinea subulifera*, were seen developing from an undivided but presumably fertilized carpogonial derivative cell attached to cell 4 (Fig. 52). Connecting filaments to 12 μm in diameter have been observed.

Auxiliary cell branches are 7-16 cells in length (x=10.7, n=72; Fig. 53). The auxiliary cell is cell 2, occasionally cell 3. As the reproductive filament differentiates, the auxiliary cell enlarges somewhat but remains orbiculate (Fig. 53a), and its immediate neighbors begin to elongate and become humerus-like, similar to cells of the carpogonial branch (Figs. 53d, e). The second cell below the auxiliary cell also enlarges but not to the extent of the immediately neighboring cells. Not infrequently, a subterminal auxiliary cell cuts off a second cell distally as the branch matures (Fig. 53b). In one instance, one of two terminal cells had divided further (Fig. 53c). When two terminal cells are present, both enlarge as the branch matures (Fig. 53e).

Contact between the auxiliary cell and the connecting filament is similar to that in other Dumontiaceae except that the connecting filament appears to divide after contact with the auxiliary cell. As in *Leptocladia binghamiae* (Fig. 47b), the auxiliary cell itself produces a protrusion that appears to effect contact. After contact, the connecting filament produces up to five outgoing connecting filaments and begins to initiate gonimoblast filaments (Fig. 54a). The cells of the gonimoblast are distinguished by their tightly appressed character (Fig. 54b), resembling cells constrained by an outer wall during spore
germination in certain species. The tightly appressed aspect of the cells of the gonimoblast is maintained even in the mature cystocarp (Fig. 54c). An ostiole develops above mature cystocarps.

Mature cells of reproductive filaments can be invaded by vegetative filaments.

The cruciate to irregularly cruciate tetrasporangia appear to be attached somewhat laterally to the second cell of a cortical filament; they were 12-17 \( \mu m \) by 16-20 \( \mu m \) in the specimens examined.

A large number of specimens of *Weeksia coccinea* were also observed. These were similar in most respects to the specimens of *W. digitata* and *W. reticulata* examined. Somewhat larger blades (to 40 cm) were seen, and these ranged in color from Pompeian red through Acajou, Jasper, and Eugenia red (Ridgway 1912). Anatomically, no unequivocal differences were observed. The lack of distinctive features separating the species of *Weeksia* suggests the need for a detailed study of this genus.

**COMMENTS**

Abbott (1968:188) proposed a new family, the *Weeksiaceae*, to include those genera of the Dumontiaceae which were believed to have non-functional auxiliary cell branches (and hence were considered to be procarpic). In this family, Abbott placed *Weeksia*, *Leptocladia*, and *Constantinea*. I have shown elsewhere (Lindstrom 1981) that *Constantinea* species do in fact have functional auxiliary cell branches. I have shown in this study that *Weeksia* and *Leptocladia* also have functional auxiliary cell
branches although I illustrate one example in which gonimoblast-like filaments, in addition to connecting filaments, appear to arise from a carpogonial fusion cell in *W. digitata*. Abbott's figure (1968:189, Fig. 23), said to be "gonimoblast being produced from a fused nutritive cell borne on the carpogonial branch," is rather gonimoblast being produced from the remnant of connecting filament attached to an auxiliary cell.

It is therefore apparent that the distinguishing character of the Weeksiaceae is not generally valid among the species placed in the family. Further comments on the Weeksiaceae appear below in Chapter IV (p. 342).

*Constantinea rosa-marina* (Gmelin) Postels et Ruprecht 1840:17, *C. simplex* Setchell 1901:127, and *C. subulifera* Setchell 1906:172

**INTRODUCTION**

Three species of the genus *Constantinea* are currently recognized, *C. rosa-marina*, *C. simplex*, and *C. subulifera*.

Gmelin (1768:102) described *Fucus rosa-marina* from specimens collected by Steller in 1742-45 near Cape Lopatka, Kamchatka Peninsula. He wrote of *Fucus rosa-marina*, "Peculiare sistit haec planta fuci specimen, cujus exemplum aluid in omni reliqua fucorum historia non occurrit." Gmelin distinguished this species by its terete percurrent stem with petaloid, frequently split blades marked by a circle in the center. He noted its membranous texture, yellowish red color and moderate size ("half a foot"). His figure shows a heavily epiphytized,
much branched thallus, with polypetalous blades terminating most branches and also sometimes occurring at 1 or 2 nodes behind the terminus. New blades appear to be arise in the centers of the terminal blades (this feature suggests that the specimen figured was collected in November—see Lindstrom 1980:146).

Postels and Ruprecht (1840:17) introduced the generic name *Constantinea*. To Gmelin's description, they added the occurrence of annular rings on the stipe and a description of the reproductive structures. They described the "sporidia" [probably tetraspores] as occurring in oval loments among numerous closely appressed antheridia [probably paraphyses] on the upper surface of the blade and the "gongyli" [probably carposporangia] as round or oval, sheathed, and mixed with linear filaments (Kützing, 1843:400, as quoted by Setchell 1906:168, believed Postels and Ruprecht's "gongyli rotundi" to be merely the starch-filled cells of the inner cortex.)

Postels and Ruprecht included 3 species, making 2 new combinations and describing one species as new. To the earlier description of *Fucus rosa-marina* they added measurements of blades ("diametro 2 pollicaris") and distance between annuli ("2-5 lineas"), also noting that the stipe can be branched to the base, that the branches do not vary much in diameter from one order to another, that the terminal peltate blades are usually composed of 5-6 obovate-spathulate segments, rarely entire, and that subterminal blades are composed of 2-4 verticillately arranged lamina cleft nearly to the branch. Postels and Ruprecht's figure of this species appears somewhat more natural than Gmelin's and also shows what appears to be new
blade initiation in the centers of the terminal blades. 

**Constantinea sitchensis** from near Sitka was described as larger than the preceding species in all aspects: terminal blades 4-6 pollicaris [a pollicaris is about 1 inch] in diameter, internodes separating annuli 4 times as long as wide (for *C. rosa-marina*, this ratio was stated to be 2); this species was also described as dichotomously branched. Postels and Ruprecht recognized the Mediterranean **Neurocaulon reniforme** (P. et R.) Zanardini as a third species of *Constantinea, C. reniforme*.

Many nineteenth century phycologists who referred to these taxa probably based their citations solely on material in the literature and not on personal observations: C. Agardh 1822:190, 1824:253, as *F. rosa-marina*; Endlicher 1843, Suppl. III:40, as Kallymenia *rosa-marina* and *K. sitchensis*; Kützing 1849:744, as *Neurocaulon rosa-marina* and *N. sitchensis*, 1867, pl. 83, as *N. rosa-marina*; J. Agardh 1851:295; and Harvey 1853:173.

Harvey (1862:172) observed what was probably *C. subulifera* (as *C. sitchensis*) in drift material collected at Victoria by Dr. Lyall. He suggested that the plants, which had lacerated blades 6-8 inches in diameter, might merely represent a luxuriant state of *C. rosa-marina*.

J. Agardh (1876:225) observed authentic specimens of *C. rosa-marina* sent from Leningrad and of *C. simplex* (as *C. sitchensis*) sent to him by Farlow from California (Setchell 1906). Despite this, his generic diagnosis followed that of his earlier paper, which according to Setchell (1906:168) was based on **Neurocaulon reniformis**, and his species diagnoses followed those of Postels and Ruprecht.
Schmitz (1889:453; Schmitz and Hauptfleisch 1897:520) also must have observed specimens of the genus for he correctly placed it in the Dumontiaceae (J. Agardh had consistently included it with Kallymenia in his tribe Kallymeneae). Schmitz and Hauptfleisch described the occurrence of the carpogonial and auxiliary cell branches and later the cystocarps in the inner cortex of the upper side of the blade only, the meshwork of sterile tissue interspersed among the carposporangia, and the pores through which the spores are released.

Okamura (1891:333) recorded Constantinea sitchensis from Akkeshi Bay, Hokkaido.

Freeman (1899:175) studied the morphology and anatomy of Constantinea subulifera (as C. sitchensis) from Puget Sound and Juan de Fuca Strait including the San Juan Islands collected from late May to early August. He noted the prominent veins on the under side of the blade and described and illustrated the three part cross-section of the blade alluded to by earlier authors (J. Agardh 1851, 1876; Schmitz and Hauptfleisch 1897)—the central layer of loosely woven filaments, an intermediate layer of starch-filled, nearly spherical cells, and an outer cortical layer of small, pseudoparenchymatous, slightly elongate cells. He also described and illustrated the anatomy of the stipe as similar to the blade except in the region of the annulus, where the cortical and intermediate layers are absent, and at the growing point, where the intermediate layer is missing. Cystocarps were absent from the material examined by Freeman. Zonate tetrasporangia averaging 22 by 108 μm occurred among paraphyses in nemathecia 3.5 to 4 mm in diameter on the
lower surface of the frond. Freeman also hypothesized that *C. sitchensis* merely represented a summer stage of *C. rosa-marina* and hence that the genus was monotypic.

Setchell (1901:127) recognized a new species of *Constantinea*, *C. simplex*, from California. He distinguished it by its low stature, generally unbranched habit, stout stem (6-12 mm) with successive annulations much closer than the diameter of the stem. Other features, including reproductive ones, appeared to be similar to other members of the genus.

Setchell (1906:172) described another species, *C. subulifera*. He distinguished the existing species thus: internode between old and new blade initially less than the diameter of stipe and remaining so—*C. simplex*, internode initially less less than diameter of stipe but elongating to 2-4 times diameter of stipe—*C. rosa-marina*, and internode between old and new blade always longer than the diameter of the stipe—*C. subulifera*. Thus, the blades of *C. rosa-marina* and *C. simplex* are peltate, becoming perfoliate only upon the appearance of a new blade whereas, according to Setchell, those of *C. subulifera* appear to be perfoliate from the very beginning. Setchell also noted the strong aggregation of what he called the mechanical tissues of the blade into conspicuous radiating strands in *C. subulifera*, a feature lacking in the other two species.

In addition to vegetative features, Setchell noted reproductive differences. *Constantinea subulifera* showed the least amount of aggregation of the tetrasporangial nemathecia, and *C. simplex*, the most. Setchell further indicated that the
tetrasporangial nemathecia of both *C. subulifera* and *C. simplex* occur on the upper surface of the blade. To his earlier description of the cystocarp in *C. simplex* (which essentially mimicked that of Schmitz and Hauptfleisch for the genus) he added that it is a reniform mass of spores subtended by a stalk or pedicel. Cystocarps develop centripetally.

Setchell included *Constantinea sitchensis* as a synonym of *C. rosa-marina*. He recognized the distribution of this species from the Kurile Islands to the coasts of Alaska, the distribution of *C. simplex* from Oregon to central California, and the intermediate position of *C. subulifera* in the vicinity of Puget Sound.

Nagai (1935:780) recorded both *Constantinea rosa-marina* and *C. subulifera* from Japan. He included original habit figures of both species and a sketch of the zonate tetrasporangia among paraphyses at the surface of the blade.

Masaki (1952:30) studied the reproductive structures of both Japanese species. He noted the occurrence of tetrasporangial nemathecia on the lower surface of the blades of both *C. rosa-marina* and *C. subulifera*. He described the tetrasporangia of *C. subulifera* as having more distinct membranes and as being slightly larger than those of *C. rosa-marina*. Carpogonial branches were described as consisting of 6, rarely 7, irregularly shaped cells, growing inward from the inner cortex but becoming reflexed such that the carpogonium comes to lie close to cell 4. Masaki wrote, "After fertilization the carpogonium fuses with this cell (nutritive cell) and the latter becomes large giving rise to several
protuberances which are supposed [presumed] to become later starting points of the connecting filaments..." In contrast to the carpogonial branches, the 10-11-celled auxiliary cell branches develop outwardly from the inner cortex. Masaki identified the auxiliary cell as third from the apex and as the largest. His Text Fig. 4(b) "shows the contact of a connecting filament with an auxiliary cell and the gonimoblast initial cut of from the latter." Masaki also described the anticlinal elongation of the inner cortical cells to provide space for the developing gonimoblast and the development of a large fusion cell at the base of the cystocarp.

Scagel (1957:146) included both C. simplex and C. subulifera in the flora of British Columbia and northern Washington.

Powell (1964) wrote a thesis on Constantinea subulifera. In it he demonstrated that new blade initiation in this species occurs in response to short-day conditions and appears to be a genuine photoperiodic response, requiring approximately 28 days of short-day (i.e., less than 9 hours of light, p. 46) conditions to induce. Although never published, this thesis has been cited frequently; it also included other important information on the species. Powell provided records of the distribution of C. subulifera from the Pacific coast of Alaska and recorded its vertical distribution as from MLLW to about 11 m below MLLW in the San Juan Islands (p. 29; plants transplanted to 12.7 m did not survive for the full period of experimentation). Blades to 63 cm in diameter were collected; internodes averaged 8-10 mm in length (11-14 mm in C. rosa-
marina from Japan). Powell was the first to estimate the age of plants based on the assumption of only one blade (and hence one blade-scar) per branch per year. Among his Brown I., Wash., plants, the average age was 6.85 years and the range, 4 to 12 years. Japanese specimens of C. rosa-marina averaged 7.15 years and ranged from 4 to 12 years, and California specimens of C. simplex averaged 6.7 years and ranged from 3 to 10.

Powell illustrated new blade initiation from a thickened cortical zone of 50-60 cells in the flattened center of the protuberant stipe of C. subulifera.

Powell was also the first to observe male reproductive organs in the genus. Spermatangial mother cells to 36 μm in length form on both surfaces of the blade in April and May and cut off spermatangia 4.2-5.4 μm long by 2.6-3.6 μm in diameter. Following release of the spermatia, the outer, fertile rim of blade tissue disintegrates leaving a sterile central portion 5-7 cm in diameter.

At the same time spermatia are released, Powell observed pores in the cortical cells over each carpogonial branch. Powell stated that the auxiliary cell branches are nonfunctional in C. subulifera and that the gonimoblast filaments develop directly from the fusion cell of the carpogonial branch.

Abbott (1968:192) studied the vegetative and reproductive anatomy of C. simplex from California. She described the initiation of new blades from a slight depression in the terminal blade; cells in the center of the platelike meristem contribute only to stipe elongation whereas those at the periphery contributing to both stipe elongation and blade
formation. Abbott described the carpogonial branches as 9-12 cells in length with inflated and bonelike nutritive cells. As Powell believed for *C. subulifera*, Abbott thought that the auxiliary cell branches of *C. simplex* were nonfunctional, the gonimoblast arising from one or two lobes of a cell of the carpogonial branch with which the carpogonium fuses after fertilization. However, Abbott footnoted an observation by R. E. Norris of gonimoblast arising from the auxiliary cell in *C. rosa-marina*. Abbott found the irregularly cruciate to irregularly zonate tetrasporangia to occur on the upper surface of the blade in *C. simplex*. She placed *Constantinea* together with *Weeksia* and *Leptocladia* in her newly created family *Weeksiaceae*.

Lindstrom (1980) studied new blade initiation in *C. rosa-marina*. She described the development of the blade from a solid core of unbranched meristematic cells in the center of a mound of tissue protruding from the middle of the previous year's blade. Cortical cells of the upper surface of the new blade arise from apical cells of the core dividing obliquely and producing branches from the convex side of their cell files. Cortical cells of the lower surface of the blade arise from filaments initiated laterally from intercalary cells near the periphery of the core. The medulla develops from elongation of the primary cells of the meristematic core. Lindstrom also showed that new blade initiation in *C. rosa-marina* also occurs only under short-day conditions and that long-day conditions slow or halt blade expansion.

Pueschel and Cole (1980) observed phytoferritin in the
chloroplasts of senescing reproductive blades of *Constantinea simplex* and *C. subulifera* but not in the chloroplasts of new blades. However, they did not report the condition of chloroplasts in nonreproductive portions of terminal or older blades. Pueschel and Parthasarathy (1984) confirmed the identity of the phytoferritin by X-ray microanalysis.

Lindstrom (1981) described and illustrated the development of the extremely lobed cells of the carpogonial branch in *C. rosa-marina*. She also described and figured gonimoblast initiation from a distant auxiliary cell. Like earlier authors, she assumed the zygote nucleus was transferred to the nutritive cell of the carpogonial branch after fertilization. Although fertilization is effected in the spring, post-fertilization development was not observed until fall. Connecting filaments were described as branched but nonseptate, contacting the second or third cell from the tip of an auxiliary cell branch (8-) 10-12 (-15) cells long. The gonimoblast was said to usually arise from the remnant of the connecting filament near its point of attachment to the auxiliary cell.

The type of *Fucus rosa-marina* or any material which could be designated a lectotype has not been located. However, in LE are specimens and fragments of this species from the Port of St. Peter and Paul, Kamschatka, collected during the Lütke expedition and labeled, perhaps in Ruprecht's hand, "Originale! Einigs sind vertheilt worden 1840 und einigs sind..." Perestenko has suggested (pers. comm., 29 June 1983) that this material be designated the neotype. I concur with Perestenko's suggestion, pending location of Gmelin's original material. Since the
species is so distinct, there can be little doubt of the identity of the neotype with the original. The geographic proximity of the two collections also supports their identity. The designation of a drawing as lectotype, as Abbott (1979) has done for Dumontia contorta, also originally described by Gmelin, seems particularly inappropriate here because the illustration presents such a fanciful concept of the species (see below).

The largest fragment in the neotype collection is about 8 cm tall and shows at least 11 blade scars. Among the material, no blade has a radius of more than 4 cm. The specimens are a golden-brown with a tinge of red, verging on black, not particularly close to any Ridgway (1912) color. Veins are not evident on the blades, which appear to be uniformly sterile. Their small diameters suggest the fertile portion has already been shed, but evidence of new terminal blades is lacking. Remains of what appear to be hydroids occur on the stems, and Spirorbus-like organisms occur on the stems and blades.

Two packets of specimens of Constantinea sitchensis, both labeled "syntype," are found in LE. Both packets contain several specimens collected at Sitka by "Kastalsky?" and determined by Postels and Ruprecht. In one packet, a label with "Sitca" on it is attributed to "(Mert. fil. scripsit)" in a second script, believed to be Ruprecht's, which further appends the label "Constantinea sitchensis PR" and "an a Kastalski's ...?". The larger of the specimens in this packet has a blade 10 cm in diameter. No veins are evident on the blade or any of the others in this collection. An outer rim of tissue 2.5 to 3.0 cm across has become faded. This rim bears tetrasporangia
among paraphyses in discrete sori on the lower surface. Mature tetrasporengia measured 30-48 by 102-158 μm (x=37 by 121 μm; n = 18), including the outer wall. A few tetraspores had just initiated in situ germination within their sporangia. New blades 2.5 mm in diameter were evident at the tops of short (about 1 mm high) hemispheric protrusions in the center of old blades of several of the specimens. That these protrusions between the two years' blades eventually elongate was suggested by the distance between nodes—7 to 20 mm—along the stipes of the plants. The smaller of the specimens had two thalli growing together from a coherent base, and one of these thalli was sparingly branched. The vegetative and reproductive condition of the plants suggest they were collected in December, probably no earlier than November nor later than January.

The second packet contains a similar assortment of specimens and fragments among which are, in addition to tetrasporic thalli, female blades containing early stages of gonimoblast production reminiscent of specimens of C. rosa-marina collected in mid October at Cape Nosappu, Japan.

The preceding observations support Setchell's determination that C. sitkensis should be considered a synonym of C. rosa-marina.

The holotype of Constantinea simplex (UC 93186) includes both tetrasporangial and carposporangial thalli. The specimens were collected at Dillon Beach, California, by W. A. Setchell and "R. E. Nabs?" in Dec. 1898. The largest blade is 11.2 cm in diameter; the stipe, 3 mm in diameter. New blades to 6 mm in diameter can be seen sitting atop old blades. Irregularly
zonate tetrasporangia, 19-21 by 70-76 µm, occur in nemathecia on the upper surface of the blade. Some carposporangia show in situ germination. Ostioles are visible on the upper surface of the blade.

The holotype of *Constantinea subulifera* (UC 93196) includes both female and tetrasporophytic fragments. The specimens were collected at Whidbey Island, Washington, by N. L. Gardner, no date given. They are moldy, wrinkled, and fragmented. Radiating veins are visible in some fragments, and the blades seem thinner than those of *C. simplex*. *Chlorochytrium* is a common endophyte. At least one specimen had incompletely differentiated reproductive filaments, and another displayed young tetrasporangia.

Specimens of *Constantinea rosa-marina* from the Lütke expedition were distributed by LE to LD, TCD, and FH (Setchell 1906:164). Specimens of *C. subulifera* were distributed by Tilden (Am. Alg. no. 203, 1897, cited by Freeman 1899:181) as *C. sitchensis*. Specimens of *C. simplex* were included as *C. sitchensis* in Farlow, Anderson, and Eaton, Algae Amer. Bor. Exsiccatea No. 148, and in Collins, Holden & Setchell, P.B.-A., No. 150, 1898 (Setchell 1901:128).

A realistic concept of the genus and its species has no doubt been hampered by the somewhat fanciful or misidentified illustrations of *Constantinea* which have been published starting with Gmelin's of *Fucus rosa-marina*. Kützing (1867, Pl. 83) modified Gmelin's drawing of the rose-like habit of the species, bringing it no closer to realism, and he has been copied by Schmitz and Hauptfleisch (1897, Fig. 277) and Kylin (1956, Fig.
Oltmanns (1904, Fig. 342) copied Freeman's illustration of *C. subulifera*, identifying it, as Freeman had done, as *C. sitchensis*. Oltmanns (1922, Fig. 494) used the same illustration but identified it as *C. rosa-marina* as did Fritsch (1945, Fig. 176). More accurate representations of the genus include illustrations of *C. rosa-marina* by Nagai (1935, Fig. 1) and Chihara (1975, p. 104), of *C. simplex* by Smith (1944, Pl. 47, Fig. 6), Scagel (1967, Fig. 79), and Abbott and Hollenberg (1976, Fig. 303), and of *C. subulifera* by Nagai (1935, Fig. 2) and Scagel (1967, Fig. 80).

**OBSERVATIONS**

The genus *Constantinea* is distinguished vegetatively by its saucer-shaped blades borne atop a cylindrical stipe. In *C. simplex*, as the name implies, a single blade terminates the usually unbranched stipe. In *C. rosa-marina* and *C. subulifera*, the stipe is branched, and each branch is terminated by a blade. In *C. subulifera*, the stipe begins to protrude through the terminal blade in late spring, and a new blade is initiated atop this protrusion in the fall. In *C. rosa-marina* and *C. simplex*, the new blade is formed in the center of the old blade, but only in *C. rosa-marina* does the stipe between the two blades elongate and then only as the new blade enlarges; in *C. simplex*, there is almost no stipe elongation between successive blades.

Blades to 65 cm in diameter have been recorded for *C. subulifera* (Powell, 1964), to 12 cm for *C. simplex* (Abbott and Hollenberg 1976; Alaskan specimens identified as this species have blades to at least 15 cm in diameter), and to 21 cm for *C.*
rosa-marina. Blades are frequently lacerated. Blades are initiated in the fall; radial growth slows in the spring and terminates as the blades become fertile. All but the central sterile approximately 5 cm radius of blade tissue is shed following release of the reproductive products. This sterile remnant may persist for up to 6 years (pers. obs. for specimens of C. rosa-marina from Kushiro, Japan), but it usually disappears in a year or two, leaving a blade scar. The number of blade scars along the main axis of the plant gives an estimate of the age of the plant. I have observed specimens of C. rosa-marina with up to 18 blade scars and of C. simplex with up to 20. Powell (1964) recorded specimens of all three species to 10-12 years of age.

The stipe of C. simplex is fairly robust, 6-12 mm in diameter (Abbott and Hollenberg 1976). It is distinctly narrower, 2-3.5 mm, in C. rosa-marina and C. subulifera. The stipe between successive blades is only 1-2 mm long in C. simplex. In C. rosa-marina, it varies from 4 mm long in low intertidal specimens to a maximum of at least 22 mm long in subtidal specimens. This apparent correlation of stipe length with water depth requires further study. The internodes of C. subulifera range from a few mm on new branches to 18 mm on older branches. In C. rosa-marina, most of the internode is composed of stipe tissue formed in conjunction with blade initiation, and in fresh material there is a junction between the darker colored 0.5-2.5 mm high mound out of which the stipe and blade arose and the lighter colored stipe subtending the new blade. In fresh material of C. subulifera, a junction is also evident, but its
position is variable, depending on the length the old stipe protruding through the previous year's blade (to 15 mm) and the length of new stipe produced in conjunction with new blade initiation (to 9 mm).

In a transverse section of the blade, three layers are recognizable. The outer pigmented cortical cells are elliptical, 8-12 μm high by 3-4 μm in diameter. Subsurface cells are approximately spherical. Five to six layers from the surface, the cells become elongate, elliptical to cylindrical in outline. These elongate cells coalesce in the center of the section to form the filamentous medulla. Rhizoidal filaments develop from inner cortical cells of the upper surface of the blade, cross the medulla, and contribute to the formation of the cortex of the lower surface of the blade (see Lindstrom 1980). Cell fusions can occur between cells of the inner cortex, resulting in the formation of secondary pit connections, but these fusions are not common and do not result in the stellate cells characteristic of Dilsea and its close relatives. As the season progresses, the inner cortical cells enlarge and become replete with starch grains. Rhizoids increase in the medullary portion of the section. Sections of sterile blades range in total thickness from about 200 μm in early spring plants of C. rosa-marinato at least 1 mm in late summer plants of C. simplex.

Axial filaments are occasionally visible in the medulla of sections, particularly in spring plants. The cells of these filaments can reach at least 2.0 mm in length in C. rosa-marinato. They have thick walls and can reach nearly 30 μm in diameter.
They are interconnected by pit connections 4-7 μm in diameter. They usually bear a single branch near their midpoint.

As suggested by the gross morphology of *C. subulifera*, the presence of distinct bundles composed of an axial filament surrounded by rhizoidal filaments is characteristic of transverse sections of this species.

The species of *Constantinea* vary from Vandyke Red-Pompeian Red (Ridgway 1912) in early spring to Brick Red-Hessian Brown by late spring to almost black by late summer.

The species are lithophytic but can occur on medium-sized rocks on sandy bottoms. Lindstrom and Foreman (1979) found *C. subulifera* to be a constant and characteristic species in the upper subtidal foliose red algal association in the Flat Top Islands area of the Strait of Georgia, B. C.

The species typically extend from the extreme low intertidal zone into the subtidal zone to a depth of about 10 m. This vertical range varies somewhat geographically. At Cape Nosappu, Japan, for example, *C. rosa-marina* occurs only below a depth of at least 2 m whereas *C. subulifera* extends into the low intertidal zone but is rare at 5 m. Druehl (1967) found the upper limit of *C. subulifera* to be depressed near the head of a British Columbia fjord (its vertical distribution correlated most strongly with summer water temperature).

*Constantinea rosa-marina* has been collected from Southeast Alaska to Hokkaido, Japan, *C. simplex* from central California to possibly the Aleutian Islands (*UBC A26997 appears to be referable to this species*), and *C. subulifera* from northern Washington to Hokkaido, Japan.
The following description of reproductive structures and post-fertilization development is based mostly on specimens of *C. rosa-marina* and *C. subulifera*.

Reproductive structures begin to develop in early spring as the radial expansion of the blades of all three species slows.

Carpogonial branches develop from inner cortical cells of the upper surface of the blade (Fig. 55a). The branches grow toward the medulla. The last 3 cells of the branch are cut off by oblique walls so that the distal end of the branch becomes recurved. As these cells are forming, a narrow protrusion begins to develop distally. It represents the trichogyne. In *C. rosa-marina*, cells 2-7 begin to enlarge as the carpogonium matures, as do their nuclei, and cells 2-5 become lobed, particularly cell 4 (Fig. 55b). Carpogonial branches are 6-9 (-12) cells in length in *C. rosa-marina* from Hokkaido, 10-17 cells long in *C. simplex* from British Columbia, and 7-17 cells long in *C. subulifera* from British Columbia and Alaska. The cells of the carpogonial branches of *C. subulifera* (Figs. 55c-f) enlarge much the same as in *C. rosa-marina*, but in *C. simplex*, cells 2-7 can become nearly as lobed as cell 4. The long, irregularly coiled trichogyne usually extends through a conical projection in the upper surface of the blade, but it can also traverse the medulla and cortex of the lower surface of the blade and project through it.

Fertilization is believed to occur in the spring. In all the species, spermatangia have been observed from April to June, after which the male thalli shed the fertile portion of their blades.
There are no recognizable changes in reproductive structures for at least several months after presumed fertilization. The zygotic nucleus appears to remain in the fertilized carpogonium, which is recognizable by its darker staining properties than a presumably unfertilized carpogonium.

Post-fertilization development in *C. subulifera* appears to be initiated by the fusion of the fertilized carpogonium with another cell of the carpogonial branch in close proximity, usually cell 4 (Fig. 56). Connecting filaments appear to issue from the carpogonial portion of the fusion cell. They are highly segmented (Figs. 55f, 56), as has been observed in *Weeksia digitata* (Fig. 52). However, these segments do not appear to mature into carposporangia as do the cells of gonimoblast filaments. Figure 58a shows the more diffuse nature of the segmented connecting filaments developing from a fertilized carpogonial branch compared to the gonimoblast filaments developing attached to an auxiliary cell branch (Fig. 58b).

Small darkly staining bodies resembling satellite condensed chromosomes appear in the lobes of cells 4-7 (-8) (Fig. 55e); these darkly staining bodies were not visible in cells from spring collections. The lobes of cell 4 also appear to segment, but these cells do not ramify as the connecting filaments do.

Auxiliary cell branches also appear to be initiated in spring but do not mature until late summer or fall. Many short, 3-6 (-8)-celled incompletely differentiated reproductive filaments occurred together with fully differentiated, if not already fertilized, carpogonial branches in a May specimen of *C.*
rosa-marina from Hokkaido. Their darkly staining apical cells indicate continued meristematic activity.

By the time connecting filaments begin to form, the auxiliary cell branches have "moved" from growing inwardly to growing outwardly. This "movement" results from the changing position of the inner cortical cells to which the accessory branches are attached. As the thallus matures, additional cortical layers are formed, and the previously formed layers enlarge and come to lie closer to the medulla.

In the maturing auxiliary cell branches of C. subulifera, the auxiliary cell is initially somewhat larger than its immediate neighbors (Figs. 57a, c). The neighboring cells soon overtake the auxiliary cell in size and can become somewhat lobed (Fig. 57d), although never as lobed as the cells of the carpogonial branch. As in the carpogonial branch, the distal 7 cells stain darkly and have enlarged nuclei (Figs. 57b, c). Auxiliary cell branches were observed to be 7-11 cells long in C. rosa-marina, 9-15 cells long in C. simplex, and 6-14 cells long in C. subulifera. Lateral cells or branches rarely occur on either carpogonial or auxiliary cell branches of any of the three species. The auxiliary cell is usually cell 2, sometimes cell 3, rarely cell 4.

Away from the carpogonial fusion cell, connecting filaments remain unbranched except in the vicinity of an auxiliary cell. Connecting filaments were observed to be about 5 μm in diameter, somewhat wider just behind their growing tip. Initiation of contact between a connecting filament and an auxiliary cell was not observed; I assume it occurs as in other Dumontiaceae. One
example was observed in which a second outgoing connecting filament had been initiated from the remnant of the connecting filament attached to the auxiliary cell. Two or three gonimoblast initials appear to develop from the gonimoblast initiator cell (Fig. 57d); the first initial is usually larger than the others.

As the gonimoblast develops, the connections between the distal cells of the auxiliary cell branch enlarge (Fig. 57e). The pit connections can also enlarge, to about 9 μm in *C. rosa-marina*, to at least 5 μm in *C. simplex*, and to a maximum of 18 μm in *C. subulifera*. However, the connections between the cells expand beyond the diameter of the pit connections, and cytoplasmic continuity between these cells and the gonimoblast initiator cell is achieved. The connections between the basal cells of the gonimoblast and the gonimoblast initiator cell also enlarge (here, the pit connections enlarge only to about 3 μm in *C. rosa-marina*, 2 μm in *C. simplex*, and 4 μm in *C. subulifera*), and a gonimoblast fusion cell is formed (Fig. 57f). (Even if the auxiliary cell remains unfertilized, pit connections between distal cells of the branch still enlarge to about 2 μm in diameter.)

Prior to maturation of cells of the gonimoblast into carposporangia, nearby cortical cells are filled with starch grains (Fig. 58c). As the carposporangia mature, the inner cortical cells lose their starch grains and shrink in diameter (Fig. 58d). Although these inner cortical cells appear to nourish the developing carposporangia, no direct connections are discernible between the diploid carposporophyte and the
enveloping haploid tissue.

Only the distal cells of the gonimoblast mature into carposporangia. The proximal cells are either incorporated into a gonimoblast fusion cell or simply remain undifferentiated.

An ostiole develops above the mature carposporophyte. Released carpospores averaged 49 \( \mu \text{m} \) in diameter from specimens of \textit{C. rosa-marina} collected at Cape Nosappu, Japan, in late November. Those of \textit{C. subulifera} appear to be somewhat larger and those of \textit{C. simplex} somewhat smaller, but no measurements of released carpospores of these two species have been made.

Following release of the spores, the fertile portion of the blade disintegrates, leaving a rim of sterile tissue around the perennial stipe.

Spermatangia are cut off spermatangial mother cells which are 1-2 \( \mu \text{m} \) wide by 20-35 \( \mu \text{m} \) long in \textit{C. rosa-marina} (Fig. 58e) and \textit{C. subulifera}. They are somewhat broader but shorter in \textit{C. simplex}. The oblong spermatangia have a central nucleus and vacuoles located both distally and proximally, similar to what has been described for the spermatangia of \textit{Bonnemaisonia nootkana} (Young 1977).

Tetrasporangia are zonately divided (Fig. 58f; they are irregularly zonate in \textit{C. simplex}) and occur among paraphyses, which appear to be tetrasporangial initials that have not yet begun to differentiated. Tetrasporangia occur on the lower surface of terminal blades of \textit{C. rosa-marina} and \textit{C. subulifera} and on either the upper or lower surface (rarely both) of \textit{C. simplex}. The smallest tetrasporangia are found in \textit{C. simplex} (28-40 by 62-82 \( \mu \text{m} \) in a pressed specimen collected in December),
the largest in *C. subulifera* (38-82 by 115-235 μm). The average size of tetrasporangia appears to increase as the season progresses until a maximum size is attained. The tetrasporangia occur in nemathecia which can become confluent, particularly in *C. rosa-marina* and *C. simplex*, as the season progresses. Tetrasporangia first appear in *C. subulifera* in June in British Columbia and July in Alaska, in *C. rosa-marina* in August in Alaska and September in Japan, and in *C. simplex* probably in November in British Columbia. Following release, the fertile portion of the blade disintegrates.

**Dumontia contorta** (Gmelin) Ruprecht 1851:295

**INTRODUCTION**

*Dumontia contorta*, in addition to being the taxonomic synonym of the type species of the family, is also its most studied and written about member. Below, I summarize the literature pertinent to our current understanding of its biology.

Abbott (1979) has reviewed the taxonomy and nomenclature of this species. Briefly, the species was originally described as *Fucus contortus* by Gmelin (1768:181) from drift material collected at Scheveningen, near The Hague, The Netherlands. The same species was subsequently described as *Ulva incrassata* by Müller (1775:7) from "Sinu Laurvigeosi Norvegiae" and as *Ulva filiformis* by Hudson (1778:570') from "Christ-Church in comitatu Hantoniensi." In creating the genus *Dumontia* (named for Charles

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Abbott's citation of *Ulva filiformis* as Hudson (1778:585) appears to be an error. Hudson described *Fucus filiformis* on p. 585; *Ulva filiformis* is described on p. 570.
Frédéric Dumont de Sainte-Croix, 1758-1830, a French ornithologist—Silva 1950:264), Lamouroux (1813:133) made the combination D. incrassata (Mueller) Lamouroux. Greville (1830:165) made the combination D. filiformis (Hornemann) Greville, Hornemann (1818(9):5) himself citing Hudson as author of the basionym. Ruprecht (1851:295) made the combination D. contorta. Ruprecht accepted Hudson's Ulva filiformis as conspecific with D. contorta, but he objected to Hornemann's Ulva filiformis on the grounds that the specimens corresponding to Hornemann's illustrations were Cystoclonium purpurascens (Hudson) Kuetzing (=C. purpureum (Hudson) Batters). Other combinations include Gastridium filiforme Lyngbye (1819:68), Halymenia filiformis C. Ag. (1822:214), and Dumontia filiformis (Lyngbye) J. Ag. (1876:257). Kützing (1849:718) and J. Agardh (1852:350) included Chondria purpurascens Greville (1824:290) under this name [Greville considered Ulva purpurascens Engl. Bot. Tab. 641 to be the basionym].

Gmelin originally described the species as thalli flat, subundulate and subcontorted with remote, minute marginal denticulae, a pale red or ochre. Subsequent authors described it as tubular, terete, threadlike or compressed, sparsely or simply branched, branches long, remote and attenuated at their base, membranaceous or mucilaginous, various shades of purple (Müller 1775, Hudson 1778, Hornemann 1818, Lyngbye 1819, C. Agardh 1824:245, Greville 1824, 1830, Kützing 1849, J. Agardh 1852:349, 1876, Harvey 1871:Pl. 59).

Wilce and Davis (1984) have recently reviewed the literature on the vegetative anatomy and morphology of D.
contorta and added their own observations. They noted the previous confusion surrounding the structure of the thallus and attributed it to the early conceptual separation of the basal crust from the upright macrothallus. A number of authors (Nägeli 1847:243, Schmitz and Hauptfleisch 1897:517, Rosenvinge 1917:156, Kylin 1923:10) apparently studied only apices of branches and concluded the thallus to be uniaxial. Reinke (1889:26) was the first to describe the crustose stage in detail and identify its capacity to perennate and initiate an upright macrothallus. However, it was Brebner (1895) who first described and illustrated the origin of the macrothallus from the elongation of a group of segmented filaments usually formed endogenously in the perennial crust; Dunn (1917:435) also noted and illustrated the origin of the macrothallus from "a group of vertical branches in the holdfast." Oltmanns (1904:273, 1922:245) attempted to reconcile these conflicting observations by stating that eventually only one filament dominates to form the macrothallus. Rietema and coworkers (Rietema and Klein 1981, Rietema 1982, Rietema and Breeman 1982, Rietema 1984), in studying environmental control of the life history of European D. contorta, also observed the multiseriate origin of the upright macrothallus. Both Rietema (1984) and Wilce and Davis (1984) have now documented the divergence of these filaments into separate uniaxial branches.

In an autoecological study of D. contorta, Kilar and Mathieson (1978) noted the increase in size of plants from their first appearance in October until February-March and then a decrease in size until their disappearance in July-August. They
related seasonal growth to temperature and nutrient availability and noted "a good correlation between seasonal growth and net photosynthesis." However, Rietema and coworkers (Rietema and Klein 1981, Rietema and Breeman 1982) found macrothallus initiation and growth to be primarily a response to photoperiod. They found macrothallus initiation to occur under short-day conditions of up to 12-13 hours of daylight in Isle of Man and Roscoff strains and up to 16 hours in Zeeland strains; initiation occurred earlier at 8°C than at 16°C and not at all at 20°C in Isle of Man material, earlier at 12°C than either 8° or 16°C and up to 24°C in Roscoff material, and earlier at 18° and up to 26°C in Zeeland material. Under longer-day conditions and if given a light break during long nights, crusts remained vegetative. Rietema (1982) found the response to consist of two parts: in the first, at least 31 short-day cycles are required to form the macrothallus initials; these develop irrespective of temperature (4° to 24°C for the Isle of Man strain). In the second part, for macrothalli to emerge from the crust, however, low temperatures are needed in addition to short days.

Despite the longstanding assumption that the thallus of D. contorta is uniaxial, little has been written on the structure of its uniaxial branches. Rosenvinge (1917) corrected earlier statements that the plane of division of the apical cell is oblique rather than transverse. Kylin (1923:10) indicated that each segment cell cuts off four pericentral cells. Wilce and Davis (1984) wrote that "the four pericentral cells constitute the cortical primordia which subsequently divide with both anticlinal and periclinal divisions to form the branch cortex,"
but they did not discuss the anatomy further. Neither of their figures of apical regions (Figs. 21 and 22) shows pit connections, and both appear to imply the occurrence of five periaxial cells.

Fritsch (1945:404, 412) indicated that the photosynthetic cells of D. contorta contain a single, large parietal chloroplast and that all vegetative cells are always uninucleate.

Greville (1830:Pl. 17) appears to have been the first to illustrate a reproductive feature of the species, showing a cystocarp composed of relatively few (ca 10) large, obpyriform carposporangia, each with a large central nucleus. Nägeli (1847:9, Fig. 6) briefly described oval, perpendicularly divided cells found in the cortex [tetrasporangia] and described and illustrated the somewhat deeper germ cell masses [cystocarps] which develop from a group of small cells in the dichotomies of whorl branches. Kützing [1849, 1866(16):Pl. 81] was the first to illustrate the subcortical cruciate tetrasporangia. Okamura (1907:65, Pl. 16) described and illustrated tetrasporangia, female reproductive structures and post-fertilization events in specimens from the Kurile Islands, noting the separation of the trichogyne from the base of the carpogonium, the fusion of the carpogonium with other cells of the carpogonial branch, and initiation of 4-5 or more nonseptate and unbranched connecting filaments from the fused carpogonium. Following Okamura, Rosenvinge (1917), Kylin (1923), and Kilar and Mathieson (1981) have provided similar descriptions and illustrations. Kilar and Mathieson observed carpogonial and auxiliary cell branches to
range from 4 to 9 cells in length. They found that the second to seventh cell from the base of the carpogonial branch could function as nutritive auxiliary cells. None of these authors have illustrated or described the fusion of the fertilized carpogonium to more than a single nutritive auxiliary cell although Okamura was nonspecific, stating, "cells of the carpogonial branch more or less fuse together into one mass." Kylin added the observation that, whereas most vegetative and reproductive cells are uninucleate, the lowermost cell of reproductive filaments is generally bi- or trinucleate. Kilar and Mathieson noted that these lower cells sometimes bear a sterile lateral. They found the position of the auxiliary cell to vary with the length of the auxiliary cell branch, being on the average the third cell from the distal end of the branch. Kylin assumed that both the nutritive auxiliary cell of the carpogonial branch and that of the auxiliary cell branch receive a diploid nucleus ("Die Auxiliarzelle muss dann aus dem Karpogone einen diploiden Kern bekommen," and "Dieser Auxiliarzelle [the one in the auxiliary cell branch] bekommen dabei einen diploiden Kern.") Despite assertions to the contrary, both Rosenvinge (Fig. 75H) and Kylin (Fig. 6C) illustrate gonimoblast development from the connecting filament remnant attached to the auxiliary cell rather than from the auxiliary cell itself.

Dunn (1916:271) discussed the cytology of tetrasporogenesis in D. contorta. She found little evidence of meiosis in specimens collected approximately hourly over a 24-hour period during the greatest of a series of spring tides. Only in
material collected at 9 a.m. were a few stages of nuclear division found (the one-celled binucleate condition).

Magne (1964:Pl. III) illustrated nuclear division in *D. contorta*. He observed 22-24 chromosomes, but since his material was sterile, he did not know whether this represented a haploid or diploid number.

Mature carposporangia have been reported to be 30-40 by 45-60 µm (Irvine 1983:16) and mature carpospores about 50 µm (Chemin 1937:368) and 52-57 µm in diameter (Kilar and Mathieson 1981:21, who also found an average of 22 sporangia per cystocarp). Mature tetrasporangia were reported to be 49 by 66 µm (Dunn 1916:272), 69-73 µm in their longer dimension (Kilar and Mathieson), and 35-65 by 55-90 µm (Irvine). Kylin (1917:9) found released tetraspores to be 35-45 µm in diameter. Discoid germination patterns for both tetraspores and carpospores have been documented by Kylin (1917) and Chemin (1937).

*Dumontia contorta* has been recorded in the NE Atlantic from Portugal (Ardré 1970) to the Barents and White Seas (Zinova 1955:69) and in the NW Atlantic from Long Island to James Bay (Taylor 1957:234). In the Pacific, it has been recorded from the southern part of the Alaska Panhandle (Lindstrom and Scagel 1981:67) around the N Pacific Rim to Peter the Great Bay (Perestenko 1980:38) and north to Port Clarence (Kjellman 1889:30).

Whelden (1928:123) noted the occurrence of *D. contorta* on stones, pebbles, and shells in a sandy tidepool in Maine. It also occurs on bedrock and epiphytically (Irvine 1983:16). It is common in tidepools from as high as +2 m in New England.
(Kilar and Mathieson 1978) to a depth of 12 m in Denmark
(Rosenvinge 1917). Young plants first appear in October or
November (Whelden 1928, Kilar and Mathieson 1978, Wilce and
Davis 1984). Rosenvinge recorded specimens to 70 cm in length,
and Whelden reported specimens to 50 cm with a maximum branch
diameter of 14 mm. As noted by Kilar and Mathieson, growth
ceases in February or March. Male and female reproductive
structures appear in mid March to mid May, and cystocarps have
been recorded from April in New England, from May in Europe
(Rosenvinge), and from July in Japan (Okamura). Female thalli
usually disappear within two months of becoming cystocarpic.
Tetrasporangial initials first appear between late March and mid
May, and tetrasporic thalli have been found to persist into
August in all areas but Alaska (pers. obs.).

Dunn (1917:437), Rosenvinge (1917:156), Grubb (1925:233),
Tazawa (1975:109), and Kilar and Mathieson (1981:21) have
described and illustrated spermatangial production in this
species. The spermatangia develop over essentially all but the
basal portion of the thallus. They are cut off the
spermatangial mother cells by oblique walls. No more than two
are seen attached to a spermatangial mother cell at any one
time, and secondary ones are produced after release of the
first. The spermatangia have a distal nucleus and a proximal
vacuolar region. According to Grubb and Tazawa, spermatangial
mother cells are cut off outer cortical cells.

I have not seen the type specimen of Dumontia contorta.
Abbott (1979) was also unable to locate the specimen Gmelin used
for his original description and illustration. She therefore
lectotypified the species name with his illustration (Plate XXII Fig. 1). This procedure is somewhat unfortunate since a habit figure gives one access only to the morphology of a specimen and not its anatomy. The morphology of Gmelin's figure, while showing the somewhat characteristic contorted and flattened aspect of the species, also shows the more unusual branching of its lateral branches.

OBSERVATIONS

As already discussed, *Dumontia contorta* has a unique axial structure, considered by some to be uniaxial and by others, multiaxial. As Wilce and Davis (1984) have shown, the thallus initially develops from a group of unbranched, small-celled filaments which elongate and begin to branch as the thallus expands. Apical cells of these filaments can eventually diverge from the coherent thallus to initiate usually unbranched lateral branches. Each of these branches terminates in a dome-shaped apical cell which divides transversely to cut off a discoid subapical cell 3-4 μm high by 11-13 μm in diameter (Fig. 59a). The subapical cell divides somewhat obliquely to produce four periaxial cells. The periaxial cells then divide anticlinally and periclinally in such a way that the corticating cells of the thallus come to be derived from a nested series of adaxial branches.

Immediately below the apical cell, the axial cells begin to elongate: 5 cells from the apex, the axial cell is 20-35 μm long by 5-7 μm wide (n=4); 10 cells from the apex, it is 140-205 μm long by 5-7 μm wide (n=4), somewhat narrower toward the middle
of the cell. Axial cells appear to elongate slightly more distally than proximally. Periaxial cells appear to be cut off slightly more toward the base of the axial cell than toward the apex; 10-15 cells from the apex, the lateral branches are attached to axial cells approximately 0.6-0.7 of the distance from the distal end of the axial cell, and in an axial cell about 1.5 mm long, the lateral branches were still attached 66% of the distance from the distal end to the proximal end of the cell. The walls of outer cortical cells are confluent, but a distinct cuticle appears to be lacking.

Axial cells enlarge to a maximum of about 25 μm in diameter including the wall and to at least 1500 μm in length. Pit connections enlarge to only 3 μm in diameter. Rhizoids occur in older parts of the thallus; they terminate in a relatively short cell in the middle of the thallus. No secondary pit connections or other vegetative cell fusions were seen. Hairs to over 700 μm in length have been measured. Refractive inclusions appear to be absent from all cells of the thallus.

Among the many studies of D. contorta, none have utilized material from the NE Pacific. The following observations are therefore based on specimens from SE Alaska except where noted. Specimens from Alaska are generally not as robust as some of those described from the N Atlantic. The largest was 27 cm tall and 3 mm across, but most specimens were 15 cm or less and only about 2 mm across. The thalli are irregularly branched to a single order. The branches are not constricted basally (branches appearing constricted basally are usually twisted at that point). The branches were of variable lengths—to a
maximum of about 9 cm—and generally 1 mm or less in diameter. The number of laterals varied from as few as 9 to a maximum of 37. The first lateral appeared 0.6 to 6.7 cm from the base of the thallus, or 4 to 43% of the distance from base to apex. The branches are of uniform diameter except for tapering gradually at their apices. The main axis tapers at the base; distally, it can taper like a lateral or terminate abruptly. Color of mature thalli prior to release of reproductive products ranges between Diamine brown and Prussian red (Ridgway 1912).

As in other Dumontiaceae, reproductive filaments develop abaxially from inner cortical cells. In *Dumontia contorta*, they are distinguished by their short length. In specimens from SE Alaska, carpogonial branches were 4-7 cells in length, and auxiliary cell branches (3-) 4-6 cells in length; they rarely bear a lateral branch basally. In specimens from Massachusetts, carpogonial branches were 4-7 cells in length, and auxiliary cell branches 5-8 cells in length; lateral branches were occasionally present. In branches 6 or more cells in length, the basal 1-2 cells were not always differentited (i.e., they were elongate and cylindrical rather than small and round).

Carpogonial branches are modestly recurved (Fig. 59b). The division between cells 2 and 3 appears to be slightly oblique and that between the carpogonium and cell 2 strongly oblique. The trichogyne is relatively short (about 100 μm long) and spirally twisted once or twice basally, and it frequently appears to be attached laterally to the base of the carpogonium (Fig. 59c). The carpogonium is relatively small and stains rather poorly with aniline blue. Cells 2 and 3 are about the
same size. Cell 4 does not enlarge to the extent of cell 5. All cells of the branch except the carpogonium have somewhat enlarged nuclei but particularly cells 4 and 5. More proximal cells, if they are present, can be multinucleate, as described previously by Kylin (1923). After presumed fertilization, the carpogonium expands and fuses with one or two cells, usually cells 4 and/or 5 (Fig. 59d), occasionally cell 6. When more than one cell is involved, the carpogonial derivative cell appears to separate into two distinct parts, and each fuses to another cell of the carpogonial branch. However, no pit connection between the two parts was seen. There can be some segmentation of the outgoing connecting filaments as they leave the carpogonium fusion cells. Connecting filaments up to at least 10 μm have been measured, but they are usually narrower (3-5 μm). Zero, one, or two diploid nuclei can remain behind in the carpogonial fusion cells after connecting filament production. The trichogyne remains attached by its wall to the carpogonium during post-fertilization development. If unfertilized, the carpogonium (and possibly other cells of the carpogonial branch) disintegrates.

The auxiliary cell is usually cell 3 in a 4-celled branch (Fig. 60a) or cell 4 in a 5-celled branch. The auxiliary cell is usually distinctly smaller than its neighbors. Its nucleus is not particularly prominent, but nuclei of two cells distal and one cell proximal to the auxiliary cell are enlarged and stain darkly with haematoxylin. These neighboring cells also have prominent walls, to 5 μm thick in many branches. A wall around the auxiliary cell was not detectable with either
haematoxylin or aniline blue staining. More proximal cells may be multinucleate, as previously described by Kylin (1923). Contact of the auxiliary cell by a connecting filament was not seen, but an immediately post-contact stage is illustrated in Fig. 60b. Two or three gonimoblast initials are produced by the gonimoblast initiator cell (Fig. 60c). Twenty-four or fewer carposporangia are produced; they are all cut off in a moderately tight cluster before enlargement begins (Fig. 60d). Maturation of carposporangia occurs centripetally. Pit connections between cells of the auxiliary cell branch can enlarge to 3 \( \mu \text{m} \) in diameter (Fig. 60e). The haploid nucleus can disappear or move into the gonimoblast initiator cell, which does not enlarge appreciably during cystocarp maturation. All cells of the gonimoblast usually mature into carposporangia 64-92 (-100) \( \mu \text{m} \) in diameter.

Spermatangia were not observed in the Alaska material.

Usually regularly but occasionally irregularly cruciately divided tetrasporangia are attached basally or subbasally to cortical cells 4 (-6) cells from the surface of the thallus. They are ovoid, 63-104 by 88-125 \( \mu \text{m} \).

Among the tetrasporic specimens examined are ones collected during an 8:54 a.m. PDT low tide at Craig, Alaska, on 12 May 1979. These specimens, like those collected by Dunn (1916) at 9 a.m. in Maine, include a number of binucleate one-celled sporangia. The nuclei of many of the other sporangial initials appear possibly meiotic by their elongate shape, but a single attempt to stain chromosomes and detect meiotic figures was unsuccessful.
**INTRODUCTION**

*Dumontia simplex* was originally described by Cotton (1906:372) from tetrasporic and cystocarpic specimens collected by Wakefield at Wonsan, Korea, in Feb. 1905: "Fronds many from a small basal disc, simple, linear-spathulate, with an attenuate filiform stipe toward the base, gelatinous. Cystocarps immersed, minute, nearly all occurring sparsely in the upper surface, carpospores largish; tetrasporangia immersed, sparse, cruciately divided [translation]."

The specimens Cotton observed consisted of 4-5 compressed fronds arising from a single base. The blades were 10-12 cm tall and about 1 cm across at their widest point 2-3 cm below the more or less blunt apex. Cotton further noted that the internal filamentous structure of the thallus showed no divergence from the usual *Dumontia* type. The large carposporangia frequently measured 80 μm in length.

Several Japanese workers have studied this species. Okamura (1928:182, Pl. 247) described and illustrated the habit of the species, its 5-celled carpogonial branches and 4-5 celled auxiliary cell branches, its small cystocarps, and its scattered tetrasporangia.

Segawa (1942:17) described and illustrated post-fertilization development in this species from specimens collected 16 May 1942 near the northern end of Ibaraki Prefecture. Among the 27 individuals collected, 24 were tetrasporophytes and 3 were female gametophytes. Segawa showed connecting filaments arising from a carpogonial fusion cell in
contact with cell 4 or with cells 4 and 5, and the gonimoblast was shown developing from the remnant of the connecting filament in cytoplasmic continuity with an auxiliary cell. All reproductive cells were shown to have thick walls.

Kawashima (1959b:74) also described and illustrated post-fertilization stages in this species, noting particularly its strong resemblance to *D. contorta* (as *D. filiformis*). He summarized its known geographic distribution from the eastern and western coasts of the Korean Peninsula north to southern Sakhalin through Tsugaru Strait and along the Pacific coast of Japan from Iwate Prefecture north to the Kurile Islands.

More recently Kang (1966:64) included it from around the coast of Korea. However, neither Funahashi (1966, 1973) nor Perestenko (1980) recorded it from the vicinity of Vladivostok. Kawai and Kurogi (1982:85) found it only at Soya Misaki along the Okhotsk Sea coast of Hokkaido. Along the east coast of Hokkaido, it has been recorded from Hidaka south (Chihara 1972:156). Tseng (1983:68) has recorded it from the Yellow Sea coast of China.

Tokida et al. (1964) studied specimens from Oshoro Bay and from near Hakodate, Japan. Plants first appear in October. Reproductive organs begin to form in November, and mature tetrasporic, male, and female plants occur from December onward. Most of the thalli disappear by the end of June. Tetrasporophytes are larger than gametophytes and reach a maximum size of 50 cm long by 5 cm wide. The maximum dimensions of female thalli were 34 cm by 3 cm. Males are distinctly smaller. The color is dark red to yellowish brown.
Tokida et al. described the medulla as consisting of "long filamentous cells with thick walls running longitudinally with rather large intercellular spaces or rarely even with a large central hollow," the cortex consisting of anticlinal rows of short cells. The presence of hairs was also noted, as was the occasional twisting and surface wrinkling of the thallus.

Tetrasporangia were recorded to be ellipsoidal, up to 64 by 75 µm. The tetraspores are released with the dissolution of the surrounding tissue. Spermatangia were described and illustrated for the first time. Female reproductive structures and post-fertilization development were also described and illustrated. In general, the observations of Tokida et al. followed earlier authors, but they noted the carpogonial branches could be 5-7 cells long and the auxiliary cell branches 4-5 cells long and that the lower cells of both branches were sometimes bi- or trinucleate. The carpogonial branches were described as covered by a thick membrane. Two to five nonseptate connecting filaments were produced from the carpogonial fusion cells in contact with cell 4 or cells 4 and 5. The connecting filaments contacted an auxiliary cell which is the third cell from the distal end of the branch. Then, according to Tokida et al. "the auxiliary cell gives rise to the gonimoblast-initials and also to one or two secondary connecting filaments which are of the same morphological and functional characters as the primary ones." However, their figures show the gonimoblast initials arising from the remnant of the connecting filament in cytoplasmic continuity with the auxiliary cell; they also appear to indicate that at least one connecting filament leaves the
auxiliary cell before a gonimoblast initial is cut off. Tokida et al. found the mature carpospores to be up to about 22 μm in diameter and to be shed, as the tetraspores are, with the dissolution of the blade.

OBSERVATIONS AND COMMENTS

Cursory observations of thalli of this species from Hokkaido, Japan, and Alaska did not reveal any significant differences in the reproductive anatomy and post-fertilization development between this species and Dumontia contorta. Vegetatively, the two species appear to differ mainly in the fact that the separate filaments constituting the thallus of D. simplex do not diverge into separate branches as in D. contorta. The anatomy and development of the vegetative macrothallus of D. simplex is the subject of an ongoing study by Dr. R. T. Wilce and A. N. Davis (pers. comm., 16 Oct. 1984). This species will not be dealt with further. Its overall similarity to D. contorta indicate that D. simplex would occur on the same branch as D. contorta as its sister taxon in any phylogenetic analysis.

Dasyphloea insignis Montagne 1842:8

INTRODUCTION

Dasyphloea insignis, originally described by Montagne (1842:8, non vidi) from Akaroa, New Zealand, has been collected only from southern Australia since that time (Mitchell 1966; Shepley and Womersley 1983), and Mitchell (1966:210) has hypothesized that the type material (in PC) was collected at Hobart, Tasmania, the last stop of the collector, Dumont
D'Urville, before reaching New Zealand. Mitchell considered *Dasyphloea tasmanica* Hooker et Harvey 1847:406 and *Nizzophloea tasmanica* J. Agardh 1876:256 to be synonyms.

Limited material of this species was available for study so the following account is based largely on the literature.

**OBSERVATIONS**

Thalli to 25 cm tall and to 4 mm in diameter have been recorded (Mitchell 1966). The thalli are irregularly, radially branched to 3 orders, and the branches taper at both base and apex.

Thalli are uniaxial. A dome-shaped apical cell 7-8 μm in diameter and 3-5 μm high cuts off discoid subapical cells which in turn cut off whorls of 4 periaxial cells by somewhat oblique angles (Fig. 61a). The periaxial cells also divide somewhat obliquely to initiate the whorl branches. The cells of a whorl branch are cut off by a series of nearly anticlinal divisions that cause the branch to grow forward. The space behind is filled by an abaxial cell on the periaxial cell that begins to divide in a similar, obliquely anticlinal manner as the main axis of the whorl branch.

Axial cells begin to elongate 5-6 cells behind the apex. Cell 5 is 4-5 μm in diameter by 4-6 μm tall, cell 10, 6-7 by 9-13 μm, and cell 20, 10-14 by 34-65 μm (n=5). As the axial cells enlarge, the pit connections between them also enlarge to at least 18 μm in diameter. The axial cells elongate more proximally than distally so that the periaxial cells remain located about two-thirds of the way toward the distal ends of
the cells. The largest axial cell measured was 600 μm long by 50 μm in diameter at its branch point.

Periaxial cells are relatively long and narrow (125 μm by 7.5 μm); they are not differentiated from more distal cells in size or shape. They are forked di- or trichotomously, giving rise to unbranched rhizoidal filaments of relatively narrow (less than 5 μm) diameter or to the similarly forked proximal cells of the whorl branches. More distally, cells of the whorl branches become cuneate and finally spherical. Shepley and Womersley (1983:206) described the periaxial cells as each "producing several orders of 3-4 elongate cells, then 2-3 layers of ovoid cells and 4-5 layers of small cells forming a compact cortex." According to them, the tetrasporophytes are more robust than the gametophytes with greater rhizoidal development in the medulla. Mitchell (Fig. 5) showed three rhizoidal filaments arrayed in a series along the abaxial side of a whorl branch cell.

Carpogonial branches are 5-6 cells long, distally recurved (the pit connections "in" and "out" of cell 2 are at 90° to each other), and are borne abaxially on periaxial cells (and possibly more distally). The base of the carpogonium is relatively small and non-descript (Fig. 61b). A long, broadly curved trichogyne emerges somewhat laterally from the base of the carpogonium. Cells 2 and 3 are also relatively small, with somewhat enlarged nuclei. Cells 4-6 are quite large and irregularly shaped; they have large nuclei. The fertilized carpogonium fuses with cells 4 and 5 without dividing (Mitchell stated that it also fuses with cell 6 when present, but I saw no examples of this). Up to
at least 6 connecting filaments are cut off the expanded carpogonial part of the fusion cell. Connecting filaments are about 5 μm in diameter and are relatively non-persistent. After connecting filament production, all but cells 2 and 3 of the branch disintegrate. If unfertilized, the carpogonium also appears to disintegrate.

Mature auxiliary cell branches are usually unbranched, 12-16 cells long, and surrounded by a relatively thick mucilaginous coat (Fig. 61c). The auxiliary cell is usually 3-6 cells from the tip of the branch. The cells are square, round, cuneate, or irregularly shaped. The basal cell of the branch may or may not be differentiated. Pit connections are prominent even before the auxiliary cell is contacted by a connecting filament, and nuclei are large throughout much of the branch (except in the undifferentiated basal cell, the auxiliary cell, and the relatively small terminal cells). The auxiliary cell is only slightly smaller than its immediate neighbors.

Although Mitchell observed 2-6 connecting filaments arising from the carpogonial fusion cell, she found that connecting filaments did not extend beyond the first auxiliary cell contacted. She described the first gonimoblast initial as arising from the auxiliary cell on the same side as its fusion with the connecting filament, but her figures suggest that it arises rather from the connecting filament in contact with the auxiliary cell. I observed up to 4 gonimoblast initials developing from the gonimoblast initiator cell attached to the auxiliary cell (Fig. 61d). The cells of the gonimoblast are initially irregular in size and shape and are relatively loosely
arranged. A fusion cell is eventually formed incorporating the first formed gonimoblast cells. As the carposporophyte matures, the pit connections between the cells of the auxiliary cell branch continue to enlarge to about 12 μm in diameter. Cells of the auxiliary cell branch adjacent to the auxiliary cell sometimes fuse as the connections between cells enlarge more than the pit connections connecting them. Mature carposporangia are relatively small and lightly staining.

Two to three spermatangia are produced by the superficial, elongate, clavate spermatangial mother cells (Mitchell 1966:215).

Zonate tetrasporangia 25 by 50 μm develop in place of a dichotomous branch about 3 cells from the surface of the thallus.

**Cryptosiphonia woodii** (J. Agardh) J. Agardh 1876:251

**INTRODUCTION**

*Cryptosiphonia woodii* and *C. grayana* were originally described by J. Agardh (1872:15) as species of *Pikea*. Although J. Agardh listed the name "*Cryptosiphonia* J. Ag. mscri. in Hb. Gray" under *Pikea* in the original work (p. 14), he did not formally introduce the genus or make the new combinations until 1876 (pp. 251-2). In diagnosing the genus, J. Agardh largely followed his earlier description of *Pikea* (changes in the 1876 circumscription are underlined; words from the 1872 version are noted in parentheses; the translation is from Latin):

*Frond somewhat terete, radially branched, gelatinous and fleshy, the young frond tubular, the older one*
somewhat filled, made up completely of jointed filaments; with a flexible axial siphon running through the tube (large, jointed flexible axial siphon) and alternately sending out di-, polychotomous branches forming a continuous cortical layer made up of short moniliform filaments (alternately excurrent in corymbose, fastigate poly-, dichotomous branches at length forming a continuous peripheral layer) on the outside. The majority of the cystocarps are (Cystocarps are developed) embedded in their characteristic branchlets, finally freed when the attached (fertile) part becomes loosened, consisting of a rather simple cystocarp inserted (suspended) among the more flaccid (interior) polychotomous filaments; the cystocarp is transformed from moniliform filaments that are short-jointed, curved, and only slightly branched, now joined into a bundle (obconical-hemispherical) and consist of somewhat larger oblong buds, angled by pressing against one another, radiating from a placental filament, and surrounded by mucous (included in a single hyaline sac). Sphaerospores [tetraspores] are numerous in the branchlets, apparently cruciately divided.

J. Agardh described the species, both of which were cystocarpic and came from near Vancouver I., as somewhat terete with short branches coming out laterally in all directions. He distinguished P. woodii as being "gelatinous yet cartilaginous ...covered with dense branchlets almost in bundles here and there, clavate, rather spinescent and warty..." For P. grayana, he wrote, "fleshy...long and slender with short branchlets scattered and spreading, fusiform and attenuate lengthwise on both sides...," adding below, "P. grayana is deep purple and hardly adheres to the paper; this plant has the appearance of the slender Chondria while you say that it is more or less the same as P. woodii rather than Ch. dasyphylla."

He placed Cryptosiphonia in the Dumontiaceae despite a vegetative structure he considered as analogous to Gloiopeltis and Endocladia (because of the loosely arranged, often paired branches from the axial filament).
In 1879 (Pl. 17), J. Agardh included the first figures of Cryptosiphonia grayana. Figure 1 shows the habit of a cystocarpic plant. Figure 2 shows an enlargement of the plant with its swollen branchlets and tips of branchlets containing aggregations of cystocarps. Figures 4 and 5 show the position of cystocarps relative to the vegetative tissue in longitudinal section. Figure 3 provides a transverse section showing the origin of a single branch from the axial cell and the relatively thin, small-celled cortex.

Subsequently, Cryptosiphonia woodii was recorded from central California by Farlow (1877:241), Anderson (1891:222), and Howe (1893:68).

Schmitz (1889:453) included Cryptosiphonia in the Dumontiaceae and designated C. grayana the type species.

Schmitz and Hauptfleisch (1897:517) continued to recognize two North Pacific species. In their description of the genus, they noted the scattered, cruciately divided tetrasporangia and the small, spherical-reniform cystocarps composed of a solid mass of cells most of which develop into carposporangia.

Both species are represented in the P.B.-A. Number 449 (May 1898), labeled Cryptosiphonia woodii, includes two collections. The upper specimen, found in pools on Duxbury Reef, Bolinas, Marin Co., California, 6 April 1897, is spermatangial in the U.B.C. set. The lower specimen, collected from dense mats on exposed rocks near high water mark, Fort Point, San Francisco, California, 21 Jan. 1898, has what appear to be young tetrasporangia in the U.B.C. volume.

Cryptosiphonia grayana is represented in P.B.-A. 1047 (May
This tetrasporic specimen was collected on intertidal rocks on the west coast of Whidbey Island, Washington, in 1897 by N. L. Gardner.

Saunders (1901:441) reported Cryptosiphonia grayana from Wrangell, Sitka, Yakutat Bay, and Kukak Bay, Alaska.

Setchell and Gardner (1903:353) recorded both species from Washington, British Columbia, and Alaska. They differentiated C. woodii as "the more densely branched, bushy species which does not collapse when removed from water" and C. grayana as "the slender plant that collapses." They stated that P.B.-A. 449 (1898) should be considered a specimen of C. grayana, not C. woodii, although they concluded, "It may be doubted whether the two species (as now recognized) represent more than divergent forms of one rather varied species!"

DeToni (1905:1623) also recognized both species.

Collins (1913:128) was the first to propose that the two species be merged into one. He favored C. woodii because of its priority of position. He recorded the species from Victoria (J. Agardh) and from Port Holmes (Macoun), and he noted the extreme variability in the pattern of division of the tetrasporangia from cruciate (but with the reservation "ni fallor"—J. Agardh) to nearly zonate.

Kylin (1925:14) found cystocarpic and tetrasporic C. woodii at San Juan Island, Washington; he also concluded that C. grayana was identical to C. woodii.

Sjöstedt (1926:4) provided the first detailed account of the vegetative and reproductive anatomy of Cryptosiphonia woodii (collected at Pacific Grove, California, July 1922, by Kylin).
He noted the oblique division of the apical cell and the production of a pair of branches at right angles to each other which are cut off alternate sides from one axial cell to the next. The branches are di- or trichotomous and terminate in a dense, small-celled cortex. Pericentral rhizoids are present in older parts of the thallus.

Carpogonial branches usually 7 cells in length and auxiliary cell branches usually 11 cells long arise independently and secondarily from basal or suprabasal cells of the lateral branches. Both branches can bear vegetative branches (which themselves can branch) on their lower cells.

Following fertilization, the carpogonium fuses with cell 4. According to Sjöstedt, the connecting filaments arise from this "primary auxiliary cell." Usually the fifth cell from the base of the branch functions as the auxiliary cell (the sixth or seventh cell from the tip of the branch in Sjöstedt's drawings). All the cells of the auxiliary cell branch, especially the auxiliary cell and its proximate cells, are enlarged, but the auxiliary cell is somewhat smaller than its immediate neighbors. Double nuclei can occur in cells of both the carpogonial and auxiliary cell branches but never in the carpogonium or the auxiliary cell. Although Sjöstedt stated that the diploid nucleus migrates into the auxiliary cell after it is contacted by a passing connecting filament, his figures of early gonimoblast initiation are consistent with a connecting filament origin of the gonimoblast. No pericarp is formed, and all cells of the gonimoblast become carposporangia.

Spermatangia were not observed. Tetrasporangia arise
secondarily and can be zonate, cruciate, or intermediate in shape.

Kylin (1930:23, 1941:8) also reported on his Pacific Grove specimens of *Cryptosiphonia*. His descriptions of both vegetative and reproductive anatomy followed those of Sjöstedt. In addition, he noted the occurrence of female structures primarily in the rhizoid-free tips of small spine-like macroscopic branches. He found carpogonial branches usually 7-9 cells long and auxiliary cell branches 9-11 cells long, and he noted that the nuclei of the middle three cells of the auxiliary cell branch are somewhat larger than the rest. He figured a fertilized carpogonium fused to cell 4 with connecting filaments issuing from the carpogonial side of the fusion cell. He also noted that the gonimoblast develops from the connecting filament side of the fusion with the auxiliary cell as in *Dumontia*, *Dudresnaya*, and *Acrosymphyton*, and his figure (13F) shows the spatial separation of the auxiliary cell and fertilization nuclei in that fusion cell.

Smith (1944:200) described and illustrated specimens from the Monterey Peninsula, and he observed that all cells of the gonimoblast produce carposporangia with the possible exception of the most proximal.

Doty (1947:163) recorded this species from Oregon. He noted the tetrasporangia to be very irregularly cruciate, 70-75 by 115-140 µm.

Scagel (1957:142) included new records of *Cryptosiphonia* from Washington and British Columbia. In 1967 (p. 188), he included it as one of the common seaweeds of British Columbia in
Norris (1957:307), in his discussion of the phylogenetic relations of the red algal family Kallymeniaceae, stated that the Dumontiaceae "is possibly linked with the polycarpogonial line by such advanced forms as Cryptosiphonia (fig. 24, A) in which several subsidiary branches issue from the lowermost cells of the carpogonial- and auxiliary-cell branches."

Abbott and Hollenberg (1976:361) reported Cryptosiphonia woodii to be a "locally abundant but inconspicuous element in the lower Gigartina papillata - Rhodoglossum affine association." They also reported that the female gametangial plants are more densely branched and shorter than tetrasporangial plants.

In the past twelve years, Cryptosiphonia woodii has been recorded from Barkley Sound, B. C. (Scagel 1973:137), Oregon (Phinney 1977:107), northern British Columbia (Hawkes et al. 1979:100), and Port Valdez, Alaska (Calvin and Lindstrom 1980:794).

As noted by Kylin (1941:8), the type material of Cryptosiphonia woodii is represented by some old fragments whereas that of C. grayana, a good individual. I have seen the original material of both species. Although the fragments of C. woodii are eroded and faded, they still display the diagnostic features of the genus at the microscopic level, including tetrasporangia, female reproductive filaments, and cystocarps.

**OBSERVATIONS**

Cryptosiphonia woodii occurs in the mid-to low intertidal
zone along the Pacific coast of North America from the outer coast to protected inside waters, from the eastern Aleutian Islands (Unalaska) to San Pedro, California. This species appears to have a patchy distribution, having not been recorded by either Doty (1946) or Widdowson (1965) in their studies of vertical distributions of intertidal species. Lindstrom (1973) found it in only 5 of 20 intertidal quadrats in the Flat Top Islands, Strait of Georgia, B. C. In her species constellation diagram, its occurrence was most highly associated (p<.001) with Polysiphonia hendryi var. garnderi, Microcladia borealis, and Leathesia difformis and less highly associated (p<.01) with Neorhodomela larix. According to Doty (1946), these species occur along the coast of Oregon from mean lower low water (0-foot tide level) to higher high low water (about 2.8-foot tide level, based on tide levels at San Francisco, California). This figure is comparable to the range of 0.5 to 2.5 feet given by Smith (1944) for this species.

Although fertile specimens of Cryptosiphonia have been found year round, some seasonality is still evident. Young sterile plants can be observed in late winter-early spring. Spermatangia have been found on specimens collected from late March to early May. Their occurrence coincides with the appearance of carpogonial branches. Cystocarps are present by early May. Young tetrasporangia are present in March; tetrasporangia showing in situ germination have been seen in August-October collections. Old sterile remnants of thalli, in which the distal fertile portions have eroded away, have been found in fall-early winter. Several collections, however, call
into question such a distinct seasonality. Mature cystocarpic thalli have been collected in December in central California and in early March in Vancouver harbor, where tetrasporic thalli were observed in January. These observations may suggest a latitudinal gradient in phenology in response to seasonal temperature fluctuations.

Among the species currently recognized as members of the Dumontiaceae, the axial structure of Cryptosiphonia is unique. The apical cell divides obliquely or sometimes transversely to produce a zigzag line of axial cells (Fig. 62). Periaxial cells are cut off one or more commonly two at a time at about 90° to each other. The zigzag effect is maintained for some distance from the apex. As the axis matures, the points of attachment of the two periaxial cells can begin to move apart in a longitudinal direction. They can also rotate such that the lateral branches appear to come off the axial cell at 180° from each other. These lateral branches curve upward, and they appear to branch predominantly abaxially-pseudodichotomously. Inner cortical cells are somewhat elongate.

Axial cells can reach a length of 850 \( \mu m \) but are more commonly 400-600 \( \mu m \) long. These cells reach a maximum width of about 145 \( \mu m \), including the outer wall. They are connected by pit connections to about 60 \( \mu m \) in diameter. The cells contain a large central nucleus. Refractive inclusions appear to be lacking.

Macroscopically, the thallus is terete and profusely distally branched to 3 to 4 orders with progressively shorter and narrower branches. Specimens from Washington northward are
commonly 10 cm or less in height, but larger specimens 20-25
(-35) cm tall are common in California (Smith 1944:200). The
main axis is 1-2 (-4) mm in diameter. Branches are radially
disposed; they are constricted at their point of attachment and
taper at their distal ends. The overall aspect of the thalli is
somewhat pyramidal. Color is an olive brown to a deep maroon.

Reproductive filaments have been found developing within
250 μm of a branch apex. Progressively more mature branches are
found further from the apex. In one specimen, stages from
gonimoblast initiation to mature cystocarp production were
present in the same macroscopic branches.

Reproductive filaments are borne on inner cortical cells of
the ultimate order of macroscopic branches. Those bearing
carpogonia are mostly 5-7 cells long. The distal 5-6 cells
stain darkly. The basal 1-2 cells are not strongly
differentiated and can bear 1-2 undifferentiated lateral
branches. The distal end of the branch is curved but not
strongly. Its curvature arises from the last two divisions of
the branch occurring somewhat obliquely (Fig. 63a). The pit
connections between the distal cells of the branch can be
located medially in contrast to their inward displacement in
most non-mucilaginous members of the Dumontiaceae (Figs. 63a-d).
The trichogyne is often coiled and can develop somewhat
laterally from the base of the carpogonium (Fig. 63b), which is
relatively small and not greatly differentiated. The nuclei of
cells 4 and 5 are larger than those of other cells of the branch
(Fig. 63d). One example was seen in which a carpogonium
terminated a branch with what appeared to be an auxiliary cell
in the position of cell 7 below it (Fig. 63c).

Following presumed fertilization, the cytoplasm of the trichogyne becomes detached from that of the base of the carpogonium (Fig. 63d), and the carpogonium grows toward and fuses with cell 4 and then cell 5 (Figs. 63e-g), at the same time initiating connecting filaments. From the limited number of examples seen, it appears that the fertilized carpogonium does not divide but rather forms a single carpogonial fusion cell attached to both cells 4 and 5 (Figs. 63e-g).

Connecting filaments are quite slender (<5 μm in diameter), stain poorly, and have been discerned only in the vicinity of a carpogonial branch or an auxiliary cell branch.

Auxiliary cell branches from 5 to 13 cells in length were observed, and I believe even longer ones may occur. The branches can terminate in the typical zigzag manner of indeterminate branches (Fig. 64a). They are branched basally, occasionally distally as well. As the auxiliary cell branch matures, its cells begin to enlarge, particularly a series of about 4 cells near the base (Figs. 64a, d). One of these cells will become the auxiliary cell, usually the third or fourth cell from the base of the branch, occasionally the fifth. Thus, the auxiliary cell ranges from cell 2 to cell 10 when the position is determined from the distal end of the branch. The auxiliary cell does not enlarge as much as the two cells below it or the cell immediately above it. These neighboring cells stain darkly and possess enlarged nuclei.

The connecting filament appears to contact the auxiliary cell before it segments. The segment contacting the auxiliary
cell enlarges somewhat in the region of contact, and one or two outgoing connecting filaments can develop from it. Three or four gonimoblast initials also arise from this segment (the gonimoblast initiator cell) in cytoplasmic continuity with the auxiliary cell (Figs. 64b, c). Both the auxiliary cell and the gonimoblast initiator cell maintain their own nuclei in their respective corners of the fusion cell (Fig. 64d). No gonimoblast fusion cell is formed, and all cells of the gonimoblast appear to mature into carposporangia. As the gonimoblast matures, the pit connections between the cells of the auxiliary cell branch continue to enlarge, particularly those in the vicinity of the auxiliary cell (Fig. 64d), and can reach at least 15 μm in diameter in some branches.

Mature carposporangia can attain a size of more than 200 μm in diameter but are usually smaller, about 60 to 85 μm in diameter.

Cystocarps form a dense aggregate in the center of the short, tapered branches which radially clothe the upright axes. Carpospores are released presumably by the erosion of these branches. No ostioles have been observed.

Spermatangia are cut off superficial spermatangial mother cells by oblique walls as is typical of most species of the Dumontiaceae (Fig. 63h). Thalli are unisexual.

Tetrasporangia are irregularly cruciate to irregularly zonate, 58-90 μm by 77-132 μm (n=39), and occur in the outer cortex. They are attached laterally to sub-basally.

COMMENTS
Although the vegetative anatomy of *Cryptosiphonia woodii* is unique in the Dumontiaceae, a similar zigzag pattern of apical cell segmentation and production of only two pericentral cells per segment, formed at approximately right angles to each other, occurs among members of the Endocladiaceae, Rhabdoniaceae, Hypneaceae, Rhodophyllidaceae, and Mychodeaceae. This diversity of families suggests an independent origin of this developmental mode a number of times in the evolutionary history of the Florideophycideae.

In addition to its distinctive mode of apical cell segmentation and periaxial cell production, *Cryptosiphonia* possesses a number of other autapomorphies. Its level of occurrence on intertidal shores is higher than that of any other member of the Dumontiaceae. The pit connections between axial cells reach a larger diameter than those of any other species in the family, and its sporangia represent the largest size attained by any member of the family.

The occurrence of large sporangia and an alternation of isomorphic generations, one per season, ally *Cryptosiphonia* with the *Dumontia* group. However, in many of its reproductive characters, *Cryptosiphonia* exhibits plesiomorphic states: the continuing acropetal production of reproductive filaments as the carposporophytes mature, a distinct vegetative appearance to basal cells of reproductive filaments, a laxly curved, relatively open carpogonial branch in which pit connections between distal cells can be medially situated, a delicate carpogonium, narrow, ephemeral connecting filaments, an auxiliary cell located near the base of a reproductive filament.
which can terminate vegetatively, no gonimoblast fusion cell, all cells of the gonimoblast potentially capable of differentiating into carposporangia, and the lack of an ostiole above maturing cystocarps. Vegetatively, Cryptosiphonia displays the pleisiomorphic character states of cylindrical, radially branched habit, uninucleate vegetative cells and lack of formation of secondary pit connections.

Hyalosiphonia caespitosa Okamura 1909:51

INTRODUCTION

The monotypic genus Hyalosiphonia was originally described by Okamura (1909:50). Okamura recognized the genus as a member of the Dumontiaceae by its characteristic reproductive filaments, but he found the nature of the central axis and cystocarps to be so distinct that he was forced to describe a new genus. He distinguished the genus by its cylindrical, radially branched thallus composed of "a hyaline longitudinal, cylindrical axis, from which infra-cortical cells verticillately arise longitudinally." In older parts of the thallus, "the infra-cortical cells...grow up into elongated hyaline cells of wider and narrower calibres taking the appearance of cylindrical cells and rhizoidal filaments," the central axis becoming indistinct from being mixed with them. The irregularly cruciate tetrasporangia occurred scattered in the thallus, and the cystocarps appeared as prominent but minute spheres above the thallus surface.

Okamura provided a much more detailed description of the species (p. 51, Pls. 64, 65, Figs. 1-6). Plants were described
as 10-30 cm tall with branches tapering at both ends, 5-10 mm long. Carpogonial branches consist of a carpogonium with a strongly twisted trichogyne, two relatively small hypogenous cells above two (or three) large, contents-rich cells with which the carpogonium fuses after fertilization. The connecting filaments develop from the carpogonium after fusion, usually but not always separated from the carpogonium by pit connections.

Okamura's description of auxiliary cell behavior is somewhat ambiguous. In particular, he stated, "The fertilized auxiliary cells, either after fusion or without fusing, very much enlarge so as to form the placental cell of nucleus." While this is occurring, the remaining cells of the auxiliary cell branch cut off lateral branches of many minute cells which contact "either by fusion or by pit-formation" sterile, vegetative cells. Okamura continued, "From the placental cell gonimoblast is formed which is faintly divided into a number of gonimolobes, and in almost all articulations of spore-filaments, spores are produced almost at once." He also described the cystocarps and illustrated them (Pl. 64, Fig. 1; Pl. 65, Figs. 5, 6) as small hemispheres, "internally composed of plexus of filaments lining the inner wall of pericarp, externally of anticlinal rows of cells." A carpostome is lacking, and the spores are released by dissolution of the pericarp.

Ohmori (1970:103) reported on spore germination in Hyalosiphonia. Both tetraspores and carpospores demonstrated Inoh's immediate discal type, but in the former, the second division occurred at right angles to the first whereas in the latter, the second segmentation usually ran parallel to the
first. Tetraspores averaged 38.5 μm in diameter (s.d. 2.7 μm) and carpospores, 56.0 μm (s.d. 3.1 μm). Ohmori collected his fertile plants in Okayama Prefecture in western Honshu on May 7.

Chihara and Yoshizaki (1971) studied the vegetative and reproductive anatomy of *Hyalosiphonia* collected at Tsuyazaki in Fukuoka Prefecture, Kyushu, Japan, in March 1969. They recorded plants to 40 cm in height and up to 2 mm in diameter, and they noted that one or more thalli arise from the same basal disc. The thallus is uniaxial; the apical cell divides transversely, and four laterals are produced by each axial cell. Tetrasporangia were observed to be attached laterally to a cell of usually the third layer of the cortex. Carpogonial branches were 7-13 cells in length and occasionally bore short, 1-5-celled laterals from their proximal cells. Their figures show the carpogonium fusing with cell 4 alone (Fig. P), cells 4 and 5 (Fig. Q), and apparently cells 5 and 6 (Fig. R) without itself appearing to divide. Two or more connecting filaments can arise from this fusion product. I interpret them as deriving from the fertilized carpogonium in their figures, but they state that the nutritive cell produces the two or three connecting filaments.

The auxiliary cell branches arise in a similar position as the carpogonial branches and can be 8-13 cells in length. Although they state that the auxiliary cell, which is the second or rarely the third cell from the tip of the branch, is larger than the other cells of the branch, their Figure S shows that it is distinctly smaller than its neighbors (Figures K-M suggest that the auxiliary cell is initially larger than its neighbors, if the authors have identified the auxiliary cell of the
immature branches correctly), but the cells immediately adjacent to it soon overtake it in size. Chihara and Yoshizaki illustrate (Fig. M) the fact that, "each cell below the larger cells of the branch is capable of producing sterile filaments distally from its outer side." Although the authors state that, "after fusion with a connecting filament, the auxiliary cell cuts off gonimoblast initials towards the side where the fusion has taken place," their figures (S and T) demonstrate that the gonimoblast arises from the remnant of the connecting filament attached to the auxiliary cell. They also state that a secondary connecting filament that goes to another auxiliary cell branch is cut off the auxiliary cell (their figures show it coming from the remnant of the connecting filament attached to an auxiliary cell), that more than two gonimoblast initials arise from one auxiliary cell, and that the auxiliary cell and adjacent cells of the auxiliary cell branch fuse as the gonimoblast matures into "a massive fused area" (here their figures are equivocal). As the cystocarp matures, they note that it gradually increases in size and eventually emerges as an outgrowth on the thallus surface.

Umezaki (1972) reported on the life history of *Hyalosiphonia* from carpospores collected May 16 on the Japan Sea coast of Honshu. The spores measured (45-) 53-55 (-58) μm in diameter. Umezaki found that the second division plane of the spore could be either perpendicular or parallel to the first. Pulvinate discs 1-2 mm in diameter and 1-2 mm high developed after six months in continuous light, 500-1500 lux, 10-15°C. These discs produced upright shoots (up to 10 per disc) which
formed tetrasporangia after three months in short-day conditions (7:17 light:dark). Released tetraspores measured 30-35 µm in diameter in one plant and 35-42 µm in another, and they germinated in a manner similar to the carpospores.

Tazawa (1975) described the development of spermatangia on unisexual thalli. On plants collected in May and June along the coast of Hokkaido, spermatangia formed over all but the lower portions of the main axis and the branches. Spermatangial mother cells about 4 µm wide by 9 µm long cut off the 3 by 7 µm spermatangia by somewhat oblique walls as is typical of most if not all Dumontiaceae.

Kang (1966:65) recorded the species from around the coast of Korea, and Tseng (1983:70) noted its occurrence on the Yellow Sea coast of China. Chihara (1975:213) recorded it from the northern and middle parts of the Pacific coast of Japan, the Inland Sea, the west coast of Kyushu, the Okhotsk Sea coast, the Japan Sea coast, Sakhalin, the Korean Peninsula, and China. He described its habitat as on rocks near the low tide line. Umezaki (1972:278) found it a little below low tide level on the Japan Sea coast. Okamura (1909:51) recorded it as sublittoral.

OBSERVATIONS

Hyalosiphonia is uniaxial. A dome-shaped apical cell divides transversely to cut off a discoid (4-5 by 11-12 µm) subapical cell (Fig. 65a). This discoid cell then cuts off four periaxial cells. The periaxial cells then divide both anticlinally and periclinally. This division pattern continues as thallus development progresses. Lateral branches can also
arise from basal cells (and subsequently from suprabasal cells) of whorl branches; they branch in a similar manner. Axial cells begin to elongate immediately: 5 cells from the apex, they are 10-11 μm long by 4-6 μm wide (n=3); 10 cells from the apex, they are 25-35 μm long by 7 μm wide (n=3); 15 cells from the apex, they are 55-65 μm long by 14-18 μm wide (n=2).

The pattern of anticlinal and periclinal divisions produces whorl branches whose major axis parallels that of the main axis. Secondary pit connections can form among the cells of these branches as occurs in *Pikea californica*. As the thallus matures, these inner cortical cells enlarge to nearly the size of the axial cells, which can reach almost 200 μm in diameter and at least 850 μm in length. However, pit connections remain small, less than 5 μm in diameter. Rhizoids develop from inner cortical cells in older parts of the thallus and anastomose, forming secondary pit connections both among themselves and with cells of the primary tissue.

Hairs are common.

A variety of reproductive stages was present in the 5 March 1969 material examined. They ran from carpogonial branch initiation to mature cystocarp formation. This diversity of stages and their arrangement in the thallus suggest that thallus growth continues during reproductive development with new structures being continually produced near the growing apex. The limited data available also suggest that this species may show a latitudinal gradient in reproduction, reaching reproductive maturity 2-3 months later in colder regions.

Reproductive filaments begin to develop from inner cortical
cells within 150 μm of a branch apex. They initially grow downward but soon become recurved distally toward the exterior. Mature carpogonial branches can occur within 650 μm of a branch apex. They are mostly (7-) 9-11 cells in length (Fig. 65b) but sometimes reach lengths of at least 16 cells. Cells 2-5 are enlarged and frequently of similar size; cell 6 is also often enlarged but less so than the other cells. Cell 2 is sometimes lobed. Short, unbranched lateral branches can occur on cell 6 or more proximal cells of the branch. In longer branches, the laterals near the base can be longer and can themselves branch. Initiation of the trichogyne can begin before any cellular differentiation has occurred. At this time, the distal end of the branch is not strongly curved. It appears to become recurved by the differential growth of the distal cells of the branch. The trichogyne is usually strongly contorted basally (Fig. 65c) and can appear to be somewhat lateral on the base of the carpogonium; it sometimes forks distally. The trichogyne is relatively thin and fragile-looking, and the carpogonium as a whole resembles the same structure in Dumontia and Cryptosiphonia. Unfertilized carpogonia appear to disintegrate through progressive vacuolization. Additionally, rhizoidal filaments can invade reproductive cells.

Following fertilization, the carpogonium enlarges and fuses with cell 4 or occasionally with both cells 4 and 5 (Fig. 65d). No definitive evidence of division of the fertilized carpogonium prior to connecting filament initiation was seen.

Connecting filament initiation and auxiliary cell contact were not seen in the material available. The former stage is
illustrated by Chihara and Yoshizaki (1971, Figs. P, Q, R).

Auxiliary cell branches range in length from at least 8 to 13 cells. Even prior to differentiation of cells of the filament, lateral branches of various lengths can be seen extending from mostly the intermediate cells of the branch (Fig. 65e), including the cell subtending the auxiliary cell, and, in one instance, the auxiliary cell itself appeared to bear a one-celled lateral. These laterals can themselves branch, and auxiliary branch cells can bear more than one lateral branch each. They are rarely rhizoidal (i.e., composed of elongate, cylindrical cells), and if they are rhizoidal, the rhizoids develop from the lower cells of the filament. The future auxiliary cell, usually the second cell from the distal end of the branch, is initially distinguishable from its neighbors by its larger size, but the adjacent cells soon overtake it. These neighboring cells develop enlarged nuclei and stain intensely with aniline blue. Unbranched incompletely differentiated branches are occasionally seen.

As in other Dumontiaceae, the gonimoblast develops from the remnant of the connecting filament attached to the auxiliary cell.

A gonimoblast fusion cell enlarges to more than 100 \( \mu \text{m} \) across as the carposporophyte matures (Fig. 65f). The fusion cell contains numerous nuclei and somewhat enlarged pit connections from the incorporated cells of the gonimoblast. Pit-connection enlargement is highly variable, ranging from less than 2 \( \mu \text{m} \) to about 4 \( \mu \text{m} \) or slightly more. The pit connections between the distal cells of the auxiliary cell branch enlarge to
5-10 μm, and branch cells immediately adjacent to the auxiliary cell can become incorporated into the fusion cell as connections between these cells broaden beyond the diameter of the pit connections. The cells of lateral branches form secondary pit connections possibly with each other and with adjacent vegetative cells, creating a plexus of tissue beneath the maturing gonimoblast. Below mature cystocarps, these cells appear somewhat emaciated, suggesting that they may play a nutritive role in gonimoblast development. The gonimoblast fusion cell is found just below the surface of the thallus, and the carposporangia protrude into a small hemispherical outgrowth on the thallus surface (Okamura, 1909; Chihara and Yoshizaki, 1971). According to these authors, the outgrowth lacks an ostiole. Its susceptibility to erosion and release of spores is supported by the observation that none of the mature female plants that I examined had protuberant cystocarps; above all the gonimoblast fusion cells, a large hole in the surface of the thallus revealed that the entire protrusion had been torn off.

Male reproductive structures were not observed.

Tetrasporangia measured 50-75 by 73-95 μm (excluding the wall) in a specimen collected near Otaru, Hokkaido, Japan, in July 1978. Some of the tetrasporangia in this specimen showed in situ germination. At least some, if not all, tetrasporangia are attached laterally.

Farlowia irregularis Yamada 1933:280

INTRODUCTION

Yamada (1933:280) described Farlowia irregularis on the
basis of sterile specimens collected at Akkeshi, Japan, presumably by himself, and on Kunashiri I. in the Kurile Is. by Mr. Y. Okada. The description covered only the gross morphology of the complanate, branched plants which can reach 25 cm in height. A habit photograph of a specimen was included.

Okamura (1936:483) included a drawing of a portion of a transverse section of the thallus together with a reproduction of Yamada's figure. The transverse section shows a cortex of 6-7 layers of spherical cells of progressively smaller diameter; the broader medulla is filled with narrow filaments oriented irregularly.

Tokida (1954:157) recorded this species from numerous sites around southern Sakhalin. The specimens he collected in July and August were sterile, but other specimens collected there in September and December bore auxiliary cell branches and young cystocarps, respectively.

Mikami (1957) believed he was describing the female reproductive filaments of Farlowia irregularis, but it now appears his observations pertain to Farlowia mollis or its western N Pacific vicariant (see Farlowia section, p. 132). Abbott's (1968) comments on Mikami's observations and specimens likewise are discussed under Farlowia.

Funahashi (1966:137) recorded Farlowia irregularis from Usuri Bay near Vladivostok at a depth of about 32 m. The specimen(s) collected in May were tetrasporic.

Chihara (1972:156) recorded this species from Hidaka and Erimo Misaki, Hokkaido. The identity of these specimens is discussed in the Farlowia chapter.
Shimizu and Masuda (1983) studied the phenology in the field and the life history in culture of *Farlowia irregularis*. In field material, they found a single hemispherical apical cell at the tips of young uprights and concluded the internal structure to be uniaxial. Also in field material, they found female gametophytes with reproductive filaments from August to December and with cystocarps from February to April. Bisporangial initials first appeared in August, and mature bisporangia 35-50 by 73-103 μm were found in March and April. Released carpospores averaged 43.4 μm in diameter (s.d. = ±6.6, n=400). Released bispores averaged 49.6 μm in diameter (s.d. = ±6.8, n=510). They developed according to Inoh's immediate discal type of spore germination. Following spore release, the fertile portions of the frond disintegrated, and proliferous branches developed from the remaining sterile portions of the thallus. In culture, separate male and female gametophytes developed from bisporangia-initiated apical segments kept for 4 months at 10°C, 8:16 light:dark.

**OBSERVATIONS**

Although branches are initiated uniaxially and terminate in a single, dome-shaped apical cell (Fig. 66a), the mature thallus appears to be multiaxial, with no central axial file of cells evident. Secondary pit connections form between inner cortical cells (Fig. 66c). These secondarily pit-connected cells elongate to form the stellate cells of the medulla of the mature thallus (Fig. 66e).

A distinct cuticle is evident on vegetative thalli (Fig.
66a), but it becomes eroded during release of spermatia (Fig. 66b).

Refractive inclusions to 10 μm in diameter have been measured in inner cortical cells of some thalli (Fig. 66d), and up to six refractive inclusions have been seen in one cell.

Female reproductive filaments are borne on inner cortical cells. They can bear 1-2 short lateral branches per cell, and the laterals themselves can branch (Figs. 67a-e). Cells of lateral branches are usually moniliform like cells of the reproductive filaments themselves but occasionally they are rhizoidal in character (Fig. 67f). Carpogonial branches 7-15 cells in length were observed (Figs. 67a-c). The trichogyne can develop from the side of the carpogonium as in Cryptosiphonia, Dumontia, and Hyalosiphonia (Figs. 67a, b). Occasionally forked trichogynes occur (Fig. 67e). As the carpogonial branches mature, their distal cells continue to enlarge (Figs. 67a-c). No clearly identifiable auxiliary cells were seen (Figs. 67d, e), and no branch lengths were obtained. Incompletely differentiated reproductive filaments can reach at least 18 cells in length.

Unusual cystocarp development was seen in specimens from Aikappu. No definitive evidence of fertilization was obtained (Shimizu and Masuda have noted the lack of recognizable males in their field-collected material.) No carpogonial fusion cells or connecting filaments were seen. Some carpogonia appeared to be disintegrating; several appeared to fuse with nearly stellate cells. Cell 4 also appeared to fuse with adjacent vegetative cells (Fig. 68a), producing a fusion cell reminiscent of the
gonimoblast fusion cell in other Dumontiaceae. As the vegetative cells fuse with cells of the carpogonial branch, they can become highly refractive (Fig. 68b). Other vegetative cells appear to become transformed into carposporangia and/or become incorporated into the "gonimoblast fusion cell" (Fig. 68d). Vegetative cells transformed into carposporangia are recognizable by their large size (about 75 μm in diameter) and by their single, central, prominent, radiating nucleus. The adjacent cells of the carpogonial branch fuse (Fig. 68e); pit connections can enlarge to about 5 μm. The cells of the lateral branches form a web of fusions with adjacent vegetative cells (Figs. 68e, f). Figure 68c shows a putative auxiliary cell fused to a vegetative cell. Distal cells of the branch have fused, but there are no obvious connections between the vegetative cell attached to the auxiliary cell and what appear to be maturing carposporangia surrounding it.

Spermatangial mother cells and spermatangia were observed on a specimen (SAPS 043089) cultured from bispores for 2 months at 10°C, 16:8 light:dark and then for 4 months at 10°C, 8:16 light:dark. They can begin to develop within 100 μm of a branch apex (Fig. 66b). Spermatangial mother cells were 1.5-3 by 7-12 μm (n=10). Spermatangia were cut off the spermatangial mother cells by oblique walls; they were 2-3.5 by 4-8 μm (n=10).

Bisporangia (and a few of what appeared to be tetrasporangia) averaged 35.0 by 89.1 μm (n=30) from pressed material collected 26 January 1979 at Cape Nosappu. Mature sporangia were observed to be attached laterally (Fig. 66f).
As suggested by Shimizu and Masuda (1983) and supported by this study, *Farlowia irregularis* has an unusual life history pattern. Putative meiosporangia appear to be predominantly bisporangia. Carposporangia appear to develop from vegetative tissue without benefit of fertilization (or if it occurs, it may only stimulate the course of these events).

The occurrence of apomeiotic uninucleate bisporangia among boreal-arctic members of the Corallinaceae has been discussed by Suneson (1982:114). Although he does not provide a rationale for its occurrence, he cites a number of instances of this phenomenon. Dixon (1973:134) has stated that in *Crouania attenuata*, in both the N Pacific and the N Atlantic, "there is good evidence to suggest that bisporangia are formed during winter months with tetrasporangia produced on the same plants during the summer."

It is assumed that the occurrence of bisporangia in *F. irregularis* is a response to cold. This species occurs along the Pacific coast from Akkeshi to Kunashiri I., where monthly mean surface temperatures during winter months dip below 0°C. [It has also been reported from the Okhotsk Sea by Tokida (1954) and from the Sea of Japan by Tokida (1954), Funahashi (1966), and Kawai and Kurogi (1982).] Such cold conditions could inhibit normal reproductive behavior in this species. Meiosis in the tetrasporangial initials could be inhibited, as could the formation of spermatangia--Shimizu and Masuda obtained spermatangia in cultures maintained at 10°C. Production of carposporangia by parthenogenesis may be another result of the
cold (a similar parthenogenetic phenomenon was detected in a
cystocarpic specimen of the Arctic species *Dilsea integra*, see
p. 266).

*Farlowia irregularis* may be restricted to an area where
mean monthly temperatures range from about -1° to about +17°C
because warm summer waters to the south and west may be
inhibitory to the growth and survival of the species. This
situation would suggest that *F. irregularis* may be a relict of
earlier times when marine temperatures in the western N Pacific
may have been less extreme. Its method of maintaining itself
under such adverse conditions deserves further study.

I will not treat the nomenclatural problem of *Farlowia
irregularis* here since I believe that it is being dealt with
elsewhere by Shimizu and Masuda.

*Dilsea* Stackhouse 1809:55 and *Neodilsea* Tokida 1943:96

INTRODUCTION

The *Dilsea*-*Neodilsea* complex is composed of multiaxial
foliose species characterized by a moderately thick cortex and a
filamentous medulla of variable thickness. The cells of the
cortex, which are usually rectangular or quadrangular near the
surface of the thallus, increase in size toward the interior.
Inner cortical cells can cut off one to several conjunctor cells
to form secondary pit connections with adjacent cortical cells.

Because of these secondary pit connections, the inner cortical
cells are multinucleate and stellate. These cells can elongate
periclinally to become medullary filaments, but the extent to
which they elongate varies from species to species. Inner
cortical cells can cut off rhizoids, which can branch in some species or generally remain unbranched in others. Although a single apical cell is sometimes discernible in early ontogeny of blades, no other evidence of a uniaxial origin of the upright thalli has been found. Thallus growth appears to be by a marginal meristem.

Reproductively, the members of the *Dilsea*-Neodilsea complex share a number of features. For example, all species begin to mature reproductively in late summer and to shed their spores in fall beginning at the distal end of the thallus. As the spores are released, the thallus erodes progressively toward the base. Cystocarps are frequently grouped in distinct patches. Most species disappear by late winter. Reproductive filaments are relatively long (8-30 cells) and are distinguished by the extent of lateral formation—in number of lateral branches formed (0-3 per cell), in their length (to 17 cells in at least one species), in their potential to differentiate into rhizoidal filaments, and in their ability to branch. All species but one also form a gonimoblast fusion cell as the carposporophyte matures by incorporation of the first-formed gonimoblast cells into the gonimoblast initiator cell that gave rise to them.

**Dilsea carnosa** (Schmidel) Kuntze 1898:404

INTRODUCTION

Schmidel (1794:75) may have been the first person to have recognized in writing that this taxon is an entity distinct from *Palmaria palmata*. However, Withering (1796:101) believed that Ray's (1724:46, No. 30) *Fucus scoticus latissimus edulis dulcis*
was probably this taxon. [Ray also listed, as No. 29, *Fucus membranaceous ceranoides*, which may have been *Palmaria palmata* (Linnaeus) Kuntze.] And in a footnote, Turner (1809) stated:

That these plants were not altogether unknown either to Hudson or Lightfoot, I have the authority of Sir Thomas Frankland for saying; as he writes to me in one of his letters: 'I never could persuade Hudson or Lightfoot that *F. edulis* was distinct from *F. palmatus*; when young it contains a pulp between two membranes and is quite succulent, and I never could find a single frond that was branched; though, when old, it spreads, and becomes rugged and lacerated, which gives it a general appearance of being so.'

I have read (in translation, thanks to Dr. Hannah Croasdale) Schmidel's discussion of *Fucus carnosus*:

Very abundant also was *Fucus* which, on account of its thickness and deeply blood-red colour, for the present I have called *Fucus carnosus*, until more may be disclosed about it; and it now is still confused with *Fucus dulcis* Gmelin. Its blades are sometimes perforated partly by waves and partly by animals and insects, by chance living off it, so that the blades appear rather like a net, wherefore I have no doubt that the *Fuci reticulati* of Seba Thef. III. Pl. 103 may pertain to it, and of Gmelin also *Agarum clathrus* and similar ones, and they may have originated from broad *Fuci* of this sort, since the plants may not be entire, but may be seen as portions. The fragments vary greatly, scarcely ever indeed do they agree exactly with the figures of *Fucus dulcis* Gmel. I have had whole rafts of it in which fronds of varying size were found, all thick, of a deep blood-red colour if they were recent, after being left several days on the shore they begin to decay, they become thinner and either turning green or they incline to a white colour.

Schmidel's comments provide a minimal description of *Fucus carnosus* in the sense of Articles 32 and 34, International Code of Botanical Nomenclature. In contrast, Esper 1799:150, who, after quoting Schmidel's "description" and commenting on it, provided a more substantive description (in translation, my own this time):

On a single stem of this seaweed, various forms of the
blade appear together, which take their exit from a common base. They are all in the lower parts, narrowed in the form of a stalk, and elaborate with increased growth that much more at the opposite ends. The margin itself is scalloped and in some also lacerated or at times toothed, but the blade itself is undulating. Some of these blades, as the Introduction indicates, are round-oblong, others lancet-shaped, but diverse in length or digitate. Others also appear as small blades or outgrowths of different forms. The color is partly pale, partly a very intense rose-red and changes into yellowish as well as dark red. In regard to the above character, the cast-up specimens change if they do not become rotten, partly into a green, partly into a white color. With the Icelandic Fucus lactuca represented in Plate 64, which has a close resemblance to this seaweed, still the blades do not have the same stoutness of substance; they are moreover smooth-rimmed and of not such an irregular form. I have the good communication of President von Schreber of Reichsacademie der Naturforscher to thank for the present Original, which has been cited by Schmidel...

Esper also included a figure (Pl. 76) showing a group of mostly oblanceolate blades emanating from a central basal region.

Withering (1796:101) was the first person to give this species the binomial Fucus edulis; he described it:

Leaves arising many in succession, of different sizes, from a discoid base. It is as thick as leather, large, veinless, transparent. From a flat discoid base arise 2, 3 to 8 or more leaves of different sizes, and of different ages, the largest are from 6 to 9 inches high, on a thick compressed, or nearly cylindrical stem. This stem suddenly dilates into a very wide, smooth, leather-like leaf, sometimes 4 or 5 inches over near the top, in shape like the lateral section of a wedge. When in fruit, the middle of the leaf, betwixt the two coats is a vascular jelly, the vessels are annular tubes chained together. The surface at this time rises into conical protuberances perforated at the top.

Withering had undoubtedly received his specimens from Stackhouse, whom he acknowledged at the end of the section.

Stackhouse published on Fucus edulis the following year (1797:58), describing it,

Root flat, membranaceous, spreading; throwing up
numerous leaves. Stem roundish, short; expanding soon into a frond. Frond simple, wedge-shaped and rounded at top; many from a common base of different sizes. Fructification internal; a chain-work of annular tubes, as the pellucid mucous appears under high magnifiers, with external visible papillae. Seeds very minute.

In the discussion that followed, Stackhouse added that it was "dull red, inclining to chocolate colour...sometimes...nearly a foot high and the large leaves about five or six inches broad at the top...Its substance is tender and succulent, of the thickness of neats leather..."

It is unclear whether Stackhouse was aware that Fucus edulis represented an earlier name of a Gmelin species. Turner (1809:113) first pointed this out, when he wrote, "The name F. edulis, having originally been given by Gmelin to a very different species, ought never to have been applied to the present." However, Turner argued that since F. edulis Gmelin belonged to F. lichenoides in his belief, he was justified in retaining F. edulis for the taxon under consideration.

Although Turner's reasoning appears to be sound, Section 45.3 of the International Code of Botanical Nomenclature states that "validly published earlier homonyms, whether legitimate or not, shall cause rejection of their later homonyms..." Silva (1979, in Farr et al.:539) has surmounted this objection by basing Dilsea edulis, the type of the genus, not on Fucus edulis Stackhouse non Gmelin but on Ceramium edule Stackhouse. Ceramium edule is the name Stackhouse listed for this taxon in his Synopsis Generum (1797:xxiv).

Turner, like other authors of the early nineteenth century, was aware of the identity of Fucus carnosus and Fucus edulis but
preferred the latter epithet. He referred to the discovery of
the fructification by Dr. Weber and Dr. Mohr in the specimens
gathered by Schmdel. From these same specimens Turner provided
an illustration of a "portion of the frond, with a part of the
epidermis rolled back, to shew the position of the seeds."

Stackhouse (1809:55) introduced the generic name Dilsea for
his Fucus edulis. Although most subsequent authors retained his
specific epithet, they adopted a variety of combinations:
Lamouroux (1813), Delesseria edulis; C. Agardh (1817, 1822,
1824), Halymenia edulis; Greville (1824), Ulva edulis; Bory
(1826), Greville (1830), Harvey (1841 1871), and Kützing (1867),
Iridaea edulis; J. Agardh (1851), Schizymenia edulis and (1876),
Sarcophyllis edulis. The name Dilsea edulis only reappears with
Wille (1885, 1887), and Schmitz (1889).

Kuntze (1898) made the combination Dilsea carnosa
(Schmdel) Kuntze, the name acknowledged or used by Papenfuss
(1950), Bert (1965), Parke and Dixon (1976), and Irvine (1983).
Other twentieth century authors have retained Dilsea edulis
(Rosenvinge 1917, Killian 1928, Newton 1931, Kylin 1956).

Irvine (1983:10) has selected a lectotype for Dilsea
carnosa: "BM (see Turner 1809, Pl. 114) France (Dieppe)." In
correspondence (22 Sept. 1983), she has indicated selection of a
specimen in BM (ex Kew) as lectotype of Dilsea edulis; it is
labeled "Mr. Stackhouse June 1798" in Turner's hand with
"Cornwall" written separately on the sheet.

Schmdel (1794) believed his plant from Dieppe in Normandy
to be near Gmelin's (1768, Pl. 26) illustrations of Fucus dulcis
from Kamchatka as stated in Esper (1799), but Esper thought them
to be different. Stackhouse (1797) placed *F. dulcis* of Gmelin into doubtful synonymy with *F. edulis* on the basis of the wedge-shaped frond of the former. Turner (1809), C. Agardh (1822), J. Agardh (1851), and Harvey (1871) also refer to Gmelin's figure when listing the synonyms of *Dilsea carnosa*. I have read Gmelin's description and studied Plate 26 and concur with Esper that *Fucus dulcis* is a taxon distinct from *Dilsea carnosa*. The membranous, thin, pellucid substance to which Gmelin refers in the description is conveyed by the drawings. The very gradual attenuation of the stipe in the illustration and the shape of the blade which can be proliferous or dichotomous according to the description, contrast with the usual habit of *Dilsea carnosa*. These features together with the locality (Oceanus Kamtschatka) suggest that *Fucus dulcis* is the taxon currently known as *Palmaria palmata* in the northwest Pacific.

*Fucus lactuca* Esper (1799:129, Pl. 64) has also been included as a synonym (J. Agardh 1851; Harvey 1871; DeToni 1905). I am unable to judge the merit of this suggestion.

*Sarcophyllis lobata* Kützing (1867:29, Pl. 97) has also been cited as a synonym (DeToni 1905); however, Kützing's transverse section resembles a *Schizymenia* more than a *Dilsea*.

These early authors described the macroscopic aspect of the plant quite accurately: gregarious, thick, dark red, frequently lacerated blades expanding distally from a narrow stalk attached to a basal disc. Stackhouse (1797) mentioned the fructification, and it is possible he was referring to the cystocarp: "Under the outer coloured skin a pellucid colourless jelly pervades the whole frond. In this undoubtedly is the
fructification. With a favourable opportunity the seeds may be seen on the surface of the frond with high magnifiers, either in clusters or stretched in strait lines..." Turner's (1809) description seems more definitive: "Fructification-minute, spherical, scarlet seeds, scattered all over the frond, placed in small clusters of no certain shape, and situated in the centre of the substance of the plant, in a pellucid mucous..." Greville (1830) included a figure showing a transverse section with cystocarps embedded at different levels in the cortex. Although some of the cystocarps appear to be embedded outward from their normal location, the transverse section is recognizable as *Dilsea carnosa* by the vertical files of cortical cells and crisscrossing medullary filaments. Greville (1830) also noted, "Fructification situate [sic] towards the extremity in wide patches, sometimes occupying the whole of the end for several inches."

Kützing (1867) appears to have been the first to illustrate tetrasporangia. Although he did not describe them, he did show them in a line two cell layers below the surface of the thallus. Rosenvinge (1917) appears to have been the first to actually describe their intercalary nature; he was also the first to illustrate the carpogonial and auxiliary cell branches. Bert (1965) also presented drawings of carpogonial and auxiliary cell branches and included one figure showing a connecting filament which had fused with a subterminal auxiliary cell. He observed the carpogonial branches to be of 10-12 (13-15?) cells and the much ramified auxiliary cell branches to be as long as 30 cells. He described post-fertilization development to involve formation
of a short protrusion from the carpogonium toward the fourth cell, development of the connecting filament from the base of the carpogonium, fusion of the connecting filament with usually the fourth cell, but sometimes the second cell, from the tip of the auxiliary cell branch, and development of the carposporangia. Bert's figures do not clearly document these events, however.

Newton's (1931) figure of catenate spermatangia requires verification since it contrasts with what has been observed in other higher Dumontiaceae.

Killian (1928) recorded the early developmental stages of blade initiation.

Newton (1931) recorded this species as common, occurring on rocks at low-water mark in the British Isles. On the Swedish and Norwegian coasts it is reported to occur subtidally (Kylin 1944; Rueness 1977). Munda (1982) found it intertidally in the Gigartina stellata zone only on exposed slopes of the peninsulas of Reykjanes and Snaefellsner in southwestern Iceland. Titley and Price (1977) recorded it as subtidal to 10 m, epilithic, and infrequent but locally abundant along the coast of Kent. Cullinane and Whelan (1981) have noted its occurrence on the tops and sides of subtidal ridges where silt and strong currents prevail. Wilce (in herb.) has collected it to 17 m off the Swedish coast.

Dilsea carnosa is found from northern Portugal (Ardé 1970) northward through the British Isles to northern Norway (Rueness 1977). Kjellman (1883) recorded specimens from Norland, Spitsbergen, and Tri-Ostrowa in the Arctic. These records need
to be verified since some of them date from prior to the recognition of *Dilsea integra* as a distinct taxon. Munda (1982) has observed it in southwestern Iceland.

Greville (1830) and Harvey (1841) have described *Dilsea carnosa* as perennial. Sterile blades among the winter collections I have observed suggest that at least some blades overwinter and may become fertile in their second year. Rosenvinge (1917) found tetrasporic specimens from February to April, and Bert (1965) recorded female reproductive organs from December to February. I have observed tetrasporangial initials in plants collected in August (W239 in MASS) and mature tetrasporangia and carposporangia in January (UBC WS 1425).

**OBSERVATIONS**

Two basic morphologies occurred among the specimens I observed (Figs. 69a, b) although intermediates were present. All blades were narrowly attenuate to about 2.5 to 7.0 cm above the basal disc. Some blades continued broadening at an angle continuous with the basal portion of the blade toward the rounded apex. Other blades flared out above the basal portion at nearly right angles. Such blades frequently became broader than tall. The size of specimens examined ranged from about 9 to 25 cm tall and 5 to 30 cm across. The cortex of *Dilsea carnosa* resembles other members of this species complex with cells increasing in size inward from the surface and forming secondary pit connections in the inner cortex (Fig. 72a). Transverse sections ranged in thickness from less than 100 μm to about 700 μm. The cortex ranged in thickness from 7 to 12 cells
and occupied from 65% to nearly 100% of the section.

Colors exhibited by the specimens include Hay's maroon, Diamine brown, and Brick red (Ridgway 1912).

Unbranched, incompletely differentiated reproductive filaments to 18 cells in length were observed in one specimen (Fig. 72b). Mature carpogonial branches ranged from 10 to 21 cells in length (Fig. 72c). The proximal cells of such branches frequently bore long, unbranched, sterile, moniliform lateral branches.

Carpogonial fusion cells were not observed in the material available.

Auxiliary cell branches were of similar lengths to carpogonial branches. The auxiliary cell was observed to be a terminal (Figs. 72d, 73) or subterminal (Fig. 74a) cell. It is about the same size or slightly smaller than neighboring cells. Each proximal cell of a mature branch usually bears one, rarely two lateral branches of round to somewhat elongate cells, the terminal cells of which can fuse with vegetative cells or cells of other reproductive filaments (Figs. 73, 74a). These lateral branches can themselves be sparingly branched (Fig. 73). As these figures illustrate, fusion of lateral branches with vegetative cells can occur before the auxiliary cell is contacted by a connecting filament. Also before contact, one can sometimes observe the broadening of pit connections between the distal cells of the branch. Connecting filaments to 10 μm in diameter were observed in contact with auxiliary cells (Fig. 74c). Following contact, the auxiliary cell becomes nearly translucent. At least two gonimoblast initials are produced
from the gonimoblast initiator cell. The proximal cells are usually squat, sometimes elongate (Figs. 74b, c, 75a) and progressively become incorporated into a gonimoblast fusion cell (Figs. 74c, 75a). The distal carposporangia enlarge to approximately 80 μm in diameter. As the carposporophyte matures, the pit connections between the cells of the auxiliary cell branch continue to enlarge (to a maximum of about 5 μm, Fig. 75b), and the connections between the cells enlarge further to form an auxiliary branch fusion cell (Fig. 75a).

Long, incompletely differentiated, sparsely branched reproductive filaments are commonly seen in cystocarpic specimens. They have been figured by Bert (1965; this study Fig. 72b). They appear to be unique to this species.

Definitive spermatangia were not observed.

The cruciately divided tetrasporangia are intercalary. They averaged 52.3 by 75.9 μm in the specimens examined (n=30; Fig. 75c).

**Dilsea californica** (J. Agardh) Kuntze 1891:892

**INTRODUCTION**

**Dilsea californica** was first described by J. Agardh (1876:265) as *Sarcophyllis californica* on the basis of cystocarpic specimens from Oregon territory sent to him by Farlow. (Farlow 1875:370 had earlier identified these plants, collected by Mr. E. Hall, as *Schizymenia edulis*.) J. Agardh described the species as, roughly translated, "Stipe flattened above, giving way to membranous, soft but firm fronds, cuneate blade fragments expanded above, upper margin rounded." In
contrast, he described *Sarophyllis edulis*, the only other species in the genus at that time, as, roughly translated, "Elongate stipe terete, gradually compressed, giving way to a membranous, soft but firm, ovate, entire frond, finally lacerated above, margins uniform..." He further differentiated *S. californica* from *S. edulis* by its being substantially thicker and of a dark purple color, drying to blackish. J. Agardh was the first to recognize this species and the previous one as members of the Dumontiaceae. He based his conclusion on the development of the gonimoblast filaments from the characteristic moniliform filaments which occur in the inner cortical layer of the fertile thalli.

I have observed specimens identified by J. Agardh as *Sarophyllis californica*. LD35898 and LD35899 are from California, and LD35900 and LD35900a are from Oregon. The latter collection has been indicated to be the type (see below). The Oregon specimens are labeled in J. Agardh's hand, "Schizymenia nov. sp., divisionis modo, forma frondis & colore atropurpurea ad Sch. edulum proxima. Oregon misit Farlow." These specimens reach a height of about 11 cm and a breadth of about 2.5 cm. They are Maroon (Ridgway 1912) to nearly black. The presence of tetrasporangial initials in one specimen and mature carpogonial branches in another suggest the thalli were

\[ ^1 \text{J. Agardh uses the term "atropurpurea:" atro comes from the Latin alter meaning black, especially dull black (Stearn 1983:390); purpurea comes from purpureus and is derived from the Greek purpura, the name of the shellfish yielding the classical purple dye of antiquity. Since the color varied according to the shellfish used and the processing applied, it came to cover various hues of red (Stearn 1983:492). Hence, a precise interpretation of this color is not possible.} \]
collected in August or September.

Kuntze (1891:892) made the combination *Dilsea californica* (J. agardh) Kuntze.

Setchell (1901:126) described *Dilsea pygmaea*, which had been distributed as *Sarcophyllis californica* f. *pygmaea* Setchell in Collins, Holden and Setchell, P.B.-A. 396 (1897), on the basis of the large (to 40 cm in diameter) crustose thallus producing marginal, short (to 8 cm tall), erect blades.

Kylin (1941:8) synonymized *D. pygmaea* with *D. californica*. He had observed J. Agardh's specimens of *D. californica*. He noted that specimen No. 35899 from California was sterile but that No. 35900 from Oregon had carpogonial and auxiliary cell branches characteristic of the Dumontiaceae and that this was the specimen especially intended to be the type by J. Agardh. Kylin also noted that *Sarcophyllis californica* of the American "Algologen" (i.e., the Phycotetheca Boreali-Americana) is in fact *Schizymenia pacifica*.

I have examined *Sarcophyllis californica* in the UBC set of the Phycotetheca Boreali-Americana (P.B.-A. 395, 1897). It is represented by two specimens collected by Setchell at Pyramid Point, Pacific Grove, California, in May 1897. One specimen is said to be cystocarpic, the other, tetrasporic. The former, as suggested by Kylin, was found to be a cystocarpic specimen of *Schizymenia pacifica*, epiphytized by *Microcladia coulteria* Harvey. The latter specimen was also found to be *S. pacifica* and sterile rather than tetrasporic; Setchell presumably misinterpreted the gland cells of this specimen as tetrasporangia although the gland cells are equally conspicuous.
in the cystocarpic specimen. Abbott (1967:164) reported that the Sarcophyllis californica of P.B.-A. 395 in GMS is a species of Iridaea.

* Dilsea californica* is represented in P.B.-A. 396 (1897), which is labeled *Sarcophyllis californica* f. *pygmea*. The UBC specimen is somewhat falcate, entire, 4.8 cm tall, and contains intercalary tetrasporangial initials. This specimen represents an isotype of *Dilsea pygmea*. The holotype of *D. pygmea* (UC 96313) was also examined (Fig. 69i). It consists of an assortment of short (to about 7 cm), falcate, cleft, orangish-black blades plus fragments. No basal crust was seen other than the small (about 1 mm diameter) disc from which the individual thalli arise. Several blades were sectioned and found to contain bands of intercalary tetrasporangial initials, some of which had divided once to form bisporangia and some of which were catenate. The label indicates in Setchell's hand that the specimens represented #1451 in his personal herbarium. Printed on the label is the following additional information also provided by Setchell: "Growing densely crowded together upon rocks near high water mark, Land's End, San Francisco, California, Nov. 6 1896," and, "This form, characterized by its dwarf size and thick, firm consistency, seems to represent a very distinct environmental form."

Chihara (1967) was among the first to publish figures of this taxon. He included figures of the intercalary tetrasporangia (p. 193, Fig. 6), carpogonial branches (p. 194, Figs. 7A-C), and immature reproductive filaments (p. 194, Figs. 7D-E), which he described as "auxiliary-cell filaments in different
stages of development." Both of his figures are erroneously labeled *Delisea californica*. In the same year, Scagel (1967) included the species in the B.C. Provincial Museum Handbook No. 27 together with several figures of its habit (p. 191, Fig. 78).

Abbott (1968) also included a habit figure (p. 183, Fig. 14) as well as one of the intercalary tetrasporangia (p. 183, Fig. 15). She described the vegetative and reproductive morphology, and following Kylin (1941), stated the type specimen to be the one from Oregon. She also followed Kylin's synonymization of *D. pygmaea* and even suggested that the Pacific taxon might be conspecific with *Dilsea carnosa* from the Atlantic.

**OBSERVATIONS**

*Dilsea californica* occurs in the low intertidal zone (from about 1 meter above extreme lower low water on the open coast); it has also been collected subtidally. It grows in patches, usually on rocks near or on sandy beaches and hence must be subject to some scouring. However, I have not seen any evidence of seasonal burial.

In British Columbia, *Dilsea californica* appears to be more a plant of the outer coast; it has not been collected from the Strait of Georgia or its associated inlets. In Alaska, it is also more commonly found in areas with at least a moderate oceanic influence, but it also occurs in the protected, somewhat estuarine waters near Juneau. There, the maximum tidal range is nearly eight meters, and low salinity coincides with low temperature during periods of glacial run-off in the summer.
Dilsea californica is widely distributed in the eastern North Pacific Ocean. Abbott and Hollenberg (1976:363) recorded its southern distribution limit as Bushnell's Beach, San Luis Obispo Co., California. Doty (1947:165) and Phinney (1977:108) included it in the macrophytic marine algal flora of Oregon. Scagel (1957:145, 1973:138) and Hawkes et al. (1979:100) have documented its occurrence in Washington and British Columbia. Somewhat more problematical is its distribution along the coast of Alaska. Lindstrom (1977), following Setchell and Gardner (1903), recorded its occurrence westward to the Shumagin Islands (I have personally collected it as far west as Kodiak Island). Recently, I examined specimens in UBC (26441, 26442, 26719, 26983) and UC (96260, 96263, 96265, 96266) from Unimak and Unalaska Islands, which I believe can be referred to Dilsea californica, thereby extending its range westward to the eastern Aleutian Islands. The UC specimens had been identified as Sarcophyllis (=Dilsea) arctica, as had P.B.-A. 1048 (1903) in UBC. The distinction between these two taxa is problematical and is discussed below under Dilsea integra.

The phenology of more than 85 collections of the species from approximately 50 sites in British Columbia was examined. Juvenile plants are first recognizable in March: plants to 3.7 cm tall were collected at Box Island on 16 March 1968 (UBC 32564), and plants to 2.5 cm tall were observed at Brady's Beach on 27 March 1982 (pers. obs.). The plants reach their mature size by June. In late June or early July, female plants begin to produce reproductive filaments. Carpogonia usually appear in July, and plants are cystocarpic by November. Spermatangia were
seen only on July and August specimens. Tetrasporangial initials become discernible from July to September; mature tetrasporangia were first observed in specimens collected in October. The blade progressively erodes to within about 2 cm of the base as spores are released from the distal end of the blade, and the blades disappear entirely from the shore sometime during the winter months. Therefore, *Dilsea californica* appears to be an annual.

*Dilsea californica* exhibits an extremely polymorphic habit (Figs. 69e, g, i, 70i). Relatively short (mature blades can be less than 8 cm tall), falcate to cuneate blades characterize plants exposed to considerable surge. These blades are usually also deeply cleft. In more protected waters and subtidally, these shapes can give way to larger, more ovate thalli. The largest blade which I have collected was 16 cm wide by 38 cm tall.

Color is highly variable. Based on Ridgway's (1912) Color Standards, thalli of the following hues have been observed: Diamine brown, Hessian brown, Vandyke red, Hay's maroon, and Victoria Lake. In general, outer coast populations tend to be maroon whereas inner coast populations are more brownish. Blades have a smooth, matte finish; they are frequently characterized by a soft tanned-leather aspect just above their short stipe. The margin of the blade can be slightly raised.

Blade thickness is also highly variable. Sterile blades can range from just over 100 µm thick to nearly 1 mm thick. Among 18 seasonal collections from Oregon to Alaska, the cortex ranged from 5-6 cells thick in spring to 10-15 cells thick by late
summer. It accounted for 23 to 40% of the total thickness of the thallus in 17 of the collections and for 73% of the total thickness in a single collection from Lawton Pt., B.C., 25 Aug. 1968 (UBC 37917). As in other species of *Dilsea* and *Neodilsea*, going from outer to inner cortex, the cortical cells initially show an increase in length toward the medulla, then formation of secondary pit connections, and finally expansion in width to form the characteristic stellate inner cortical cells. Rhizoidal filaments arising from the inner cortical cells are frequently branched in some specimens and almost completely unbranched in others. At times, certain cells can contain a refractive inclusion; at other times, the stellate medullary cells are themselves refractive.

Reproductive filaments develop from inner cortical cells. Figures 76a and b show two carpogonial branches initiating trichogynes. Carpogonial branches were 7-19 cells in length and averaged 12-13 cells in length (n=236) in specimens from Oregon, Washington, and Alaska. One or two short laterals frequently occur on the lower cells of mature branches. Distal cells of mature branches show the enlarged nuclei characteristic of members of the Dumontiaceae (Fig. 76c).

Following fertilization, the carpogonium divides (Fig. 76d), and the two cells fuse with cells 4 and 5 or 6 of the carpogonial branch (Fig. 76e). From these fusion cells arise connecting filaments (Fig. 77a) which seek out auxiliary cells. The connecting filaments in *D. californica* can be 9 μm in diameter but are usually narrower.

Auxiliary cell branches arise in the same position as
carpogonial branches. They were 6-9 cells in length (n=18) in one specimen from British Columbia and 8-20 cells in length (n=24) in one specimen from Oregon. The auxiliary cell is usually cell 2 or cell 3, occasionally cell 4, and it is frequently distinctly smaller than neighboring cells (Fig. 77b). The auxiliary cell is contacted by a connecting filament as in *N. natashae* (Figs. 85c-f). An outgoing connecting filament can segment more than once at varying distances after leaving an auxiliary cell (Figs. 77c, 78a).

Following contact, two gonimoblast initials are usually produced (Fig. 78b; I have seen as few as one and as many as three). The proximal cells of one gonimoblast filament are frequently distinctly larger than those of the other. As the carposporophyte develops, the connections between the distal five or six cells of the auxiliary cell branch enlarge beyond the size of the pit connections, which have enlarged to 3-6 μm in diameter (Fig. 71d). At the same time, the gonimoblast initiator cell enlarges, in part by incorporation of the basal cells of the gonimoblast filaments. The net result is the formation of an auxiliary-gonimoblast fusion cell (Figs. 71d, 78c, 79a) including both haploid and diploid nuclei. These nuclei appear to maintain their integrity and their relative positions within the fusion cell. At the same time, the proximal cells of the branch develop a profusion of small-celled laterals, usually two per branch cell. These laterals can themselves branch; they form secondary pit connections with surrounding rhizoidal filaments (Fig. 79a).

Carpospores released from a plant collected 12 Dec. 1981 at
Brady's Beach averaged 25.1 ± 3.4 μm (s.d., n=50) in diameter.

Spermatangia form a superficial layer cut off by oblique walls from the somewhat elongate spermatangial mother cells; they were 2.5-3.0 μm by 4.0-7.0 μm on a specimen from Boiler Bay, Oregon, collected 9 Aug. 1975. They are illustrated in Fig. 79b

The mature, intercalary tetrasporangia are cruciately divided (Fig. 79c), 32-45 μm wide by 51-77 μm long in a collection of thalli from Porpoise Harbour, B.C., 12 Oct. 1981 (average = 37.7 ± 3.9 by 65.8 ± 5.5 μm, n=30). It is possible, though not common, to have two tetrasporangia form a chain. Tetraspores released from plants collected at Brady's Beach, 12 Dec. 1981, averaged 25.2 ± 2.7 μm (s.d., n=56).

COMMENTS

As indicated by Kylin (1941), *Dilsea californica* has been confused on occasion with *Schizymenia pacifica*. This confusion may be due to their similarly cleft habit when growing intertidally on exposed coasts. I have annotated a number of specimens in UC originally identified as *Sarcophyllis arctica* (another taxon under which *D. californica* has been identified) as *Schizymenia pacifica* (UC 96259, 96261, 96262, 96264), and one sheet of specimens originally identified as *Schizymenia pacifica* has been placed in *D. californica* (UC 392736). I also found that *Schizymenia pacifica* and *Neodilsea americana* (NLG No. 2362 in UC) had been confused as had *N. americana* and *D. californica* (UC 276506).

Some inconsistencies exist between my observations on the
morphology of *D. californica* and those of Abbott (1968:186). In most of the specimens observed, I found a gradual transition between cortical layers rather than two distinct layers, as described and illustrated by Abbott. Also, in most of my specimens, the medulla occupied more of the transection than the cortex in contrast to the 20% allotted by Abbott. In her description of the genus, Abbott stated carpogonial branches are 10-14 cells in length and auxiliary cell branches 10-18 cells long, but under the species, she stated them to be 10-22 cells and 8-18 cells long, respectively. I concur with her on the degree of variability in their length, having found them to be 7-19 cells and 6-20 cells long, respectively. I also found the tetrasporangia to be notably larger (32-45 μm by 51-77 μm) than the 13-15 μm by 34-40 μm Abbott recorded. Abbott followed Newton (1931) in stating that spermatangia in the genus occur in short superficial chains, forming a sorus. From my observations of *D. californica*, I would describe the spermatangia as forming a superficial layer. Since most of the specimens examined by Abbott came from California, the possibility exists that the differences in the characters we observed reflect real population differences between plants at the southern extreme of the distribution of the species and more northerly populations. Furthermore, this study does not exclude the possibility that, in fact, there may be two species currently classified as *D. californica*; however, I consider this possibility unlikely.
Dilsea integra was described first as Kallymenia? integra from specimens collected at Spitsbergen (Kjellman 1875) although it is possible that the Iridaea edulis that Postels and Ruprecht (1840:II) mention from the Kara Sea is this taxon. (Postels and Ruprecht also record Iridaea edulis from the White Sea, but Zinova (1961) has stated that this specimen from the area of Tri Ostrowa is a species of Turnerella.) Later, based on specimens collected at Novaya Zemlya and Vaygach, Kjellman (1877:17) suggested the specific epithet arctica for this species because he found older and fully developed plants not to be entire but to be more or less divided into lobes. Kjellman also quoted a letter from J. Agardh in which the latter concluded that Kjellman's specimens were a species of Sarcophyllis very near to the common Iridaea edulis. Although at least one of the similarities between the two species cited by J. Agardh seems to be based on a misinterpretation of an endophyte as the remains of a cystocarp (from a footnote by Kjellman), J. Agardh recognized "die eigenthümlichen Faden...characteristisch für den Dumontiaceen," which he saw in a specimen collected 22 July 1875. These reproductive filaments characteristic of the family were first figured by Kjellman (1883, Pl. 14, Fig. 2), who concluded that "late autumn is its proper period for producing carpospores" although he also figured what he considered nearly mature cystocarps in a July specimen. In this work, Kjellman (1883) also recorded specimens from the Siberian Sea and Cumberland Sound. He noted that a collection made by Moravian missionaries either on the west coast of Greenland or along the coast of Labrador contained a couple of specimens of this
I have had an opportunity to examine specimens collected by Kjellman in the Eurasian Arctic. Among these are specimens collected during the winter (1872-73) he spent at Mussel Bay, Spitsbergen, in 1875 along the coasts of Novaya Zemlya and Vaygach, and during the trans-Polar expedition of the Vega (1878-79) at Konyam Bay, near Kolyuchin Bay, in Port Clarence, and on St. Lawrence Island (Nordenskjold 1882). Most of these specimens are sterile, but a few have tetrasporangial initials or reproductive filaments. All specimens but those collected at Mussel Bay were identified by Kjellman as *Sarcophyllis arctica* Kjellman. The two collections from Mussel Bay were labeled *Kallymenia*? *integra* Kjellman. I have chosen a group of about 20 specimens collected 23 December 1872 as the lectotype (Fig. 69h). A single collection from Bering Island labeled *S. arctica* is *Turnerella mertensiana* (Postels et Ruprecht) Schmitz.

Rosenvinge (1898:19), recording specimens collected in 4-7 fathoms (7-13 m) at Scoresby Sound and cast ashore at Cape Stewart, Greenland, made the combination *Dilsea integra*. He noted that most of his specimens, collected in July and August, contained reproductive filaments with carpogonia and auxiliary cells and some contained cystocarps. He figured a number of these reproductive filaments, showing the recurved tips of the branches bearing carpogonia. One figure also shows a connecting filament originating from a cell of the carpogonial branch and fusing with a cell of a separate reproductive filament. Because of their sketchiness, Rosenvinge's figures do not lend themselves to further unqualified interpretation. Rosenvinge
also noted that the cystocarps, prominent on dried specimens, are frequently disposed in small groups.

Zinova (1961:84) transferred the species from *Dilsea* to *Neodilsea* on the basis of the similarity of the carpogonial and auxiliary filaments to those of *N. vendoana* and the location of the (undivided) tetrasporangia in the outer rather than inner cortical layer. She also stated that occasionally cytoplasmic strands were seen connecting the tetrasporangia with two end cells of cortical filaments, but in most cases the tetrasporangia were lateral shoots of basal cells of the outer cortical layer. She noted further the possibility that the formation of tetrasporangia in *D. integra* represents an intermediate link between *Dilsea* and *Neodilsea*.

Chihara (1967:189) described specimens of *N. integra* collected at Cape Thompson, Alaska, in August 1965 and included figures of tetrasporangial initials, incompletely differentiated reproductive filaments, and carpogonial branches. His specimens were 300-400 μm thick. Carpogonial branches were (7-) 8-10 (-11) cells in length and bore 1-3 lateral filaments near the base. He appears to have interpreted all immature reproductive filaments as auxiliary cell branches.

Masuda (1973b:468) described a variety of *N. integra* from Japan. This taxon, *N. integra* var. *longissima* Masuda, is elevated to specific status below.

Masuda (1982) included figures of spermatangia (Fig. 5C) and carpogonial (Fig. 6J-L) and auxiliary cell branches (Fig. 6M) from Greenland specimens.

*Dilsea integra* is considered to be a subtidal species. Lund
(1959) recorded it from 5-38 m off Greenland. South and Hooper (1980) stated that in Newfoundland it "grows on rocks mainly in fjord-type situations with strong thermal stratification in summer" and with "most growth while water temperature is below 2°C (from December to June)" although they recorded its presence year-round. They have observed it as shallow as 2 m but state that it usually occurs below 15 m and can extend to below 30 m. Wilce (in herb.) has also found it to occur through a wide vertical range--from tidepools and just below low water mark (W-744) to about 30 m (308-54, 309-54).

*Dilsea integr*a can be considered a truly Arctic species. It has been recorded from the north and west coasts of Spitsbergen and from the Barents, Kara, and Siberian Seas (Kjellman 1883:153). Zinova (1961) recorded it from the Chukchi Sea as well and added that there were no authenticated records from either the White Sea or the Murmansk area. It has been found off Greenland (Rosenvinge 1898:21, Lund 1959:189) and the coast of Canada, from Nova Scotia (Edelstein et al. 1967:197) in the south through the Canadian Arctic (Collins 1927:15, Lee 1980:52), including Hudson Bay (Howe 1927:25). Along the coast of Alaska, it has been collected at Collinson Point, Port Clarence, Oliktok, Cape Lisburne, Beaufort Lagoon, Cape Deceit, and Cape Thompson (Collins 1927:15, Dube in herb., Chihara 1967:189) south at least to Cape Peirce (ALA unnumbered, leg. 21 June 1977) and possibly to the Aleutian Islands (UC 96269, UC 96263, UC 96265, and UC 96266 are indeterminable as to whether they are specimens of *D. integr*a or *D. californica*).
OBSERVATIONS

The phenology of *Dilsea integra* is uncertain. I have observed carpogonial branches in specimens collected from June to October. Cystocarps were seen only in one specimen collected in June (NFLD 24961) and one in July (Wilce in herb., W-744). Male plants have been collected from June to September. Plants bearing tetrasporangial initials have been found from June to October. None of these specimens had completely divided tetrasporangia. Since sterile plants have been collected year-round, I believe that at least some blades are biennial if not perennial.

Vegetatively, *Dilsea integra* resembles other species of *Dilsea* and *Neodilsea*. Most specimens are small (less than 15 cm tall), entire, and possess a long stipe broadening very gradually into an oblanceolate blade (Fig. 69d). The blades of other specimens can flare out at nearly 90 degrees above the relatively long stipe, as sometimes occurs in *D. carnosa* (compare Figs. 69a and c). One unusually large specimen from Labrador occupied an entire herbarium sheet. Blades usually occur in clusters of 10-25 from a common discoid holdfast. Specimens are typically Burnt Lake, Hay's maroon, or Diamine brown (Ridgway 1912). Cells appear to lack a refractive inclusion, but the medullary cells are refractive in some specimens. Blades tend to be thin, ranging from 60-260 μm thick among the specimens I have examined.

Reproductive filaments bearing carpogonia and auxiliary cells develop from inner cortical cells. The lengths of these reproductive filaments varied significantly from specimen to
specimen. In one specimen collected 28 June 1979, carpogonial branches averaged 7.1 cells (n=59) and ranged from 6 to 11 cells in length. In another specimen collected on the same date the carpogonial branches averaged 14.9 cells (n=31) and ranged from 8 to 24 cells in length (Fig. 80a). A third specimen, collected 23 June 1972, had branches ranging from 7 to 14 cells and averaging 10.9 cells (n=41) in length. Carpogonia develop as in other species of Dilsea and Neodilsea (Fig. 80a).

Incompletely differentiated reproductive filaments are usually unbranched although some cells can have two or rarely three nuclei. Mature filaments can bear one or two short (to 8 cells) lateral branches from their proximal cells. Lateral branches on one filament were becoming rhizoidal.

No carpogonial fusion cells were observed. In one instance, what might be interpreted as a connecting filament appeared to be issuing from a carpogonium which had not fused with any other cells of the reproductive filament.

The mature auxiliary cell is cell 2 or cell 3 (Fig. 80b). It is not differentiated in size from neighboring cells but it stains much less intensely.

Nothing could be made of the cystocarps present on one of the 28 June 1979 specimens because of the poor preservation of the material. In the 22 July 1955 specimen, the carposporangia appeared to be transformed inner cortical cells; this was determined by noting the pit connections between the "carposporangia" and other cells shaped like inner cortical cells, some of which bore one or more reproductive filaments. These "sporangia" were rather large, to 47 by 69 μm.
Spermatangia are cut off spermatangial mother cells by a slightly oblique wall. They are 3-4.5 μm wide by 4.5-7 μm long, obovate to spherical and with a distal nucleus. The spermatangial mother cells producing them can be elongate, 2-2.5 μm wide by 7-11 μm long, or rectangular (as illustrated by Masuda 1982, Fig. 5C).

Tetrasporangial initials were observed in specimens collected from June to October. They are recognizable as enlarged deeply pigmented cortical cells forming a layer 1-2 cells below the surface of the thallus. Most were attached basally or sub-basally. Pit connections to distal cells were not observed. The size of initials in the specimen from Cape Peirce ranged from 17 to 26 μm wide and to 65 μm tall. The initials terminate a cortical filament and elongate predominantly distally (Fig. 80c). Only in specimens collected in October were there indications of infurrowing preceding presumed tetraspore formation. However, no bisporangia or tetrasporangia were observed.

COMMENTS

Since tetrasporangial initials in *Dilsea integra* are attached basally, or at times what might be called sub-basally, I believe the transfer of *Dilsea integra* to *Neodilsea* (Zinova 1961) was unwarranted. The presence of an extensive layer of these initials in the cortex is reminiscent of the two species of *Dilsea* and not the species of *Neodilsea*. The size of the sporangia, at least in the Cape Peirce specimen, is close to that of *D. californica*. One expects, when looking at such
specimens, so great is the similarity, to see a file of one or more cells attached terminally to the sporangia, but such a chain of cells has yet to be reported.

Inadequate material has necessitated the exclusion of *Dilsea integra* from the phylogenetic analysis. It is clear that this species is closely related to *Dilsea carnosa* and *D. californica*, but its precise relationship to these two species cannot be resolved at this time. A number of possibilities exist: (1) It is the Arctic form of *D. carnosa*. The apparent continuity in distribution between the two species in the Atlantic together with their gross morphological similarity argues for this option. Differences in the branching of the reproductive filaments (they have few but long laterals in *D. carnosa*) argues against it. (2) It is the Arctic form of *D. californica*. There appears to be no abrupt disjunction between *D. integra* and *D. californica* in the Bering Sea-Aleutian Islands region. I was unable to assign most of the specimens from the eastern Aleutian Islands to one or the other of these two species with certainty. (3) It is the Arctic form of a single species which has been identified as *D. carnosa* at one geographical limit and as *D. californica* at the other limit. (4) It is a distinct taxonomic entity, possibly a polyploid or an aneuploid, which can reproduce only asexually. The lack of mature tetrasporangia and the possible vegetative origin of carposporangia suggest a deficient reproductive mechanism that might be the result of a genetic problem. However, the observations on sporangia can also lend support to the argument that this is merely the Arctic form of another taxon and that it
is the severe environment rather than the genetic constitution
of the plants which is responsible for their anomalous
reproductive behavior.

**Neodilsea yendoana** Tokida 1943:96

**INTRODUCTION**

*Neodilsea yendoana*, the type of the genus, was described by
Tokida (1943:96). This species, common in the northern part of
Japan, had previously been identified under the name *Dilsea
edulis* (Yendo 1909), and under that name Okamura (1921:115, Pl.
180) had included a description of the plant as well as figures,
indicating that it also occurs in the Kurile Islands. Tokida
segregated the Japanese plant from the European species on the
basis of its lateral tetrasporangia. He also pointed out some
reproductive differences between the female and male plants of
the two species, some of which are still valid.

The type sheet of *Neodilsea yendoana* was borrowed from HAK.
The sheet (Fig. 69f) contains four specimens collected by Prof.
J. Tokida on 6 Dec. 1942 at Oshoro, Hokkaido, Japan. The two
upper specimens are tetrasporic and fit Tokida's circumscription
of the species. Tetrasporangia are quite variable in size; the
larger ones measured 24-41 μm by 46-67 μm. In the upper left
specimen, some of the tetrasporangia showed *in situ* germination.
The two lower specimens are bisexual, with both spermatangia and
cystocarps on the same thalli; they represent what is called
*Schizymenia dubyi* (Chauvin) J. Agardh in Japan.

The International Code of Botanical Nomenclature states
that the type of a name of a species of most non-vascular plants
"may consist of more than one individual which ought to be conserved permanently on one herbarium sheet or in one preparation." However, if it is found that the type sheet contains parts belonging to more than one taxon, "the name must remain attached to that part (lectotype) which corresponds most nearly with the original description." Since Tokida (1943) did not indicate a particular specimen in his paper, I am selecting the upper right specimen as the lectotype of *Neodilsea yendoana*. This specimen is favored because of its larger size and its typical appearance. Also, the label indicating the type sheet is closest to this specimen, perhaps suggesting that Tokida intended this plant to be the type specimen. The upper left specimen is therefore an isotype.

Mikami (1957) studied the development of the female reproductive structures in more detail. He found them to be similar to those in *Farlowia*, which he also studied (see **COMMENTS** under *Farlowia mollis* (p. 133) regarding the identity of his material). He noted that the strongly recurved carpogonial branches grow from the inner cortex toward the medulla, the fourth cell from the tip of the branch is the largest and becomes the nutritive auxiliary cell, and the auxiliary cell is the second cell from the tip of its branch and is somewhat smaller than its neighbors. The most striking difference noted between *Neodilsea* and *Farlowia* was the profusion of lateral branches from the basal cells of the reproductive filaments in *N. yendoana*. His description of immediate post-fertilization events is somewhat ambiguous, but he does describe and figure three connecting filaments leaving
the carpogonial fusion cell via pit connections. However, as other authors have done, he incorrectly attributes the origin of gonimoblast filaments to be from the auxiliary cell rather than the connecting filament attached to the auxiliary cell.

Tazawa (1956) described the male reproductive structures: the entire surface of the frond is covered with spermatangia cut off by oblique walls from spermatangial mother cells 3-4 by 12-15 μm or 4-5 by 8-10 μm. The spermatangia they produce are 4-5 by 10-12 μm and 4-5 by 5-7 μm, respectively. Later, Tazawa (1975) wrote that spermatangial mother cells 4 by 12 μm produce 4 by 8 μm spermatangia, and spermatangial mother cells 3 by 6 μm produce 4 by 5 μm spermatangia.

Masuda (1973a, 1973b, 1982) has included comments on and figures of this species in several of his publications. In particular, he has provided data on spore dimensions (1973b 1982), illustrations of early spore germination (1982), young blades in culture (1973a), stipe morphology (1982), tetrasporangia and carpogonial and auxiliary cell branches (1982), and a variation polygraph of thallus shape (1982).

Yoshizaki and Hommersand (MS) also studied the reproductive morphology of this species. They observed tetrasporangia to be 39-50 μm by 55-70 μm, averaging 43 by 64 μm, and spermatangia, which were 3-4 μm by 5-7 μm, but their main contribution was a detailed examination of post-fertilization development. They recognized that the connecting filaments arise from a fusion cell of carpogonial origin, which they said involved "the third [cell 4 in this study] and fourth [cell 5 in this study] cells and sometimes other cells of the carpogonial branch apparatus."
They also observed that, "Growth of a connecting filament is apical and there may or may not be a septum at its point of origin." The connecting filaments they show coming from the carpogonial fusion cell(s) can reach 10 \( \mu m \) or more in diameter.

They also observed that the gonimoblast filaments arise from "a bulge" on the side of the auxiliary cell where the connecting filament attached. The auxiliary cell is the second or third cell from the tip of a branch; their figures show it to be slightly smaller than its neighboring cells although they described it as "especially well developed." Although they stated that "usually more than two gonimoblast initials arise from one auxiliary cell," their figures do not show this clearly. Their statement that the gonimoblast branches dichotomously also is not supported by their figures. They also stated that they had seen but do not illustrate gonimoblast filaments arising directly from the carpogonial fusion cell. They show the branching, elongation, and fusion to medullary filaments of the laterals coming from the proximal cells of the auxiliary cell branch; they also figure a divided trichogyne (Fig. 8).

**OBSERVATIONS**

*Neodilsea yendoana* is a plant of the lower intertidal-upper subtidal zone although Chihara (1975:209) stated it is found in the mid intertidal zone. I found it associated with *Neorhodomela larix* (Turner) Masuda and *Symphyocladia latiuscula* (Harvey) Yamada at Muroran and with other low intertidal-upper subtidal species at other sites along the coast of Hokkaido,
Japan. Nagai (1941:161) recorded it as "growing on rocks in the upper sublittoral zone, preferring somewhat sheltered place" in the Kurile Islands whereas Tokida (1954:156) described it as "growing on rocks in the littoral belt" in southern Sakhalin.

**Neodilsea yendoana** is the most widely distributed species of the genus in the western North Pacific. To the northeast, it extends to Paramshir I., Kurile Is. (Masuda 1982:257). It is found along the coast of southern Sakhalin (Tokida 1954:156) and occurs around the coast of Hokkaido, through Tsugaru Strait, and along the Pacific coast of northern Honshu south to Ibaraki Prefecture (Masuda 1982:257). To the west, Funahashi (1966:137) and Perestenko (1980:40) have recorded its occurrence near Vladivostok in the Sea of Japan. I have collected it along the coast of Hokkaido from Nemuro in the east to Yoshioka in the southwest and near Otaru and at Oshoro on the coast of the Sea of Japan.

**Neodilsea yendoana** displays the phenology typical of *Dilsea* and *Neodilsea*: young blades appear in spring, mature in summer, fruit in fall, and disappear in winter. I have collected a few plants in spring which appear to have overwintered (SCL 2228, 2402).

The initially slightly ob lanceolate blades expand distally and become cleft as they develop (Fig. 69f). Intertidal plants typically remain rather small (less than 15 cm tall). Subtidal plants become somewhat larger. The widths of the plants not uncommonly exceed their lengths (e.g., one blade 10.5 cm tall was 18.5 cm wide, and another 17 cm tall measured 23 cm across). Color ranged through Vandyke red, Victoria Lake, Hay's maroon,
Diamine brown, Brick red, Hay's russet, and Mars brown (Ridgway 1912) among the specimens I collected in Japan.

Blades increase in thickness as they mature. Blades collected in April had 3-5 cortical layers and were less than 100 μm thick; in October, blades had 8-10 cortical layers and were nearly 600 μm thick. In these latter blades, the cortex comprised approximately 70% of the transections. The length of cortical cells increases from the surface of the thallus inward 5-6 cells and not uncommonly reaches 40 μm. Inward from these cells, the cells begin to expand laterally and can form secondary pit connections with neighboring cells. A small refractive inclusion (to about 5 μm in diameter) commonly occurs in both cortical and medullary cells.

Carpogonial branches ranged from 7-12 cells and averaged 9.8 cells in length (n=18) in the specimens I examined.

Like Yoshizaki and Hommersand, I also observed the auxiliary cell to be cell 2 or cell 3 and to be somewhat smaller than neighboring cells.

Specimens were not available with intermediate stages of maturity comparable to those observed by Yoshizaki and Hommersand, but later stages were observed. Pit connections in the auxiliary cell branch enlarge to 5 μm, and the connections between the cells also expand. The cells of the gonimoblast filaments show much morphological diversity. The inner cells remain short and squat. Pit connections expand to only about 2 μm prior to incorporation of these cells into a gonimoblast fusion cell (Figs. 71e, 81a). Other cells may enlarge somewhat or become more elongate before producing carposporangia.
I observed tetrasporangia to average 30μm by 58 μm (n=18) in specimens collected 5 October 1978 at Oshoro, Japan. This compared to 26 μm by 58 μm (n=16) in Tokida's (1943) figures and 43 μm by 64 μm reported by Yoshizaki and Hommersand (MS) in specimens from Muroran. A portion of a transection of thallus showing the attachment and disposition of tetrasporangia is shown in Fig. 81b.

Fertile plants of *N. yendoana* were collected at Oshoro, Japan, the type locality, 12 December 1978. Released tetraspores averaged 27.6 μm ± 1.7 μm (n=25) in diameter, and carpospores, 27.6 ± 2.9 μm (n=35). These diameters are significantly smaller than those observed by Masuda (1982) who measured 600 tetraspores and 700 carpospores, presumably from plants collected at Muroran (where he conducted his research on the genus). He found tetraspores to average 32.0 ± 1.7 μm and carpospores to average 33.8 ± 2.1 μm (figures are interpreted from his graph). These differences in spore sizes between the two sites are thought to reflect natural variation between populations. My observations on early stages of spore germination followed his but at a slower pace. My 11-day stage (at 10°C, 8:16) was about the size of his 5-day stage (at 14°C, 14:10).

**COMMENTS**

Although I did not have the same stages available to me as those observed by Yoshizaki and Hommersand, I would like to comment on their observations based on their figures and those stages I did observe. Their figures suffer in part from being
too detailed, and in a number of cases certain incongruities have led me to believe the illustrations may not be completely accurate (e.g., Fig. 21 has what appears to be two distinct tips to an auxiliary cell branch). In at least one figure (Fig. 14) they show what appear to be two separate carpogonial fusion cells although this situation is described nowhere in the text. Although it is possible that gonimoblast filaments could arise directly from the carpogonial fusion cell (Fig. 25), I would like to see additional documentation of this observation since it is very easy to misinterpret the origin of cells in post-fertilization development.

**Neodilsea crispata** Masuda 1973:37 and **N. integra** var. **longissima** Masuda 1973:468

**INTRODUCTION**

**Neodilsea crispata** and **N. integra** var. **longissima** were described by Masuda (1973a:37, 1973b:468) from Hokkaido, Japan. The former species is restricted to the Okhotsk Sea coast of the province and adjoining Nemuro Strait. The latter occurs along the Pacific coast from Hidaka to Muroran. Both taxa occur in the low intertidal to upper subtidal zone.

Both **N. crispata** and **N. integra** var. **longissima** are described as linear-lanceolate. **N. crispata** reaches a maximum length of about 45 cm, and **N. integra** var. **longissima** has been reported to attain lengths of about 65 cm. The latter taxon is also reported to have a thicker blade (330-580 µm compared to 200-350 µm in **N. crispata**); it has 6-10 cortical cell layers compared to 5-8 in **N. crispata**. **Neodilsea crispata** is
distinguished from *N. integra* var. *longissima* and other species in the genus by its curled margin. *Neodilsea crispata* is reported to be dark red, *N. integra* var. *longissima*, deep red.

Reproductive filaments are similar in both species. Carpogonial branches are 10-12 cells long in *N. crispata* and 9-14 cells long in *N. integra* var. *longissima*, and auxiliary cell branches are 8-12 cells long and 7-16 cells long, respectively. Cell 2 or cell 3 becomes the auxiliary cell. Both types of reproductive filaments bear lateral branches from their lower cells. Carpospores are reported to be 25-45 μm in diameter in *N. integra* var. *longissima*, averaging 32.5 μm. Masuda (1973a 1982) provides no data on their size in *N. crispata*.

Spermatangia are reported to be 4-5 μm by 6-7 μm in *N. crispata* and 3.5-4 μm by 4.5-5 μm in *N. integra* var. *longissima*.

Tetrasporangia are cruciately divided, 40-50 μm by 67-83 μm in *N. crispata* and 30-40 μm by 50-55 μm in *N. integra* var. *longissima*. Tetraspores released from field-collected plants were 31.5 to 40 μm in diameter, with a mean value of 34.5 μm in *N. crispata*; in *N. integra* var. *longissima*, they were 22.5-37.5 μm, with a mean value of 28.3 μm.

Masuda (1973a 1973b) cultured tetraspores of both species and obtained upright shoots from the basal discs at 14°C under both 14:10 and 10:14 light:dark photoperiods. Uprights of *N. crispata* were 1-2 mm high 21 days after germination under 14°C, 14:10 culture conditions; those of *N. integra* var. *longissima* reached a length of 10-12 mm one month after germination under the same conditions.
OBSERVATIONS AND COMMENTS

In addition to a similarity in shape (Figs. 70a, b), size, and section, N. crispata and N. integra var. longissima share a number of other characteristics. In neither species did I observe refractive cellular inclusions or refractive medullary cells. In both species, I observed the occasional transformation of a reproductive filament into a vegetative filament (Fig. 82a). I found carposporangia to be larger in N. integra var. longissima than implied by Masuda's measurements of carpospores; I measured carposporangia up to 70 by 77 μm; this contrasts with measurements of carposporangia up to 45 by 65 μm and 40 by 70 μm in N. crispata (Masuda did not publish figures on the size of released carpospores in this species). I found tetrasporangia to be somewhat smaller than recorded by Masuda for both species (see Table III). The specimens of N. integra var. longissima which I observed (pressed material) ranged from Brick red through Hay's russet and Kaiser brown to Hazel (Ridgway 1912); specimens of N. crispata were observed to be Victoria Lake, Diamine brown, Brick red, and Hessian brown.

Masuda (1973a) did not observe a carpogonial fusion cell in N. crispata; for N. integra var. longissima, he wrote, "The fourth cell from the distal end of the carpogonial branch is usually larger than other cells and becomes a nutritive cell which fuses directly with the carpogonium after fertilization." Two paragraphs later, he stated, "The proximal portion of the carpogonium fuses with the third cell (the nutritive cell) below the carpogonium (Fig. 2-D). The nutritive cell produces several connecting filaments, each of which elongates and fuses with an
auxiliary cell." His Fig. 2-E does show the carpogonium fused with the fourth cell but the two connecting filaments are issuing from the enlarged carpogonium attached to the nutritive cell rather than from the nutritive cell itself. Figure 2-F is somewhat harder to analyze but also appears to show the connecting filaments arising from the carpogonial fusion cell. I did not observe this stage in the material of *N. integra* var. *longissima* available to me; the one example I saw in *N. crispata* indicated that the connecting filaments come from a single carpogonial fusion cell attached to cell 4 (Fig. 82b).

As observed by Masuda, I also found the auxiliary cell to be cell 2 or occasionally cell 3 in both species, but sometimes I observed it to be the terminal cell in *N. integra* var. *longissima* (Fig. 82c). Although Masuda stated that it is the auxiliary cell which cuts off the two or more gonimoblast initials in both species, his figures show and my observations confirm that the gonimoblast initials are cut off the remnant of the connecting filament attached to the auxiliary cell as in other members of the Dumontiaceae. The auxiliary cell is of approximately the same size as neighboring cells in *N. crispata* (Fig. 82d) but is often somewhat smaller in *N. integra* var. *longissima* (Fig. 82e).

Both species display a profusion of lateral branches from the proximal cells of the reproductive filaments, especially those bearing auxiliary cells. These lateral branches are particularly well developed on the auxiliary cell branches of *N. integra* var. *longissima*, which can have up to 3 lateral branches per cell (Fig. 83a) and in which the cells of the lateral
branches can enlarge (Fig. 83b; this latter characteristic is
unique to this taxon). These enlarged cells may play a
nutritive role since their emaciated homologues have been
observed in thalli with mature cystocarps. In both species, the
lateral branches themselves can branch; they can also form
secondary pit connections with nearby vegetative cells.

*Neodilsea crispata* and *N. integra* var. *longissima* are both
distinguished by the extreme enlargement of the pit connections
in the auxiliary cell branch (Fig. 71f) and the formation of a
large (over 100 μm across) gonimoblast fusion cell during
carposporangial maturation. Only in *N. crispata* is there any
indication of cell fusions in the auxiliary cell branch itself.
The proximal cells of the gonimoblast filaments which are
eventually incorporated into a fusion cell tend to be ovate.
Their pit connections enlarge somewhat prior to incorporation.
Figure 83c shows a portion of a gonimoblast fusion cell in *N.
integra* var. *longissima*.

These two species appear to represent vicariants possibly
resulting from a lowering of sea level at some time during the
Pleistocene. Such an event would have isolated an Okhotsk Sea
or a Sea of Japan population from a North Pacific population.
Masuda (1973b) attempted an interspecific cross between male *N.
crispata* and female *N. integra* var. *longissima* but was unable to
produce cystocarps. He therefore concluded that these two taxa
are reproductively isolated.

Masuda (1973b) judged *N. integra* var. *longissima* to be
close to *N. integra* on the basis of the following characters:
"Shape of young plant being linear, basal portion of thallus
being attenuate, thallus margin being entire (Fig. 3, Pl. 1) and thallus surface being plane [sic]." He went on to enumerate their differences. I have argued above that N. integra is most closely related to D. carnosa and D. californica and that it should be returned to the genus Dilsea. Since Masuda observed N. crispata and N. integra var. longissima to be reproductively isolated, I support the elevation of the latter to specific status and propose the new combination:

**Neodilsea longissima** (Masuda) comb. nov.

Basionym: **Neodilsea integra** var. **longissima** Masuda, 1973:468, Pl. 1, Fig. J.

Holotype: SAPS 29790, tetrasporangial specimen collected at Masuichi-hama, Muroran, 14 August 1972.

**Neodilsea natashae** Lindstrom 1984:29

**INTRODUCTION**

Lindstrom (1984:29) has described a new species of **Neodilsea, N. natashae**, from Alaska. Her observations are summarized below.

**OBSERVATIONS**

**Neodilsea natashae**, occurs from extreme lower low water into the upper subtidal zone. It can occur on small rocks or on bedrock. Specimens have been collected along the coast of Alaska, from the Aleutian Islands to the Alaska Panhandle. Plants are annuals; young plants 6-21 cm in height have been collected in April (Fig. 70g); reproductive filaments begin to
develop in June; carpogonia appear in July or August; cystocarps and tetrasporangia begin to mature in September, and disintegrating cystocarpic and tetrasporic plants have been collected in November. Mature plants are orbiculate (Fig. 70h).

The blades range in thickness from 125-180 (320) μm in the upper part, 165-220 (290) μm in the central part, and 185-240 (350) μm in the lower part. (Numbers in parentheses refer to reproductive specimens.) The cortex of 4-7 layers of cells is composed of anticlinally arranged filaments of cells of progressively smaller diameter toward the surface (Fig. 84a). The outermost cells are uninucleate and 5-8 μm wide by 4-7 μm high. Cells of the fourth and fifth layer become elongate horizontally; they are 14-16 μm by 11-12 μm and 21-27 μm by 13-15 μm, respectively, and they can contain more than one nucleus presumably due to the formation of secondary pit connections via small conjunctor cells as occurs in other members of the genus. The filamentous medulla is composed of multinucleate stellate cells to 850 μm long and 5-13 μm wide; these cells are frequently highly refractive (Fig. 71b). The unbranched rhizoidal filaments traversing the medulla are also frequently refractive.

The reproductive filaments arise from inner cortical cells. Carpogonial branches are 9-20 cells in length (Figs. 84b, c). Auxiliary cell branches are 9-24 cells in length. A mature auxiliary cell is slightly larger, about the same size or slightly smaller than neighboring cells, and it can be cell 1-4 of the branch bearing it (Figs. 85a-h). Mature reproductive filaments can bear lateral branches of moniliform cells, some of
which can become distally recurved, or the laterals can be rhizoidal (Figs. 84c, 85b, g). The laterals themselves rarely branch, and in one instance a lateral on a carpogonial branch bore an auxiliary cell.

Following presumed fertilization, the carpogonium expands and can divide to produce two carpogonial derivative cells (Figs. 84d-f). The proximal cell (or the undivided carpogonium if no division occurred) usually fuses with cell 4, and the distal cell, if it is cut off, can fuse with cell 5 or cell 6 (Figs. 84d, e). Connecting filaments arise directly from the carpogonial derivative cells; they have been seen to arise even in those instances when another cell of the carpogonial branch has not been contacted (Fig. 84f). The connecting filaments are cut off by a pit connection when nuclear division occurs; when no nuclear division occurs, the diploid nucleus vacates the carpogonial derivative cell and moves into the connecting filament, and no pit connection is formed (Fig. 84f).

Auxiliary cells are contacted by connecting filaments in the following manner: First, the connecting filament passes an auxiliary cell (Fig. 85c); the connecting filament then divides (following nuclear division; Fig. 85d), and the proximal portion of the filament containing one nucleus contacts the auxiliary cell while the distal portion of the filament with its nucleus continues on presumably toward another auxiliary cell (Fig. 85e). The gonimoblast initiator cell produces 2-3 gonimoblast initials (Figs. 85f, g). All but a few of the proximal cells of the highly branched gonimoblast differentiate into carposporangia 30-40 μm in diameter (Fig. 85h). The gonimoblast
initiator cell and the auxiliary cell retain their respective nuclei although they remain in cytoplasmic continuity throughout carposporophyte development (Fig. 85h). As seen in Fig. 85h, the innermost gonimoblast cells are not incorporated into the gonimoblast initiator cell to form a gonimoblast fusion cell as I have observed in all the other species of Dilsea and Neodilsea.

Cystocarps are immersed in the thallus and are 145-233 μm wide by 82-227 μm high; they mature first near the base of the blade.

A continuous layer of tetrasporangia occurs on both surfaces of the thallus except near the base. A tetrasporangium is cut off as a side branch of the anticlinal cortical filaments and enlarges basipetally as seen by its lateral point of attachment (Fig. 85i). The cruciate tetrasporangia are 38-48 μm by (15) 20-28 μm.

**Neodilsea americana** Abbott 1968:187

**INTRODUCTION**

*Neodilsea americana* was described by Abbott (1968:187) from specimens collected in the San Juan Islands, Washington. Significant features of her description are incorporated in the observations below. Lindstrom (1977) recorded its occurrence in Cook Inlet and Southeast Alaska.

To date, I have been unable to locate the type specimen of *N. americana*, which Abbott (1968) indicated was deposited in UCSB but which is currently missing from its folder (Neushul, pers. comm.).
OBSERVATIONS

**Neodilsea americana** is essentially a subtidal species (I've collected it twice intertidally, both times on the lowest tides of the year, one of which was also the lowest tide of the century). Although it can occur on bedrock, it frequently occurs on small rocks (one to several cm in longest dimension) in sand, mud, shell debris or on bedrock. Lindstrom (1973:48) included it in her sandy bottom association in the species constellation diagram [misidentified as *Kallymenia oblongifructa* (Setchell) Setchell].

**Neodilsea americana** occurs from Puget Sound northwestward at least to Kodiak Island in the Gulf of Alaska. As far as I have been able to ascertain, it does not occur in Oregon: Phinney (1977) does not record its occurrence there; the specimen from the Wilkes expedition (in NY; Fig. 70d) which Abbott (1968) refers to being from Oregon is labeled in typeset "Oregon and Washington Territory" and in hand "Puget Sound." The Puget Sound locale is further suggested by the botanical report of the Wilkes expedition (Bailey and Harvey 1862), in which *Iridaea mertensiana* Postels et Ruprecht, the name under which the **Neodilsea** specimen was identified, was included in the list of algae from "Northwest America, chiefly Puget Sound." Setchell (1912:255) also observed this specimen and mentioned its existence under *Weeksia fryeana* but without making any attributions. **Turnerella mertensiana** has not been recorded from Oregon although *Schizymenia epiphytica* (Setchell et Lawon) Smith et Hollenberg, with which it can be confused, has. Additional specimens of **Neodilsea americana** from the Puget Sound
area were found in UC under *Weeksia fryeana* (UC 194773, 194554, 276199). Another specimen (UC 276505) identified as *N. americana* from Sunset Beach, south of Cape Arago, Oregon, was found to be *Dilsea californica*.

Small, immature thalli of *Neodilsea americana* can be found year-round. Tetrasporangial plants have been collected from May through February. Male plants have been found from July to November. Female plants are first recognizable in June, and carposporophytes first appear in October and can persist until the following July. Therefore, *N. americana* might be described as biennial since reproductive thalli persist through the winter months into the following spring.

Young specimens are lanceolate. The mature thallus flairs fairly abruptly from a 2-4 mm long stipe into an orbiculate blade which can reach more than one meter in diameter (Hansen, pers. comm.). Abbott (1968) described *N. americana* as brownish red. Although none of Ridgway's (1912) standard colors match that well, the colors which seem closest are Eugenia red, Acajou red, Oxblood red, and Vandyke red. I would describe the thallus colour as dark red to reddish black. The surface of *N. americana* can undulate slightly and frequently has a somewhat shiny lustre. The margin can be slightly raised but is never as crispate as *N. crispata*.

The cortex of a mature plant is comprised of 6-10 cell layers. It is like other members of the genus in size and shape of cells and in formation of secondary pit connections and rhizoidal filaments. The medulla consists of a few stellate cells and branched or unbranched rhizoidal filaments, frequently
with distinct walls. Thalli are typically about 350 μm thick in transverse section. Many cells contain a refractive inclusion which stains darkly with aniline blue (Fig. a), suggesting a proteinaceous substance. Staining with Acid Fuchsin and Fast Green produced negative and positive results, respectively, suggesting that if proteinaceous, the inclusions are strongly basic. These inclusions can reach 12 μm in diameter.

Reproductive filaments develop from inner cortical cells. Carpogonial branches can be 7-17 cells in length but are typically 10-12 cells in length. One or two short lateral branches frequently occur on the lower cells of the mature branches (Figs. 86a-c).

Fertilized carpogonia are distinguishable from unfertilized carpogonia because they stained more darkly with iron haematoxylin (Fig. 71c). Only three fertilized carpogonia were seen for the hundreds of carposporophytes observed developing attached to auxiliary cells. Of these, only one had divided, fused to cells 4 and 5 of the carpogonial branch, and begun to initiate connecting filaments. This single example is not figured because its disposition precluded clear illustration.

Auxiliary cell branches are 7-14 cells in length (x=10,n=59, in a plant collected at Bath Island, B.C., 5 Oct. 1982, Figs. 87a, b). The auxiliary cell is usually cell 2, but the terminal cell can also become the auxiliary cell. Rarely, cell 3 serves as the auxiliary cell. The auxiliary cell is usually but not always slightly smaller than neighboring cells. The auxiliary cell is contacted by a connecting filament as in N. natashae (Figs. 87c, d, 88a, b). Following contact, the
moderately darkly staining auxiliary cell usually becomes translucent except for the nucleus. The gonimoblast initiator cell cuts off 3-5 gonimoblast initials (Figs. 88c, d, 89a), at least one of which is composed of somewhat elongate cells. As the carposporophyte matures, a small gonimoblast fusion cell is usually formed (Fig. 89b).

Mature carposporangia are relatively small. A sample of 18 measured 28 μm in their longer dimension.

The mature cystocarps are mostly about 250 μm in diameter and can be distributed fairly homogeneously near the margin of the blade, but they tend to occur in circular to elliptical patches about 2-5 mm in diameter over the rest of the blade. These patches become colorless and erode as the carpospores are released. A distinct ostiole is lacking.

The proximal cells of reproductive filaments can bear one or two lateral branches, which themselves can bear lateral branches (Fig. 87c). These lateral branches are usually short (fewer than 10 cells in length) although they can terminate in rhizoidal filaments of indeterminable length. No secondary pit connections were seen between cells of the reproductive filament system and vegetative cells.

Spermatangia are 2.0 to 5.5 μm wide by 2.5 to 8.0 μm long. They are cut off the distal ends of the slightly elongate (2-4 μm wide by 9-14 μm long) spermatangial mother cells by a somewhat oblique wall (Fig. 89c). The spermatangial nucleus is located distally.

A sample of 68 mature tetrasporangia from six different collections were 15-30 by 26-58 μm, averaging 22.3 by 44.6 μm,
notably larger than the size reported by Abbott (1968). Tetrasporangia are attached laterally to the third cell from the surface and are cruciately divided. A sample of 100 tetraspores from a plant collected 5 Oct. 1982 at Bath I., B.C., averaged $20.7 \pm 2.2 \mu m$ (s.d.), and a sample of 100 tetraspores from a plant collected 9 Nov. 1982 at the same site averaged $22.8 \pm 2.2 \mu m$ (s.d.). These means are statistically different at $p<.001$.

Tetraspores were cultured, initially at $9^\circ C \ 9:15$ light:dark and later at $10^\circ C \ 8:16$ and $16:8$. After 3 weeks (1 of which was at $16:8$), the germinating discs in long-day conditions were $50 \mu m$ in diameter. After 5 weeks they were $120 \mu m$ in diameter, and after 8 weeks they were $300 \mu m$ in diameter. The discs in short-day conditions grew more slowly and were only $200-250 \mu m$ in diameter after 8 weeks. However, after 13 weeks in short-day conditions, discs to $500 \mu m$ were present. The discs began to produce upright thalli less than one month after the cultures were initiated. As with the basal discs, the upright thalli in long-day conditions grew more rapidly. The presence of a single enlarged cell on the surface of the basal disc or a small protrusion indicated the site of upright initiation. Despite the presence of such a cell, no other morphological features were observed suggesting a uniaxial ontogeny of the multiaxial $Neodilsea$ blade.

In the process of trying to obtain a loan of the holotype of $Neodilsea \ americana$, Dr. M. Neushul of UCSB sent me a group of specimens including four isotypes of $Schizymenia \ borealis$ Abbott. I have examined these specimens plus two additional isotypes (US 086053, US 086054). (The holotype of $Schizymenia$
borealis appears to be missing; J. Norris, pers. comm.) These specimens were all collected by M. Neushul at Blakely Island, Washington, on 20 Sept. 1962. The specimens include both tetrasporic and female thalli. The tetrasporangia are mostly immature, attached laterally to cortical cells. Ten mature tetrasporangia measured 20-26 by 35-50 μm, including the outer wall. Female specimens possess reproductive filaments, some of which terminate in mature carpogonia although a large number of these filaments are sterile or are just starting to initiate trichogynes from an incompletely divided terminus. A few filaments appear to be differentiating into auxiliary cell branches.

Vegetatively, these specimens are distinguished by a cortex of 5-6 cell layers, the inner cells of which become stellate. Stellate cells are also found in the medulla. Unbranched rhizoidal filaments run anticlinally from cortex to cortex and periclinally through the length of the plant. The walls of the medullary cells stand out particularly distinctly. A large refractive inclusion (to about 10 μm in diameter) is present in most cells. Color of the specimens is closest to Garnet brown and Pompeian red (Ridgway 1912). All of the specimens are large; almost all cover most of the herbarium sheet, some with their edges folded over, others with parts trimmed away. The basal part of the plant, including the attachment organ, is not present on any of the specimens.

The vegetative and reproductive characters described above do not conform to our present understanding of the genus Schizymenia. Stellate cells are absent from the cortex and
medulla of Schizymenia, and, although both anticlinal and periclinal rhizoidal filaments are present, their walls are not particularly prominent. Refractive inclusions are unknown in cells of this genus. The characteristic gland cells of Schizymenia were not observed in any of the specimens of S. borealis although the immature tetrasporangia in some specimens superficially resembled these structures when stained with aniline blue (reports of tetrasporangia in foliose thalli of Schizymenia spp. require careful scrutiny since the foliose gametophyte of S. dubyi has been found to alternate with a crustose tetrasporophyte--Ardre 1977). Further, the female reproductive structures of the present specimens differ from those of Schizymenia.

On the other hand, the present specimens possess characters conforming to those of the species currently known as Neodilsea americana along this part of the Pacific coast. The name Schizymenia borealis was validly published in 1967, the name Neodilsea americana in 1968. It is therefore necessary to propose the following combination:

Neodilsea borealis (Abbott) comb. nov.
Basionym: Schizymenia borealis Abbott 1967b:169, Figs. 7, 8
Synonym: Neodilsea americana Abbott 1968:187, Figs. 12, 13

The absence of the holotype of Schizymenia borealis requires the selection of a lectotype from among the extant isotypes. I have selected one of the female isotypes in UCSB (Fig. 70e) as lectotype pending discovery of the missing
holotype.

The transfer of *Schizymenia borealis* to *Neodilsea* necessitates the revision of the species description. An emended diagnosis (based on Abbott's original one) follows:

Thallus saxicolous, membranous, fleshy, the base cordate, with a distinct stipe, the mature blade very broadly undulate and ruffled, dark red to blackish red, occasionally brownish red. When young, blades twice as long as broad, when mature, as large as 2 meters in diameter. Sections mostly about 350 μm in thickness. Cortex of 5-8 (10) cell rows. Inner cortical cells stellate. Medulla of both anticlinal and periclinal filaments and stellate cells. Gland cells absent, but most cells containing a round, refractive inclusion to about 12 μm in diameter.

Carpogonial branches 7-17 cells in length. Connecting filaments issuing from the divided, fertilized carpogonium in contact with more proximal cells of the carpogonial branch. The auxiliary cell terminal or subterminal on its reproductive filament, 7-14 cells in length, usually slightly smaller than its neighboring cells. Three to five gonimoblast initials arising from the connecting filament near its point of contact with the auxiliary cell.

Cystocarps to 250 μm in diameter, producing small, hemispherical bumps on the thallus surface. Most cells of the cystocarp maturing into carposporangia. Ostiole absent. Spermatangia 2-6 μm wide by 2-8 μm long. Tetrasporangia 15-30 μm wide by 26-58 μm long, attached laterally, cruciately divided, scattered over the thallus.
**Neodilsea tenuipes** Yamada et Mikami in Mikami 1954:83

**INTRODUCTION**

*Neodilsea tenuipes* was described by Mikami (1954:83) based on specimens collected at Horoman and Samani, Hidaka Province, Hokkaido, Japan (the type specimen was collected by Mikami at Horoman on 7 Aug. 1951). The obovate to oblong specimens to 16 cm wide and 29.5 cm tall were found cast ashore attached to small pieces of rock. The plants were distinguished from *N. yendoana* in part by their thin, membranous, plain (not wrinkled) fronds with undulating margins. The blades were 300-550 μm thick with a cortex of 5-7 cell layers. Carpogonial branches of 8-12 cells were observed as were auxiliary cell branches of about 10 cells, but no post-fertilization stages were seen. The tetrasporangia were described as obliquely cruciate, 35-45 μm.

Tazawa (1956) observed spermatangial mother cells and spermatangia in the species. He found them to measure 4-5 by 8-10 μm and 3-4 by 4-5 μm, respectively. Subsequently, he (1975) reported that the oblong spermatangial mother cells measured 4 by 6 μm, and the nearly spherical spermatangia attained a diameter of about 4 μm.

Masuda (1974) reported on the life history of *N. tenuipes* in culture and included some morphological observations. He reported fronds to 28 cm wide by 65 cm tall and described the surface as wrinkled. He found spermatangia to be 4-5 by 6-7 μm in field material and 4-5.5 by 5-7 μm in cultured plants. His cultures were started from carpospores, which measured 27.5-38.5 μm in diameter. The carpospores developed into plants bearing tetrasporangia 25-30 by 47.5-50 μm; released tetraspores were
22.5-30 μm in diameter. These tetraspores grew into separate male and female gametophytic plants, the latter of which, 3 months after fertilization, produced carpospores 27.5-36.3 μm in diameter. He also concluded that this species was closest to *N. americana*, but that further study of the latter was required to determine their exact taxonomic relationship.

Post-fertilization stages in *N. tenuipes* have been illustrated by Masuda (1982). Figures 6-E and 6-F show the formation of a carpogonial fusion cell, which appears to contact only cell 4 and to initiate a number of connecting filaments. Masuda also illustrated a mature auxiliary cell branch (Fig. 6-D), contact of an auxiliary cell branch by a connecting filament (Fig. 6-G, 6-H), and initiation of gonimoblast filaments (Fig. 6-I).

Masuda (1982) reported the geographic distribution of *N. tenuipes* to be on the Pacific coast of Hokkaido from Akkeshi to Muroran.

**OBSERVATIONS AND COMMENTS**

*Neodilsea tenuipes* is similar to *N. borealis* in color, texture, thickness, and shape (compare Figs. 70c and f). Both species occur in similar habitats. Sporangia are of similar sizes (see Table III). Anatomically, they also share many similarities. Fig. 90a shows the initiation of connecting filaments from the two carpogonial fusion cells in *N. tenuipes*. Gonimoblast initiation is similar (compare Fig. 89a and Fig. 90b), and gonimoblast fusion cells are fairly small in both species (compare Fig. 89b and Fig. 90c.). Pit connections in
the auxiliary cell branch enlarge to 2.5 μm during
carposporophyte maturation in *N. borealis* and to about 4.5 μm in
*N. tenuipes* (Fig. 90d). Both species can possess refractive
inclusions in their vegetative cells although they are usually
larger in the cells of *N. borealis*. The auxiliary cell can be
the terminal cell of a reproductive filament in both species.
*Neodilsea borealis* reaches a larger size than *N. tenuipes* and
its color may be somewhat duskier. Lateral branches on
reproductive filaments tend to be somewhat more abundant and
longer in *N. borealis*. These two species are believed to be
derived from a single North Pacific taxon which was separated
into eastern and western populations by one of the Pleistocene
Ice Ages. Whether the two species are distinct or merely
disjunct populations of a single species remains to be
demonstrated.

*Neoabbottiella araneosa* (Perestenko) Lindstrom 1985:264

In 1975, Perestenko described *Abbotia araneosa*, which she
tentatively placed in the Dilseaceae, a segregate family of the
Dumontiaceae not generally recognized. Abbott (1982:301)
followed Perestenko in attributing the species to the
Dumontiaceae (not recognizing the Dilseaceae) but transferred it
to *Neodilsea*, making the combination *Neodilsea araneosa*.
Perestenko (1982:30), claiming the generic uniqueness of this
taxon but recognizing that *Abbotia* Perestenko is a later homonym
of *Abbotia* Rafinesque 1836 (Juncaginaceae), renamed the genus
*Neoabbottiella*. However, Perestenko did not make the new
combination *Neoabbottiella araneosa*. I have therefore proposed
the combination elsewhere (Lindstrom 1985).

I have had an opportunity to examine the holotype and other specimens of *Neoabbottiella araneosa* identified by Perestenko and housed in LE. In these specimens, the carpogonia and auxiliary cells occur among compact and highly branched clusters of accessory filaments reminiscent of the ampullae characteristic of the Cryptonemiaceae. In contrast, in the Dumontiaceae, carpogonia and auxiliary cells occur on distinctly percurrent accessory branches. Because of these reproductive features, *Neoabbottiella araneosa* has been transferred from the Dumontiaceae to the Cryptonemiaceae (Lindstrom 1985).
CHAPTER IV. RESULTS AND DISCUSSION

CHARACTER ANALYSIS

The characters and character states used in the phylogenetic analysis are listed in Table IV together with the criteria used to polarize the character states. The character states of the 35 taxa used in the phylogenetic analysis appear in Table V. Besides the species discussed in the preceding chapter, I have included two additional undescribed species, *Dudresnaya puertoricensis* from Puerto Rico (specimens of which were loaned to me by Dr. R. B. Searles) and *Dudresnaya "hawkesii"* (specimens of which were loaned to me by Dr. M. W. Hawkes).

Some species are not included in Table V. Lack of material of *Dudresnaya minima* and *Thuretellopsis japonica* prevented their inclusion; as already noted (p. 101), they are closely related to *Dudresnaya peggiana* and would probably appear on the cladogram as sister taxa of that species. *Dilsea integra* was also omitted, and its close relationship to the vicariant pair *Dilsea californica* and *Dilsea carnosa* has been noted (p. 268). As already indicated, I could not clearly separate the previously recognized species of *Weeksia* and *Pikea*, and a single species is accepted as representing each genus in Table V and Fig. 91. The species pairs *Leptocladia binghamia-Leptocladia peruviana* and *Dumontia contorta-Dumontia simplex* represent sister species within well-delimited genera, and only one species of each pair was used in the analysis (for all but possibly one or two of the characters, their character state profiles were identical). Similarly, I represented each of the
species pairs *Neodilsea crispata*-Neodilsea longissima and *Neodilsea borealis*-Neodilsea tenuipes by a single taxon, since here also the character states of each species pair differed at only one or two characters; in all earlier analyses containing all four species, the members of each pair always segregated as sister taxa. Finally, for *Constantinea*, I relied on observations of all three species; for the characters examined, I observed only one conflict among the species, and in that case I chose the plesiomorphic condition in the family as representing the genus.

In addition to the 35 taxa in the Dumontiaceae, a hypothetical ancestor, i.e., a taxon with the plesiomorphic state for all characters was also included in the analysis (Table V). Use of such a "dummy" in the analysis does not alter either the data or the results, but it does provide for separation of the basalmost (i.e., most plesiomorphic) taxa on the cladogram through providing space for the transformation from plesiomorphic to apomorphic states of those few apomorphic traits possessed by these relatively primitive taxa.

The methods employed for character polarization and data analysis are described in Chapter 2 (p. 17 ff.). The Wagner's option of the PHYSYS program produced two trees of length=197. Figure 91 shows the consensus of these two trees using the Nelson option of PHYSYS. The consistency index for the cladogram in Fig. 91 is 37.06. Consistency indices for individual characters are listed in Table VI.

Approximately 8% of the data in Table V is coded as 9. This 8% represents three categories of missing data: (1) Character
coding not applicable, e.g., the maximum diameter of axial cells in species that do not have distinct axial cells; this category represents 0.7% of the total characters in the matrix. (2)
Character state not clearly interpretable, e.g., a cell size or shape that does not clearly fall into the designated states; this category represents 1.1% of the total matrix. (3)
Character state not known, e.g., the size, shape, and attachment of tetrasporangia in heteromorphic species that have not been cultured in the laboratory; this category represents 6.2% of the total matrix, with approximately half of this amount, or 3.0% of the total, being due to lack of information on the tetrasporophyte of heteromorphic species.

Below, I discuss each of the characters included in the cladistic analysis. I first discuss the plesiomorphic condition in the family. This condition, based on outgroup comparison for a majority of characters, was upheld by the cladistic analysis to be the plesiomorphic condition in the family for all characters. I then discuss the character transformations as I coded them for the cladistic analysis. Finally, I discuss the character transformations produced by the cladistic analysis and what they imply about evolution in the Dumontiaceae. I recognize the two distinct, advanced lineages in Fig. 91 as the tribes Farlowieae and Dumontiaeae. These tribes are discussed in a subsequent section on taxonomic conclusions (p. 341).

CHARACTER EVOLUTION

Axiality (Characters 1 and 2). Although limited studies have been done on the vegetative anatomy of the Helminthocladiaceae,
the available evidence (Fritsch 1945:468, Kylin 1956:101) indicates a type of multiaxiality in which indeterminate axes are poorly differentiated from determinate ones. Indeterminate axes lack the usual characteristics one associates with an indeterminate axis; i.e., they lack a distinct apical cell subtended by a file of cells that produce directly or indirectly laterals of limited or unlimited growth.

Such a vegetative construction also characterizes certain members of the Dumontiaceae, particularly Gibsmithia (and possibly Kraftia--apical portions of the thallus were missing from the material examined). In some species of Dudresnaya, distinguishable apical segments also appear to be lacking. In D. hawaiensis and D. capricornica, indeterminate branches are not recognizable as such until 20-30 cells and 5-15 cells behind the "apex," respectively. A plate showing upright initiation from a basal crust in D. japonica (sent to me by Dr. S. Migita, Nagasaki Univ., Japan) revealed that even in young thalli of this species the percurrent axis is not recognizable by its apical or even subapical cell, but it becomes evident 4-6 cells behind the "apex." In D. patula, the only identifiable axial filament seen in this study (Fig. 19a) also terminated in an assimilatory filament. Assimilatory filament terminations to axial filaments were also observed in D. crassa (Fig. 10a) and D. verticillata (Fig. 7a), but recognizable apical cells were also seen in these two species. In other species of Dudresnaya (and in the remaining uniaxial genera of the family), apical cells and axial files were present. Within Dudresnaya, one is therefore able to observe the development of an organized axis
from one in which vegetative filaments are all relatively undifferentiated to one in which differentiation occurs sooner and sooner after a cell has been cut off.

A further elaboration of the development of a differentiated axis can be seen in the degree of differentiation of the apical file in the species of *Dudresnaya*. As already noted, apical cells subtended by a file of discoid cells are entirely absent in *D. hawaiiensis*, *D. japonica*, and probably *D. patula*. *Dudresnaya bermudensis*, *D. colombiana*, *D. georgiana*, *D. lubrica*, *D. peggiana*, and *D. puertoricensis* all show little enlargement of subapical cells until about 8-10 cells below the apex, *D. crassa* and *D. "hawkesii"* about 10-15 cells below the apex, and *D. australis* and *D. verticillata* about 20 cells below the apex.

The development of a distinct axial file through a series of stages (character 2) has a consistency index of 62.50 for the cladogram in Fig. 91. *Kraftia dichotoma* and *Dudresnaya capricornica* are the only species that appear to show reversals in the developmental trend. *Dudresnaya "hawkesii"* appears to have developed in parallel with *Dudresnaya crassa* an axial file in which cells do not begin to enlarge until 10-15 cells from the apex.

In the Dumontieae and Farlowieae, axial cells begin to enlarge within 10 cells (in some species, within 5 cells) of the apex. This observation suggests to me that these tribes are more likely derived from a less specialized ancestor than, say a *Dudresnaya australis*, in which axial cell enlargement is not initiated until 20 or more cells below the apex. However, in *Dumontia* and *Constantinea*, one observes (bundles of) files of
more than 20 subapical discoid cells forming the primordium of new thallus growth. I am unable to relate this condition to the character state of any other species in the family. The cladistic analysis in Fig. 91 suggests that this condition arose independently in Dumontia and Constantinea.

Coupled with an increase in thallus organization in Dudresnaya is a trend away from multiaxiality toward uniaxiality. Whereas the uniaxial condition is clearly evident in most species of Dudresnaya, it has not been clearly established in D. hawaiensis, D. japonica, D. patula, and possibly D. colombiana. [Its putative occurrence in D. capricornica (Robins and Kraft 1985) should be reexamined.] Although axial cells are discernible in some branches of thalli of these species, it is unclear whether the entire thallus originates from a basal crust as a single axial file or as an aggregate of filaments that later differentiate into individual branches. Analyses coding these taxa as uniaxial or as multiaxial do not differ in the topology of the cladograms produced. In Table V, the character state is coded as unknown for these species.

The cladogram in Fig. 91 suggests that a transition to the uniaxial condition occurred in the ancestor of Dudresnaya japonica, D. patula, and the more advanced members of the family. Such a transition at this point must be questioned since it appears that D. japonica and D. patula should probably be considered multiaxial and that two of the more advanced members (Dudresnaya colombiana and Dumontia spp.) may also possess the plesiomorphic multiaxial condition. Alternately, at
least for *Dumontia*, the multiaxial condition may be secondarily derived, as suggested in Fig. 91. The distinctive structure of the individual filaments of which *Dumontia* is composed does not readily ally the genus with any known species of lower Dumontiaceae, but the aggregation of the filaments into a coherent thallus is reminiscent of the most primitive members of the family.

Among higher Dumontieae, *"Farlowia" irregularis* demonstrates a transition from the uniaxial to the multiaxial condition. In the related but somewhat more advanced genera *Dilsea* and *Neodilsea*, the only evidence of uniaxiality that remains is the uniaxial tip of the blade at the earliest stages of upright initiation (seen in *D. carnosia*, Killian 1928) or a single enlarged cell on the surface of the basal crust at the point where upright initiation is to occur (seen in *N. borealis*).

In the Farlowieae, the multiaxiality of *Constantinea* is shown in Fig. 91 to be independently and secondarily derived rather than plesiomorphic, as it was coded. Norris (1971) demonstrated the derivation of multiaxiality in *Weeksia* during the ontogeny of the initially uniaxial, upright thallus. Since this character state transition appears to be an autapomorphy for *Weeksia*, it was not used in the cladistic analysis (see p. 20).

The open type of vegetative anatomy possessed by ancestors of the Dumontiaceae may be considered largely responsible for the variety of forms the axial condition assumes within the family. This plasticity has allowed a degree of experimentation
with types of axially and forms of branching that a more canalized vegetative anatomy, as appears to be characteristic of many other family-level groups, could not.

Axial cell width, pit connections between axial cells (Characters 3 and 4). With the emergence of a distinct axial file came the concommitant enlargement of cells of the file. Among primitive members of the family, the narrowest medullary cells are those of *Gibsmithia* and *Kraftia*. Distinctly wider cells (approximately 70-90 μm in diameter) are found in *D. hawaiienensis*, *D. japonica*, *D. patula*, and *D. puertoricensis*, and cells to 100 μm in diameter have been observed in *D. colombiana*. In the remaining species of the genus, observations of axial cells showed maximum diameters ranging from 125 μm in *D. georgiana* to 300 μm reported in *D. capricornica* (Robins and Kraft 1985).

Among the more advanced members of the family, genera of the Farlowieae show a range of maximum axial cell diameters from about 150 μm in *Pikea*, 90 μm in *Farlowia conferta*, 70 μm in *Weeksia*, 65 μm in *Orculifilum* and *Leptocladia*, 30 μm in *Constantinea*, and 22 μm in *Farlowia mollis*. These diameters show an inconsistent pattern in relation to the hypothesized phylogeny of the tribe. In the Dumontieae, diameters of axial filaments of most species are relatively small, 25 μm or less, but diameters of 145 μm and 200 μm have been measured in thalli of *Cryptosiphonia woodii* and *Hyalosiphonia caespitosa*, respectively.

A consistency index of 25.00 for axial cell width reflects
three apparently independent origins of large axial cells—one among species of Dudresnaya, once in the Farlowieae (seen in Pikea), and once in the Dumontieae (seen in Cryptosiphonia and Hyalosiphiphia). Dudresnaya puertoricensis does not appear to possess the large axial cells expected from its position in the cladogram.

Among most members of the family, pit connections between axial cells are relatively small (< 5 µm in diameter). However, in the Farlowieae, they enlarge to at least 6 µm in Farlowia mollis, 7 µm in Constantinea, 8 µm in Weeksia, 13 µm in Farlowia conferta, 15 µm in Orculifilum, and 25 µm in Leptocladia. In the Dumontieae, only Dasyploea (to at least 20 µm) and Cryptosiphonia (60 µm) have pit connections larger than 5 µm. The consistency index of 40.00 for this character reflects the general lack of a trend in the data.

Rhizoids (Characters 5 and 6). Rhizoids are secondarily formed, nonassimilatory, usually unbranched filaments of relatively narrow (of the order of 5-10 µm in diameter) but elongate cells. These filaments grow downward, filling out the lower portions of the thallus. Among some advanced species of Dudresnaya, a tendency toward increasing diameter of these rhizoidal filaments occurs. Among these species, maximum diameters have been recorded as follows: D. peggiana—18 µm, D. lubrica—25 µm, D. verticillata—40 µm, D. georgiana—75 µm, D. capricornica—85 µm, D. australis—120 µm, and D. crassa—135 µm.

Some species of Dudresnaya (D. australis, D. capricornica, D. georgiana, D. peggiana, and D. verticillata), exhibit the
development of whorl branches from cells of rhizoidal filaments. This feature is especially pronounced in *D. peggiana*, in which a single whorl branch characteristically develops from each rhizoidal cell in older parts of the thallus.

The consistency index of 50.00 for rhizoid diameter results from the apparent independent enlargement of rhizoids in *Dudresnaya lubrica*. The consistency index of 33.33 for whorl branch development from rhizoids results from the independent origin of this character in *D. peggiana* and its absence in *D. crassa*.

**Branching patterns** (Characters 7 and 8). Although the manner of periaxial cell formation and the relative dominance of apical and lateral shoots has received a fair bit of attention in the literature, particularly in the Ceramiales, the actual sequence and orientation of subsequent divisions of lateral cells and the resulting shape of the branch have received notably less. The pattern of branch development is one of the major features distinguishing the Dumontieae from the Farlowieae. In both tribes (with the exception of *Cryptosiphonia* and the multiaxial genera) two pairs of whorl branches are cut off each subapical cell by a type of hemiblastic branching (Hommersand 1963:298). In *Pikea, Farlowia*, and *Orculifilum* at least the first pair of periaxial cells is cut off obliquely with reference to the established plane of the thallus (Figs. 27a, 34a, 42). The second pair of periaxial cells can also be somewhat off-center. The first pair bears the major whorl branches, the second pair, the minor whorl branches. [Because species with distinct axial
files in the Dumontieae are cylindrical, with the exception of "Farlowia" irregularis, for which adequate material was not available for study, the differentiation between major and minor whorl branches does not apply in this tribe.] In the Farlowieae, cells of the major whorl branch axis are cut off by a series of divisions whose angle of interception with the main axis is approximately 45°, at least initially. This angle of division causes the branches to sweep upward. To fill in the cortex between whorl branches, corticating branches are cut off the transverse periaxial cells and cells of the major whorl branches. In addition, distally to medially situated cells of the major whorl branches can initiate abaxial branches that develop much like the parent branch and aid in filling in the thallus between consecutive whorl branches. Norris (1971:208) clearly illustrated this pattern of branching in young, uniaxial fronds of Weeksia coccinea.

In contrast, in the Dumontieae, the cells of the whorl branches are cut off by a series of anticlinal and periclinal divisions. The first division of a periaxial cell is usually anticlinal, i.e., perpendicular to the surface of the thallus. It is generally followed by a periclinal division, i.e., one parallel to the surface of the thallus. The resulting cells follow the same sequence, first dividing anticlinally, then perclinally, and so on. If one considers the major axis of the branch the file of cells produced by successive anticlinal divisions of the periaxial cell and its derivatives, then branching of the whorl branch would be considered abaxial, as in the Farlowieae, but it is initiated beginning with the periaxial
cell and progressing in strict sequence distally. This branching pattern also produces an upward direction to the whorl branches, but whereas the upward sweep of whorl branches in species of the Farlowieae is concave, the pattern in the Dumontieae could be considered convex. The pattern of lateral branch formation exhibited by Cryptosiphonia appears derivable from the Dumontia pattern within the context of the unique form of apical cell segmentation exhibited by Cryptosiphonia.

The different patterns of branching of whorl branches in the Farlowieae and the Dumontieae were initially coded as independently derived character states. Analyses run in which the Farlowieae pattern was assumed to be derived from that of the Dumontieae did not alter the cladistic relationship between these two tribes, which continued to be derived from a common dudresnayan ancestor. These two branching patterns are coded as independently derived in Table V.

Annulations (Character 9). Annulations, i.e., rings of whorl branches surrounding a single axial cell that give the margins of the thallus an undulating aspect, are sometimes recognized on young thalli of D. australis, D. crassa, and D. verticillata, but on no other species in the family. This character thus appears to represent a synapomorphy for these three species. This feature is also characteristic of species of Crouania and Gulsonia in the Ceramiaceae and may account for Gulsonia nodulosa (Ercegovic) Feldmann et Feldmann originally being described as a species of Dudresnaya.
Cortical branching (Character 10). The average number of cells from the distal end of a whorl branch where branching first occurs was determined for all the taxa included in the phylogenetic analysis. The average for most species ranged from 1.0 in *Dasyphloea* to 7.4 in *Gibsmithia hawaiensis*. However, three species stood out as distinct with averages of 9.5, 10.1, and 10.3; these were *Dudresnaya hawaiensis*, *D. japonica*, and *D. capricornica*. The phylogenetic analysis does not support this character state as a synapomorphy.

Cell shapes (Characters 11 and 12). Terminal cells of whorl branches of both species of *Gibsmithia* and most species of *Dudresnaya* are distinctly cylindrical or bullet-shaped. Among these species, *G. hawaiensis* and *D. georgiana* display terminal cells that are notably shorter and in *G. hawaiensis* somewhat broader than those of the other species. This trend in length reduction is also seen in *D. colombiana* and *D. puertoricensis*, whose terminal cells appear somewhat intermediate in shape between the distinct bullet-shaped cells of *G. hawaiensis* and *D. georgiana* and the oval-obpyriform shape of *D. bermudensis* and *D. lubrica*. The smaller terminal cells characteristic of *G. hawaiensis*, *D. georgiana*, *D. puertoricensis*, *D. colombiana*, *D. bermudensis*, and *D. lubrica* were coded as apomorphic, and most of these species occur in a sequence sandwiched between the most primitive and the most derived species of *Dudresnaya*. The very long, narrow terminal cells of *D. hawaiensis* and *D. capricornica*, when coded as a second apomorphic condition, did not appear as a synapomorphy in the cladistic analysis, and they
were excluded from the analysis represented in Fig. 91.

In some species of *Dudresnaya*, intermediate cells of whorl branches become distinctly forked di- or trichotomously. This forking, which was observed in *D. colombiana*, *D. patula*, and *D. puertoricensis*, also appears not to represent a synapomorphy (Fig. 91).

Refractive inclusions (Character 13). Refractive inclusions were observed in cells of many species in the family. Whereas their occurrences are diagnostic or nearly so in certain species (e.g., *Neodilsea borealis*, *Leptocladia binghamiae*, and *Weeksia coccinea*), their occurrences in other species are erratic. Large crystal-like refractive inclusions have been recorded by Robins and Kraft (1985) in *D. australis*, *D. capricornica*, and *D. verticillata*. I observed them also in *D. crassa*, *Dudresnaya "hawkesii"*, *D. puertoricensis*, and *Leptocladia peruviana*. Although the occurrence of these crystal-like inclusions in *D. australis*, *D. capricornica*, *D. crassa*, and *D. verticillata* appears to represent a synapomorphy, their occurrence in other taxa appears to represent homoplasy.

Refractive inclusions have not been recorded in cells of species of the Helminthocladiaceae. However, their occurrence has been documented in the Ceramiaceae, in which they have been studied cytologically (Young 1979) and biochemically (Wetherbee et al. 1984). These workers found the inclusions to be proteinaceous. Wetherbee et al. noted the basic character of the inclusions, which appears to be the case in at least *Neodilsea borealis* in the Dumontiaceae.
Habit (Character 14). It is in habit that the Dumontiaceae surpasses all other families of red algae in its diversity. Most primitive members of the family are mucilaginous to lubricous, and most advanced members are cartilaginous. Thalli vary from terete to slightly to markedly flattened. I assumed a terete thallus to be plesiomorphic in the family (all species in the Helminthocladiaceae are terete except for some species of Liagora and Liagoropsis). Gibsmithia spp. also have terete thalli (although their unique habit cannot be readily explained in terms of the morphologies of any other species of either the Dumontiaceae or Helminthocladiaceae). The analysis in Fig. 91 suggests that the somewhat flattened habit developed early in the evolution of the family and that the terete habit only reappeared with the attainment of the uniaxial condition in Dudresnaya. In the Dumontieae, the multiaxial, somewhat compressed Dumontia contorta produces cylindrical uniaxial branches. According to Fig. 91, Dumontia contorta or its immediate ancestor was ancestral to a group of uniaxial, terete taxa (Dasyphloea, Cryptosiphonia, and Hyalosiphonia). Analyses in which the terete habits of Dasyphloea, Cryptosiphonia, and Hyalosiphonia were coded as derived from the somewhat flattened habit of Dumontia did not differ in cladogram topology from analyses in which the terete habits of these three genera were coded as identical to the presumed plesiomorphic state of the family. The character state of these three genera is coded as plesiomorphic in Table V.

An alternate analysis (in which the unique habit of Gibsmithia spp. was coded as 9) suggested that the ancestor of
the Dumontiaceae may have been slightly flattened.

The foliose habit has developed independently in the Dumontieae and the Farlowieae. In the Dilsea-Neodilsea complex, an elaboration of the foliose habit appears to have developed from the branched but flattened "Farlowia" irregularis through the linear Neodilsea crispata and N. longissima, the ovate Dilsea carnosa, D. californica, and N. yendoana, to the orbiculate N. natashae, N. borealis, and N. tenuipes. In the Farlowieae, Weeksia and Constantinea spp. have apparently developed the foliose habit independently. (Although the habit of Constantinea is coded as 3 in Table V, its cylindrical stipe and branches call into question this coding; coding the habit as 9 produces the same cladogram as that seen in Fig. 91).

Secondary pit connections (Character 15). The Nemaliales is characterized by a lack of secondary pit connections. I have not observed secondary pit connections in Gibsmithia, Kraftia, Dudresnaya, Dasyphloea, Dumontia, Cryptosiphonia, Farlowia, Orculifilum, Leptocladia, or Weeksia, but I have observed them in Pikea, Hyalosiphonia, "Farlowia" irregularis, Dilsea, and Neodilsea. In these latter genera, I have also observed the multinucleate condition of cells that results from the formation of secondary pit connections. In Constantinea, I have seen evidence of secondary pit connections (cortical cells connected to two nonrhizoidal cells proximally as well as two or more cells distally), but I was unable to ascertain the nuclear condition of such cells.

Doty (1963:459) described the anastomosing of cells of
different branches in *Gibsmithia hawaiensis*. He illustrated the "reconnecting" of these branches and noted that "pit connections appear between all cells concerned." I have observed the fusion of cells from different branches of *Gibsmithia* from the Great Barrier Reef. Such fusions occur without benefit of conjunctor cells. Rather, they are effected by a lateral outgrowth of a cell that fuses directly to a nearby cell. Hence, no secondary pit connections are formed.

Shepley and Womersley (1983:211) noted that the medullary filaments of *Kraftia dichotoma* are "laterally connected by frequent secondary pit-connections." I have seen no such connections in the material from Flinders, Victoria, Australia.

Wilce and Davis (1984:340) indicated that secondary pit connections are formed in *Dumontia contorta*. Norris (1971:211) reported that anticlinal rhizoidal filaments may form secondary pit connections with inner cortical cells on the opposite side of the blade in *Weeksia coccinea*, and Abbott (1968: Fig. 26) illustrated this situation in *W. digitata*. I have been unable to confirm the occurrence of secondary pit connections in either *Dumontia* or *Weeksia*.

Secondary pit connections appear to have arisen independently several times in the Dumontiaceae (Fig. 91). In the Farlowieae, they are known for certain in *Pikea*. In Table V, I have coded this character as 9 for *Constantinea* and *Weeksia* because of the uncertainty of occurrence of secondary pit connections in these genera. When secondary pit connections are coded as occurring in these two genera, the most parsimonious cladogram shows the derivation of secondary pit connections in
the ancestor of *Pikea* and the more advanced genera of the tribe and loss in the ancestor of *Leptocladia* and *Orculifilum*. Loss of ability to form secondary pit connections seems unlikely, and one must therefore question the characters that produce a cladogram with such a topology.

In the Dumontieae, occurrence of secondary pit connections in the ancestor of *Hyalosiphonia* made possible a change in thallus morphology that attains its ultimate expression in the foliose habit of *Dilsea* and *Neodilsea*. In the Dumontieae, secondary pit connections produce an inner cortex of stellate cells. In progressively more advanced species, we see an obscuring and eventual loss of the axial siphon and its replacement by a plexus of secondarily pit-connected, stellate medullary cells derived ontogenetically from cells of the inner cortex.

**Cuticle** (Character 16). The presence of a "cuticle" has been recognized at the surface "of some of the coarser forms" of red algae (Fritsch 1945:399). The cuticle of *Porphyra umbilicalis* has been characterized; it contains about 80% protein (Hanic and Craigie 1969).

The absence of a cuticle in *Gibsmithia*, *Kraftia*, and *Dudresnaya* suggests independent origins of the cuticle in the Dumontiaceae and in other families of red algae. A cuticle also appears to be absent, or at best rudimentary, in *Dumontia* and *Dasyploea*. This observation suggests that a cuticle developed in the Farlowieae independently of its development in the Dumontieae.
Vegetative phenology (Character 17). Species with ephemeral, annual, and perennial thalli occur in the Dumontiaceae. [For heteromorphic species, this classification refers to only the gametophytic phase.] Although the species of Gibsmithia are perennial, they have been observed to shed their "branches" on a periodic basis. Many, if not most, species of Dudresnaya appear to be ephemeral, with the macroscopic gametophyte occurring over a period of only 3 to 6 months.

Among the Farlowieae, all species appear to be perennial. In the Dumontieae, Dumontia, Cryptosiphonia, and Hyalosiphonia might be considered ephemerals because of the relatively short season during which they are present as macrothalli. "Farlowia" irregularis appears to be a perennial (Shimizu and Masuda 1983). Thalli of Dilsea carnosa and D. integra also seem to persist for more than one year, but those of D. californica and species of Neodilsea appear to be annuals. Neodilsea borealis may persist into a second year, but whether these plants reach reproductive maturity a second time is unknown.

The cladogram in Fig. 91 is equivocal about whether the ancestor of the Dumontiaceae was a species with an ephemeral gametophyte. The first dichotomy leads to one group of ephemeral species and one group of perennial species. However, the branches of the perennial Gibsmithia spp. are shed periodically, lending support to the idea of an ephemeral ancestor.

Habitat (Character 18). The primitive genera are all recorded to be subtidal. Dasyphloea also appears to be restricted to a
subtidal habitat, but the remaining species of the Dumontieae (except *Cryptosiphonia*, which is strictly intertidal) all occur near low-water mark, sometimes extending into the upper subtidal zone. *Farlowia* and *Pikea* are also genera of the lower intertidal-upper subtidal region. The species of *Constantinea* occur from the low intertidal to moderate depths (about 10 m), but the remaining genera of the Farlowieae appear to be restricted to the subtidal zone. This restriction of *Orculifilum*, *Leptocladia*, and *Weeksia* to a subtidal habitat appears to be secondarily derived in the Dumontiaceae.

**Temperature zone** (Character 19). The species of Dumontiaceae range from being strictly tropical to being distinctly arctic. I have assumed that their occurrence in a particular environment—tropical-subtropical, warm temperate, or cool temperate—reflects a suite of heritable physiological traits that, like morphological characters, will show a conservative evolutionary progression. However, this character had one of the lowest consistency indices (22.22) of any of the characters included in the analysis.

**Life history** (Character 20). The Dumontiaceae includes species with both an alternation of isomorphic generations and an alternation of heteromorphic generations. Although outgroup comparison suggests that the primitive condition in the family is an alternation of heteromorphic generations, the species of *Gibsmithia* appear to have an alternation of isomorphic generations. The tetrasporic phase of *Kraftia dichotoma* is
unknown. Among the species of *Dudresnaya*, both types of life histories have been reported, but an alternation of isomorphic generations appears to be the derived condition based on the cladistic analysis (the same cladogram was obtained whether an isomorphic or a heteromorphic alternation of generations was assumed to be the primitive condition in the family). In the Farlowieae, a heteromorphic alternation of generations is the primitive condition. In the Dumontieae, all species appear to have an alternation of isomorphic generations although unusual reproductive processes have been suggested in *Farlowia irregularis* and *Dilsea integra* (both species appear to lack completely divided tetrasporangia, and carposporangia appear to arise from transformed vegetative cells).

The pattern that results from the two modes of alternation of generations is more than a difference in whether the two ploidy levels occur in plants of similar or dissimilar morphologies. [Like most other red algae, the gametophyte is always a macroscopic individual, and the tetrasporophyte is either isomorphic or a crust.] An alternation of heteromorphic generations means, in the Dumontiaceae as well as many other red algae, that the haploid and diploid generations reproduce in different seasons. In most instances, the gametophyte appears in spring and matures in summer; the tetrasporophyte may be the only stage of the plant that persists through fall and winter.

[This situation is typical of most species of Florideophycidae with an alternation of heteromorphic generations.] Species with this life history pattern appear to be ideally suited for cobble substrates and other unstable habitats that may be subjected to
winter perturbation, and a number of Dumontiaceae have been recorded from just such habitats. Species with an alternation of isomorphic generations may also show distinct seasonal changes in form (e.g., *Dumontia*), but ploidy level alternates on an annual basis, rather than semiannually, so that one year's gametophyte produces next year's tetrasporophyte, and vice versa. This type of life history produces populations that are out of phase by a year for all annual species. How these species maintain their genetic integrity is a question that still needs to be addressed.

**Sexuality** (Character 21). Whether thalli are unisexual or bisexual is another character showing a low consistency among the members of the Dumontiaceae. This character could not be polarized by outgroup comparison since thalli of species of the Helminthocladiaceae have been reported to be unisexual, bisexual, or both unisexual and bisexual. In the Dumontiaceae, both unisexual and bisexual thalli have been observed in *Gibsmithia hawaiiensis*, *D. australis*, *D. crassa*, *D. verticillata*, *Farlowia mollis*, *Orculifilum denticulatum*, and *Weeksia reticulata*. Only bisexual thalli have been reported for *Kraftia dichotoma*, *Dudresnaya capricornica*, *D. georgiana*, *D. hawaiiensis*, *D. peggiana*, and *D. puertoricensis*. The remaining species in the family appear to have strictly unisexual thalli.

Analyses were performed coding all taxa that exhibited the bisexual condition in any population as having the plesiomorphic condition. These analyses produced cladograms with consistency indices of 14.27-16.67 for that character, and all cladograms
exhibited the plesiomorphic state as the putative ancestral condition. Analyses carried out assuming that taxa that had any populations with unisexual thalli possessed the apomorphic condition produced cladograms with consistency indices of 16.67-20.00 for that character, and 2 out of 3 cladograms exhibited the apomorphic state as the putative ancestral condition. Finally, an analysis assuming a transformation from the bisexual through both bisexual and unisexual to the strictly unisexual condition produced a cladogram with a consistency index of 25.00 for that character. This is the character state transformation shown in Table V. However, the cladogram in Fig. 91 does not support the validity of this transformation series. Taxa with both unisexual and bisexual populations tend to occur at the advanced ends of lineages rather than in more primitive positions in Fig. 91, and species with unisexual thalli appear to be ancestral to species with bisexual thalli, a phenomenon that runs counter to the generally observed pattern in red algal evolution.

The carpogonial branch (Characters 22-25). Relatively long branches terminating in carpogonia help characterize the Dumontiaceae; they are also found in various species of the Helminthocladiaceae (e.g., Trichogloea lubrica—Butters, 1903, T. requienii—Papenfuss 1946, Dotyophycus spp.—Abbott and Yoshizaki 1981). Within the Dumontiaceae, the lengths of carpogonial branches vary greatly. I coded species with maximum branch lengths of 11 cells or less as plesiomorphic (based on branch lengths of 6-9 cells in Gibsmithia hawaiiensis and a
breaking point in the data at about 10-12 cells maximum length). Species with maximum branch lengths of 12 cells or more were coded as apomorphic. I obtained a consistency index of 16.67 for this character, the same value I obtained when the character polarity was reversed. This result suggests that this character, as coded, is not particularly useful in recognizing evolutionary trends in the Dumontiaceae.

Even in some species of the Helminthocladiaceae one can see a degree of differentiation of cells immediately below the carpogonium. Whereas proximal cells of these carpogonial branches are cylindrical, like cells of assimilatory filaments, more distal cells are quadrate to horizontally elliptical. I do not necessarily subscribe to the idea that the Dumontiaceae is derived from a helminthocladean ancestor in which cells of the carpogonial branch are as differentiated as what we see in, say Dotyophycus pacificum (Abbott and Yoshizaki 1981:223); however, I would suggest that the differentiation of cells of the carpogonial branch that occurs in the Dumontiaceae may be an underlying synapomorphy (Saether 1983:343) shared with certain members of the Helminthocladiaceae.

Among the most primitive species of the Dumontiaceae, one can observe carpogonial branches that show relatively little differentiation in size and shape of cells (e.g., Gibsmithia sp. from the Great Barrier Reef or Dudresnaya hawaiensis, Fig. 14b). Other species of Dudresnaya show progressively more differentiated carpogonial branches, but I was unable to create a character transformation series for this change. For example, Dudresnaya japonica shows greater differentiation in cell shape
and size than *D. hawaiensis*, but irregularity of the cell shapes and sizes (Fig. 13b) suggests that it still possesses a degree of plasticity not observed in more advanced species.

In the Dumontieae, the carpogonial branches of *Dumontia*, *Cryptosiphonia*, and perhaps *Dasyphloea* do not appear to exhibit any greater degree of differentiation than some of the species of *Dudresnaya* or *Kraftia dichotoma*. However, the remaining members of the tribe display distinctly wedge-shaped distal cells. In the Farlowieae, *Farlowia* and *Pikea* possess wedge-shaped distal carpogonial branch cells, and other genera show further modifications of these cells. In *Leptocladia* and *Weeksia*, cells 4 and 5 in particular expand laterally to form what Abbott (1968) has described as humerus-like cells. An apparent modification of this lateral distension is seen in *Orculifilum* and *Constantinea* in which cells 4 and 5, and to a lesser extent cells distal and proximal to these two cells, develop lobes. The cladistic analysis in Fig. 91 suggests such lobing developed independently (another underlying synapomorphy, sensu Saether 1983) in *Orculifilum* and *Constantinea*. This character has a consistency index of 57.14 for the entire cladogram.

In *Farlowia*, *Pikea*, *Weeksia*, and *Constantinea*, cell 3 is often if not usually smaller than cell 2; the opposite is true in *Orculifilum* and *Leptocladia* and most other members of the Dumontiaceae (in *Gibsmithia* spp., however, cell 3 is distinctly smaller than all other cells of the branch). There is also a slight difference in size in favor of cell 2 in some carpogonial branches of *Dudresnaya capricornica*, *D. hawaiensis*, *D.*
georgiana, D. peggiana, and D. puertoricensis. In D. hawaiiensis, this difference may be a result of its close relationship with Gibsmithia. The occurrence of this character state in D. georgiana, D. peggiana, and D. minima, may indicate a closer relationship between these taxa and the Farlowieae than that suggested in Fig. 91. This character has a consistency index of 20.00.

Curvature of the carpogonial branch also underwent a metamorphosis during the evolution of the Dumontiaceae. As shown by Abbott (1981:55), carpogonial branches of the Helminthocladiaceae are relatively straight, terminating distally in an elongate trichogyne. In all Dumontiaceae, some distal curvature of the branch occurs. In Gibsmithia spp., Dudresnaya hawaiiensis, and D. patula, this curvature may amount to little more than the carpogonium being displaced to one side of cell 2, presumably by a somewhat oblique final division of the branch. However, in most species of Dudresnaya, one also observes a differential enlargement of distal cells of the branch. Cell 3 in particular, but also cell 2 and sometimes other cells of the branch, become slightly wedge-shaped due to unequal enlargement (this fact has already been noted by Robins and Kraft 1985 for D. capricornica and D. hawaiiensis). Such a condition also obtains in Kraftia. In several species of Dudresnaya (D. lubrica, D. peggiana, and D. verticillata), the last two divisions of the carpogonial branch appear to be oblique. Such divisions result in the carpogonium being placed adjacent to cell 4 without any further cell enlargement being required to achieve such a disposition (the importance of this
placement is discussed below). In the Dumontieae, it is unclear whether the two final divisions are both oblique in Dumontia and Dasyphloea; the mature carposporangial branches of these genera reveal an open aspect suggestive of cell enlargements, and it is possible that the enlargements have occurred after oblique divisions of the branch as appears to occur in Cryptosiphonia. I have coded this character as a 1 for both genera. The remaining members of the Dumontieae and all members of the Farlowieae have distinctly recurved carposporangial branches. In certain Farlowieae (Farlowia conferta, Orculifilum denticulatum), carposporangial branches are not just distinctly recurved but the cells can remain tightly appressed after being cut off, forming a knot-like cell-cluster at the distal end of the branch.

Curvature of the carposporangial branch has a consistency index of 28.57. Since reversal in this character seems improbable (see below, p. 326), I sought an equally parsimonious cladogram that did not contain reversals. Such a cladogram can be constructed by recognizing the independent development of branch curvature in Kraftia dichotoma, an earlier divergence of Dudresnaya patula than D. japonica, and a separation of these two latter taxa solely on the basis of branch curvature.

The trichogyne (Characters 26 and 27). As previously noted, curvature of the carposporangial branch affects the disposition of the carposporangium and its trichogyne. In branches with little curvature, the distally directed trichogyne projects straight toward the surface of the thallus. In species of Dudresnaya that show moderate to marked curvature of the branch, the
trichogyne must curve back on itself in order to exit the thallus; thus, the trichogyne can be broadly (Fig. 7c) or abruptly (Fig. 18c) curved at it base and sometimes distally as well. In *Dudresnaya lubrica*, the trichogyne appears to exit the base of the carpogonium somewhat laterally. This lateral displacement may represent an attempt to accommodate the advantages and/or disadvantages of the distally recurved branch. Whether we assign an adaptational explanation to it or not, the occurrence of a lateral trichogyne appears to mark a particular developmental line in the Dumontiaceae, namely, the Dumontieae. The lateral displacement of the trichogyne is evident particularly in *Dumontia*, *Dasyphloea*, and *Cryptosiphonia*, and is also sometimes distinguishable in *Hyalosiphonia* and "*Farlowia*" *irregularis*. This character has a consistency index of 33.33.

In contrast to most species of *Dudresnaya* in which the trichogyne is relatively straight and curves only broadly or in distinct crooks, *Dudresnaya peggiana* and *D. puertoricensis* bear trichogynes that can spiral basally. This character state is present in all members of the Dumontieae except *Dasyphloea*. It is also found in the Farlowieae although somewhat more irregularly. Character 27 has a consistency index of 25.00.

*Spermatangia* (Character 28). More than one pattern of spermatangial production has been recorded for species of the Helminthocladiaceae and for the more primitive species of the Dumontiaceae. Based on their occurrence in *Gibsmithia hawaiiensis* and *Dudresnaya hawaiiensis*, spermatangia occurring in double whorls around branch cells were coded as
plesiomorphic. Double-whorled spermatangia also occur in *D. capricornica*, *D. japonica*, and possibly *D. australis*. This character has a consistency index of 33.33 in Fig. 91.

**Division of the fertilized carpogonium** (Characters 29 and 30).

One of the distinguishing features of the Dumontiaceae is the division of the carpogonium after fertilization and its fusion with usually two other cells of the branch. This initial post-fertilization division has been interpreted in two different ways.

One interpretation suggests that this division is homologous to the transverse division of the fertilized carpogonium in certain species of Helminthocladiaceae, such as species of *Dotyophycus*, *Helminthocladia*, *Helminthora*, *Nemalion*, *Trichogloea*, and *Trichogleopsis*. In support of this argument, one could note production of gonimoblast filaments (i.e., connecting filament homologues) from both carpogonial derivative cells in most of the genera mentioned above.

The second interpretation, which has been followed by Lee (1963), Littler (1974), and Robins and Kraft (1985) in terminology if not in substance, holds that the initial outgrowth of the fertilized carpogonium is a primary connecting filament, and that the two carpogonial derivative cells that fuse with other cells of the branch represent two ontogenetically distinct entities (fertilized carpogonium and primary connecting filament, respectively). [This viewpoint seems inherently less satisfactory because of this initial invocation of nonidentity in two structures that otherwise
appear to behave identically.) This viewpoint suggests that the Dumontiaceae is derived from a species in which the carpogonium did not divide transversely following fertilization. Among genera in the Helminthocladiaceae lacking such a division are Cumagloia, Dermonema, Liagoropsis, and Yamadaella.

Although variability in the division of the fertilized carpogonium has been noted, particularly in species of Dudresnaya (Taylor 1950, Robins and Kraft 1985), the standard pattern is an initial division of the carpogonium followed by fusion with cells 4 and 5. [It is because of the occurrence of these fusions that the development of a recurved branch makes sense; without a distinctly recurved branch, the fertilized carpogonium must grow 10-20 μm before cell 4 can be contacted (see Fig. 14c).] This standard pattern is found in Gibsmithia, Kraftia, Dudresnaya, Farlowia, and Pikea. In the remaining genera of the Farlowieae, carpogonial fusion cells were either not observed (Orculifilum and Leptocladia) or a modified post-fertilization development occurs. In the Dumontieae, the situation is also somewhat unclear. Although fusion with more than a single cell can occur in most species, it is unclear for many of the species, when it does occur, whether the fertilized carpogonium has actually divided into two cells, with pit connection formation, or whether it has merely been pinched or pulled in two.

The homology of connecting filaments with gonimoblast filaments has been proposed by Drew (1954:66) and supported by Robins and Kraft (1985). Drew envisioned the ontogeny of connecting filaments from laterally spreading gonimoblast
filaments characteristic of certain Nemaliales. These laterally spreading gonimoblast filaments are abundantly septate. I have therefore assumed that a connecting filament that is initially septate on leaving the carpogonial fusion cell represents the plesiomorphic state in the Dumontiaceae. Such connecting filament septation has been observed in Gibsmithia from the Great Barrier Reef, Kraftia, Dudresnaya hawaiiensis, D. japonica, and D. patula.

In Weeksia digitata and Constantinea subulifera, I have observed abundantly divided filaments initiated from carpogonial fusion cells. These filaments superficially resemble gonimoblast filaments, but true gonimoblast filaments arising from gonimoblast initiator cells attached to remote auxiliary cells were also seen in both species, as were more typical connecting filaments arising from carpogonial fusion cells or their products. Whether these divided filaments actually produce viable carpospores has not been demonstrated. Development of gonimoblast filaments from carpogonial fusion cells has also been reported to occur in Neodilsea yendoana (Yoshizaki and Hommersand MS) and in Dudresnaya hawaiiensis (Robins and Kraft 1985).

The auxiliary cell branch (Characters 31-33). The occurrence of the auxiliary cell on a branch distinct from the carpogonial branch is another distinguishing feature of the Dumontiaceae. This feature also sets the family apart from the Nemaliales and has been used to include the family in the order Cryptonemiales. The apparent homology of the auxiliary cell branch, which
terminates in an assimilatory filament in most primitive species, with other vegetative branches has provided the basis for a recent proposal merging the Cryptonemiales and the Gigartinales (Kraft and Robins 1985). As noted above, the most primitive Dumontiaceae are distinguished by undifferentiated or incompletely differentiated axial filaments. Lateral assimilatory filaments are similarly poorly differentiated—varying numbers are produced per axial cell in no particular order. This situation makes it impossible in these primitive species to identify any lateral branch when it is first formed as primary or secondary, indeterminate or determinate, vegetative or reproductive. [Rhizoids, in contrast, are generally identifiable soon after initiation by their characteristic position, direction of growth, cell size, and lack of pigmentation.] What is noteworthy is that, as the axial structure of members of the Dumontiaceae becomes more organized, the development of the auxiliary cell branch ceases to be assimilatory in character and becomes more rhizoid-like. In these more organized taxa, the branch is cut off a periaxial cell or other proximal whorl branch cell in a position commonly occupied by a rhizoid rather than distally as are assimilatory filaments and reproductive filaments of more primitive taxa. In the Farlowieae and the Dumontieae, auxiliary cell branches are distinctly rhizoidal in position and sometimes even character (recall, e.g., the instances in which a carpogonium has been described as reverting to vegetative—i.e., rhizoid-like—growth). Because the auxiliary cell branches of the primitive members of the family are distinctly assimilatory in character,
however, we are forced to recognize the rhizoidal character of these branches as secondarily derived and hence an example of convergence. This distinction is necessary because Kraft (1975:289) has argued that "...the past divergence of lower cryptonemialean algae may have taken place from the simpler gigartinalean types through modifications of some rhizoidal filaments, possibly in a sequence that included Adelophyton-like stages." We have seen above that the auxiliary cell branches of the Dumontiaceae appear to be homologous to assimilatory filaments and not rhizoidal filaments, and we therefore reject the premises of Kraft's argument. We must also question the conclusion that lower cryptonemialean algae (Kraft is thinking here specifically of some members of the Dumontiaceae) are derived from simpler gigartinalean types.

A further question remains regarding the possible homology of assimilatory filaments bearing auxiliary cells in the Dumontiaceae and the so-called normal vegetative filaments of members of the Calosiphoniaceae or Nemastomataceae. I will not argue the fact that branches in all these families are derived from assimilatory filaments; rather I will ask whether the modification of such branches to serve an auxiliary function occurred once, representing homology, or more than once, representing homoplasy. One could argue that even among the most primitive species of these families the branches bearing auxiliary cells look different. Modification of a row of cells, one of which may be slightly to distinctly smaller than its immediate neighbors, is simply not found in species of either the Calosiphoniaceae or the Nemastomataceae; yet, this feature
characterizes all members of the Dumontiaceae. However, for me, the strongest case against the homology of branches bearing auxiliary cells in the Dumontiaceae and those of the Calosiphoniaceae or Nemastomataceae is that there is no evidence in the evolution of any of the other characters in the Dumontiaceae to indicate a derivation from a gigartinalean ancestor. One is therefore forced to conclude that the similarities manifested by members of the Dumontiaceae and the more primitive Gigartinales must represent either symplesiomorphies or homoplasies.

In most Dumontiaceae, the mature auxiliary cell is slightly to distinctly smaller than immediately adjacent cells, which are usually round and enlarged relative to other branch cells. However, in Gibsmithia spp., Dudresnaya georgiana, D. lubrica, and D. puertoricensis, the auxiliary cell is not differentiated in size from adjacent cells. In the cladogram in Fig. 91, an undifferentiated auxiliary cell was assumed to be primitive. With such an assumption, one still observes the origin of one group of species of Dudresnaya with undifferentiated auxiliary cells from other species in the genus in which the auxiliary cells are differentiated. When the polarity of the character is reversed, the same result obtains.

Auxiliary cells are frequently recognizable in immature reproductive filaments by their initially larger size (larger than other cells of the branch). In mature filaments, they are typically about 8-10 μm in diameter and may or may not be smaller than adjacent cells, as discussed in the preceding paragraph. In Orculifilum, Leptocladia, and Weeksia, the
auxiliary cell usually reaches 15-20 µm in diameter, and the cells adjacent to it are humerus-like or lobed. These greatly enlarged auxiliary cells appear to represent a synapomorphy.

The relative position of an auxiliary cell in its branch has changed during the evolution of the Dumontiaceae. In most primitive species, the auxiliary cell is found near the base of the branch, but the precise number of cells from the base of the branch often varies greatly. Kraftia is an exception with the auxiliary cell located closer to the distal than the proximal end of the branch. However, auxiliary cell branches in Kraftia are distinct from all other species of Dumontiaceae, suggesting that its distal auxiliary cell does not represent a synapomorphy with other Dumontiaceae. The relative position of the auxiliary cell in Dumontia is equivocal. Reproductive filaments of this genus are so short, usually only 4-6 cells long, that it is unclear whether the auxiliary cell, which is usually cell 3 or cell 4, should be considered proximal or distal. I have coded it the same as Kraftia, Cryptosiphonia, Dasyphloea, and Pikea, recognizing the possibly transitional position of the auxiliary cell in these genera. In Cryptosiphonia, the auxiliary cell is 2-10 cells from the distal end of the branch, in Dasyphloea 3-6 cells, and Pikea 2-6 cells. In the remaining genera of the Dumontiaceae and the Farlowieae, the auxiliary cell is within four cells of the branch tip. A consistency index of 40.00 for this character reflects the independent development of a distal cell in Kraftia and the separate development of an auxiliary cell within 4 cells of the branch tip in the Farlowieae and Dumontiaceae, and a possible reversal in auxiliary cell position.
from distal to intermediate in *Pikea*.

**Post-fertilization changes in the auxiliary cell branch**

(Characters 34-37). In *Dudresnaya crassa*, *D. hawaiiensis*, and *D. japonica*, several cells distal to the auxiliary cell can become swollen and vacuolate as a carposporophyte develops attached to the auxiliary cell. This character state represents an instance of homoplasy, according to the analysis in Fig. 91.

Concomitant with carposporophyte maturation in association with an auxiliary cell branch, pit connections between the cells of the auxiliary cell branch, particularly those adjacent to the auxiliary cell, enlarge in most species. Although little (to 2.0 \(\mu m\) in diameter) to no enlargement has been detected in *Dudresnaya australis*, *D. colombiana*, *D. georgiana*, *D. hawaiiensis*, *D. patula*, and *D. peggiana*, for at least several of these species, this observation may reflect the immaturity of the associated carposporophyte development in the specimens examined. In *Gibsmithia* spp., *Dudresnaya lubrica*, *D. verticillata*, *Kraftia*, *Pikea*, *Farlowia*, *Weeksia*, *Constantinea simplex*, *Dumontia*, "Farlowia" *irregularis*, *Dilsea carnosa*, *Neodilsea yendoana*, and *N. tenuipes*, a maximum enlargement of 3-5 \(\mu m\) was measured. Among species of *Dudresnaya*, only *D. crassa* and *D. japonica* show greater enlargement, in both cases to a maximum diameter of 7 \(\mu m\). In the *Farlowieae*, the pit connections of *Orculifilum* and *Leptocladia* enlarge to 7 and 6 \(\mu m\) in diameter, respectively. Enlarged pit connections in *Cryptosiphonia*, *Dasyploea*, and *Hyalosiphonia*--15, 12, and 10 \(\mu m\), respectively--are thought to represent a synapomorphy. I
have therefore interpreted the enlarged pit connections of *Neodilsea crispata* and *N. longissima* as inherited from a common ancestor (whether through a common ancestor with *Farlowia* *irregularis* is hard to establish because of the unusual post-fertilization development observed in that species). The distinctly smaller pit connections (4-6 µm) found in the remaining species of *Dilsea* and *Neodilsea* appear to be secondarily derived from the enlarged pit connections of their ancestors and not directly from the plesiomorphic state exhibited by more primitive genera in the family. I now believe the maximum size of pit connections measured in *N. borealis* (2.5 µm) reflects the immaturity of the cystocarps examined since the remaining species in the genus, including its vicariant *N. tenuipes*, have pit connections that reach 4-6 µm in diameter. The maximum diameter of pit connections in cystocarps of *N. borealis* is being re-examined.

Enlarged pit connections in the auxiliary cell branch might be interpreted as a synapomorphy uniting the Dumontiaceae. It is unclear whether pit connections in carpogonial branches (i.e., branches bearing carposporophytes) of members of the Helminthocladiaceae enlarge as they do in auxiliary cell branches of the Dumontiaceae. In studies of members of the Helminthocladiaceae (Papenfuss 1946, Womersley 1965, e.g.), reference to widening of pit connections appears to refer only to the pores between cells and not to the proteinaceous plug I call the pit connection. Ramm-Anderson and Wetherbee (1982), who studied ultrastructurally post-fertilization events in *Nemalion helminthoides*, also did not indicate a widening of the
proteinaceous plugs during fusion cell formation in that species.

The fusion of carpogonial branch cells subtending a developing carposporophyte has been observed in *Trichogloea requienii* (Papenfuss 1946), *Nemalion helminthoides*, *Helminthora lindaueri*, *H. australis*, *Helminthocladia dotyi*, *H. beaugleholei*, *H. densa*, *H. australis*, *Liagora harveyiana*, *L. wilsoniana* (Womersley 1965), *Yamadaella cenomyce* (Abbott 1970), and *Dotyophycus pacificum* (Abbott and Yoshizaki 1981). Despite the prevalence of this character state in the Helminthocladiaceae, the primitive state in the Dumontiaceae appears to be absence of cell fusions in the auxiliary cell branch. Auxiliary cell branch fusions are present in the Dumontieae in *Dasyphloea*, *Hyalosiphonia*, and most species of *Dilsea* and *Neodilsea* (they appear to be secondarily lost in *N. natashae*, *N. borealis*, and *N. tenuipes*). Auxiliary cell branch fusions also occur in *Pikea* and *Constantinea* in the Farlowieae.

A comparison of pit connection enlargement and widening of intercellular connections between carpogonial branches of the Helminthocladiaceae and auxiliary cell branches of the Dumontiaceae might appear to be an analogy. However, I will make a case for their homology based not on the homology of carpogonial and auxiliary cell branches, a homology that I believe cannot be supported in the Dumontiaceae, but on the association of each, in their respectively families, with the development of the carposporophyte. Pit connection enlargement and widening of intercellular connections appear to be responses of the gametophyte to the attached carposporophyte. The
proximity of the carposporophyte provides the stimulus for the
gametophytic response. The kind of response the gametophyte
produces must be programmed in its genetic code, and that
response can be elicited from any cell of that genotype given
the appropriate conditions (namely, association with a
carposporophyte). I therefore suggest that the response of
cells of the auxiliary cell branch in the Dumontiaceae be
considered homologous to the response of the cells of the
carpogonial branch in the Helminthocladiaceae.

The production of involucral filaments around the
carposporophyte is another example of possible homology between
post-fertilization development in the Helminthocladiaceae and
the Dumontiaceae. Involucral, or sterile, filaments occur in
Dotyophycus, Helmithora, Helminthocladia, Liagora, Nemalion, and
Trichogloea (Papenfuss 1946, Womersley 1965, Abbott and
Yoshizaki 1981). Although involucral filaments may be initiated
prior to fertilization, at least in the Dumontiaceae, they do
not achieve their full development until after carposporophyte
initiation. They occur on auxiliary cell branches of
Gibsmithia, Dudresnaya georgiana, D. lubrica, D. peggiana, and
D. puertoricensis. The homology of the lateral branches on
cells of auxiliary cell branches in Kraftia is uncertain. In
the Dumontieae, they occur in Cryptosiphonia, Hyalosiphonia,
"Farlowia" irregularis, Dilsea and Neodilsea. In the Dumontieae
in all but Cryptosiphonia, the involucral filaments form a
plexus of branches that can fuse secondarily with non-
reproductive cells of the thallus. The occurrence of involucral
filaments in Dudresnaya spp. and in members of the Dumontieae
appears to be secondarily derived according to the cladogram in Fig. 91.

**Gonimoblast fusion cell** (Character 38). Although fusions among first-formed gonimoblast filaments occur in some Helminthocladiaceae (e.g., *Dotyophycus pacificum*, *Helminthocladia dotyi*, *H. australis*, *Liagora harveyiana*—Abbott and Yoshizaki 1981, Womersley 1965), lack of such fusions appears to be plesiomorphic in the Dumontiaceae. Gonimoblast fusion cells appear in members of both the Dumontieae and the Farlowieae. In the Dumontieae, they are seen in all genera but *Dumontia* and *Cryptosiphonia*. They are very large in *Dasyphtloea*, *Hyalosiphonia*, "*Farlowia* irregularis*, *Neodilsea crispata*, and *N. longissima*, extending more than 100 μm across. In the other species of *Dilsea* and *Neodilsea*, they become progressively smaller until in *N. natashae* they appear to be entirely lacking. Gonimoblast fusion cells occur in *Leptocladia* and *Constantinea* in the Farlowieae; they apparently arose independently in these two genera (Fig. 91).

**Spore and sporangial size** (Characters 39 and 44). Although spore size has been shown to be a poor specific character for tropical benthic algae (Ngan and Price 1979:285), it was found to have some utility in the present study. Spores or sporangia were found to be uniformly small (i.e., less than 30 μm in diameter for carpospores/carposporangia and less than 25 by 55 μm for tetrasporangia) in primitive members of the family and in the Farlowieae. [They are also small in the Helminthocladi-
In the Farlowieae, only in Constantinea are larger spores encountered. The Dumontieae, with the exception of Dasyphloeae, is characterized by its large spores. Only the carpospores of Dilsea californica, Neodilsea yendoana, N. borealis, and N. tenuipes are less than 30 μm, and this small size appears to be secondarily derived according to the cladogram in Fig. 91. [I have already noted that Masuda (1982) found significantly larger spores in N. yendoana from Muroran than I found in the same species from Oshoro.] Tetrasporangia of the Dumontieae (excluding Dasyphloeae) show a transformation from the very large sporangia of Dumontia and Cryptosiphonia, through the medium large sporangia of Hyalosiphonia, "Farlowia" irregularis, and Dilsea carnosa, to the medium sporangia of D. californica, Neodilsea crispata, and N. yendoana, and the medium small sporangia of N. longissima, N. natashae, N. borealis, and N. tenuipes. Among other members of the Dumontiaceae, a size difference can be observed between the smaller, cruciate or zonate tetrasporangia (7-17 by 15-31 μm) of Gibsmithia from the Great Barrier Reef and the Farlowieae, except Farlowia mollis and Constantinea spp., and the zonate tetrasporangia (10-25 by 25-55 μm) of Dudresnaya, Dasyphloeae, and Farlowia mollis. The smaller size was coded as plesiomorphic based on outgroup comparison. Cruciate tetrasporangia of Gibsmithia hawaiiensis (25-30 by 29-39 μm) do not clearly fit either category.

Ostiole (Character 40). An ostiole above maturing cystocarps is found only among certain members of the Farlowieae. Orculifilum appears to possess a less well-developed ostiole than do
Leptocladia, Weeksia, and Constantinea. This observation argues for a more primitive position for Orculifilum than that shown in Fig. 91.

Tetrasporangia (Characters 41-43). Based on outgroup comparison, the plesiomorphic condition for tetrasporangial shape is cruciate. This pattern is exhibited by Gibsmithia, Dudresnaya peggiana, all members of the Dumontieae except Dasyphloea, and Pikea and Weeksia in the Farlowieae. A zonate pattern is reported for Dudresnaya australis, D. capricornica, D. crassa, D. minima, D. verticillata, Dasyphloea, Farlowia, Leptocladia, and Constantinea. Irregularly cruciate or irregularly zonate tetrasporangia have been observed in Dudresnaya capricornica, Dumontia, Cryptosiphonia, Farlowia, Leptocladia, Weeksia, and Constantinea. The zonate pattern appears to be derived within the family at least twice (Fig. 91).

Tetrasporangia are borne laterally (plesiomorphic state) or terminally (apomorphic state) on outer cortical cells. [In Dudresnaya capricornica both states occur.] The tetrasporangia may be attached basally or sub-basally (plesiomorphic state), laterally (a condition found among certain members of the Dumontieae and derived from the sub-basal condition), or intercalarly (a condition diagnostic of the genus Dilsea and apparently derived from the lateral condition). The cladogram in Fig. 91 suggests either an independent origin of intercalary tetrasporangia in the two species of Dilsea or a reversal of the intercalary state back to the lateral state in the more advanced
species of Neodilsea.

**Spore germination pattern** (Character 45). Based on outgroup comparison, Farlowia, Pikea, and all species of Dudresnaya that have been examined display the plesiomorphic diprotocellular spore germination pattern. The immediate discal type of spore germination has been observed in Constantinea and in all species of the Dumontieae that have been studied. The germination pattern appears to be correlated with spore size; all species with relatively large spores possess the immediate discal pattern. The maintenance of this pattern in species of Dilsea and Neodilsea with spores no larger than some species of Dudresnaya suggests a genetic basis for this character state in at least part of the family. This character has a consistency index of 50.00.

**Non-coded characters.** A number of additional characters, not included in the phylogenetic analysis for one reason or another (e.g., uncertainties in occurrence or in coding), may shed additional light on the affinities of members of the Dumontiaceae.

An absence of hairs has been noted in Dudresnaya capricornica, D. hawaiensis, D. japonica, and D. patula. I did not observe hairs on any species of the Farlowieae. Other authors have noted that the occurrence of hairs may be a reflection of environmental conditions rather than the genetic potentiality of the species. I was therefore reluctant to use this character in the analysis.
The most cryptic species in the family are *Dudresnaya bermudensis*, *D. georgiana*, *D. "hawkesii," D. lubrica*, *D. minima*, *D. peggiana*, and *D. puertoricensis*. These species are known from relatively few collections (several species from only single collections). What this rarity indicates about these species is difficult to define, but these species do appear to share a natural affinity in the cladogram in Fig. 91. Furthermore, these species are all relatively small; some reach only 2-4 cm in height (*Dudresnaya georgiana*, *D. "hawkesii," D. *minima*, *D. peggiana*, and *D. puertoricensis*), the remaining two species, *D. bermudensis* and *D. lubrica*, reaching 9 and 7 cm, respectively.

The further growth of a differentiated but unfertilized carpogonial branch into a vegetative filament has been noted in a variety of species of the Dumontiaceae. It has also been observed in species of *Helminthocladia* (Doty and Abbott 1961, Womersley 1965). This character was not used in the phylogenetic analysis because of an anticipated high probability of miscoding the character (i.e., confusing not observing it with its non-occurrence) and a possibly high probability of parallel losses.

A thick wall around cells of the auxiliary cell branch has been noted in *Dudresnaya crassa*, *D. hawaiiensis*, *D. japonica*, *Dumontia* spp., and *Dasyphloea insignis*. Although this character may have some phylogenetic utility, the variability seen in *Dudresnaya hawaiiensis* from different localities suggests that it is not altogether reliable. I therefore excluded it from the analysis.
For most species examined, the diameter of connecting filaments was 5 μm or less. Connecting filaments to 7 μm in diameter were observed in *Dudresnaya lubrica* and to 8 μm in *D. hawaiiensis* and *D. patula*. In the Dumontieae, only *Dilsea carnosa*, *D. californica*, and *Neodilsea yendoana* have connecting filaments reaching 9 or 10 μm in diameter. In the Farlowieae, however, enlarged connecting filaments appear to be characteristic of *Orculifilum* (to 14 μm), *Leptocladia*, *Weeksia*, and *Constantinea* (12 μm) although in the last species, the connecting filaments are usually much narrower.

A protrusion of the auxiliary cell toward a passing connecting filament was observed in *Farlowia mollis*, *Leptocladia binghamiae*, *Weeksia digitata*, and possibly *Dumontia contorta* and *Neodilsea borealis*. Insufficient observations of imminent contact of the connecting filament and the auxiliary cell in most species of the Dumontiaceae make it impossible to ascertain the distribution of this character state or possible variations on it in the family.

Color was not regarded as a reliable character for many of the species studied because I observed many species only in a dried or pickled state. However, among the species of *Dilsea* and *Neodilsea* two apomorphic conditions were recognized as derived from the plesiomorphic maroon of "*Farlowia*" *irregularis*. These conditions were the brownish red of *N. natashae* and the carmine red of *N. borealis* and *N. tenuipes*.

TAXONOMIC CONCLUSIONS

The cladistic analysis in Fig. 91 generally supports the
character polarization based on outgroup comparison. These results suggest that the ancestor of the Dumontiaceae was multiaxial, with narrow, poorly differentiated axial filaments, small pit connections, narrow rhizoidal filaments, irregularly branched, possibly pseudodichotomous assimilatory filaments of cylindrical cells lacking hexagonal crystals, secondary pit connections, and a cuticle. The results are ambiguous as to whether the ancestor was terete or slightly flattened. The ancestor was probably ephemeral; it occurred subtidally in the tropics and the bisexual gametophytic thalli probably alternated with a heteromorphic tetrasporophyte with small, lateral, basally attached, cruciate tetrasporangia. Carpogonial branches were probably of variable length, relatively straight, and with terminal cells little differentiated from other branch cells. Cell 3 was probably smaller than adjacent cells. The carpogonium terminated distally in a long, straight trichogyne. Spermatangia occurred in double whorls around spermatangial mother cells. Following fertilization, the carpogonium divided transversely and the filaments that developed after fusion to cells of the carpogonial branch were proximally septate but distally nonseptate. It is unclear whether the auxiliary cell of the ancestor was a cell differentiated from neighboring cells. At any rate, the auxiliary cell occurred near the base of a branch somewhat differentiated from other assimilatory filaments. Enlargement of pit connections in the auxiliary cell branch did not exceed 5 μm, and fusions between cells of the auxiliary cell branch or between cells of the gonimoblast were lacking. The carposporangia were small. It is uncertain
whether involucral filaments subtended the auxiliary cell. Spores germinated in a diprotocellular pattern.

The character state transitions that occur in the initial dichotomy of the cladogram, leading either to Gibsmithia or to the remaining taxa in the family, are candidates for considering polarization reversal for the family (i.e., if the polarities of the binary characters that appear here are reversed, a cladogram of identical length and topology is produced, but the character state transitions would appear on the segments of the dichotomy opposite where they now appear). One must therefore entertain the notion that the ancestor of the Dumontiaceae may have been somewhat flattened, with a perennial phenology, an alternation of isomorphic generations, carposporogial branches over 12 cells in length, a differentiated auxiliary cell, and no involucrudeveloping from cells subtending the auxiliary cell.

Character state changes that occurred during the evolution of the family were noted in the preceding section. The changes produced a family of extreme vegetative diversity and rather monotonous reproductive uniformity—at least in the female reproductive structures and post-fertilization events.

Most vegetative features and some reproductive ones are not unique to the family: Thalli are uniaxial or multiaxial, crustose or upright, terete or slightly to distinctly flattened, branched or unbranched. Tetrasporophytes are heteromorphic or isomorphic with gametophyte, or absent. Tetrasporangia are cruciate, zonate, or intermediate in shape; bisporangia are present in at least one species. Sexual thalli are bisexual, unisexual, or both bisexual and unisexual. Carpogonia terminate
long, separate filaments of differentiated cells. Following fertilization, the carpogonium may or may not divide.

Most other female reproductive structures and post-fertilization events are diagnostic of the family: The cell(s) derived from the fertilized carpogonium fuse(s) with usually cells 4 and 5 of the carpogonial branch; they initiate long, sometimes proximally septate but distally nonseptate connecting filaments that grow through the thallus. Adjacent to an auxiliary cell on a separate, differentiated filament, the connecting filament divides, the distal segment grows onward to locate other auxiliary cells, and the proximal segment fuses with the auxiliary cell. The diploid nucleus remains in the connecting filament segment attached to the auxiliary cell and can initiate one or more additional connecting filaments and 2-5 gonimoblast initials. The gonimoblast initials divide to produce a relatively large cluster of cells, most of which mature into carposporangia.

J. Agardh (1876:250) included three tribes in the Dumontiaceae, the Cryptosiphonieae, the Dumontieae (this name was originally used by J. Agardh 1852:348 but in a much different context), and the Farlowieae. He included Cryptosiphonia, Pikea, and Dasyphloea (as Nizzophloea?) in the Cryptosiphonieae; he described the Cryptosiphonieae as [in translation], "a tubular or filled frond, with a monosiphonous axial filament supporting the outer layer; with cystocarps often occurring in their own, barely-modified branches." The Dumontieae included Dumontia and Halosaccion and was described also as a tubular frond, but "with anastomosing filaments more
sparse and running around the empty inner space with no central siphon." Finally, he described the Farlowieae as "frond filled with very dense interior filaments, with no axial siphon of its own; with the cystocarps formed within the frond;" he included Farlowia and Sarcophyllis in the Farlowieae.

I have chosen to resurrect and redefine two of J. Agardh's tribes for the two distinct evolutionary lineages that encompass the relatively advanced species of the Dumontiaceae. The Dumontieae is distinguished as follows:

Thallus terete or compressed, branching radial or distichous-flabellate, or unbranched and foliose, uniaxial, multiaxial, or transitional in axiality. Cells of whorl branches dividing in an alternate anticlinal/periclinal sequence, or in a pattern derived from this sequence. Trichogyne spiralled basally and, in some genera, attached laterally. Distal cells of carpogonial branch round or oblong-cuneate. Following fertilization, the carpogonium does not necessarily divide; one or two carpogonial fusion cells are formed. Involucre present (absent in Dumontia and Dasyphloea). Carposporangia and tetrasporeangia relatively large, or smaller but derived from larger ones. Carpospores released by erosion of distal end of thallus; ostiole absent. Tetrasporeangia cruciately divided (zonate in Dasyphloea). Spore germination immediate distal type. Alternate generations ismorphic.

Although most of the analyses I performed suggested that the genus Dumontia is the sister group of the remaining members of the tribe and hence could be segregated into a tribe of its own, I have tentatively chosen to include Dumontia with the
remaining genera to avoid an unnecessary multiplication of subfamilial categories. The Tribe Cryptosiphonieae remains available to accept the remaining genera should subsequent studies favor the segregation of Dumontia from the other genera. Both options produce monophyletic groups. The Tribe Dumontieae, as reconstructed, contains Dumontia, Dasyphloea, Cryptosiphonia, Hyalosiphonia, "Farlowia" irregularis, Dilsea, and Neodilsea. The apparent paraphyly within the Dilsea-Neodilsea complex was not resolved in this study.

The tribe Farlowieae is characterized as follows:

Thallus terete or compressed, branching distichous or unbranched and foliose; uniaxial, multiaxial, or transitional in axiality. Cells of whorl branches producing upwardly sweeping branches from which laterals develop abaxially, or a condition derived from this pattern. Trichogyne terminal. Distal cells of carposgonial branches oblong-cuneate, elongate (humerus-like), or distinctly lobed. Following fertilization, the carposgonium divides to form two fusion cells, or a condition modified from this (formation of a single fusion cell). Involucre absent. Carpospores released by erosion of distal end of thallus, or ostiole present. Carposporangia and tetrasporangia small (large only in Constantinea). Tetrasporangia zonately divided (cruciate in Pikea and Weeksia, unknown in Orculifilum). Spore germination diprotocellular type (immediate discal type only in Constantinea). Alternate generations heteromorphic or isomorphic.

As reconstructed, the Tribe Farlowieae contains Farlowia (excluding Farlowia irregularis), Pikea, Orculifilum,
Leptocladia, Weeksia, and Constantinea.

Subgroups of both the Dumontieae and the Farlowieae have been recognized as distinct families in the past. Bert (1965) recognized the Dilseaceae, in which he included only Dilsea and Neodilsea, on the basis of the distinct multiaxial habit of these two genera. Abbott (1968) described the Weeksiaeae on the basis of the purportedly nonfunctional auxiliary cell branches and included in it Weeksia, Leptocladia, and Constantinea. Although the present analysis supports the monophyletic character of these two groups of genera, it demonstrates that to recognize these groups at either the family or tribal level would create paraphyly in the Dumontiaceae.

The cladogram in Fig. 91 suggests that both the Farlowieae and the Dumontieae have arisen from species of Dudresnaya although possibly from different ancestors within Dudresnaya. These results indicate that Dudresnaya is paraphyletic and suggests the need for dividing the genus into monophyletic subunits. I prefer to refrain from erecting tribes for the remaining species in the family until a better supported cladogram for these more primitive taxa has been obtained and more natural supraspecific taxa have been established.

In addition to producing a hypothesis of phylogenetic relations (Fig. 91), this study has also dealt with other systematic and some taxonomic issues in the family. Table VII lists the species that I recognize as members of the Dumontiaceae. Changes made by this study include the removal of the genera Acrosymphyton and Neoabbottiella from the family, the reinstatement of Neodilsea integra in Dilsea, the synonymization
of *Thuretellopsis* with *Dudresnaya*, the recognition of "*Farlowia* irregularis" as representing a distinct genus, the raising of *Neodilsea integra* var. *longissima* to specific rank, the discovery of older specific names for *Neodilsea americana* and *Weeksia fryeana*, the description of a new genus and species, and suggested synonymization of *Thuretellopsis japonica* with *Dudresnaya minima*, *Farlowia compressa* with *F. mollis*, *Pikea robusta* with *P. californica*, *Weeksia digitata* with *W. reticulata* and possibly both of these species of *Weeksia* with *W. coccinea*.

**BIOGEOGRAPHY**

The Dumontiaceae is primarily a family of the Pacific basin. Species from the Atlantic and adjoining seas are clearly derived from Pacific taxa. To date, records from the Indian Ocean are those of Pacific species, and these records are so far limited to southern and western Australia. The Dumontiaceae is conspicuously absent from the northern and western Indian Ocean.

The Dumontiaceae appears to have originated in the southwestern Pacific Ocean based on the occurrence of the putatively mostly primitive members of the family there—*Gibsmithia hawaiiensis*, *Gibsmithia* sp. from the Great Barrier Reef, *Kraftia dichotoma*, and *Dudresnaya hawaiiensis*. Early radiation from this area appears to have been northward and eastward. *Dudresnaya japonica* and *Dudresnaya "hawkesii"* represent possible vicariants of *D. hawaiiensis* to the north and the south, respectively. *Dudresnaya patula* also appears to be a product of an early eastward radiation, and much subsequent diversification of the genus has occurred in the eastern
Pacific-western Atlantic region. *Dudresnaya colombiana*, e.g., may represent the Pacific vicariant of the Atlantic *D. patula*. *Dudresnaya bermudensis, D. puertoricensis* (both western Atlantic species) and *D. lubrica* (a Hawaiian species) show affinities, as do *D. georgiana* (western Atlantic) and *D. peggiana* (northeast Pacific). The biogeographic pattern represented by the remaining species of *Dudresnaya* is unclear. *Dudresnaya crassa* and *D. verticillata* may represent western Atlantic and eastern Atlantic vicariants, respectively, but their putative relationships with the distinctly Australian *D. capricornica* and *D. australis* are difficult to explain biogeographically.

The species of the Farlowieae and the Dumontieae also reflect the Pacific basin bias of the Dumontiaceae, but they show centers of diversification on opposite sides of the N Pacific—the Farlowieae reaches its greatest diversity in the eastern N Pacific, the Dumontieae in the western N Pacific.

The Farlowieae includes a single biogeographic outlyer, *Pikea californica*, from the Scilly Isles off the SW coast of England. Although it is possible that this occurrence marks a recent introduction, it appears equally likely that this N Atlantic disjunction represents the remnants of an archaic panboreal distribution of the species, a distribution that was interrupted by the continued cooling of the Arctic, the N Pacific and the N Atlantic since at least the Miocene. The three currently disjunct populations (in SW England, central Japan, and western North America) of what has been recognized as a single species may have been produced in such a manner. Whether these three populations have maintained their genetic
integrity and can still interbreed has not been addressed. [This problem may not be amenable to solution through intraspecific crosses since Chihara (1972) has observed direct development of gametophytes upon germination of carpospores in Japanese material.]

The remaining genera in the Farlowieae are restricted to the Pacific. Farlowia mollis, like Pikea californica, has been found on both sides of the N Pacific. In Japan it exhibits a more northerly distribution than P. californica, but in the eastern N Pacific the two species have essentially identical distributions, from Baja California, Mexico, to Prince William Sound, Alaska. Here again the cooling of the N Pacific during the Cenozoic appears to be responsible for the observed disjunction.

With the exception of Constantinea, two species of which are distributed in a non-disjunct manner, from western North America to northern Japan, the remaining species of the Farlowieae are eastern Pacific endemics. Farlowia conferta is restricted to the southern Oregon to central California coast. Orculifilum denticulatum is known only from near Juneau, Alaska. Leptocladia spp. occur from southern California south to Peru, and Weeksia spp. from Baja California, Mexico, north to Southeast Alaska. The species of Constantinea occur from central California to northern Japan—all three apparently occur along the coast of Alaska.

It is unclear what vicariant events might be invoked to explain the patterns of distribution of Constantinea, Weeksia, Leptocladia, and Orculifilum. One is tempted to point out
possible vicariant pairs in *Orculifilum denticulatum* and *Leptocladia binghamiae*, *Leptocladia* spp. and *Weeksia* spp., *Leptocladia* spp. and *Constantinea* spp., *Constantinea simplex* and *C. rosa-marina*, and *C. simplex* and *C. subulifera*. However, since all these speciation events appear to be restricted to the eastern N Pacific, no obvious mechanism of lineage splitting is evident. In *Constantinea* at least, it is possible that episodes of Pleistocene glaciation segregated populations into eastern and western N Pacific pairs that have extended their ranges to overlap their congeners during interglacial periods.

In contrast to the Farlowieae, whose center of distribution is the eastern N Pacific, the Dumontieae has a center of distribution in the western N Pacific. In the eastern N Pacific, none of the species extends further south than San Pedro, California. Both species of *Dumontia* occur in the western N Pacific eastward to the Alaska Panhandle. The occurrence of *D. contorta* in the N Atlantic is believed to represent a vestige of an earlier continuous distribution through the Arctic, a distribution that was disrupted perhaps less than a million years ago, as a permanent ice sheet formed over the polar sea. It is possible that *Dumontia contorta* and *Cryptosiphonia* represent a western and an eastern N Pacific vicariant pair. It is also possible that *Hyalosiphonia* and *Cryptosiphonia* represent such a pair. The origin of *Dasyphtloe* remains problematical because of its southern Australian endemism. The species pairs *Hyalosiphonia caespitosa-*"Farlowia"* irregularis* and *Dumontia simplex*- *Dumontia contorta* may represent vicariant pairs derived from a period in which the Sea of Japan was separated from the N
Pacific. The first species of each species-pair shows a more southwesterly distribution than the second species. A similar vicariant event, this time involving the Sea of Japan or possibly the Okhotsk Sea and the N Pacific, has been hypothesized for the species-pair Neodilsea crispata and N. longissima. At some point in the history of the Dilsea-Neodilea complex, an extension of the range of one of the species occurred, leading to its expansion from the western N Pacific into the eastern N Pacific, the Arctic, and the Atlantic. Although distinct species have been described from each of these areas—Neodilsea yendoana, Dilsea californica, D. integra, and D. carnosa, the exact relationship of these taxa to each other, particularly of D. integra to the other two species of Dilsea, needs to be studied in more detail. The phylogenetic analysis is ambiguous about the relationships of these species to each other. Neodilsea borealis and N. tenuipes appear to represent an eastern and western N Pacific vicariant pair. Neodilsea natashae may vicariate with N. yendoana or D. californica or their common ancestor on the one hand and with N. tenuipes, N. borealis, or their ancestor on the other.

**SOME FURTHER THOUGHTS**

Further reflection on characters used in the cladistic analysis, on some of those not used, and on the biogeography of the species in the family suggest several areas of the cladogram that need to be investigated more thoroughly.

*Dudresnaya lubrica* resembles *Gibsmithia hawaiiensis* in a number of characters. In addition to several symplesiomorphies
(relatively short carpogonial branches, involucral filaments), both have relatively small terminal cells on assimilatory filaments, and both show a somewhat lateral attachment of the trichogyne. Both species occur on Oahu, Hawaiian Is., where they are represented by unisexual thalli. A more detailed examination of the similarities and differences between these two species is needed.

The position of *Dudresnaya capricornica* in the cladistic analysis is biogeographically anomalous. Although it appears to share a suite of synapomorphies with *D. verticillata*, *D. crassa*, and *D. australis* (viz., large rhizoids, hexagonal crystals, relatively small, terminal, zonate tetrasporangia), it also shares some derived character states with *D. hawaiiensis* (sparse branching of assimilatory filaments, elongate terminal cells of assimilatory filaments, spermatangia in double whorls). Biogeographically, it fits better with *D. hawaiiensis* than where the analysis places it. A similar argument might be made for *D. australis* and other western Pacific congeners. The similarities of *D. crassa* to *D. hawaiiensis* and *D. japonica* (enlarged cells distal to the auxiliary cell, thick wall around the auxiliary cell branch) suggest the need for further critical examination of these species as well.

The affinities of the Dumontieae are problematical. *Dumontia* itself has a number of distinctive attributes (e.g., multiaxial origin of the flattened thallus from a group of filaments, very short reproductive filaments) that exacerbate its placement within the family. *Dasyploea*, with its alternation of isomorphic gametophytic and tetrasporophytic
generations, the latter with zonate tetrasporangia, and with its austral distribution evokes a question of its possible relationship with *D. australis*. This region of the cladogram also requires further investigation.

CONCLUSION

I have argued above that the Dumontiaceae is best understood as a direct descendant of a helminthocladean ancestor. The final question I will address is whether the Dumontiaceae (or any of its members, past or present) can be viewed as ancestral to any known genus, family, or order of red algae not in the Dumontiaceae. The Rhodymeniales and most families of the Cryptonemiales and Gigartinales can be immediately excluded from consideration because of lack of synapomorphies—these families are multiaxial, have short carpogonial branches that do not divide into two cells after fertilization, both cells initiating connecting filaments after contacting other cells of the carpogonial branch. In these other families, gonimoblast filaments are initiated from a single gonimoblast initial cut off by an auxiliary cell and/or the auxiliary cell is a primary cell of an pseudoparenchymatously constructed thallus. Although the most primitive members of the Ceramiaceae bear some vegetative resemblance to some of the more advanced species of *Dudresnaya*, details of reproductive structures and post-fertilization events provide no synapomorphies, and other characters (e.g., bipolar spore germination in the Ceramiales) also support independent origins for these two families.
A striking similarity to species of the Dumontiaceae is shown by \textit{Polyides rotundus} (Hudson) Greville. Like some of the more primitive Dumontiaceae, \textit{Polyides} has an undifferentiated multiaxial structure. Although male and female reproductive structures occur in nemathecia, the female reproductive organs in particular resemble equivalent structures in the Dumontiaceae: The carpogonium occurs somewhat laterally on a relatively long branch of 8-14 cells. Cells of the branch are differentiated from nonreproductive filaments and are filled with floridean starch or are birefringent; they can become multinucleate (Rao 1956). As has also been noted in the Dumontiaceae, the trichogyne can begin to develop before the carpogonium is separated from the hypogynous cell. The trichogyne can spiral basally and can become relatively long; it persists after fertilization.

Post-fertilization development in \textit{Polyides} is somewhat different from the Dumontiaceae. As in the Dumontiaceae, division of the fertilized carpogonium and fusion with cells 4 and 5 or cells 4 and 6 have been observed (Rao 1956: Figs. 4A and B). Rao noted that only 12 such fusions were seen, the more usual event being direct connecting filament production by the carpogonium. Rao believed the fusions to occur secondarily, i.e., after initial connecting filament production. In contrast to the Dumontiaceae, the connecting filament is septate. Although gonimoblast initiation occurs from the connecting filament in contact with an auxiliary cell (as in the Dumontiaceae), only a single gonimoblast initial produces each cystocarp, and connecting filament segments not in direct
contact with auxiliary cells can also initiate gonimoblast filaments. The nuclei and pit connections of cells in the auxiliary cell branch increase in size, and nuclei can increase in number during carposporophyte development. As in the Dumontiaceae, cystocarps are relatively large, to 300 μm in diameter. Carposporangia are of moderate size, 20-35 μm in diameter by 45-50 μm long (Dixon and Irvine 1977:180). The cruciate tetrasporangia, 35-55 μm by 700-100 μm, resemble those of species of the Dumontieae.

Although the similarities between Polyides and members of the Dumontiaceae are striking, most of these character states appear to be plesiomorphic. This result suggests that Polyides might be better viewed as a member of a sister-group to the Dumontiaceae or as part of a group that arose parallel to the Dumontiaceae from closely related taxa within the Helminthocladiaceae.

Polyides is part of a group of species comprising the families Polyidaceae, Peyssonneliaceae, and Rhizophyllidaceae. These families are united by the production of reproductive structures in nemathecia. In most species, spermatangia are cut off laterally from cells of special filaments. Rhodopeltis in particular bears a striking resemblance to the helminthocladean genus Yamadaella. Both are calcified, and calcification is also observed among most species of Peyssonnelia. However, calcification appears to be absent (lost?) in Polyides, species of Rhizophyllidaceae, and some species of Peyssonnelia. Post-fertilization development usually involves the fusion of an outgrowth of the carpogonium with a subtending cell of the
carpogonial branch prior to connecting filament production. Gonimoblast filaments arise directly from the connecting filament, either near its point of contact with an auxiliary cell or at some distance. Segmentation of the connecting filament in conjunction with auxiliary cell contact appears to occur in at least some of the species (Nozawa 1970: Fig. 4A).

The apparent phylogenetic separation of the Dumontiaceae from the remaining families of the Cryptonemiales and Gigartinales, except perhaps the Peyssonneliaceae, Polyidaceae, and Rhizophyllidaceae, is not an entirely unexpected conclusion. The restricted geographic distribution of the family, including even its primitive members, speaks for a relatively recent origin, an origin too recent to allow the Dumontiaceae a place in the phylogenetic development of such widely distributed families as the Cryptonemiaceae, Kallymeniaceae, or Nemastomataceae. In fact, one gets the distinct impression that the Dumontiaceae merely represents the latest of many nemalialean-derived families that have evolved higher forms of vegetative and reproductive development.
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Table I. Species currently recognized as members of the Dumontiaceae.

Acrosymphyton caribaeum (J. Agardh) Sjoestedt 1926:9
A. firmum Hawkes 1982:448
A. purpuriferum (J. Agardh) Sjoestedt 1926:9
A. taylori Abbott 1962:845
A. tenax Millar et Kraft 1984:140

Constantinea rosa-marina (Gmelin) Postels et Ruprecht 1840:17
C. simplex Setchell 1901:127
C. subulifera Setchell 1906:172

Cryptosiphonia woodii (J. Agardh) J. Agardh 1876:251

Dasyphloea insignis Montagne 1842:8

Dilsea californica (J. Agardh) Kuntze 1891:892
D. cariosa (Schmidel) Kuntze 1898:404

Dudresnaya australis Setchell 1912:245
D. bermudensis Setchell 1912:244
D. capricornica Robins et Kraft 1985:23
D. colombiana Taylor 1945:162
D. crassa Howe 1905:572
D. georgiana Searles 1983:309
D. hawaiiensis R. K. S. Lee 1963:315
D. japonica Okamura 1908:209
D. lubrica Littler 1974:149
D. minima Okamura 1932:86
D. patula Eiseman et J. N. Norris 1981:188
D. verticillata (Withering) LeJolis 1863:117

Dumontia contorta (Gmelin) Ruprecht 1851:295
D. simplex Cotton 1906:372

Farlowia compressa J. Agardh 1876:262
F. conferta (Setchell) Abbott 1968:186
F. irregularis Yamada 1933:280
F. mollis (Harvey et Bailey) Farlow et Setchell 1901:898

Gibsmithia hawaiiensis Doty 1963:458

Hyalosiphonia caespitosa Okamura 1909:51

Kraftia dichotoma Shepley et Womersley 1983:209

Leptocladia binghamiae J. Agardh 1892:96
L. peruviana Howe 1914:176

Neoabbottiella araneosa (Perestenko) Lindstrom 1985:264

Neodilsea americana Abbott 1968:187
N. crispata Masuda 1973:37
N. integra (Kjellman) Zinova 1961:84
N. natashae Lindstrom 1984:29
N. tenuipes Yamada et Mikami in Mikami 1954:83
N. yendoana Tokida 1943:96

Pikea californica Harvey 1853:246
P. robusta Abbott 1968:184

Thuretellopsis japonica Segawa et Ichiki 1958:5
T. peggiana Kylin 1925:13

Weeksia digitata Abbott 1968:191
W. fryeana Setchell 1912:254
W. howelli Setchell et Gardner 1937:77
W. reticulata Setchell 1901:128
Table II. Comparison of characters of four species of *Weeksia* (based on Abbott 1968).

<table>
<thead>
<tr>
<th></th>
<th><em>W. reticulata</em></th>
<th><em>W. fryeana</em></th>
<th><em>W. howellii</em></th>
<th><em>W. digitata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Size</strong></td>
<td>to 20 cm</td>
<td>15-30 cm broad</td>
<td>20-30 cm high</td>
<td>60 cm high</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15-60 cm high</td>
<td></td>
<td>segments 3-15 cm across</td>
</tr>
<tr>
<td><strong>Habit</strong></td>
<td>in cabbage-like</td>
<td>---</td>
<td>elongate to orbiculate</td>
<td>dissected</td>
</tr>
<tr>
<td></td>
<td>cluster, reniform</td>
<td></td>
<td>to rounded</td>
<td></td>
</tr>
<tr>
<td><strong>Color</strong></td>
<td>Magenta to Schoenfeld purple</td>
<td>Rose red to Geranium purple</td>
<td>---</td>
<td>Corinthian red to Mars violet</td>
</tr>
<tr>
<td><strong>Veins</strong></td>
<td>basally prominent, can run to margins</td>
<td>absent</td>
<td>absent</td>
<td>basally</td>
</tr>
<tr>
<td><strong>Transverse section</strong></td>
<td>250-400 (500)</td>
<td>200-300</td>
<td>150-200 (dried)</td>
<td>300-350 μm</td>
</tr>
<tr>
<td><strong>Cortex</strong></td>
<td>3-5</td>
<td>---</td>
<td>3-4</td>
<td>4-5 cell layers</td>
</tr>
<tr>
<td><strong>Carpogonial branch</strong></td>
<td>8-15</td>
<td>10-12</td>
<td>7-9</td>
<td>8-10 cells long</td>
</tr>
<tr>
<td><strong>Cystocarps</strong></td>
<td>---</td>
<td>79-100</td>
<td>60-70</td>
<td>120 μm in diameter</td>
</tr>
<tr>
<td><strong>Tetrasporangia</strong></td>
<td>10 x 15</td>
<td>---</td>
<td>18-20 x 26-30</td>
<td>8 x 16 μm</td>
</tr>
<tr>
<td><strong>Texture</strong></td>
<td>soft</td>
<td>filmy</td>
<td>---</td>
<td>rather firm</td>
</tr>
<tr>
<td><strong>Sexuality</strong></td>
<td>bisexual</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>Spermatangia</strong></td>
<td>1-2 x 3-4 μm</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table III. Comparison of sizes (in micrometers) of spores and sporangia in Dilsea and Neodilsea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Tetrasporangia</th>
<th>Tetraspores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>This study</td>
<td>Other studies</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td><em>D. californica</em></td>
<td>21-45x51-78</td>
<td>34x64</td>
</tr>
<tr>
<td><em>D. carnosa</em></td>
<td>42-80x52-100</td>
<td>52x76</td>
</tr>
<tr>
<td><em>N. borealis</em></td>
<td>15-30x26-58</td>
<td>22x45</td>
</tr>
<tr>
<td><em>N. crispata</em></td>
<td>32-57x42-78</td>
<td>42x59</td>
</tr>
<tr>
<td><em>N. longissima</em></td>
<td>25-30x38-51</td>
<td>27x45</td>
</tr>
<tr>
<td><em>N. natashae</em></td>
<td>15-28x38-48</td>
<td>22x42</td>
</tr>
<tr>
<td><em>N. tenuipes</em></td>
<td>17-35x32-54</td>
<td>24x42</td>
</tr>
<tr>
<td><em>N. yendoana</em></td>
<td>24-36x50-70</td>
<td>30x58</td>
</tr>
</tbody>
</table>

Carpospores/carposporangia

<table>
<thead>
<tr>
<th>Species</th>
<th>This study</th>
<th>Other studies</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. californica</em></td>
<td>25</td>
<td></td>
</tr>
<tr>
<td><em>D. carnosa</em></td>
<td>to 80</td>
<td></td>
</tr>
<tr>
<td><em>N. borealis</em></td>
<td>to 28</td>
<td></td>
</tr>
<tr>
<td><em>N. crispata</em></td>
<td>to 55</td>
<td></td>
</tr>
<tr>
<td><em>N. longissima</em></td>
<td>to 50</td>
<td>34</td>
</tr>
<tr>
<td><em>N. natashae</em></td>
<td>to 40</td>
<td></td>
</tr>
<tr>
<td><em>N. tenuipes</em></td>
<td>to 28</td>
<td>32-34</td>
</tr>
<tr>
<td><em>N. yendoana</em></td>
<td>28</td>
<td>34</td>
</tr>
</tbody>
</table>

1 Abbott 1968
2 Masuda 1973a
3 Masuda 1982
4 Masuda 1973b
5 Masuda 1974
6 Tokida 1943
Table IV. Characters and their coded states for the 45 characters used to construct a hypothesis of phylogenetic relationships among the species and genera of the Dumontiaceae.

<table>
<thead>
<tr>
<th>Char. Character No.</th>
<th>Character Name</th>
<th>Character Code and States</th>
<th>Polarization Rationale</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Axiality</td>
<td>0: Multiaxial</td>
<td><em>OG, IG¹-³, OC</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Uniaxial</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2: Uniaxial-multiaxial (&quot;F.&quot; irregularis)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3: Multiaxial (Dilsea, Neodilsea)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Axis organization</td>
<td>0: No obvious organization</td>
<td><em>OG, IG¹-³, OC</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Axial file recog. 20-30 cells from apex</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2: Axial file recog. w/i 5-15 cells of apex</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3: Apical cell present; cells enlarge 5-10 cells from apex</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>4: Apical cell present; cells enlarge 10-15 cells from apex</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>5: Apical cell present; cells enlarge more than 20 cells from apex</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Maximum axial cell diam.</td>
<td>0: Less than 100 µm</td>
<td><em>OG, IG¹-³</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Greater than 100 µm</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Pit connections between axial cells</td>
<td>0: Small, less than 10 µm</td>
<td><em>OG, IG¹-⁷</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Medium, 10-25 µm</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2: Large, greater than 50 µm</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Maximum rhizoid diameter</td>
<td>0: Less than 15 µm</td>
<td><em>OG, IG¹-³</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: 15-40 µm</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2: Greater than 40 µm</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Assimilatory filaments from rhizoids</td>
<td>0: Absent</td>
<td><em>OG, IG¹-³</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Present</td>
<td></td>
</tr>
</tbody>
</table>

*OG refers to the taxonomic outgroup (the Helminthocladiaceae); IG¹-n refers to species of the Dumontiaceae used as functional outgroups as they are numbered in Table V; OC refers to a recognized developmental trend.*
<table>
<thead>
<tr>
<th></th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>Branching of whorl branches-I</td>
<td>0: Pseudodichot., irreg., other OG, IG^1-17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Anticlinal/periclinal</td>
</tr>
<tr>
<td>8</td>
<td>Branching of whorl branches-II</td>
<td>0: Pseudodichot., irreg., other OG, IG^1-17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Upward sweep</td>
</tr>
<tr>
<td>9</td>
<td>Annulations</td>
<td>0: Absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Present</td>
</tr>
<tr>
<td>10</td>
<td>Branching of outer cortical cells</td>
<td>0: Moderate to abundant OG, IG^1-3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Sparse</td>
</tr>
<tr>
<td>11</td>
<td>Whorl br. terminal cells</td>
<td>0: 2-5 by 8-24 μm</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: (2-) 3-7 by (3-) 4-10 (-11) μm</td>
</tr>
<tr>
<td>12</td>
<td>Whorl br. intermed. cells</td>
<td>0: Cylindrical/cuneate IG^1,2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Forked</td>
</tr>
<tr>
<td>13</td>
<td>Hexagonal crystals</td>
<td>0: Absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Present</td>
</tr>
<tr>
<td>14</td>
<td>Habit</td>
<td>0: Cylindrical, branched OG</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Somewhat flattened, branched</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2: Distinctly flattened, branched</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3: Distinctly flattened, unbranched (blade)</td>
</tr>
<tr>
<td>15</td>
<td>Secondary pit connections</td>
<td>0: Absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Present</td>
</tr>
<tr>
<td>16</td>
<td>Cuticle</td>
<td>0: Absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Present</td>
</tr>
<tr>
<td>17</td>
<td>Phenology</td>
<td>0: Ephemeral/annual</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Perennial</td>
</tr>
<tr>
<td>18</td>
<td>Habitat</td>
<td>0: Strictly subtidal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Low intertidal/upper subtidal</td>
</tr>
<tr>
<td></td>
<td>Term</td>
<td>0:</td>
</tr>
<tr>
<td>---</td>
<td>-------------------------------</td>
<td>---------------------------------</td>
</tr>
<tr>
<td>19</td>
<td>Temperature zone</td>
<td>Tropical/subtropical</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cool temperate</td>
</tr>
<tr>
<td>20</td>
<td>Life history</td>
<td>Heteromorphic</td>
</tr>
<tr>
<td>21</td>
<td>Sexuality</td>
<td>Bisexual</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Strictly unisexual</td>
</tr>
<tr>
<td>22</td>
<td>Carpogonial branch max. length</td>
<td>11 cells or less</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>Carpogonial branch cell shape</td>
<td>Cylindrical/quadrate</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Carpogonial branch curv.</td>
<td>Relatively straight</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Carpogonial branch cell 2 size</td>
<td>Larger than cell 3</td>
</tr>
<tr>
<td>26</td>
<td>Trichogyne shape</td>
<td>Straight</td>
</tr>
<tr>
<td>27</td>
<td>Trichogyne attachment</td>
<td>Distal</td>
</tr>
<tr>
<td>28</td>
<td>Spermatangia</td>
<td>Double whorls</td>
</tr>
<tr>
<td>29</td>
<td>Carp. division after fertilization</td>
<td>Transverse</td>
</tr>
<tr>
<td>No.</td>
<td>Description</td>
<td>0: Present</td>
</tr>
<tr>
<td>-----</td>
<td>-------------------------------------------------</td>
<td>--------------------------</td>
</tr>
<tr>
<td>30</td>
<td>Connecting filament segmentation</td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>Differentiated aux. cell</td>
<td>0: Present</td>
</tr>
<tr>
<td>32</td>
<td>Enlarged auxiliary cell</td>
<td>0: Usually less than 10 μm</td>
</tr>
<tr>
<td>33</td>
<td>Aux. cell position</td>
<td>0: More than 10 cells from apex</td>
</tr>
<tr>
<td>34</td>
<td>Enlarged cells distal to auxiliary cell</td>
<td>0: Absent</td>
</tr>
<tr>
<td>35</td>
<td>Enlarged pit connections in aux. cell branch</td>
<td>0: Less than 5 μm</td>
</tr>
<tr>
<td>36</td>
<td>Auxiliary cell branch cell fusions</td>
<td>0: Absent</td>
</tr>
<tr>
<td>37</td>
<td>Involucre</td>
<td>0: Present</td>
</tr>
<tr>
<td>38</td>
<td>Gonimoblast fusion cell</td>
<td>0: Absent</td>
</tr>
<tr>
<td>39</td>
<td>Size of carposporangia</td>
<td>0: Small, less than 30 μm</td>
</tr>
<tr>
<td>40</td>
<td>Ostiole</td>
<td>0: Absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1: Incipient</td>
</tr>
</tbody>
</table>
|     |                                                 | 2: Present               |                          | }
41 Tetrasporangia position

0: Lateral
1: Terminal

42 Tetrasporangia attachment

0: Basal, sub-basal
1: Lateral
2: Intercalary

43 Tetrasporangia division pattern

0: Cruciate
1: Irreg. cruciate/zonate
2: Zonate

44 Tetrasporangia size

0: Small, less than 20 μm
1: Medium, to 25 by 55 μm
2: Large, 58-104 by 77-132 μm
3: Med. large, 35-80 by 52-103 μm
4: Medium, 21-57 by 42-83 μm
5: Med. small, 15-40 by 26-58 μm

45 Spore germination pattern

0: Diprotocellular type
1: Immediate distal type
Table V. Character states for the species and genera of the Dumontiaceae used in the phylogenetic analysis in Fig. 91.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Character Code</th>
</tr>
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<tbody>
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<td>Hypothetical ancestor</td>
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<tr>
<td>Gibsmithia hawaiiensis</td>
<td>000000000012345</td>
</tr>
<tr>
<td>G.B.R. Gibsmithia</td>
<td>000000000012345</td>
</tr>
<tr>
<td>Kraftia dichotoma</td>
<td>000000000012345</td>
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<tr>
<td>Dudresnaya australis</td>
<td>151021001000111</td>
</tr>
<tr>
<td>D. bermudensis</td>
<td>131000000010100</td>
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<tr>
<td>D. capricornica</td>
<td>121021001010000</td>
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<tr>
<td>D. colombiana</td>
<td>930000000011010</td>
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<td>D. crassa</td>
<td>141020001000101</td>
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<tr>
<td>D. georgiana</td>
<td>131021000100000</td>
</tr>
<tr>
<td>D. hawaiiensis</td>
<td>910000000010000</td>
</tr>
<tr>
<td>D. &quot;hawkesii&quot;</td>
<td>140010000010000</td>
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<tr>
<td>D. japonica</td>
<td>920000000010010</td>
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<tr>
<td>D. lubrica</td>
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<tr>
<td>D. patula</td>
<td>920000000010100</td>
</tr>
<tr>
<td>D. peggiana</td>
<td>131011000009000</td>
</tr>
<tr>
<td>D. puertoricensis</td>
<td>130000000011100</td>
</tr>
<tr>
<td>D. verticillata</td>
<td>151021001000000</td>
</tr>
<tr>
<td>Dasyphloea insignis</td>
<td>130100100100000</td>
</tr>
<tr>
<td>Dumontia spp.</td>
<td>030000000100000</td>
</tr>
<tr>
<td>Cryptosiphonia woodii</td>
<td>131200100010000</td>
</tr>
<tr>
<td>Hylasiphonia caespitosa</td>
<td>131090100010000</td>
</tr>
<tr>
<td>&quot;Farlowia&quot; irregularis</td>
<td>239000100010211</td>
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<td>Dilsea carnosa</td>
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<td>D. californica</td>
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<td>Neodilsea crispata</td>
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<td>N. yendoana</td>
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<td>N. borealis</td>
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<td>Farlowia mollis</td>
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<tr>
<td>Conifera</td>
<td>130100100010000</td>
</tr>
<tr>
<td>Pikea californica</td>
<td>131090100010211</td>
</tr>
<tr>
<td>Ocu liliifolium denticulatum</td>
<td>130109100010211</td>
</tr>
<tr>
<td>Leptocladia spp.</td>
<td>130100100010211</td>
</tr>
<tr>
<td>Weeksia spp.</td>
<td>130000010010000</td>
</tr>
<tr>
<td>Constantinea spp.</td>
<td>030000010010000</td>
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</table>
Table VI. Consistency indices for individual characters for the cladogram in Fig. 91.

<table>
<thead>
<tr>
<th>Character</th>
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<th>3</th>
<th>4</th>
<th>5</th>
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<td>100.00</td>
<td>100.00</td>
<td>33.33</td>
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<td>25.00</td>
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<td>50.00</td>
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<td>18</td>
<td>19</td>
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</tr>
<tr>
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<td>25.00</td>
<td>33.33</td>
<td>22.22</td>
<td>20.00</td>
</tr>
<tr>
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<td>24</td>
<td>25</td>
</tr>
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<td>57.14</td>
<td>28.57</td>
<td>20.00</td>
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<td>27</td>
<td>28</td>
<td>29</td>
<td>30</td>
</tr>
<tr>
<td>C-Index</td>
<td>33.33</td>
<td>25.00</td>
<td>33.33</td>
<td>100.00</td>
<td>33.33</td>
</tr>
<tr>
<td>Character</td>
<td>31</td>
<td>32</td>
<td>33</td>
<td>34</td>
<td>35</td>
</tr>
<tr>
<td>C-Index</td>
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<td>100.00</td>
<td>40.00</td>
<td>33.33</td>
<td>28.57</td>
</tr>
<tr>
<td>Character</td>
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<td>37</td>
<td>38</td>
<td>39</td>
<td>40</td>
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<tr>
<td>C-Index</td>
<td>20.00</td>
<td>20.00</td>
<td>57.14</td>
<td>16.67</td>
<td>66.67</td>
</tr>
<tr>
<td>Character</td>
<td>41</td>
<td>42</td>
<td>43</td>
<td>44</td>
<td>45</td>
</tr>
<tr>
<td>C-Index</td>
<td>33.33</td>
<td>66.67</td>
<td>33.33</td>
<td>45.46</td>
<td>50.00</td>
</tr>
</tbody>
</table>
Table VII. Species recognized as members of the Dumontiaceae by this study.

**Constantinea rosa-marina** (Gmelin) Postels et Ruprecht 1840:17
C. *simplex* Setchell 1901:127
C. *subulifera* Setchell 1906:172

**Cryptosiphonia woodii** (J. Agardh) J. Agardh 1876:251

**Dasyphloea insignis** Montagne 1842:8

**Dilsea californica** (J. Agardh) Kuntze 1891:892
D. *carnosa* (Schmidel) Kuntze 1898:404
D. *integra* (Kjellman) Rosenvinge 1898:19

**Dudresnaya australis** Setchell 1912:245
D. *bermudensis* Setchell 1912:244
D. *capricornica* Robins et Kraft 1985:23
D. *coombiana* Taylor 1945:162
D. *crassa* Howe 1905:572
D. *georgiana* Searles 1983:309
D. *hawaiensis* R. K. S. Lee 1963:315
D. *japonica* Okamura 1908:209
D. *lubrica* Littler 1974:149
D. *minima* Okamura 1932:86

Syn.: **Thuretellopsis japonica** Segawa et Ichiki 1958:5
D. *patula* Eiseman et J. N. Norris 1981:188
D. *peggiana* (Kylin) comb. nov.
D. *verticillata* (Withering) LeJolis 1863:117

**Dumontia contorta** (Gmelin) Ruprecht 1851:295
D. *simplex* Cotton 1906:372

F. *conferta* (Setchell) Abbott 1968:186
F. *mollis* (Harvey et Bailey) Farlow et Setchell 1901: 898

"Farlowia" **irregularis** Yamada 1933:280

**Gibsmithia hawaiensis** Doty 1963:458

**Hyalosiphonia caespitosa** Okamura 1909:51

**Kraftia dichotoma** Shepley et Womersley 1983:209

**Leptocladia binghamiae** J. Agardh 1892:96
L. *peruviana* Howe 1914:176

**Neodilsea borealis** (Abbott) Lindstrom 1985:264

Syn.: **N. americana** Abbott 1968:187
N. *crispata* Masuda 1973:37
N. *longissima* (Masuda) Lindstrom 1985:262
N. *natashae* Lindstrom 1984:29
N. *tenuipes* Yamada et Mikami in Mikami 1954:83
N. *yendoana* Tokida 1943:96
Orculifilum denticulatum gen. et sp. nov.

Pikea californica Harvey 1853:246
  Syn.: P. robusta Abbott 1968:184

Weeksia coccinea (Harvey) comb. nov.
  Syn.: W. fryeana Setchell 1912:254
  W. howellii Setchell et Gardner 1937:77
  W. reticulata Setchell 1901:128
    Syn.: W. digitata Abbott 1968:191
  W. templetonii Setchell et Gardner 1937:76
FIGURE ABBREVIATIONS

1,2,3,4... Cell number beginning at distal end of a carpogonial or auxiliary cell branch. Because these reproductive filaments vary in length, counting is done from the less variable end (i.e., the distal end in most species).

ab = auxiliary cell branch
ac = auxiliary cell
af = assimilatory filament
cdc = carpogonial derivative/fusion cell
cf = connecting filament
cp = carpogonium
cs = carposporangium
gf = gonimblast filament
gfc = gonimoblast fusion cell
gi = gonimoblast initial
gic = gonimoblast initiator cell
i = intermediate cell (cell on a periaxial cell bearing both an assimilatory filament and a rhizoid)
ib = involucral branch
icf = incoming connecting filament
l = lateral branch on a reproductive filament
ocf = outgoing connecting filament
pa = periaxial cell
r = rhizoid (secondary medullary filament)
rb = refractive inclusion
smc = spermatangial mother cell
sp = spermatangium
v = vegetative cell
A = axial cell
B = (cell of) abaxial branch
M = (cell of) major whorl branch
N = (cell of) minor whorl branch
Figure 1

Fig. a. Gibsmithia sp. Assimilatory filaments. Reef 7, Great Barrier Reef, Australia, 13 Aug. 1981, 20m, PWG collection.

Fig. b. Gibsmithia hawaiiensis. Assimilatory filaments. Makua Bay, Oahu, Hawaii, 19 Oct. 1969, leg. M. Littler, MML 1020 in US.

Fig. c. Gibsmithia sp. Carpogonial branch in which carpogonium has disintegrated (former attachment indicated by arrow). Note that the carpogonial branch is one of three branches borne on an axial cell. Great Barrier Reef, Australia, 16 Nov. 1982, 10 m, PWG collection.

Fig. d. Gibsmithia hawaiiensis. Tetrasporangia and tetrasporangial initials borne corymbosely on 1-few-celled pedicels. Released tetrasporangium denoted by empty walls (dashed line). Kaneohe Bay, Oahu, Hawaii, 3 Aug. 1959, A. J. Bernatowicz in BISH.

Fig. e. Gibsmithia sp. Tetrasporangium and tetrasporangial initial. Same collection as Fig. a.

Scale bar = 20 μm
**Figure 2**


Fig. a. Carpogonial branch and auxiliary cell branch borne on the same periaxial cell. Note that the auxiliary cell branch is borne abaxially relative to the carpogonial branch. Involucral filaments have already been initiated on cells subtending the future auxiliary cell.

Fig. b. Auxiliary cell branch with involucral filaments developing on cells subtending the future auxiliary cell.

Fig. c. Spermatangia borne on lateral branches to about 7 cells in length. Spermatangial mother cells can occur in double whorls around proximal branch cells. Not all spermatangia and spermatangial mother cells are depicted in this drawing.

Scale bar = 20 μm
Figure 3

Gibsmithia sp. The Bommie off NW Heron I., Great Barrier Reef, Australia, 16 Nov. 1982, 10 m, PWG collection.

Mature cystocarp showing involucral branches, the gonimoblast initiator cell attached to the auxiliary cell, and two of the gonimoblast initials. Note the thick wall evident on cells adjacent to the auxiliary cell.

Scale bar = 20 μm

Fig. a. Cortical filaments. Elongate, darkly stained cell is characteristic of cells bearing floridean hairs (hair not shown).

Fig. b. Immature carpogonial branch.

Fig. c. More mature carpogonial branch. Note the 90° angle relationship of the pit connections attaching cell 3 to its neighboring cells. Also note the relatively small basal portion of the carpogonium.

Fig. d. Mature carpogonial branch with very large cells 4 and 5 and one-celled laterals on some proximal cells of the branch. The carpogonium and cells 2 and 3 are behind cells 4 and 5. This is the same configuration of carpogonial branch cells as that shown in Fig. 5.

Fig. e. Carpogonial branch showing either abortive trichogyne development or early post-fertilization enlargement.

Scale bar = 20 μm

Connecting filament production from carpogonial derivative cells in contact with cells 4 and 5 of the carpogonial branch. The carpogonial derivative cells and cells 2 and 3 are behind cells 4 and 5, as in Fig. 4d. A total of 17 connecting filament were observed leaving this carpogonial branch.

Scale bar = 20 μm

Fig. a. Mature auxiliary cell branch. Note displacement of enlarged auxiliary cell out of the line of the branch and the abundance of lateral branches on cells both distal and proximal to the auxiliary cell. A filament of proximally differentiated cells but of a distally rhizoidal character is borne on the vegetative cell just below the one bearing the auxiliary cell branch.

Fig. b. Auxiliary cell with attached gonimoblast initiator cell producing both outgoing connecting filaments and gonimoblast initials.

Fig. c. Auxiliary cell branch with early gonimoblast production.

Scale bar = 20 μm
Dudresnaya verticillata

Fig. a. "Indeterminate" branch terminating in an assimilatory filament (arrow). Worlbarrow Tout, Kimmeridge, Dorest, England, 30 July 1977, 13 m, leg. S. I. Honey, BM.

Fig. b. Periaxial cell showing ascending whorl branch, descending rhizoid, and three intermediate cells that bear both whorl branches and rhizoids. Same collection as Fig. a.

Fig. c. Carpogonial branch showing characteristically elongate, medially constricted (arrow) base of carpogonium. Same collection as Fig. a.

Fig. d. Branch bearing spermatangia on bisexual thallus. Note distal position of spermatangia on terminal or lateral spermatangial mother cells. Same collection as Fig. a.

Fig. e. Branch initiating spermatangia from files of relatively short, squat cells on unisexual thallus. Roscoff, France, 12 July 1927, leg. H. Kylin, AHF 5984.

Fig. f. Spermatangia clustered around files of relatively short, squat cells on unisexual thallus. Same collection as Fig. e.

Scale bar = 50 μm

Fig. a. Carpogonial branch with characteristic elongate, medially constricted (arrow) base of carpogonium. Note final two oblique divisions yielding a recurved branch. A basally differentiated filament occurs laterally.

Fig. b. An immature reproductive filament (possibly an auxiliary cell branch) bearing from the same cell two lateral, basally differentiated filaments.

Fig. c. Auxiliary cell branch showing auxiliary cell slightly smaller than its neighbors, but with a nucleus nearly as large.

Fig. d. Auxiliary cell branch with gonimoblast initiator cell, two outgoing connecting filaments, and two elongate gonimoblast initials. A single-celled lateral occurs distal to the auxiliary cell.

Fig. e. Part of a maturing cystocarp showing gonimoblast initiator cell in cytoplasmic continuity with auxiliary cell. Pit connections between the auxiliary cell and its neighbors have enlarged. All but the basal cells of the gonimoblast have differentiated into carposporangia.

Scale bar = 50 μm
Figure 9

Assimilatory filaments


Fig. b. *Dudresnaya australis*. Flinders, Victoria, Australia, 8 January 1981, leg. M. H. Hommersand, WS in NCU.

Fig. c. *Dudresnaya crassa*. Hamilton Harbor, Bermuda, 13 May 1953, leg. A. J. Bernatowicz 53-335, US 38098.

Fig. d. *Dudresnaya verticillata*. Worlbarrow Tout, Kimmeridge, Dorset, England, 30 July 1977, 13 m, leg. S. I. Honey, BM.

Scale bar = 50 μm
**Figure 10**

**Dudresnaya crassa**

Fig. a. "Indeterminate" branch terminating in an assimilatory filament. N. Content Key, Florida, 2 April 1969, leg. M. H. Hommersand, WS in NCU.

Fig. b. Carpogonial branches showing small, nondescript carpogonium and moderate curvature. Carteret Co., North Carolina, 20 July 1973, 20 m, leg. R. Searles, DUKE.

Fig. c. Auxiliary cell branch with relatively small auxiliary cell flanked by two very large cells. Buildings Bay, Bermuda, 30 March 1915, leg. A. B. Hervey, US 074390.

Fig. d. Branch bearing spermatangia on bisexual thallus. Note distal position of spermatangia on terminal or lateral spermatangial mother cells. Same collection as Fig. a.

Fig. e. Branches bearing spermatangia clustered around relatively short cells on unisexual thallus. Gunner Bay, Bermuda, 9 April 1949, leg. A. J. Bernatowicz 49-686, MICH.

Scale bar = 50 μm

Fig. a. Very early gonimoblast initiation from a gonimoblast initiator cell after contacting an auxiliary cell showing only slight differentiation in size from that of its neighbors.

Fig. b. A slightly later stage in gonimoblast initiation.

Fig. c. A maturing cystocarp showing some enlargement of pit connections between cells of the auxiliary cell branch. The empty space between cells of the auxiliary cell branch and maturing carposporangia suggests the presence of a thick wall surrounding the auxiliary cell although such a wall was not visible directly. Note that one of the cells (arrow) distal to the auxiliary cell is swollen. The gonimoblast initiator cell is directly behind the auxiliary cell.

Fig. d. A mature cystocarp showing pronounced enlargement of pit connections between cells of the auxiliary cell branch. Only some of the basalmost cells of the carposporophyte are shown. Note that at least one of the cells (arrow) distal to the auxiliary cell is swollen.

Scale bar = 50 μm
Figure 12

*Dudresnaya australis*. Flinders, Victoria, Australia, 8 January 1981, leg. M. H. Hommersand, NCU.

Fig. a. Carpogonial branches. The carpogonium and cell 2 are disintegrating (these were in a thallus with mature cystocarps).

Fig. b. Auxiliary cell branch showing an auxiliary cell slightly smaller than its neighbors. The nucleus is also somewhat smaller.

Fig. c. Early gonimoblast initiation from a gonimoblast initiator cell. The cell subtending the auxiliary cell bears a lateral.

Fig. d. Maturing cystocarp. Note relatively loose arrangement of gonimoblast filaments and lack of enlargement of pit connections in the auxiliary cell branch except for slight enlargement of the pit connection between the auxiliary cell and its subtending cell (arrow).

Scale bar = 20 μm
Figure 13

Dudresnaya japonica. Chojakasaki, Hayama, Kanagawa-ken, Japan, 12 March 1971, leg. M. Yoshizaki, WS in NCU.

Fig. a. Assimilatory filaments showing characteristic cell size and branching pattern.

Fig. b. Carpogonial branches with characteristic elongate carpogonium and irregularly shaped cells.

Fig. c. Connecting filament production from a carpogonial fusion cell in contact with cell 5. Another layer of connecting filaments is not shown. Note spermatangia attached to the tip of the trichogyne, which is about 2.5 X the length shown here.

Fig. d. Auxiliary cell branch showing differentiation in size between the auxiliary cell and its neighbors.

Fig. e. Gonimoblast initiation from a gonimoblast initiator cell. One outgoing connecting filament (arrow) appears to have converted to gonimoblast production.

Fig. f. Mature carposporophyte with relatively loosely arranged gonimoblast filaments, the basalmost of which appear not to differentiate (the distalmost are not shown). Note the thick wall around the auxiliary cell branch and the enlarged pit connections between the auxiliary cell and its immediate.

Scale bar = 50 μm
**Dudresnaya hawaiensis**

Fig. a. Characteristic sparsely branched assimilatory filament of long, narrow cells. Reef #7, E side, Great Barrier Reef, Australia, 14 Aug. 1981, leg. R. Wetherbee, PWG collection.

Fig. b. Carpogonial branch showing little differentiation of cells and little curvature. The trichogyne wall is thickened at its base. Same collection as Fig. a.

Fig. c. Connecting filament initiation from carpogonial fusion cells in contact with cells 4 and 6. Note the distance the fertilized carpogonium must grow in order to contact other cells of the branch. Also note that this branch and that in Fig. d. have cells more differentiated and are more recurved than the branch in Fig. b. Same collection as Fig. a.

Fig. d. Connecting filaments issuing from a carpogonial fusion cell in contact with cell 4. Another layer of connecting filaments emanates from a carpogonial fusion cell attached to cell 5 above the plane of the drawing, but it was too faint to observe in detail. Ned's Beach, Lord Howe Island, Australia, 6 December 1978, leg. G. T. Kraft, PWG collection.

Scale bar = 50 μm
Dudresnaya hawaiiensis

Fig. a. Auxiliary cell branch showing slight differentiation between the auxiliary cell and its neighbors. Reef #7, Great Barrier Reef, Australia, 14 August 1981, leg. R. Wetherbee, P. Gabrielson collection.

Fig. b. Early gonimoblast initiation from a gonimoblast initiator cell in contact with an auxiliary cell. Same collection as Fig. a.

Fig. c. A later stage showing relatively tightly appressed gonimoblast cells. Same collection as Fig. a.

Fig. d. A maturing cystocarp. Note the three swollen cells distal to the auxiliary cell. Ned's Beach, Lord Howe Island, Australia, 6 Dec. 1978, leg. G. T. Kraft, P. Gabrielson collection.

Scale bar = 50 μm
**Figure 16**

*Dudresnaya bermudensis*

Fig. a. Apex of an indeterminate branch showing dense whorl branches almost from initiation. Coopers Island, Bermuda, 1881, leg. W. G. Farlow, #49 in part, upper right specimen, FH.

Fig. b. Distal end of whorl branch showing characteristic obpyriform apical cells and presence of refractive bodies in some cells. Coopers Island, Bermuda, 1881, cast ashore, leg. W. G. Farlow, UC 160726 (isotype).

Fig. c. Carpogonial branch showing long, relatively straight trichogyne and modestly curved and differentiated branch cells. Same specimen as Fig. b.

Fig. d. Auxiliary cell branch showing enlarged cells on either side of the relatively small auxiliary cell. Same specimen as Fig. b.

Fig. e. Spermatangia showing dense, seemingly catenate arrangement terminating assimilatory filaments. Buildings Bay, Bermuda, 30 March 1960, leg. W. R. Taylor 30016, MICH.

Scale bar = 20 μm
Figure 17

**Dudresnaya colombiana**

Fig. a. Indeterminate branches being initiated on adjacent vegetative cells of the main axis. Note that the cells of the branches remain closely appressed. Isla Estanque, Mexico, 27 April 1974, 9-10.6 m, leg. J. N. Norris, US 091654.

Fig. b. Assimilatory filament showing the characteristic oval shape of the distal cells of a whorl branch. More proximal cells commonly become bi- or trifurcate. Isla Mejía, Mexico, 23 April 1974, leg. J. N. Norris, US 91656.

Fig. c. Distal ends of two carpogonial branches showing slight curvature of the branch. Same collection as Fig. a.

Fig. d. Early gonimoblast initiation from a gonimoblast initiator cell. Note the slight difference in size between the auxiliary cell and its neighbors. Also note the oval shape of these cells and the bifurcate and trifurcate nearby vegetative cells. Isla Estanque, Mexico, 27 April 1974, 9-10.6 m, leg. J. N. Norris, US slide #3772.

Fig. e. Spermatangia clustered distally on terminal or sub-terminal spermatangial mother cells. Same collection as Fig. a.

Scale bar = 50 μm

Fig. a. Indeterminate branch showing lateral assimilatory filaments reaching the level of the apical cell.

Fig. b. Assimilatory filament showing characteristic obpyriform shape of distal cells.

Fig. c. Carpogonial branch showing final two oblique divisions. Note the slightly lateral displacement of the trichogyne.

Fig. d. Auxiliary cell branch showing slight differentiation of the auxiliary cell from its neighbors and relatively little differentiation of other cells of the branch. Note involucral filaments on cells subtending the auxiliary cell.

Fig. e. Terminally clustered spermatangia showing catenate appearance.

Scale bar = 20 μm
Dudresnaya patula

Fig. a. "Indeterminate" branch terminating in an assimilatory filament. Singer I., Palm Beach Co., Florida, 28 March 1979, 48.8 m, JSL-I-650, US slide #3337.

Fig. b. Characteristic branching of assimilatory filaments within thallus. Same slide as Fig. a.

Fig. c. Carpogonial branch showing characteristic length and differentiation. Singer Island, Palm Beach Co., Florida, 8 July 1978, JSL-I-517, leg. M. O. Hall and E. Melton, US slide # 3334.

Scale bar = 20 μm
Figure 20


Fig. a. Connecting filament production from two carpogonial fusion cells. One connecting filament appears to be in the process of contacting an auxiliary cell on a separate branch.

Fig. b. Gonimoblast developing from a gonimoblast initiator cell attached to an auxiliary cell.

Scale bar = 50 \( \mu \text{m} \)
Dudresnaya georgiana. Gray's Reef, Georgia, 26 June 1980, 21.5 m., leg. R. B. Searles, holotype slide collection, DUKE.

Fig. a. Indeterminate branch and whorl branch arising from adjacent cells. Note that cells of the indeterminate branch are smaller and bear more laterals than those of the whorl branch.

Fig. b. Periaxial cell showing ascending whorl branch, descending rhizoids, and three intermediate cells that bear both assimilatory filaments and rhizoids.

Figs. c, d, e. Initiation and development of the carpogonium. Note that distal cells of the branch are not cut off by strongly oblique divisions; the branch becomes recurved by differential growth of cell 2. Also note the elongate base of the carpogonium.

Fig. f. Gonimoblast initiator cell with incoming and outgoing connecting filaments and a single, slightly elongate gonimoblast initial. Note the three involucral branches attached to the basal cell of the branch.

Fig. g. Spermatangia borne distally on terminal and subterminal spermatangial mother cells. Note refractive inclusions in most cells of the branches.

Scale bar = 50 μm
Thuretellopsis peggiana

Fig. a. Habit of cystocarpic plant. Note numerous hairs extending from the thallus in this figure and the next. Dixon I., B. C., 16 June 1982, 6.5 m, leg. M. W. Hawkes and T. Klinger, UBC.

Fig. b. Apex showing bullet-shaped apical cell densely surrounded by whorl branches. Several spermatangia are visible on whorl branches a short distance below apex. Dixon I., B. C., 13 April 1984, 12 m, leg. M. W. Hawkes and L. Yip, UBC.

Fig. c. Whorl branch (assimilatory filament) of cylindrical cells pseudodichotomously branched. Same collection as Fig. a.

Fig. d. Relatively short assimilatory filaments arising perpendicularly from cells of rhizoidal filaments clinging to axial filament. Same collection as Fig. b.

Scale bar: a = 200 \( \mu \)m, b, d = 50 \( \mu \)m, c = 20 \( \mu \)m
Thuretellopsis peggiana

Fig. a. Carpogonial branch showing strong curvature due to final two oblique divisions. Dixon I., B. C., 13 April 1984, 12 m, leg. M. W. Hawkes and L. Yip, UBC.

Fig. b. Carpogonial derivative cell fused to cell 4; a single connecting filament has been initiated. Auxiliary cell branch on right bears typical subtending involucral branches. Dixon I., 16 June 1982, 6.5 m, leg. M. Hawkes and T. Klinger.

Fig. c. Connecting filament showing darkly staining tip containing the nucleus, with nearly invisible wall material collapsing behind it. Same collection as Fig. b.

Fig. d. Auxiliary cell branch which terminates vegetatively. Except for the auxiliary cell and its immediate neighbors, which are both initiating lateral branches (the distal neighbor already bears one lateral), no other cells of the branch are differentiated. Same collection as Fig. a.

Fig. e. Two mature auxiliary cell branches with darkly staining auxiliary cell flanked by somewhat inflated neighboring cells with enlarged, darkly staining nuclei. Note the single, centrally situated nucleus in the vegetative cells. Same collection as Fig. b.

Scale bars: a - e = 20 μm
**Figure 24**

*Thuretellopsis peggiana*

Fig. a. Immature auxiliary cell branch with auxiliary cell larger than its neighbors. Dixon I., B. C., 3 June 1977, UBC.

Fig. b. Mature auxiliary cell which has not been fertilized; terminal cell of branch is disintegrating. Dixon I., 16 June 1982, 6.5 m, leg. M. Hawkes and T. Klinger, UBC.

Fig. c. Contact of auxiliary cell by connecting filament, which grows onward to contact other auxiliary cells. An incompletely differentiated auxiliary cell branch that terminates vegetatively is seen in the background. Same collection as Fig. b.

Fig. d. Young gonimoblast developing from gonimoblast initiator cell. Auxiliary cell nucleus is not in focus, but it lies in the corner opposite attachment of gonimoblast initiator cell. Same collection as Fig. b.

Fig. e. Mature cystocarp surrounded by a mucilaginous wall and obscuring the branch bearing it. Same collection as Fig. b.

Fig. f. Distal spermatangia on spermatangial mother cells cut off by oblique walls. Note distal nucleus in each spermatangium. Dixon I., 13 April 1984, 12 m, leg. M. Hawkes and L. Yip, UBC.

Scale bars: a - e = 20 μm, f = 10 μm
Figure 25

Pikea californica

Fig. a. Lectotype. Golden Gate, California. Sept. 1851. Sheet C, 50 in part. TCD.

Fig. b. Upper specimen, isotype; lower specimens, Farlowia compressa. Golden Gate, California. Sept. 1851. Sheet C in TCD.

Fig. c. Upper specimen in Fig. b.

Fig. d. Pikea pinnata. Holotype (right specimen). Fort Point, San Francisco, California. 18 Feb. 1898. UC 95041.

Scale bars: a, b, d, = 10 cm; c = 5 cm
Figure 26

Pikea californica

Fig. a. Pikea pinnata. Isotype. Arrows indicate cystocarps. Fort Point, San Francisco, California. 18 Feb. 1898. UC 95041.

Fig. b. P.B.-A. 897 in UBC. Pacific Beach, California. No date given.

Fig. c. Pikea robusta. Holotype. Carmel Beach, California. 20 July 1939. US 084196.

Fig. d. Scilly Isles, England. 3 July 1983. UBC A22722.

Scale bars: a, b = 5 cm; c, d = 10 cm
897. *Pikea Californica* Hart.


Pacific Coast, California.

Fig. a. Apex of an indeterminate axis showing the characteristic cell shapes and disposition of branches. Stippling indicates cells of minor whorl branches.

Fig. b. Longitudinal section showing the axial structure in a more mature part of the thallus. Note the characteristic branching pattern of major whorl branches, the occurrence of secondary pit connections (arrows), and the production of corticating rhizoids from inner cortical cells.

Fig. c. Spermatangia and spermatangial mother cells. Note the distal location of the nucleus in the spermatangium.

Scale bars: a and c = 20 μm, b = 50 μm
Figure 28

Fig. a. Mature axial structure of *Farlowia mollis*. Davenport Landing, Calif., 9 Aug. 1979, leg. M. Hommersand, WS in NCU.

Fig. b. Axial structure of *Orculifilum denticulatum* a short distance below apex of a branch. Fritz Cove, Alaska, 22 Jan. 1980, UBC 67492.

Fig. c. Axial structure of *Pikea californica*. Note the way that lateral branches become appressed to the central axis and to each other. Carmel Pt., Calif., 19 July 1974, leg. M. Hommersand, WS in NCU.

Fig. d. Axial structure of *Leptocladia binghamiae*. Note enlarged pit connections and distal attachment of lateral branches. Punta Eugenia, Mexico, 11 June 1972, leg. M. Hommersand, WS in NCU.

Scale bars = 200 μm
Figure 29


Figs. a, b. Initiation of the trichogyne prior to the final cell division separating cell 2 from the carpogonium.

Figs. c, d. Immature carpogonial branches showing enlargement of the distal cells of the branch and elongation of the trichogyne as the branch matures.

Fig. e. Mature carpogonial branch six cells in length.

Fig. f. Mature carpogonial branch in which the carpogonium appears to have just been fertilized, and the trichogyne has become detached from the basal part of the carpogonium.

Scale bar = 20 μm
Figure 30


Fig. a. Fertilized carpogonium which has enlarged and is in the process of dividing (arrow); one of the derivative cells is fusing with cell 5.

Fig. b. Fertilized carpogonium that has divided into two carpogonial derivative cells, one of which has fused with cell 5.

Fig. c. Two old carpogonial fusion cells showing remnants of outgoing connecting filaments (arrows point at pit connections).

Fig. d. Young carpogonial fusion cells showing initiation of one outgoing connecting filament from each.

Fig. e. A carpogonial branch which is becoming vegetative. Note the formation of a pit connection between the base of the "carpogonium" and the "trichogyne."

Scale bar = 20 µm
Figure 31


Fig. a. Unbranched auxiliary cell branch in which the auxiliary cell is subterminal.

Fig. b. Auxiliary cell branch in which the auxiliary cell is cell 4. Note the one-celled lateral branch on cell 5.

Fig. c. Auxiliary cell branch in which the auxiliary cell is cell 4. Note the one-celled lateral branch on cell 3.

Fig. d. Auxiliary cell branch in which the auxiliary cell is cell 5. A one-celled lateral branch is borne on the basal cell.

Fig. e. Auxiliary cell branch in which the auxiliary cell is cell 3 and itself bears a one-celled lateral branch.

Fig. f. Auxiliary cell branch in which the auxiliary cell is cell 6. A one-celled lateral branch is borne on the basal cell.

Fig. g. Auxiliary cell branch in which lateral branches borne on proximal cells are rhizoidal in character.

Scale bar = 20 µm

Fig. a. Auxiliary cell in the process of being contacted by a connecting filament that has already divided.

Fig. b. Gonimoblast initiator cell in contact with an auxiliary cell, initiating a second outgoing connecting filament.

Fig. c. Early stage in gonimoblast development from three somewhat elongate gonimoblast initials.

Fig. d. A young cystocarp. Note the dark granules, in addition to the enlarged nucleus, in the terminal cell of the auxiliary cell branch.

Scale bar = 20 μm
Figure 33

Farlowia mollis. Variations in habit.

Fig. a. Langara Pt., B. C., 16 July 1979, UBC A60865.

Fig. b. Barney Rocks, B. C., 13 May 1975, UBC A53185.

Fig. c. McLean I., B. C., 24 Aug. 1959, UBC A11927.

Fig. d. Glacier Pt., B. C., 13 June 1979, UBC A62733.

Fig. e. Part of Pikea californica type collection in TCD, identified as Farlowia compressa by W. A. Setchell. No. 78.

Fig. f. Klucksiwi, B. C., 14 July 1946, UBC A881.

Fig. g. Holotype of Gigartina mollis. Puget Sound. No date. TCD.

Fig. h. Glacier Pt., B. C., 22 Nov. 1968, UBC A39123.

Scale bars = 10 cm
Figure 34

Farlowia mollis

Fig. a. Apex of indeterminate axis (A) showing manner of major whorl branch (M) formation and formation of corticating minor whorl branches (N). Only corticating branches stippled. Sooke, B.C., 7 Mar. 1982, leg. T. Klinger, UBC.

Fig. b. Composite drawing showing branching pattern of mature thallus. The main axis (A) bears one of its minor whorl branches (N) and one of its major whorl branches (M). The basal 1-4 cells of the major whorl branch bear only two corticating branches (N) and occasionally rhizoidal filaments. Other cells of the major whorl branch bear an abaxial branch (B) plus two corticating branches. Unless labeled otherwise, all cells are members of corticating or rhizoidal filaments. Note the two carpogonial branches replacing rhizoidal filaments. Davenport Landing, Calif., 9 Aug. 1979, leg. M. Hommersand, WS in NCU.

Fig. c. The development of three successive indeterminate axes from a primary, secondary, and tertiary branch, respectively. These branches represent a major whorl branch, an abaxial branch, and a minor whorl branch, respectively. Yankee Pt., Calif., culture from crust, terminated 3-4-77 (no other data provided with specimen), UC.

Scales as indicated
Farlowia mollis

Fig. a. A transverse section showing the disposition of mature cystocarps. Brady's Beach, Bamfield, B. C., 29 Jan. 1972, UBC A46133.

Fig. b. Two carpogonial branches developing from inner cortical cells. Sombrio Pt., B. C., 17 July 1958, UBC A14513.

Fig. c. Carpogonial branch showing initiation of the trichogyne before the last cell of the branch is cut off. 55°45'40"N, 132°29'08"N, Prince of Wales I., Alaska, 11 Aug. 1980, SCL 6101.

Fig. d. A young carpogonium with its nucleus at the base of the trichogyne. Same collections as Fig. c.

Fig. e. Immature auxiliary cell branches in the presence of a mature carpogonial branch. Same collection as Fig. c.

Fig. f. A mature auxiliary cell branch. Davenport Landing, Calif., 9 Aug. 1979, leg. M. Hommersand, NCU.

Fig. g. A connecting filament contacting an auxiliary cell. Same collection as Fig. f.

Fig. h. An outgoing connecting filament after its proximal segment has contacted an auxiliary cell. Arrowhead indicates pit connection between the two segments of the connecting filament. Port Renfrew, B. C., 26 Nov. 1969, UBC 41040.

Fig. i. Initiation of carposporangia from the gonimoblast initiator cell (see Fig. 38e). Same collections as Fig. h.

Scale bars: a = 200 µm; b, e = 50 µm; c, d, f, g, h, i = 20 µm
Farlowia mollis

Fig. a. Carpogonial branch showing initiation of the trichogyne before the last cell of the branch is cut off. 55°45'40"N, 132°29'08"W, Prince of Wales I., Alaska, 11 Aug. 1980, SCI 6101.

Fig. b. Carpogonial branch showing the last cell division in the branch. Crescent Beach, Wash., 28 Aug. 1969, leg. M. Hommersand, NCU.

Fig. c. A carpogonial branch after the final cell division but before cell enlargement and trichogyne elongation. Same collection as Fig. a.

Fig. d. A maturing carpogonial branch. Same collection as Fig. b.

Fig. e. A maturing carpogonial branch with a 2-celled lateral. Same collection as Fig. b.

Fig. f. A maturing carpogonial branch with a 5-celled lateral on the basal cell of the branch. Same collection as Fig. b.

Scale bar = 20 μm
Farlowia mollis

Figs. a, b. Initiation of connecting filaments from the two carpogonial derivative cells attached to cells 4 and 5 of the carpogonial branch. Crescent Beach, Wash., 28 Aug. 1969, leg. M. Hommersand, NCU.

Fig. c. Seven connecting filaments coming from the two carpogonial fusion cells. Port Renfrew, B.C., 26 Nov. 1969, UBC A41040.

Scale bar = 20 μm
Farlowia mollis

Fig. a. A connecting filament in which nuclear division has already occurred after passing a subterminal auxiliary cell. Crescent Beach, Wash., 28 Aug. 1969, leg. M. Hommersand, NCU.

Fig. b. A connecting filament after it has contacted a subterminal auxiliary cell. Same collection as Fig. a.

Fig. c. A connecting filament after it has contacted an auxiliary cell and is initiating a second outgoing connecting filament (behind). Same collection as Fig. a.

Fig. d. View showing the gonimoblast initiator cell attached to the auxiliary cell with the incoming connecting filament, two outgoing connecting filaments, and a gonimoblast initial. Davenport Landing, Calif., 9 Aug. 1979, leg. M. Hommersand, NCU.

Fig. e. Gonimoblast development from the gonimoblast initiator cell (see Fig. 34i). Port Renfrew, 26 Nov. 1969, UBC A41040.

Scale bar = 20 μm
Figure 39

Farlowia mollis

Fig. a. Young gonimoblast derived in part from a segmented outgoing connecting filament. Glacier Pt., B. C., 13 June 1979, UBC A61654.

Fig. b. A mature cystocarp showing the integrity of the auxiliary cell nucleus and the gonimoblast initiator cell nucleus. Note the enlargement of the pit connection below the auxiliary cell and the lack of gonimoblast fusions. Brady's Beach, Bamfield, B. C., 29 Jan. 1972, UBC A46133.

Fig. c. A carpogonial branch which appears to be reverting to vegetative growth. Crescent Beach, Wash., 28 Aug. 1969, leg. M. Hommersand, WS in NCU.

Fig. d. Spermatangia. Cree I., B. C., 29 June 1969, UBC A41534.

Fig. e. Spermatangia. Roller Bay, B. C., 13 Sept. 1970, UBC A49056.

Scale bar = 20 μm
Figure 40

**Farlowia conferta**

Fig. a. Moss Beach, Calif., 8 July 1963, UBC A20099.

Fig. b. Moss Beach, Calif., 14 Mar. 1966, UBC A50629.

**Farlowia mollis**

Fig. c. Horoman, Hidaka, Hokkaido, Japan, 7 aug. 1951, SAPS 042253.

Fig. d. Horoman, Hidaka, Hokkaido, Japan, 20 Oct. 1951, SAPS 042254.

Scale bars: a, b = 10 cm; c, d = 5 cm
Figure 41

Fig. a. Leptocladia binghamiae. Shell Beach, San Luis Obispo Co., Calif., 4 June 1966, UBC A18004.

Fig. b. Leptocladia peruviana. Parachique, Piura, Peru, 7 July 1977, Acleto 1889.

Fig. c. Leptocladia peruviana. Playa de Paita, Peru, 10 Aug. 1965, Acleto 991.


Fig. e. Orculifilum denticulatum. Fritz Cove, Alaska, 22 Jan. 1980, UBC A67492.

Fig. f. Orculifilum denticulatum. Holotype. Coghlan I., Alaska, 13 June 1974, UBC A67496.

Scale bars = 10 cm
Figure 42


Apex of an indeterminate axis showing the characteristic cell shapes and branching patterns. Stippling indicates cells of minor whorl branches. Numbered cells are those of the axial file beginning with the apical cell.

Scale bar = 20 μm
**Figure 43**


Outlines of protoplasts of axial cells 20, 30, 40...100 cells from the apex of an indeterminate branch showing the cask-like shape of these cells and the position of lateral branch attachment.

Scale bar = 20 μm

Fig. a. A mature carpogonial branch showing the enlargement and lobing of distal cells of the branch. Clear areas in enlarged cells indicate vacuoles.

Figs. b, c. Auxiliary cell branches. The cells on either side of the auxiliary cell are also enlarged and can be lobed.

Scale bar = 20 μm

Fig. a. An early stage in the initiation of gonimoblast filaments from a gonimoblast initiator cell attached to a subterminal auxiliary cell that has separated somewhat from the terminal cell of the branch. Note enlargement of pit connections between cells of the auxiliary cell branch proximal to the auxiliary cell.

Fig. b. Portion of a mature carposporophyte showing lack of gonimoblast fusion cell.

Scale bar = 20 μm
Leptocladia binghamiae

Fig. a. Carpogonial branch showing initiation of the carpogonium as a narrow projection. Note the presence of a lateral which can also branch. Santa Cruz I., Calif., 17 Aug. 1969, leg. M. Hommersand, NCU.

Fig. b. An immature carpogonial branch showing enlargement of the distal cells of the branch. Note enlargement of the nuclei. Same collections as Fig. a.

Fig. c. A mature carpogonial branch showing enlargement of the distal cells of the branch, particularly cells 4 and 5. Puerto Santo Tomás, Mexico, 8 Nov. 1969, leg. M. Hommersand, NCU.

Fig. d. The distal end of a carpogonial branch in which the carpogonium appears to have been fertilized. The basal part of the carpogonium has expanded, and its cytoplasmic connection with the trichogyne has been broken. Same collection as Fig. a.

Fig. e. The presumably fertilized carpogonium appears to have cut off a cell that might be destined to fuse with cell 4 or cell 5 or which might signal the initiation of a connecting filament. Same collection as Fig. a.

Scale bar = 20 μm

Fig. a. A mature auxiliary cell branch showing enlargement of distal cells of the branch, particularly the cells on either side of the auxiliary cell. Note the slight constriction of these cells at the nucleus.

Fig. b. Contact of the proximal part of a passing connecting filament by an auxiliary cell. Note the slight protrusion of the auxiliary cell toward the gonimoblast initiator cell.

Fig. c. A gonimoblast initiator cell with two gonimoblast initials and remnants of two or three outgoing connecting filaments.

Scale bar = 20 μm
Leptocladia binghamiae. Punta Eugenia, Mexico, 12 June 1972, leg. M. Hommersand, NCU.

A gonimoblast fusion cell which has developed by incorporation of first-formed gonimoblast cells into the gonimoblast initiator cell. Note the presence of the auxiliary cell nucleus in its own part of the cell and the enlargement of the pit connections between all cells of the auxiliary cell branch. Pit connections and most nuclei incorporated into the fusion cell are not shown.

Scale bar = 20 µm
Fig. a. *Leptocladia binghamiae*. The arrangement of cells of the gonimoblast filaments outside the fusion cell: most inner cells do not enlarge; intermediate cells are frequently somewhat elongate; only distal cells differentiate into carposporangia. Punta Eugenia, Mexico, 12 June 1972, leg. M. Hommersand, WS in NCU.

Fig. b. *Leptocladia peruviana*. The arrangement of spermatangial mother cells and spermatangia to form an outer cortical layer. Note the distal location of the spermatangial nucleus. Parachique, Peru, 7 July 1977, leg. C.Acleto 1889, MICH.

Fig. c. *Leptocladia binghamiae*. Irregularly cruciate to irregularly zonate tetrasporangia developing terminally on subcortical cells. Santa Cruz I., Calif., 17 Aug. 1969, leg. M. Hommersand, WS in NCU.

Scale bar = 20 \( \mu \text{m} \)
Figure 50

Fig. a. *Weeksia reticulata*. Holotype. Pacific Grove, Calif., 28 March 1896, UC 96497.

Fig. b. *Weeksia reticulata*. Abbott's "technical type." Pacific Grove, Calif., 30 July 1896, FH.

Fig. c. *Weeksia digitata*. Holotype. Mission Pt., Calif, 1 Aug. 1964, Abbott 4011 in US (084201).

Fig. d. *Schizymenia? coccinea*. Holotype. Griffin Bay, Washington, March 1858, TCD.

Fig. e. *Weeksia fryeana*. Holotype. Deer Harbor, Washington, 1 July 1904, UC 96308.

Fig. f. *Schizymenia? coccinea*. Holotype close-up. Arrows indicate some of the veins.

Fig. g. *Weeksia templetonii*. Portion of holotype collection. Arrows indicate some of the veins. Isla Cedros, Mexico, 15 Aug. 1932, CAS 236484 in UC.

Scale bars: a - e = 10 cm; f, g = 5 cm

Figs. a, b. Immature carpogonial branches showing enlargement of distal cells of the branch during maturation.

Fig. c. A carpogonial branch showing post-fertilization fusion of the divided carpogonium with cells 4 and 5 of the branch. The meaning of the cells cut off cells 2 and 4 (arrows) is unknown (also see Figs. 52, 56).

Scale bar = 20 µm
Figure 52


A presumably fertilized carpogonium fused to cell 4 and initiating, in addition to unbranched connecting filaments, branched filaments resembling gonimoblast filaments. Arrow indicates what appears to be a non-reproductive cell cut off cell 2 (see also Figs. 51, 56).

Scale bar = 20 μm
Figure 53


Fig. a. Immature auxiliary cell branch showing the somewhat enlarged auxiliary cell prior to maturation of neighboring cells.

Fig. b. Immature auxiliary cell branch in which a second (arrow) separate distal cell has been cut off the auxiliary cell.

Fig. c. Immature auxiliary cell branch bearing two separate cells distally, one of which has divided.

Fig. d. A maturing auxiliary cell branch showing enlargement of cells neighboring the auxiliary cell.

Fig. e. A mature auxiliary cell branch showing the typical size and shape of distal cells of the branch.

Scale bar = 20 μm
Figure 54

Fig. a. *Weeksia digitata*. An early stage in gonimoblast initiation from a gonimoblast initiator cell attached to a subterminal auxiliary cell. Note the number of outgoing connecting filaments from the gonimoblast initiator cell and the presence of a long, unbranched lateral on the basal cell of the filament. Coronado, San Diego, Calif., 14-16 Sept. 1969, leg. M. Hommersand, NCU.

Fig. b. *Weeksia digitata*. Early gonimoblast initiation from an initiator cell attached to an auxiliary cell. Note the clustered arrangement of developing gonimoblast cells. Same collection as Fig. a.

Fig. c. *Weeksia coccinea*. A portion of a mature cystocarp showing the clustered arrangement of developing carposporangia, the lack of a gonimoblast fusion cell, and the enlarged pit connections between cells of the auxiliary cell branch. Salmon Bank, Wash., 18 Apr. 1980, UBC A61726.

Scale bar = 20 μm
Figure 55

Fig. a. *Constantinea rosa-marina*. Immature carpogonial branch showing origin from inner cortical cells and curvature toward upper surface of blade. Cape Nosappu, Japan, 8 Apr. 1970, leg. M. Kurogi, WS in SAPS.

Fig. b. *Constantinea rosa-marina*. Distal end of mature carpogonial branch showing characteristic lobing of cells and basally spiralled trichogyne. Same collection as Fig. a.


Fig. e. *Constantinea subulifera*. Mature carpogonial branch showing enlarged nuclei of lobed cells. Arrows indicate extranuclear heterochromatin-like material. Some collection as Fig. c.

Fig. f. *Constantinea subulifera*. Mature carpogonial branch (left and lower sides of figure) that has been fertilized. Part of the segmented connecting filaments originating from the fertilized carpogonium are in focus in the upper right of the figure.

Scale bars = 20 μm

Segmented connecting filament production from a presumably fertilized carpogonium in contact with cell 4 (pair of solid arrows point at connection isthmus). Hollow arrow indicates a detached segment of cell 4; this segment appears to lack a nucleus (see Figs. 51, 52). Not all connecting filament segments are shown. This is an enlargement of the carpogonial fusion cell shown in Fig. 58a.

Scale bar = 20 μm
Fig. a. *Constantinea subulifera*. Immature auxiliary cell branches in which the auxiliary cell is still larger than adjacent cells. Buck I., Alaska, 25 Aug. 1980, SCL collection.

Fig. b. *Constantinea subulifera*. Mature auxiliary cell branch showing characteristic enlargement of cells adjacent to the auxiliary cell. Also note the very large nuclei in these cells. Same collection as Fig. a.

Fig. c. *Constantinea subulifera*. Immature and mature auxiliary cell branches. Same collection as Fig. a.

Fig. d. *Constantinea subulifera*. Gonimoblast initiation from remnant of gonimoblast initiator cell attached to subterminal auxiliary cell. Note auxiliary cell nucleus appressed to wall opposite gonimoblast initiator cell attachment. E of Crancroft I., B.C., 10 Sept. 1970, UBC A49063.

Fig. e. *Constantinea rosa-marina*. An immature cystocarp attached to an auxiliary cell. Note enlargement of connections between cells of the auxiliary cell branch. Cape Nosappu, Japan, 17 Oct. 1978, leg. S. Lindstrom, WS 1455 in UBC.

Fig. f. *Constantinea rosa-marina*. Incorporation of cells of gonimoblast into a gonimoblast fusion cell. Auxiliary cell branch fusion cell is seen out of focus to the left. Cape Nosappu, 29 Nov. 1978, leg. S. Lindstrom, WS 1457 in UBC.

Scale bar = 20 \(\mu m\)
Fig. a. *Constantinea subulifera*. Peel showing segmented connecting filament production in the vicinity of the fertilized carpogonial branch shown in Fig. 57 (orientation rotated 90°). Some of the outlying connecting filaments that are no longer segmented are indicated by arrows. Buck I., Alaska, 25 Aug. 1980, SCL collection.

Fig. b. *Constantinea subulifera*. Peel showing gonimoblast production attached to auxiliary cells. Note that these cystocarps appear much less diffuse than the connecting filament production shown in Fig. a. Hornby I., B. C., 15 Oct. 1984, leg. D. Renfrew and G. Kendrick, SCL collection.

Fig. c. *Constantinea rosa-marina*. Transverse section of a female blade with immature carposporangia. Note that the inner cortical cells are filled with starch grains. Cape Nosappu, 17 Oct. 1978, leg. S. Lindstrom, WS 1455 in UBC.

Fig. d. *Constantinea rosa-marina*. Transverse section of a female blade with mature carposporangia. Note that the inner cortical cells have lost most of their starch grains and have shrunken in diameter. Cape Nosappu, 29 Nov. 1978, leg. S. Lindstrom, WS 1457 in UBC.

Fig. e. *Constantinea rosa-marina*. Spermatangia borne on elongate superficial spermatangial mother cells. Kushiro, 26 May 1978, WS 1456 in UBC.

Fig. f. *Constantinea subulifera*. Zonate tetrasporangia situated among "paraphyses" on the lower surface of the blade. Cape Nosappu, 17 Oct. 1978, SCL collection.

Scale bars: a–d, f = 100 μm; e = 20 μm
Figure 59

*Dumontia contorta*

Fig. a. Apex of an indeterminate axis showing the characteristic pattern of axial cell enlargement and the characteristic anticlinal-periclinal branching pattern of whorl branches of the Dumontieae. Stippling indicates axial cells and cells of the main axis of two of the four whorl branches. Seitucte, Massachusetts, 8 Apr. 1981, leg. M. Hommersand, WS in NCU.

Fig. b. Two young carpogonial branches just starting to initiate trichogynes. Buck I., Alaska, 26 May 1979, SCL collection.

Fig. c. Carpogonial branch showing lateral attachment and characteristic basal spiral of the trichogyne. Same collection as Fig. b.

Fig. d. Connecting filament production from two carpogonial derivative cells attached to cells 4 and 5. Note some segmentation of connecting filaments adjacent to the carpogonial derivative cells. Same collection as Fig. b.

Scale bar = 20 μm

Fig. a. Mature auxiliary cell branch. Note thick wall surrounding all branch cells but the auxiliary cell.

Fig. b. Auxiliary cell branch just after contact by passing connecting filament.

Fig. c. Early gonimoblast initiation from a gonimoblast initiator cell. Arrows point to anucleate fragments that may represent either remains of outgoing connecting filaments or defective gonimoblast cells.

Fig. d. Immature cystocarp prior to carposporangial enlargement. Twenty-two gonimoblast cells were counted, probably close to the final number for the cystocarp.

Fig. e. Mature cystocarp showing the very large mature carposporangia. Only about half the total number of carposporangia are depicted here.

Scale bar = 20 μm
**Figure 61**

*Dasyphtoea insignis.* Southport, Tasmania, Australia, 21 Dec. 1980, leg. M. Hommersand, WS in NCU.

Fig. a. Apex of an indeterminate axis showing the pattern of axial cell enlargement characteristic of the species and the anticlinal-periclinal branching pattern characteristic of the Dumontieae of one pair of opposite whorl branches.

Fig. b. Distal end of carpogonial branch. The nucleus of the carpogonium appears to be disintegrating.

Fig. c. Mature auxiliary cell branch prior to contact by a connecting filament.

Fig. d. Part of a maturing cystocarp developing attached to an auxiliary cell branch. Note (arrows) fusion of some of the proximal cells of the gonimoblast.

Scale bar = 20 μm
Figure 62


Apex of indeterminate branch showing the characteristic pattern of cell divisions. Only axial cells and cells of one of a pair of major whorl branches are shown.

Scale bar = 20 μm
Cryptosiphonia woodii

Fig. a. Immature carpogonial branch showing that the final two divisions of the branch are oblique. Pt. Conception, California, 13 June 1949, leg. M. Hommersand, WS in NCU.

Fig. b. Immature carpogonial branch showing the lateral trichogyne. Same collection as Fig. a.

Fig. c. Reproductive filament that appears to have both a differentiated auxiliary cell and a terminal carpogonium. Abundant proximal lateral branches and the zigzag aspect of the distal end of the branch also suggest the auxiliary-cell-branch nature of this filament. Lighthouse Park, West Vancouver, B. C., 3 March 1982, UBC.

Fig. d. Fertilized carpogonium. Trichogyne remains attached to carpogonium by only wall material. Third Beach, Stanley Park, B. C., 4 Feb. 1981, leg. D. Garbary and L. Golden, UBC A63340.

Fig. e. Fertilized carpogonium that has enlarged to fuse with cells 4 and 5 of the branch to produce a single carpogonial fusion cell. Trichogyne remains attached to carpogonium by only wall material. Same collection as Fig. d.

Fig. f. Carpogonial fusion cell attached to cells 4 and 5 of carpogonial branch. What may be remnants of two connecting filaments are attached to one end of the fusion cell although the presence of distinct wall material and their position suggest rather remains of the trichogyne. Pt. Higgins, Alaska, 5 June 1981, SCL collection.

Fig. g. Carpogonial fusion cell attached to cells 4 and 5. Several connecting filaments are also shown. Same collection as Fig. f.

Fig. h. Spermatangia. Sooke, B. C., 7 Mar. 1982, leg. T. Klinger, SCL collection.

Scale bar = 20 μm
Cryptosiphonia woodii

Fig. a. Mature auxiliary cell branch (basalmost cells not shown). Lighthouse Park, West Vancouver, B. C., 3 March 1982, UBC.


Fig. d. Auxiliary cell branch to which a mature cystocarp is attached (only three carposporangia are shown). Arrows indicate the attachment points of the gonimoblast initials to the gonimoblast initiator cell. Both the auxiliary cell nucleus and the gonimoblast initiator cell nucleus are evident in their respective parts of the fusion cell. Same collection as Fig. a.

Scale bar = 20 μm
Hyalosiphonia caespitosa

Fig. a. Apex of an indeterminate axis showing pattern of axial cell enlargement characteristic of the species and anticlinal-periclinal branching pattern characteristic of the Dumontieae of one pair of opposite whorl branches. Other cells not stippled.

Fig. b. Carpogonial branch showing characteristic cell enlargements and presence of lateral branch on lower cells of filament.

Fig. c. Carpogonial branch showing somewhat lateral trichogyne.

Fig. d. Recently fertilized carpogonium fusing with cell 5. Trichogyne remains attached by only wall material.

Fig. e. Auxiliary cell branch with abundant laterals.

Fig. f. Gonimoblast fusion cell attached to an auxiliary cell branch also exhibiting cell fusions. Small, nonstippled cells are those of lateral branches of the auxiliary cell branch. Most carposporangia not incorporated into the gonimoblast fusion cell have already been released.

Scale bar = 20 μm
Figure 66

Farlowia irregularis

Fig. a. Apex of thallus grown in culture from bisporangia. Note single apical cells and thick cuticle. FI-30, SAPS 043087.

Fig. b. Apex of spermatangial thallus grown in culture from bispores. Note break-down of cuticle above spermatangia. Same collection as Fig. a.

Fig. c. Transverse section showing secondary pit connection formation (arrows) among inner cortical cells. Aikappu, Japan, 22 June 1971, UBC A50141.

Fig. d. Transverse section showing refractive inclusions in inner cortical cells. Cape Nosappu, 29 Nov. 1978, SCL collection.

Fig. e. Peel of thallus showing characteristic stellate cells and rhizoidal filaments of the medulla. Cape Nosappu, 16 Aug. 1966, MY7-156 in NCU.

Fig. f. Bisporangia showing lateral attachment (arrow). Aikappu, Hokkaido, Japan, 2 Feb. 1977, leg. T. Shimizu, SAPS 043079.

Scale bars: a, b, e = 100 μm; c, d, f = 20 μm
Farlowia irregularis

Figs. a, b. Carpogonial branches showing characteristic cell sizes and shapes. Note the somewhat lateral trichogyne, which spirals basally in Fig. a. Lateral branches on proximal cells of the branch are evident in the lower right of Fig. a and the upper right of Fig. b. Aikappu, Japan, 2 Feb. 1977, leg. T. Shimizu, SAPS 043079.

Fig. c. Carpogonial branch with a forked trichogyne. Note that only wall material remains where cell 3 had been. Also note lateral branches from proximal cells of branch. Same collection as Fig. a.

Figs. d, e. Auxiliary cell branches showing abundant lateral branches on proximal cells. Same collection as Fig. a.

Fig. f. An immature reproductive filament in which cells of lateral branches are distinctly rhizoidal. Aikappu, 6 Apr. 1977, leg. T. Shimizu, SAPS 043085.

Scale bars = 20 μm
**Farlowia irregularis**

Fig. a. "Carposporangia" appear to be developing from a "gonimoblast" fusion cell attached to cell 4 of a carpogonial branch. Aikappu, Japan, 2 Feb. 1977, leg. T. Shimizu, SAPS 043079.

Fig. b. "Gonimoblast" fusion cell which appears to have fused with at least one vegetative cell (arrows indicate stellate arms of the vegetative cell). Note cluster of cells in lower left associated with lateral branch proliferation from a reproductive filament. Same collection as Fig. a.

Fig. c. An auxiliary cell branch that has formed an auxiliary fusion cell. The presumed auxiliary cell is attached to a large, dark cell that does not appear to be connected to any other cells (i.e., gonimoblast cells). Same collection as Fig. a.

Fig. d. Incorporation of cells of the "gonimoblast" into a "gonimoblast" fusion cell. Aikappu, Japan, 6 Apr. 1977, leg. T. Shimizu, SAPS 043085.

Fig. e. A "gonimoblast" fusion cell. Small, darkly stained cells on the right belong to several different reproductive filaments. Same collection as Fig. d.

Fig. f. Transverse section of thallus showing cystocarps in inner cortex-outer medulla. Note characteristic darkly staining cells of lateral branches associated with reproductive filaments at lower left of cystocarp. Same collection as Fig. d.

Scale bars: a-c = 20 μm; d, e = 50 μm; f = 100 μm
Figure 69

Fig. a. *Dilsea carnosa*. Kristineberg, Sweden, 10 Jan. 1959, W-158 (#725) in MASS.

Fig. b. *Dilsea carnosa*. Kristineberg, Sweden, 23 July 1946, UBC A23825.

Fig. c. *Dilsea integra*. Point Lay, Alaska, 17 Aug. 1972, W-750 in MASS.

Fig. d. *Dilsea integra*. W-748 in MASS.

Fig. e. *Dilsea californica*. Pt. Higgins, Alaska, 5 June 1981, SCL 6281.

Fig. f. Upper specimens, *Neodilsea yendoana*. Lectotype, upper right. Lower specimens, "*Schizymenia dubyi*." Oshoro, Hokkaido, Japan, 6 Dec. 1942, HAK.

Fig. g. *Dilsea californica*. Narrow Cape, Alaska, 3 July 1981, SCL 6511.

Fig. h. *Kallymenia? integra*. Lectotype. Mussel Bay, Spitsbergen, 23 Dec. 1872, UPS.

Fig. i. *Dilsea pygmaea* (=*Dilsea californica*). Holotype. San Francisco, California, 6 Nov. 1896, UC 96313.

Scale bars = .10 cm
Figure 70

Fig. a. *Neodilsea crispata*. Holotype. Utoro, Hokkaido, Japan, 23 Sept. 1969, SAPS 029716.

Fig. b. *Neodilsea integra* var. *longissima*. Holotype. Masuichihama, Hokkaido, Japan, 14 Aug. 1972, SAPS 029790.

Fig. c. *Neodilsea tenuipes*. Holotype. Horoman, Hokkaido, Japan, 7 Aug. 1951, SAPS 027551.

Fig. d. *Neodilsea borealis*, as *Iridaea mertensiana*. Wilkes Expedition. Puget Sound?, Wash., NY.

Fig. e. *Schizymenia borealis*. Lectotype. Blakely I., Wash., 20 Sept. 1962, UCSB.

Fig. f. *Neodilsea borealis*. Anton Larsen Bay, Alaska, 4 July 1981, UBC A39292.

Fig. g. *Neodilsea natashae*. Juvenile thalli. Pt. Louisa, Alaska, 11 June 1979, UBC A65917.

Fig. h. *Neodilsea natashae*. Upper specimen, holotype. Between Indian and Coghlan Is., Alaska, 6 Oct. 1978, UBC A65915.

Fig. i. *Dilsea californica*. "Sunshine Cove," Alaska, 27 Aug. 1980, SCL 6252.

Scale bars = 10 cm
Figure 71

Fig. a. **Neodilsea borealis.** Portion of a transverse section showing stellate shape of inner cortical cells due to the formation of secondary pit connections and the large, darkly stained refractive inclusions characteristic of inner cortical cells of this species. Blakely I., Wash., 20 Sept. 1962, leg. M. Neushul, isotype in UCSB.

Fig. b. **Neodilsea natashae.** Planar section of blade showing refractive (stained with aniline blue) stellate medullary cells. Rogers Reef, B. C., 2 June 1973, SCL collection.

Fig. c. **Neodilsea borealis.** A fertilized carpogonium which has started to expand but which has not yet divided or contacted other cells of the branch. Bath I., B. C., 5 Oct. 1982, leg. S. Lindstrom, WS 1442 in UBC.

Fig. d. **Dilsea californica.** A gonimoblast fusion cell attached to an auxiliary cell branch. Note the fusion (arrow) of distal cells of the auxiliary cell branch. Bamfield, B. C., 20 Oct. 1982, leg. S. Lindstrom, WS 1448 in UBC.

Fig. e. **Neodilsea yendoana.** A mature cystocarp showing the extent of a gonimoblast fusion cell. Oshoro, Hokkaido, Japan, 25 Nov. 1978, leg. Y. P. Lee, SCL 3331.

Fig. f. **Neodilsea crispata.** A gonimoblast fusion cell attached to an auxiliary cell branch. Note the greatly enlarged pit connections (arrows) between distal cells of the branch. Utoro, Hokkaido, Japan, 23 Sept. 1969, leg. M. Masuda, SAPS.

Scale bars: a, c - f = 20 μm, b = 200 μm
Figure 72


Fig. a. Part of a transverse section of the thallus showing outer cortical files of rectangular to elliptical cells and inner cortical stellate cells joined by conjunctor cells (arrow) and producing rhizoidal filaments.

Fig. b. Immature reproductive filament.

Fig. c. A mature carpogonial branch. The basal cell of the branch also bears three incompletely differentiated lateral branches.

Fig. d. A reproductive filament bearing what may be a terminal auxiliary cell and several moniliform lateral branches.

Scale bar: a = 50 μm; b - d = 20 μm
A reproductive filament bearing what may be a terminal auxiliary cell. The proximal cells of the auxiliary cell branch bear laterals, many of which come to resemble rhizoidal filaments distally and some of which fuse via conjunctor cells (arrows) to vegetative (rhizoidal) cells.

Scale bar = 20 μm
**Figure 74**


Fig. a. An auxiliary cell branch bearing a subterminal auxiliary cell and lateral branches fused to vegetative cells via conjunctor cells.

Fig. b. Production of gonimoblast filaments (=carposporangia) from a gonimoblast initial (the gonimoblast initiator cell is not shown here).

Fig. c. A gonimoblast initiator cell with the outgoing connecting filament still attached. Some of the gonimoblast filaments arising from the initiator cell have already been incorporated into a gonimoblast fusion cell.

Scale bar = 20 µm

Fig. a. A gonimoblast fusion cell showing incorporation of gonimoblast cells into the fusion cell. The cells of the auxiliary cell branch have also fused into a single cell which is continuous with the gonimoblast fusion cell through the point (arrow) of original contact between the connecting filament and the auxiliary cell.

Fig. b. An earlier stage in fusion cell formation in which the pit connections between the distal cells of the auxiliary cell branch have enlarged but no cell fusions have taken place. Note that the half of the pit connection closer to the auxiliary cell is always somewhat broader.

Fig. c. Two tetrasporangia showing their intercalary attachments. (Black dots at both ends of sporangia represent pit connections.)

Scale bar = 20 μm
Dilsea californica

Fig. a. Carpogonial branch prior to the final division cutting off the carpogonium. La Push, Washington, 27 Aug. 1969, leg. M. Hommersand, NCU.

Fig. b. Carpogonial branch after the carpogonium has been cut off but prior to elongation of the trichogyne. Same collection as Fig. a.

Fig. c. A mature carpogonial branch showing enlarged nuclei in the distal cells of the branch. Bamfield, B. C., 20 Oct. 1982, leg. S. Lindstrom, WS 1448 in UBC.

Fig. d. A carpogonial branch showing post-fertilization division of the carpogonium. Same collection as Fig. a.

Fig. e. A carpogonial branch showing post-fertilization fusion of the divided carpogonium with cells 4 and 6. A diploid nucleus is present in each carpogonial derivative cell but is not shown. Same collection as Fig. a.

Scale bar = 20 μm
Dilsea californica

Fig. a. Connecting filaments arising from the carpogonial derived cell attached to cell 4 (it is not clear whether the piece behind cells 5 and 6 is part of the divided carpogonium or part of a connecting filament or whether it is attached to another cell). Haystack Rock, Ore., 22 Oct. 1973, leg. J. Markham, UBC A49257.

Fig. b. A mature auxiliary cell branch. Note the size relations of the distal cells of the branch and the enlarged nuclei of these cells. La Push, Wash., 27 Aug. 1969, leg. M. Hommersand, NCU.

Fig. c. An auxiliary cell branch after contact by a connecting filament showing a segmented outgoing connecting filament and gonimoblast initiation from several of the segments. Same collection as Fig. a.

Scale bar = 20 μm
Dilsea californica

Fig. a. An auxiliary cell branch after contact by a connecting filament showing segmented outgoing connecting filament and carposporangial initiation from several of the segments. Haystack Rock, Ore., 22 Oct. 1973, leg. J. Markham, UBC A49257.

Fig. b. Initiation of carposporangia from a gonimoblast initiator cell. Bamfield, B. C., 20 Oct. 1982, leg. S. Lindstrom, WS 1448 in UBC.

Fig. c. Formation of a gonimoblast fusion cell from incorporation of first-formed gonimoblast cells into the gonimoblast initiator cell. Concomitantly, the connections between cells of the auxiliary cell branch enlarge and join these cells to the fusion cell. Same collection as Fig. b.

Scale bar = 20 \( \mu \text{m} \)
Dilsea californica

Fig. a. An auxiliary cell branch bearing a maturing carposporophyte (not shown) with a profusion of lateral branches developing from the lower cells of the branch and fusing (via conjunctor cells) with rhizoidal filaments in the medulla. Bamfield, B. C., 20 Oct. 1982, leg. S. Lindstrom, WS 1448 in UBC.

Fig. b. Segment of cortex showing spermatangial mother cells each bearing one or two spermatangia. Jockey Cap Rock, Ore., 25 Sept. 1972, leg. J. Markham, UBC A49207.

Fig. c. Typical tetrasporangia, one showing its intercalary position in the cortex. Porpoise Harbour, B. C., 12 Oct. 1981, leg. D. Garbary and H. Vandermeulen, WS 1430 in UBC.

Scale bar = 20 μm
**Dilsea integra**

Fig. a. Carpogonial branch prior to the final cell division cutting off the carpogonium. St. Mary's Bay, Newfoundland, 28 June 1979, NFLD 24961.

Fig. b. A mature auxiliary cell branch. Same collection as Fig. a.

Fig. c. Tetrasporangial initials showing point of attachment to vegetative cells (arrows). Cape Peirce, Alaska, 21 June 1973, ALA unnumbered.

Scale bar = 20 μm
Figure 81

Neodilsea yendoana

Fig. a. Gonimoblast fusion cell showing the incorporation of the proximal gonimoblast cells into a fusion cell. Oshoro, Hokkaido, Japan, 25 Nov. 1978, leg. Y. P. Lee, SCL 3331.

Fig. b. Portion of cortical layer showing initiation of tetrasporangia and attachment of mature tetrasporangia. Oshoro, Hokkaido, Japan, 5 Oct. 1978, SCL 10067804 (slide).

Scale bar = 20 μm
Figure 82

Fig. a. Neodilsea longissima. A reproductive filament, reminiscent basally of one destined to bear a carpogonium or an auxiliary cell that has become rhizoidal. Muroran, Hokkaido, Japan, 11 Sept. 1935, SAPS 029757.

Fig. b. Neodilsea crispata. A connecting filament arising from a carpogonial derivative cell attached to cell 4. It is unclear whether the cell (question mark) is derived from the initial division of the fertilized carpogonium and has yet to fuse with cell 5 or whether it is just a connecting filament. Utoro, Hokkaido, Japan, 23 Sept. 1969, leg. M.-Masuda, SAPS.

Fig. c. Neodilsea longissima. Distal end of an auxiliary cell branch showing a terminal auxiliary cell. Muroran, Hokkaido, Japan, 11 Oct. 1970, leg. M. Masuda, WS in SAPS.

Fig. d. Neodilsea crispata. An auxiliary cell branch in which the auxiliary cell is approximately the same size as neighboring cells. Same collection as Fig. b.

Fig. e. Neodilsea longissima. An auxiliary cell branch in which the auxiliary cell is somewhat smaller than neighboring cells. Same collection as Fig. c.

Scale bar = 20 μm
Figure 83


Fig. a. An auxiliary cell branch showing abundant development of lateral branches.

Fig. b. An auxiliary cell branch showing enlargement of some cells of lateral branches during early cystocarp development.

Fig. c. A portion of a gonimoblast fusion cell after incorporation of proximal gonimoblast cells.

Scale bar = 20 μm
Figure 84


Fig. a. Transverse section of the cortex.

Fig. b. Distally recurved carpogonial branch (note absence of lateral branches on all but the basal cell at this stage).

Fig. c. Carpogonial branch with undifferentiated lateral branches similar to the branch bearing them.

Fig. d. Division of the fertilized carpogonium and fusion of the two carpogonial derivative cells with cells 4 and 5.

Fig. e. A slightly later stage than Fig. d. Note that the nuclei remain in their respective cells despite fusion and that the trichogyne remains attached by wall material to one of the carpogonial derivative cells.

Fig. f. One carpogonial derivative cell has fused with cell 4 and has cut off a single outgoing connecting filament; the other carpogonial derivative cell, with the trichogyne attached by wall material, has not fused with another cell, and its nucleus has become the nucleus of a connecting filament.

Upper scale bar refers to Fig. a; lower scale bar refers to Figs. b – f
Neodilsea natashae


Fig. b. Auxiliary cell branch with a terminal auxiliary cell (note two type of lateral branches). Same collection as Fig. a.

Figs. c – f. Steps in connecting filament contact of a terminal auxiliary cell and gonimoblast initiation. Fig. c. Connecting filament passing the auxiliary cell. Fig. d. Connecting filament following nuclear division; note constriction behind proximal nucleated segment. Fig. e. Proximal nucleated connecting filament segment fusing with auxiliary cell. Fig. f. Gonimoblast initiator cell with two gonimoblast initials attached to an auxiliary cell. Same collection as Fig. a.

Fig. g. Young cystocarp developing from a gonimoblast initiator cell attached to a subterminal auxiliary cell. Same collection as Fig. a.

Fig. h. Part of a mature cystocarp showing lack of gonimoblast fusion cell. Note the maintenance of the auxiliary cell and gonimoblast initiator cell nuclei in their respective cells despite cytoplasmic continuity; also note outgoing connecting filament still loosely attached). Amalga Harbor, Alaska, 17 Nov. 1974, SCL 289.

Fig. i. Mature tetrasporangia showing points of attachment (arrows) characteristic of the genus. Same collection as Fig. a.

Upper scale bar refers to Figs. a – g
Lower left scale bar refers to Fig. h
Lower right scale bar refers to Fig. i
Figure 86


Fig. a. Immature carpogonial branch.

Fig. b. Immature carpogonial branch slightly more mature than the branch in Fig. a.

Fig. c. Mature carpogonial branch.

Scale bar = 20 μm
Figure 87


Figs. a, b. Mature auxiliary cell branches with subterminal auxiliary cells.

Fig. c. A mature subterminal auxiliary cell being passed by a connecting filament.

Fig. d. A mature terminal auxiliary cell near which a connecting filament has passed and divided into an outgoing connecting filament and a gonimoblast initiator cell. The proximal end of the gonimoblast initiator cell has constricted to sever the incoming connecting filament.

Scale bar = 20 μm

Figs. a, b. Gonimoblast initiator cells contacting subterminal auxiliary cells as the outgoing connecting filaments grow on toward other auxiliary cells.

Figs. c, d. Initiation of gonimoblast filaments from gonimoblast initiator cells attached to subterminal auxiliary cells.

Scale bar = 20 μm
Figure 89

**Neodilsea borealis**

Fig. a. A developing cystocarp attached to a terminal auxiliary cell. The gonimoblast initiator cell has cut off three gonimoblast initials from which gonimoblast filaments are radiating. Bath I., B. C. 5 Oct. 1982, leg. S. Lindstrom, WS 1442 in UBC.

Fig. b. The small gonimoblast fusion cell attached to an auxiliary cell. Bath I., B. C., 9 Nov. 1982, leg. S. Lindstrom, WS 1443 in UBC.

Fig. c. Portion of cortex showing spermatangial mother cells each bearing one or two spermatangia. Sitka, Alaska, 30 July 1980, leg. S. Lindstrom, SCL 5389.

Scale bar = 20 μm
**Figure 90**


**Fig. a.** Connecting filament initiation from two carpogonial fusion cells.

**Fig. b.** A developing carposporophyte attached to a subterminal auxiliary cell. The gonimoblast initiator cell has cut off three gonimoblast initials from which gonimoblast filaments are radiating.

**Fig. c.** A gonimoblast fusion cell.

**Fig. d.** An auxiliary cell branch bearing a mature carposporophyte. Note the enlargement of the pit connections, particularly between the distal cells of the branch, and the development of lateral branches from the proximal cells of the branch.

Scale bar = 20 μm
Cladogram of species and genera of the Dumontiaceae produced by the Wagner’s and Nelson options of the PHYSYS program from data in Table V. The cladogram has a length of 197 and a consistency index of 37.06. Bars indicate character state transitions—open bars indicate reversals; closed bars, advancements. Numbers refer to Character Number in Table IV and the text; subscripts, to changes to more advanced states for multistate characters. Taxa designations are abbreviated to the first four letters of the generic and specific epithets. Character state transitions for individual taxa are listed below. Numbers preceded by an "X" refer to a reversal in that character.

Gibshawa: 11,21,23,27,30
Dudrhawa: 10,34
Krafich: X2,X37; 11,33
Dudrpatu: X19,X24; 12
Dudrjapo: X28; 10,34,35
Dudrcolo: 12
Dudrhawk: X11; 24,5,13
Dudrlubr: 24,27
Dudrpuer: X3,X5; 12,13
Dudrpegg: 6,19,24,41
Dudrcapr: X2,X28; 10,20
Dudrcras: X6; 34,35
Dudrvert: 19,24
Dudraust: X22
Farlconf: 4

Farlmoll: 21,44
Pikecali: X43,X33; 3,15,36
Orcudent: 21,23,40
Leptbing: 13,19,38
Weeksias: 14
Constant: X1;14,23,36,38,39,44,45
Dumocont: X1; 39,44
Dasyinsi: X18,X26; 4,36,38,43
Crypwood: 4
Farlirre: 17
Neodyend: X39
Dilscal: X39,42
Dilscarn: 17,42,44
Neodnata: 38
Neodbore: X35,X39
APPENDIX: REPRESENTATIVE SPECIMENS EXAMINED

Geographical abbreviations

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*Gibsmithia hawaiensis*

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**Gibsmithia sp.**

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**Kraftia dichotoma**

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**Dudresnaya verticillata**

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**Dudresnaya crassa**

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3 Type specimen of *Pikea robusta*
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| Tenakee Inlet, AK              | 9-12 Feb. 1975| ABL 636, 650, 658 |
| ²Griffin Bay, WN               | Mar. 1858     | TCD          |
| Princess Royal In., BC         | 26 Mar. 1976  | UBC A55546   |
| Cape Scott, BC                 | 11 Apr. 1970  | UBC A42954   |

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Salmon Bank, WN 18 Apr. 1980 UBC A61726
Brown I., WN 11 May 1963 UCSB
Clayoquot Sd., BC 25 May 1977 UBC A58750
Harmony I., BC 23 June 1975 UBC A53538
Orcas I., WN 27 June 1904 UC 96309
'Deer Harbor, WN 1 July 1904 UC 96308
Hein Bank, WN 15 July 1968 GMS 5867
Gabriola Reefs, BC 23 July 1976 UBC A57815
Naked I., AK 1 Aug. 1979 UBC A61312
Sear I., BC 31 Aug. 1971 UBC A46981
Decatur I., WN 17 Sept. 1962 UCSB
Blakely I., WN 20 Sept. 1962 UCSB
Salmon Bank, WN 4 Oct. 1979 UBC A61538
Arab Cove, BC 12 Oct. 1968 UBC A39248
Turnagain I., BC 15 Nov. 1974 UBC A51849
Bamfield, BC 3 Dec. 1978 UBC A59312
Hood Canal, WN 13 Dec. 1968 MJW 2377 in MICH
Tugboat I., BC 29 Dec. 1976 UBC A56583

* Weeksia templetonii *

2Isla Cedros, MX 15 Aug. 1932 CAS 236484 in UC
Isla Cedros, MX 15 Aug. 1932 UC 543986

* Weeksia howellii *

2Natividad I., MX 17 Aug. 1932 CAS 237496 in UC
Natividad I., MX 17 Aug. 1932 CAS 482550 in UC
Natividad I., MX 17 Aug. 1932 UC 543981

* Weeksia digitata *

Carmel Canyon, CA 5 Apr. 1962 US 086140
Carmel Canyon, CA 15 Apr. 1962 US 51078
Carmel Beach, CA 5 May 1965 UC 1362319
Carmel Canyon, CA 16 May 1961 US 081654
Carmel Beach, CA 17 June 1969 UC 1455023
Moss Beach, CA 10 July 1962 UC 1362318

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**Cryptosiphonia woodii**

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**Hyalosiphonia caespitosa**

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**Neodilsea crispata**

1. Utoro, HOKK
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   - 23 Sept. 1969 | SAPS 029719
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   - 23 Sept. 1969 | SAPS 029721
4. Utoro, HOKK
   - 23 Sept. 1969 | WS in SAPS
5. Rebuncho, HOKK
   - 22 Oct. 1968 | SAPS 029734

**Neodilsea longissima**

1. Masuichihama, HOKK
   - 14 Aug. 1972 | SAPS 029790
2. Masuichihama, HOKK
   - 14 Aug. 1972 | SAPS 029768
3. Shizusho, HOKK
   - 11 Sept. 1935 | SAPS 029757
4. Muroran, HOKK
   - 21 Sept. 1970 | WS in SAPS
5. Muroran, HOKK
6. Denshihama, HOKK
   - 1 Nov. 1970   | SAPS 029788

**Dilsea carnosa**

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**Dilsea integra**

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**Neodilsea tenuipes**

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