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Generic Assignments, Strain Histories and Properties of Pure Cultures of Cyanobacteria

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On the basis of a comparative study of 178 strains of cyanobacteria, representative of this group of prokaryotes, revised definitions of many genera are proposed. Revisions are designed to permit the generic identification of cultures, often difficult through use of the field-based system of phycological classification. The differential characters proposed are both constant and readily determinable in cultured material. The 22 genera recognized are placed in five sections, each distinguished by a particular pattern of structure and development. Generic descriptions are accompanied by strain histories, brief accounts of strain properties, and illustrations; one or more reference strains are proposed for each genus. The collection on which this analysis was based has been deposited in the American Type Culture Collection, where strains will be listed under the generic designations proposed here.

INTRODUCTION

The cyanobacteria constitute one of the largest sub-groups of Gram-negative prokaryotes. As a result of their traditional assignment to the algae, the classification of these organisms was developed by phycologists, working under the provisions of the Botanical Code (Stafleu *et al.*, 1972). Almost entirely on the basis of observations on field materials, about 150 genera and well over 1000 species have been described. The discriminatory properties, both generic and specific, are either structural or ecological, these being virtually the only characters determinable in the field. Types are represented by herbarium specimens or, failing these, by descriptions and illustrations; cultures are not recognized as valid type materials under the Botanical Code.

The attempt to identify cyanobacteria in culture through this field-based system of classification leads to many difficulties and ambiguities. The limited and necessarily provisional taxonomic goal of the present article is to redefine certain cyanobacterial genera in such a way that simple and clear-cut generic assignments can be made for cultures. It is based on our experience over the past decade with pure strains representative of all major sub-groups of cyanobacteria. As far as possible, we have attempted to maintain the system of generic nomenclature and the generic definitions now used by phycologists (Bourrelly, 1970; Geitler, 1932; Desikachary, 1959). However, when the discriminatory characters that nominally distinguish two genera are either not determinable on cultures or within the range of variation of a single strain, the existing genera have been combined. Some of the proposed generic definitions include discriminatory characters that have not hitherto received taxo-

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nomic recognition because they were discovered only through investigations of cultures. The present article also presents full strain histories and succinct surveys of outstanding properties of strains assigned to each genus.

The cyanobacterial collection on which this study was based, hereafter termed the Pasteur Culture Collection, has recently been deposited in the American Type Culture Collection, where the strains will be carried under the generic designations proposed here.

Specific names have been applied to only two strains: those on which descriptions of the type species of two monotypic genera, *Chlorogloeopsis* (Mitra & Pandey, 1966) and *Gloeobacter* (Rippka *et al.*, 1974), are based. Under the rules of the Bacteriological Code (Lapage *et al.*, 1975), both strains would be holotypes; under the Botanical Code (Stafleu *et al.*, 1972), only *Chlorogloeopsis* has nomenclatural status.

The reasons which have led us not to attach specific names to strains of other genera deserve brief discussion. The most important has been the difficulty of making unambiguous identifications in the complete absence of living type materials. This problem is further compounded by the very large number of nomenspecies (frequently associated with descriptions having minimal information content) that already exist in many genera of cyanobacteria. In a recent taxonomic review of two genera of unicellular cyanobacteria, *Synechococcus* and *Synechocystis*, Komarek (1976) accepts as valid 39 species in the former genus and 17 in the latter. The species are distinguished primarily by the dimensions of the cell (rod-shaped in *Synechococcus*, spherical in *Synechocystis*), in some cases supplemented by information about habitat. Since cell dimensions may vary with culture conditions, and information concerning the habitat is often lacking, culture-based studies on cyanobacterial speciation cannot be satisfactorily fitted into the present *nomenclatural* framework, even if specific entities can be well characterized both genetically and phenetically. The Botanical Code (Stafleu *et al.*, 1972) provides no remedy, since types are considered immutable. On the other hand, the recognition that living type materials are indispensable for culture-based taxonomic research has led to inclusion in the Bacteriological Code of Rule 18h (revision of 1976), specifically designed to deal with this problem. Under Rule 18h, a bacterial type represented by a herbarium specimen, description or illustration can be replaced by a subsequently isolated culture of the organism in question, which thereafter becomes the holotype. Under the provision of Rule 18h (which was not in effect in 1974), cultures of myxobacteria (McCurdy, 1974) would have constituted holotypes, rather than representative strains.

A proposal to bring cyanobacteria under the rules of the Bacteriological Code has recently been submitted to the Judicial Commission (Stanier *et al.*, 1978). If successful, this change of jurisdiction would permit the progressive replacement of the existing dead type materials by living holotypes. As an interim measure, one (or sometimes more) reference strains have been designated for the genera recognized here. These have been selected because they appear to be reasonably typical of the genera in question, although they do not necessarily represent or closely resemble the type species. Reference strains lack nomenclatural standing, even under the Bacteriological Code (Lapage *et al.*, 1975), but may be useful for comparative cultural studies as long as living type materials are unavailable.

METHODS

Abbreviations. P, Pure culture; I, impure culture; ATCC, American Type Culture Collection; PCC, Pasteur Culture Collection; UTEX, Culture Collection of Algae at the University of Texas (formerly IUCC, Indiana University Culture Collection); CCAP, Culture Collection of Algae and Protozoa, Cambridge, England; SAUG, Sammlung von Algenkulturen am Pflanzenphysiologischen Institut der Universität, Göttingen, German Federal Republic.

Organisms. A majority of the cyanobacterial strains of the Pasteur Culture Collection

were isolated and purified over the last 15 years by past or present members of our research group. Such strains are identified only by a generic name, a PCC number and an ATCC number. Other strains were received either from algal culture collections or from other investigators, often as impure cultures. After purification, such strains were assigned PCC numbers and incorporated into the collection. In the histories of strains received from these sources, the names and/or strain designations which they bore prior to accession to the PCC have been included where the information was available and the purity of cultures checked upon receipt.

Maintenance media and conditions of cultivation. All strains are maintained under photoautotrophic growth conditions in one of the media listed in Table 1. Medium BG-11 and its variant BG-11_0 (BG-11 with omission of $NaNO_3$) are used for strains of freshwater, soil or thermal origin and for some strains isolated from marine source materials which do not display the ionic requirements characteristic of indigenous marine cyanobacteria (Stanier & Cohen-Bazire, 1977). All strains which fix nitrogen aerobically, i.e. heterocystous cyanobacteria and members of the unicellular genus *Gloeothece*, are maintained in BG-11_0. It was noted that prolonged maintenance of heterocystous cyanobacteria in BG-11 sometimes leads to the selection of mutants which have lost the ability to fix nitrogen aerobically and which either form abnormal heterocysts or, more rarely, have become aheterocystous.

Most cyanobacteria from marine sources cannot grow in BG-11, even if it is supplemented with 3% (w/v) NaCl; analysis of their nutritional properties (Stanier & Cohen-Bazire, 1977) showed that such cyanobacteria, hereafter defined as marine strains, have elevated requirements for Na^+, Cl^-, Mg^{2+} and Ca^{2+}. Most of them are maintained in medium MN, which has a natural seawater base and is supplemented with the minerals of medium BG-11 at half strength. Some marine strains grow poorly on MN and are maintained in a synthetic seawater medium, ASN-III. These are: PCC 7302, 7303, 7304, 7305, 7306, 7345, 7310 and 7418.

A few strains have an absolute requirement for vitamin B_{12}, and these are cultivated in the appropriate maintenance medium containing 10 μg vitamin l^{-1} (filter-sterilized).

Solid media are prepared by mixing a separately autoclaved aqueous solution of Difco Bacto-agar with the mineral medium, to give a final agar concentration of 1% (w/v) (Allen, 1968). Nearly all cyanobacteria grow well on agar and appear to remain viable longer on solid than in liquid media, provided that cultures are kept at low light intensities. We therefore recommend agar slants for routine maintenance.

Stock cultures are grown under continuous illumination with Osram Fluorescent White or Osram L Interna lamps, at a relatively low intensity (< 500 lux). Higher intensities should be avoided, since many strains (particularly those containing phycoerythrin) are light-sensitive. With the exception of strains of thermal origin, stock cultures are incubated at 25 °C. For convenience, thermal strains are kept at 37 °C, even though this temperature is close to their minimum for growth. Many cyanobacteria die rapidly when placed at 0 to 4 °C; cultures should therefore never be stored in a refrigerator. Other aspects of cultivation have been discussed previously (Stanier *et al.*, 1971).

It should be emphasized that the media and conditions described above have been selected for their simplicity and convenience in the maintenance of a large and diverse collection. The determination of optimal growth conditions is a different problem, which requires separate study for each strain.

Control of purity. The presence of contaminating bacteria can nearly always be detected by microscopic examination, particularly of old cultures. As a routine control of purity, a heavy streaking on two media is recommended: the solidified maintenance medium, supplemented with 0·2% (w/v) glucose and 0·02% Casamino acids; and nutrient agar. Both should be incubated in the dark at 25 to 30 °C.

Characterization of strains: structural properties. The structural properties on which generic definitions are based are, with one exception, determinable by light microscopy. The

Table 1. *Composition of standard mineral media*

Ingredient	Amount (g l^{-1}) in medium		
	BG-11	MN	ASN-III
NaCl	—	—	25·0
$MgCl_2.6H_2O$	—	—	2·0
KCl	—	—	0·5
$NaNO_3$	1·5	0·75	0·75
$K_2HPO_4.3H_2O$	0·04	0·02	0·02
$MgSO_4.7H_2O$	0·075	0·038	3·5
$CaCl_2.2H_2O$	0·036	0·018	0·5
Citric acid	0·006	0·003	0·003
Ferric ammonium citrate	0·006	0·003	0·003
EDTA (disodium magnesium salt)	0·001	0·0005	0·0005
Na_2CO_3	0·02	0·02	0·02
Trace metal mix A5+Co*	1 ml l^{-1}	1 ml l^{-1}	1 ml l^{-1}
Sea water	—	750 ml	—
Deionized water	1000 ml	250 ml	1000 ml
pH after autoclaving and cooling	7·4	8·3	7·5

* Trace metal mix A5+Co contains (g l^{-1}): H_3BO_3, 2·86; $MnCl_2.4H_2O$, 1·81; $ZnSO_4.7H_2O$, 0·222; $Na_2MoO_4.2H_2O$, 0·390; $CuSO_4.5H_2O$, 0·079; $Co(NO_3)_2.6H_2O$, 0·0494.

exception is the absence of thylakoids, characteristic of *Gloeobacter*; this property can only be determined by electron microscopy (Rippka *et al.*, 1974). Although a certain amount of information can be derived from the light microscopic examination of mass cultures, semi-continuous observations of development on agar media are often necessary to reveal determinatively important developmental properties, such as planes of successive divisions, formation of baeocytes, and formation and structure of hormogonia. The Cooper dish culture technique (Waterbury & Stanier, 1978) is particularly useful for the study of the two former properties, although it cannot be successfully applied to some small-celled cyanobacteria as a result of its optical limitations. In such cases, slide culture techniques (Allen & Stanier, 1968) must be used.

Many filamentous cyanobacteria (Sections III to V) form motile hormogonia structurally distinguishable from the vegetative filaments. The formation of motile hormogonia can be followed by inoculating material on the centre of an agar plate, and examining at intervals of 2 to 3 d the filaments in the expanding peripheral region, where hormogonia are enriched as a result of their gliding movement. With highly motile cyanobacteria, gliding motility is also readily evident in wet mounts, prepared by crushing a small piece of agar from a plate culture under a coverslip; the crushed agar provides a substrate which facilitates gliding movement. However, in organisms of Section II, gliding movement is transient, being displayed only by baeocytes; and in organisms of Section I, it is relatively slow. For such organisms, the phototactic response of plate cultures exposed to unidirectional illumination (Stanier *et al.*, 1971; Waterbury & Stanier, 1978) is the most reliable method of demonstrating motility.

The structural properties described are those displayed by cultures growing photoautotrophically in the appropriate maintenance medium. The use of medium BG-11_0 is essential for the characterization of heterocystous cyanobacteria (Sections IV and V), since most of these organisms do not develop heterocysts when cultivated with a combined nitrogen source.

All photomicrographs were taken with a Zeiss Universal microscope, equipped with Neofluar objectives, under bright field or phase contrast illumination.

Characterization of strains: physiological properties. Photoheterotrophy was demonstrated by growth of strains in the light in the appropriate mineral medium, supplemented with an organic substrate and with 10^{-5} M-dichlorophenyldimethylurea (Rippka, 1972). Substrates

tested universally were the carbohydrates glucose, fructose and sucrose (0·3 to 0·5%, w/v). Growth on ribose (0·5%, w/v), glycerol, acetate and glycollate (0·1%, w/v) was tested for all strains with the exception of members of Section II. Acetate and glycollate did not support photoheterotrophic growth of any strain examined; data on the utilization of carbohydrates are given in the descriptions of strains belonging to each genus.

Most strains incapable of aerobic nitrogen fixation were screened for their ability to synthesize nitrogenase under strictly anaerobic conditions, by a special technique described elsewhere (Rippka & Waterbury, 1977). This property is noted in strain descriptions.

All cyanobacteria so far examined synthesize chlorophyll *a* and three blue, water-soluble phycobiliproteins: phycocyanin (λ_{max} 620 nm), allophycocyanin (λ_{max} 650 nm) and allophycocyanin B (λ_{max} 670 nm). With respect to pigmentation, the only property now known to be of determinative significance within the group is the presence or absence of an additional phycobiliprotein with an absorption maximum at a wavelength shorter than that of phycocyanin. Several different chromoproteins of this type have been identified in cyanobacteria (reviewed by Stanier & Cohen-Bazire, 1977). They include C-phycoerythrin (λ_{max} 550 to 570 nm); other phycoerythrins, showing an additional peak at a shorter wavelength; and phycoerythrocyanin (λ_{max} 565 nm; shoulder at 590 nm). The presence of such compounds, hereafter termed collectively phycoerythrinoid pigments, can often be detected by determining the absorption spectrum of a crude cell-free extract, or even of a cell suspension; however, a definitive characterization usually requires isolation in a spectrally pure state. In strain descriptions, phycoerythrinoid pigments are tentatively designated as C-phycoerythrin, other phycoerythrins (distinct from C-phycoerythrin) or phycoerythrocyanin.

Techniques for the extraction and purification of DNA, and for the determination of mean DNA base composition, are described by Herdman *et al.* (1979).

RESULTS AND DISCUSSION

Primary sub-divisions

Differences in structure and development permit the recognition among cyanobacteria of five large sub-groups (Table 2). These sub-groups do not, for the most part, correspond precisely to major taxa now recognized by phycologists; they will be described here as sections.

Section I is composed of unicellular organisms that reproduce either by binary fission or by budding; the cells are spherical, cylindrical or oval. These are the simplest cyanobacteria, structurally speaking, and have counterparts in other major groups of Gram-negative, unicellular bacteria.

The members of Section II are characterized by a special type of reproduction – multiple fission – which has not been reported in any other prokaryotic group. They all share one property: the vegetative cell is always enclosed by an additional fibrous layer closely investing the outer membrane layer. Multiple fission (rapid binary fission of a vegetative cell within the fibrous wall layer without accompanying growth) leads to the formation of small, spherical reproductive cells (baeocytes) that are subsequently released by rupture of the fibrous layer of the parental cell wall (Waterbury & Stanier, 1978). The number of baeocytes produced from one parental cell ranges from 4 to over 1000. In the phycological literature, the reproductive cell characteristic of members of this section is termed an endospore. The alternative name, baeocyte (Greek: 'small cell'), was recently proposed in order to avoid confusion in the prokaryotic context (Waterbury & Stanier, 1978). In most members of Section II, synthesis of the fibrous wall layer is repressed during multiple fission, and the baeocytes at the time of their release possess walls that contain only peptidoglycan and outer membrane layers. These baeocytes display gliding motility, but become immotile as their size increases and synthesis of the fibrous wall layer begins. In other members of Section II, synthesis of the fibrous wall layer accompanies multiple fission. Consequently,

Table 2. *Major sub-groups of cyanobacteria*

<table>
<tr><td rowspan="2">Unicellular; cells single or forming colonial aggregates held together by additional outer cell wall layers</td><td colspan="3">Reproduction by binary fission or by budding</td><td>Section I</td></tr>
<tr><td colspan="3">Reproduction by multiple fission giving rise to small daughter cells (baeocytes), or by both multiple fission and binary fission</td><td>Section II</td></tr>
<tr><td rowspan="3">Filamentous; a trichome (chain of cells) which grows by intercalary cell division</td><td rowspan="3">Reproduction by random trichome breakage, by formation of hormogonia and (Sections IV and V only) sometimes by germination of akinetes</td><td>Trichome always composed only of vegetative cells</td><td>Division in only one plane
Section III</td></tr>
<tr><td rowspan="2">In the absence of combined nitrogen, trichome contains heterocysts; some also produce akinetes</td><td>Division in only one plane
Section IV</td></tr>
<tr><td>Division in more than one plane
Section V</td></tr>
</table>

the baeocytes already have a thin fibrous wall layer at the moment of their release. Such baeocytes are never motile. Members of the genera *Dermocarpa* and *Xenococcus* divide only by multiple fission. In *Dermocarpella, Myxosarcina, Chroococcidiopsis* and the Pleurocapsa group, baeocyte enlargement is followed by a series of binary fissions, resulting in the formation of an aggregate of vegetative cells, which remain firmly adherent to one another. Some or all of the cells in the aggregate later undergo multiple fission and release baeocytes.

The unit of structure in cyanobacteria of Sections III to V is a filament of cells, or trichome. Elongation of the trichome is accompanied by an increase in cell number, as a result of repeated intercalary cell divisions. Transverse wall formation occurs through centripetal ingrowth of the peptidoglycan layer, followed by that of the outer membrane layer. The extent to which the outer membrane layer participates in the formation of the transverse walls is evidenced by the degree of constriction between the cells that compose the trichome. Reproduction is effected by breakage of the trichome into shorter lengths. These short, reproductive filaments are often distinguishable from the mature trichome by their gliding motility. Phycologists (e.g. Geitler, 1932) have applied the term hormogonium to any motile trichome fragment released from an immotile, ensheathed parental trichome. This term can now be extended (in the specific context of the heterocystous cyanobacteria) to designate filaments, either motile or immotile, that are distinguishable from the parental trichome by cell size, cell shape, gas vacuolation or the absence of heterocysts, even when grown without a source of combined nitrogen.

The vegetative trichomes of filamentous cyanobacteria are often enclosed by tubular sheaths. If trichome breakage occurs within a sheath, subsequent elongation may result in the protrusion of one or both daughter filaments through the sheath wall, eventually bringing them into angular apposition. This configuration, often evident in ensheathed cyanobacteria belonging to Sections III to V, is termed 'false branching' in order to distinguish it from the 'true' (i.e. dichotomous) branching (Bourrelly, 1970; Geitler, 1932) that is characteristic of most cyanobacteria in Section V.

In cyanobacteria of Section III, the trichome is composed solely of vegetative cells, and is always uniseriate (one cell thick), since cell divisions occur regularly in a plane at right angles to the long axis of the trichome.

The filamentous cyanobacteria of Sections IV and V are collectively distinguished from those of Section III by their capacity for cellular differentiation. In the absence of a combined nitrogen source, a small fraction of the cells in the trichome develop into heterocysts,

distinguishable from vegetative cells by their thick walls, relatively weak pigmentation and refractile polar granules (Figs 43, 44, 49). When mature, the heterocyst can neither divide nor dedifferentiate; it is the specific cellular site of nitrogen fixation under aerobic conditions (Stewart *et al.*, 1969). Polar granules form near the point(s) of attachment of the heterocyst to adjacent vegetative cells. An intercalary heterocyst thus has a granule at each pole; a terminal heterocyst has a granule at only one pole. Many members of Sections IV and V can also produce thick-walled resting cells known as akinetes (Stanier & Cohen-Bazire, 1977; Fogg *et al.*, 1973). The development of akinetes (Figs 36, 46, 69, 85) occurs as cultures approach the stationary phase, and it is usually not dependent on the nature of the nitrogen source.

Sections IV and V are distinguished by one basic character: the polarity of successive cell divisions during growth of the trichome. In Section IV, intercalary cell divisions always occur in a plane at right angles to the long axis of the trichome, which is consequently uniseriate and unbranched (though it may display false branching) (Figs 59, 62). In Section V, hormogonia are uniseriate and unbranched at the time of their release. However, as growth proceeds, some cell divisions occur in planes that are not at right angles to the long axis of the trichome. In those members of Section V that retain a filamentous structure throughout growth (*Fischerella*), the primary trichome becomes partly multiseriate and develops lateral branches which are uniseriate and composed of small cylindrical cells. At this stage in development, the cellular continuity of the primary trichome is often interrupted by the deposition of a fibrous wall layer between adjacent cells (Thurston & Ingram, 1971; Martin & Wyatt, 1974); such interruptions of cellular continuity are evidenced by the frequent presence of terminal heterocysts in an intercalary position within the primary trichome (Figs 70, 72, 75). Hormogonia that are initially uniseriate, unbranched and devoid of heterocysts, even in medium BG-11_0, are formed from the lateral branches. Heterocyst differentiation in a hormogonium is almost invariably intercalary. In the mature trichome, heterocysts are either intercalary, terminal or lateral. Lateral heterocysts possess only one polar granule: they are heterocysts that have differentiated from vegetative cells that divided in a plane parallel to the long axis of the trichome (Figs 75, 76, 95, 96).

In the special case of *Chlorogloeopsis*, the filamentous structure is lost relatively early in development and the cylindrical cells of hormogonia become rounded and start to divide in several planes. Associated detachment of groups of cells, enclosed in a common sheath, eventually leads to a virtually unicellular mode of growth (*Gloeocapsa*-like). Conditions which favour rapid cell division give rise to hormogonia within such cellular aggregates (Figs 91 to 93).

The fundamental difference between Sections IV and V, the polarity of successive cell division, is also expressed in the mode of akinete germination. In members of Section IV, the germination of an akinete gives rise to a new uniseriate trichome by division in only one plane (Figs 47, 55 to 58, 69). Rapid cell division of this trichome leads in some genera to the formation of hormogonia as defined here. In Section V, however, germination of an akinete gives rise to a multicellular aggregate by division in several planes. Subsequent division in only one plane leads to hormogonia formation (*Chlorogloeopsis*; Figs 91 to 93) or to the development of lateral branches (*Fischerella*; Fig. 76).

Genera of Section I

The 57 strains of this section are assigned to six form genera, distinguished by the characters shown in Table 3.

Unicellular cyanobacteria with cylindrical to ovoid cells that reproduce by binary transverse fission are placed in three genera: *Synechococcus* Nägeli 1849, *Gloeothece* Nägeli 1849 and *Gloeobacter* Rippka, Waterbury & Cohen-Bazire 1974.

In *Synechococcus*, cells occur singly, in pairs or in short chains and are devoid of sheaths (Figs 1, 2). Nägeli (1849) proposed another genus, *Aphanothece*, for organisms like *Synecho-*

Table 3. *Section I: Unicellular cyanobacteria that divide by binary fission or by budding*

		Division in one plane	Division in two or three planes
Reproduction by binary fission	Thylakoids absent	Sheath present *Gloeobacter*	
	Thylakoids present	Sheath present *Gloeothece*	Sheath present *Gloeocapsa*
		Sheath absent *Synechococcus*	Sheath absent *Synechocystis*
Reproduction by budding	Thylakoids present	*Chamaesiphon*	

coccus that develop as irregular aggregates united by a common slime layer. Although many strains of *Synechococcus* produce considerable quantities of extracellular slime in culture, none develops in the form of aggregates. The maintenance of the genus *Aphanothece* appears questionable, particularly since Nägeli (1849) himself suggested that it might be united with *Synechococcus*. A new genus *Cyanothece* has recently been proposed by Komarek (1976) to accommodate some species hitherto placed in *Synechococcus*. Its principal distinguishing character is that cells occur either singly or in pairs, but never in chains. Since the extent of chain formation in organisms of the *Synechococcus* type is strongly dependent on the conditions of culture, Komarek's proposal is not accepted here. The extreme genetic diversity of the strains now included in the form genus *Synechococcus* is shown by the very wide span of mean DNA base composition (Stanier *et al.*, 1971; Herdman *et al.*, 1979). This character, in conjunction with phenetic properties, may eventually make possible the recognition of additional genera; but to propose a generic split without taking the base compositional data into account appears unwise.

The genus *Gloeothece* is distinguished from *Synechococcus* by sheath formation: well-defined laminar sheaths enclose both individual cells and small cell groups that produce characteristic aggregates (Fig. 3). Sheath formation is both stable and constant in culture, being possessed by strains some of which have been maintained for 15 years. The five *Gloeothece* strains of the collection also share a distinctive physiological property not possessed by any other strains of Section I: the ability to fix nitrogen aerobically (Wyatt & Silvey, 1969; Rippka *et al.*, 1971). This may eventually prove to be a second discriminatory character of *Gloeothece*.

The genus *Gloeobacter* was created (Rippka *et al.*, 1974) for an ensheathed, unicellular cyanobacterium which has the appearance of a small-celled *Gloeothece* strain by light microscopy (Fig. 4), but shows an ultrastructure unlike that of any other known cyanobacterium. Both thylakoids and typical phycobilisomes are absent from the cells of *Gloeobacter*. A cytoplasmic membrane of simple contour is the only unit membrane system within the cell, and this bears a cortical layer of phycobiliproteins on its inner surface.

Unicellular cyanobacteria with spherical cells that divide in two or three successive planes at right angles to one another are assigned to either *Synechocystis* Sauvageau 1892 or *Gloeocapsa* Kützing 1843.

At least five different genera have been proposed for unicellular, spherical cyanobacteria that do not produce well-defined sheaths. In both *Microcystis* Kützing 1833 and *Aphanocapsa* Nägeli 1849 a common slime layer unites the cells into irregular aggregates: cells of *Microcystis* often contain gas vacuoles, those of *Aphanocapsa* do not (Geitler, 1932). Planes of successive divisions are not specified. The genera *Merismopedia* Meyen 1839 and *Eucapsis*

Clements & Shantz 1909 are distinguished by the formation of rectangular plates and cubical packets of cells, respectively; these reflect regular divisions in two or in three planes. The genus *Synechocystis* Sauvageau 1892 is distinguishable from the preceding four genera by the failure to produce aggregates, cells occurring singly or in pairs. This is the characteristic growth habit in culture of all strains of unsheathed, spherical cyanobacteria in our collection, and *Synechocystis* therefore appears to be the most appropriate form genus for such organisms (Figs 5, 6).

When cell separation occurs soon after division, the planes of successive divisions cannot be easily determined, as noted by Sauvagcau (1892). However, most strains of *Synechocystis* appear to divide in two planes at right angles to one another (Stanier *et al.*, 1971; Komarek, 1976; unpublished observations). When cell separation does not occur, the formation in culture of *Merismopedia*-like aggregates may occasionally occur (Stanier *et al.*, 1971). One strain, PCC 6906, which does not now form aggregates in culture, was observed on first isolation to produce cubical packets of cells, and should therefore divide in three planes. Pending further study, we propose that *Synechocystis* be defined as comprising unicellular cyanobacteria with spherical cells that divide successively in more than one plane.

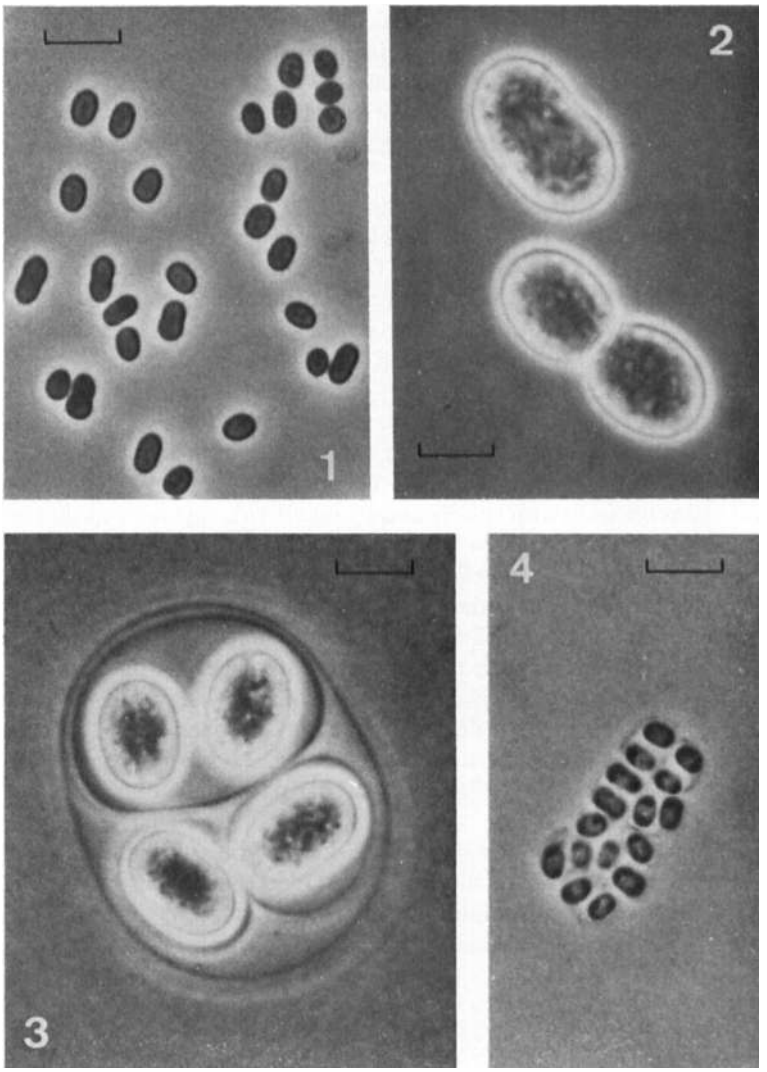
Two genera, *Gloeocapsa* Kützing 1843 and *Chroococcus* Nägeli 1849, have been proposed for ensheathed cyanobacteria with spherical cells that divide regularly in three planes. These genera are nominally distinguished by the structure of the sheath (relatively loose and wide in *Gloeocapsa*) and by the shape of cells immediately after division (rounded in *Gloeocapsa*, hemispherical in *Chroococcus*). Geitler (1932) has emphasized that it is often difficult to make the generic distinction on field material, and we have had a similar experience with cultures. Within a single strain, both rounded and hemispherical post-divisional cells may be observed. The factor that determines post-divisional cell shape – obviously often a variable character – is probably the degree of compression exerted by the common sheath that encloses the two daughter cells. We consider that only one genus for ensheathed cyanobacteria with spherical cells is required; and in this event, *Chroococcus* becomes a later synonym of *Gloeocapsa* (Figs 7, 8).

The generic assignment of the two strains in Section I that reproduce by forming successive spherical buds from one pole of the ovoid cell (Waterbury & Stanier, 1977) presents no problem. This is the mode of reproduction ('exospore formation' in phycological terminology) distinctive of the genus *Chamaesiphon* Braun & Grunow 1865 emend. Geitler 1925 (Figs 9, 10).

Genus Synechococcus Nägeli 1849

Many of the PCC strains were first described by Stanier *et al.* (1971). The three strains which these authors placed in group IB of *Synechococcus* (PCC 6802, 6901 and 6903) have been transferred to the genus *Pseudanabaena* (Section III). One strain which they assigned to group IA (PCC 6605) has been transferred to *Chamaesiphon*, since it has been found to reproduce by budding (Waterbury & Stanier, 1977). Four strains of group IA (PCC 6706, 6707, 6708 and 6709) were isolated from the same water sample as PCC 6710 and appear to be identical with it; they have therefore been eliminated from the collection. With the addition of nine strains isolated since the publication of Stanier *et al.* (1971), *Synechococcus* is now represented by 28 strains. Two of these (PCC 7335 and 7424) are shown in Figs 1 and 2. The histories of the strains are as follows:

ATCC 27144 PCC 6301 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ M. B. Allen $\overset{I}{\leftarrow}$ W. A. Kratz [*Anacystis nidulans* (Kratz & Myers, 1955), strain Tx20 (Stevens & Myers, 1976)], fresh water, Texas, U.S.A., 1952. Named as *Anacystis nidulans* in CCAP (1405/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971), SAUG (1402/1) (Koch, 1964) and UTEX (625 and 1550) (Starr, 1964, 1966).



Figs 1 and 2. *Synechococcus* PCC 7335 and PCC 7424, respectively. Fig. 3. *Gloeothece* PCC 6909. Fig. 4. *Gloeobacter violaceus* PCC 7421. All phase contrast; bar markers represent 5 μm.

ATCC 27147 PCC 6307 (Stanier *et al.*, 1971). ← G. C. Gerloff (*Coccochloris peniocystis* 1020), lake water, Wisconsin, U.S.A., 1949 (Gerloff *et al.*, 1950). Named as *Coccochloris peniocystis* in UTEX (1548) (Starr, 1966).

ATCC 27145 PCC 6311 (Stanier *et al.*, 1971). M. M. Allen, fresh water, California, U.S.A., 1963. Named as *Anacystis* sp. in UTEX (1549) (Starr, 1966).

ATCC 27167 PCC 6312 (Stanier *et al.*, 1971). M. M. Allen (*Anacystis* sp.), fresh water, California, U.S.A., 1963.

ATCC 27168 PCC 6603 (Stanier *et al.*, 1971). M. M. Allen, pond water, California, U.S.A., 1966.

ATCC 27174 PCC 6710 (Stanier *et al.*, 1971). R. Kunisawa, fresh water, California, U.S.A., 1967.

ATCC 27177 PCC 6713 (Stanier *et al.*, 1971). R. Kunisawa, fresh water, California, U.S.A., 1967.

ATCC 27149 PCC 6715 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ D. S. Berns $\overset{I}{\leftarrow}$ D. L. Dyer (*Synechococcus lividus*), hot spring Yellowstone National Park, U.S.A., 1961 (Dyer & Gafford, 1961).

ATCC 27179 PCC 6716 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ R. Castenholz (*Synechococcus lividus* OH-53s), Hunter's Hot Spring, Oregon, U.S.A., 1967 (Castenholz, 1970).

ATCC 27180 PCC 6717 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ R. Castenholz (*Synechococcus lividus* Y-52s), hot spring, Yellowstone, U.S.A., 1967 (Castenholz, 1970).

ATCC 29138 PCC 6904. A. Neilson, shallow stream, Sierra Valley, California, U.S.A., 1969.

ATCC 27148 PCC 6907 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ UTEX $\overset{I}{\leftarrow}$ E. G. Pringsheim, pond water, Cambridge, England (Pringsheim, 1951). Named as *Synechococcus elongatus* Naeg. in CCAP (1479/1a) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971) and UTEX (563) (Starr, 1964).

ATCC 27146 PCC 6908 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ UTEX $\overset{I}{\leftarrow}$ E. B. Gassner $\overset{I}{\leftarrow}$ W. Arnold, source unknown. Named as *Synechococcus* in UTEX (1191) (Starr, 1964).

ATCC 27191 PCC 6910 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ G. C. Gerloff (*Gloeocapsa alpicola* 1051), lake water, Wisconsin, U.S.A., 1949; does not correspond to original description (Gerloff *et al.*, 1950).

ATCC 27192 PCC 6911 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ R. Haselkorn ← R. Safferman ← P. R. Gorham (*Microcystis aeruginosa* NRC-1), lake water, Ontario, Canada, 1954; does not correspond to original description (Hughes *et al.*, 1958; Zehnder & Gorham, 1960).

ATCC 27194 PCC 7001 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ C. Van Baalen (*Anacystis marina* 6), intertidal mud, City Island, New York, U.S.A., 1961 (Van Baalen, 1962).

ATCC 27264 PCC 7002. $\overset{P}{\leftarrow}$ C. Van Baalen (*Agmenellum quadruplicatum* PR-6), mud sample from 'fish pens', Magueyes Island, Puerto Rico, 1961 (Van Baalen, 1962).

ATCC 27265 PCC 7003 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ C. Van Baalen (*Coccochloris elabens* 17a), sand sample at edge of clam bed, Greenwich, Connecticut, U.S.A., 1960 (Van Baalen, 1962).

ATCC 29203 PCC 7009. A. Neilson, low salinity brine pond, Newark, California, U.S.A., 1970.

ATCC 29139 PCC 7117. A. Neilson, low salinity brine pond, Port Hedland, Western Australia, 1971.

ATCC 29140 PCC 7202. $\overset{I}{\leftarrow}$ Algothèque du C.N.R.S., Gif-sur-Yvette $\overset{I}{\leftarrow}$ M. Lefèvre, alkaline pond, Chad, 1963. Named as *Synechococcus cedrorum* in CCAP (1479/2a and 1479/2b) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 29403 PCC 7335. J. B. Waterbury, snail shell, intertidal zone, Puerto Penasco, Mexico, 1971.

ATCC 29404 PCC 73109. $\overset{P}{\leftarrow}$ C. Van Baalen (*Agmenellum quadruplicatum* BG-1), sea water, City Island, New York, U.S.A., 1961 (Van Baalen, 1962).

ATCC 29534 PCC 7418. $\overset{I}{\leftarrow}$ Y. Cohen (*Aphanothece halophitica*), Solar Lake, Israel, 1972 (Garlick *et al.*, 1977).

ATCC 29155 PCC 7424. $\overset{I}{\leftarrow}$ P. Roger (*Aphanothece* sp.), rice paddy, Senegal, 1972.

ATCC 29141 PCC 7425. $\overset{I}{\leftarrow}$ P. Roger, rice paddy, Senegal, 1972.

ATCC 29172 PCC 7502. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

ATCC 29154 PCC 7511. R. Rippka, calcareous rock, Aareschlucht, Meiringen, Switzerland, 1972.

The span of mean DNA base composition in *Synechococcus* extends from 39 to 71 mol % GC (Stanier *et al.*, 1971; Herdman *et al.*, 1979); within this range there are three compositional sub-groups with spans of 39 to 43, 47 to 56 and 66 to 71 mol % GC. However, this

Table 4. *Properties of Synechococcus strains*

Mean DNA base composition (mol % GC)	PCC no.*	Facultative photoheterotroph, using: Glucose	Fructose	Sucrose	Glycerol	Synthesis of nitrogenase in anaerobiosis	Synthesis of C-PE†	Marine‡	Thermophil§	Vitamin B_{12} requirement‖	Cell width > 3 μm
39–43	7202	−	−	−	−	−	−	−	−	−	−
	7418	−	−	−	−	ND	−	+	−	$+^{s}$	+
	7424	−	−	−	−	+	+	−	−	−	+
	7502	−	−	−	−	−	−	−	−	−	−
	7511	+	−	+	−	−	−	−	−	−	−
47–56	6301	−	−	−	−	−	−	−	−	−	−
	6311	−	−	−	−	−	−	−	−	−	−
	6908	−	−	−	−	−	−	−	−	−	−
	6312	−	−	−	−	−	−	−	−	−	−
	6715	−	−	−	−	ND	−	−	+	−	−
	6716	−	−	−	−	ND	−	−	+	−	−
	6717	−	−	−	−	ND	−	−	+	−	−
	6910	−	−	−	−	−	−	−	−	−	−
	7002	(+)	−	−	+	−	−	−	−	$+^{o}$	−
	73109	(+)	(+)	−	+	−	−	−	−	$+^{o}$	−
	7003	(+)	−	−	+	−	−	+	−	$+^{o}$	−
	7117	−	−	−	−	−	−	−	−	−	−
	7335	−	+	−	−	+	+	+	−	−	−
	7425	−	−	−	−	+	−	−	−	−	+
66–71	6307	−	−	−	−	−	−	−	−	−	−
	6603	−	−	−	−	−	−	−	−	−	−
	6710	−	−	−	−	−	−	−	−	−	−
	6713	−	−	−	−	−	−	−	−	−	−
	6904	−	−	−	−	−	−	−	−	−	−
	6907	−	−	−	−	−	−	−	−	−	−
	6911	−	−	−	−	−	−	−	−	−	−
	7001	−	−	−	−	−	−	−	−	−	−
	7009	−	−	−	−	−	−	−	−	$+^{s}$	−

ND, Not determined; (+), weak growth.

* Strains bracketed together are probably independent isolates of the same species.

† C-PE, C-phycoerythrin.

‡ Requirement for high concentrations of Na^{+}, Mg^{2+} and Ca^{2+}.

§ Maximum growth temperature, 53 °C.

‖ o, Obligate requirement for vitamin B_{12}; s, vitamin B_{12} stimulates growth, but is not an obligate requirement.

extreme genetic heterogeneity is mirrored only to a limited extent by known phenotypic properties (Table 4). Most strains possess small cells, less than 2 μm wide. Permanent immotility is the rule; only PCC 6910 has been observed to glide (Stanier *et al.*, 1971). The great majority of strains are obligate photoautotrophs. Phycoerythrinoid pigments are produced by only two strains.

Four strain clusters (bracketed in Table 4) are each probably composed of independent isolates belonging to one species.

In view of the diversity in base composition characteristic of this form genus, it appears desirable to designate three reference strains, each representative of one base compositional group. **Reference strains: PCC 7202 for the low GC group**
PCC 6301 for the intermediate GC group
PCC 6307 for the high GC group

Genus Gloeothece Nägeli 1849

One of the five strains assigned to this genus is shown in Fig. 3. Strains PCC 6501 and 6909 were described by Stanier *et al.* (1971) as *Gloeocapsa* spp., on the basis of an earlier observation (Allen & Stanier, 1968) which had suggested that the former strain could divide in more than one plane. Re-examination has shown that PCC 6501 and 6909 divide in only one plane (unpublished observations) and therefore should be assigned to *Gloeothece*. Three additional *Gloeothece* strains have since been added to the collection. The histories of the strains are as follows:

ATCC 27151 PCC 6501 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ M. M. Allen, fresh water, California, U.S.A., 1965 (Allen & Stanier, 1968). Named as *Gloeocapsa* sp. in CCAP (1430/2) (*Culture Collection of Algae and Protozoa: Second Amendments to the* 1971 *List of Strains*, 1973).

ATCC 27152 PCC 6909 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ UTEX ← W. R. Taylor ← W. Markle, source unknown, 1926. Named as *Gloeocapsa* sp. in CCAP (1430/3) (*Culture Collection of Algae and Protozoa: Second Amendments to the* 1971 *List of Strains*, 1973) and UTEX (795) (Starr, 1964).

ATCC 29163 PCC 7109. J. B. Waterbury, limestone cave, Bermuda, 1971.

ATCC 29116 PCC 73107. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

ATCC 29164 PCC 73108. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

The range of mean DNA base composition is 40 to 43 mol% GC (Herdman *et al.*, 1979). Motility has never been observed. All strains are obligate photoautotrophs, and all are capable of fixing nitrogen aerobically. With the exception of PCC 73107, all produce a phycoerythrinoid pigment distinct from C-phycoerythrin.

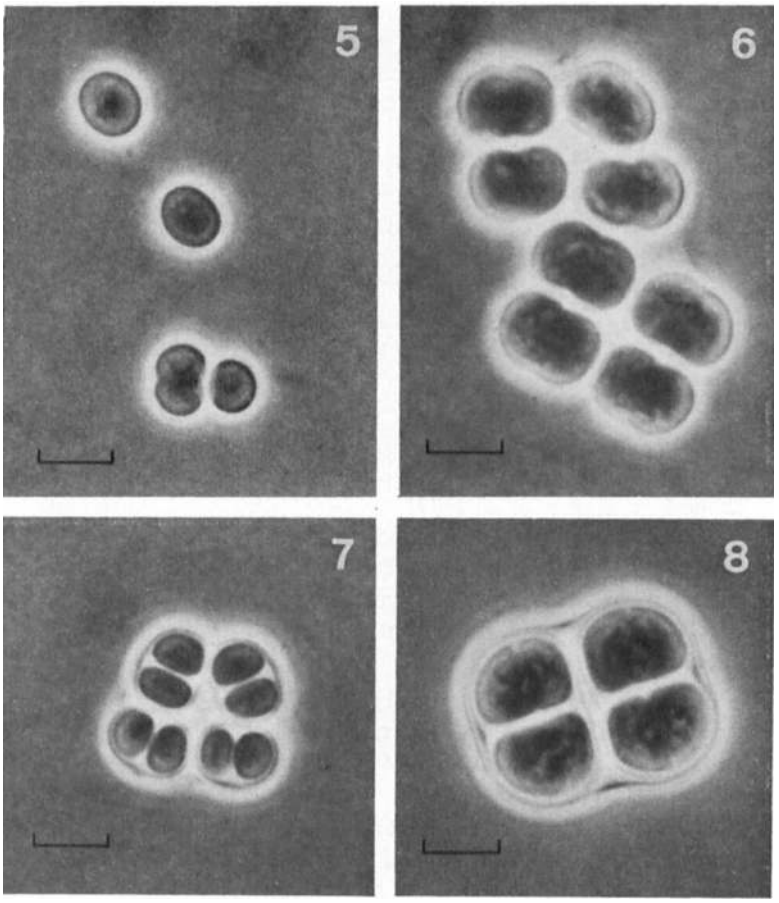
Reference strain: PCC 6501

Genus Gloeobacter Rippka, Waterbury & Cohen-Bazire 1974

Strain PCC 7421, the only representative of this genus so far isolated, is shown in Fig. 4; it has the following history:

ATCC 29082 PCC 7421. R. Rippka, calcareous rock, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972. Holotype of the type species, *Gloeobacter violaceus* (Rippka *et al.*, 1974).

This strain has a DNA base composition of 64 mol% GC (Rippka *et al.*, 1974), very different from that of *Gloeothece* strains. It is an immotile, obligate photoautotroph that



Figs 5 and 6. *Synechocystis* PCC 7509 and PCC 6808, respectively. Figs 7 and 8. *Gloeocapsa* PCC 7428 and PCC 73106, respectively. All phase contrast; bar markers represent 5 μm.

fails to synthesize nitrogenase in anaerobiosis; it produces a phycoerythrinoid pigment distinct from C-phycoerythrin. For further information, see Rippka *et al.* (1974).

Genus Synechocystis Sauvageau 1892

Two representatives of *Synechocystis* are shown in Figs 5 and 6. A majority of the strains of this genus were originally described by Stanier *et al.* (1971) either as *Aphanocapsa* (group IIA) or as *Microcystis* (group IIC). Komarek (1976) pointed out that the strains of group IIA conform to the definition of *Synechocystis* since they do not normally develop in culture as cell aggregates, an interpretation with which we agree. The one strain of group IIC (PCC 7005) was received by Stanier *et al.* (1971) from an algal culture collection as *Microcystis aeruginosa*. The cells, which occur singly, contained phase-bright granules interpreted by Stanier *et al.* (1971) as gas vacuoles, and on this basis assignment to *Microcystis* was maintained. However, subsequent work has shown that these granules are not gas vacuoles. Although it cannot be stated categorically that PCC 7005 did not at one time produce gas vacuoles, it has not done so since its purification in 1970 and should therefore be assigned, like the strains of group IIA, to *Synechocystis*. One of the strains described by Stanier *et al.* (1971), PCC 6807, has since been lost. Six new strains of this genus (PCC 6902, 6905, 6906, 7008, 7201 and 7509) have been added to the collection. The histories of all strains are as follows:

ATCC 27150 PCC 6308 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ G. C. Gerloff (*Gloeocapsa alpicola* 1051), lake water, Wisconsin, U.S.A., 1949 (Gerloff *et al.*, 1950). Named as *Gloeocapsa alpicola* in UTEX (1598) (Starr, 1971) and CCAP (1431/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 27170 PCC 6701 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ J. Hauxhurst (*Aphanocapsa* HA), fresh water, California, U.S.A., 1967.

ATCC 27171 PCC 6702 (Stanier *et al.*, 1971). $\overset{P}{\leftarrow}$ J. Hauxhurst (*Aphanocapsa* HD), fresh water, California, U.S.A., 1967.

ATCC 27175 PCC 6711 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), California, U.S.A., 1967.

ATCC 27178 PCC 6714 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), fresh water, California, U.S.A., 1967.

ATCC 27184 PCC 6803 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), fresh water, California, U.S.A., 1968.

ATCC 27185 PCC 6804 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), fresh water, California, U.S.A., 1968.

ATCC 27186 PCC 6805 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), fresh water, California, U.S.A., 1968.

ATCC 27187 PCC 6806 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), fresh water, California, U.S.A., 1968.

ATCC 27189 PCC 6808 (Stanier *et al.*, 1971). R. Kunisawa (*Aphanocapsa* sp.), California, U.S.A., 1968.

ATCC 29108 PCC 6902. A. Neilson, brackish water, Oregon, U.S.A., 1969.

ATCC 29109 PCC 6905. A. Neilson, low salinity brine pond, Newark, California, U.S.A., 1969.

ATCC 27266 PCC 6906. $\overset{I}{\leftarrow}$ J. West (*Eucapsis* sp.), hypersaline lake, Salton Sea, California, U.S.A., 1969.

ATCC 27153 PCC 7005 (Stanier *et al.*, 1971). $\overset{I}{\leftarrow}$ SAUG (1450/1) (Koch, 1964) $\leftarrow$ G. C. Gerloff (*Microcystis aeruginosa* 1036), Lake Mendota, Wisconsin, U.S.A., 1946 (Gerloff *et al.*, 1950, 1952). Named as *Microcystis aeruginosa* in CCAP (1450/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 29110 PCC 7008. A. Neilson, shallow pond, Point Reyes Peninsula, California, U.S.A., 1970.

ATCC 29152 PCC 7201. J. B. Waterbury, hemispherical macroscopic colony, bank above high water, Bodega, California, U.S.A., 1970.

ATCC 29235 PCC 7509. R. Rippka, rock scraping, Schöllenen, below Teufelsbrücke, Switzerland, 1972.

Strains of this genus fall into two sub-groups, distinguishable by their mean DNA base composition: 35 to 37 and 42 to 48 mol% GC (Stanier *et al.*, 1971; Herdman *et al.*, 1979). All strains of low GC content are obligate photoautotrophs, whereas most strains of high GC content (9 out of 12) are facultative photoheterotrophs (Table 5). The latter include seven strains of independent origin that are similar in all respects and probably represent independent isolates of one species. Some strains in both base compositional groups display gliding motility. Phycoerythrins are produced only by some strains of the low GC group. As for *Synechococcus*, reference strains representative of each base compositional sub-group are designated. **Reference strains: PCC 6308 for the low GC group**
PCC 6714 for the high GC group

Table 5. *Properties of Synechocystis strains*

Mean DNA base composition (mol % GC)	PCC no.*	Motility	Facultative photoheterotroph, using: Glucose	Sucrose	Glycerol	Synthesis of nitrogenase in anaerobiosis	Synthesis of C-PE†	Marine‡	Vitamin B_{12} requirement§
↑	6308	−	−	−	−	−	−	−	−
	6701	−	−	−	−	−	+	−	−
35–37	6711	+	−	−	−	−	+	−	−
	6804	+	−	−	−	−	−	−	−
↓	6808	+	−	−	−	−	+	−	−
↑	6702	−	+	−	−	−	−	−	−
	6714	−	+	−	−	−	−	−	−
	6803	+	+	−	−	−	−	−	−
	6805	−	+	−	−	−	−	−	−
	6806	−	+	−	−	−	−	−	−
	6905	+	+	−	−	−	−	−	−
42–48	7201	+	+	−	−	−	−	−	−
	6902	+	−	−	−	−	−	−	−
	6906	−	(+)	−	+	−	−	+	+s
	7005	−	−	−	−	−	−	−	−
	7008	−	−	−	−	−	−	−	−
↓	7509	−	+	+	−	ND	−	−	−

ND, Not determined; (+), weak growth.
* Bracketed strains are probably independent isolates of the same species.
† C-PE, C-phycoerythrin.
‡ Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.
§ s, Vitamin B_{12} stimulates growth, but is not an obligate requirement.

Genus Gloeocapsa Kützing 1843

The four strains that conform to the definition of this genus are recent isolates and none has been described previously. Two of them (PCC 7428 and 73106) are shown in Figs 7 and 8. The strain histories are as follows:

ATCC 27928 PCC 73106. R. Rippka, sphagnum bog, Switzerland, 1972.

ATCC 29159 PCC 7428. $\overset{I}{\leftarrow}$ A. Neilson, moderate hot spring, Amparai District, Maha Oya, Ceylon, 1973.

ATCC 29113 PCC 7501. J. B. Waterbury, rock scraping, Pont Neuf, Paris, France, 1975.

ATCC 29115 PCC 7512. $\overset{I}{\leftarrow}$ J. B. Waterbury, rock scraping, Pont Neuf, Paris, France, 1975.

The range of DNA base composition is narrow (40 to 46 mol% GC; Herdman *et al.*, 1979) and similar to the ranges both for *Gloeothece* (40 to 43 mol% GC) and for the high GC cluster of *Synechocystis* (42 to 48 mol% GC). The four strains are phenotypically distinguishable by the characters shown in Table 6.

Reference strain: PCC 73106

Genus Chamaesiphon Braun & Grunow 1865 emend. Geitler 1925

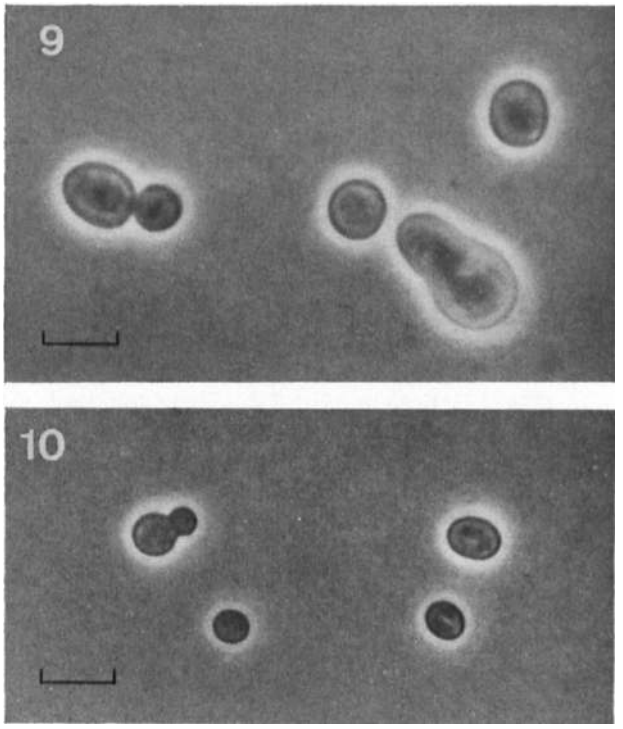
The two strains of *Chamaesiphon* (Figs 9 and 10) have both been in culture for many years, but were wrongly identified in earlier publications: PCC 6605 as *Synechococcus* sp. (Stanier *et al.*, 1971) and PCC 7430 as *Chroococcidiopsis* sp. (Komarek & Hindak, 1975). Their histories are as follows:

ATCC 27169 PCC 6605 (Stanier *et al.*, 1971). M. M. Allen, stream water, Berkeley, California, U.S.A., 1966.

Table 6. *Properties of Gloeocapsa strains*

Mean DNA base composition (mol % GC)	PCC no.	Motility	Facultative photoheterotroph, using: Glucose	Fructose	Ribose	Sucrose	Glycerol	Synthesis of nitrogenase in anaerobiosis	Synthesis of:* C-PE	X-PE
↑	73106	+	−	−	−	−	−	−	+	−
40–46	7428	−	+	+	+	+	−	−	−	−
	7501	+	+	−	−	−	−	−	−	+
↓	7512	−	−	−	−	−	−	−	+	−

* C-PE, C-phycoerythrin; X-PE, phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin.



Figs 9 and 10. *Chamaesiphon* PCC 7430 and PCC 6605, respectively. Both phase contrast; bar markers represent 5 μm.

ATCC 29397 PCC 7430 (Waterbury & Stanier, 1977). $\overset{I}{\leftarrow}$ J. Komarek $\leftarrow$ F. Hindak (*Chroococcidiopsis* sp., strain 1963/133), stream water, Sarka Valley near Prague, Czechoslovakia, 1963 (Komarek & Hindak, 1975; Komarek, 1972).

Although these two strains are identical in mean DNA base composition (47 mol% GC; Herdman *et al.*, 1979), they differ phenotypically in many respects and clearly represent two different species (Waterbury & Stanier, 1977). Strain PCC 6605 has much smaller cells than PCC 7430. It is an obligate autotroph, whereas PCC 7430 can grow photoheterotrophically with glucose, fructose and sucrose. Both strains produce C-phycoerythrin and PCC 6605 exhibits chromatic adaptation (Waterbury & Stanier, 1977).

Reference strain: PCC 7430

Table 7. *Section II: Unicellular cyanobacteria that reproduce by multiple fission*

	○ Baeocytes without fibrous outer wall layer ◎ Baeocytes with fibrous outer wall layer	
Reproduction only by multiple fission	Motile baeocytes ○ Immotile baeocytes ◎	*Dermocarpa* *Xenococcus*
Reproduction by both binary fission and multiple fission	Binary fission leads to pear-shaped structure composed of one or two basal cells and one apical cell; subsequent multiple fission of the apical cell yields motile baeocytes ○	*Dermocarpella*
	Binary fission yields cubical cellular aggregates; subsequent multiple fission yields: motile baeocytes ○ immotile baeocytes ◎	*Myxosarcina* *Chroococcidiopsis*
	Binary fission yields irregular cellular aggregates (pseudofilamentous); subsequent multiple fission yields motile baeocytes ○	Pleurocapsa group

Genera of Section II

The 32 strains of this section are assigned to five genera, all long recognized by phycologists, and to one provisional assemblage, termed the Pleurocapsa group (Table 7). The choice of generic names and the problem of generic definitions in Section II are discussed by Waterbury & Stanier (1978). Although diverse in structural and developmental respects, the members of Section II differ very little in mean DNA base composition: the overall range is 38 to 47 mol% GC (Herdman *et al.*, 1979). Consequently DNA base composition is not a useful character for distinguishing genera, or (with one exception: see Table 10) for making intrageneric sub-divisions.

Genus Dermocarpa Crouan & Crouan 1858

A marine strain, PCC 7301, is carried in two algal culture collections as *Dermocarpa violacea*, type species of the genus; however, no justification for this specific name has been published. Two freshwater strains, PCC 7437 and 7438, were described on the basis of the study of impure cultures (Komarek & Hindak, 1975) as *Chroococcidiopsis cyanosphaera*: subsequent structural and developmental study of the pure strains showed that they were typical members of the genus *Dermocarpa* (Waterbury & Stanier, 1978). A representative of this genus is shown in Fig. 11. The histories of the strains are as follows:

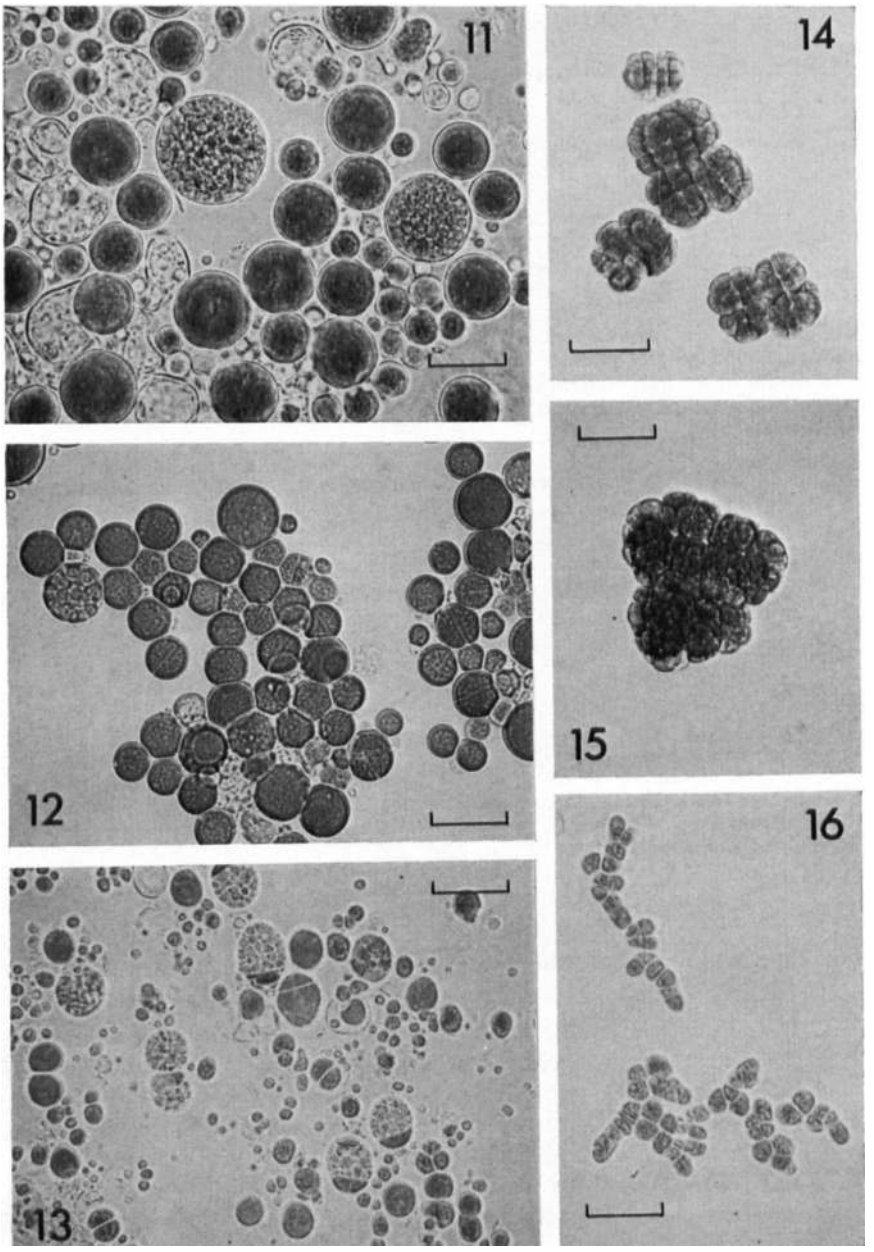
ATCC 29367 PCC 7301 (Waterbury & Stanier, 1978). $\overset{P}{\leftarrow}$ R. A. Lewin, marine aquarium, Scripps Institute of Oceanography, La Jolla, California, U.S.A., 1964. Named as *Dermocarpa violacea* in CCAP (1416/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971) and UTEX (1635) (Starr, 1971).

ATCC 29368 PCC 7302 (Waterbury & Stanier, 1978). J. B. Waterbury, sea water tank, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

ATCC 29369 PCC 7303 (Waterbury & Stanier, 1978). J. B. Waterbury, sea water tank, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

ATCC 29370 PCC 7304 (Waterbury & Stanier, 1978). J. B. Waterbury, epiphyte on *Rhodochorton* sp., high intertidal zone, Bodega Marine Laboratory, California, U.S.A., 1970.

ATCC 29371 PCC 7437 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek $\leftarrow$ F. Hindak (*Chroococcidiopsis cyanosphaera*, strain 1965/25), pool, botanical garden,



Figs 11 to 16. Representatives of the pleurocapsalean genera. *Dermocarpa* PCC 7437 (Fig. 11), *Xenococcus* PCC 7306 (Fig. 12), *Dermocarpella* PCC 7326 (Fig. 13), *Myxosarcina* PCC 7312 (Fig. 14), *Chroococcidiopsis* PCC 7431 (Fig. 15) and Pleurocapsa strain PCC 7319 (Fig. 16). All bright field; bar markers represent 20 μm.

Havana, Cuba, 1965 (Komarek & Hindak, 1975; Komarek, 1972; Komarek *et al.*, 1975).

ATCC 29372 PCC 7438 (Waterbury & Stanier, 1978). $\overset{1}{\leftarrow}$ J. Komarek $\leftarrow$ F. Hindak (*Chroococcidiopsis cyanosphaera*, strain 1965/26), mineral spring, near Santa Fé, Cuba, 1965 (Komarek & Hindak, 1975; Komarek, 1972).

Some strain properties are shown in Table 8.

Reference strain: PCC 7301

Table 8. *Properties of Dermocarpa strains*

PCC no.	Facultative photoheterotroph, using: Glucose	Fructose	Sucrose	Synthesis of nitrogenase in anaerobiosis	Synthesis of:* C-PE	X-PE	Marine†	Vitamin B_{12} requirement‡
7301	+	+	+	+	+	−	+	+^{o}
7302	−	−	−	−	+	−	+	+^{s}
7303	−	−	−	+	+	−	+	+^{s}
7304	+	−	+	−	−	+	+	−
7437	+	−	+	−	+	−	−	−
7438	+	+	−	−	−	+	−	−

* C-PE, C-phycoerythrin; X-PE, phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin.

† Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

‡ o, Obligate requirement for vitamin B_{12}; s, vitamin B_{12} stimulates growth markedly, but is not an obligate requirement.

Table 9. *Properties of Xenococcus, Dermocarpella and Myxosarcina strains*

Genus	PCC no.	Facultative photoheterotroph, using: Glucose	Fructose	Sucrose	Synthesis of nitrogenase in anaerobiosis	Synthesis of:* C-PE	X-PE	Marine†
Xenococcus	7305	−	−	−	+	−	+	+
	7306	−	−	−	−	−	+	+
	7307	+	−	+	−	−	+	+
Dermocarpella	7326	+	+	+	−	+	−	+
Myxosarcina	7312	−	−	+	+	−	+	+
	7325	+	−	+	−	+	−	+

* C-PE, C-phycoerythrin; X-PE, phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin.

† Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

Genus Xenococcus Thuret 1880

One of the three strains in this genus is shown in Fig. 12. The histories of the strains are as follows:

ATCC 29373 PCC 7305 (Waterbury & Stanier, 1978). $\overset{P}{\leftarrow}$ R. A. Lewin (*Dermocarpa* sp.), marine aquarium, Scripps Institute of Oceanography, La Jolla, California, U.S.A., 1971.

ATCC 29374 PCC 7306 (Waterbury & Stanier, 1978). J. B. Waterbury, rock chip, high intertidal zone, Pillar Point, California, U.S.A., 1970.

ATCC 29375 PCC 7307 (Waterbury & Stanier, 1978). J. B. Waterbury, rock chip, high intertidal zone, Horseshoe Cove, Bodega Marine Laboratory, California, U.S.A., 1970.

Some strain properties are shown in Table 9.

Reference strain: PCC 7305

Genus Dermocarpella Lemmermann 1907

This genus is so far represented by only one strain, illustrated in Fig. 13, which has the following history:

ATCC 29376 PCC 7326 (Waterbury & Stanier, 1978). J. B. Waterbury, snail shell, intertidal zone, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

Some properties of the strain are summarized in Table 9.

Genus Myxosarcina Printz 1921

One of the two strains in this genus is shown in Fig. 14. Their histories are as follows:

ATCC 29377 PCC 7312 (Waterbury & Stanier, 1978). J. B. Waterbury, snail shell, intertidal zone, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

ATCC 29378 PCC 7325 (Waterbury & Stanier, 1978). J. B. Waterbury, snail shell, intertidal zone, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

Some properties of the strains are shown in Table 9.

Reference strain: PCC 7312

Genus Chroococcidiopsis Geitler 1933

A representative of this genus (PCC 7431) is shown in Fig. 15. One strain (PCC 6712) was described by Stanier *et al.* (1971) as *Chlorogloea* sp., since the formation of baeocytes was not observed. A second strain (PCC 7203) was received as *Myxosarcina chroococcoides*, but was transferred to *Chroococcidiopsis* as a result of the observation that it produces immotile baeocytes (Waterbury & Stanier, 1978). The strain histories are as follows:

ATCC 27176 PCC 6712 (Stanier *et al.*, 1971; Waterbury & Stanier, 1978). R. Kunisawa, water sample, reservoir, Marin County, California, U.S.A., 1967. Named as *Chlorogloea* sp. in CCAP (1411/2) (*Culture Collection of Algae and Protozoa: Second Amendments to the* 1971 *List of Strains*, 1973).

ATCC 27900 PCC 7203 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ CCAP $\overset{I}{\leftarrow}$ Ernst-Moritz Arndt-University, soil sample, near Greifswald, East Germany, 1962 (Komarek, 1972). Named as *Myxosarcina chroococcoides* in CCAP (1451/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 29379 PCC 7431 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek (*Chroococcidiopsis thermalis*, strain 1964/48), mineral spring, near San Diego, Cuba, 1964 (Komarek & Hindak, 1975; Komarek, 1972).

ATCC 29380 PCC 7432 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek ← F. Hindak (*Chroococcidiopsis thermalis*, strain 1965/21), spring, near Santa Fé, Cuba, 1965 (Komarek & Hindak, 1975; Komarek, 1972).

ATCC 29381 PCC 7433 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek ← F. Hindak (*Chroococcidiopsis thermalis*, strain 1966/27), soil, dried pool, Pinar del Rio, Cuba, 1966 (Komarek & Hindak, 1975; Komarek, 1972).

ATCC 29382 PCC 7434 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek ← F. Hindak (*Chroococcidiopsis cubana*, strain 1965/19), pool, botanical garden, Havana, Cuba, 1965 (Komarek & Hindak, 1975; Komarek, 1972).

ATCC 29383 PCC 7436 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek ← F. Hindak (*Chroococcidiopsis cubana*, strain 1965/108), drainage ditch, Nueva Gerona, Cuba, 1965 (Komarek & Hindak, 1975).

ATCC 29384 PCC 7439 (Waterbury & Stanier, 1978). $\overset{I}{\leftarrow}$ J. Komarek ← F. Hindak (*Chroococcidiopsis doonensis*, strain 1968/64), sand beach, near Mamaia, Romania, 1968 (Komarek & Hindak, 1975).

Some properties of *Chroococcidiopsis* strains are summarized in Table 10. Excluding PCC 6712, and possibly 7434, the strains of this genus are probably independent isolates of one species: they cannot be distinguished by DNA base composition, structure and development, or other major phenetic properties. It should be noted that an earlier study of structure and development conducted with impure cultures (Komarek & Hindak, 1975) resulted in the assignment of some of these strains to three different species of *Chroococcidiopsis* (see histories).

Reference strain: PCC 7203

Table 10. *Properties of Chroococcidiopsis strains*

PCC no.*	Mean DNA base composition (mol % GC)	Facultative photoheterotroph, using: Glucose	Fructose	Sucrose	Synthesis of nitrogenase in anaerobiosis	Synthesis of:† X-PE	PEC
6712	40	+	+	+	+	+	−
7203	46	+	+	+	+	−	+
7431	46	+	+	+	+	−	+
7432	46	+	+	+	+	−	+
7433	46	+	+	+	+	−	+
7436	46	+	+	+	+	−	+
7439	46	+	+	+	+	−	+
7434	46	−	+	−	+	−	−

* The bracketed strains are probably independent isolates of the same species.

† X-PE, Phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin; PEC, phycoerythrocyanin.

The Pleurocapsa group

This is a provisional designation and is given to a group of strains that are diverse and variable in development; an example (PCC 7319) is shown in Fig. 16. This group of strains corresponds broadly to the organisms included by phycologists in the genera *Pleurocapsa* (Thuret) Hauck 1885, *Hyella* Bornet & Flahaut 1888, *Hydrococcus* Kützing 1833, *Onkonema* Geitler 1933 and *Tryponema* Ercegovic 1929 (family *Pleurocapsaceae* or *Hyellaceae*). The histories of the strains are as follows:

ATCC 29385 PCC 7310 (Waterbury & Stanier, 1978). J. B. Waterbury, snail shell, intertidal zone, Arizona Marine Station, Puerto Penasco, Mexico, 1971.

ATCC 29386 PCC 7314 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29387 PCC 7317 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29388 PCC 7319 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29389 PCC 7320 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29390 PCC 7321 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29391 PCC 7322 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29392 PCC 7324 (Waterbury & Stanier, 1978). Isolator and source as for ATCC 29385.

ATCC 29393 PCC 7327 (Waterbury & Stanier, 1978). ← R. Castenholz (*Pleurocapsa minor* OH-69-pm), Hunter's Spring, Oregon, U.S.A., 1969 (Castenholz, 1970).

ATCC 29394 PCC 7440 (Waterbury & Stanier, 1978). J. B. Waterbury, rock chip, high intertidal zone, Deauville, Normandy, France, 1974.

ATCC 29395 PCC 7506 (Waterbury & Stanier, 1978). J. B. Waterbury, rock chip, collected by T. Le Campion-Alsumard, Marseille, France, 1964.

ATCC 29396 PCC 7516 (Waterbury & Stanier, 1978). ← T. Le Campion-Alsumard (*Hyella caespitosa*), rock chip, station B, l'Ile Riou, Marseille, France, 1974 (Le Campion-Alsumard, 1972).

Some strain properties of the Pleurocapsa group are shown in Table 11. No reference strains are proposed.

Table 11. *Properties of strains of the Pleurocapsa group*

PCC no.	Facultative photoheterotroph, using: Glucose	Fructose	Sucrose	Synthesis of nitrogenase in anaerobiosis	Synthesis of:* C-PE	X-PE	Thermophil†	Marine‡	Vitamin B_{12} requirement§
7310	−	−	+	−	+	−	−	+	+[s]
7314	−	+	+	+	+	−	−	+	−
7317	+	−	−	−	+	−	−	+	+[o]
7319	−	+	+	−	−	+	−	+	−
7320	+	+	+	+	−	+	−	+	−
7321	−	−	+	+	−	+	−	−	−
7322	+	+	+	+	+	−	−	+	−
7324	−	−	−	+	+	−	−	+	−
7327	−	−	+	+	+	−	+	−	−
7440	−	−	−	−	+	−	−	+	−
7506	+	−	−	−	−	ND	−	+	−
7516	−	−	+	+	+	−	−	+	−

ND, Not determined.

* C-PE, C-phycoerythrin; X-PE, phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin.

† Maximum growth temperature, 55 °C.

‡ Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

§ o, Obligate requirement for vitamin B_{12}; s, vitamin B_{12} stimulates growth, but is not an obligate requirement.

Genera of Section III

Of the 44 non-heterocystous, filamentous strains placed in this section, only 19 could be given definite generic assignments; the remainder are included in a provisional group (Table 12, Diagram 1). Many genera have been proposed for members of this large cyanobacterial assemblage, and phycologists are far from agreed about its generic sub-division. Geitler (1932) recognized 25 genera, reduced in a more recent treatment to 11 (Bourrelly, 1970).

Sheath formation has traditionally had a prominent place in the classification of these cyanobacteria, some genera being defined exclusively by properties such as the consistency of sheath material (*Lyngbya* Agardh 1824, *Phormidium* Kützing 1843); false branching, a consequence of the consistency of the sheath, (*Plectonema* Thuret 1875); and special arrangements of trichomes within a common sheath (*Microcoleus* Desmazières 1823, *Schizothrix* Kützing 1843). Consequently characters expressed by the structure of the trichome itself have served only to define genera that produce little or no sheath material, such as *Spirulina* Turpin 1827, *Oscillatoria* Vaucher 1803 and *Pseudanabaena* Lauterborn 1915.

Although many strains of Section III can form sheaths, characters connected with sheath formation have for the most part proved determinatively unsatisfactory for the generic identification of cultures. Only in strain PCC 7419 is the trichome regularly surrounded by a firm sheath under all growth conditions; this strain might accordingly be assigned to *Lyngbya* on the basis of its sheath structure. In other strains that produce sheaths, this character is much influenced by environmental parameters: cultivation in liquid or on solid media, presence or absence of a utilizable sugar, and age of cultures at the time of examination. In several strains received as *Plectonema* spp., false branching was so rare as to be virtually undetectable under conditions that supported abundant and apparently normal growth. Three strains received as *Microcoleus* spp. never showed in culture the arrangement of trichomes surrounded by a common sheath nominally characteristic for this genus. We concluded, therefore, that sheath-associated properties are too unreliable to permit generic identifications for strains that belong to Section III.

On the other hand, certain strains of Section III can be readily identified in culture as members of three form genera that produce motile trichomes not surrounded by well-marked sheaths; each genus is traditionally defined by the properties of the trichomes.

Table 12. *Section III: Filamentous non-heterocystous cyanobacteria that divide in only one plane*

Trichome helical	Cells composing trichome are isodiametric, cylindrical or disc-shaped; little or no constriction between adjacent cells; reproduction by transcellular trichome breakage (?)	Trichome motile, either not ensheathed or thinly sheathed *Spirulina*
Trichome straight	Cells composing trichome are disc-shaped and not separated by deep constrictions; reproduction by transcellular trichome breakage	Trichome motile, either not ensheathed or thinly sheathed *Oscillatoria*
		Trichome immotile, enclosed by heavy sheath; motility restricted to sheathless or thinly sheathed hormogonia **LPP group A**
	Cells composing trichome are isodiametric or cylindrical; variable degree of constriction between adjacent cells; reproduction by transcellular or intercellular trichome breakage	Trichome motile, not ensheathed; cells contain polar gas vacuoles and are separated by deep constrictions *Pseudanabaena*
		Not as above; with or without sheath, motile or immotile **LPP group B**

The trichome of *Oscillatoria* Vaucher 1803 is straight and composed of disc-shaped cells between which there is little if any constriction. The latter implies that the outer membrane layer participates little in the formation of the transverse walls (Lamont, 1969). Consequently, the trichome does not fragment very easily and often attains a considerable length (> 1 cm). Reproduction occurs only by sacrificial (transcellular) trichome breakage, a process well described by Lamont (1969). The straight trichome of *Pseudanabaena* Lauterborn 1915 differs from that of *Oscillatoria* in several respects: the cells are cylindrical, they are separated by deep constrictions and they contain gas vacuoles, revealed by microscopic examination under phase contrast illumination as a light refractile granule at each cell pole (Figs 22 to 24). Reproduction occurs readily by intercellular trichome breakage, and the trichomes of many strains are very short (2 to 8 cells). Gas vacuolated species of *Oscillatoria* and *Spirulina* do not display the polar location of the gas vacuoles characteristic of *Pseudanabaena*.

It should be emphasized that the definitions of *Pseudanabaena* and *Oscillatoria* presented above are considerably more restrictive than those of many phycologists, being based on the described properties of the respective type species, *Pseudanabaena catenata* Lauterborn 1915 and *Oscillatoria princeps* Vaucher 1803.

The trichome of *Spirulina* Turpin 1827 is also composed of cells between which there is little constriction, and reproduction probably also occurs by transcellular fragmentation. In contrast to *Oscillatoria*, the trichome of *Spirulina* is helical, and its cells may be either disc-shaped, isodiametric or cylindrical. Bourrelly (1970) combines *Oscillatoria* and *Spirulina*; however, the helical shape of the trichome of *Spirulina* is a stable and constant property in culture.

The abandonment of genera defined by sheath-associated characters, as well as the relatively restrictive definitions of the three genera recognized, leaves many strains in Section III without clear-cut generic assignments. They are here provisionally placed in the

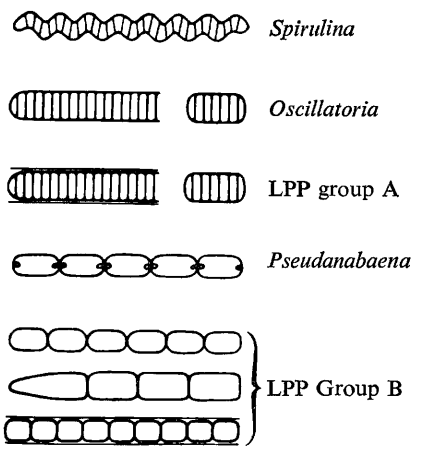


Diagram 1. Schematic presentation of the genera assigned to Section III. Thin lines surrounding trichomes designate sheath material. Polar bodies (*Pseudanabaena*) represent gas vacuoles.

LPP group, so called because many of the strains included fall within the broad confines of the genera *Lyngbya, Phormidium* and *Plectonema.*

Genus Spirulina Turpin 1827

Only two strains, with markedly different properties, belong to this genus (see Figs 17, 18). Their histories are as follows:

ATCC 29542 PCC 6313 (Kenyon *et al.*, 1972). M. M. Allen, brackish water, Berkeley, California, U.S.A., 1963.

ATCC 29408 PCC 7345. $\overset{P}{\leftarrow}$ R. A. Lewin (*Arthrospira platensis*), saline marsh, Del Mar Slough, California, U.S.A., 1969.

Strain PCC 6313, briefly described by Kenyon *et al.* (1972), forms thin (2 μm) trichomes without gas vacuoles; although isolated from brackish water, it is not a marine strain. Strain PCC 7345 forms wide (16 μm), more loosely coiled trichomes, which contain abundant gas vacuoles; it is a true marine strain. Both strains are obligate autotrophs, unable to synthesize nitrogenase anaerobically. Mean DNA base compositions are 44 and 54 mol% GC for PCC 7345 and 6313, respectively (Herdman *et al.*, 1979).

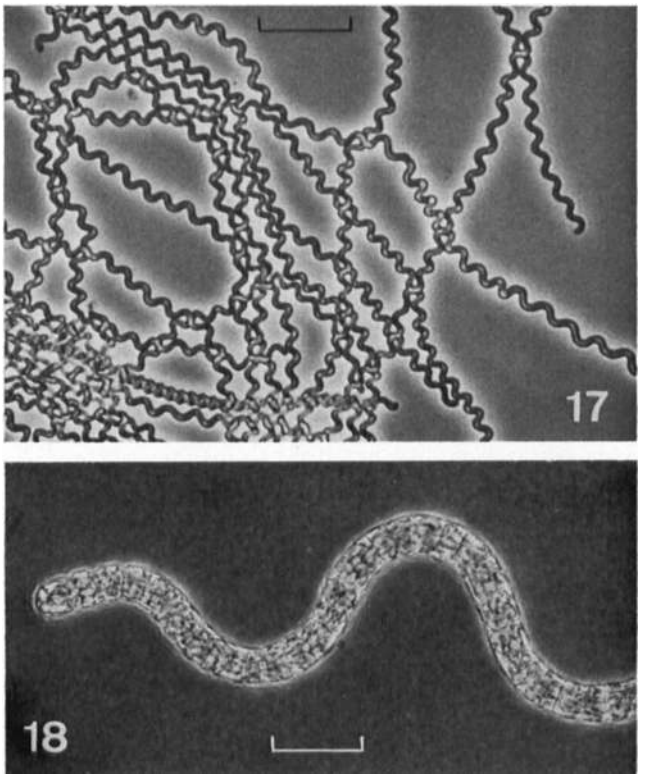
Strain PCC 7345, received as *Arthrospira platensis*, has the relatively thick trichome, containing cross-walls readily evident by light microscopy, that defines this form genus. However, the traditional generic distinction between *Arthrospira* Stizenberger 1852 and *Spirulina* Turpin 1827 appears trivial and is not recognized by Geitler (1932). The substantial difference in mean DNA base composition between strains PCC 6313 and 7345 nevertheless suggests that more solid genetic grounds for recognizing these two genera may eventually be found. **Reference strain: PCC 6313**

Genus Oscillatoria Vaucher 1803

Nine strains are included in this genus. Three representatives are illustrated in Figs 19 to 21. The histories of the strains are as follows:

ATCC 27930 PCC 6304 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ M. B. Allen, source unknown. Named as *Microcoleus vaginatus* in SAUG (1449/3) (Koch, 1964).

ATCC 29215 PCC 6401 (Kenyon *et al.*, 1972). M. M. Allen, marine mud, California, U.S.A., 1964.



Figs 17 and 18. *Spirulina* PCC 6313 and PCC 7345, respectively. Both phase contrast; bar markers represent 20 μm.

ATCC 27906 PCC 6407 (Kenyon *et al.*, 1972). M. M. Allen, fresh water, California, U.S.A., 1964.

ATCC 29205 PCC 6412 (Kenyon *et al.*, 1972). M. M. Allen, fresh water, California, U.S.A., 1964. Named as *Lyngbya* sp. in UTEX (1546) (Starr, 1966).

ATCC 29081 PCC 6506 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ E. G. Pringsheim, source unknown; does not correspond to description by isolator (Pringsheim, 1966). Named as *Lyngbya kuetzingii* in UTEX (1547) (Starr, 1966).

ATCC 27935 PCC 6602 (Kenyon *et al.*, 1972). M. M. Allen, fresh water, California, U.S.A., 1966.

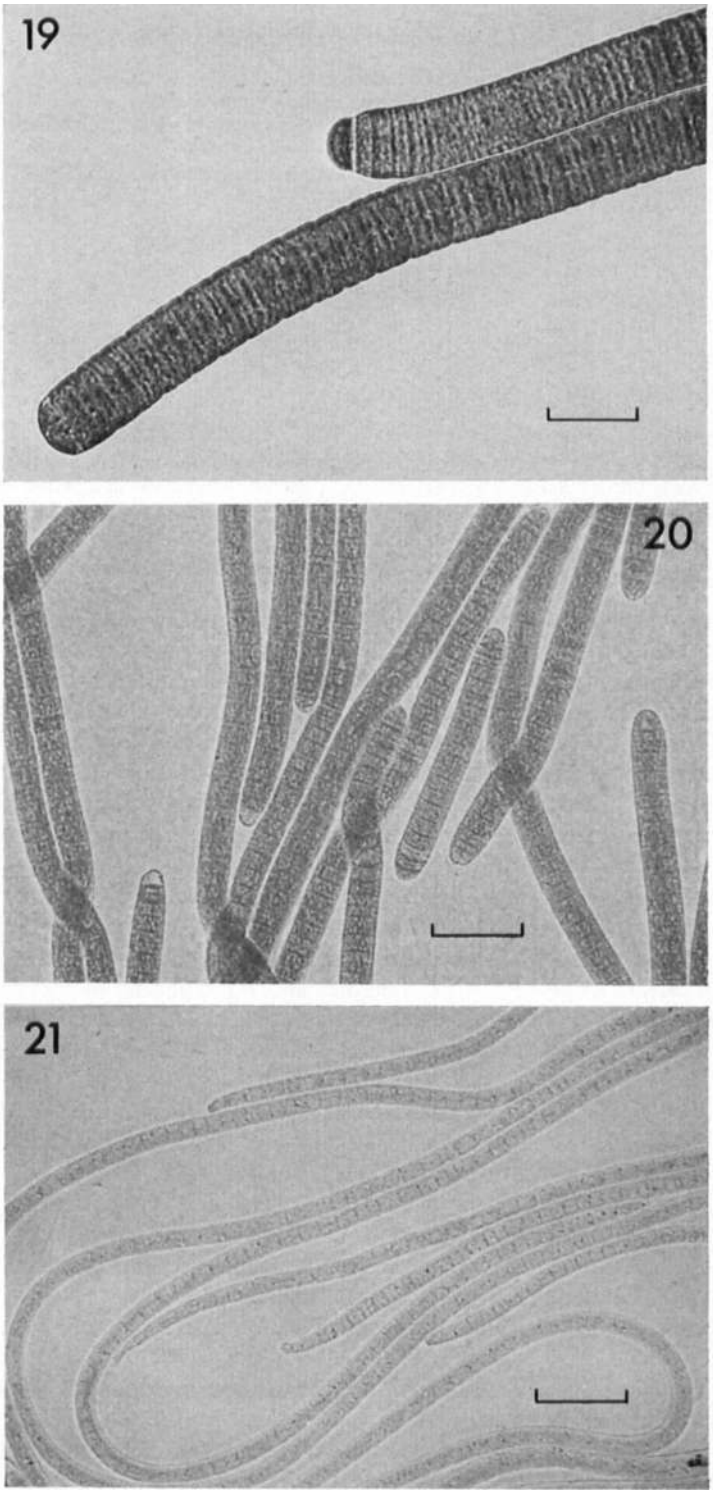
ATCC 29134 PCC 7112. A. Neilson, soil, orchid house, San Francisco, U.S.A., 1970.

ATCC 29135 PCC 7412. $\overset{I}{\leftarrow}$ A. Neilson, greenhouse water tank, Stockholm, Sweden, 1972.

ATCC 29209 PCC 7515. $\overset{I}{\leftarrow}$ A. Neilson, greenhouse water tank, Stockholm, Sweden, 1972

The range of mean DNA base composition is relatively narrow (40 to 50 mol% GC; Herdman *et al.*, 1979) and no clear-cut intrageneric sub-groups can be distinguished on this basis. As shown in Table 13, the strains fall into three sub-groups distinguished by the width of the trichome. In the sub-group with the narrowest trichomes (4 to 5 μm), two clusters of strains appear to be independent isolates of a single species, distinguished by differences with respect to facultative heterotrophy and the capacity to synthesize nitrogenase anaerobically.

Reference strain: PCC 7515



Figs 19 to 21. *Oscillatoria* PCC 7515, PCC 7112 and PCC 6506, respectively. All bright field; bar markers represent 20 μm.

Table 13. *Properties of Oscillatoria strains*

PCC no.*	Cell width (μm)	Facultative photoheterotroph, using: Glucose	Facultative photoheterotroph, using: Fructose	Synthesis of nitrogenase in anaerobiosis	Synthesis of:† C-PE	Synthesis of:† X-PE
6304	4–5	–	–	–	–	–
6401	4–5	–	–	–	–	–
7412	4–5	–	–	–	–	–
6407	4–5	(+)	–	+	–	–
6412	4–5	(+)	(+)	+	–	–
6506	4–5	(+)	–	+	–	–
6602	4–5	+	+	+	+	–
7112	7–8	–	–	–	+	–
7515	15–16	+	+	+	–	+

(+), Weak growth.

* Strains bracketed together are probably independent isolates of the same species.

† C-PE, C-phycoerythrin; X-PE, phycoerythrinoid pigment tentatively designated as being spectroscopically distinct from C-phycoerythrin.

Genus Pseudanabaena Lauterborn 1915

These cyanobacteria are found in widely diverse aquatic habitats including hot springs (Anagnostidis, 1961), the sulphide-rich anaerobic layer of ponds (Lauterborn, 1915) and marine environments. Nevertheless, some phycologists have long expressed doubts about the validity of the genus, since the trichomes resemble those of an *Anabaena* sp. without heterocysts (Geitler, 1932). Bourrelly (1970) recently reported that, exceptionally, *Pseudanabaena* spp. may form heterocysts and considered the boundary between this genus and *Anabaena* to be imprecise. However, Pringsheim (1968) had shown earlier that two strains of *Pseudanabaena* were incapable of fixing nitrogen aerobically or of forming heterocysts under a wide variety of growth conditions. We have confirmed Pringsheim's observations for many additional strains. The boundary *vis-à-vis Anabaena* is, accordingly, clear-cut.

Three of the eight strains assigned to this genus (PCC 6802, 6901 and 6903) were originally described by Stanier *et al.* (1971) as *Synechococcus* spp., since all form short trichomes, typically 2 to 6 cells in length. Polar gas vacuoles and rapid gliding movement are the principal properties that distinguish short-trichome strains of *Pseudanabaena* from *Synechococcus*. Three *Pseudanabaena* strains are shown in Figs 22 to 24. The strain histories are as follows:

ATCC 29118 PCC 6406. $\overset{I}{\leftarrow}$ M. M. Allen, fresh water, California, U.S.A., 1964.

ATCC 27183 PCC 6802 (Stanier *et al.*, 1971). A. Neilson (*Synechococcus* sp.), pond water, University of California, Berkeley, U.S.A., 1968.

ATCC 27263 PCC 6901 (Stanier *et al.*, 1971). A. Neilson (*Synechococcus* sp.), shallow stream, Tres Pinos, California, U.S.A., 1969.

ATCC 27190 PCC 6903 (Stanier *et al.*, 1971). A. Neilson (*Synechococcus* sp.), brackish pool, Coos Bay, Oregon, U.S.A., 1969.

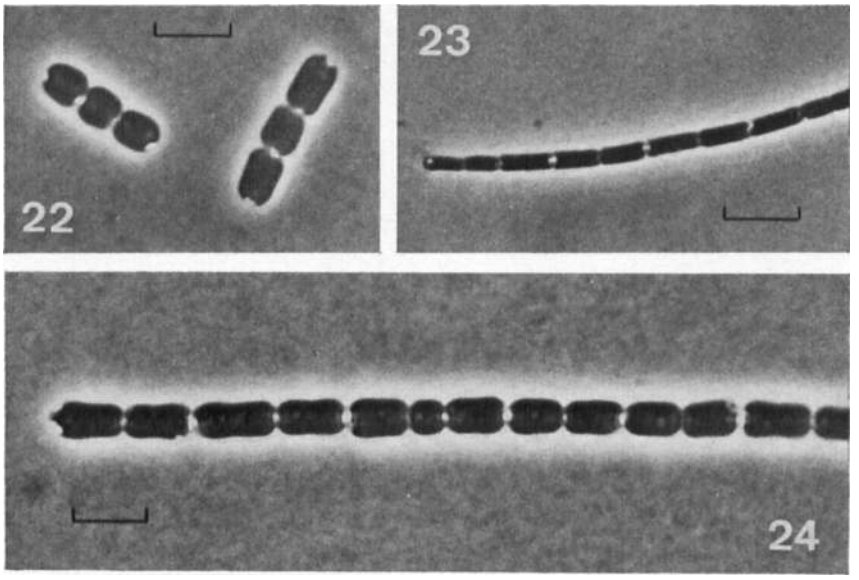
ATCC 29137 PCC 7367. J. B. Waterbury, snail shell, intertidal zone, Puerto Penasco, Mexico, 1971.

ATCC 29207 PCC 7402. $\overset{I}{\leftarrow}$ J. A. Houghton, pond heavily polluted with pig manure, Ireland, 1972.

ATCC 29210 PCC 7403. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

ATCC 29536 PCC 7429. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

The range of mean DNA base composition is 44 to 52 mol% GC (Stanier *et al.*, 1971;



Figs 22 to 24. *Pseudanabaena* PCC 7402, PCC 6406 and PCC 7429, respectively. All phase contrast; bar markers represent 5 μm.

Table 14. *Properties of Pseudanabaena strains*

PCC no.	No. of cells in a trichome	Cell width (μm)	Synthesis of nitrogenase in anaerobiosis	Synthesis of:* C-PE	Synthesis of:* PEC	Motility†	Marine‡
6802	1–3	2·0–2·5	+	+	−	−	−
6901	3–6	1·3–1·8	−	−	−	+	−
6903	3–6	2·5–3·0	−	−	−	+	−
7402	3–6	2·0–2·5	−	−	−	+	−
7403	3–6	1·8–2·3	+	−	−	−	−
7367	4–10	1·3–1·8	−	+	−	+	+
6406	>10	0·8–1·3	+	−	+	+	−
7429	>10	2·0–2·5	−	−	−	+	−

All strains are obligate photoautotrophs.

* C-PE, C-phycoerythrin; PEC, phycoerythrocyanin.
† −, Loss of motility on repeated subculturing in liquid medium.
‡ Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

Herdman *et al.*, 1979) and no clear-cut intrageneric separations can be made on this basis. All strains are obligate photoautotrophs. Other properties are shown in Table 14.

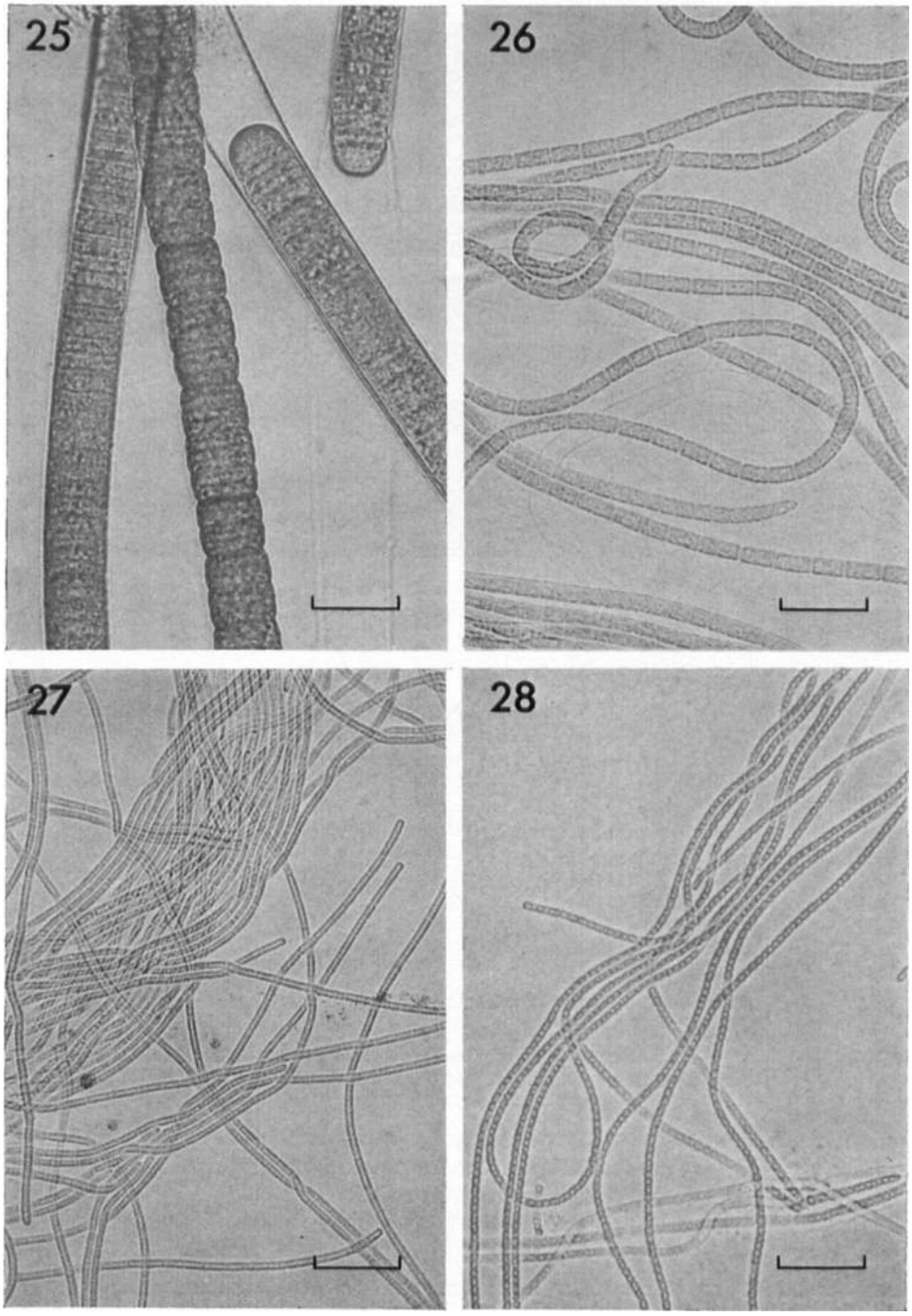
Reference strain: PCC 7429

The LPP group

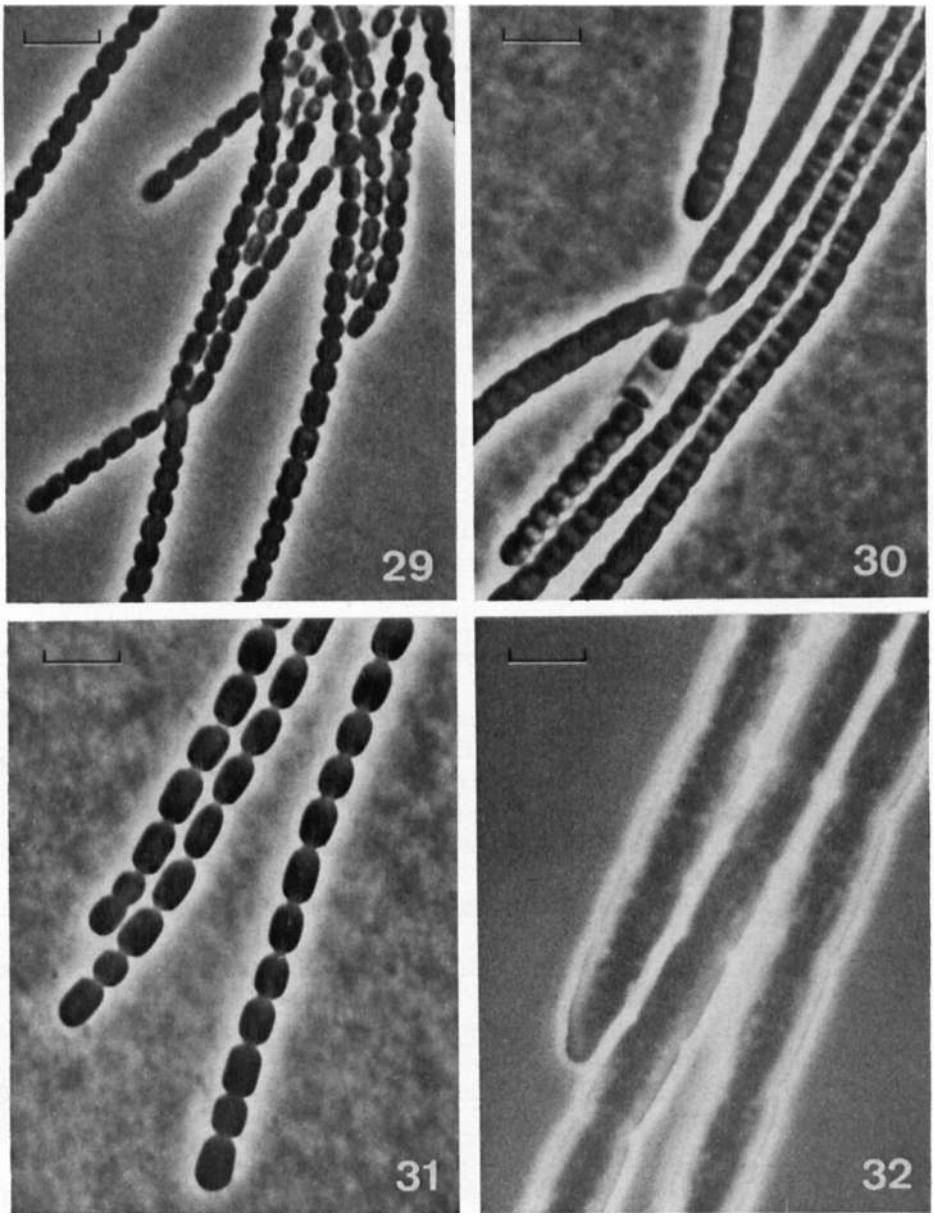
Some representatives of the 25 strains assigned to this provisional assemblage are shown in Figs 25 to 32. The histories of the strains are as follows:

ATCC 27894 PCC 6306 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ M. B. Allen $\overset{P}{\leftarrow}$ M. Dyar (*Plectonema notatum*), source unknown (Allen, 1952). Named as *Plectonema boryanum* in UTEX (581) (Starr, 1964) and (1542) (Starr, 1966) and in CCAP (1463/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 27902 PCC 6402 (Kenyon *et al.*, 1972). M. M. Allen, pond water, California, U.S.A., 1964. Named as *Plectonema* sp. in UTEX (1541) (Starr, 1966).



Figs 25 to 28. Representatives of the LPP group. Strain PCC 7419 (Fig. 25), strain PCC 7113 (Fig. 26), strain PCC 7105 (Fig. 27) and strain PCC 7505 (Fig. 28). All bright field; bar markers represent 20 μm.



Figs 29 to 32. Representatives of the LPP group at a higher magnification to illustrate cell shape. Strain PCC 7376 (Fig. 29), strain PCC 7505 (Fig. 30), strain PCC 7408 (Fig. 31) and strain PCC 7420 (Fig. 32). All phase contrast; bar markers represent 5 μm.

ATCC 29119 PCC 6409 (Kenyon *et al.*, 1972). M. M. Allen, pond water, California, U.S.A., 1964. Named as *Phormidium* sp. in UTEX (1540) (Starr, 1966).

ATCC 27907 PCC 6703 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ G. Cohen-Bazire, Lake Washington, U.S.A., 1967.

ATCC 27913 PCC 7004 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ C. Van Baalen (*Schizothrix calcicola* MAN), mangrove root, Lydia Ann Channel, Port Aransas, Texas, U.S.A., 1962.

ATCC 29117 PCC 7104 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ C. Van Baalen (*Lyngbya lagerheimii*

MONT), rock at shoreline, Montauk Point, Long Island, New York, U.S.A., 1960 (Van Baalen, 1962).

ATCC 29120 PCC 7105. $\overset{P}{\leftarrow}$ C. Van Baalen (*Oscillatoria williamsii* MEV) $\overset{I}{\leftarrow}$ J. J. A. McLaughlin, Haskins Laboratories, 1960, source unknown (Van Baalen & Marler, 1963).

ATCC 29206 PCC 7113. A. Neilson, soil, orchid house, San Francisco, U.S.A., 1971.

ATCC 29121 PCC 7114. A. Neilson, soil, orchid house, San Francisco, U.S.A., 1971.

ATCC 29122 PCC 7123. A Neilson, soil, orchid house, San Francisco, U.S.A., 1971.

ATCC 29123 PCC 7124. A. Neilson, low salinity brine pond, Port Hedland, Western Australia, 1970.

ATCC 29409 PCC 7375. $\overset{P}{\leftarrow}$ R. A. Lewin (*Phormidium ectocarpi*) $\overset{I}{\leftarrow}$ P. Strout, plankton, Woods Hole region, Massachusetts, U.S.A., 1958.

ATCC 29410 PCC 7376. $\overset{P}{\leftarrow}$ R. A. Lewin (*Phormidium fragile*) $\overset{I}{\leftarrow}$ F. Haxo $\leftarrow$ P. Strout, source unknown, 1958.

ATCC 29407 PCC 73110. $\overset{P}{\leftarrow}$ M. Shilo $\leftarrow$ UTEX $\leftarrow$ M. Dyar (unidentified filamentous alga no. 3), source unknown (Allen, 1952). Named as *Plectonema boryanum* in UTEX (594) (Starr, 1964).

ATCC 29165 PCC 7404. $\overset{I}{\leftarrow}$ R. Kunisawa, Lake Washington, U.S.A., 1967.

ATCC 29125 PCC 7406. $\overset{I}{\leftarrow}$ A. Neilson, epiphyte on *Azolla filiculoides*, Berkeley, California, U.S.A., 1971.

ATCC 29126 PCC 7407. $\overset{I}{\leftarrow}$ SAUG (*Microcoleus vaginatus*), 1970, source unknown.

ATCC 29344 PCC 7408. $\overset{I}{\leftarrow}$ SAUG, E. G. Pringsheim, 'by river Thames', England, 1940 (Pringsheim, 1951). Named as *Pseudanabaena catenata* in CCAP (1464/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971), SAUG (1464/1) (Koch, 1964) and UTEX (425) (Starr, 1964).

ATCC 29541 PCC 7409 $\overset{I}{\leftarrow}$ A. Neilson, *Azolla filiculoides*, Berkeley, California, U.S.A., 1971.

ATCC 29136 PCC 7410. $\overset{I}{\leftarrow}$ A. Neilson, swimming pool, Davis, California, U.S.A., 1972.

ATCC 29127 PCC 7411. $\overset{I}{\leftarrow}$ A. Neilson, sulphide-rich water, Keene Wonder Mine, Death Valley, U.S.A., 1972.

ATCC 29346 PCC 7419. J. B. Waterbury (*Lyngbya* sp.), salt marsh, Woods Hole, Massachusetts, U.S.A., 1974.

ATCC 29128 PCC 7420. J. B. Waterbury (*Microcoleus* sp.), salt marsh, Woods Hole, Massachusetts, U.S.A., 1974.

ATCC 29129 PCC 7427. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

ATCC 29170 PCC 7505. $\overset{I}{\leftarrow}$ A. Neilson, moderate hot spring, Amparai District, Maha Oya, Ceylon, 1973.

Table 15 summarizes structural and physiological properties of the 25 strains placed in the LPP group. The range of mean DNA base composition for 24 strains extends from 42 to 59 mol% GC (Herdman *et al.*, 1979), without any sharp discontinuity. One exceptional strain, PCC 7411, has a DNA base composition of 67 mol% GC.

Seven strains form straight, highly motile trichomes which produce little or no sheath material. In five of them (PCC 7113, 7420, 7105, 7407 and 7411), there are no marked constrictions between adjacent cells of the trichome and some authors would no doubt assign them to the genus *Oscillatoria*, broadly defined. We have excluded them because the cells of the trichome are cylindrical, not disc-shaped. The trichomes of PCC 7408 and 7409 resemble those of *Pseudanabaena*, the cylindrical cells being separated by deep constrictions. PCC 7408 was, in fact, identified as *Pseudanabaena catenata* by its original isolator, E. G. Pringsheim, and is carried impure under this name in the UTEX, CCAP and SAUG collections. Both strains have been excluded from *Pseudanabaena* because they do not produce polar gas vacuoles.

Table 15. *Properties of strains in the LPP group*

Mean DNA base composition (mol % GC)	PCC no.*	LPP group	Cell shape†	Cell width (μm)	Constrictions between cells	Sheath	Polar gas vacuoles	Motility	Facultative photoheterotroph, using: Glucose	Fructose	Ribose	Sucrose	Glycerol	Synthesis of nitrogenase in anaerobiosis	Synthesis of C-PE‡	High C-PE/PC ratio‡ (red colour)	Marine§	Vitamin B_{12} requirement‖
↑	7419	A	d	15–16	–	+	–	(+)	(+)	–	–	–	–	+	–	–	+	–
	7420	B	c	4·5–5·0	–	(+)	–	+	–	–	–	–	–	–	–	–	+	–
	7113	B	c	3·5–4·0	–	(+)	–	+	–	–	–	+	–	+	+	–	–	–
	7406	B	c	1·5–2·0	(+)	(+)	v	(+)	–	–	–	–	–	+	–	–	–	–
	7375	B	c	1·0–1·5	(+)	–	–	–	ND	ND	ND	ND	ND	+	+	+	+	+°
	7376	B	c	1·3–1·8	(+)	–	–	–	–	–	–	–	–	ND	+	+	+	+°
	7404	B	c	0·8–1·3	(+)	(+)	v	(+)	–	–	–	–	–	–	–	–	–	–
	7427	B	c	1·0–1·5	(+)	–	–	–	–	–	–	–	–	+	–	–	–	–
	7408	B	c	2·0–2·5	+	–	–	+	–	–	–	–	–	+	+	–	–	–
42–52	7409	B	c	1·0–1·5	+	–	–	+	–	–	–	–	–	+	+	–	–	–
	6306	B	i	1·8–2·3	(+)	(+)	–	(+)	+	+	+	+	–	+	–	–	–	–
	6402	B	i	1·8–2·3	(+)	(+)	–	(+)	+	+	+	+	–	+	–	–	–	–
	73110	B	i	1·8–2·3	(+)	–	–	(+)	+	+	+	+	–	+	–	–	–	–
	7410	B	i	1·8–2·3	(+)	(+)	–	(+)	+	+	+	+	–	+	–	–	–	–
	7505	B	i	1·8–2·3	(+)	(+)	–	(+)	+	+	+	+	–	+	–	–	–	–
	7004	B	i	1·8–2·3	(+)	(+)	v	(+)	+	+	+	+	–	+	–	–	–	–
	6409	B	i	1·8–2·3	(+)	(+)	–	(+)	+	+	–	–	–	+	+	–	–	–
	6703	B	i	1·8–2·3	(+)	–	–	–	–	–	–	–	–	–	+	–	–	–
↓	7114	B	i	1·5–2·0	(+)	(+)	–	(+)	+	–	–	+	–	–	–	–	–	–
↑	7105	B	c	2·0–2·5	–	(+)	–	+	(+)	(+)	–	(+)	+	–	–	–	+	+ˢ
	7407	B	c	1·5–2·0	(+)	(+)	–	+	+	+	+	–	–	–	–	–	–	–
53–59	7123	B	c	1·0–1·5	(+)	(+)	v	(+)	+	+	–	+	–	–	–	–	–	–
	7104	B	c	1·0–1·5	(+)	(+)	–	(+)	+	+	–	+	–	+	–	–	–	–
↓	7124	B	c	1·0–1·5	(+)	(+)	v	(+)	+	+	–	+	–	+	–	–	–	–
67	7411	B	c	2·5–3·0	–	(+)	–	+	–	–	–	–	–	–	–	–	–	–

ND, Not determined; v, variable; (+), present, but not pronounced.

* The bracketed strains are probably independent isolates of the same species.

† d, Disc-shaped; c, cylindrical; i, isodiametric.

‡ C-PE, C-phycoerythrin; PC, phycocyanin.

§ Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

‖ o, Obligate requirement for vitamin B_{12}; s, vitamin B_{12} stimulates growth, but is not an obligate requirement.

In other strains of the LPP group, motility is less evident and appears to be restricted to hormogonia. Strain PCC 7419 (LPP group A) is distinguished by the width of its trichome (15 to 16 μm), composed of disc-shaped cells not separated by marked constrictions. Reproduction occurs by transcellular trichome breakage. Each trichome is enclosed by a firm sheath, a character that might permit assignment of this strain to the genus *Lyngbya*. In terms of trichome structure, it closely resembles PCC 7515, the reference strain of *Oscillatoria*.

The remaining 17 strains of the LPP group all produce trichomes less than 3 μm wide and composed of cells that are either cylindrical or isodiametric. Some of them (PCC 7406, 7404, 7004, 7123 and 7124) have occasionally been observed to form polar gas vacuoles. However, in contrast to *Pseudanabaena*, gas vacuolation in these strains seems to be variable and is not displayed under all culture conditions. A cluster of freshwater strains (PCC 6306, 6402, 73110, 7410 and 7505) appear to be independent isolates of one species. They are structurally indistinguishable (except for the sheathless strain 73110); they synthesize nitrogenase anaerobically; they grow extremely well with glucose, fructose, sucrose and ribose, of which the latter is rarely used by other cyanobacteria; and the DNA base compositional span is narrow (46 to 50 mol% GC; Herdman *et al.*, 1979). Strains PCC 6306, 6402 and 73110 were received as *Plectonema* spp. and the first two strains display rare false branching in old cultures. This structural property is absent from PCC 73110 since it does not form a sheath. Strain PCC 73110 (as *Plectonema boryanum* 594) has been used for studies on anaerobic nitrogen fixation (Stewart & Lex, 1970), heterotrophy (Raboy *et al.*, 1976) and the development of cyanophage LPP-1 (Padan *et al.*, 1967; Ginzburg *et al.*, 1968).

Stam & Venema (1977) have determined by DNA–DNA hybridization *in vitro* the genetic relatedness of 13 filamentous cyanobacteria known to be hosts for cyanophage LPP-1 (Safferman & Morris, 1963, 1964) and carried by UTEX. All, including PCC 6306 (UTEX 581) and PCC 73110 (UTEX 594), share such a high level of genetic homology that they can be construed as members of one genospecies. UTEX numbers of genetically related strains not carried in the PCC are: 426, 485, 487, 488, 597, 598 and 790 (axenic), and 427, 482, 595 and 596 (impure). Certain of these strains are listed in the UTEX catalogue as three different species of *Plectonema*, as two different species of *Phormidium* and as a *Lyngbya* sp. Four of the strains examined by Stam & Venema (UTEX 485, 488, 594 and 597) had also been included in an earlier DNA–DNA hybridization study by Kelly & Cowie (1971). Kelly & Cowie's results concerning the genetic relatedness of these strains were similar to those obtained by Stam & Venema but, in addition, they found the same high degree of homology with a strain of yet another generic assignment: *Oscillatoria prolifera* (UTEX 1270). No better illustration of the nomenclatural chaos that prevails in this group of cyanobacteria could be provided.

Genera of Section IV

The 36 strains of this section are assigned to six genera, all long recognized by phycologists. However, many of these genera are defined and distinguished (Table 16, Diagram 2) by developmental properties that have no place in the traditional definitions. These properties are difficult to determine on field material, but are readily evident in pure cultures.

In some genera of Section IV, exemplified by *Anabaena* Bory de St Vincent 1822, reproduction occurs by random fragmentation of the vegetative trichomes into shorter cell chains that are structurally indistinguishable from the parental trichomes. If akinetes are formed, they germinate to produce short filaments that are likewise structurally indistinguishable from mature vegetative trichomes. In other genera, exemplified by *Nostoc* Vaucher 1803, reproduction occurs both by random trichome breakage and by the formation of hormogonia. As first described in detail by Harder (1917), hormogonia arise from vegetative cells of the mature trichome under conditions that favour rapid cell division (e.g. transfer to fresh medium). This becomes clearly evident (in medium BG-11_0) in *Nostoc*

species that produce hormogonia composed of cells that are markedly reduced in size. In such strains the small-celled hormogonia are initially located adjacent to one heterocyst or between two heterocysts that differentiated from the vegetative cells in the mature trichome, and consequently share their larger dimensions (Figs 41, 45). Subsequently, the heterocysts degenerate and the (heterocyst-less) hormogonia are released.

The distinction between *Nostoc* and *Anabaena* has been traditionally based on the character of colony formation; however, the gelatinous colonies typical of *Nostoc* spp. growing under natural conditions are rarely formed in culture. In their descriptions of *Nostoc*, Bornet & Flahaut (1888*b*) and Geitler (1932) imply that strains of this genus undergo a developmental cycle that is absent from *Anabaena* species. Furthermore, the developmental stages of numerous *Nostoc* species have been described in detail (Thuret, 1844; Sauvageau, 1897; Harder, 1917; Lazaroff & Vishniac, 1961; Mollenhauer, 1970). Nevertheless, the presence or absence of a developmental cycle has never been proposed as a discriminatory character. Its taxonomic utility was first recognized by Kantz & Bold (1969) as the outcome of a comparative study in culture of many strains identified as *Nostoc* or *Anabaena* species. They observed that in typical *Anabaena* strains all trichomes are motile: in typical *Nostoc* strains, on the other hand, motility is restricted to hormogonia, the cells of which are often smaller than those of the vegetative trichomes. Present observations confirm the validity of this distinction.

A generic differentiation based essentially on motility, however, does not permit the placement of immotile strains, not uncommon in the *Nostoc–Anabaena* group. In such cases, smaller cell size, gas vacuolation and the absence of heterocysts can serve as additional properties that distinguish hormogonia from mature trichomes. On this basis, strains that produce non-heterocystous immotile hormogonia, either composed of smaller cells than the mature trichomes (PCC 6314, 7524) or containing gas vacuoles (PCC 6719), have been assigned to *Nostoc*. Although some *Nostoc* strains are said to divide in a plane parallel to the long axis of the trichome in the course of development (Bornet & Flahaut, 1888*b*; Harder, 1917; Geitler, 1932; Lazaroff & Vishniac, 1961), we have never observed a change in the plane of division in any of the strains included in *Nostoc*. This observation is confirmed by the fact that none of the *Nostoc* strains forms lateral heterocysts.

As shown in Table 16, the other genera of Section IV are also distinguishable by hormogonium formation or its absence. Like *Anabaena*, *Cylindrospermum* Kützing 1843 and *Nodularia* Mertens 1822 do not produce hormogonia. These two genera are readily distinguished from *Anabaena* by the traditional discriminatory properties, always displayed in culture. The vegetative cells in the trichome of *Nodularia* are disc-shaped, not spherical or cylindrical. The trichomes of *Cylindrospermum* bear a terminal heterocyst at each end and form subterminal akinetes as growth approaches the stationary phase.

Members of the genus *Scytonema* Agardh 1824 and *Calothrix* Agardh 1824 share with *Nostoc* the ability to form differentiated hormogonia, but their subsequent development diverges from that of *Nostoc*. In all three genera, the hormogonia are initially devoid of heterocysts. As shown by Kantz & Bold (1969) and confirmed here, the developing hormogonium of *Nostoc* soon differentiates two heterocysts, both usually terminal (Figs 39, 43, 53, 54). Subsequent growth and elongation of the hormogonium gives rise to mature trichomes in which intercalary heterocysts may also be produced. In *Scytonema* and *Calothrix* only one heterocyst, invariably terminal, is formed in the developing hormogonium (Figs 60, 61, 66, 67).

In *Scytonema*, growth and elongation of the developing hormogonium eventually leads to the differentiation of trichomes of even width, in which the heterocysts are predominantly intercalary. In *Calothrix*, the juvenile hormogonia are composed of small cells of even width (Figs 64 to 67). The basal–apical tapering characteristic of this genus is determined by the location of the first terminal heterocyst produced, which is invariably a small one since its development begins at the juvenile stage. However, as development proceeds, the subterminal vegetative cell itself differentiates into a terminal heterocyst, the dimensions of

Table 16. *Section IV: Filamentous heterocystous cyanobacteria that divide in only one plane*

Reproduction by random trichome breakage, and (in some) by germination of akinetes, to produce trichomes indistinguishable from the mature vegetative trichomes	Heterocysts are intercalary or terminal; position of akinetes (if produced) is variable	Vegetative cells are spherical, ovoid or cylindrical *Anabaena*
		Vegetative cells are disc-shaped *Nodularia*
	Heterocysts are exclusively terminal and are formed at both ends of the trichome; akinetes are always adjacent to heterocysts	Vegetative cells are isodiametric or cylindrical *Cylindrospermum*
Reproduction as above, and also by formation of hormogonia distinguishable from mature trichomes by the absence of heterocysts and by one or more of the following characters: rapid gliding motility, smaller cell size, cell shape and gas vacuolation	Hormogonia give rise to young filaments that bear a terminal heterocyst at both ends of the cellular chain	Vegetative cells are spherical, ovoid or cylindrical; akinetes (if produced) are not initiated adjacent to heterocysts and are often formed in chains *Nostoc*
	Hormogonia give rise to young filaments that bear a terminal heterocyst at only one end of the cellular chain	Mature trichome is composed of cells of even width; heterocysts are predominantly intercalary; vegetative cells are disc-shaped, isodiametric or cylindrical *Scytonema*
		Mature trichome tapers from base, which bears a terminal heterocyst, to apex; vegetative cells are disc-shaped, isodiametric or cylindrical *Calothrix*

which will depend on the degree of tapering attained at the time of its differentiation. In some strains, a whole series of terminal heterocysts may remain attached to the basal end of the developing trichome, thus demonstrating nicely the course of developmental events (Figs 62, 66). Any break in the filament [e.g. by necridium formation (Lamont, 1969)] may lead to the development of a new terminal heterocyst on one or both sides of the break (Fig. 62). Hormogonia are always formed from the apical end of the trichome. The size of the cells composing hormogonia is constant for any given strain, whereas the size of cells in maturing trichomes increases with age.

From the summary account of the development of *Calothrix* given above, it follows that cell dimensions of these organisms in the mature (tapering) state are wholly without taxonomic significance: the only reliable estimate of cell size is that determined on the juvenile hormogonium.

The genera *Rivularia* (Roth 1802) Agardh 1812 and *Gloeotrichia* Agardh 1842 are traditionally distinguished from *Calothrix* Agardh 1824 by their development under natural conditions as gelatinous, usually hemispherical, colonies (composed of non-akinete forming and akinete producing tapered trichomes, respectively). Strains PCC 7111, 7116 and 7204 were isolated from natural colonies identified as *Rivularia* spp. but do not produce gelatinous colonies in culture. They have accordingly become indistinguishable from *Calothrix* spp. and are included in this genus.

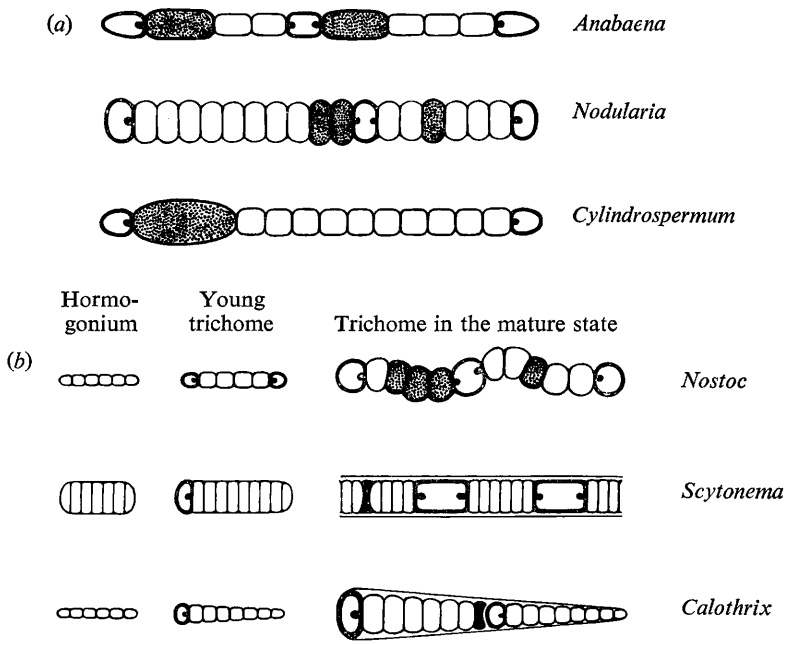


Diagram 2. Schematic presentation of the genera assigned to Section IV: (*a*) without developmental cycle; (*b*) with developmental cycle. Heavy walled cells with polar granules represent heterocysts; heavy walled cells that are dotted represent akinetes; thin lines surrounding trichomes designate sheath material.

Genera based on the occurrence of coiled and multiple trichomes enclosed by a common sheath (e.g. *Dichothrix* Zanardini 1858 and *Polythrix* Zanardini 1872) have also been ignored, since our observations suggest that this phenomenon is a crowding effect of rapidly growing trichomes within a firm sheath and therefore of no taxonomic value (Fig. 63).

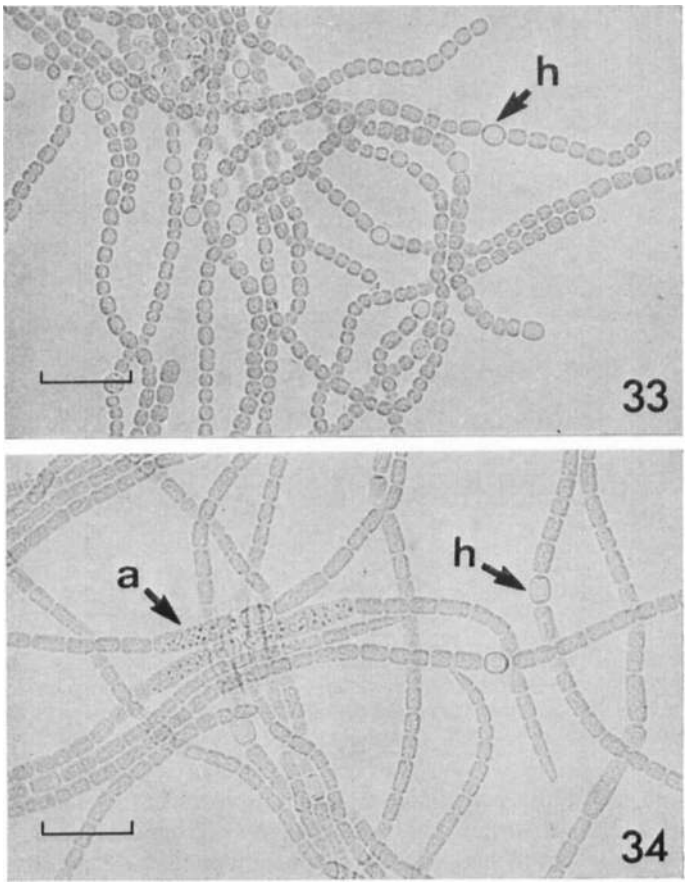
The mean DNA base composition characteristic of all heterocystous cyanobacteria is narrow: values for the 36 strains of Section IV range from 38 to 47 mol% GC (Herdman *et al.*, 1979). This character is of little value for making either intergeneric or intrageneric distinctions.

Genus Anabaena Bory de St Vincent 1822

Examples of this genus (PCC 7120 and 7122) are shown in Figs 33 and 34. Two strains (PCC 7119 and 7120) were originally described as *Nostoc muscorum* (Adolph & Haselkorn, 1971) but do not possess the character of the genus *Nostoc* as defined here. Strain PCC 7118, originally identified as *Anabaena variabilis* (Kratz & Myers, 1955), has been incapable of fixing nitrogen or forming heterocysts in culture for over 20 years (Kratz & Myers, 1955; Leach & Carr, 1971). Its identity as an *Anabaena* sp. was recently confirmed by the isolation of a spontaneous heterocystous mutant, capable of aerobic nitrogen fixation (Rippka & Stanier, 1978). The strain histories are as follows:

ATCC 29211 PCC 6309 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ M. Shilo ← UTEX, source unknown. Named as *Anabaena variabilis* Kütz. in UTEX (377) (Starr, 1964) and in CCAP (1403/4b) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971); named as *Anabaena cylindrica* Lemm. in SAUG (1403/4b) (Pringsheim, 1951).

ATCC 27898 PCC 6411 (Kenyon *et al.*, 1972). M. M. Allen, pond water, California, U.S.A., 1964. Named as *Nostoc* sp. in UTEX (1597) (Starr, 1971).



Figs 33 and 34. *Anabaena* PCC 7120 and PCC 7122, respectively: h, heterocysts; a, akinetes. Both bright field; bar markers represent 20 μm.

ATCC 29208 PCC 7108. J. B. Waterbury, intertidal zone, Moss Beach, California, U.S.A. 1970.

ATCC 27892 PCC 7118. $\overset{P}{\leftarrow}$ N. G. Carr $\overset{P}{\leftarrow}$ J. Myers (*Anabaena variabilis* Kütz.) $\leftarrow$ R. C. Hecker (*Cylindrospermum* sp.), source unknown (Kratz & Myers, 1955).

ATCC 29151 PCC 7119. $\overset{P}{\leftarrow}$ R. Haselkorn $\overset{P}{\leftarrow}$ University of Wisconsin (*Nostoc muscorum* UW), source unknown (Adolph & Haselkorn, 1971).

ATCC 27893 PCC 7120. $\overset{P}{\leftarrow}$ R. Haselkorn $\overset{P}{\leftarrow}$ Iowa State University (*Nostoc muscorum* ISU), source unknown (Adolph & Haselkorn, 1971).

ATCC 27899 PCC 7122. $\overset{P}{\leftarrow}$ D. Arnon $\overset{P}{\leftarrow}$ UTEX $\overset{P}{\leftarrow}$ G. E. Fogg $\overset{P}{\leftarrow}$ S. P. Chu, pond water, Cambridge, England, 1939 (Fogg, 1942). Named as *Anabaena cylindrica* Lemm. in CCAP (1403/2a) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971), SAUG (1403/2) (Pringsheim, 1951), UTEX (629) (Starr, 1964).

All strains assigned to *Anabaena* are obligate autotrophs. The range of mean DNA base composition is 38 to 44 mol% GC (Herdman *et al.*, 1979). As shown in Table 17, they are divisible into two sub-groups, each of which shares many common properties. The bracketed strains are almost certainly independent isolates of a single species. In strains that form akinetes, these always develop from vegetative cells adjacent to a heterocyst.

Reference strain: PCC 7122

Table 17. *Properties of Anabaena strains*

PCC no.*	Motility	Conical end cells	Akinetes produced	Lysed by phage N-1†	Synthesis of PEC‡	Grows as even suspension in liquid culture
6411	−	−	−	+	+	+
7118	−	−	−	+	+	+
7119	−	−	−	+	+	+
7120	−	−	−	+	+	+
6309	+	+	+	−	+	−
7122	+	+	+	−	+	−
7108	+	+	+	−	+	−

All strains are obligate photoautotrophs.

* Bracketed strains are probably independent isolates of the same species.
† Spot test on a lysate produced by the host strain *Anabaena* PCC 7120.
‡ PEC, Phycoerythrocyanin.

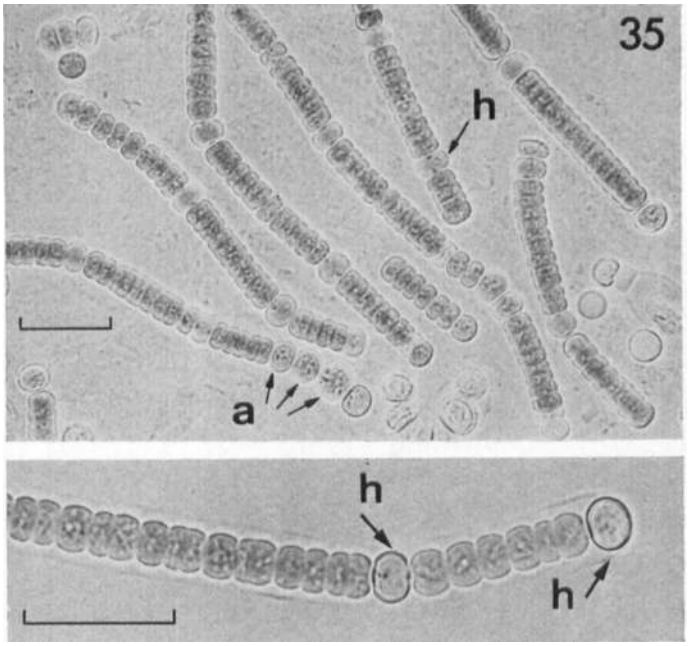


Fig. 35. *Nodularia* PCC 73104: h, heterocysts; a, akinetes. Bright field; bar markers represent 20 μm.

Genus Nodularia Mertens 1822

Only one strain of this genus is represented in the PCC collection; it is illustrated in Fig. 35.

ATCC 29167 PCC 73104. $\overset{I}{\leftarrow}$ R. N. Nordin, highly alkaline pond, British Columbia, Canada.

This strain is a facultative heterotroph which grows with glucose, fructose and, more poorly, with sucrose. The mean DNA base composition is 40·5 mol% GC (Herdman *et al.*, 1979). Heterocysts are predominantly intercalary; akinetes are formed, often in chains, either adjacent to heterocysts or distant from them. No phycoerythrinoid pigment is formed. Although this strain can synthesize nitrogenase aerobically, aerobic growth at the expense of N_2 is very slow.

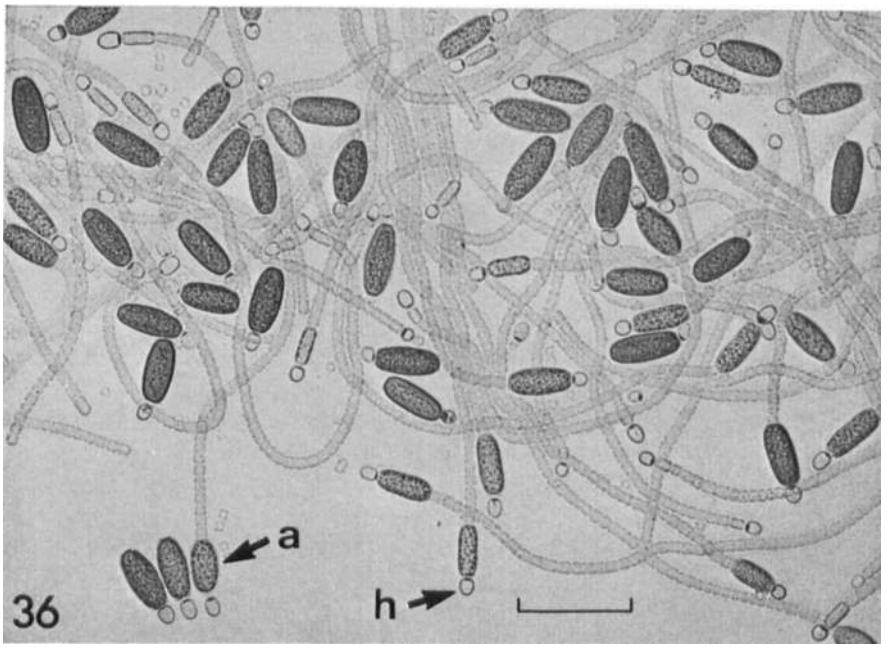
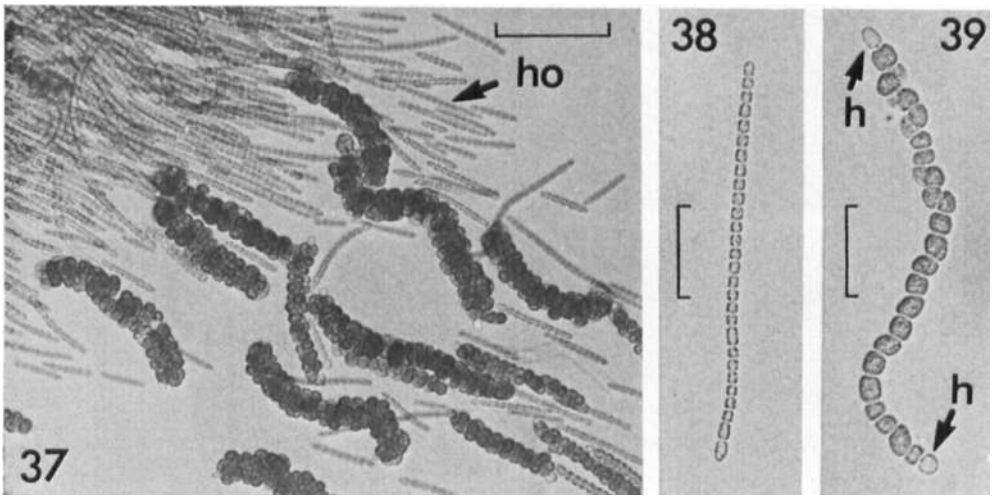


Fig. 36. *Cylindrospermum* PCC 73101: h, heterocysts; a, akinetes. Bright field; bar marker represents 50 μm.



Figs 37 to 39. *Nostoc* PCC 73102. Fig. 37 shows coiled vegetative filaments together with hormogonia (ho). Fig. 38 shows an enlarged view of a hormogonium, and Fig. 39 shows a mature, but still uncoiled vegetative trichome, with terminal heterocysts (h). All bright field; bar markers represent 50 μm in Fig. 37 and 20 μm in Figs 38 and 39.

Genus Cylindrospermum Kützing 1843

One of the three strains in this genus (PCC 73101) is shown in Fig. 36. The histories of the strains are as follows:

ATCC 29535 PCC 73101. $\overset{I}{\leftarrow}$ SAUG *Cylindrospermum stagnale*; source unknown.

ATCC 29204 PCC 7417. $\overset{I}{\leftarrow}$ A. Neilson, soil, greenhouse, Stockholm, Sweden, 1972.

ATCC 33001 PCC 7604. $\overset{I}{\leftarrow}$ M. Wilcox [*Cylindrospermum maius* (CCAP 415/2) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971)]←J. Komarek.

The three strains are similar in structure. The range of DNA base composition is 42 to 47 mol% GC (Herdman *et al.*, 1979). Strains PCC 73101 and 7604 are obligate autotrophs whereas 7417 is a facultative heterotroph that grows on fructose and sucrose. All produce phycoerythrocyanin. **Reference strain: PCC 7417**

Genus Nostoc Vaucher 1803

The diversity of the strains comprising this genus and some aspects of their developmental processes are illustrated in Figs 37 to 58. Several strains included in this genus were received under other generic designations: PCC 6302 and 6310 as *Anabaena* spp., 6720 as *Anabaenopsis* and 7413 as *Cylindrospermum*. Partial descriptions of several strains, designated as '*Anabaena*-type', are given in Kenyon *et al.* (1972). The strain histories are as follows:

ATCC 27897 PCC 6302 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ M. B. Allen, source unknown. Named as *Anabaena* sp. in UTEX (1551) (Starr, 1966).

ATCC 27896 PCC 6310 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ M. Shilo (*Anabaena spiroides*), fish pond, Northern Galilee, Israel, 1963. In UTEX (1552) (Starr, 1966).

ATCC 27904 PCC 6314 (Kenyon *et al.*, 1972). M. M. Allen, crude algal material, 1963. Named as *Nostoc muscorum* in UTEX (1545) (Starr, 1966).

ATCC 29131 PCC 6705 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ G. Cohen-Bazire, Botanical Garden, University of California, Berkeley, U.S.A., 1967.

ATCC 29105 PCC 6719 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ D. Branton (*Nostoc muscorum* UC142), soil water culture, microgarden collection, University of California, Berkeley, U.S.A. (Waaland & Branton, 1969; Waaland *et al.*, 1970).

ATCC 27895 PCC 6720 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ R. A. Lewin $\overset{P}{\leftarrow}$ A. Watanabe (*Anabaenopsis circularis*), soil sample, Sumatra, 1950 (Watanabe, 1959). In CCAP (1402/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 29150 PCC 7107. A. Neilson, shallow pond, Point Reyes Peninsula, California, U.S.A., 1970.

ATCC 29133 PCC 73102. R. Rippka, root section, *Macrozamia* sp., Australia, 1973.

ATCC 29106 PCC 7413. $\overset{I}{\leftarrow}$ G. E. Fogg (*Cylindrospermum licheniforme*), surface garden soil, St Albans, Hertfordshire, England, 1950 (purified by ultraviolet radiation).

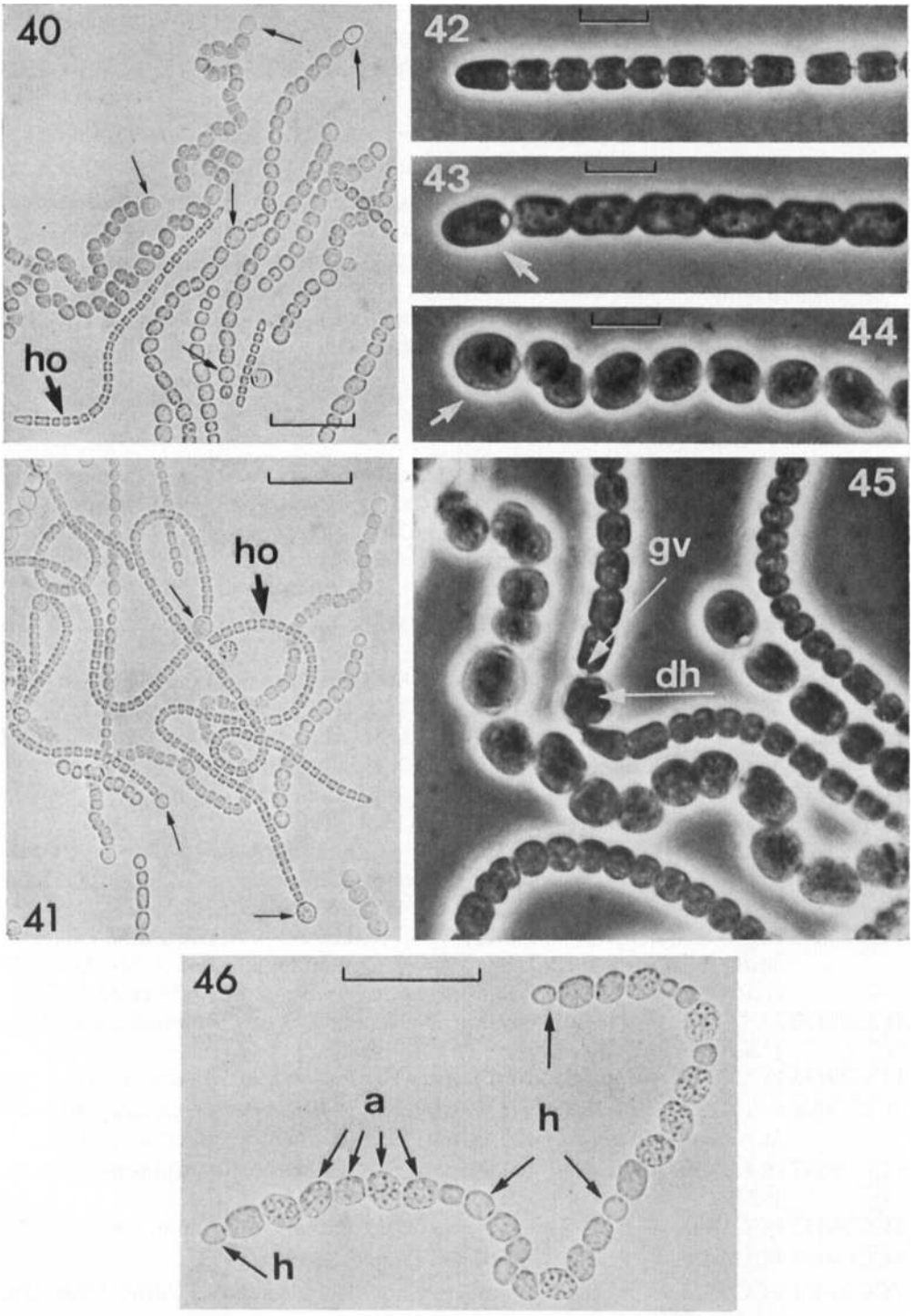
ATCC 29107 PCC 7416. A. Neilson, shallow pool, San Andreas valley, California, U.S.A., 1972.

ATCC 29132 PCC 7422. $\overset{I}{\leftarrow}$ A. Neilson, root section, *Cycas* sp., Stockholm, Sweden, 1972.

ATCC 29168 PCC 7423. $\overset{I}{\leftarrow}$ P. Roger, dried soil sample, Senegal, 1973.

ATCC 29411 PCC 7524. $\overset{I}{\leftarrow}$ A. Neilson, moderate hot spring, Amparai District, Maha Oya, Ceylon, 1973.

The range of mean DNA base composition for the 13 *Nostoc* strains is very narrow: 39 to 45 mol% GC (Herdman *et al.*, 1979). In phenotypic respects (Table 18) the strains appear highly diverse: only PCC 7107 and 7416 are sufficiently similar to suggest that they are independent isolates of a single species. Most strains produce akinetes, often formed in


40
ho
42
43
44
ho
41
45
gv
dh
46
a
h
h

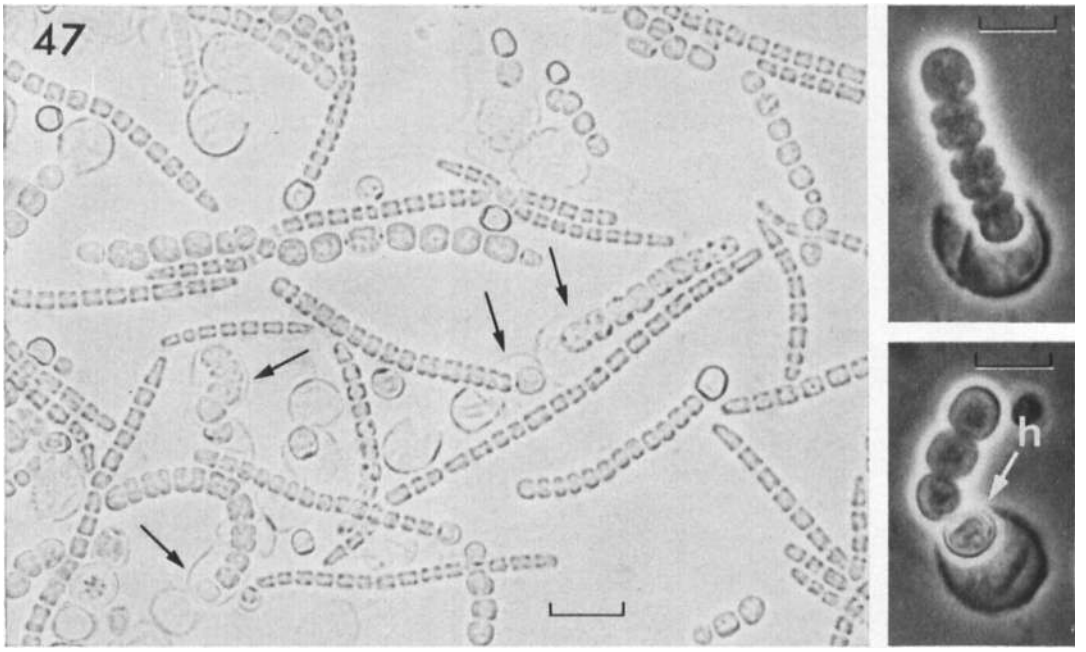
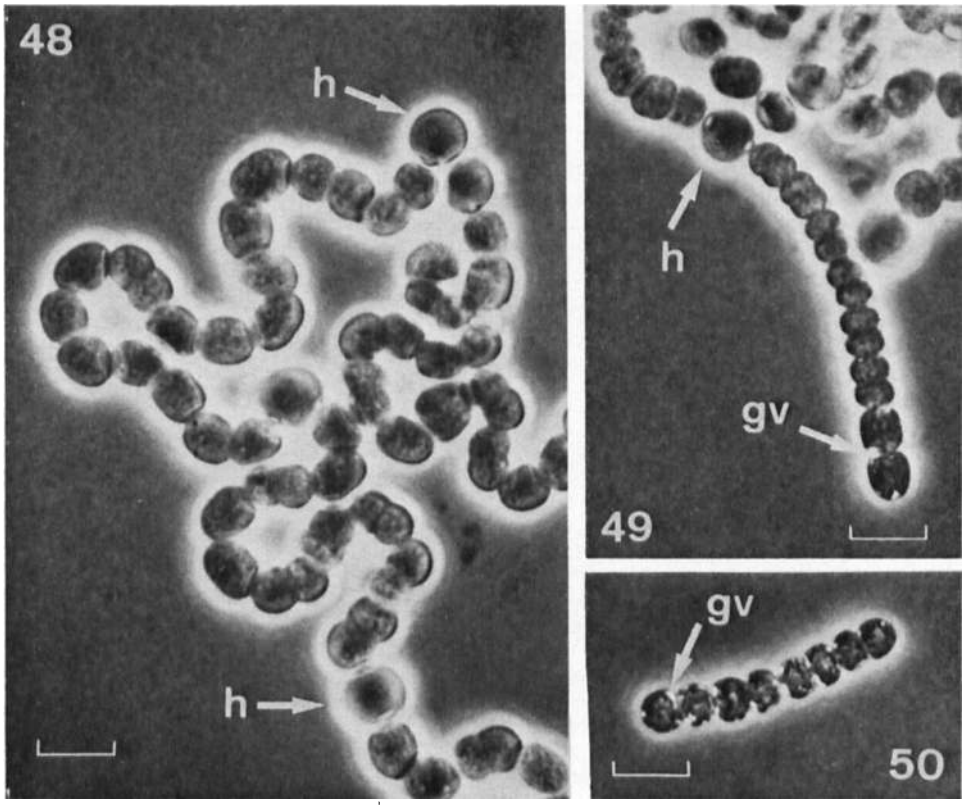


Fig. 47. *Nostoc* PCC 6720. Germination of akinetes (arrows). Note that germination does not give rise to a differentiated hormogonium (in this strain characterized by polar gas vacuoles, Fig. 42) but to a short trichome composed of cells that differ little from the cells in a vegetative trichome. Heterocysts (h) may be formed at a relatively early stage of akinete germination. Bright field (insets, phase contrast); bar marker represents 10 μm (insets, 5 μm).

chains. Akinete development is never initiated adjacent to heterocysts, as it is in the akinete-producing strains of *Anabaena* carried in the PCC. The majority of strains are photoheterotrophs. Most strains produce either C-phycoerythrin or phycoerythrocyanin. PCC 6302, 6314 and 7524 have lost the ability to fix nitrogen aerobically as a result of prolonged cultivation in medium BG-11. Dark growth and chromatic light have been reported to influence the developmental cycle of *Nostoc muscorum* (Lazaroff, 1966) and *Nostoc commune* 584 (Robinson & Miller, 1970). A systematic survey of these parameters on *Nostoc* strains in the PCC collection is in progress.

Reference strain: PCC 73102

Figs 40 to 46. *Nostoc* PCC 6720. Fig. 40 shows mature filaments and hormogonia (ho); arrows indicate heterocysts. Bright field. Fig. 41 shows the formation of hormogonia (ho) next to heterocysts (arrows) that differentiated from the vegetative cells in the mature trichome and consequently share their larger dimensions. Bright field. Figs 42 to 44 show the successive developmental stages of a freshly released hormogonium to a mature vegetative trichome. Note the resemblance of the hormogonium (Fig. 42) to a *Pseudanabaena* species (intercellular constrictions, polar gas vacuoles) as well as the cellular enlargement, loss of gas vacuolation and the formation of heterocysts (arrows) that accompany hormogonial development (Figs 43, 44). Phase contrast. Fig. 45 shows a degenerating intercalary heterocyst (dh) from which a rapidly dividing, newly formed hormogonium will subsequently detach; gas vacuoles (gv) are already present in the cells adjacent to the heterocyst. Phase contrast. Fig. 46 shows a mature trichome with rows of akinetes (a). As typical for *Nostoc* (Bornet & Flahaut, 1888*b*), akinete differentiation is initiated midway between two heterocysts (h), never adjacent to a heterocyst. Successive akinete differentiation on both sides of the first akinete produced may eventually also lead to akinetes that are adjacent to heterocysts. Bright field. Bar markers represent 20 μm in Figs 40, 41 and 46 and 5 μm in Figs 42 to 45.



Figs 48 to 50. *Nostoc* PCC 6705, a strain that produces hormogonia containing irregularly distributed gas vacuoles (gv). Fig. 48 shows mature trichomes with terminal and intercalary heterocysts (h). Fig. 49 shows the manner of hormogonium formation immediately prior to its release. Fig. 50 shows a short gas vacuolated hormogonium. All phase contrast; bar markers represent 5 μm.

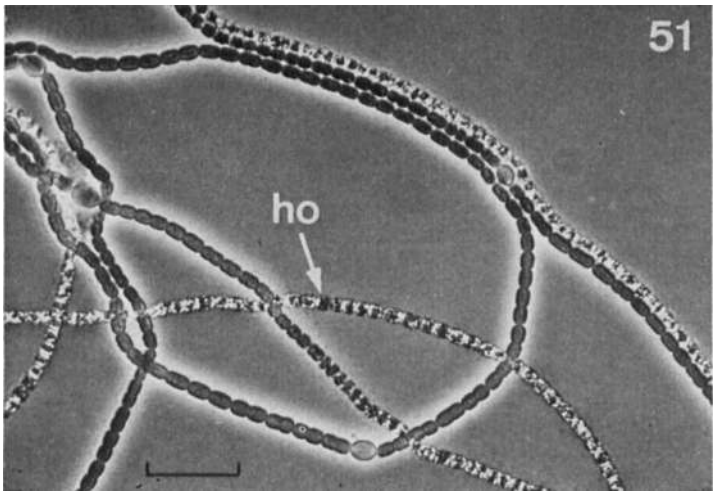
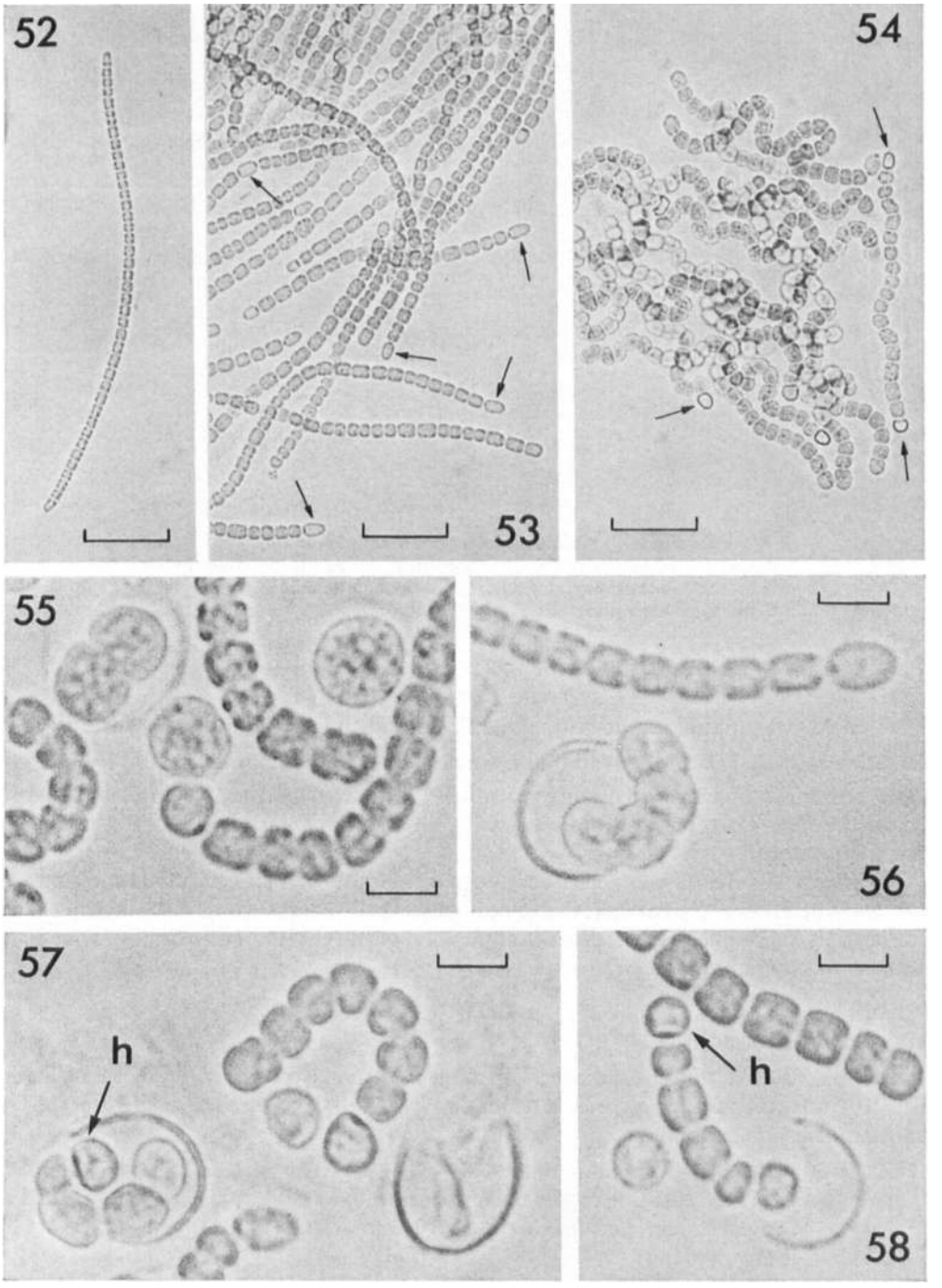


Fig. 51. *Nostoc* PCC 6719 (strain of Waaland & Branton, 1969), showing the long, gas vacuolated hormogonia (ho) that are characteristic of this strain. Phase contrast; bar marker represents 20 μm.



Figs 52 to 58. *Nostoc* PCC 7107. Figs 52 to 54 show the development of a hormogonium to a mature vegetative trichome; arrows indicate heterocysts. Figs 55 to 58 show stages in the germination of akinetes: two-celled stage (Fig. 55); four-celled stage (Fig. 56); five-celled stage, including a heterocyst (h) (Fig. 57); six-celled stage, including a heterocyst (h) (Fig. 58). All bright field; bar markers represent 20 μm in Figs 52 to 54 and 5 μm in Figs 55 to 58.

Table 18. *Properties of Nostoc strains*

PCC no.*	Permanently immotile	Hormogonia gas vacuolated†	Akinetes produced	Trichomes break up in old cultures into isolated cells	Facultative photoheterotroph, using: Glucose	Fructose	Ribose	Sucrose	Synthesis of:‡ C-PE	PEC
6302	−	−	+	−	+	+	+	+	+	−
6310	−	−	+	−	+	+	(+)	+	+	−
6314	+	−	+	+	−	−	−	+[v]	−	+
6705	−	+[1]	+	−	−	−	−	+[v]	−	+
6719	+	+[1]	−	−	−	−	−	−	−	+
6720	−	+[2]	+	−	+	+	−	−	−	+
7107	−	−	+	−	−	+	−	−	−	+
7416	−	−	+	−	−	+	−	−	−	+
73102	−	+[2]	+	−	+	+	+	(+)	+	−
7413	−	−	−	−	−	−	−	−	−	−
7422	−	−	−	−	−	−	−	−	+	−
7423	+	−	+	−	−	+	−	−	−	−
7524	+	−	+	+	−	−	−	+	−	+

(+), Weak growth; +[v], variable, probably reflecting mutation.
* Bracketed strains are probably independent isolates of the same species.
† 1, Gas vacuoles throughout cells; 2, gas vacuoles confined to cell poles.
‡ C-PE, C-phycoerythrin; PEC, phycoerythrocyanin.

Genus Scytonema Agardh 1824

The one representative is shown in Figs 59 and 60. It has the following history:

ATCC 29171 PCC 7110. J. B. Waterbury, Crystal Cave (limestone), Bermuda, 1971.

This strain is a facultative heterotroph which grows with glucose, fructose and sucrose. The mean DNA base composition is 44 mol% GC (Herdman *et al.*, 1979). Phycoerythrocyanin is produced.

The mature filaments, characterized by frequent false branching, produce cylindrical intercalary heterocysts; no akinetes have been observed. In hormogonia, the single terminal heterocyst is hemispherical. A distinctive feature of PCC 7110, best displayed on plate cultures, is its aerial growth.

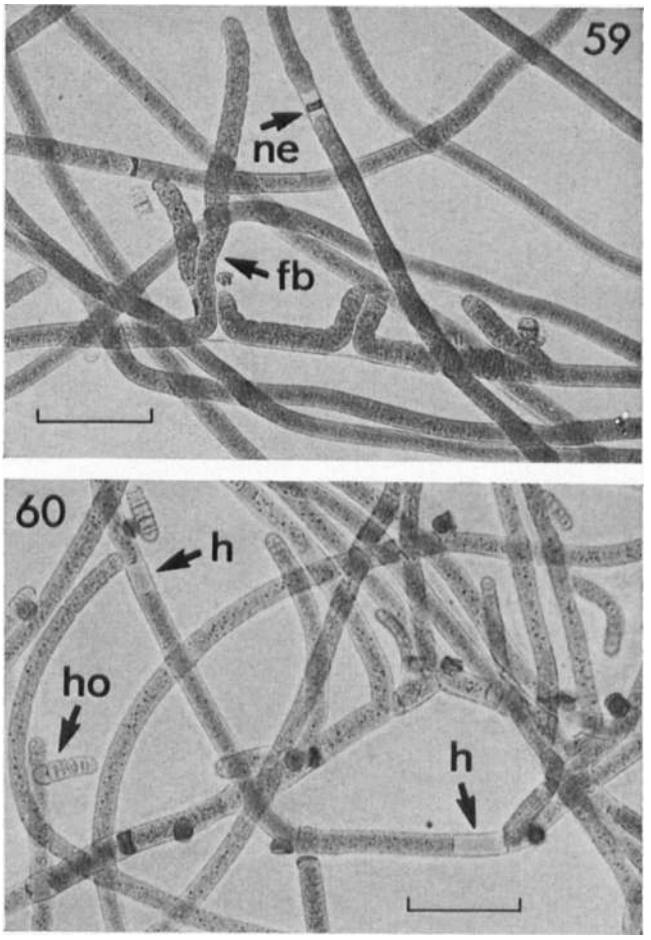
Genus Calothrix Agardh 1824

Structural features of some members of this genus are illustrated in Figs 61 to 69. Strain PCC 7101 was received as *Tolypothrix tenuis* and PCC 7103 as *Nodularia sphaerocarpa*. The strain histories are as follows:

ATCC 29156 PCC 6303 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ M. B. Allen ← G. C. Gerloff (*Calothrix parietina* 1018), lake water, Wisconsin, 1948 (Gerloff *et al.*, 1950). Named as *Calothrix parietina* in CCAP (1410/3), SAUG (1410/3) and UTEX (484) (Starr, 1964).

ATCC 27914 PCC 7101 (Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ SAUG (1482/3) (Koch, 1964) $\overset{P}{\leftarrow}$ A. Watanabe (*Tolypothrix tenuis* Kütz.), soil sample, Borneo, 1950 (Watanabe, 1959). In CCAP (1482/3a and 1482/3b) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

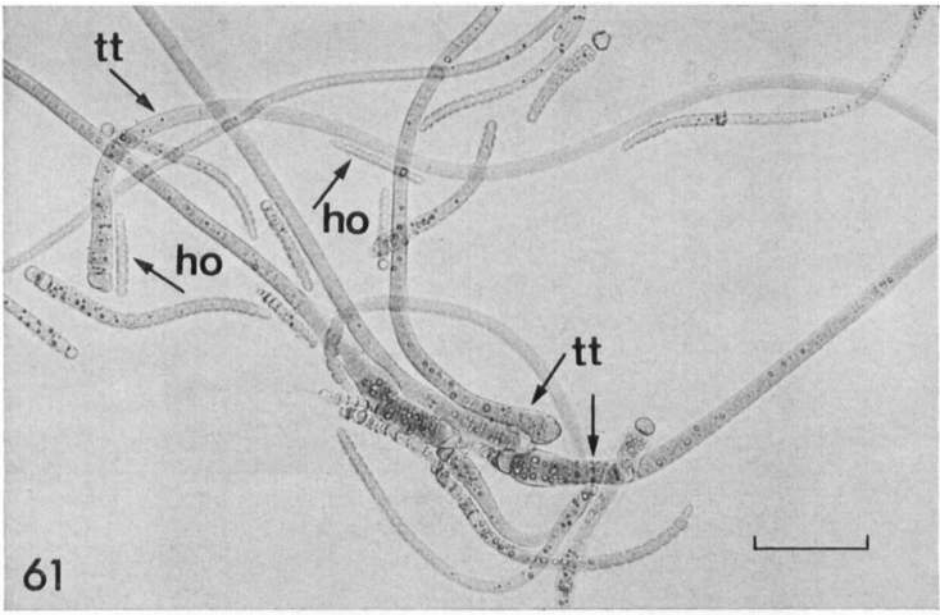
ATCC 27901 PCC 7102 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ SAUG $\overset{I}{\leftarrow}$ G. H. Schwabe (*Calothrix desertica*), fine desert sand, near La Pertada, Antofagasta, Chile, 1958 (Schwabe, 1960).

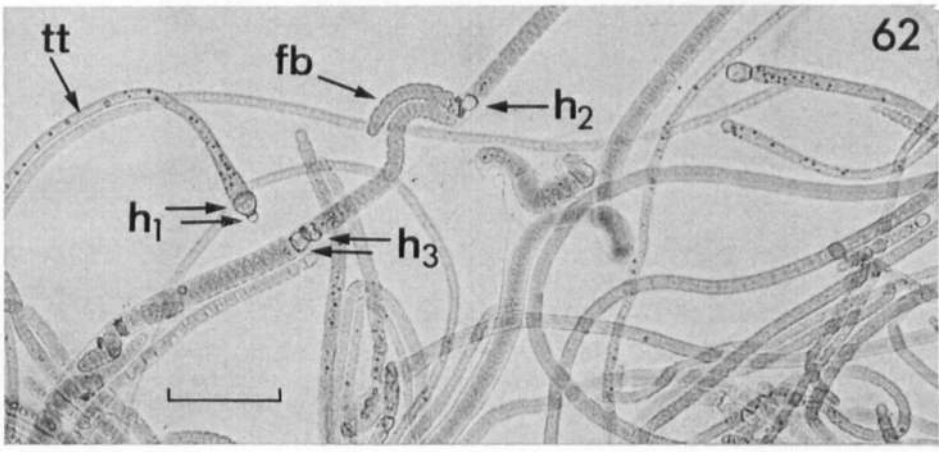


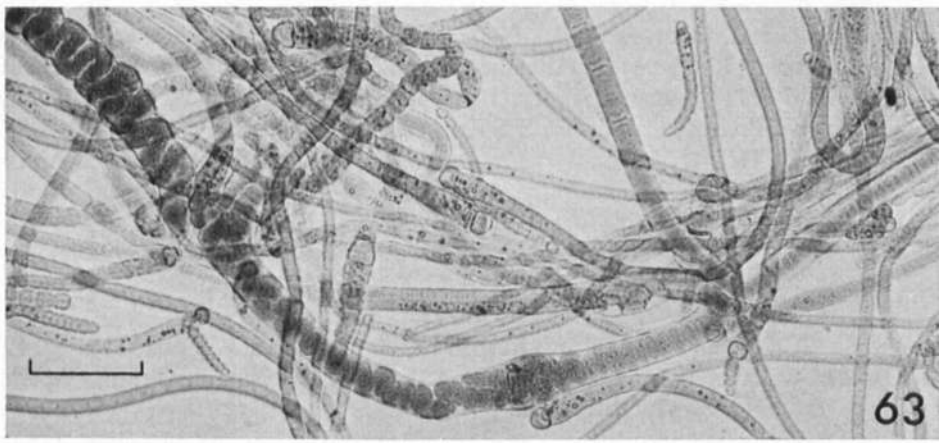
Figs 59 and 60. *Scytonema* PCC 7110, grown in BG-11 (Fig. 59) and BG-11_0 (Fig. 60), showing necridia (ne) and false branching (fb) (Fig. 59) and mature trichomes with intercalary heterocysts (h) and a short hormogonium (ho) bearing a terminal heterocyst (Fig. 60). Both bright field; bar markers represent 50 μm.

ATCC 27905 PCC 7103 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ SAUG (1466/1) *Nodularia sphaerocarpa* (Koch, 1964) ← M. B. Allen, source unknown. In UTEX (583) (Starr, 1964).
ATCC 29199 PCC 7111. J. B. Waterbury, hemispherical macroscopic colony, intertidal zone, Bodega, California, U.S.A., 1970.
ATCC 29111 PCC 7116. A. Neilson $\overset{I}{\leftarrow}$ R. A. Lewin, La Paz, Baja California, U.S.A., 1968.
ATCC 29190 PCC 7204. J. B. Waterbury, hemispherical macroscopic colony, intertidal zone, Bodega, California, U.S.A., 1970.
ATCC 29157 PCC 7415. A. Neilson, soil, greenhouse, Stockholm, Sweden, 1972.
ATCC 29345 PCC 7426. J. B. Waterbury $\overset{I}{\leftarrow}$ G. Guglielmi (*Isactis* sp.), flattened thallus on rock, intertidal zone, Banyuls-sur-Mer, France, 1974.
ATCC 29158 PCC 7504. $\overset{I}{\leftarrow}$ A. Neilson, fresh water aquarium, Stockholm, Sweden, 1972.
ATCC 29112 PCC 7507. R. Rippka, sphagnum bog, near Kastanienbaum, Vierwaldstättersee, Switzerland, 1972.

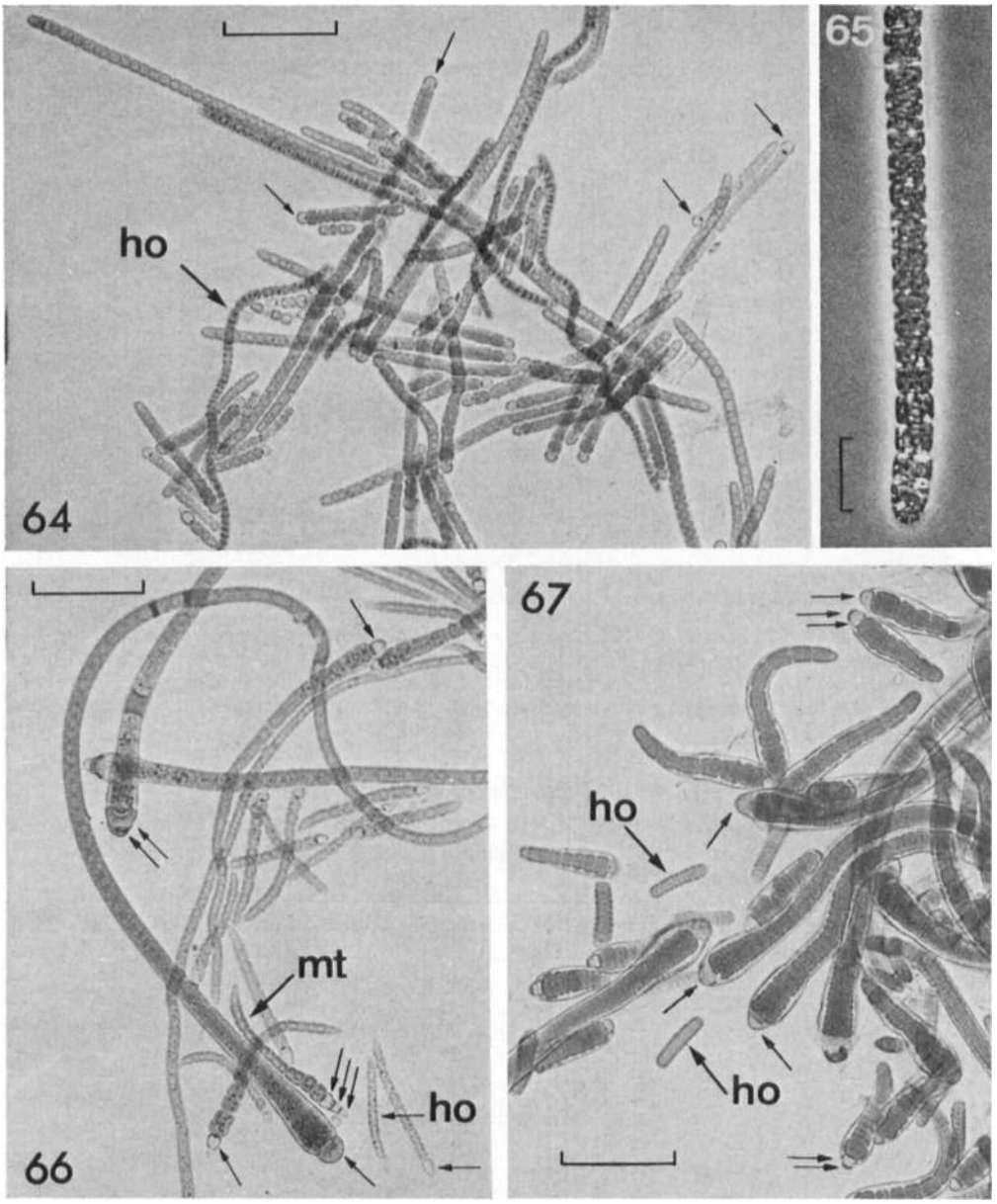
The range of mean DNA base composition is 40 to 44 mol% GC (Herdman *et al.*, 1979). Other strain properties are shown in Table 19. Hair formation, nominally typical for many *Calothrix* species (Bourrelly, 1970; Geitler, 1932), has recently been found to be dependent







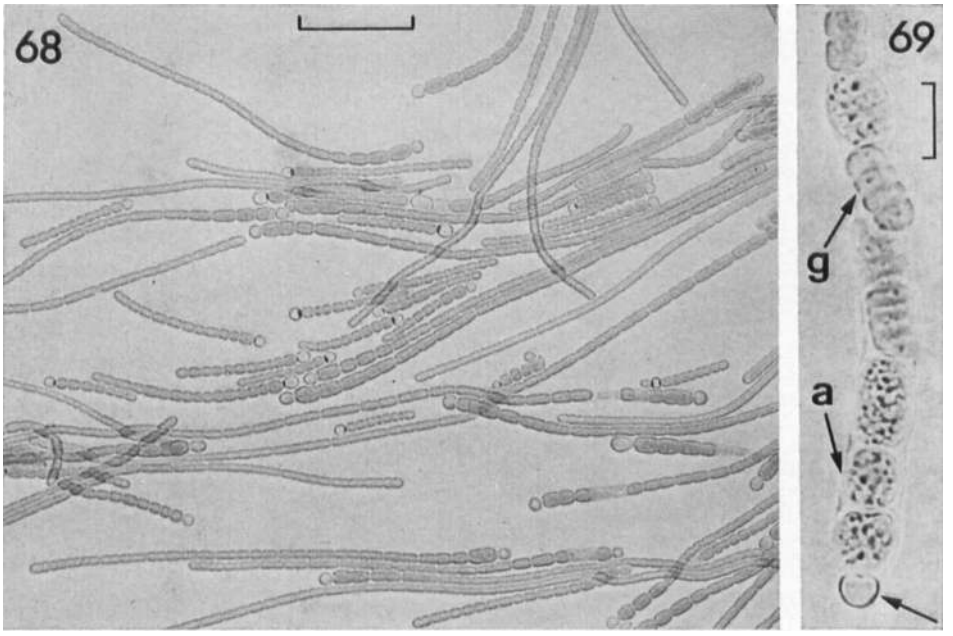
Figs 61 to 63. *Calothrix* PCC 7102. Fig. 61 shows the characteristic tapering of mature trichomes (tt) bearing basal heterocysts, aheterocystous hormogonia (ho) composed of cells of even width, and various stages of filament development. Fig. 62 shows a tapering trichome (tt) with two basal heterocysts (h_1) of markedly differing size, demonstrating the increase in cell width during the course of filament development. Also visible in this field are: false branching (fb) at the level of a terminal heterocyst (h_2) within the trichome; and two terminal heterocysts (h_3), which have differentiated on adjacent sides of a dead cell (necridium). Fig. 63 shows the coiling within a tightly enclosing sheath often found in *Calothrix* 7102, nominally distinctive for the genera *Dichothrix* and *Polythrix*. All bright field; bar markers represent 50 μm.



Figs 64 and 65. *Calothrix* PCC 7101 ('*Tolypothrix tenuis*', Watanabe, 1959). Fig. 64 shows the low degree of tapering of the mature trichomes, the exclusively terminal heterocysts (arrows) and the long gas-vacuolated hormogonia (ho). Bright field. Fig. 65 is an enlargement of a hormogonium, showing the irregularly distributed gas vacuoles typical of this strain. Phase contrast. Bar markers represent 50 μm in Fig. 64 and 10 μm in Fig. 65.

Fig. 66. *Calothrix* PCC 7103. Note the high degree of tapering of this strain, the aheterocystous hormogonia (ho) and the terminal heterocysts (arrows). One maturing trichome (mt) bears three terminal heterocysts of different sizes, demonstrating the increase of cell width during the course of successive heterocyst differentiation. Bright field; bar marker represents 50 μm.

Fig. 67. *Calothrix* PCC 7116. Note the sheathless aheterocystous hormogonia (ho) and the heavily ensheathed tapering trichomes that bear terminal heterocysts (arrows). Bright field; bar marker represents 50 μm.



Figs 68 and 69. *Calothrix* PCC 7507, the only strain of this genus that produces akinetes. Fig. 68 shows the relatively low degree of tapering characteristic of this strain. Fig. 69 shows part of a mature filament bearing a basal heterocyst (arrow) adjacent to a chain of akinetes (a), several of which are in the course of germination (g). Both bright field; bar markers represent 50 μm in Fig. 68 and 10 μm in Fig. 69.

Table 19. *Properties of Calothrix strains*

PCC no.*	Hormogonia gas vacuolated	Heterocysts sometimes intercalary	Akinetes produced	Facultative photoheterotroph, using: Glucose	Fructose	Ribose	Sucrose	Synthesis of:† C-PE	PEC	Marine‡
6303	−	−	−	−§	−	−	+	+	−	−
7101	+	−	−	+	+	+	−	+	−	−
7504	+	+	−	+	+	+	−	+	−	−
7102	−	−	−	+	+	−	−	−	−	−
7103	−	−	−	+	+	−	+	+	−	−
7111	−	−	−	+	(+)	−	+	−	−	−
7116	−	−	−	(+)	(+)	(+)	+	−	+	+
7204	−	−	−	+	(+)	−	+	−	+	−
7415	−	+	−	+	+	−	+	+	−	−
7426	−	−	−	(+)	(+)	+	+	−	+	+
7507	−	+	+	−	+	−	−	−	+	−

(+), Weak growth.

* Bracketed strains are probably independent isolates of the same species.

† C-PE, C-phycoerythrin; PEC, phycoerythrocyanin.

‡ Requirement for high concentrations of Na^+, Mg^{2+} and Ca^{2+}.

§ Although previously reported to grow on glucose (Kenyon *et al.*, 1972), subsequent tests were always negative.

on phosphate and iron deficiency (Whitton & Sinclair, 1976) and is rarely observed under the culture conditions employed here. Although heterocysts are typically terminal in this genus, a few strains (PCC 7415, 7504 and 7507) produce rare intercalary heterocysts in longer trichomes. Only PCC 7507 has been observed to produce akinetes (Fig. 69); akinetes begin to develop adjacent to the terminal heterocyst, and may occur in chains. All 11 strains are heterotrophs, with differing patterns of sugar utilization. With the exception of PCC 7102 and 7111, all produce either C-phycoerythrin or phycoerythrocyanin. Only PCC 7101 and 7504 are sufficiently similar in both structural and physiological respects to suggest that they may be independent isolates of one species.

Reference strain: PCC 7102

Genera of Section V

The nine strains placed in this section are assigned to two genera: *Fischerella* Gomont 1895 and *Chlorogloeopsis* Mitra & Pandey 1966, distinguished by the properties shown in Table 20 and Diagram 3.

Choice of the generic name *Fischerella* for the branched, filamentous strains of Section V, all of which are thermophiles, is based on the following considerations. A thermophilic cyanobacterium of this type was first described by Schwabe (1837) as *Fischera thermalis*. Cohn (1863) described in detail a similar organism from the same hot spring as *Mastigocladus laminosus*; creation of the new genus was justified primarily by smaller cell size. Since the name *Fischera* had previously been applied to a genus of higher plants, it was changed to *Fischerella* by Bornet & Flahaut (1887), who reduced this taxon to a subgenus of *Stigonema*. Gomont (1895) once again elevated *Fischerella* to the generic level.

In subsequent phycological treatises (e.g. Geitler, 1932; Bourrelly, 1970), both *Fischerella* and *Mastigocladus* are recognized. However, the descriptions of the genus *Mastigocladus* presented are widely divergent and depart more or less extensively from the original description by Cohn (1863). The status of this genus consequently has now become very confused. For this reason, we have chosen to assign the branching filamentous strains of Section V to *Fischerella* Gomont 1895.

The structure and development of *Chlorogloeopsis fritschii*, type species of this monotypic genus, were well described by Mitra (1950), Fay *et al.* (1964) and by Mitra & Pandey (1966). Recently, Evans *et al.* (1976) studied the effect of culture conditions on the morphology of *Chlorogloeopsis fritschii* (strain PCC 6912) and found that the filamentous phase of development is repressed under photoheterotrophic and chemoheterotrophic growth conditions. The ability of this heterocystous organism to divide in more than one plane precludes an assignment to *Nostoc*, which was suggested by Schwabe & El Ayouty (1966). The significance of its division pattern was first recognized by Mitra & Pandey (1966), who suggested inclusion of the new genus in the order Stigonematales, even though *Chlorogloeopsis* never displays the branched, filamentous structure characteristic for other members of this order. The placement of *Chlorogloeopsis* proposed by these authors is adopted here, since Section V is taxonomically equivalent to the phycological order Stigonematales.

The mean DNA base composition of the strains of Section V ranges from 42 to 46 mol% GC (Herdman *et al.*, 1979).

Genus Fischerella Gomont 1895

Six of the seven strains assigned to this genus were received as *Mastigocladus* sp. or *Mastigocladus laminosus*. The confusion surrounding the names *Fischerella* and *Mastigocladus* is discussed above. Three representative *Fischerella* strains are shown in Figs 70 to 78. The strain histories are as follows:

ATCC 27929 PCC 7115. $\overset{P}{\leftarrow}$ A. Neilson $\overset{P}{\leftarrow}$ F. Haxo (*Mastigocladus* sp. H_2), thermal spring, Tassajara, California, U.S.A., 1971.

Table 20. *Section V: Filamentous heterocystous cyanobacteria that divide in more than one plane*

Reproduction by random trichome breakage, by formation of hormogonia and (if produced) by germination of akinetes	Hormogonia composed of small cylindrical cells which enlarge and become spherical; heterocysts develop in terminal and intercalary positions	Cells in the mature trichome divide in more than one plane; associated detachment of groups of cells leads to irregular *Gloeocapsa*-like aggregates containing terminal heterocysts; hormogonia are produced within such aggregates ***Chlorogloeopsis***
	Hormogonia composed of small cylindrical cells which enlarge and become rounded; heterocysts develop almost exclusively in an intercalary position	Cells in the mature trichome divide in more than one plane to produce a partly multiseriate trichome with lateral uniseriate branches; heterocysts in the primary trichome are predominantly terminal or lateral; hormogonia are produced from the ends of trichomes or from lateral branches ***Fischerella***

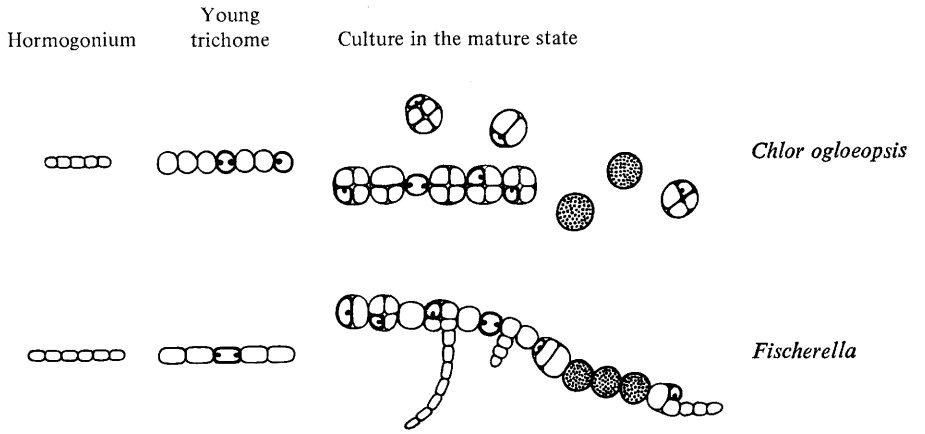


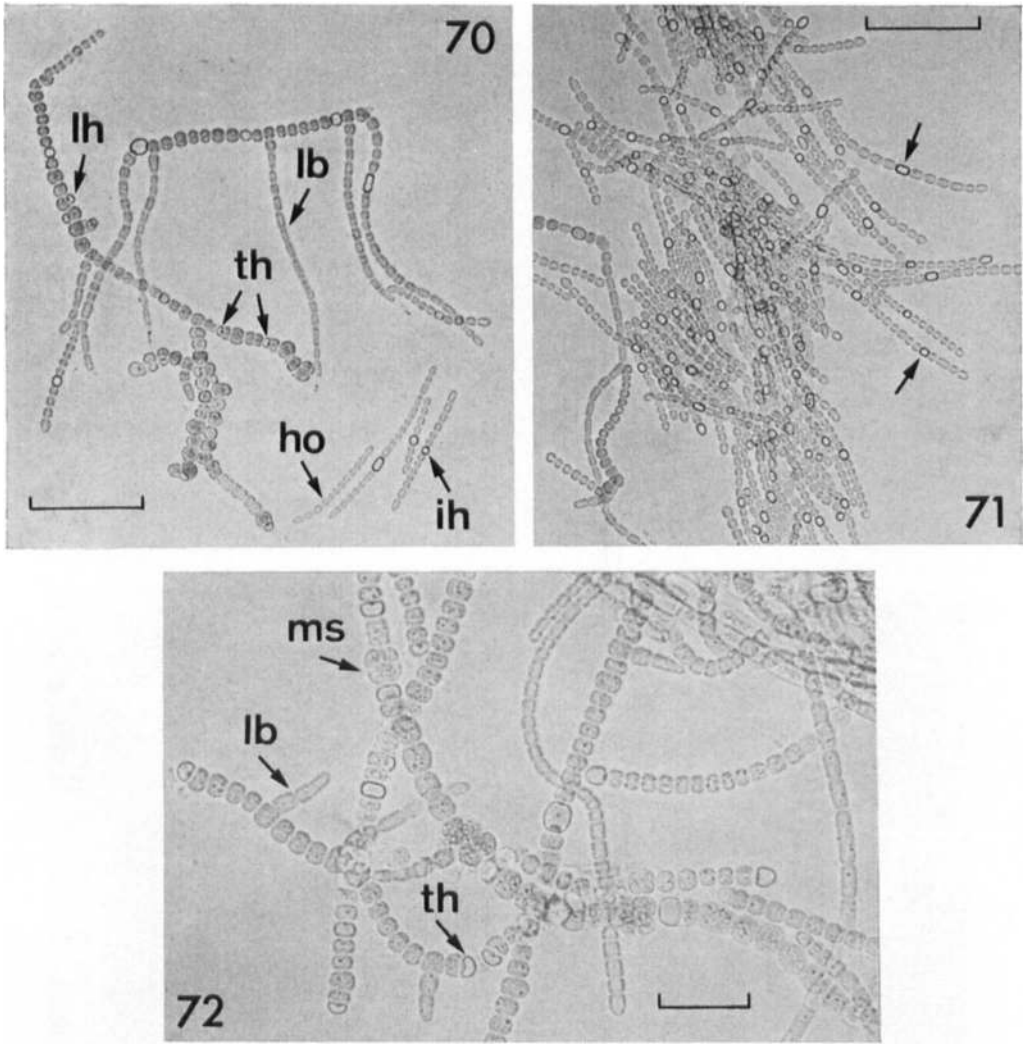
Diagram 3. Schematic presentation of the genera assigned to Section V. Heavy walled cells with polar granules represent heterocysts; heavy walled cells that are dotted represent akinetes; thin lines surrounding groups of cells designate sheath material.

ATCC 29114 PCC 73103. $\overset{I}{\leftarrow}$ SAUG (1427/1) (Koch, 1964) ← A. K. Mitra (*Fischerella muscicola*), rice field, near Allahabad, India (Mitra, 1951). In CCAP (1427/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971) and UTEX (1301) (Starr, 1966).

ATCC 29161 PCC 7414. $\overset{I}{\leftarrow}$ SAUG (1447/1) ← G. E. Fogg (*Mastigocladus laminosus*), hot spring, New Zealand. In CCAP (1447/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971).

ATCC 29537 PCC 7520. $\overset{P}{\leftarrow}$ R. Castenholz (*Mastigocladus laminosus* I-Kris-m), hot spring, Krisuvik, Iceland.

ATCC 29538 PCC 7521. $\overset{P}{\leftarrow}$ R. Castenholz (*Mastigocladus laminosus* Y-16-m), hot spring,



Figs 70 and 71. *Fischerella* PCC 7115. Fig. 70 shows mature trichomes with lateral branches (lb) from which hormogonia (ho) arise; heterocysts in the developing hormogonia are in an intercalary position (ih). The mature and partly multiseriate trichomes have intercalary heterocysts, terminal heterocysts (th) in an intercalary position, as well as lateral heterocysts (lh). Fig. 71 shows young trichomes composed of small cylindrical cells, with intercalary heterocysts (arrows). Both bright field; bar markers represent 50 μm.

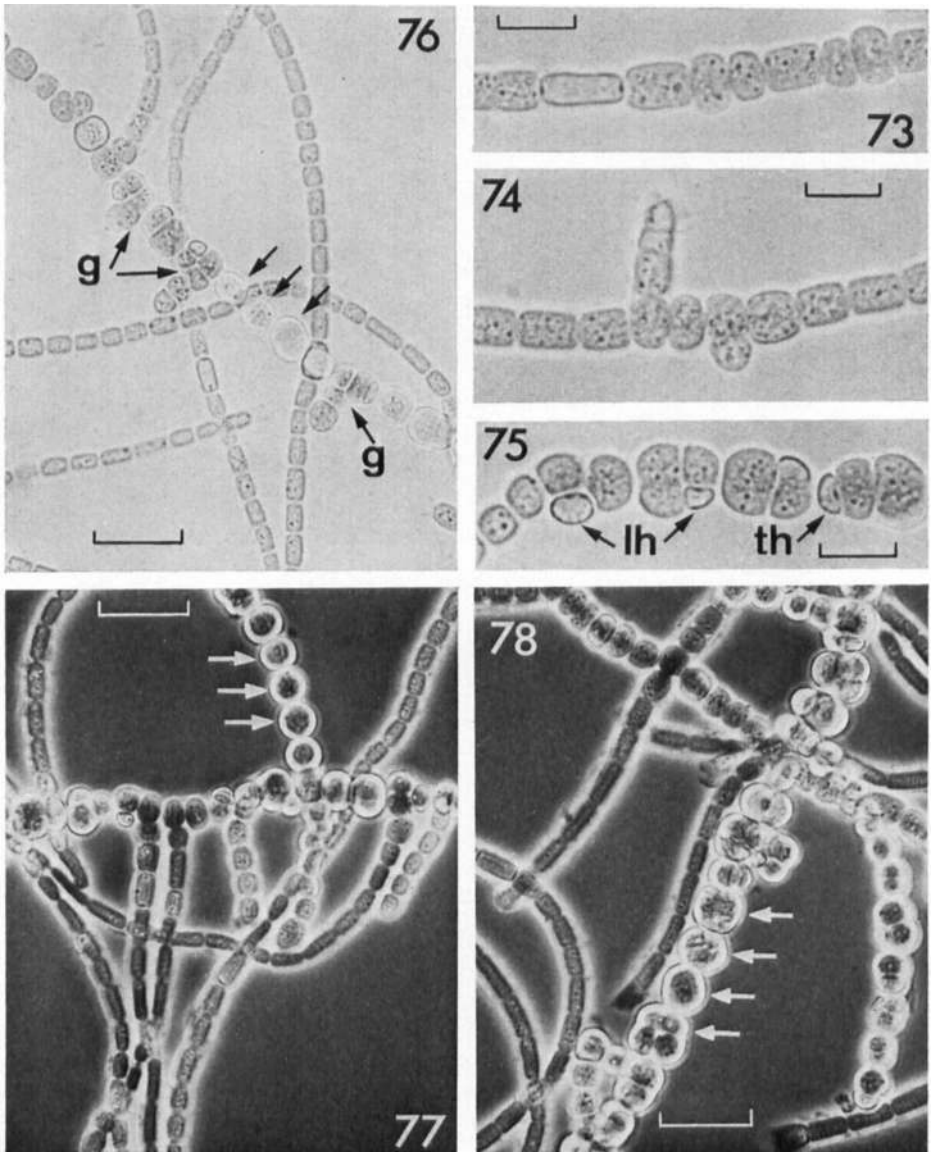
Fig. 72. *Fischerella* PCC 7521 ('*Mastigocladus laminosus*' MTF, Y-16-m, Castenholz, 1969). Note the terminal heterocysts (th) in an intercalary position within the primary trichome, the lateral branches (lb) and multiseriate parts of the primary trichome (ms). Bright field; bar marker represents 20 μm.

Mammoth Sinkhole III, Yellowstone National Park, U.S.A., 1969 (Castenholz, 1969).

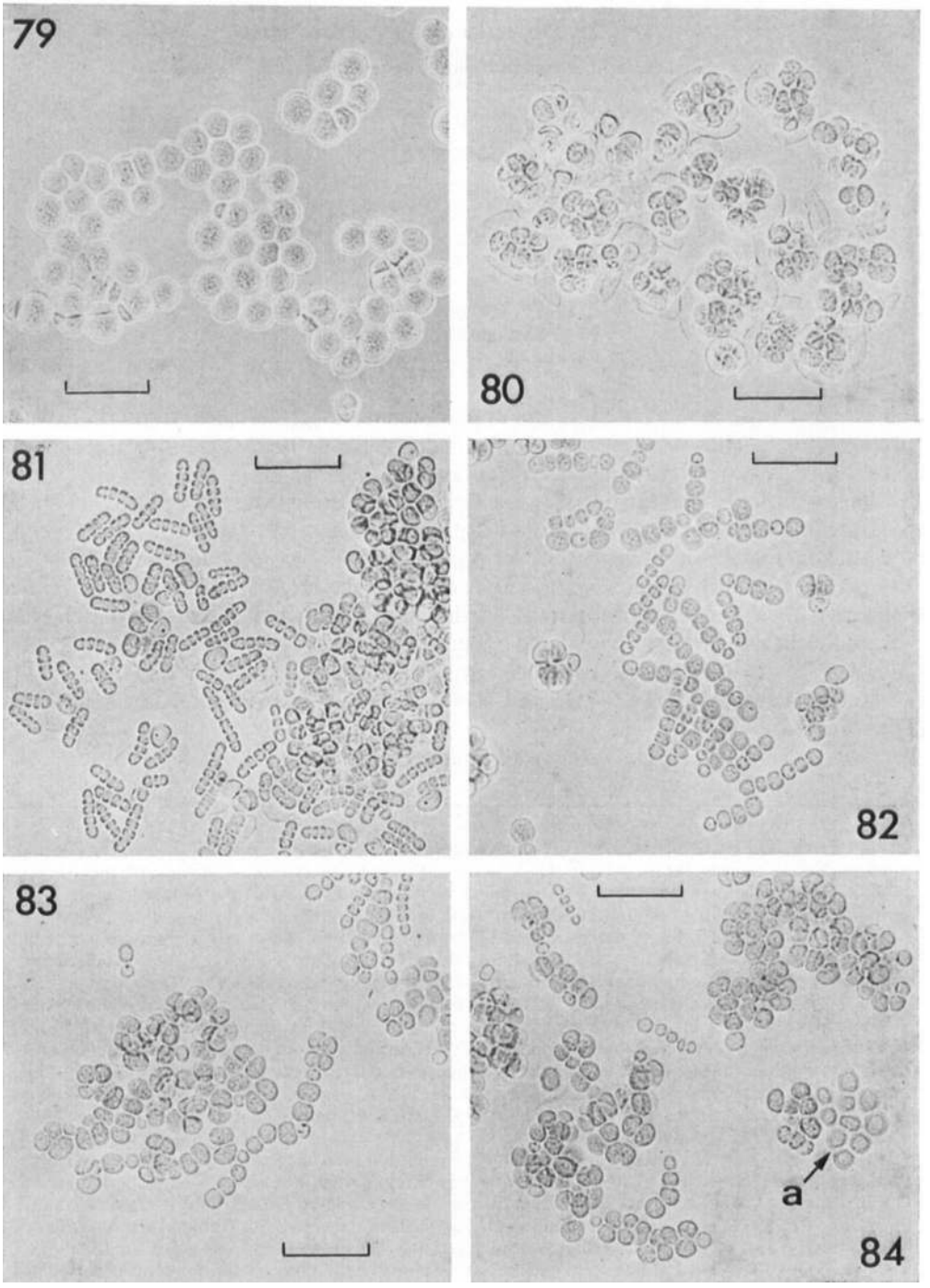
ATCC 29539 PCC 7522. $\overset{P}{\leftarrow}$ R. Castenholz (*Mastigocladus laminosus* NZ-86-m), hot spring, Whakarewarewa, New Zealand, 1969.

ATCC 29540 PCC 7523. $\overset{P}{\leftarrow}$ R. Castenholz (*Mastigocladus laminosus* OH-CW-m), hot spring, Oregon, U.S.A.

The mean DNA base composition of the *Fischerella* strains ranges from 42 to 46 mol% GC (Herdman *et al.*, 1979). The seven strains, despite their highly diverse geographical



Figs 73 to 78. *Fischerella* PCC 7414. Figs 73 and 74 show successive developmental stages in the formation of lateral branches: trichome just prior to branch formation (Fig. 73); lateral branches at the two-celled stage and at the four-celled stage (Fig. 74). Bright field. Fig. 75 shows part of a multiseriate trichome with lateral (lh) and terminal (th) heterocysts. Note the distinctive gaps between groups of cells attributable to the intercellular deposition of a fibrous wall layer (Thurston & Ingram, 1971). Bright field. Fig. 76 shows a mature filament with rows of akinetes (arrows), several of which are in the course of germination (g) giving rise to lateral branches. Bright field. Figs 77 and 78 show comparable fields taken under phase contrast illumination to reveal more clearly the light refractile akinetes (arrows). Bar markers represent 10 μm in Figs 73 to 75 and 20 μm in Figs 76 to 78.



Figs 79 to 84. Developmental stages of *Chlorogloeopsis fritschii* PCC 6718. Fig. 79 shows a field of akinetes in a culture in late-stationary phase of growth. Fig. 80 shows the same culture several days after transfer to fresh medium. Akinete germination occurs by division in several planes and leads to a *Gloeocapsa*-like mode of growth. Note the shedding of the extra wall layers that enclosed the akinetes. Subsequent division of many cells in only one plane leads to massive production of short trichomes (hormogonia), that are composed of small cylindrical cells (Fig. 81). The development of hormogonia leads to the formation of trichomes of larger cell size and the differentiation of terminal and intercalary heterocysts (Fig. 82). Figs 83 and 84 show fields of cultures in early-stationary phase of growth, with young akinetes (a). All bright field; bar markers represent 20 μm.

Table 21. *Properties of Fischerella strains*

PCC no.	Facultative photoheterotroph, using: Glucose	Fructose	Ribose	Sucrose	Akinetes readily evident	Synthesis of PEC*	Thermophil†
7115	+	+	−	+	+	+	+
73103	+	+	−	+	−	+	+
7414	+	+	−	+	+	+	+
7520	+	+	−	+	−	+	+
7521	+	+	(+)	+	−	+	+
7522	+	+	+	−	−	+	+
7523	+	+	+	+	−	+	+

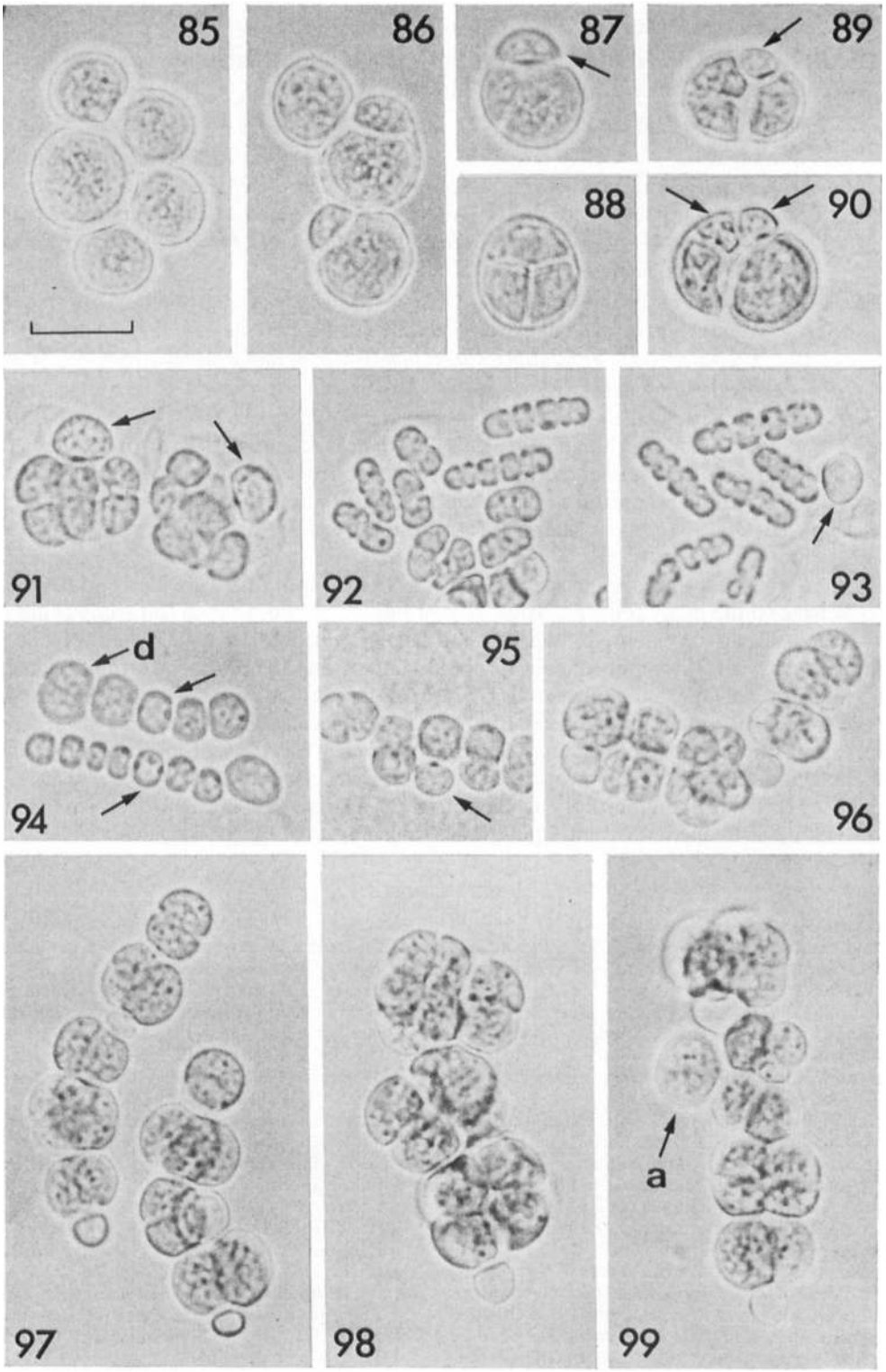
(+), Weak growth.
* PEC, Phycoerythrocyanin.
† Maximum growth temperature, 50 °C.

origins, differ little in morphology, and appear similar in physiological respects (Table 21). All strains are facultative heterotrophs, growing on glucose, fructose and sucrose; some also utilize ribose. All synthesize phycoerythrocyanin.

Akinetes in *Fischerella* are not always readily recognizable (Martin & Wyatt, 1974), and the large round cells of the primary trichome that are enclosed by the fibrous wall layer may be mistaken for young akinetes or vice versa. The only property (observable by light microscopy) that distinguishes mature akinetes from the large round cells of the primary trichome is their weaker pigmentation. Furthermore, since the germination of akinetes as well as the development of the round vegetative cells leads to the formation of lateral branches, the distinction between the two types of cells often becomes very difficult. Only two strains of *Fischerella* (PCC 7115 and 7414) form akinetes that can readily be recognized (Figs 76 to 78).

Reference strain: PCC 7414

Figs 85 to 99. Details of the developmental stages of *Chlorogloeopsis fritschii* PCC 6718. Fig. 85 shows a field of akinetes. Figs 86 to 90 show the early stages in akinete germination. Uneven cell division in more than one plane without concomitant growth leads to the formation of cells of differing size. After the first uneven division, the daughter cell often differentiates into a heterocyst (arrow) (Fig. 87). However, heterocyst differentiation may also occur only after additional cell divisions, thus resulting in a heterocyst (arrow) of smaller size (Fig. 89). More than one heterocyst (arrows) per germinating akinete may occasionally be observed (Fig. 90). Fig. 91 shows two cell clusters that developed from akinetes by division in several planes (arrows indicate heterocysts). Note the extra cell wall layers of the original akinetes that surround both groups of cells. Fig. 92 shows division stages in only one plane by which a single cell produces a four- to six-celled hormogonium. At this stage of development, one observes a high frequency of heterocysts that are shed by the rapidly gliding aheterocystous hormogonia (Fig. 93, arrow; also see Fig. 81). Fig. 94 shows two filaments that developed from a hormogonium. Note the increase in cell size, the intercalary heterocysts (arrows) and a cell that is dividing in a plane parallel to the long axis of the trichome (d). Fig. 95 shows part of a maturing filament in which cell divisions have occurred parallel to the long axis of the trichome. One of the resulting cells has differentiated into a lateral heterocyst (arrow). Further cell division in several planes leads to trichomes composed of multicellular clusters as seen in Figs 96 to 99. They may bear terminal, intercalary or lateral heterocysts. Terminal and intercalary heterocysts (Figs 96 to 99) differentiated from vegetative cells of the young and uniseriate trichomes (Fig. 94, but also see Fig. 82); lateral heterocysts developed only after cell divisions had occurred in planes other than that at right-angles to the long axis of the trichome. Trichomes as seen in Figs 96 to 99 easily fall apart into irregular cell aggregates and can readily be observed only after growth on solid medium. Fig. 99 shows strain PCC 6718 just prior to the breaking up of the trichomes and massive differentiation of akinetes (a). All bright field; bar marker (applicable to all figures) represents 10 μm.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Genus Chlorogloeopsis Mitra & Pandey 1966

Details of the development of one of the two strains in this genus are shown in Figs 79 to 99. The histories of the strains are as follows:

ATCC 27193 PCC 6912 (Stanier *et al.*, 1971; Kenyon *et al.*, 1972). $\overset{P}{\leftarrow}$ D. Hoare, University of Texas $\overset{P}{\leftarrow}$ CCAP $\overset{P}{\leftarrow}$ A. K. Mitra, soil sample, Allahabad, India (Mitra, 1950). Strain on which description of the type species, *Chlorogloeopsis fritschii*, is based (Mitra & Pandey, 1966). Named as *Chlorogloea fritschii* in CCAP (1411/1) (*Culture Collection of Algae and Protozoa: List of Strains*, 1971) and SAUG (1411/1) (Koch, 1964).

ATCC 27181 PCC 6718 (Kenyon *et al.*, 1972). $\overset{I}{\leftarrow}$ Botany Department, University of California, previous history unknown. Named as *Chlorogloeopsis* sp. in CCAP (1411/1b) (*Culture Collection of Algae and Protozoa: Second Amendments to the* 1971 *List of Strains*, 1973).

These two strains appear to be identical in all respects. The mean DNA base compositions are 42 to 43 mol% GC (Herdman *et al.*, 1979). Both are facultative heterotrophs; they grow especially well with sucrose, but can also utilize glucose, fructose and ribose. Both synthesize phycoerythrocyanin and produce akinetes in stationary phase of growth.

Reference strain: PCC 6912

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