
A consideration of the evolutionary trends in the blue-green algae with palaeontological evidences

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Blue-green algae are known right from the Precambrian to Recent. Evolutionary concepts have largely been based on comparative morphology of extant forms as revealed by culture studies. Broadly speaking, two trends came into vogue: (i) the 'retrogressive' concept elucidated by Geitler (1925), and (ii) the 'progressive' one laid out well by Fritsch (1942). Because relatively few fossil blue-green algae were then known, palaeobotanical evidence played only a small part in these approaches. Korde (1971) was the first to present a consolidated picture of the phylogenetic trends as revealed by fossils. Evidences that one looks for among the fossils relate to the origin of the filamentous condition, appearance of the heterocysts and the origin of heterotrichous habit and true branching. Most of the trends seen in the present day filamentous organization appeared in the Precambrian. Trichomatous condition developed in a major way in the Precambrian itself. The first uncontroverted record of a heterocyst apparently comes from Cambrian strata. The hormogone and spore types appeared earlier than the heterocyst. Records of heterocystous forms seem to point to an evolution of heterocystous types later. These forms parallel the homocystous morphotypes known earlier. True branching types seem to have come much later than the Cambrian. The fossil record of these forms seems to clearly support a 'progressive' type of evolution in two phyletic lines, the homocystous/heterocystous line preceding the heterocystous line. This evidence clearly supports Elenkin's concept of parallel evolution but not his 'retrogressive' projections. Reduction may be relevant only in smaller clines. The blue-green algae as a whole seem to be a conservative group where major developments occurred very early before the end of Proterozoic and do not exhibit any great degree or rate of change during later periods as do many other groups of biota. More work on these fossils is the need especially in the Indian subcontinent.

Key-words—Cyanophyceae, Evolution, Precambrian fossils.

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सारांश

पुरातात्विक प्रमाणों सहित नील-हरित शैवालों में विकासीय प्रवृत्तियों का महत्व

टी० वी० देसिकाचार्य

नील-हरित शैवाल क्रीमिय-पूर्व कल्प से वर्तमान तक मिलते हैं। विकासीय परिकल्पनायें अधिकतर वर्तमान प्ररूपों के तुलनात्मक आकारिकीय अध्ययन पर आधारित हैं। इस प्रकार दो चरण विकसित हुए (1) जीटलर (1925) द्वारा प्रस्तावित धारणा से, एवं (2) फ्रिट्च (1942) द्वारा प्रस्तावित 'प्रगामी' धारणा से। चूँकि उस समय अपेक्षाकृत अशिमत नील-हरित शैवाल कम विदित थे अतः उन्नत प्रस्तावित धारणाओं में पुरावनस्पतिक अवशेषों को कम महत्व दिया गया। सबसे पहले फिआर्डे (1971) ने अशिमत शैवालों पर आधारित एक ठोस अवधारणा प्रस्तावित की। अशिमत प्रमाणों से सूत्रवत् प्ररूपों, हेट्रोसिस्ट की उत्पत्ति तथा इनका वास्तविक द्विशाखन व्यक्त होता है। इस समय मिलने वाले सूत्रवत् शैवाल प्ररूपों के कई लक्षण क्रीमिय-पूर्व कल्प में विकसित हो गये थे। हेट्रोसिस्ट का पहला अभिलेख क्रीमिय-पूर्व स्तरों से ही ज्ञात है। होमोगोन तथा बीजाणु-प्ररूपों का विकास हेट्रोसिस्ट की उत्पत्ति के पहले हुआ है। शाखित प्ररूप क्रीमिय कल्प से काफी बाद में विकसित हुए हैं। ये सभी पादपाशम अभिलेख 'प्रगामी' प्रकार के विकास की पुष्टी करते हैं। ये प्रमाण एलेन्किन द्वारा प्रस्तावित समानान्तर विकास अवधारणा की भी पुष्टी करते हैं लेकिन उन्हीं द्वारा प्रस्तावित अधोगामी अवधारणा की नहीं। अधोगमन की प्रवृत्ति छोटे प्ररूपों में सम्भव हो सकती है। कुल मिलाकर नील-हरित शैवाल एक ऐसा पादप-समूह है जिनमें प्रोटीरोजीवी कल्प की समाप्ति के काफी पहले ही विकास हो चुका था और महत्वपूर्ण यह है कि अन्य पादप-समूहों की भाँति इनमें प्रोटीरोजीवी कल्प के बाद के कल्पों में अधिक परिवर्तन नहीं हुए। इन अशिमत शैवालों पर विशेषतया भारतीय उपमहाद्वीप में अभी और अनुसंधान की आवश्यकता है।

THE Cyanophyta of India was published in 1959 and only a few blue-green fossils were then known (see Desikachary, 1959). Further, fossils known from

elsewhere were similarly few and, as Fritsch (1942) has rightly said, the fossils referred to the blue-green algae at that time afforded no morphological data of value in the elucidation of evolutionary sequences and heterocysts were not known among the fossils till much later. Many records were largely of sheath-like structures probably belonging to the blue-green algae.

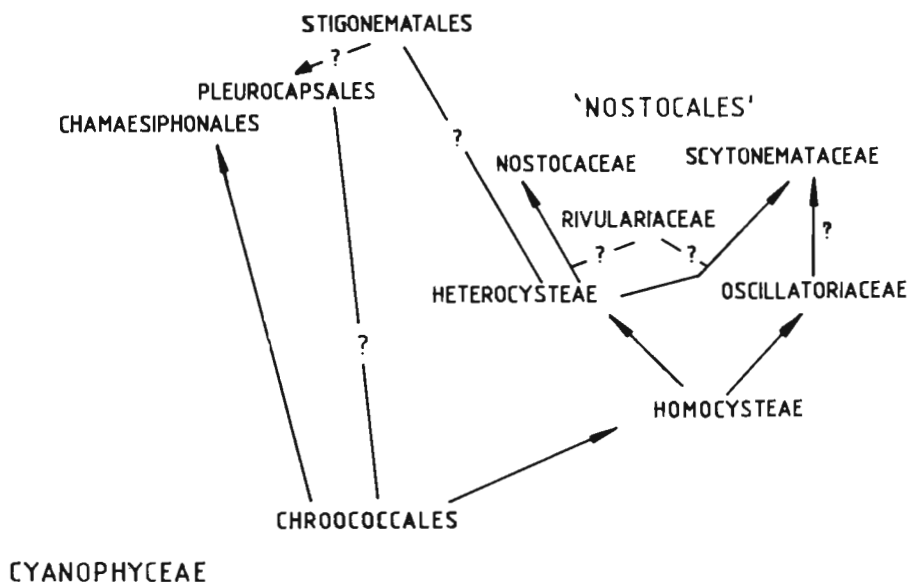
Later, in the sixties, many additional fossils were discovered from other lands. This was largely due to the great impetus given to Precambrian studies by Barghoorn, Schopf, and others (see Schopf, 1983).

Two concepts had crystallized by 1959 (for a complete review, see Fritsch, 1942). Geitler (1925, 1932; see also Chadefaud, 1951; Elenkin, 1969) formulated a theory which can be called 'Retgressive' evolution and Fritsch (1942) formulated the 'progressive' evolution (see Text-figure 1). Geitler derived the Pleurocapsales from the coccoid Entophysalidaceae and the Stigonematales with many 'advanced' features such as heterotrichous habit, hormogones, heterocysts, thallus structure, etc. were probably derived from forms similar to *Siphononema*. The other heterocystous and homocystous forms were derived from Stigonematales by a reduction series or simplification. Fritsch (1942) considered Pleurocapsales which have a heterotrichous condition with 'advanced' organization, cannot easily be derived from simple pseudofilamentous ancestors represented by Entophysalidaceae, a coccoid group. He thought, in agreement with Borzi (1916), that the relatively high degree of

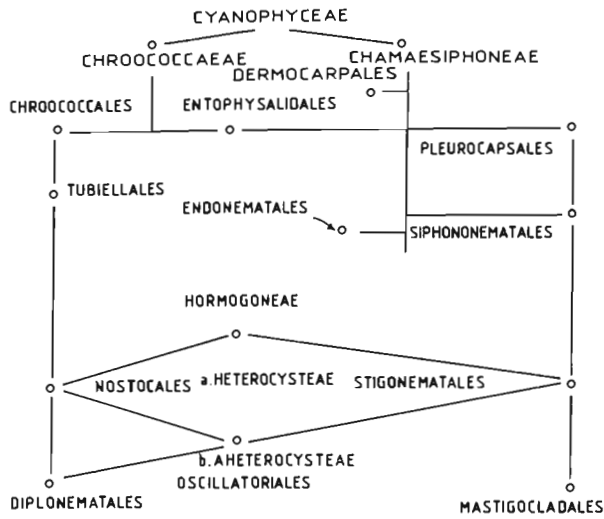
morphological elaboration and the heterotrichous habit do not lend support to Geitler's view of regarding the Stigonematales as the most primitive and the non-heterocystous or homocystous simple trichomatous forms as secondary or recent.

Fritsch, on the contrary, derived diverse Nostoclean forms directly from the unicellular forms (see also Iyengar & Desikachary, 1946). He considered the Pleurocapsales and Stigonematales as the end products of two parallel lines of development from diverse origins and any inter-relationship between the two groups as still unclear. The latter were probably derived from the line that gave rise to the Nostocales.

In some interesting cases, especially scytonemataceous forms the entire trichome may become fragmented into a number of short fragments which may become free by the break down of the sheath at point(s) all around or selectively near the ends of such fragments. In such cases the hormogones may not become free but grow out with one end remaining tucked into the parent sheath giving the appearance of a prolific false branching. Such instances have served as *raison d'être* for considering false branching, both the incipient ones in the imperceptibly sheathed forms or the patterned false branching in the thick sheathed forms, as analogous to *in situ* germination of intercalary hormogones (Bharadwaja, 1933; Fritsch, 1942; Desikachary, 1959, 1973). It is becoming evident that in some individuals these hormogones/free fragments do not possess obvious autochthonous movements and probably get



Text-figure 1—Scheme of possible inter-relationships of blue-green algae (after Fritsch, modified).



Text-figure 2—Scheme of inter-relationships (after Elenkin).

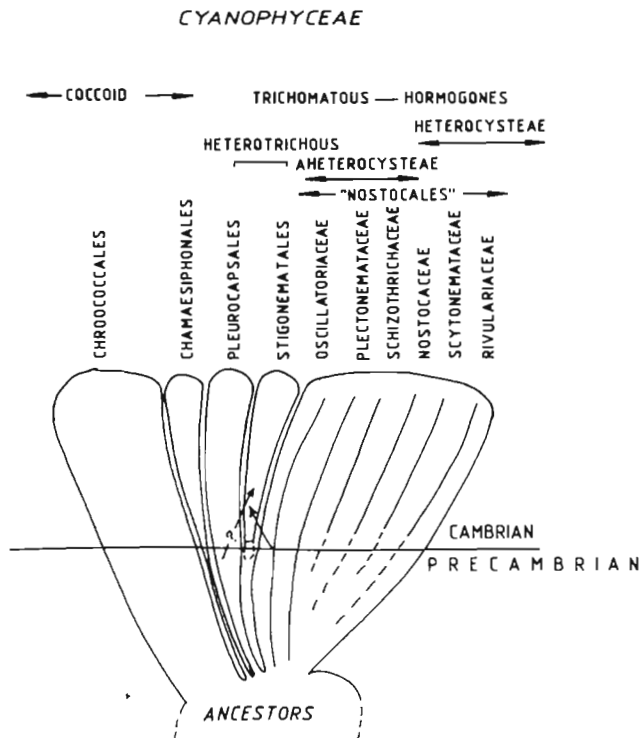
dispersed in a manner similar to other planktonic elements. Individual trichomes in bundle sheathed forms and in 'phormidioid thalli' often show oscillatoriacean movements within the mucilage. These genera as now constituted seem to hold both types of trichomatous forms, with or without such active movements. There are very tangible reasons

for not only splitting these genera but also recognizing the families Lyngbyaceae, Schizotrichaceae; etc. The origin of this group of Oscillatoriaceous genera included by various authors in Oscillatoriaceae, Lyngbyaceae, Plectonemataceae and Schizotrichaceae have parallels in Nostocaceae, Scytonemataceae, Rivulariaceae, etc. The recognition and delimitation of the various families is a larger question beyond the scope of the present paper. Indications of hormogone formation are available in the recorded fossil forms. Some of the oscillatoriacean fossils clearly exhibit a tendency to become attenuated towards the apex in a manner similar to what is seen among some present day Scytonemataceae, Rivulariaceae, etc. It is important to note that (1) these two sets of families essentially differ in the presence or absence of heterocysts and akinetes (perennating spores). Taking up the latter one first, it may be stated that reproductive cells common among the extant coccoid forms, such as endospores or exospores, are now known in the Precambrian, though one does not know more exactly the time of their first appearance. Akinetes, or thick-walled perennating spores, formed by trichomatous forms by the transformation of whole cells are not known among the Precambrian forms (except an unpublished report presented during the deliberations here). Fossil forms so far discovered do not exhibit akinetes adjoining the heterocysts as seen in the extant forms.

Heterocysts hold the key to an evaluation of the concepts, of Geitler and of Fritsch. Three decades of research has yielded no reliable structures resembling the heterocyst with its characteristic structure from the Precambrian times. The few instances known from the Cambrian and the Devonian are the only accepted ones (see Croft & George, 1959; Sastri *et al.*, 1972). Thus, the concept that the Stigonematales were ancestral to the Nostocales is not borne out by evidences from the fossils. The second point that stands against accepting that proposition is that all the morphotypes seen in the extant homocystous Nostocales are already seen in the Precambrian.

Fritsch (1942, p. 142) considered that the heterocyst is probably a very ancient structure. He envisaged that multicellular forms arose directly from a common group of simple coccoid types and that the Oscillatoriaceae diverged before the evolution of the heterocysts. This latter conclusion appears to be still true today. Heterotrichous thalli seem to have appeared after the Precambrian (see Korde, 1972, p. 163).

Desikachary (1973) discussed the situation as it



Text-figure 3—Schematic representation of the inter-relationships between major groups of blue-green algae (Cyanophyceae/Myxophyceae/Cyanobacteria) as discussed in the text.

obtained then. Summarizing palaeontological evidences, Korde (1972) and Tappan (1980) have shown that the complexities seen in thallus construction among the homocystous forms have already been evidenced in the early ones themselves. Nevertheless, one cannot definitely indicate the exact origin and divergence of the major lines of evolution. Our knowledge is much the same even now except in that one is prone to rely on the assumption that with the inception of the heterocyst, the diverse heterocystous groups evolved parallelly from similar but different homocystous groups (see Text-figure 3). That the former might have probably had different starting points is borne out by the fact that all the evolutionary tendencies have not been seen together in the Precambrian and therefore probably had a staggered evolution at different times in the Precambrian and in the early succeeding ages. One should bear in mind that we are dealing with a large period of the time in geological history and biostratigraphic subdivisions are not yet available. Ideas on evolution of blue-greens ('hypobradytic' of Schopf) as evidenced by fossils in the nearly 3Ga are still shrouded in rational conjectures. We may have to wait a long time before these ideas are tested against the ground realities when more extensive and precise knowledge of origin and evolution of the different groups of blue-green algae are available.

Elenkin (1936) separated the non-heterocystous forms (homocystous forms) and divided the heterocystous forms of the Nostocales (*sensu lato*) into distinct and parallel orders and families. Looking at the panorama of taxa presently known, fossil records of homocystous forms are not accompanied by parallel heterocystous forms. Elenkin's segregation into two series seem to present a more correct picture at this point. Yet one is unable to agree with the evolutionary lines presented by him, a simulation of Geitler's view (see Text-figure 2).

Trichomatous condition and hormogone formation are the characteristics that are common to the majority of blue-greens barring the 'coccoid' forms. Hormogones are small portions/fragments of the trichomes which are formed often by their separation from the rest of the trichome by necridia developed by the alga. These are considered to be endowed with movement nearly akin to that seen in *Oscillatoria*. Hormogones are noticed in some forms only by careful observation and are formed generally from the free apices of trichomes. In hairforming taxa these are formed below the hair region ('intercalary meristematic region') and become free after the hair is discarded (e.g., Rivulariaceae,

Nostochopsidaceae).

Evolutionary thoughts were based on comparative and developmental morphological evidences. Phenotypic variations, as revealed by culture studies (for e.g. see Drouet, 1962; Padmaja & Desikachary, 1967), also influenced taxonomic and evolutionary concepts. The first point dealt with was the origin of filamentous condition in the blue-greens. Iyengar and Desikachary (1946) thought this condition could be visualized to have been derived by the daughter cells from a transverse division in an entophysalidacean or pseudofilamentous alga continuing to remain attached to each other instead of separating as they do in the coccoid forms. Summarizing plasticity of morphological features as reflected by variations exhibited in culture conditions (see Desikachary & Padmaja, 1970), Desikachary (1973) concluded that morphological variations exhibited by extant forms resembled forms lower down in the evolutionary line according 'progressive' evolution.

Korde's account (1972) probably represents a picture consistent with our present knowledge of fossils. Again one does not know, given the period of time covered by the Precambrian, whether one can correctly assess the validity of so many distinct phyletic lines represented by Korde and also correctly envisage the inter-relationships between them or inter-relationships of their ancestors, or evaluate the time of divergence of the individual lines from the ancestral stock.

Many investigations have revealed a wealth of forms from the Precambrian of USA, Canada, Russia, China, South Africa and Australia. We have in India many areas which have been accepted as having Precambrian deposits. But we have only a few publications which deal with the Early Precambrian flora. It is of utmost importance that more of these are thoroughly investigated.

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