Gibsmithia hawaiiensis gen. n. et sp. n.[1]

MAXWELL S. DOTY[2]

ABSTRACT: A new genus, *Gibsmithia,* is described and tentatively placed in the Dumontiaceae of the red algal order Cryptonemiales. Its diagnostic features are: possession of auxiliary cells in specialized filaments separate from those bearing the carpogonia; the known sexual structures occurring in sori at the tips of soft, gelatinous branches which arise from perennial round stems so as to form a hemispherical head; cruciate tetraspores borne on filaments protruding from the surface of the branches and these same branch filaments often bearing terminal seirospores. The type species of the genus is *G. hawaiiensis,* known only from the island of Oahu in the Hawaiian Islands.

THE ALGA described here was first collected by Dr. J. T. Conover in 1943, and from 1951 on has been found by eight other individuals collecting in Hawaii. It seems to comprise a new genus of the Cryptonemiales in the Rhodophyta, and we take pleasure in naming it in honor of the late Prof. G. M. Smith, of Stanford University, whose publications and teachings have probably done more to facilitate work with the algae in America than has the work of any other phycologist.

Gibsmithia hawaiiensis genus et species nova

Figs. 1–17

DESCRIPTIO TYPI: Thalli ramis gelatinosis fasciculatis, e stipite erecto fere cartilaginose lignoso egredientibus, formam hemisphaericam simulantes. Frondes e filamentis uniseriatis, sicut in genere *Callithamnio,* compositae. Filamenta interdum pilis uniseriatis, multicellularibus e superficie gelatinosa ramorum exstantibus terminata. Tetrasporangia cruciformiter divisa, subsphaerica, in pilis supra descriptis unilateraliter in cymulis fortasse velut in genere *Spermothamnio* producta. Cystocarpia modo *Cryptonemialium* simili crescentia.

The holotype (Fig. 1) was found drifting in the water at Waikiki, Honolulu, Oahu, Hawaii (21° 161 min N, 157° 49.5 min W), on January 12, 1960; 19263.[3] It is cystocarpic. The type material, consisting of a liquid-preserved isotype specimen and a dried holotype herbarium specimen, is being deposited in the Bernice P. Bishop Museum in Honolulu, Hawaii. Tetrasporic material has been collected from the vertical surface of a dredge-cut in the reef at Waikiki, first on January 5, 1961, by Dr. D. W. Strasburg. This specimen (8525) is also being deposited in the Bishop Museum herbarium. Other collections are listed below.

DESCRIPTION OF GENUS AND SPECIES: Thalli (Figs. 1, 2), as generally collected, consisting of 'woody' stems and a number of soft, but not slippery, gelatinous ultimate branches. Forming bright-pink, hemispherical tufts often 8 cm high, the stems are up to 3 mm in diameter, blackish when dried, and they bear rings believed to be indicative of successive crops of the ultimate branches. The stems are cylindrical or, when large, compressed toward the apex and sometimes branched once or twice. When the stems are fresh they are colored approximately Eugenia Red or darker to Acajou Red

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[2] Department of Botany, University of Hawaii, Honolulu 14, Hawaii.

[3] Such 4- and 5-digit numbers are the collection or herbarium numbers of the author.

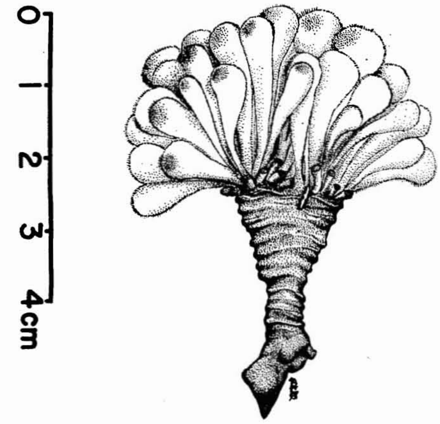


FIG. 1

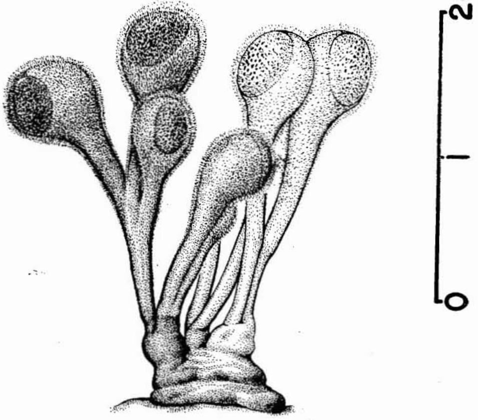


FIG. 2

FIGS. 1–2. Gross aspects of *Gibsmithia hawaiiensis* (type specimen 19263). *1,* Whole thallus illustrating the rounded stem with growth rings. *2,* A few of the soft gelatinous branches enlarged to show asymmetrical placement of the sexual sori and the superficial filaments which, in tetrasporic thalli, would bear the tetraspores and seirospores. Below is shown some of the stem material of very different, almost woody, nature and the origins and rebranching of the ultimate branches of the thallus.

(Ridgway, 1913). The soft, gelatinous, ultimate branches are lighter red in the same series or their bases are lighter and their apical portions darker. The branches are often up to 4 cm long, and they gradually enlarge apically until they are club-shaped and up to 1 cm in diameter near their tips. These ultimate branches rarely arise singly from the parent stem; more often (Fig. 2) they arise from a disk that is a flattened expanse of the same gelatinous nature and which divides somewhat dichotomously into the branches.

The gelatinous branches are made up of callithamnioid filaments (Fig. 3). The exact nature of the central axis of the thallus has not been determined, but the alga is believed to be multiaxial in structure. The major axes in the medulla bear, most often, opposite branches which seem to arise near the apical cell. Toward the exterior the branching of the filaments is pseudodichotomous, and the surface of a gelatinous branch is generally covered densely, especially toward the tip, with free tufts of such filaments.

Branches of the axial filaments in the medulla often give rise to recurrent branches (*A* in Figs. 3–5) or rhizoids, which anastomose with a particular cell of another branch (Fig. 3), the supporting cell of the branch (Fig. 4), or with the next cell below in the same branch (Fig. 5). Pit connections appear between all cells concerned in these cases. In content, the cells of such anastomosing branches, like those reported and figured by Feldmann-Mazoyer (1940: 142, 393, fig. 48) in *Pleonosporium borreri,* are not particularly different from the cells of similar nearby filaments.

Reproductive structures of three kinds have been found in the collections studied. These are interpreted as seirospores, as tetrasporangia, or as various stages and structures leading toward carpospore production. The same thallus may produce both tetraspores and seirospores, a situation I have seen in *Seirospora,* and which is reported (Feldmann-Mazoyer, 1940) in *Dohrniella.* The evidences of sexuality have been seen positively in only the type and two other collections. Unfortunately the critical stages involving the primary and secondary connecting filaments between the carpogonia and auxiliary cells have not been found. Thus, though for the present *Gibsmithia* seems certainly to be a member of the Dumontiaceae as this family is circumscribed by Kylin (1956), the description of the sexual reproduction and discussion of the systematic disposition within the family are of necessity brief.

The seirospores are borne in unbranched chains at the tips of the exterior filaments in the asexual material. At some place along a branch bearing seirospores (*B* in Fig. 5) the chromatophore and central vacuole disappear rather abruptly and the cytoplasm (after killing in Karpetchenko's seawater fluid) is then more densely granular and with a refractory body becoming conspicuous as the cells age. The spores, which are about 9 μ in diameter, appear to become more spherical with maturity, as in *Seirospora.* Their ultimate fate is unknown, but they are broken off easily in preserved material and presumably in nature.

The subspherical tetrasporangia appear on the more basal portions of scattered external filaments similar to those bearing the seirospores. They are, for the most part, in acropetalous series (Fig. 6) on the adaxial side of the filaments on which they are produced. In a few cases immature tetrasporangia were seen below an otherwise acropetalous series. In some instances what appeared to be chromosome groups undergoing meiosis were distinguished within immature tetrasporangia. The tetrasporangia are apically dehiscent, as in *Antithamnion,* and at least the terminal sporangia were pedicellate. The first division of the cytoplast in the tetrasporangium (Fig. 7) is near the equatorial plane. Usually the tetraspore pairs are at right angles to each other, i. e., decussately cruciate (Figs. 8, 9); only rarely is a somewhat tetrahedral (Fig. 10) or other (Fig. 11) arrangement seen. The tetraspore groups in the collection 12343 are often as long as 25 or 30 μ in their major dimension.

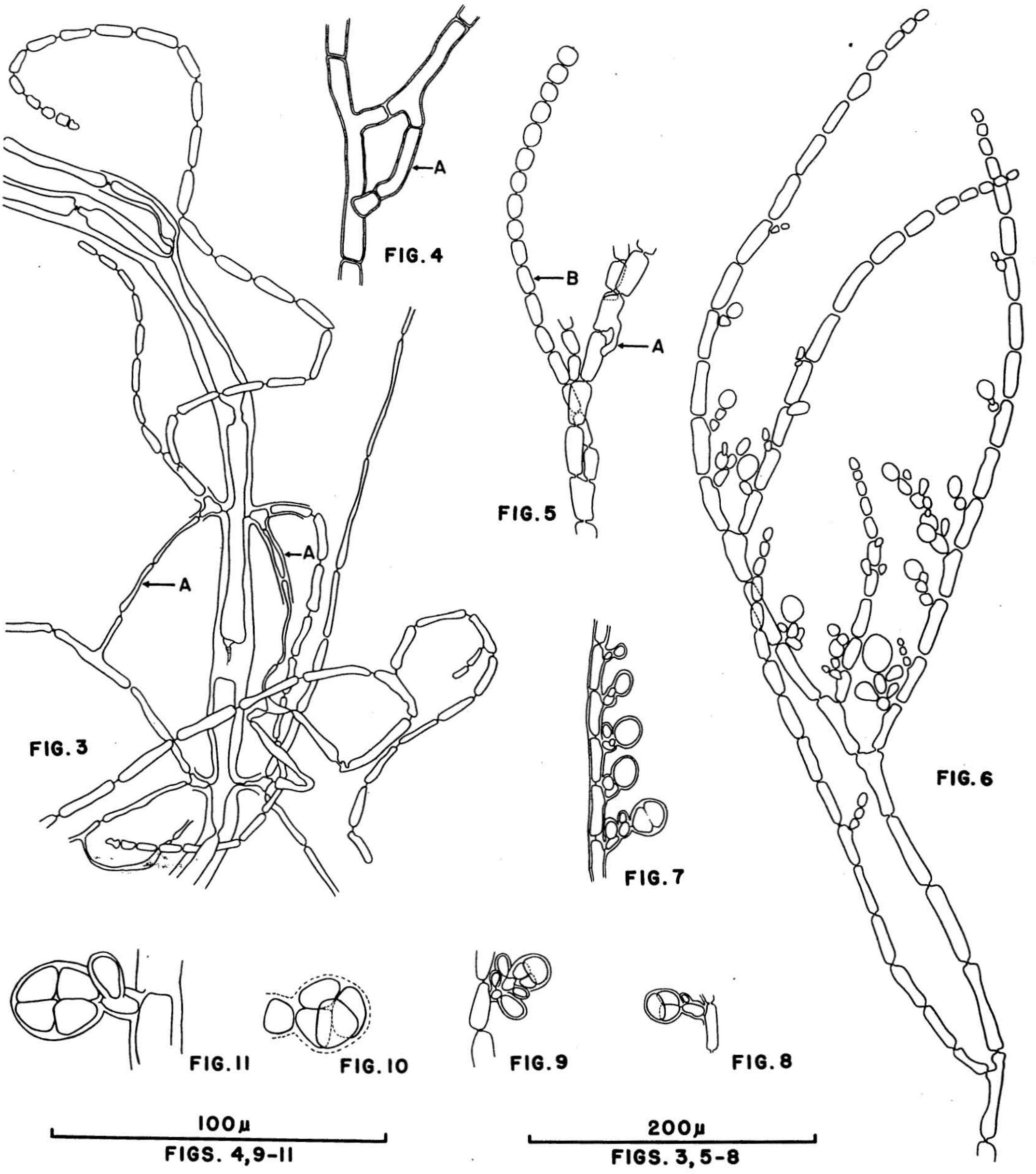
The maturing cystocarps, when stained, appear as dots in raised asymmetrically placed welts (Figs. 1, 2) near the tips of the branches. The largest thalli collected, 10386, were believed to be sterile until smears made of the branch tips were examined. When this was done what are accepted as carpogonial branches (Figs. 12–14) bearing nonfertilized carpogonia were found.

The carpogonial branch of *Gibsmithia* is the terminal portion of a modified member of the two lateral branch systems arising (Fig. 13) from a cell in a medullary filament. Upon occasion both lateral branch systems bear carpogonia; less frequently only one of the members is carpogonial, and the other is vegetative but reduced in its development. Only monocarpogonial branch systems have been seen. Branching from the cells below the special cells of the carpogonial branch is variable. In some cases there are no such branches (Fig. 12), and in others (e. g., Figs. 13, 14) up to three branches of one to six small cells each occur. The cells of these branches, except for size, are of the same appearance as the homologous cells in vegetative branches nearby.

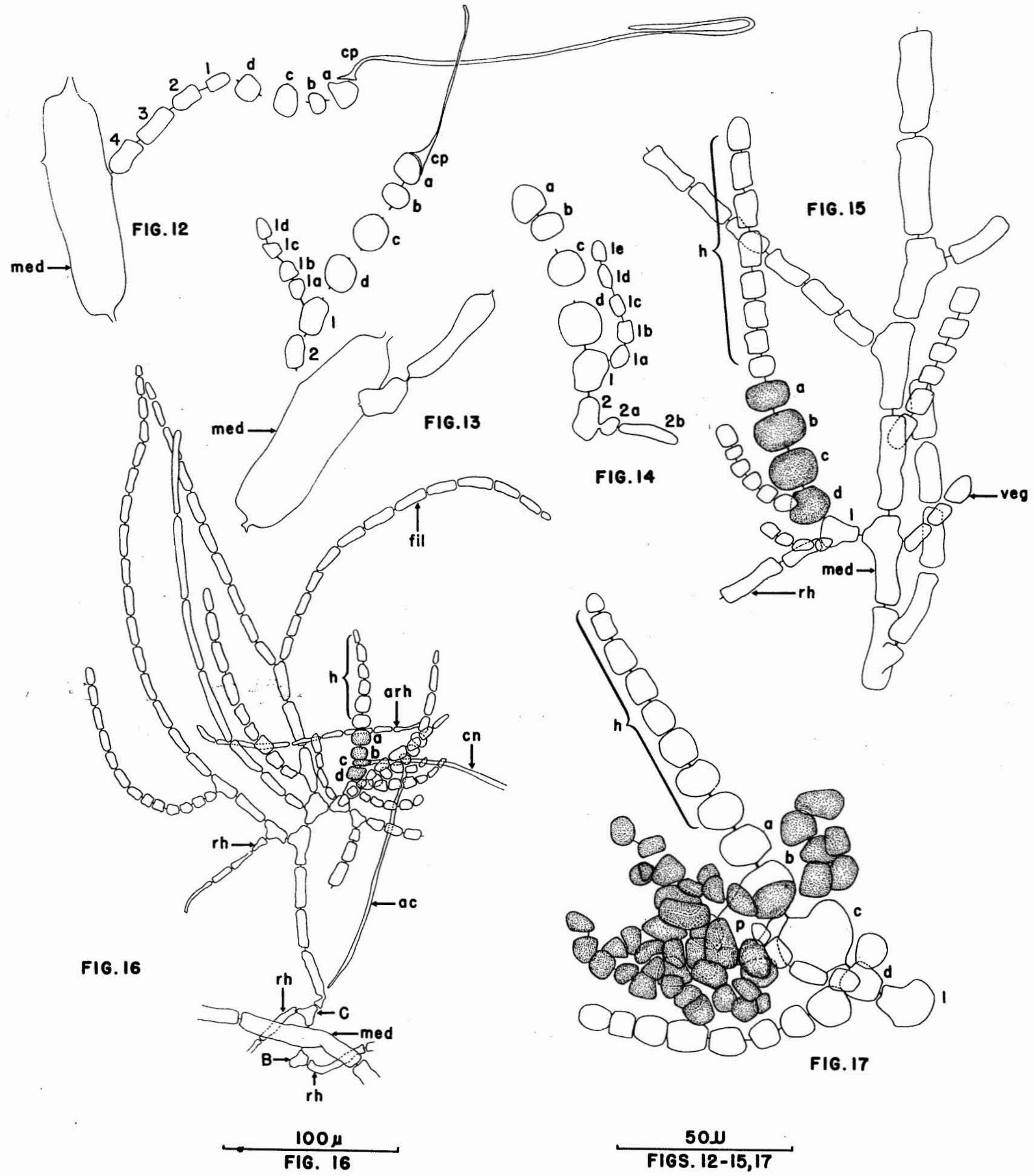
The carpogonial branch itself is consistently composed of five cells (*cp, a, b, c,* and *d* in Figs. 12–14), though the terminal carpogonium is (Fig. 14) not always present. The antepenultimate cell (*b* in Figs. 12, 13) is smaller than the other hypogynous cells. Its contents are often of different appearance and it is flattened, so that its axial length is noticeably less than its diameter. The other three hypogynous cells are more spherical, similar in content, and the largest one (*c* in Figs. 12, 13) is usually about 9 to 13 μ in diameter. The remaining two (*a, d* in Figs. 12, 13) are usually similar in size.

The carpogonium is borne on the first[4] hypogynous cell excentrically, often by a displacement from the axis of the carpogonial branch of about 45 degrees. The carpogonium (*cp* in Figs. 12, 13) is usually relatively small and does not stain strongly in aniline-blue, in contrast to the other cells of the carpogonial branch.

In the material available, stages were not found which would enable a satisfactorily complete description of sexual reproduction. However, my impression is that the heavily aniline-blue stained condition of almost all carpogonial branches seen is a result of development beyond the fertilizable point. Most such branches consist of either only the cells *a* through *d* (Fig. 14) or have in addition what are interpreted as remnants of a carpogonium. Such carpogonial branches are relatively straight and not



FIGS. 3–11. Vegetative and asexual reproductive microscopic structural details of *Gibsmithia hawaiiensis* (collection No. 12343). *3,* An axial filament from the medullary region of a gelatinous branch of the thallus showing the opposite ramification of the medullary filaments and, *A,* characteristic reconnecting rhizoidal branches. *4,* A more simple reconnecting rhizoidal branch, *A,* from one of the subdichotomous cortical filaments. *5,* A seirospore-bearing ultimate branchlet on a subdichotomous cortical filament with, *A,* a very simple reconnecting filament or rhizoid. Such lateral nonrebranched filaments, *B,* with a terminal series of seirospores were found arising from almost every second cell in the vegetative axis of this part of the filament system. The origins of but three such seirosporic branches are shown here. *6,* A tetrasporangium-bearing cortical filament system. Divisions within the tetrasporangia are not shown and no attempt was made to represent all pit connections. *7–11,* Tetrasporangia in various stages of maturity. The arrangement of spores is always at first cruciate but, as indicated by Figure 10, in age they may not be in a strictly cruciate arrangement.



FIGS. 12–17. Microscopic sexual reproductive features of *Gibsmithia hawaiiensis.* The specialized cells, *a–d,* are similar in nature whether in a carpogonial or auxiliary-cell branch. On the latter, the piliform extension, *h,* shows as a multicellular hair, the cells of which are in staining reaction and appearance, rather like vegetative cells of similar size and relative terminal position elsewhere. *12–14,* Carpogonial branches with or without nonfertilized carpogonia, *cp.* The hypogynous cells *a–d* were always densely granular and their contents took up aniline-blue from aqueous solution much more than did the other nearby cells. Cell *b* was usually smaller and the contents were usually different from the rest. Cell *c* was almost always the largest. The numbered cells, 1, 2, 3, etc., represent cells that looked like the strictly vegetative cells of similar size and position nearby and connected the carpogonial branch to a medullary cell, *med.* The cytologically similar cells of the sterile branchlets are indicated as *1a, 1b, 1c,* etc. (Collection No. 10386.) *15,* A nonfertilized auxiliary-cell branch arising from one of two opposite branch systems of the same medullary cell, *med,* the one vegetative branch system, *veg,* being of only three cells, the other more extensive and bearing an auxiliary-cell branch.

strongly curved apically, as is usual in the Dumontiaceae. In a very few cases carpogonium-bearing branches that are more curved are found with hypogynous cells that are less highly differentiated in staining quality and in form. In these cases the hypogynous and carpogonial cells are more nearly similar in staining quality and are smaller; such (Fig. 12) are judged to be more nearly normal.

Primary connecting filaments[4] were not seen, and no clues as to the origin of the abundant, presumed secondary, connecting filaments that connect to the auxiliary cells were found. In a very few cases the carpogonium as well as the cell beneath it were seen to have some indication of protuberances extending toward one another or toward the smallest of the hypogynous cells. This could have been the effect of smearing the material for microscope examination.

The auxiliary-cell branches (Fig. 15) develop farther from the apex than the carpogonial branches. It may be that initiation, or at least maturation, of an auxiliary-cell branch system is dependent upon fertilization, for in 10386, where many nonfertilized carpogonial branches were found, especially of the forms illustrated in Figures 13 and 14, branches bearing mature auxiliary cells were not observed. They are usually in the same positions as carpogonial branches, or, at times, appear to have developed (Fig. 16) after the lateral branch system had grown further.

While the complement of cells in the auxiliary-cell branches is similar in number, form, arrangement, and appearance to the hypogynous cells in a carpogonial branch, there are two major differences: in place of the carpogonium there is a reduced terminal branch or row of vegetative cells, and there are more sterile filaments developed laterally from and near the base. The auxiliary cell itself is an intercalary cell, and, contrary to the condition illustrated in Figures 15 and 16, is usually the cell there labeled as *b*.

The presumed secondary, connecting filaments (*cn* in Fig. 16) were seen fused with the auxiliary cells (*c* in Fig. 16). The tissue of the weltlike sori (Fig. 2) in which cystocarps develop is the toughest of all parts of the branch surface and this toughness seems to be related to the great abundance of sterile branches appearing in the fertile system, as well as to numerous, presumed secondary, connecting filaments. In addition, multicellular rhizoidal branches from the bases of the branch filaments (*rh* in Figs. 15, 16, and possibly *A*

This particular auxiliary-cell branch would seem to be peculiar, for usually one of the two cells labeled *b* and *c* is about half the size of the cells labeled *a* and *d*, which are similar in size. The other cell, *c* or *b*, is usually distinctly the largest of the four. A rhizoidal branch, *rh*, arises from the single vegetative cell, *l*, connecting this auxiliary-cell branch system to the medullary system. (Collection No. 19263.) *16,* A lateral branch system arising as one of a pair, *B* and *C*, from a single medullary cell, *med*, and producing vegetative filaments, *fil*, and rhizoidal filaments, *rh*, in a normal manner, and showing (at *c*) a fertilized auxiliary cell. Two other types of filaments are illustrated here: what may be labeled as an accessory rhizoid, *arh*, of multicellular nature arising near a fertilized auxiliary cell and, *ac*, an accessory connecting filament. The auxiliary cell, *c*, is shown with a connecting filament, *cn*, associated. The actual relationships of cells, *c*, *cn*, and *ac*, to one another were not entirely clear at the highest magnifications. (Collection No. 19263.) *17,* A young gonimoblast showing the apparent carposporogenic cells heavily stippled. Cell *1*, seemed to correspond to cells *B* and *C* in Figure 16. Cell *d* bore three vegetative branches in addition to the auxiliary-cell branch. No connecting filament could be distinguished. Seemingly, the auxiliary cell, *b*, had produced the gonimoblast to the left at the tip of the expansion, *p*, from but one gonimoblast initial. The six cells to the right seemed unattached and were interpreted as having been broken free from the mass at the left. (Collection No. 19263.)

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[4] The author is attempting to apply terms to the post-fertilization morphological phenomena in such a way that they are consistent with general biological usage, and so that the frequent special cases and variations from the normal do not require a special nomenclature. Thus, the term "zygote" is used for the post-fertilization carpogonium and its contents, and "primary connecting filament" for the connection between the zygote and the auxiliary cell without distinguishing whether a "carpogonial" or "generative" auxiliary cell is concerned. "Secondary connecting filament" is used to refer to any connecting filament ("ooblast" of the older nomenclature) arising from an auxiliary cell. Similarly, the term "hypogynous" is used for any of the specialized cells of the carpogonial branch other than the carpogonium itself; these are referred to as *a, b, c,* etc., or the "first," "second," etc., proceeding away from the carpogonium.

in Fig. 3) are abundant, and undoubtedly contribute to the strength of the otherwise weak, gelatinous, branch substance.

The surface of the auxiliary cell (*b* in Fig. 17), beneath the connecting filament, apparently develops a protrusion that moves the connecting filament away from the auxiliary-cell branch axis. From this protuberance of the auxiliary cell (*p* in Fig. 17) gonimoblast initials arise. While the gonimoblast, upon smearing, reveals its fundamentally filamentous nature (Fig. 17), in the undisturbed condition it is a dense almost spherical mass. Older gonimoblasts have one (or a few) very large cells at the center: all the other cells appear to be uniform, as though all could become carposporangia in time.

MATERIALS EXAMINED (all from the island of Oahu, Hawaii; the collection numbers are the author's, except the first): *J. T. Conover,* 200 BERKELEY,[5] tetrasporic, found about 550 ft along a line extending about 113° from the old marine laboratory at Waikiki on underside of a coral head about halfway out on the reef at a depth of 1.2 m, VIII-43; *D. W. Strasburg,* 8525 (BISHOP) tetrasporic and seirosporic, University of Hawaii old beach laboratory, Waikiki, Honolulu (21° 16.2′ N, 157° 49.6′ W), I-51; *M. Doty,* 8562 (STANFORD), another branch of the same thallus as 8525, but collected 25 days later; *George Ikeda,* 10385 (AUSTRALIA) tetrasporic, Lae o Kaoio, Kualoa, Kaaawa, one of two clumps seen in 5 ft of water, II-52; *George Ikeda,* 10386 (STANFORD, BERKELEY) carpogonial, in 4-5 ft of water on limestone bottom (same area as Ikeda collection of II-52, above), V-52; *Jack Randall,* 17020 (BERKELEY) seirosporic, drifting freely below the surface off Oahu, Hawaii, VI-52; *M. Doty,* 12343 (STANFORD) tetrasporic, floating freely at the surface just north of the mouth of Koloa stream south of Laie, I-54; *M. Doty,* 12286 (HOKKAIDO) first of a series of collections from the same tetrasporic thallus growing about 7 ft below the surface along the inshore edge of the swimming channel in front of the new University of Hawaii beach laboratory at Waikiki, Honolulu, XII-52; *M. Doty,* 12652 and 12647 (PARIS) tetrasporic, both same thallus as 12286, about X-54; 17019 (BISHOP) sterile, same thallus as 12286, III-55; *Jan Newhouse* and *Malvern Gilmartin,* 12671 (VANCOUVER) tetrasporic, beyond the reef, Waikiki, Honolulu, XI-54; HOLOTYPE, *M. Doty* and *B. C. Stone,* TYPE 19263 (BISHOP) cystocarpic, drifting at the surface, Waikiki, Honolulu, (near 21° 16′ N, 157° 49.5′ W), I-60; *Elvin Fong,* 19478 (STANFORD) cystocarpic and tetrasporic, on a 3 by 4 ft rock in 15 to 20 ft of water 150 yd off Haleiwa Army Beach near the channel at Haleiwa, VI-55.

This is one of the less common algae occurring along the shores of Oahu in Hawaii. It has been found adrift in a few cases, but for the most part it is found growing 1 to 2 m below low tide on reef flats. The hemispherical pale thalli were often found growing in a concavity or on a vertical surface. One individual thallus, near the University's aquarium and beach laboratory at Waikiki in Honolulu, was watched and pieces were harvested from it at irregular intervals for about 3 yr. The deepest collection was that made by Jan Newhouse and Dr. Malvern Gilmartin from the base of a coral patch on rock bottom in 7 m of water about 1000 m beyond the reef opposite the Natatorium at Waikiki.

The stem, the perennial nature of the thallus and some of the reproductory features of *Gibsmithia* show some resemblance to the much recopied small portion of Gmelin's specimen (1768: pl. 5, fig. 2) of *Constantinea*[6] (e. g., Kylin, 1956: fig. 102).

It is to be noted that at least three collections of *Gibsmithia,* including the type, were of free-floating branches. It would appear that the

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[5] Names appearing in this position refer to the following repositories of the particular material: BISHOP, B. P. Bishop Museum, Honolulu, Hawaii; STANFORD, Hopkins Marine Station of Stanford University, Pacific Grove, Calif.; BERKELEY, Herbarium of the University of California, Berkeley, Calif.; PARIS, Laboratoire de Cryptogamie du Museum National d'Histoire Naturelle; AUSTRALIA, Herbarium of the University of Adelaide, Adelaide, S. Australia; HOKKAIDO, Herbarium of the Faculty of Science, Hokkaido University, Sapporo, Japan; VANCOUVER, Herbarium of the University of British Columbia, Vancouver, British Columbia.

[6] The figure given by Okamura (1912: pl. 77, figs. 1, 2) conveys a rather different conception of this alga—a more correct one it would seem.

branches are deciduous at maturity, as is the disklike peltate blade of *Constantinea simplex.* However, the many quite different features of *Constantinea,* especially as revealed by Masaki (1952), indicate that *Constantinea* could be, at best, but remotely related to *Gibsmithia.*

Some of the anatomical features, the seirospores, and tetrasporangia are reminiscent of the Ceramiaceae. Yet I believe *Gibsmithia* should be placed among the primitive Cryptonemiales for several reasons, most notable of which is the occurrence of the carpogonia and the auxiliary cells in separate but similar special branch systems. In their general morphology and in having a small differentiated cell among the enlarged hypogynous cells, the carpogonial branches of *Gibsmithia* (if, indeed, we have seen normal carpogonial branches) recall both the carpogonial and auxiliary-cell branches of *Dudresnaya crassa,* as I have seen them in material collected by Dr. A. J. Bernatowicz in Bermuda (his number 51-580), and as they are illustrated by Taylor (1950: figs. 5–7, 38) in his splendid account of the reproduction of that species.

The terminal row of sterile cells distinguishes an auxiliary-cell filament from a carpogonial branch with its terminal trichogyne. While the terminal row of sterile cells is distinct from the terminal part of a normal vegetative branch, it is less specialized than the "hair" to be seen in *Dudresnaya crassa* and which Taylor (1950: figs. 36, 37) refers to as a "piliform extension." In other features *Gibsmithia* also recalls such a genus as *Dudresnaya* rather than any of the polycarpogonial forms discussed by Norris (1957), which are far more complex. It is like *Thuretellopsis* (Kylin, 1925: 14) in that the carpogonial and auxiliary-cell branches are alike; but in *Gibsmithia* they are less compact and less specialized. In having a terminal row of sterile cells and in having a larger number of cells, the auxiliary-cell filaments of *Gibsmithia* would seem to be more primitive than those of *Thuretellopsis.*

A point of some systematic interest is the development of low, wartlike sori containing the cystocarps. The tetrasporangia are borne quite differently, being exposed as in the Ceramiaceae. These two features seem to set this genus apart from most of the other genera now placed in the Dumontiaceae. The possession of cruciately divided tetrasporangia further distinguishes *Gibsmithia* from the type genus of the Dumontiaceae and likens it to families such as the Squamariaceae of the Cryptonemiales which have cruciate tetrasporangia and the reproductive structures in nemathecia. Until the simpler cryptonemiaceous families are better known, it seems best to place *Gibsmithia* tentatively among the Dumontiaceae.

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