The Life History of the Freshwater Red Alga Tuomeya fluviatilis Harv.

Rex Nathaniel Webster

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Edited by

J. E. Potzger
The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana’s vegetation in past decades. Authors were Butler faculty, current and former master’s degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler’s first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal’s publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor’s degrees and 75 master’s degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master’s students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daubenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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THE LIFE HISTORY OF THE FRESHWATER RED ALGA *TUOMEYA FLUVIATILIS* HARV.¹ ²

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**INTRODUCTION**

Of the several genera of freshwater Rhodophyta belonging to the subclass Florideae, *Tuomeya fluviatilis* Harv. is probably one of the rarest forms. In North America there are five genera of freshwater Florideae: namely, *Chantransia* (*Andoniella* in Smith, 1850), *Batrachospermum*, *Theora*, *Lemanea* and *Tuomeya*.

*Tuomeya* was first found in Alabama by Professor Tuomey about 1857 and at about the same time near Fredericksburg, Virginia, by J. W. Bailey. Tuomey (1858) sent some dried specimens of the alga to W. H. Harvey who named and described it in volume three of *Nereis Boreali-Americana* published in 1858. Kuetzing also described it from specimens presumably sent him by Bailey, and named the plant *Baileya americana*. The generic name *Baileya*, however, had already been applied to a genus of Compositae by Asa Gray (1848) and for that reason the name *Tuomeya* has been allowed to stand.

In North America, the present known range of *Tuomeya fluviatilis* Harv. extends from the Laurentian mountains of Quebec to Louisiana. In 1933 I found new localities for the alga in Pennsylvania, in Mountain Creek, and Tom's Run Creek in the village of Pine Grove Furnace, Cumberland County, in the Michaux State Forest. Plants in Mountain Creek were growing in great abundance on rocks about a foot below the surface of the water of this rapidly flowing stream.

The general structural features of *Tuomeya* resemble somewhat those of *Batrachospermum*. In plants of *Tuomeya* however, the frond is much more compact, and the whole body is so much more rigid that when plants are removed from the water, they retain their form and do not collapse into a gelatinous mass. Specimens when dried become quite hard and brittle.

*Tuomeya* is a bushy plant composed of branching, cylindrical fronds.

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¹ This paper is based on a dissertation submitted as partial fulfillment of the requirements for the degree of Doctor of Philosophy from the Johns Hopkins University.

² Additional information obtained from further study of this plant has been included in this paper.
which taper at their tips. It usually grows from 1 to 5 cm. high but may occasionally attain a height of 6.5 cm. (Plate 1, Fig. 1). The adult frond is uniaxial, but from each cell of the axis a whorl of lateral assimilative branches grows. The compact growth of the lateral branches gives *Tuomeya* its characteristic rigidity (Plate 2, Figs. 13-16).

Setchell (1890) in his study of *Tuomeya* made a comparison of *Tuomeya* with *Batrachopus* and *Lemanea*. Setchell was unable to make clear the development after fertilization and the formation and fate of the carpospore of *Tuomeya*. The formation of a chlamydomoid or juvenile stage was hinted by him, but he did not illustrate any such structures. For this reason, it seemed appropriate to try to settle some of the unknown and doubtful phases of the life cycle.

After considerable study it was found that Setchell had misinterpreted the function of certain structures: in confusing carpospores for spermatia (antheridia), Setchell was unable to ascertain the formation, structure, and fate of the carpospore. Because of this a re-investigation of the life history was undertaken.

METHODS

The specimens used in this study were determined as *Tuomeya floridalis* Harv. by Professor Wm. Randolph Taylor and by Dr. Marshall Howe then director of the New York Botanical Garden.

Both living and preserved plants were used. These to be sectioned were usually fixed in the field or in the laboratory shortly after collection. The following fixing agents were used: Flemming's solution weak and strong mixtures; various chromic acid mixtures; formol-acetic-alcohol; Juell's mixture of zinc chloride, alcohol, and acetic acid; and Carnoy's fluid. Of these the Flemming's weaker solution, formol-acetic-alcohol and Juell's mixture appeared to give the best results.

Dehydration was accomplished in one of three ways: namely, by ethyl alcohol, by tertiary butyl alcohol or by dioxane. Little difference could be noted between the ethyl alcohol and tertiary butyl alcohol, since both gave good results; but not much success was obtained using dioxane, although it was not used to the same extent as were the preceding two dehydrating agents.

Material dehydrated in ethyl alcohol was cleared with xylene or chloroform. No clearing agent was necessary when the other two dehydrating agents were used. Paraffin infiltration was begun after pure tertiary butyl alcohol or dioxane dehydration.

Sections were stained with Haidenhain's iron hematoxylin method. Other stains employed were iodine and crystal violet, safranine and fast green and basic fuchsin for the Feulgen nucleic acid reaction. Best results were obtained with iron tannate stain for general plant crush. No special stain for general plant crush was used.

The carpophore is not attached to the cell wall (Plate 2, Figs. 5, 6). At germination the protuberance forms a cylindrical cell (Plate 5, 6). The carpophore which they are usually called the carpophore.
with iron hematoxylin and iodine-crystal violet. The Feulgen reaction did not appear to be specific for the nuclei of Tuomey. Fresh portions of the plant crushed out on slides were sometimes stained with Mayer's haem-alum.

**VEGETATIVE STRUCTURE**

The carpospore of Tuomey after germination, forms a juvenile plant called the chontransioid stage, which is quite different from the adult shoot into which it develops.

At germination a papilla is formed on the wall of the spore, and the protoplasm flows out into it while it is elongating. Cross walls appear after the protuberance reaches a length of three to four times the diameter of the spore wall (Plate 1, Figs. 4-5). In silica gel cultures, carpospores germinated after a few days and grew to about twenty cells in length, but the germlings did not thrive well. It was evident that no rhizoid-like outgrowths were formed on the cell next to the old spore wall as Kylin (1917) has shown for Batrachospermum. The carpospore wall soon falls away leaving a filament of cylindrical cells each about four to six times as long as it is broad (Plate 1, Figs. 5, 6). Each cell, except the basal one, possesses a parietal chromatophore which is somewhat band-shaped. The filaments may branch, although they are usually composed of several cells before branching occurs.

Young plants scraped from the rocks have supplied the only other source of material for the study of juvenile stages. These appear as small dark green humps on the rocks, to which they adhere tenaciously. These humps or “turf,” referred to by Setchell as the possible juvenile stage, may be one to four millimeters in diameter and consist of basal heavy-walled cylindrical cells (with granular cytoplasm and poorly developed chromatophores) united into filaments that branch and intertwine repeatedly. They give rise to erect filaments which are sometimes branched but usually are simple and composed of six to eight more or less moniliform cells (Plate 1, Figs. 7, 8). The apical cell of the erect filament is swollen into a monosporangium (Plate 1, Figs. 7, 8) with dense cytoplasm, from which a spore is liberated by rupture of the monosporangium wall. A new sporangium proliferates on the same filament growing up within the ruptured wall of the previous one while
often several old walls may be seen still adhering to the base of the new sporangium (Plate 1, Fig. 8).

The basal filaments of the juvenile plant give rise to the sexual shoots of *Tuomey* (Plate 1, Figs. 9, 10). The first sign of this formation is observed when a short apical cell is formed instead of the usual long cylindrical cell. This is destined to be the growing point of the sexual frond. By the activity of this apical cell short sub-apical cells are produced on which lateral branch initials arise (Plate 1, Figs. 9, 10, 11). The development of these lateral outgrowths or branch initials is essentially the same as that which takes place on the mature plant except that, at the time the frond is initiated, the cells have extremely thick walls, they are less compact, and the chromatophores are poorly developed. As growth and division take place, the sexual branch pushes up above the juvenile plant.

**DEVELOPMENT OF THE MATURE PLANT**

The adult plant develops by means of a dome-shaped apical cell which cuts off short cells that at first average 1.5 to 2.0 microns long and 9.0 to 14 microns in diameter (Plate 2, Fig. 12). These give rise by considerable elongation to the large axial cells (Plate 2, Fig. 16) which in older parts of the frond may attain a length of over 200 microns and a diameter at the nodes of over 28 microns (Plate 2, Fig. 13).

In general outline these axial cells are more or less cylindrical, but they are larger at the base than at the apex (Plate 2, Figs. 13, 14). The cytoplasm appears reticulate in young fronds (Plate 2, Fig. 14). In comparison with the size of the cell, the nucleus is very small but can sometimes be seen in fresh material when crushed out on a slide. In stained sections the ovoid nucleus is shown to consist of a faintly staining nuclear plasma surrounding a darkly staining nucleolus.

Usually three or four cells below the apical cell, lateral branch initials arise from the axial cells (Plates 1, 2, Figs. 11, 12) and at first are papilla-like. They increase in size and become cut off from the mother cell by vertical cross walls. Usually six such cells form a whorl around each node of the central axis (Plate 2, Fig. 15). These initials usually give rise at their distal end to two or three separate cells, each of which in turn gives rise to two or three cells and so on until ultimately there is formed a much forked lateral branch (Plate 2, Figs. 13, 16).

The young axial cells continue to elongate greatly whereas the lateral branch initials do not; but by the increase in size of all the cells, branch initials come in contact with the base of the axial cell above so that in older parts of the frond they appear to arise from two axial cells (Plate 2, Fig. 16).

When mature, the frond appears to be made up of an inner and an outer stratum, the inner composed of large cortical cells, the outer of smaller cells...
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THE MATURE PLANT
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DEVELOPMENT OF THE SPERMATIUM
T. amoena produces spermatangia at the tips of lateral branches. The sper-

of the outer assimilative cells may obscure the other cell contents. The chro­

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be made up of an inner and an outer cortical cells, the outer of smaller cells

(Plate 2, 16). The outer cells however are not united as in L. amoena, into a rigid parenchymatous tissue; although in old portions of the frond they are closely apposed. Each cell contains a parietal chromatophore which in the outer assimilative cells may obscure the other cell contents. The chrom-

The cells of the inner stratum increase in size as the frond grows and when mature are five to six times as large as when initiated. The cytoplasm appears to be hyaline with the exception of bright refractive granules which some-
times occur in large numbers and which turn red when treated with iodine. It is possible that the large cells of the cortex are used for storage and these granules are a reserve food.

The assimilative cells are much smaller than cells of the inner stratum (Plate 2, Fig. 16). They form a layer one to three cells thick; the outermost cells are smallest and ovoid in shape while the inner are somewhat ellip-
soidal, usually twice as long as broad. A large parietal chromatophore makes it difficult to see the small nucleus except in sectioned material. A few re-

From the base of the branch initial cell, corticating filaments grow down-
ward around the central axis (Plate 2, Figs. 16, 17). These simple, rarely branched filaments, consist of cylindrical, thick-walled cells, about four times as long as broad, with thread-like or ribbon-like chromatophores. They may traverse the axis for several nodes and completely obscure it in older portions of the plant, filling the space between the internodes and the lateral branches so that the frond appears to be a solid structure.

In longitudinal and cross sections, assimilative branches spread out tree-
like from the node and join others at the periphery thus forming a cylindrical frond (Plate 2, Figs. 13, 15, 16).

One-celled projections which have been called hair cells may occur at the tips of assimilative cells. These are composed of a swollen basal part which narrows to a fine hair. The cytoplasm is granular and no chromatophore is present. The nucleus is small, occurring either in the swollen part or often in the hair.

The function of the hair cells has not been ascertained; but I noticed that they developed much more extensively on plants kept in aquaria than on plants in their natural habitat.
3, Fig. 19). There is a well-developed chromatophore at the distal end, under which the nucleus lies somewhat hidden, and large refractive granules occur in the cytoplasm.

The spermatangia are small, ovoid cells somewhat flattened where they are joined to the mother-cells (Plate 3, Fig. 18). They grow out successively from the mother-cells one or two at a time and are then cut off from them by cross walls. They attain a size of 3.5 to 4.0 microns. At first they each possess a parietal chromatophore (Plate 3, Figs. 20, 21) which later appears to break down. This may be seen in sections stained with Haidenhain's iron hematoxylin where the chromatophore does not take a rich bluish stain as the normal chromatophore of an assimilative cell does but appears rather a brownish color. In the mature cell only a small remnant of the chromatophore remains.

In the spermatium of Trachemys the cytoplasm appears reticulate. The nucleus is small and in young cells appears to be in an interphase stage with a prominent nucleus surrounded by a more or less clear plasma (Plate 3, Fig. 21). As the cell matures, the nucleus undergoes changes; it now appears to be in a prophase stage showing usually 7 to 9 granules (Plate 3, Figs. 18, 22).

The spermatium is discharged as what appears to be a naked, non-motile protoplast, by the rupture of the distal end of the spermatangium wall. It is globular in shape at this time and possesses a single, small nucleus which still appears to be in a prophase stage. Shortly after discharge the protoplast forms a wall around itself which is clearly visible when the spermatium becomes attached to the trichogyne. The cytoplasm of the cell is reticulate and rather granular, and only part of the old chromatophore is apparent as a small globule. The chromatophore stains poorly with iron hematoxylin, appearing as a yellow or orange body, and is not apparent in spermatia attached to the trichogyne.

In discharged spermatia I have found what appears to be a mitotic division of the nucleus (Plate 3, Fig. 23). In the figures seen, the chromatin was oriented at metaphase between two poles of a spindle; but because of the small size of the nucleus, I have been unable to ascertain the number of chromosomes present at this stage. Around the spindle there is an area of more lightly staining plasma the size of the original nucleus, which may indicate that the spindle is intranuclear. When attached to the latter, the spermatium possesses two darkly staining granules (Plate 3, Figs. 24, 25) which I believe are nucleoli of two daughter nuclei resulting from the division. In a few cases I have observed a clear zone around each of these granules, similar to the clear plasma of the interphase nucleus, and the size of the nuclei appears to be approximately the same as that of male nuclei seen within the trichogyne.

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cells somewhat flattened where they are seen. They grow out successively and are then cut off from them by to 4.0 microns. At first they each possess a chromatophore at the distal end, under Jen, and large refractive granules occur in the cytoplasm. The twisting of the branch is quite characteristic. Occasionally, the cells of the proximal half of the branch produce short filaments of cylindrical cells which bear assimilative cells at their tips and grow out toward the periphery of the frond (Plate 3, Fig. 26). Each cell of the distal half of the branch produces a row of one to four short, rounded cells which function as nutritive cells for the gonimoblast (Plate 3, Fig. 26; Plate 4, Figs. 27, 28), and which are comparable to those "nutritive cells" on the carpogonial branch of the Nemalionales, which are described by Kylin (1935) as food suppliers for the development of the gonimoblast.

The cells of this branch possess a central vacuole, and when young there is a well developed chromatophore. At maturity those cells of the proximal half retain their chromatophores, but those of the distal half break down into a dense granular plasma (Plate 4, Figs. 27, 28). Each cell possesses a single nucleus similar in structure to those already described for the vegetative cell. The young carpogonium is at first elongated and somewhat constricted near the tip but is still not differentiated into the three portions of the mature one (Plate 4, Fig. 29). There is in the young carpogonium a parietal chromatophore which soon breaks down, leaving only a small chromatophore rudiment at the base (Plate 4, Fig. 27). This globular body takes a dull gray stain with iron hematoxylin. In Turneya there was no evidence of a chromatophore stretching up into the trichogyne from the carpogonium. A single nucleus is present near the base of the cell in the young carpogonium. At a later stage, but before fertilization, a division apparently takes place, for the carpogonium appears to be bi-nucleate (Plate 4, Figs. 28, 30). One nucleus occurs in the carpogonium and the other in the trichogyne. The trichogyne nucleus has a small nucleolus and around it a lightly staining zone which is sometimes hard to differentiate from the cytoplasm. The trichogyne, at maturity, becomes so granular that it is difficult to say exactly what becomes of the nucleus; but just prior to fertilization it is not apparent and may be in a state of degeneration.

At the time for fertilization the procarp of Turneya consists of a swollen basal portion, the carpogonium, in which lies the egg nucleus, a larger somewhat elongated, pear-shaped trichogyne at the distal end, and a narrow, tu-

THE CARPOGONIAL BRANCH

The carpogonium is borne at the tip of a special branch which arises from the basal cell of a lateral assimilative branch (Plate 3, Fig. 26; Plate 4, Figs. 27, 28). There may be one or two carpogonial branches borne at each node; they grow upward into the hollow space between the cells of lateral branches and the main axis.

The carpogonial branch is a spirally twisted structure composed of usually ten to fourteen somewhat egg-shaped cells with the larger end of each toward the convex side of the spiral (Plate 3, Fig. 26). Each cell of the distal half of the branch produces short filaments of cylindrical cells which bear assimilative cells at their tips and grow out toward the periphery of the frond (Plate 3, Fig. 26). Each cell of the distal half of the branch produces a row of one to four short, rounded cells which function as nutritive cells for the gonimoblast (Plate 3, Fig. 26; Plate 4, Figs. 27, 28), and which are comparable to those "nutritive cells" on the carpogonial branch of the Nemalionales, which are described by Kylin (1935) as food suppliers for the development of the gonimoblast.

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The non-motile spermatia, after being discharged from the spermatangia, are carried to the trichogyne by currents of water. Often as many as five or six spermatia may be attached to one trichogyne.

The spermatium, as we have seen, is bi-nucleate when it comes in contact with the trichogyne (Plate 3, Figs. 24, 25), and after the intervening walls have dissolved, the nuclei pass into the trichogyne (Plate 3, Fig. 24; Plate 4, Fig. 31). Sometimes a small amount of cytoplasm is left within the old spermatium wall (Plate 4, Fig. 32). One of the two nuclei passes down through the pedicel into the carpogonium while the other remains in the trichogyne. Soon after, the protoplasmic connection between the carpogonium and the trichogyne is broken by a thickening of the wall of the pedicel (Plate 3, Fig. 24; Plate 4, Figs. 32, 33).

Fusion of the male and female nuclei appears to take place soon after the male nucleus enters into the carpogonium (Plate 3, Fig. 24; Plate 4, Fig. 32). In a single frond, various stages occur from fertilized carpogonia near the upper end to carpospore-forming stages below, and only a few stages show fusion. In the carpogonium both nuclei appear to be in an interphase condition.

After fertilization the carpogonium bulges out at one side, and a longitudinal wall divides it into two cells, each of which possesses a single nucleus (Plate 3, Fig. 25; Plate 4, Figs. 33, 34). These two cells then divide, thus forming a quartet of cells, which form a row at the tip of the carpogonial branch.

The gonimoblasts in *Tuomeya*, which develop from the four cells described above consist of two parts, a primary and secondary gonimoblast (Plate 4, Fig. 35; Plate 5, Fig. 37). The former are composed of short chains of more or less polygonal cells (Plate 4, Figs. 35, 36; Plate 5, Figs. 37, 38, 39), the outermost of which dichotomize at the distal end and thus form a cluster of cells around the old carpogonium. The secondary gonimoblast is composed of long filaments of cylindrical cells. Two such filaments may arise from each of the end cells of the primary gonimoblasts and grow out toward the periphery of the frond and there give rise to the carpospores (Plate 5, Fig. 37).

In *Tuomeya* the cytoplasm of cells of the distal half of the carpogonial branch and the primary gonimoblast is densely granular and of similar consistency (Plate 4, Fig. 35; Plate 5, Figs. 36, 39, 40). Later the primary
The two (Plate 4, Fig. 27). The through the pedicel between the carpo-

sition discharged from the spermatangia, 

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The former are composed of short chains 

and their nutritive cells. Thus, a large fusion cell or gonimoblast placenta is 

formed which gives rise to secondary gonimoblast filaments (Plate 4, Figs. 

35, 36; Plate 5, Figs. 37, 38, 39, 40, 41). The fusion of cells into this gon- 

imoblast placenta is so complete that it is difficult to tell one cell from an- 

other. The placenta is densely granular and usually contains numerous large 

nuclei which are budded off as nuclei of the primary gonimoblast cells. Oc- 

asionally I have found these nuclei undergoing mitotic division (Plate 5, 

Figs. 39, 40). 

At metaphase of the divisions seen in the nuclei of the gonimoblast pla- 

centa, the chromat in occurs in about eight or nine small chromosomes. This 

would seem to indicate that a reduction division has taken place, for as 

nearly as can be estimated, it corresponds with the number of granules in the 

spermatium. The number of granules seen in the prophase stage of the spermatium I have considered indicative of the haploid chromosome number. 

Although reduction division has not been observed in T. unneyei, it is 

likely that it occurs at the first division of the zygote as it does in other 

haplobiontic red algae. Two observations seem to indicate that this may be 

true: first the development of the fertilized carpogonium into four gonimo- 

blast initials; second, the presence of the same number of chromosomes in 

the dividing nuclei of the gonimoblast as were seen in the discharged spermatium. 

Cells of the secondary gonimoblast possess a parietal chromatophore that 

is irregularly thread-like with frequent thickenings of the thread (Plate 4, 

Fig. 35; Plate 5, Fig. 39). As a rule these filaments do not branch until they 

are near the periphery of the frond, where they usually dichotomize once or 

twice (Plate 5, Figs. 37, 40, 41) and at the surface of the frond bud off suc- 

cessive carposporangia (Plate 5, Figs. 41, 42). The latter are terminal cells of 

these filaments. 

Each carposporangium produces a single carpospore which may be some- 

what cylindrical when first formed but becomes a swollen egg-shaped struc- 

ture when mature (Plate 5, Fig. 41). The carposporangium is densely filled 

with protoplasm and the chromatophore is prominent. As the spore increases 

in size, the chromatophore diminishes until ultimately it does not show as 

such, but only as small globules of pigment. The carpospore chromatophore ap- 

pears reticulate and granular. The nucleus, as a rule, occupies the central 

portion of the cell. The discharge of the spore occurs by rupture of the distal 

der of the carposporangium wall (Plate 5, Figs. 41, 42); and, after it is 

freed, a new carposporangium may arise within the wall of the preceding one. 

The carpospore rounds up after being discharged and soon may germinate 

to form the juvenile plant described previously.
DISCUSSION

In 1858, Tuomeya floridana was named and placed in the sub-class Chlorospermae, now known as the Chlorophyceae, by Harvey. He believed that Batrachospermum and Lemanea were "inseparably connected by the genus Tuomeya." Setchell (1890), from his study of Tuomeya, came to the conclusion that this genus was an intermediate one between Batrachospermum and Lemanea. In subsequent classifications, Tuomeya has been placed in the Lemaneaceae. Kylin (1937) left Tuomeya in the Lemaneaceae, but stated that it might equally well be placed in the Batrachospermaceae. From my study of Tuomeya however, I am inclined to regard this genus as a member of the Batrachospermaceae.

As in Batrachospermum moniliforme (Kylin, 1917) the spermatangium: mother-cell of Tuomeya cannot be distinguished from an ordinary assimilatory cell, whereas in Lemanea it is distinctly different. The spermatia of Lemanea are developed in special areas or sori. The presence of a chromatophore in the spermatium of Tuomeya also resembles the development of a similar parietal chromatophore in the spermatium of Batrachospermum as reported by Davis (1896), Schmidle (1899), Osterhout (1900), and Kylin (1917).

The granules appearing in the nucleus of the spermatangial cell as observed in Tuomeya are not uncommon among the Florideae. In Batrachospermum and Nemalion these granules were thought by Kylin (1916, 1917) to indicate a prophase stage as I believe to be true in Tuomeya: and in many of the Florideae investigated it has been established that the nucleus is in a prophase stage when the spermatium is liberated.

A mitotic division of the nucleus of the spermatium as observed in this study of Tuomeya has also been reported in Nemalion (Kylin, 1916; Cleland, 1919) and Batrachospermum (Schmidle, 1899). Spermatia attached to the trichogyne of Batrachospermum were observed by Kylin (1917) to possess two darkly staining granules which he said may indicate a binucleate condition. He pointed out that the spermatium when it is first discharged is in a prophase stage, and later, when it lies in the carposporangium prior to the fusion with the egg nucleus, it is in the interphase condition. He believed this to be evidence that a nuclear division has taken place and regarded the observation of Schmidle as correct.

It is likely that the only spermatia Setchell (1890) saw in Tuomeya were those attached to the trichogyne, for he undoubtedly confused spore-bearing gonimoblast filaments for spermatangial branches, the carpospores, produced at the ends of long secondary gonimoblast filaments he confused with spermatia or antheridia. His description of the spermatium fits the carposporangium quite accurately. He did not describe the carpospore but did state that "as far as could be seen, strings of spores similar to those formed in Batracho-
and placed in the sub-class Chlorophyceae, by Harvey. He believed that "inseparately connected by the genus..."

"...the study of..."

"...he came to the conclusion..."

"...he has been placed in the..."

"...but stated..."

"...he believed this genus as a member..."

"...the spermatangium distinguished from an ordinary assimilating cell..."

"...the spermatium as observed in this..."

"...the trichogyne nucleus is liberated..."

"...the spermatium..."

"...the trichogyne nucleus disappears but is present up to about the time of fertilization..."

"...in this respect..."

"...the male nucleus is in a prophase stage when discharged..."

"...after fertilization in..."
gonimoblast is nourished through the cells of the carpogonial branch, but these do not fuse with each other. However, the fusion of sterile cells with the gonimoblast is reported in *Nemalion* by Kylin (1916). In *Bonnemaisonia asparagoidea* Svedelius (1935) said, there is a fusion of the carpogonium with the hypogynous cells and the nutritive cells borne on it. These cells furnish only part of the food of the gonimoblast. The greater part of the food is obtained from other cells of the mother plant and is not conducted to the gonimoblast through the carpogonial branch. In *Aparagopsis armata* Svedelius said the cells of the carpogonial branch fuse with one another and their content is used as food for the development of the gonimoblast; here though, the food from all cells is transported to the gonimoblast through the carpogonial branch.

It has been noted previously concerning the nucleus of the spermatium of *Tuomeya* that a number of granules which were thought to be chromosomes appear. The nucleus was thought to be haploid and in a prophase stage. The number of granules in the spermatium nucleus seems to agree with the number seen in the gonimoblast nuclei undergoing mitosis. For this reason it would appear that reduction division had taken place; about 7 to 9 granules or chromosomes occurred in the spermatium nucleus and in the gonimoblast, a structure which follows fertilization. In *Semiais furcellata* (Svedelius, 1915), *Aparagopsis armata* and *Bonnemaisonia asparagoidea* (Svedelius, 1933), the number of granules which was seen in a prophase stage of the spermatium nucleus was considered to be the haploid number. Kylin has said that in the case of *Nemalion multifidum* and *Batschichospernum moniliforme*, the granules of the mature spermatium nucleus correspond with the haploid number. Yamazouchi (1906) refers to granules occurring in the spermatium of *Polysiphonia violacea* as prochromosomes that are connected by weakly staining threads of linin. These prochromosomes he said, increase in size and become rod-shaped chromosomes. Kylin (1916) stated that the characteristic granules in the mature spermatium nucleus are observed in all Florideae. Thus, although reduction division was not observed in *Tuomeya* it would seem likely that it occurs at the first division of the zygote nucleus, and Kylin (1937) states that such is the case in other haplobiontic red algae. According to Kylin (1917), if the first division of the zygote in *Batrachospernum* is heterotypic, the second would be homotypic, and the four cells resulting from these two divisions would be homologous with the tetrarosperms which arise after reduction division in the higher red algae. Two observations seem to indicate that this may be true in *Tuomeya flavitidis*: first, the development of the fertilized egg into four gonimoblast initials which are similar to those found in *Batrachospernum* where meiosis occurs in the zygote nucleus; second, the presence of what is considered to be the haploid number of chromosomes in dividing nuclei in the gonimoblast.

The carpospore formed singly in the terminal cells of the secondary
The cells of the carpogonial branch, but never, the fusion of sterile cells with those by Kylin (1916). In Bornemisia, there is a fusion of the carpogonial nutritive cells borne on it. These cells are gonimoblasts. The greater part of the mother plant and is not conducted along the passage through the primary gonimoblast initials. But this fusion is not observed in other haplobiontic red algae. Two divisions take place; about 7 to 9 granules of nuclei and in the gonimoblast, 1. In Simarum fuscellatum (Svedelius, 1882), two gonimoblast initials fuse with one another and develop the gonimoblast; here is observed in the secondary gonimoblasts. In T. jilfricella (Svedelius, 1882), the gonimoblast initials which are connected by weakly tending cells, are considered to be the haploid zygote. In the gonimoblast, a terminal cell of the secondary gonimoblasts of *T. fusiformis* is unlike the carpospore development in *Lemanea*. Smith (1930) partly characterizes the family Lemaneaceae by the fact that "carpospores are formed by all the cells of the gonimoblast instead of from the terminal cells only." Of the Batrachospermaeae he says, "the gonimoblasts formed from the carpogonia develop carpospores from their terminal cells only."

When the aspect, general morphology, and cytology are considered, it is evident that *T. fusiformis* is out of place in the family Lemaneaceae and should be placed in the Batrachospermaeae.

### SUMMARY

1. Carpospores of *T. fusiformis* germinate to form a juvenile plant on which monospores are formed.
2. Basal filaments of the juvenile plants give rise to the mature plants.
3. Spermatia are borne at the tips of the lateral assimilative branches and are discharged from the spermatangia undergo mitosis.
4. When first attached to the trichogyne, the spermatia are bi-nucleate.
5. The unfertilized carpogonium is also bi-nucleate; one nucleus lies at the base of the carpogonium while the other is in the trichogyne.
6. Fusion of the male and female nuclei occurs soon after the male nucleus enters into the carpogonium.
7. The fertilized egg cell divides to form four cells from which gonimoblasts are developed, with two types of cells are developed.
8. Fusion of numerous cells takes place to provide a gonimoblast placenta which gives rise to primary and secondary gonimoblasts.
9. Carpospores are produced singly at the tips of secondary gonimoblast filaments at the edge of the frond.
10. Mitotic divisions in the gonimoblast placenta show about eight chromosomes; the same number was thought to be present in the haploid spermatium.
11. Reduction division is thought to occur at the first division of the fertilized egg cell.
12. It is suggested that *T. fusiformis* Harv. be placed in the family Batrachospermaeae rather than the Lemaneaceae where it now stands.

### EXPLANATION OF PLATES

Lettering of figures: ae, assimilative cell; cae, central axis cell; cf, corticating filament; ch, chromatophore; epg, carpogonium; cpgb, carpogonial branch; spm, spermatium; sp, spermatangium; gti, gonimoblast initial; lbi, lateral branch initial; mpm, monosporangium; ac, nutritive cell; p, pedicel of carpogonium; pgf, primary gonimoblast filament; sgf, secondary gonimoblast filament; sp, spermatium; spn, spermatangium; spsc, spermatangium mother-cell; tr, trichogyne; tn, trichogyne nucleus; N, male nucleus; F N, female nucleus.
PLATE 1

Fig. 1. Photograph of mature plants of Taxonomy, 1/4 natural size. Fig. 2. Germinating carpospore. X600. Fig. 3. Germinating spore on parent plant. X425. Fig. 4. Young germling after bary wall has fallen off and first cross-wall has formed. X600. Fig. 5. Young germling. X625. Fig. 6. Later stage showing sporing of nine cells. X625. Fig. 7. Photomicrograph of juvenile plant showing the basal mat of interwoven branched filaments and the erect filaments of moniliform cells. Monospores at the tips of the erect filaments may be seen. Fig. 8. Outline drawing of juvenile plant with terminal monosporangia. X600. Figs. 9-11. Stages in the development of sexual frond from cells of the basal mat of the juvenile plant. X625.
Fig. 1. Young germling after spore germination, live cells, x625. Fig. 2. Germinating cryptospore. x625. Fig. 3. Young sporeling. live cells, x625. Fig. 4. Longitudinal section of a mature frond, showing elongated central axis cells, x892. Fig. 5. Young sporeling. live cells, x625. Fig. 7. Photomicrograph of branched filaments and the empty filaments of lamens may be seen. Fig. 8. Outline drawing of Figs. 9-11. Stages in the development of a plant. x625.

PLATE 2

Fig. 12. Apical region of asexual frond, showing spore cells cut off from its base by vacuoles due to lateral branches. x1000. Fig. 13. Photomicrograph of longitudinal section of a mature frond, showing elongated central axis cells, x892. Fig. 14. Photomicrograph of a younger portion of frond showing the differentiation of axis cells at base and apex. Fig. 15. Cross section through a mature young portion of frond showing origin of lateral assimilative branches and main axis branch. x892. Fig. 16. Longitudinal section of a young frond showing the elongating central axis cells, lateral branch system and corticating filaments. x892. Fig. 17. Photomicrograph of crushed material showing the origin of corticating filaments from base of lateral branch initial.
Fig. 18. Portion of plant showing spermatangia mother-cells and spermatangia. The nuclei of two spermatangia are in the prophase stage. X2000. Fig. 19. Spermatangia mother-cells after they have become heart-shaped from production of spermatangia. Spermatia have been discharged. X1785.

Fig. 20, 21. Spermatangia showing parietal chromatophores. X 1785. Fig. 22. Portion of Fig. 18 enlarged, showing spermatangium nucleus in prophase stage with eight granules visible. X3000.

Fig. 23. Spermatangia after discharge from the spermatangium showing nuclear division at metaphase. X3000. Fig. 24. Spermatia attached to trichogyne showing binucleate condition in one. Two other spermatia visible, each with a single nucleus. Three male nuclei occur in the trichogyne and one in the process of fusing with the egg nucleus. The fourth spermatium is not visible. X2000.

Fig. 25. Two spermatia in binucleate condition, attached to trichogyne; the first division of the fusion nucleus has taken place. X1000. Fig. 26. Outline drawing from an aceto-carmine smear showing carpogonial branch and its relation to the central axis. X1000.
Spermatangia mother cells after they have fused. Spermatia have been discharged. X 1783. Fig. 28. Portion of Fig. 18 showing spermangium showing nuclear division at metaphase showing binucleate condition in one. Two male nuclei occur in the trichogyn and 5. The fourth spermatium is not visible. X 2000.

PLATE 4

Fig. 27. Carpogonial branch showing chromatophore rudiment in the carpogonium and degeneration of chromatophores of distal end of branch. X 1000. Fig. 28. Same structure showing nuclei in trichogyn. X 1000. Fig. 29. Young carpogonial branch showing trichogyne and growth of nutritive cells. X 1000. Fig. 30. Portion of a carpogonial branch showing binucleate carpogonium. X 2000. Fig. 31. Carpogonium after fertilisation showing male and female nuclei. X 2000. Fig. 32. Carpogonium after fusion of male and female nuclei. About 14 granules were evident. X 500. Fig. 33. First division of the carpogonium after fertilisation. X 892. Fig. 34. First division of the carpogonium after fertilisation. X 892. Fig. 35. Carpogonial branch showing fusion of four gametoblast initials and development of primary and secondary gametoblast cells. X 1000. Fig. 36. Portion of branch at an earlier stage showing fusion of gametoblast initials and first primary gametoblast cells being formed. X 1000.
PLATE 3

Fig. 37. Outline drawing showing fusion cell or gonimoblast placenta with secondary gonimoblast filaments bearing carposporangia. X1000. Fig. 38. Carpogonial branch showing fusion of branch node with nutritive cells. X1000. Fig. 39. Later stage showing fusion. Secondary gonimoblast filaments may be seen arising from the primary cells. X1000. Fig. 40. Gonimoblast placenta with one nucleus undergoing nuclear division. Eight granules may be seen in polar view. X1000. Fig. 41. Secondary gonimoblast filament bearing two carposporangia within the wall of two grana carposporangia. X1000. Fig. 42. The same, showing branching of filament and walls of old carposporangia. X1000.
simultaneous plasmodia with secondary gonimoblasts
in which branch showing fusion of branch and
gonimoblast. X1000. Fig. 38. Later stage show-}

ing nuclear division. Eight gametes may be seen
immersed in a cytoplasmic mass within the
plasmodium. X 42. The same, showing branching of

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