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 Daudenmire, 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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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* (*Audouinella* in Smith, 1930), *Batrachospermum*, *Thorea*, *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 Borealis Americana* published in 1858. Kuetzing also described it from specimens presumably sent him by Bailey, and named the plant *Batylea americana*. The generic name *Batylea*, 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.

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 *Batrachospermum* 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 chlamysoid 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 floribulbis* 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. Those 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; formal-acetic-alcohol; Juel's mixture of zinc chloride, alcohol, and acetic acid; and Carnoy's fluid. Of these the Flemming's weaker solution, formal-acetic-alcohol and Juel'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, safranin and fast green and basic fuchsin for the Feulgen nucleic acid reaction. Best results were obtained with iron fuchsin. The stain for plant crush did not appear.
with iron hematoxylin and iodine-crystal violet. The Feulgen reaction did not appear to be specific for the nuclei of *Tuomeya*. Fresh portions of the plant crushed out on slides were sometimes stained with Mayer's haem-alum.

and that Setchell had misinterpreted confusing carpospores for spermatia. Since this was clear the formation, structure, and fate of the carposporangium rounded up forming a globular body. The carpospore may germinate within a few days after being discharged and the young germling (Plate 1, Fig. 2) looks much like those Kylin (1916a.), (1917) has shown for *Nemalion multifidum* and *Batrachospermum moniliforme*. Frequently, with plants growing in aquaria, the carpospore germinates into a filament several cells long while still attached to the parent plant (Plate 1, Fig. 3).

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 germings 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, Fig. 7). 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 **Tuomeya** (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 papillate. 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.
still adhering to the base of the new plant give rise to the sexual shoots of first sign of this formation is observed of the usual long cylindrical cell. By the activity lateral branch initials usually give rise at their distal end of the L1, as seen in fresh preparations. In stained sections the ovoid nucleus is usually twice as long as broad. A large parietal chromatophore makes it difficult to see the small nucleus except in sectioned material. A few refractive granules may occur in these cells also.

From the base of the branch initial cell, corticating filaments grow downward 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.

DEVELOPMENT OF THE SPERMATIUM

Tuambee produces spermangia at the tips of lateral branches. The spermangium mother-cell cannot at first be distinguished from an ordinary assimilatory cell (Plate 3, Fig. 18); it is ovoid, but as successive spermangia are produced on the mother-cell it becomes more or less heart-shaped (Plate 2, Fig. 16). The outer cells however are not united as in Lemaee, 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 chromatophore of the inner cortical cells is less conspicuous and is composed of several disc-shaped bodies connected by a thin thread-like portion while in others it is ribbon-like.

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 sometimes 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 elliptical, usually twice as long as broad. A large parietal chromatophore makes it difficult to see the small nucleus except in sectioned material. A few refractive granules may occur in these cells also.

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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 T. seymiae 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.

In T. seymiae free spermatia found in apparent nuclear division seem to indicate a division occurs before attachment of the spermatia to the trichogyne. 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.
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). 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 *Tomoeya* 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 *Tomoeya* 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-
bular portion called the pedicel connecting the two (Plate 4, Fig. 27). The granular protoplasm is continuous through the pedicel between the carpogonium and trichogyne.

**FERTILIZATION**

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
ing discharged from the spermatangia. The pedicel between the carpogonia is bi-nucleate when it comes in contact with water. Often as many as five or six nuclei are found in the intercalary wall of the pedicel (Plate 3, Fig. 24; Plate 5, Figs. 37, 38, 39, 40, 41). The fertilized carpogonia and also with cells of the distal end of the branch 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 gonimoblast placenta is so complete that it is difficult to tell one cell from another. The placenta is densely granular and usually contains numerous large nuclei which are budded off as nuclei of the primary gonimoblast cells. Occasionally 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 placenta, the chromatin 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. numeoyla*, 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 gonimoblast 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 successive carposporangia (Plate 5, Figs. 41, 42). The latter are terminal cells of these filaments.

Each carposporangium produces a single carpospore which may be somewhat cylindrical when first formed but becomes a swollen egg-shaped structure 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 appears 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 end 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 Chlorosperma, now known as the Chlorophyceae, by Harvey. He believed that _Batrachospermum_ and _Lemaerea_ 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 _Lemaerea_. In subsequent classifications, _Tuomeya_ has been placed in the Lemanaceae. Kylin (1937) left _Tuomeya_ in the Lemanaceae, 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 montiforrne_ (Kylin, 1917) the spermatangia: mother-cell of _Tuomeya_ cannot be distinguished from an ordinary assimilatory cell, whereas in _Lemaerea_ it is distinctly different. The spermatia of _Lemaerea_ 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 carpogonium prior to the fusion with the egg nucleus, it is in the interphase condition. He believed this to be evidence that a nuclear division had 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 carpospore 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 _Batrachospermum_ are not present in _Tuomeya_."

A chromosome study of _Tuomeya_ by Schmidle would be desirable to see if the chromosome number is the same as in _Tuomeya_.

Among the species of _Tuomeya_ it appears that the antheridia are not developed in the trichogyne. Osterhout's (1900) _Tuomeya_ has not been studied, but it appears to have the character of _Tuomeya_._

After the zygote is formed the earlier stages of development of the _Tuomeya_ develop in the trichogyne and it is not until a later stage that the zygote appears on the surface of the _Tuomeya_.
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The spermatium and egg nuclei in *Tuomeyia* appear to be in the inter­

stage of mitosis at the time of fertilization as is true of *Batrachosper­
mesus* (Kylin, 1917) and *Nemalion* (Wille, 1894; Kylin, 1916; Cleland,

The development of a gonimoblast placenta, by the fusion of the primary
gonimoblast cells with the four gonimoblast initials at the distal end of the
carpogonial branch and their nutritive cells as observed in *Tuomeyia*, does not

The spermatium and egg nuclei in *Tuomeyia* appear to be in the inter­

appears, Kylin (1923) also reported a nucleus present in the trichogyne

**BalrachoJpermum** are not similar in this respect, for this type

**Asparagopsis armata** by Svedelius (1915). Svedelius said

it is not unusual but certainly not common for the gonimoblasts in the Rho­
dophyta to differentiate into a central part and another spore-bearing part.

*Tuomeyia* and *Batrachospermum* are not similar in this respect, for this type

development has never been reported for the latter.

**Carpospores** of *Tuomeyia* however, are not produced in "strings" but are borne singly at the ends of long cylin­

drical gonimoblast filaments. A chromatophore which stretches up into the trichogyne from the carpo­
gonium has been reported present in *Batrachospermum* by Davis (1896),

**Schmidle** (1899), Osterhout (1900), and Kylin (1917). I was never able to see such a chromatophore in *Tuomeyia*, nor was one reported by Setchell in his study of this plant.

Among the Florideae which have been studied according to Kylin (1917),
it appears as if the trichogyne normally contains a nucleus. The presence of a trichogyne nucleus in *Batrachospermum* was reported by Davis but Schmidle, Osterhout and Kylin were unable to demonstrate such a nucleus. In *Nema­

**Sverdelius**, 1915). Svedelius said

... **Grif­

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development has never been reported for the latter.
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 asparagoides*, Svedelius (1935) said, there is a fusion in 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 *Asparagopsis 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 *Scurria forcellata* (Svedelius, 1915), *Asparagopsis armata* and *Bonnemaisonia asparagoides* (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 *Batrachospermum moniliforme*, the granules of the mature spermatium nucleus correspond with the haploid number. Yamanouchi (1906) refers to granules occurring in the spermatium of *Polysiphonia violacea* as prochromosomes that are connected by weakly staining threads of lignin. 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 *Batrachospermum* is heterotypic, the second would be homotypic, and the four cells resulting from these two divisions would be homologous with the tetraspores which arise after reduction division in the higher red algae. Two observations seem to indicate that this may be true in *Tuomeya flavililis*: first, the development of the fertilized egg into four gonimoblast initials which are similar to those found in *Batrachospermum* 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 Bouin's fluid, there is a fusion of the carpogonial nutritive cells borne on it. These cells gonimoblast. The greater part of the mother plant and is not conducted into the terminal cells only."

Of the Batrachospermae 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 *Trommaya* is out of place in the family Lemaneaceae and should be placed in the Batrachospermae.

**SUMMARY**

1. Carpospores of *Trommaya* 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 when 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, 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 *Trommaya fluviatilis* Harv. be placed in the family Batrachospermae rather than the Lemaneaceae where it now stands.

**EXPLANATION OF PLATES**

Lettering of figures: ac, assimilative cell; cae, central axis cell; cf, corticating filament; ch, chromatophore; cg, carpogonium; cgbe, carpogonial branch; csm, carposporangium; gi, gonimoblast initial; lbi, lateral branch initial; msp, monosporangium; nr, nutritive cell; p, pedicel of carpogonium; pgb, primary gonimoblast filament; sgf, secondary gonimoblast filament; sp, spermatium; spm, spermatangium; spsc, spermatangium mother-cell; tr, trichogyne; tn, trichogyne nucleus; M N, male nucleus; F N, female nucleus.

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Fig. 1. Photograph of mature plants of *Taxomyces* var. *fusoides*. X625. Fig. 2. Germinating carpospore. X625. Fig. 3. Carpospore germination on parent plant. X625. Fig. 4. Young germ tube after pore wall has fallen off and host cross-wall has formed. X625. Fig. 5. Young spore, X625. Fig. 6. Later stage showing sporulation of nine cells. X625. Fig. 7. Photomicrograph of juvenile plant showing the basal part of the young, branched filament 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 sexual monosporangia. X625. 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. X25. Fig. 2. Germinating spores. X25. Fig. 3. Young sporeling, live cells, long cells. X625. Fig. 4. Young sporeling, live cells, long cells. X625. Fig. 5. Young sporeling, live cells, long cells. X625. Fig. 6. Young sporeling, live cells, long cells. X625. Fig. 7. Photomicrograph of branched filaments and the empty filaments of lamellae 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 sexual frond, showing apical cell; young axial cells cut off from its base have given rise to lateral branches. X1000. Fig. 13. Photomicrograph of longitudinal section of a mature frond, showing elongated central axis cells, cortical filaments, and lateral branch origin and development. X14. Photomicrograph of a younger part of the frond, showing the differentiation of axis cells at base and apex Fig. 15. Cross section through a 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 origin and cortical filaments, X892. Fig. 17. Photomicrograph of crushed material showing the origin of cortical filaments from base of lateral branch initial.
Fig. 18. Portion of J. pbnt showing spermangia mother-cells and spermangia. The nuclei of two spermangia are in the prophase stage. X2000.

Fig. 19. Spermangia mother-cells after they have become heart-shaped from production of spermangia. Spermatozoids have been discharged. X1785.

Fig. 20, 21. Spermangia showing parietal chromatophores. X1785.

Fig. 22. Portion of Fig. 18 enlarged, showing spermangium nucleus in prophase stage with eight granules visible. X3000.

Fig. 23. Spermangium after discharge from the spermangium showing nuclear division at metaphase. X3000.

Fig. 24. Spermangia attached to trichogyne showing binucleate condition in one. Two other spermangia visible, each with a single nucleus. Three male nuclei occur in the trichogyne and one is in the process of fusing with the egg nucleus. The fourth spermangia is not visible. X2000.

Fig. 25. Two spermangia in binucleate condition, attached to trichogyne; the first division of the fusion nucleus has taken place. X972.

Fig. 26. Outline drawing from an acet-o-carmine smear showing carpogonial branch and its relation to the central axis. X1000.

Fig. 27. Diagram of growth in J. pbnt. X2000.

Plate 3
sperm cells and spermatangia. The nuclei of two spermatangia mother cells after they have fused, spermatia have been discharged. X1785. Fig. 18. Portion of Fig. 17 showing spermato-angia. Spermangia have been discharged. X1785. Fig. 19. Portion of Fig. 18 showing spermato-angia. Spermangia have been discharged. X1785.

Fig. 27. Carpogonial branch showing chromatophore rudiment in the carpogonium and degeneration of chromatophores of distal end of branch. X1000. Fig. 28. Same structure showing nuclei in trichogynae. X1000. Fig. 29. Young carpogonial branch without chromatophores showing degeneration of trichogynae and growth of nutritive cells. X1000. Fig. 30. Portion of a carpogonial branch showing earliest appearance of carpogonium. X2000. Fig. 31. Carpogonium after fertilization showing male and female nuclei. X2000. Fig. 32. Carpogonium after fusion of male and female nuclei. About 14 granules were evident. X2000. Fig. 33. Early cell division of the carpogonium after fertilization. X892. Fig. 34. Early cell division of the carpogonium after fertilization. X892. Fig. 35. Carpogonial branch showing fusion of two gonimoblast initials and development of primary and secondary gonimoblast cells. X1000. Fig. 36. Portion of a carpogonial branch at an earlier stage showing fusion of gonimoblast initials and first primary gonimoblast cells being formed. X1000.
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 and nutritive cells with gonimoblast initials and primary gonimoblasts. 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 the primary gonimoblast. X1000. Fig. 42. The same, showing branching of filament and walls of old carposporangia. X1000.
LITERATURE CITED


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