Structure and Reproduction of Chrysophaeum Lewisii[1])

Wm. Randolph Taylor

Professor of Botany, University of Michigan

In 1924, while working on the marine algae of the Dry Tortugas Islands off the southern tip of Florida, the writer frequently noticed growing on the coral rocks and sand, and on the lower parts of coarse algae scattered over the sea bottom in shallow water, light yellowish-brown tufts of the utmost delicacy. Faced by the complexity of the Florida flora for the first time, without previous tropical experience, he was not able to make a careful study of this plant, which clearly did not fit any Phaeophycean category with which he was acquainted, nor could he do so on subsequent visits. When in 1928 Dr. Ivey F. Lewis proposed to carry on Phaeophycean studies at the same station, the writer recommended this plant for consideration. Dr. Lewis did make careful observations, and mentioned the organism in his preliminary report (Lewis 1928), but to date has not published any definite account of it. When the writer found the same plant at Bermuda, he inquired regarding the state of the investigations, and was generously advised by Dr. Lewis to proceed to give his own description of the plant.

These delicate tufts consist of dichotomous filaments with defined but gelatinous walls and light yellow-brown chromatophores in the cells; in reproduction they gelatinize yet more completely and the cells are transformed into unequally biflagellate zoöspores. In brief, we are directed at once out of the Phaeophyceae and faced with the surprising probability that these plants are Chrysophycean in their affinities. Very few marine Chrysophyceae are known, and probably no Chrysophyceae as large. The classification applicable to our plants

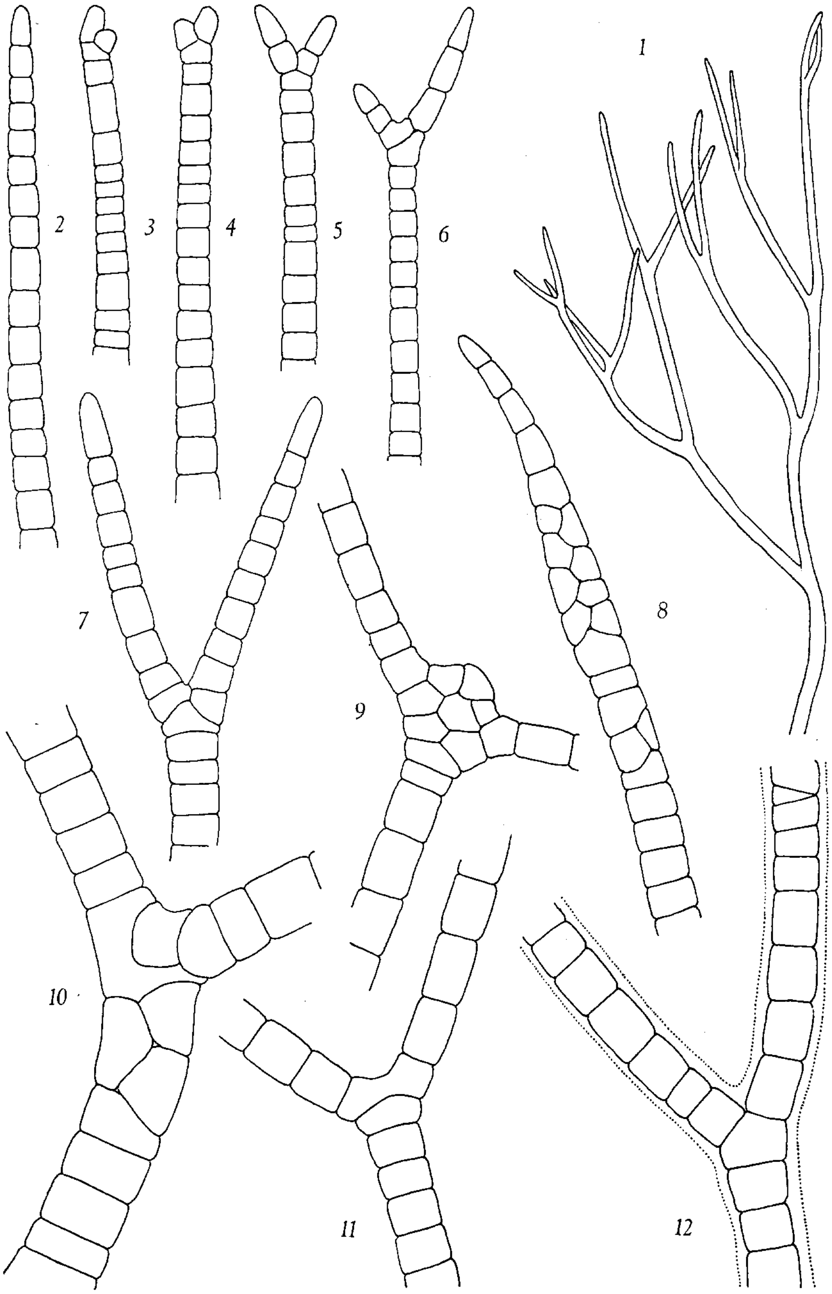
[1]) This work was facilitated by a Grant from funds placed at the disposal of the Bermuda Biological Station by the American Philosophical Society. For this generous aid, and for the very cordial coöperation of the former Director of the Station, Dr. D. E. S. Brown, of the Station staff, and of his assistant under the Grant, Mr. Albert J. Bernatowicz, the writer is exceedingly grateful. Publication no. 161 from the Bermuda Biological Station.

first appeared with PASCHER's paper (1914) where he showed that the flagellate genera with golden brown chromatophores had filamentous relatives which return to a flagellate phase in reproduction, and, for our purpose, that in the order Chrysotrichales he could define a family Chrysotrichaceae (1914, p. 143) with *Ochromonas*-like zoöspores, that is, zoöspores with two unequal flagella. In a later paper (1925, pp. 497, 509, 562) he makes a change from *Chrysothrix* to *Nematochrysis* because the name was preëmpted, and with it changes the family name to Nematochrysidaceae. While he specifies that this family consists of unbranched species with *Ochromonas*-like zoöspores, primarily the marine *Nematochrysis*, and while in the type genus the zoöspores escape through individual pores in the rather firm cell walls, his alternative in the scheme of classification would put our plant with the freshwater *Phaeothamnion*, which it does not resemble in structure or branching, though similar in reproduction. FRITSCH in his general survey of the algae (1935, pp 512, 556) accepts the classification of PASCHER without adding any categories more applicable to our plant. CARTER (1937, p. 49) offers the new genus *Chrysomeris* with sparingly branched uni- or pluriseriate filaments and uniflagellate zoöspores, placing it also in the Nematochrysidaceae, and thus widening our conception of it. While one may look askance at the inclusion of a plant with uniflagellate or *Chromulina*-type zoöspores, one must admit that PASCHER put *Chrysoclonium* in the family Phaeothamniaceae in spite of the presence of but one flagellum on zoöspores of that genus, and that the presence of the second flagellum is generally exceedingly difficult to confirm in these plants. Professor F. E. FRITSCH, in correspondence regarding this plant, kindly called the attention of the writer to a paper by SCHUSSNIG (1940, p. 323, textf. 4), among others, in which is described *Nematochrysis pusilla*, an unbranched little thing, but with the peculiar type of chromatophore shown by *Chrysophaeum Lewisii*, of which it might well be a germling except for a possibly firmer wall. When PASCHER (PASCHER and VLK 1941—42) had to place a *Radiofilum*-like Chrysophycean without known zoöspores in his system he left it in the order Chrysotrichales, without closer delimitation. In such a relatively little-known group of plants it is to be expected that many changes in the families and orders must occur before the natural limitations of the groups are clear, and the writer prefers to associate his plant with the Nematochrysidaceae even though certain peculiarities seem to require that it be placed in a new family.

This small alga seems to be somewhat local in its distribution but because of its inconspicuous character and superficial resemblance to clumps of *Schizonema* or ill-developed *Ectocarpus* it may often have escaped recognition. It is a plant of well-illuminated situations in warm, shallow water, generally growing within at most two or three decimeters of the surface at low tide, on rock, stones, sand or on other algae, such as *Chondria* or *Sargassum*, though on one occasion it was dredged from relatively shallow water. In the places where the writer has collected it the sand and the related rocks have always been calcareous, derived from coral fragments or shells. The two areas from which it is known are both well to the north of the tropics, but both have a typically tropical marine vegetation. In Bermuda the plant was not noted during the summer season, but in Florida it occurred in July, when the water was very warm, which counters any suggestion that the plant is more characteristic of cooler seasons or waters. The writer has collected at numerous places in the Caribbean without chancing upon it, but nowhere with the leisure to make a deliberate search for inconspicuous species.

The plants are commonly a centimeter tall, or even two or three, but because of their exceedingly delicate nature it is hard to be sure that a given clump is continuous, and not in part broken and displaced, or to recognize any single point of attachment. The lower filaments reach diameters of 16—38 μ, most commonly of about 30 μ, tapering gradually toward the tips where the ultimate divisions are 4.5—7.7 μ diam., with the cells 0.5—1.0 diameters long, or a little more or less. The tip cells are blunt, somewhat tapering, about 3.5 μ diam., 1.5—2.0 diameters long (Figure 13). The cell walls are very delicate throughout, thin and very inconspicuous near the tips, but reaching about a ninth of the diameter of the axes below (Figures 17, 18). While the filaments were in good health it was not possible to recognize optically a firmer wall near the protoplasts, but when they began to disintegrate it was sometimes possible to make such a distinction in the oldest parts. No cellulose reaction was obtained with freshly tested chlor-ioide of zinc. The character of the wall is thus entirely different from the clearly delimited structures of the filamentous Phaeophyceae. Excessive shrinkage of the protoplasts in dried material caused the gelatinous layer to seem much thicker in herbarium specimens. In fact, only when thinly spread and dried on mica do herbarium specimens have much record value, those on paper not recovering well enough when soaked up to permit accurate observations. All of the drawings accompanying this account were made from living material. Dried material is very much darker than the same material had been in life.

The habit of branching is characteristically dichotomous (Figure 1), the divisions rather stiffly divergent at angles of 30°—60°, with relatively inconspicuous irregularities and no systematic production of adventitious branches. However, it is clear that the apical cells do



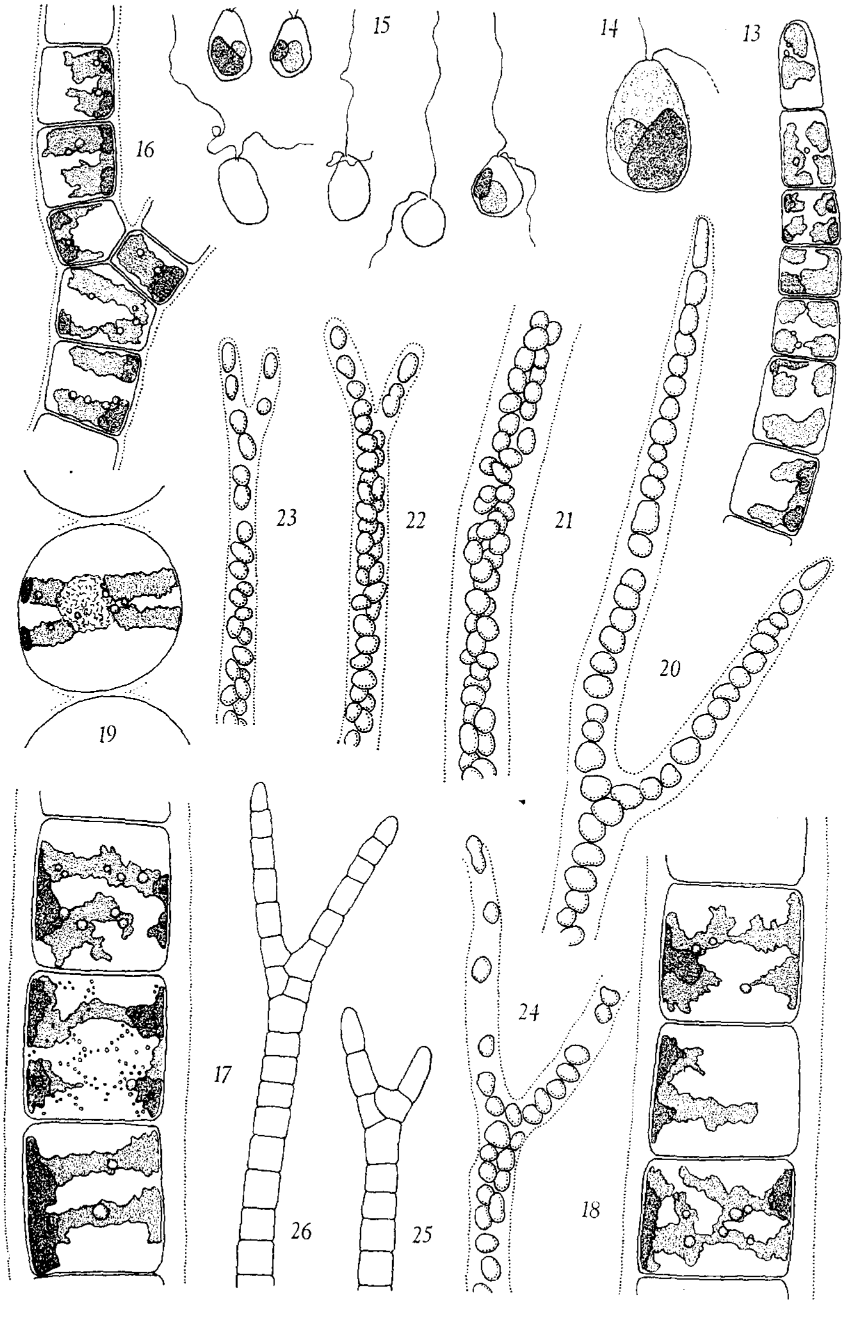
1
2
3
4
5
6
7
8
9
10
11
12

not divide longitudinally, and the false dichotomy is probably produced by a quickly cut off upgrowth from the subterminal cell, which displaces the apical cell from the median line (Figures 3—7, 25, 26). The two divisions usually grow with equal vigor and fork in turn at the same level, but one may outstrip the other The anatomy of the fork is characteristically diverse in this plant, the cell supporting the fork sometimes equally, sometimes unequally truncate, sometimes extended laterally, or sometimes after the forking has been established dividing irregularly and even producing a parenchymatous mass (Figures 7—12). Oblique divisions, causing the axes to become irregularly pluriseriate, are not rare, but generally occur locally in the older branches, though sometimes one finds the same in lesser degree near the tip of a branch (Figure 8).

The cell structure seems to be rather simple. No satisfactory staining of nuclear material was effected. The iodine test for starch, demonstrating the absence of this reserve food, failed to give a clue to the nucleus. Picronigrosin and acetocarmine applied to fresh material both caused the filaments to disintegrate without effecting a nuclear stain, and an attempt to mordant dried material and stain with haematoxylin produced no differentiation within the cells. It is assumed from the absence of suitable multiple bodies in the cell, rather than by any direct recognition, that there is a single nucleus. The chromatophores are light yellowish brown, with somewhat erose margins, two or perhaps four in number, oval to band-shaped. In young cells there quite often seem to be four, but one may easily overlook delicate bridges between parts of chromatophores (Figure 13). The chromatophores elongate as the cells get older and take up lateral positions around the cell, being commonly irregular, lobed, or perhaps fused, to conceal the basic condition (Figures 16—18). Refractive colorless round bodies (leucosin?) are generally associated with the chromatophores; they did not seem to be pyrenoids or any other fixed character (Figure 17). Other smaller granules are present in the general cytoplasm, but have not been figured except in one cell (Figure 17). Specimens kept for some time under a coverglass soon begin to deteriorate, and the cells generally round up, with an increase in the sharpness of the vacuole boundary accompanying a displacement of the chromatophores toward one side of the cell, or, occasionally, an increase in their distinctness and association with

---

Figures 1—12. *Chrysophaeum Lewisii.* Fig. 1. Habit of distal branching, × 116. Figs. 2—7. Origin and early development of typical forks at branch apices, × 500. Fig. 8. A branch with pluriseriate portion near the tip, × 500. Figs. 9—12. Various mature forks, showing different cellular arrangements below the branches; in fig. 12 the gelatinous wall is indicated, × 500.



16
15
14
13
23
22
21
20
19
17
26
25
24
18

a single protoplasmic mass which may contain the nucleus (Figure 19).

The reproductive state of this plant proved very difficult to secure. It was examined fresh from nearby shoal water on many occasions, was kept in glass bowls for days with both running and still sea water, was kept in dim light and in sunlight, was exposed to strong electric light at night, and treated in various other ways, without any certain effect. In fact, only once did the writer succeed in securing zoöspores in abundance, although on numerous occasions the initial stages appeared, only to succumb. The process is essentially a simple one. The walls of the filaments swell and the cells round up (Figures 20—24). They probably usually divide once or twice (Figure 21), but in other cases do not seem to do so. Without further preparation the cells organize as zoöspores. The inner jelly of the filaments seems to become somewhat softer than the outer at this stage, and the zoöspores become restless in an almost fluid matrix. Quite commonly the flagellar apparatus develops before they emerge, but at other times equally active zoöspores seem to have been extruded without flagella, developing them as they lie near the parent filament, and then swimming away. Egress may be through the tip of the filament, or through ill-defined holes in the side, but under the artificial conditions of microscopic observation a large proportion never emerge at all. Production of zoöspores seemed only to be effective in the outer divisions of the plant, perhaps the last two or three forks, and while the walls of the lower axes became softened and the cells rounded and even divided, they were not seen to complete the process. It is evident that there are no morphologically distinct sporangia concerned in this process, which suggests that the filaments pass from a specialized form back to a somewhat palmelloid condition, from which we have numerous examples in different algal groups of the direct production of zoöspores.

The zoöspores are pyriform, ovoid or nearly round, 6—7 μ in diameter, and 8—9 μ long (Figures 14, 15). They have two oval

---

Figures 13—26. *Chrysophaeum Lewisii.* Fig. 13. Normal branchlet tip showing the chromatophores in the cells, × 1200. Fig. 14. Diagrammatic representation of zoöspore showing verrucosity of the wall, the flagella curtailed. Fig. 15. Semidiagrammatic tracings of six zoöspores, some with the chromatophores and flagella shown, × 1200. Fig. 16. Normal fork of a branch from the upper central part of a clump, showing gelatinous wall and chromatophores, × 1200. Figs. 17, 18. Normal axes from the lower central portion of a clump where the cell structure is still typical, × 1200. Fig. 19. A cell from a dissociating filament showing the changes in cell appearance, × 500. Figs. 20—24. Various states in the rounding up, division of the cells and softening of the walls, preparatory to liberation of zoöspores, × 500. Figs. 25, 26. Two stages in the development of typical forks at branch apices, × 500.

chromatophores of more or less unequal size toward the posterior end. Nucleus, vacuole and stigma were all unobservable with the equipment at hand. The cell membrane under oil-immersion appeared to be inconspicuously verrucose toward the forward end. There was one distinct anterior flagellum about three times as long as the cell diameter, directed forward, and in a few instances there was clearly seen a second very inconspicuous one twice as long as the cell diameter, lying close about the forward end of the cell or trailing. In most cases it could not be seen. The function of these swarmers was not demonstrated, but sexuality is almost unknown in the Chrysophyceae. They probably are neutral zoöspores, but they either disintegrated or simply rounded up on the slide, and neither paired nor attached themselves.

Chrysophaeum n. gen.[1] — Plants filamentous; filaments dichotomously forked, the cells with especially the lateral walls gelatinous, the 2—4 chromatophores yellowish-brown; zoöids (zoöspores?) produced after further gelatinization and swelling of the filament walls with rounding up of the cells, the zoöids pyriform, with two chromatophores and two unequal flagella.

Chrysophaeum Lewisii n. sp. — Plants as in the genus, 1—3 cm. tall, bushy, exceedingly delicate, filaments 30—38 μ diam. below, tapering to 4.5—7.7 μ near the tips, the cells subcylindrical, a little turgid, with very thin walls between; zoöids pyriform, 7—8 μ diam., 8—9 μ long.

DISTRIBUTION: BERMUDA. St. Georges I., occasional turfts on *Amphiroa* about 10 cm. below low tide level on the Biological Station jetty, W. R. Taylor and A. J. Bernatowicz *no. 49-320*, 17 March 1949. Hamilton I., occasional tufts on marine grasses about 10 cm. below low tide level, Stovel Bay, *no. 49-912*, 24 April, 1949. Port Royal Bay, Hunt I., locally abundant on rocks and algae about 10 cm. below low tide level, *no. 49-1722 (TYPE)*, 11 May 1949.

---

[1]) *Chrysophaeum* N. Gen. — Plantae filamentosae; filamenta iterum atque iterum dichotome furcata, parietes laterales cellularum gelatinosi, chromatophori 2—4, flavescenti-brunnei; zoosporae, filamentis gelatinosioribus factis atque tumescentibus, per cellulas rotundatas effectae, pyriformes, duos chromatophoros atque duo flagella inaequa habentes.

Chrysophaeum Lewisii N. Sp. — Plantae ut in genere descriptae, 1—3 cm. altitudine, fruticosae, maxime tenues, 30—38 μ diam., inferne, ad 4.5—7.7 μ diam. prope cacumina attenuatae, cellulae subcylindricae, turgidulae, parietibus inter eas tenuissimis; zoosporae pyriformes 7—8 μ diam., 8—9 μ long. Specimen typicum in loco dicto Hunt I., Bermuda, coll. W. R. Taylor et A. J. Bernatowicz *no. 49-1722*, 11 Maii, 1949.

FLORIDA, DRY TORTUGAS I s.s. Dredged off White Shoal (in water of very moderate depth), W. R. Taylor *no. 24-327*, 10 July 1924. Garden Key, *no. 25-622*, 9 June 1925. Loggerhead Key, west side in shallow water, *no. 25-1000*, 26 June 1925. *Ibid.*, I. F. Lewis, 2 July, 1928. Garden Key, on coral sand on the west side, 46 meters south of the Laboratory Wharf at about 5 dm. below the surface, 2 July, 1928.

REFERENCES

CARTER, N. 1937. - New or Interesting Algae from Brackish Water. *Arch. Protistenk.* 90: *1—68*, pls. 1—8, 3 textfigs.

FRITSCH, F. E. - The Structure and Reproduction of the Algae, Vol. 1. xviii + 791 pp., 245 textfigs. Cambridge, England, 1935.

LEWIS, I. F. 1928. - Studies of Brown Algae. *Carnegie Inst. Washington Yearb.* 27: *278—279.*

PASCHER, A. 1914. Über Flagellaten und Algen. *Ber. dtsch. bot. Ges.* 32: *136—160.*

——— 1925. - Die braune Algenreihe der Chrysophyceen. *Arch. Protistenk.* 52: *489—564*, pl. 15, 56 textfigs.

——— and W. VLK 1914-42. - Zur Kenntniss der Chrysophyceen des salz-haltigen Flachmoores Hrabanow bei Lissa a. E. *Lotos* 88: *163—177*, 10 textfigs.

SCHUSSNIG, B. 1940. - Über einige neue Protophyten aus der Adria. *Arch. Protistenk.* 93: *317—330*, 7 textfigs.