CULTURAL EVIDENCE FOR THE MORPHOLOGIC PLASTICITY OF ENTOPHYSALIS DEUSTA (MENEGHINI) DROUET AND DAILY (CHROOCOCCALES, CYANOPHYCEAE)

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1. INTRODUCTION

Drouet and Daily (1956) in their revision of the coccoid *Myxophyceae*, unite under *Entophysalis deusta* (Meneghini) Drouet and Daily a number of often recorded marine littoral rock-inhabiting and lime-penetrating *Cyanophyceae*, such as *Gloeocapsa crepidinum* Thur. *ex* Born. & Thur. (traditionally *Chroococcaceae)*, *Entophysalis granulosa* Kütz. (traditionally *Chroococcales*, *Entophysalidaceae)*, *Pleurocapsa fuliginosa* Hauck (traditionally *Pleurocapsales*, *Pleurocapsaceae)*, *Hyella caespitosa* Born. & Flah., *Hyella balani* Lehmann (traditionally *Pleurocapsales*, *Hyellaceae)*. In all Drouet and Daily synonymize 100 specific and infraspecific names with *E. deusta*. Of these, 22 are nomenclatural synonyms, so 78 putative taxa belong, according to these revisers, to one species. However, the large majority of these names are never used in recent publications on cyanophycean taxonomy. In Parke and Dixon's 'Revised check-list of British marine algae' (1964) 8 marine *Chroococcales* are enumerated that should be ranged under *Entophysalis deusta* according to the taxonomic concepts of Drouet and Daily.

2. MATERIAL AND METHODS

Old oyster-shells, infected with various species of perforating algae, were collected near Wemeldinge (Oosterschelde, Netherlands). These shells appeared to contain '*Hyella caespitosa*' filaments.

In order to kill algae growing attached to the surface these shells were scrubbed and dipped in 50 % aethanol during about 5 to 10 seconds. Fragments of such shells were subsequently cultured in culture tubes containing Erdschreiber-chalk-agar covered by a thin layer of Erdschreiber.

After 6 weeks characteristic blackish-green gloeocapsoid colonies (*c.* 1 to 3 mm in diameter) had appeared on the surface of the agar (fig. 1), among a number of other perforating algae. Unialgal cultures were isolated from the above gloeocapsoid colonies and grown in tubes with Erdschreiber-chalk-agar covered by a thin layer of Erdschreiber. After 3 weeks typical gloeocapsoid colonies had appeared, to a part of which small transparant fragments of oyster-shells were added. The Erdschreiber-chalk-agar was prepared from a mixture of 1 l Erdschreiber, 18 g agar and 10—20 g chalk. For preparation of Erdschreiber, cf. Dammann, 1930.

Entophysalis-colonies (not the other perforating algae!) grew best on agar with a thin top layer of fluid (Erdschreiber) that subsequently disappeared by evaporation and absorption by the agar. Growth on agar without a fluid top layer or with too much fluid was clearly much smaller.

The cultures were kept in culture rooms of 20° C and 12° C and in daily 18 hours'

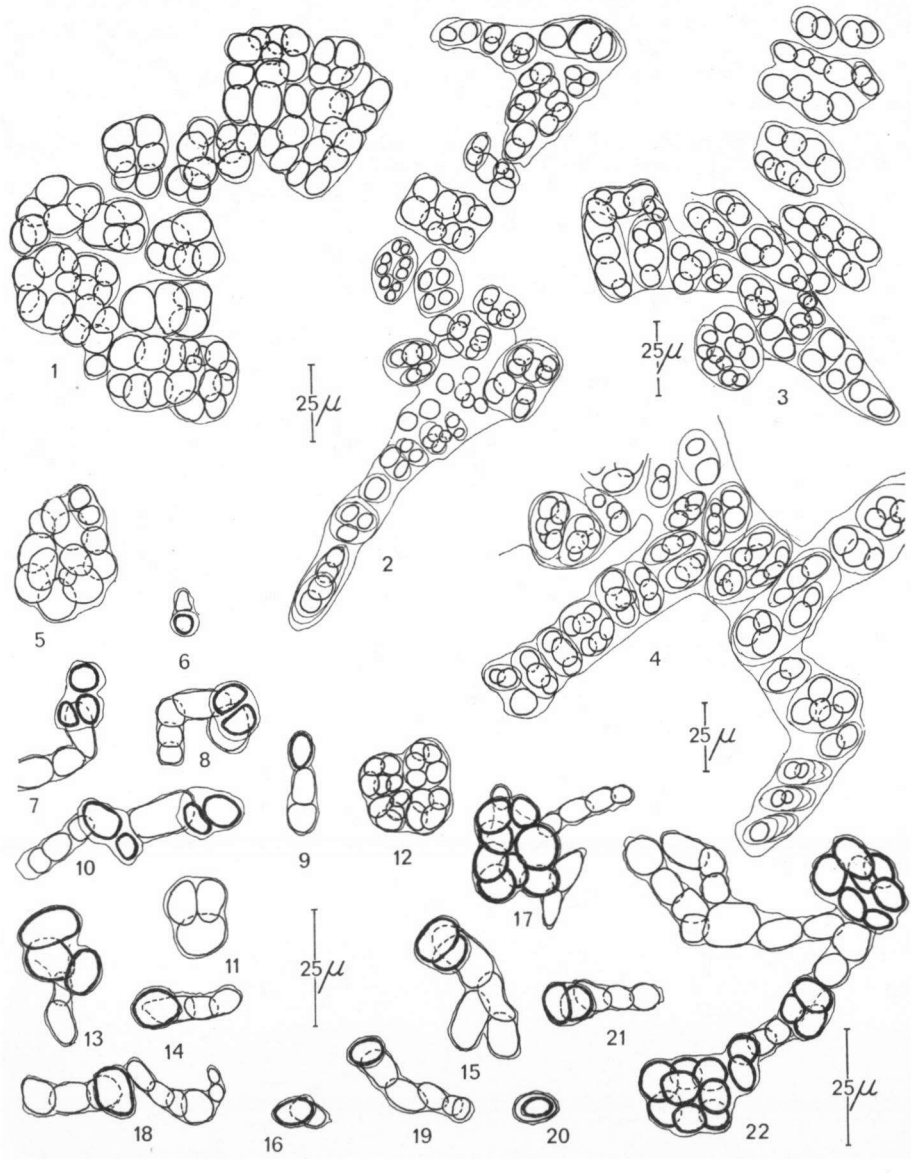
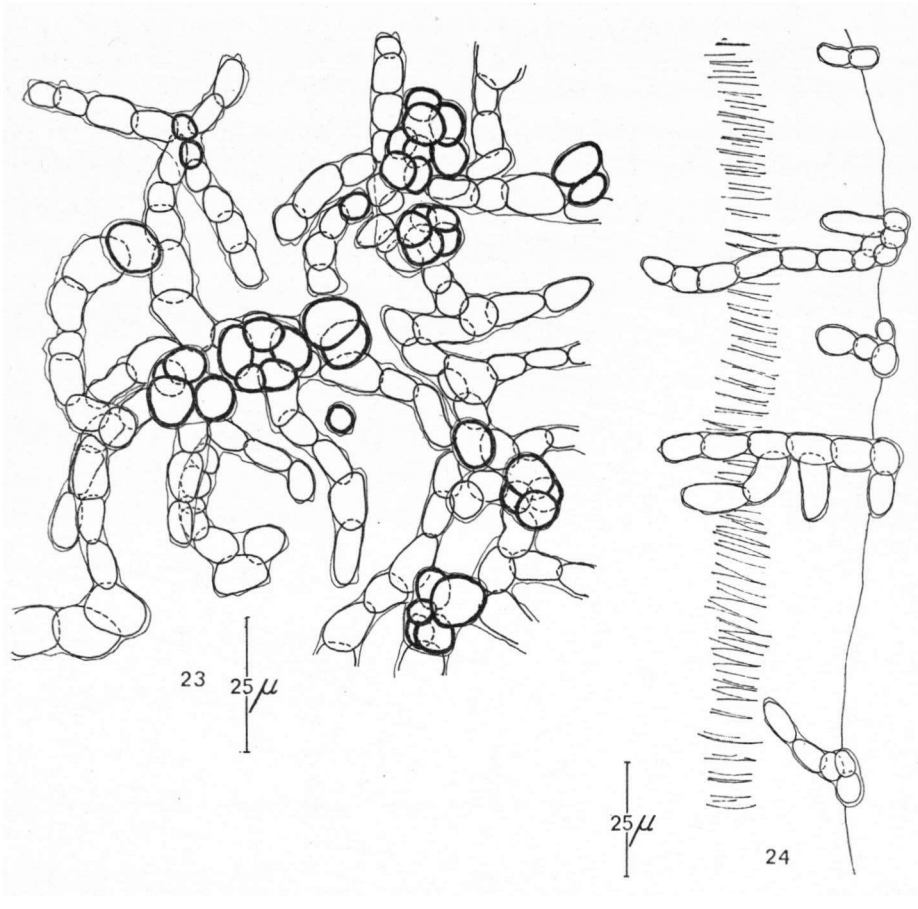


Fig. 1. Gloeocapsoid colonies grown directly from aethanol treated cells. — Figs. 2—4. Unialgal Entophysalis-like colonies, fig. 4 with Hormathomena-like cells (unilateral thickening of sheath). Figs. 5—24. Colonies grown in contact with fragments of oyster-shell. Thick-lined cells growing outside the shell, thin-lined cells growing inside the shell. The penetrating cells form Hyella-like filaments. Figs. 5—23 surface views, fig. 24 cross-section of shell with Hyella-like filaments.

photoperiods. The two different temperatures did not have any appreciable influence on the results.

Plants growing in the transparant fragments of shells were directly observed under the



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microscope. Some fragments were decalcified with a 5 % solution of Na_2-EDTA (ethylenediaminetetraacetic acid, disodium salt) in Erdschreiber. After two days the fragments were decalcified and the cyanophyte was still living. Cross-sections of such fragments were made by hand with a razor-blade.

3. RESULTS AND DISCUSSION

1. Morphology of colonies grown directly from aethanol treated shells. The blackish-green, shining colonies, macroscopically as well as microscopically, showed the typical morphology of '*Gloeocapsa crepidinum*' (fig. 1). Gelatinous irregular colonies of rounded or mutually flattened cells, surrounded by colourless, not obviously lamellated sheaths. Cell-divisions in all directions. Cells often seemingly in groups of two or four (in surface view). Transitions to '*Entophysalis granulosa*' are present. Diameter of cells 4—15 μ.

2. Morphology of unialgal cultures growing on agar and isolated from material described under 3.1. Macroscopical aspect as under 3.1. Partly resembling '*Gloeocapsa crepidinum*', partly '*Entophysalis granulosa*', both aspects merging into each other. Cell-divisions in all directions, but with a preference for the direction perpendicular to the surface, as a result of which the cells are arranged in vertical cellrows. Lamellation of the sheaths more obvious than under 3.1. The sheaths quite often unilaterally more developed giving rise to cells or cell-groups similar to '*Hormathonema*' spp. (cf. Ercegovic, 1929 b, Geitler 1930—32) (fig. 4). The '*Entophysalis granulosa*'-aspect is the characteristic result of crowding in well-growing cultures. In nature old crusts of the 'black zone' of the upper intertidal belt exhibit this aspect. Diameter of cells 2.5—10 μ (fig. 2—4).

3. Morphology of colonies grown in contact with fragments of oyster-shells. Such colonies reacted in accordance with Drouet and Daily's description of *Entophysalis deusta* by forming a profusion of basal filaments penetrating into the shell-fragments (fig. 6—24). Such filaments arise from '*Gloeocapsa*'-like cell-groups (fig. 17, 22, 23, 24) or from isolated cells (fig. 14, 18, 19, 21, 24). The filaments show true branching, but often they are unbranched. The sheaths of the penetrating filaments do not have an obvious lamellation. Gloeocapsoid cell-groups may be also found inside the shell. The penetrating filaments are sometimes composed of two to several cell-rows. The penetrating phase is identical with forms described as *Hyella caespitosa* and *H. balani*. Particularly cells or cell-groups with initial perforation cover *Pleurocapsa minuta* Geitler (1930—32, p. 355) (fig. 6, 7, 8, 13, 14).

4. Conclusions and discussion. These results support the concept of *Entophysalis deusta* as a morphologically highly plastic cyanophyte, whose different morphological possibilities are often encountered in the literature as *Gloeocapsa crepidinum*, *Entophysalis granulosa*, *Pleurocapsa fuliginosa*, and *Hyella caespitosa*. Results of investigations of naturally occurring material are in accordance with this opinion (cf. Koumans-Goedbloed, 1966; van den Hoek, 1958; personal experience of the second author).

Drouet and Daily, in their 'Revision of the coccoid *Myxophyceae*', reduce a number of about 2800 names (including the nomenclatural synonyms) to a total of 32 taxa. Geitler, on the other hand, in his compilatory work on the *Cyanophyceae* (1930—32) which serves as an identification work for the more traditionally thinking algologists, recognizes 322 species as belonging to this group.

Drouet and Daily's revision provoked much criticism, part of which very severe (Bourrelly, 1957; Geitler, 1960; Skuja, 1956). These two authors' comparative investigations and documentation of large numbers of dried specimens are considered naively uncritical ('naivste Kritiklosigkeit') (Geitler). As to *Entophysalis deusta* we do not agree with Geitler, since Drouet and Daily's concept of this species is better founded and documented than those of the entities synonymous with it and described in the general compilation works. However, one can admit that a more exhaustive treatment of the taxonomic principles underlying their work and figures illustrating their viewpoints would have facilitated a more constructive discussion.

The above reviewers criticize Drouet and Daily for not having investigated living populations, because the taxonomically valid characters can only be observed in living material (in fact the authors investigated much living material, particularly from the United States). The criteria traditionally used to differentiate in this group are: a) structure of thallus (unicellular, multicellular, in rows or not so, branched or not so, etc.), b) form of cells, c) mode of cell-division, d) formation of nannocytes or endospores, e) structure

and colour of sheaths, f) dimensions, g) presence or absence of gas vacuoles, h) habitat (epiphytic, endolithic, epilithic), i) colour of cell-contents. Of these criteria only the last one is apt to be much modified in dried material. In practice, it is used as a criterion of minor importance. Further many dried cyanophycean specimens survive long periods.

26 of the 102 synonyms of *Entophysalis deusta* are teated in Geitler's compilation, namely 1) *Entophysalis granulosa* Kützing 1843, 2) *Gloeocapsa crepidinum* Thuret 1876, 3) *Dermocarpa violacea* Crouan fr. 1858, 4) *Placoma vesiculosa* Schousboe & Thuret in Bornet & Thuret 1876, 5) *Pleurocapsa fuliginosa* Hauck 1885, 6) *Hyella caespitosa* Bornet & Flahault 1888, 7) *Hyella caespitosa* var. *spirorbicola* Hansgirg 1892, 8) *Aphanocapsa littoralis* Hansgirg 1892, 9) *Hyella caespitosa* var. *nitida* Batters 1896, 10) *Pleurocapsa crepidinum* Collins 1901, 11) *Hyella balani* Lehmann 1903, 12) *Hyella littorinae* Setchell & Gardner 1918, 13) *Placoma violacea* Setchell & Gardner 1918, 14) *Pleurocapsa entophysaloides* Setchell & Gardner 1918, 15) *Pleurocapsa gloeocapsoides* Setchell & Gardner 1918, 16) *Solentia stratosa* Ercegovic 1927, 17) *Solentia intricata* Ercegovic 1927, 18) *Aspalatia crassior* Ercegovic 1927, 19) *Aspalatia tenuior* Ercegovic 1927, 20) *Dalmatella buaënsis* Ercegovic 1929, 21) *Hormathonema paulocellulare* Ercegovic 1929, 22) *Tryponema endolithicum* Ercegovic 1929, 23) *Scopulonema hansgirgianum* Ercegovic 1930, 24) *Hormathonema luteo-brunneum* Ercegovic 1930, 25) *Hormathonema violaceo-nigrum* Ercegovic 1930, 26) *Pleurocapsa minuta* Geitler 1932.

The descriptions (and most figures) of the following entities have been borrowed, with slight alteration, directly or indirectly, from the original authors: 1, 3, 5, 6, 7, 8, 9, 11, 12, 13, 14, and 16—25, so 21 out of 26 descriptions.

Exsiccata are cited for 1, 2, 3, 4, 10, 12, and 14, so for 7 out of 26. The exsiccata cited for 2, 4 and 10, the latter two representing nomenclatural type-material, have been probably investigated by Geitler.

Geitler possibly investigated living material of only nr. 26 (a new species based on one collection), though this is not apparent, as all characters used can be studied in dried material.

Many of the descriptions and figures borrowed by Geitler have been made after preserved material, viz. of 1, 3, 4, 5, 7, 8, 9, and 16—25, so 17 out of 26.

Geitler (1960), Skuja (1956), and Bourrelly (1957) consider study of figures and descriptions (apparently including those made after preserved material) a better basis for taxonomic work in this group than study of dried specimens. Nonetheless a consequence of this approach is the inclusion in Geitler's *Cyanophyceae* (and in several other compilatory works) of species that have been described as *Cyanophyta* by the original authors but not belong to this division (e.g. *Aphanocapsa littoralis* Rabenhorst, *Gloeocapsa montana* Kütz., *G. confluens* Kütz., *G. muralis* Kütz., *G. polydermatica* Kütz., *G. quaternata* Kütz.; cf. van den Hoek, 1963).

Only the unsurpassed descriptions and figures of Bornet and Thuret (1876) show the advantage of the study of living material. The above analysis shows that, as to the entities here considered, a compilatory work such as Geitler's *Cyanophyceae* (1930—32) does not conform to the standards now generally accepted for taxonomic revisions. As a compilation it still is a monumental work, and important for algal taxonomy. Koster (1961, 1966) drew attention to other incongruities in traditional cyanophycean taxonomy.

Varma (1965), as a result of a cultural study on cyanophytes provisionally identified as *Gloeocapsa decorticans*, *G. rupestris*, *G. dermochroa*, *Gloeothece samoensis*, *Gloeothece rupestris*, and *Aphanothece pallida*, came to the conclusion that the traditionally accepted generic divisions in the *Chlorococcales* are unnatural, and that these genera should be merged into one genus, in accordance with the taxonomic concepts of Drouet and Daily.

However, according to these two authors *Gloeocapsa decorticans* is a synonym of *Anacystis thermalis*, *Gloeocapsa rupestris* of *Coccochloris stagnina*, *Gloeocapsa dermochroa* of *Entophysalis rivularis* f. *rivularis*, and *Gloeothece rupestris* and *Aphanothece pallida* of *Coccochloris stagnina*.

It is interesting to record Nadson's (1932) conclusion that entities described by Ercegovic (1927—1934) as species of the genera *Hyella*, *Dalmatella*, *Scopulonema*, *Solentia*, *Aspalatia*, and *Hormathonema* are all growth forms of *Hyella caespitosa*. He also included *Gloeocapsa*-like, *Pleurocapsa*-like, *Entophysalis*-like, and *Chroococcus*-like colonies in the morphological range of the species. Nadson, therefore, independently from Drouet and Daily came to the same taxonomic concept.

According to Parke (1961) non-motile phases of the coccolithophorids *Syracosphaera carterae* and *Syracosphaera* sp. show a morphological plasticity comparable to that of *Entophysalis deusta* (cf. also Valkanov, 1962). The morphological aspects of this non-motile phase are similar to chrysophycean algae previously described as species of the genera *Chrysosphaera*, *Gloeochrysis*, *Nematochrysis*, *Thallochrysis*, *Apistonema*, *Chrysonema*, and *Chrysotila*. Such algae were described as important constituents of the high-littoral algal vegetation of chalk-cliffs in England (Anand, 1937).

Our own experiments have demonstrated that at least one population of '*Hyella caespitosa*'-like plants is able to show the morphological plasticity ascribed to *Entophysalis deusta* by Drouet and Daily. It is imaginable that other populations would react in more or less different ways. Other methods than those used in the traditional cyanophycean taxonomy and by Drouet and Daily are required to detect such variation. It seems rather probable, however, that such more refined methods (including extensive comparative cultural experiments) would not shatter *Entophysalis deusta* as a natural taxon; perhaps it would change the appreciation of its taxonomic level.

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SUMMARY

Cultural experiments with *Entophysalis deusta* support Drouet and Daily's concept of this species as a morphologically highly plastic taxon, showing forms traditionally identified as *Gloeocapsa crepidinum*, *Entophysalis granulosa*, *Pleurocapsa fuliginosa*, and *Hyella caespitosa*. These results are in accordance with observations on populations forming part of the 'black zone' of the upper intertidal belt. It is shown that Drouet and Daily's taxonomic principles, leading to a broad and more natural concept of this species, are sounder than those underlying Geitler's Cyanophyceae in which several entities included by them in *Entophysalis deusta* are treated as species.

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