

Observations on Two Species of *Liagora* (Rhodophyta)¹

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ALTHOUGH THE ONTOGENY of the cystocarp has been studied in a number of species of the nemalionalean genus *Liagora* (Butters, 1911; Børgesen, 1915–20, 1927; Kylin, 1930; Yamada, 1938; Levring, 1941; Abbott, 1945), gaps still exist in our knowledge of the development of this structure. Thus, little precise information is at hand concerning the place of origin of the so-called involucreal filaments and as regards the presence or absence of a fusion-cell in the mature cystocarp of certain species (see Papenfuss, 1946: 433, 434). The present account is based upon a study of two Hawaiian species, *L. maxima* Butters and *L. Papenfussii* Abbott, material of which was kindly placed at the disposal of the writer by Professor Papenfuss.

LIAGORA MAXIMA

Described by Butters (1911) from the Hawaiian Islands, this species was again reported by Abbott (1945). The material studied by the writer was collected by Papenfuss on the Island of Oahu (1.8 miles west of Nanakuli) on May 16, 1941.

STRUCTURE OF THALLUS: The general habit and structure of *Liagora maxima* have been well described by both Butters and Abbott. Although the thallus varies greatly in length, some specimens may attain a height of as much as 40 cm., which marks this species as one of the largest in the genus. The plants are very much calcified. The main branches arise at or near the base and constitute per-

current axes from which issue branches of limited growth. The main axes and their branches are composed of a central core of compact, vertical filaments (the medulla) from which are produced radially directed assimilatory laterals (the cortex). The lateral filaments are repeatedly dichotomously branched—up to the sixth order (Fig. 1*a*). The length of the cells of these filaments and the distance between the dichotomies gradually diminish toward the surface of the thallus. In younger parts the assimilatory filaments often terminate in long hairs.

REPRODUCTION: *Liagora maxima* is dioecious. The spermatangia are borne in clusters at the extremities of the assimilatory filaments (Fig. 1*b, e, f*). At the tips of these filaments from one to six spermatangial mother cells are formed, each of which produces one to three spermatangia.

The carpogonial branches are produced laterally on the assimilatory filaments (Figs. 1*c, d, g, 2 d*) and usually in the younger parts of the thallus—at times even before the assimilatory filaments are fully developed (Fig. 1*d, g*). They are generally formed on the cells behind the third or fourth furcation and are characteristically composed of three cells (Figs. 1*d, 2a, b, d, b*) but are sometimes four-celled. The mature carpogonium has a long trichogyne which projects beyond the periphery of the thallus. In a few instances spermatia were seen attached to the tip of the trichogyne (Fig. 2*d*).

After fertilization the content of the trichogyne is separated from that of the carpogonium proper (Fig. 2*a, b, b*). The carpogonium then divides by a transverse septum, forming a stalk cell and a gonimoblast initial (Figs. 2*e, 3e*) from which is produced the gonimoblast (Fig. 2*c*). The gonimoblast con-

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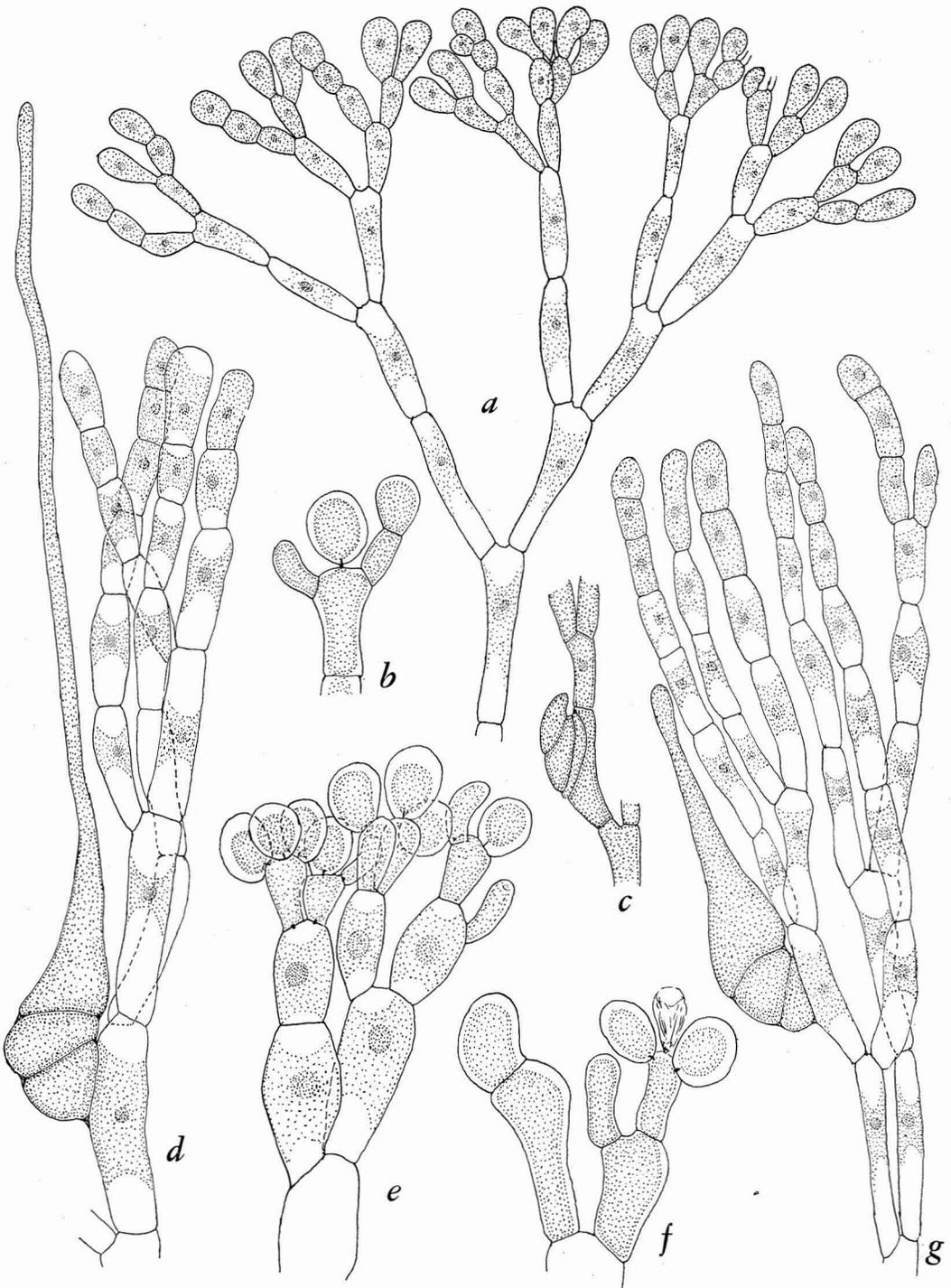


FIG. 1. *Liagora maxima* Butters. *a*, Assimilatory filament, $\times 553$; *b*, *e*, *f*, antheridia, $\times 2266$; *c*, *d*, *g*, carpogonial branches, $\times 1133$.

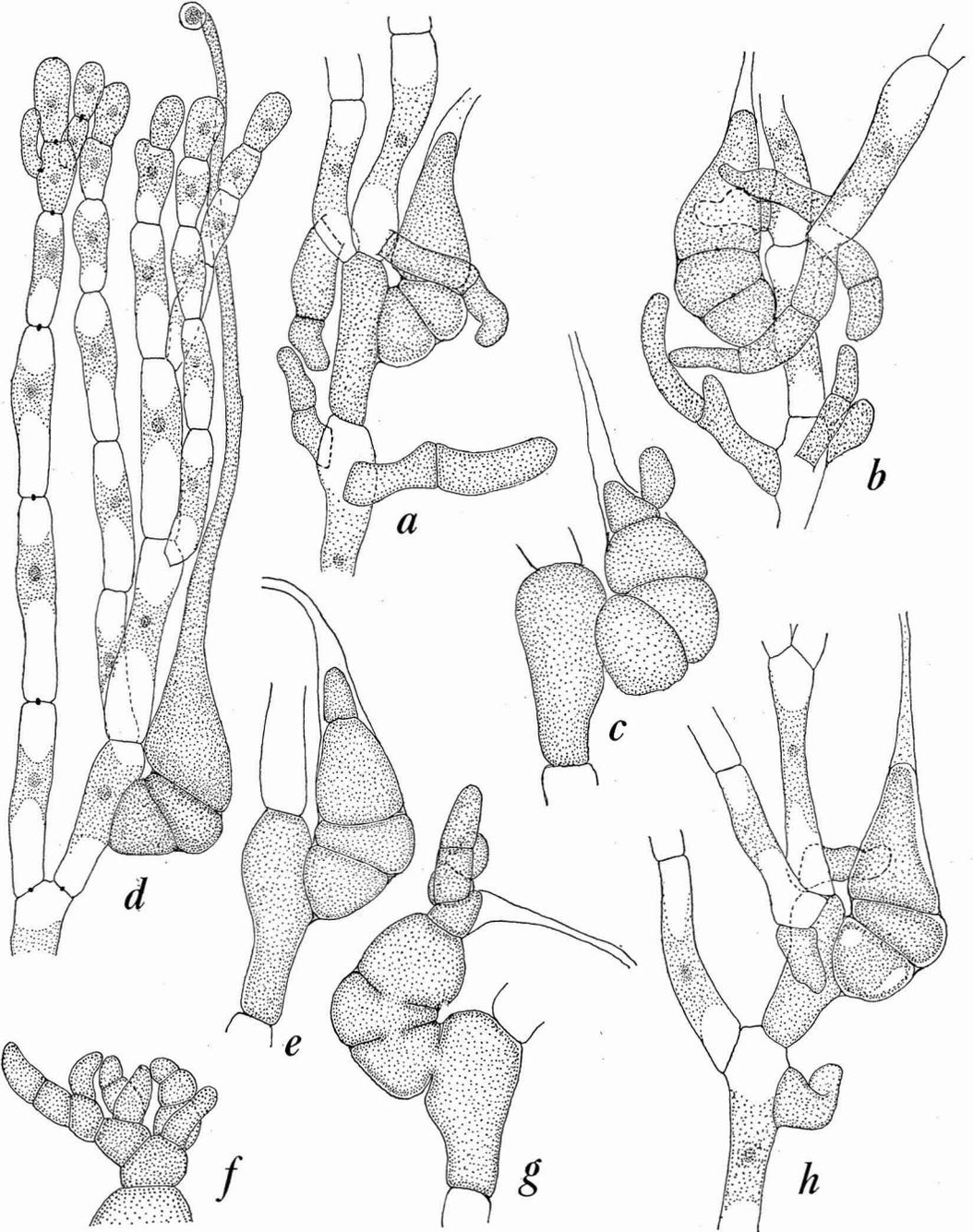


FIG. 2. *Liagora maxima* Butters. *a-c*, *e-h*, Post fertilization stages; *d*, carpogonial branch showing trichogyne with attached spermatium. All $\times 1020$.

sists of branched filaments (Figs. 2*f*, *g*, 3*a-c*) which form terminal carposporangia (Fig. 3*c*, *d*).

Soon after fertilization of the carpogonium, involucrel filaments are initiated. These filaments are formed by the vegetative cells above and below the supporting cell and rarely also by other vegetative cells in the neighborhood of the carpogonial branch (Fig. 2*a*, *b*, *b*). The involucrel filaments grow up and around the developing gonimoblast and are very much branched (Fig. 3*a*). They are generally narrower than the gonimoblast filaments and have a dense cytoplasmic content. Later, as the development of the gonimoblast advances, vacuolization of the cells of the involucrel filaments becomes evident and the filaments ultimately lose most of their contents and become colorless (Fig. 3*c*).

Concurrently with the formation of the gonimoblast, changes occur in the cells of the carpogonial branch. These cells acquire a dense content and increase in size, often becoming two or three times larger than they originally were (Fig. 2*c*, *g*). The protoplasmic connections between the cells gradually widen, resulting finally in the establishment of a large fusion-cell, comprised of the supporting cell, the cells of the carpogonial branch, and the stalk cell (Figs. 2*g*, 3*b*, *f*). The gonimoblast initial is not incorporated in the fusion-cell. At first, the fusion-cell has a dense content but later, as the gonimoblast continues growth, the content gradually becomes vacuolated and less dense.

The account of the development of the gonimoblast of *Liagora maxima* presented here is, in some respects, at variance with the description as given by Abbott (1945). According to her the carpogonial branch is four-celled when mature. In the present investigation, the mature carpogonial branches were almost always observed to be three-celled—only rarely do they become four-celled. This is the only species of *Liagora*, in addition to *L. viscida* (Kylin, 1930), in which a fusion-cell has been observed. According to Abbott the

involucrel filaments are formed from the supporting cell, but in the present study they were observed to be produced by the vegetative cells above and below the supporting cell—never from the supporting cell.

LIAGORA PAPANFUSSII

This species was described by Abbott (1945) from material collected by Papanfuss on the Island of Oahu. The writer's observations are based on part of the same material. *Liagora Papanfussii* is the fourth of the known species of *Liagora* in which the gonimoblast has been observed to produce tetrasporangia instead of carposporangia (i.e., monosporangia). The other three species are *L. tetrasporifera* Børgesen (1927), Japanese specimens of *L. pinnata* Harvey (Yamada, 1938), and *L. brachyclada* Decaisne (Levring, 1941). Børgesen (1927) and Kylin (1930) have made detailed studies of *L. tetrasporifera*. In its development this species differs in some respects from *L. viscida* as observed by Kylin (1930). A short account of the main features of *L. Papanfussii* follows. The author's observations on this species agree entirely with those of Abbott and point to the distinctness of the species.

STRUCTURE OF THALLUS: The thallus is composed of a core of large axial filaments from which issue radially directed assimilatory filaments. These lateral filaments are divided four to six times, the distance between the branches being quite short (Fig. 4*a*, *b*). The cells are short and barrel-shaped toward the axial part of the thallus and decrease in length toward the periphery. They have a thick wall and are joined by conspicuous cytoplasmic connections. In the younger parts of the thallus the assimilatory filaments often terminate in short hairs.

REPRODUCTION: *Liagora Papanfussii* is monoecious. The spermatangia are produced in clusters at the tips of the assimilatory filaments. From the terminal cell of an assimilatory filament two to three spermatangial mother cells are generally cut off, each of

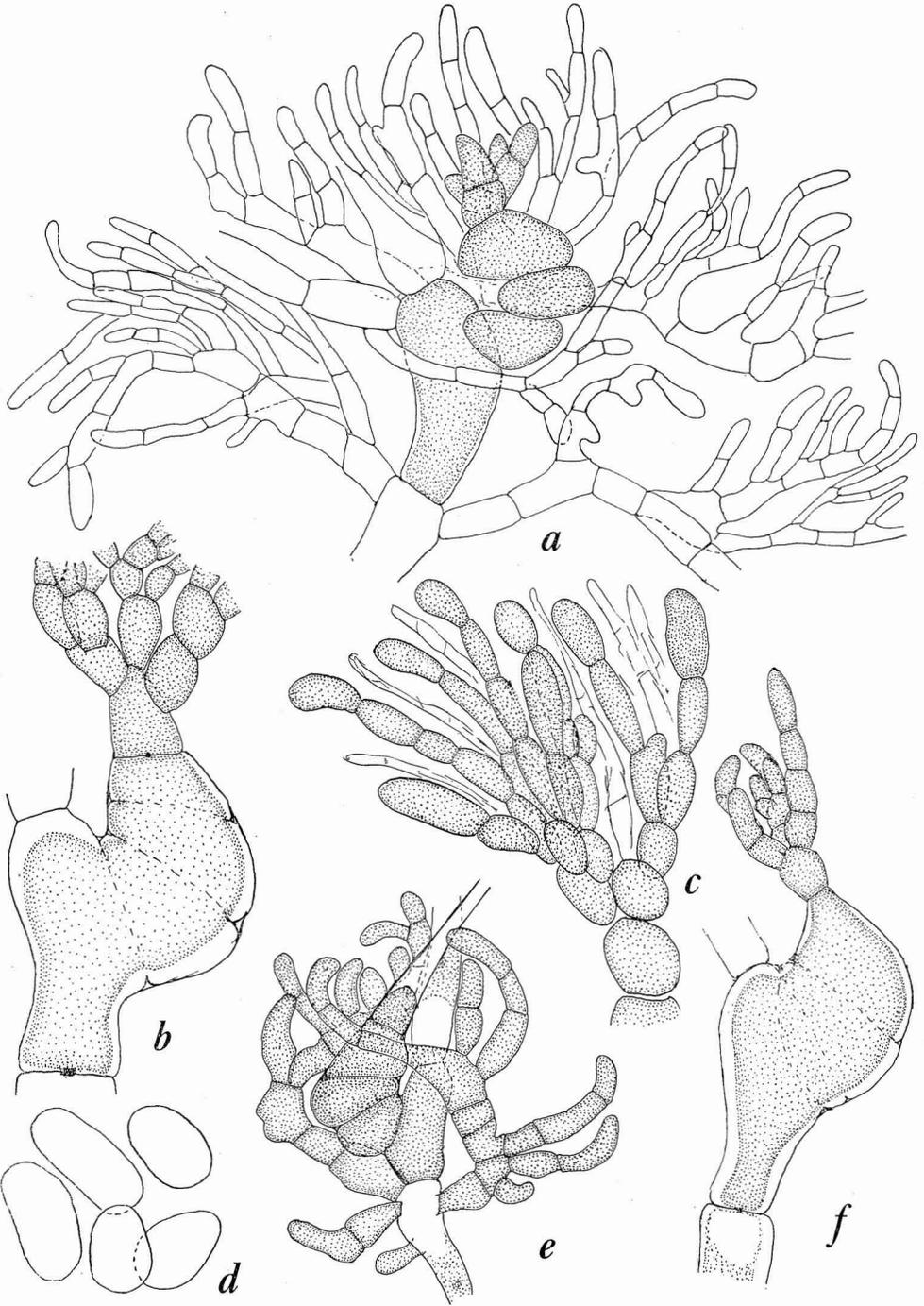


FIG. 3. *Liagora maxima* Butters. *a-c, e, f*, Post fertilization stages; *d*, carpospores. *a*, $\times 605$; *b-f*, $\times 935$.

which gives rise to two or three spermatangia (Fig. 4*a, b*).

The carpogonial branches are produced as lateral accessory branches on the assimilatory filaments and usually behind the third or fourth furcation of these filaments. The carpogonial branch initial is cut off as a lens-

shaped cell (Fig. 4*e*). By repeated division it gives rise to a four-celled branch, the terminal cell of which is the carpogonium (Fig. 4*c, d, f, g*). In the mature condition the carpogonium has a long trichogyne which extends to the surface of the thallus (Fig. 5*a*).

After fertilization the cytoplasm of the

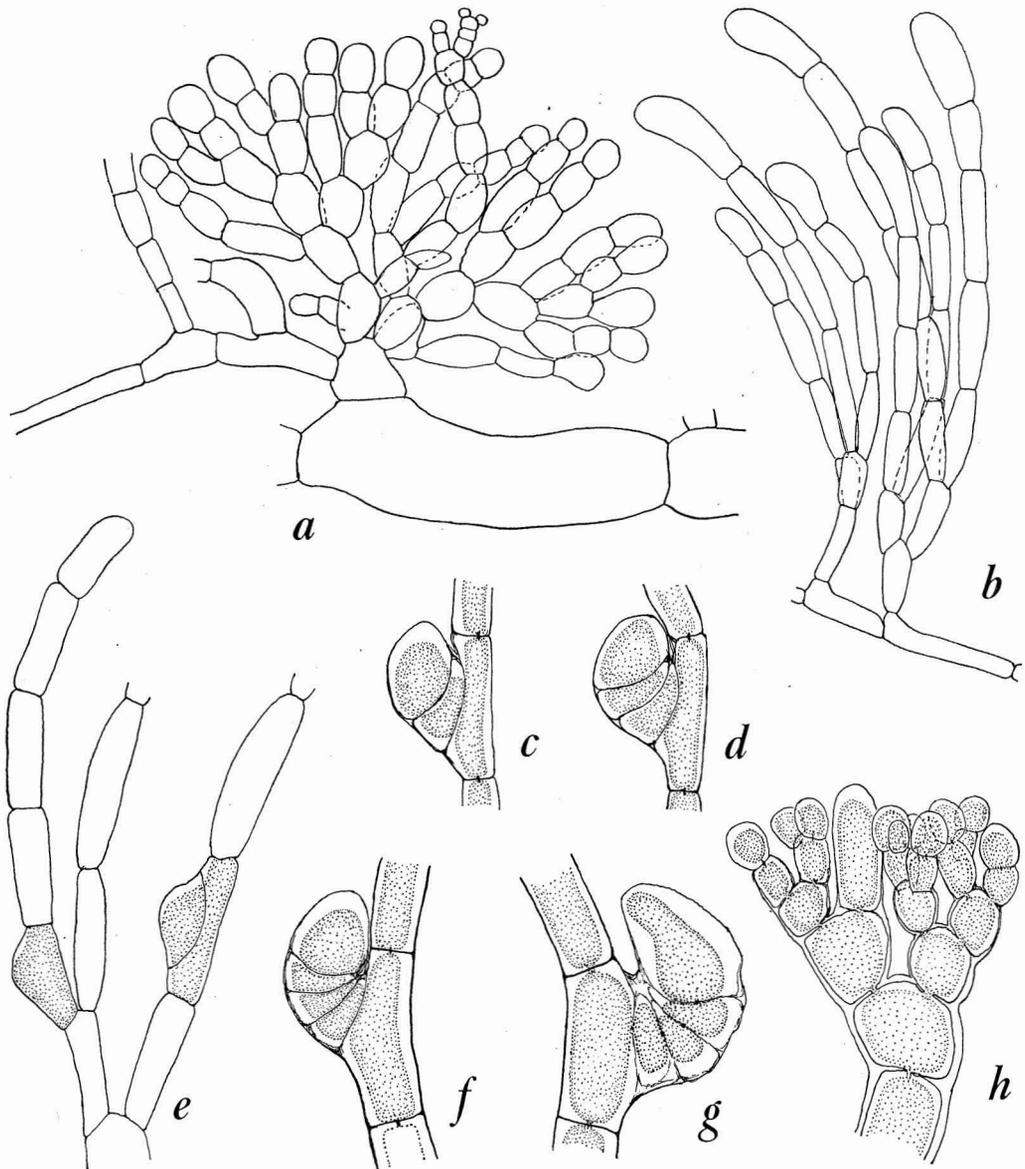


FIG. 4. *Liagora Papenfussii* Abbott. *a, b*, Old and young assimilatory branches, respectively; *c-g*, development of carpogonial branches; *b*, antheridia. *a*, $\times 270$; *b*, $\times 660$; *c-b*, $\times 1020$.

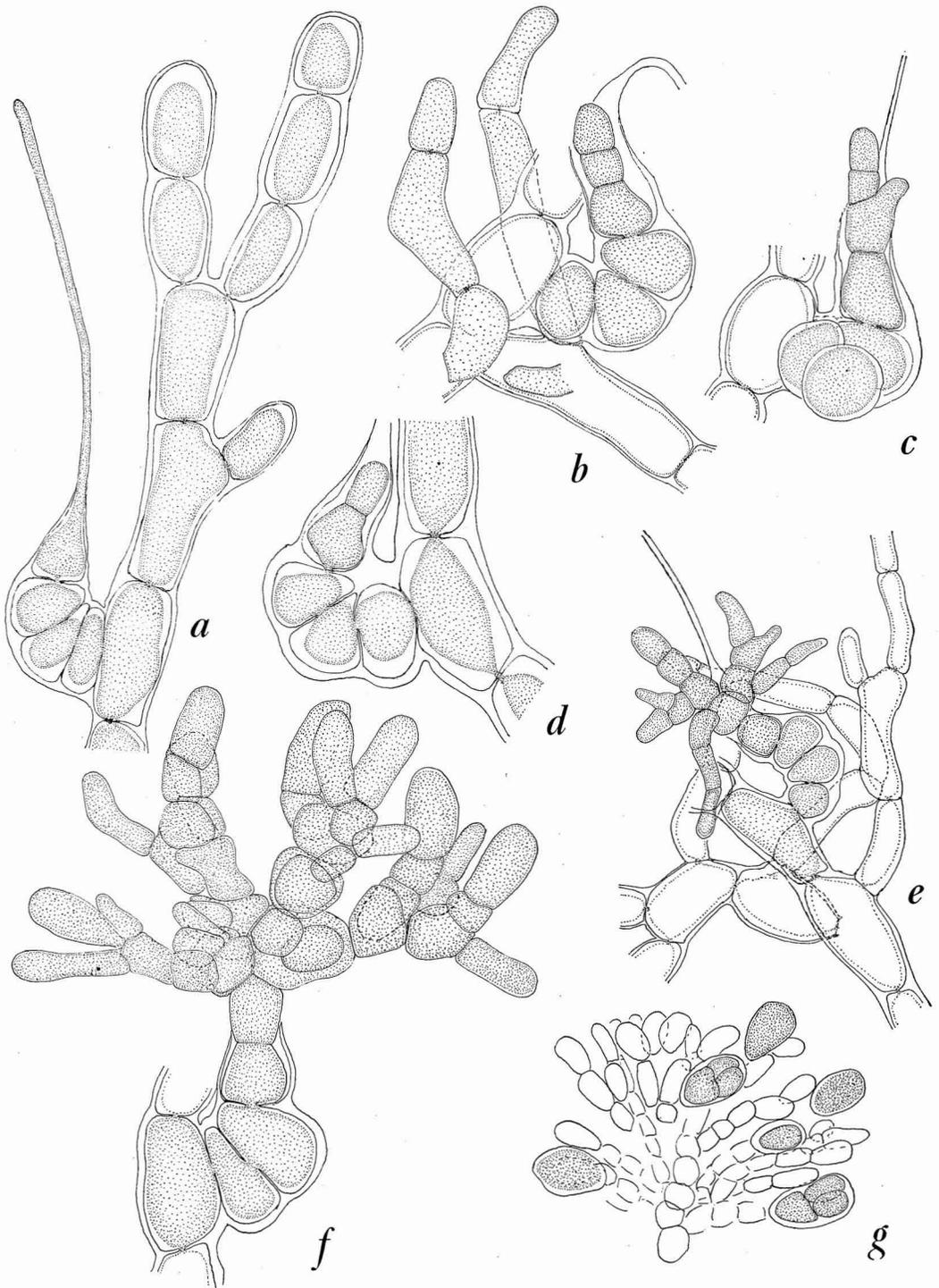


FIG. 5. *Liagora Papenfussii* Abbott. *a-f*, Post fertilization stages; *g*, old cystocarp showing tetrasporangia. *a-d, f*, $\times 765$; *e*, $\times 495$; *g*, $\times 373$.

trichogyne is separated from that of the carpogonium proper and the carpogonium then divides by a transverse wall (Fig. 5*d*) into a stalk cell and the gonimoblast initial. The gonimoblast initial gives rise to a much-branched gonimoblast (Fig. 5*b, c, e, f*). The gonimoblast filaments form terminal tetrasporangia (Fig. 5*g*).

A fusion-cell is apparently not formed in this species. At times, however, a distinct enlargement of the cytoplasmic connections occurs (Fig. 5*d, f*).

Only a slight development of involuclral filaments occurs (Fig. 5*b, e*). A few filaments are formed from the vegetative cells above the supporting cell and occasionally from cells of the other vegetative filaments near the supporting cell.

DISCUSSION AND SUMMARY

The observations on *Liagora maxima* and *L. Papenfussii* have contributed to an elucidation of two points, in particular, in the development of the cystocarp in *Liagora*.

Previously the occurrence of a fusion-cell in the cystocarp of *Liagora* has been reported only in *L. viscida* (Kylin, 1930). The observation of such a cell in *L. maxima* shows that this is a condition which may occur also in some of the other species of *Liagora*. An investigation of the numerous species of this genus with respect to this feature would be of interest.

Involuclral filaments have been reported as present in the cystocarp of a number of species of *Liagora*. In most instances authors have neglected to state from which cells these filaments are derived. It is also not possible to obtain this information from the published illustrations. According to Kylin (1930: 9), involuclral filaments are not produced in *L. viscida*. Hamel (1930: 76), however, states that such filaments are present in this species and that they are formed by the cells of the carpogonial branch. Abbott (1945: 148) described the involuclral filaments as issuing

from the supporting cell in *L. maxima*. The present writer's observations show that in the latter species they are produced by the vegetative cells above and below the supporting cell and rarely also by other vegetative cells in the vicinity of the carpogonial branch. Precise information on the place of origin of these filaments in the various species of *Liagora* in which they occur is highly desirable.

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