THE RELATIONSHIP BETWEEN BACTERIA AND MYXOPHYCEAE

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An attempt to clarify the relationships between Bacteria and Myxophyceae[2] hardly needs an excuse. If one or other reader were induced to contribute facts or considerations that constituted a step forwards, it would be the best justification for this review. The imperfect state of the conclusions reached is partly due to the unequal value of the literature which is so extensive and scattered that the writer found it impossible to use it as fully as he had intended.

The errors often encountered consist in the reference of certain microörganisms to Bacteria or Myxophyceae or their interpretation as intermediate forms between these two large classes on the basis of superficial resemblances. In such minute and often little differentiated organisms detailed study and steadily improved methods of investigation are requisite in order to determine what characteristics are of taxonomic importance. Certain errors have persisted long after

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[2] "The name Myxophyceae has priority over the possibly more suitable designation Cyanophyceae. The class is also often named Schizophyceae or Phycochromaceae." (Fritsch, 1945, p. 769). The popular name is Blue-green Algae.

the means for their removal were available owing to the lack of trained investigators sufficiently interested in theoretical questions of general microbiology. It is the aim of this article to show what conclusions can be reached with the help of the available facts, and to indicate where renewed investigations would probably yield far-reaching results.

The idea that Bacteria and Myxophyceae were closely related originated from Cohn (1853). He had discovered apochlorotic Algae, i.e., unpigmented organisms obviously derived from pigmented ancestors by the loss of chromatophores. This led him to compare other colorless microörganisms with pigmented ones, and to group together in his system of classification those organisms of either kind that showed the greatest similarity. At that time it was an established principle to use only morphological features for taxonomic purposes, while color was regarded as a secondary, merely physiological property. In Cohn's day it was easier to find colorless counterparts to pigmented forms since both were far less known.

Cohn's further aim was to find a means of arranging the chaotic host of Bacteria by differentiating them by their shape and behavior, and he thus became the father of scientific bacteriology. He expressed his opinion of their status in the following words: "The Bacteria (Vibriones) appear all to belong to the Vegetable Kingdom, showing a near and immediate similarity to obvious Algae." The Algae he had in mind were the Myxophyceae which were referred to the Algae because of their possession of assimilatory pigments. Eighteen years later Cohn (1871/72) published his natural system of the cryptogams. He recognized that the Bacteria had no relation to yeasts and moulds, as was then often held, and referred them to a new group, the Schizosporeae, to which he subsequently gave the more suitable name Schizophyta. The latter comprise the Schizophyceae (Myxophyceae) and the Schizomycetes (Bacteria). In a communication on the "Verwandtschaftsbeziehungen der Bacterien" (1875) Cohn gave a more detailed account of his views. The Bacteria were considered to be near, though primitive allies of the Myxophyceae, adapted to a saprotrophic or parasitic mode of life. While refuting any relation to Animals or Fungi, Cohn stated that "The Bacteria are at the lower end of the line of Myxophycean evolution," although a closer relation between certain forms of the two classes was assumed.

An inclination to include unpigmented forms among the Algae wherever possible became widespread. Rabenhorst (1864/68) referred the entire Bacteria to the Myxophyceae; thus *Sarcina* is grouped with the Chroococcaceae, *Bacillus*, *Spirillum*, *Sphaerotilus*, etc., with the Oscillariaceae. For some time Cohn's views were widely accepted, in part owing to the influence of Sachs' textbook (1868 and later) which was predominant (cf. Pringsheim 1932b, pp. 184 seq). A few biologists, however, opposed early. Van Tieghem (1880, p. 177) in his communication on the "Affinités des Bactériacées et des Phycochromacées" claimed to have found green Bacteria which were not Myxophyceae, and colorless Myxophyceae which were not Bacteria. He therefore emphasized the wide gap between the two classes and mentioned as the main differentiating features the mode of spore-formation in the Bacteria and the pigments associated with chlorophyll in the Myxophyceae, although their nature was not known at that time.

De Bary (1884) also opposed Cohn's system of classification. Under his influence the "Fungi" were again regarded as a distinct group, separate from pigmented plant organisms. Some authors even went so far as to regard as a "Fungus" every colorless non-flowering plant. At the present day pigment-free forms recognizable as belonging to a definite group of chlorophyll-containing plants are referred to that group, while of others it can only be said that they appear to be descended from a long series of colorless ancestors (Pringsheim, 1941).

This point of view was initiated by Cohn himself. At first (1875, p. 202) he combined colorless and pigmented groups quite logically because he believed that "genera founded on pigmentation have only conventional value." Such differences he regarded merely as physiological and therefore not significant for systematic purposes. By degrees, however, he became aware of the difficulties of grouping together Schizophyceae and Schizomycetes. The flagella detected in motile bacteria in particular made him cautious. "The existence of flagella in *Spirillum volutans*, which constitute an approach to the Flagellata renders the natural position of these organisms doubtful because no Oscillatoriacea (i.e., motile Myxophyceae) possesses flagella" (Cohn, 1871/72, p. 187). Thus he very early recognized one of the main obstacles to a close affinity between Bacteria and Myxophyceae, and it is surprising that van Tieghem does not refer to it. Cohn was followed by his collaborator Schroeter (1889, p. 141), who again emphasized the endogenous spore-formation of Bacteria as a feature differentiating them from the Myxophyceae.

Gradually more and more opinions against the habitual grouping together of Bacteria and Myxophyceae found expression, so that eventually it was almost completely abandoned but for some nomenclatural relics.

Pascher (1931, p. 330) is outspoken in his rejection of a common taxonomic unit embracing the Bacteria and the Myxophyceae. Although he groups the Cyanophyta (Myxophyceae) together with the Schizomykophyta (Bacteria) as "Plantae holoplastideae" by contrast to other vegetable organisms or "Plantae euplastideae," he regards them as completely independent tribes. "The fact that there are also colorless blue-green Algae by no means justifies the assumption that the Bacteria are an apochromatic line parallel to the Myxophyceae. Myxophyceae and Bacteria (the latter in the real [eigentlichen] meaning of the word) at present possess no relation to one another. I share completely Geitler's view. Very diverse structures are still accepted as Schizomycetes: true Bacteria, apochromatic blue-green Algae, probably also very reduced Fungi, and possibly organisms of yet another origin." Which "Bacteria" Pascher would include in the last two instances he does not say.

Bháradvája (1940, p. 203) devotes a chapter to the "Relation between the Myxophyceae and the Thread-bacteria," stating that "no convincing evidence has yet been available to lend support to any affinity between them."

Stanier and van Niel (1941), on the contrary, come to the conclusion that the Myxophyta (Myxophyceae) resemble the true Bacteria far more closely than they do any of the other algal groups (p. 450). They believe that Bacteria and blue-green Algae have originated from common ancestors and summarize their common characteristics as follows: (1) absence of true nuclei, (2) absence of sexual reproduction, (3) absence of plastids (p. 449).

These three features are employed to define the "Kingdom of Monera" (p. 456), a term Stanier and van Niel prefer in place of Cohn's Schizophyta. The entirely negative characteristics upon which this group is based should be noted, and the possibility of a convergent evolution of the two classes be seriously considered. Stanier and van Niel's conclusion (p. 450) that "it seems at least possible that the blue-green Algae of the *Chroococcus* type have developed from the Eubacteriales as a second photosynthetic line, at first paralleling morphologically the Purple Bacteria, but undergoing in the course of time a far more complex morphological evolution", is so interesting that it will be considered more fully later.

Fritsch (1945, p. 860) again is not in favor of grouping Bacteria and Myxophyceae together. "With the true Bacteria, despite an analogous lack of cell differentiation, any close affinity appears to be ruled out." In relation to *Beggiatoa* and *Thiothrix* he says: "The facts . . . suggest the possibility that these types belong to a plurality of evolutionary lines diverging from a remote ancestry, from which the Myxophyceae also arose." These cautious statements are characteristic of the modern reluctance to admit phylogenetic relations without very distinct evidence.

Dubos, who may be cited as a representative of the bacteriologists, is less cautious when he says (1945, p. 6): "One finds among bacteria organisms which show strong resemblances to certain of the blue-green algae, to the fungi, to the myxomycetes, or to the protozoa, and which can only be distinguished from these microorganisms by their much smaller size." It may be surmised that he has in mind the Beggiatoaceae, the Actinomycetes, the Myxobacteria, and the Spirochetes, but the statement as to the nature of the differences must be rejected. The Beggiatoaceae are not smaller than their pigmented counterparts, the Oscillatoriaceae; on the contrary *Beggiatoa mirabilis* is the largest member of both families, and *Achromatium* may likewise be very big (cf. p. 68). The other groups, which Dubos may have had in mind, exhibit no more than a superficial resemblance to Bacteria and to the organisms he mentions.

Dubos continues: "Some investigators have looked upon bacteria as a primitive, homogeneous group from which higher types have arisen. It appears more likely, however, that these microorganisms constitute a heterogeneous group of unrelated forms. Even among the Eubacteriales—the so-called true bacteria—one finds strange bedfellows, such as small Gram negative autotrophic organisms, the Gram positive proteolytic spore-formers, the acid-fast bacilli, which differ so profoundly from each other in metabolism, structure, and even mode of division as to have little in common except microscopic dimensions." This statement should have been more clearly substantiated. If there are any investigators of weight, who regard the Bacteria as a homogeneous group, they should have been named. The differences in metabolism are now known not to be so great as to justify wide taxonomic separation. What differences in cell-division has Dubos in mind? If he is certain of the gaps between the various groups of Eubacteria, why does he not submit a scheme of classification for which bacteriologists are waiting?

I. TAXONOMY OF BACTERIA AND NATURAL RELATIONSHIPS

The answer to the question whether there is an affinity between Bacteria and Myxophyceae depends so much on the delimitation of these groups that some space must be devoted to a discussion of these matters. In the case of the Myxophyceae it is relatively easy to define the class. All authorities agree that they are a natural group without affinities to other algal classes (Fritsch, 1945, p. 859), except a most doubtful one to the Bangiales, and differing from the other microörganisms under discussion in possessing true chlorophyll. The so-called Chlorobacteriaceae or Cyanochloridinae (Geitler and Pascher, 1925) alone remain of doubtful affinity (cf. p. 80).

The taxonomy of the Bacteria in the widest sense is much more difficult. It has unfortunately been customary, in order to secure any kind of practical arrangement, to divorce the classification of the forms from the problem presented by their natural grouping based on phylogenetic considerations. Hence the deplorable state of bacterial classification (Pringsheim, 1923), severely criticized again by Stanier and van Niel (1941, p. 439).

The paucity of differentiating morphological features makes it imperative to employ every available character in order to describe the vast number of bacterial species (Pringsheim, 1923, p. 364). The main problem is to define the importance of these characters in relation to the distinction of larger and smaller taxonomic entities respectively. To the morphological characters provided by cellshape, mode of flagellation and presence or absence of spores, which are used in the first instance, the gram stain has been added as a characteristic of equal importance (Pringsheim, 1923, p. 375). This latter has meanwhile been found to "divide the bacterial world into two groups which differ profoundly" (Dubos, 1945, p. 294).

By making use of all these means the genera *Pseudomonas*, *Vibrio*, and *Spirillum* have been recognized as allied. These genera were removed from the Bacillaceae and called Spirillaceae (Pringsheim, 1923, p. 376). The latter might well, however, be regarded as of higher rank than a family (cf. p. 81). Why later authors took *Pseudomonas* instead of *Spirillum* as the type-genus and called the family Pseudomonadaceae (Kluyver and van Niel, 1936, p. 388; Stanier and van Niel, 1941, pp. 441, 453) is not apparent. Bergey (1939, p. 82) attributes the name Pseudomonadaceae, used in that sense, to Winslow *et al.* (1917, p. 555); but these authors use it in a narrower sense, with the exclusion of *Vibrio* and *Spirillum*. Moreover, the group Rhodobacteriales was established to include the photosynthetic bacteria as opposed to the colorless sulphur bacteria (Pringsheim, 1923, p. 374), with which they had long been associated (Stanier and van Niel, 1941, p. 448).

Most recent authors, though accepting these propositions, do not go far enough in utilizing all available evidence of differentiation or of affinity among bacteria for taxonomic purposes. When the taxonomy of other groups of organisms was in an embryonic state comparable to that of bacteria at the present day the first advance always consisted in singling out assemblages of species which were obviously closely allied. Between such groupings sets of more or less intermediate forms could be recognized, until there remained only a few aberrant forms. A similar procedure has been adopted in the Bacteria, but often without sufficient consciousness of the necessity of bringing together the species with the largest number of common features. Otherwise such unnatural groups as the Thiobacteriales, the Trichobacteriales, and the Caulobacteriales, would not have been established.

The Thiobacteriales are supposed to be characterized by the presence of sulphur or of red pigment or of both in their cells, without the latter forms constituting a phylogenetic bridge between the two other groups, so that this classification is neither natural nor practical. The only common characteristic of the Trichobacteriales is the filamentous habit, although they do not comprise all filamentous bacterial forms. The only common features of the Caulobacteriales (Henrici and Johnson, 1935) are their stalk-like exudations, the nature of which is unknown in most of them, and where it is known, is not the same in all cases.

Single characteristics never suffice for the creation of natural groups (Pringsheim, 1923, p. 364) and in most bacteria morphological features are inadequate for the purpose. If therefore one is not to be deceived by superficial resemblances, affinities must be tested in every possible way, physiological features being considered side by side with morphological ones, which should certainly include sporulation and flagellation. Natural and readily recognizable groups in this sense are, for instance: the Escherichia-Salmonella group; the Pseudomonas-Vibrio-Spirillum group; the Subtilis-Mycoides group; the Corynebacterium group; the Sphaerotilus group, and many more. Features regarded as characteristic of a whole group may occasionally have to be abandoned as a result of new observations, as happened when spore-forming species of *Sarcina* and *Vibrio* were found. These genera are, however, too well characterized by other features to be affected by an alteration in the diagnosis.

The difficulties of establishing a system of classification that shall serve both the practical need of a clear grouping and afford an expression of natural relationship, are due to: (1) the small size of most bacterial cells as a result of which they do not show many differentiating features; (2) the multitude of similar forms; (3) the lack of sexual reproduction and of the morphological characteristics associated with it which are of prime taxonomic importance in many other groups; (4) the frequent neglect of numberless species in favor of those of practical importance. These difficulties increase with the discovery of more and more species, because bacteriologists who specialize in certain groups do not have a sufficiently wide outlook, while those interested in the class as a whole often lack a detailed knowledge of its various groups.

The necessity for the inclusion of numerous forms, many of them more interesting for their enzymatic activity than for their natural relationship, has led to the establishment of systems of classification primarily on physiological characteristics which, although perhaps not unsuitable for the differentiation of species, have to be used with caution. Otherwise one obtains wholly unnatural groups, embodying forms of widely differing relationship; quite a number of them could be cited.

For example the most modern classification of bacteria, that of Stanier and van Niel (1941), which is by far the best, still retains a relationship of the Myxobacteria and the Spirochaetae to the Eubacteria. The former two groups might, however, more naturally be regarded as having an origin quite different from the latter, being possibly derived from common ancestors with the Myxophyceae, and resembling true Bacteria only in shape and dimensions, a question which will be considered subsequently.

II. RESEMBLANCES AND DIFFERENCES BETWEEN BACTERIA AND MYXOPHYCEAE

1. Morphology. The Myxophyceae differ from Bacteria in a greater structural complexity and diversity. The Stigonematales possess a thallus differentiated into prostrate and erect systems of trichomes, an elaborate organization unknown in any member of Bacteria even in the widest sense accepted. In fact there are few morphological parallels between the two groups. The filaments of Bacteria are in general not comparable to those of the Nostocales; *Streptococcus*, it is true, has some similarity to *Pseudanabaena catenata*, and *Sphaerotilus* to *Lyngbya*, but the resemblances are superficial (cf. p. 77). *Beggiatoa* will be discussed below.

While bacteria, as a rule, do not form distinct colonies in nature, colonial Chroococcaceae are imitated to some degree by a few of them. A parallelism is recognizable between the blue-green *Merismopedia*, the cells of which divide along two planes and show a regular arrangement in a single tabular layer, and the purple sulphur bacterium *Thiopedia*, and *Lampropedia* among Eubacteria, in which the same arrangement is found. *Eucapsa* among Myxophyceae, which is characterized by division along three planes, has its parallel in *Sarcina* among Bacteria. *Chroococcus* divides in the same way, although the cells cohere only as groups of four or eight within mucilaginous envelopes, so that it has a certain similarity to *Gonococcus*, *Meningococcus*, and *Micrococcus tetragenus*.

Similarity between Bacteria and Myxophyceae as regards their external morphology is therefore very restricted and not really helpful in assessing their relations to one another. The fact that only the least specialized Myxophyceae, if lacking color and motility, could possibly, as suggested (Benecke, 1912, p. 244; Stanier and van Niel, 1941, p. 449), be confused with Bacteria, is not in favor of more than a very remote relationship.

Among Myxophyceae even relatively simple cell rows, like those of *Oscillatoria*, are more highly organized than bacterial filaments. The former possess differentiated terminal cells, often with a calyptra; zones of intercalary division; and defined propagatory structures in the form of hormogonia. The greater differentiation of Myxophyceae as compared with Bacteria is also expressed in the existence of protoplasmic connections between adjacent cells (Stigonemataceae), in the formation of spores in definite positions (*Cylindrospermum*, *Gloeotrichia*), in hormogonium formation being often initiated by the death of certain cells (*Scytonema*), and in the false branching occasionally being related to the development of heterocysts (*Tolypothrix*) and in such instances being more regular than in *Cladothrix* among Bacteria.

Certain bacteria, for instance *Sphaerotilus*, *Lineola*, and *Caryophanon* exhibit the first steps towards a differentiation between cells. In the two last, instead of the periodic hormogone formation of *Oscillatoria*, there is a progressive formation of steadily deepening constrictions until that first formed and situated approximately at equal distances from either end, divides the whole trichome into two halves, within which further constrictions have arisen repeatedly between those first formed. No species of *Oscillatoria* seems to develop such constrictions which at an early stage define the place of fragmentation.

As repeatedly pointed out in the literature, spore formation also differs in the two classes. No Myxophycea produces endospores comparable to those of Bacteria. Where so-called endospores are formed, as in *Dermocapsa* and many Pleurocapsales they are different in organization from those of Bacteria, while the spores (akinetes) of Nostocales are entire transformed cells, for which there is no parallel in any bacterium.

2. Pigmentation. The cells of most Bacteria do not contain assimilatory pigments, while those of Myxophyceae possess chlorophyll a, carotins, phycocyanin, and often phycoerythrin, although a few genera are colorless (cf. p. 61). Among Bacteria the Purple and Green Bacteria contain, in addition to other pigments, green ones similar to chlorophyll (cf. p. 79), but differing in the two groups. The pigmentation does not afford any indication of relationship between Bacteria and Myxophyceae.

3. Cytology. The myxophycean cell is differentiated into two regions: an inner, the central body or centroplasm, and a peripheral one, the chromoplasm, containing chlorophyll and accessory pigments. The presence of two regions is not established beyond doubt in every case (Chodat, 1894; Geitler 1936, p. 6; and own observations). The central part of the cell is characterized by an accumulation of reserve substances and perhaps a certain degree of independence during division (Fritsch, 1945, p. 780), while the chromoplasm appears to be different mainly by its pigmentation and is not sharply demarcated. The centroplasm also often contains rod-shaped structures, simulating the chromosomes of other organisms without exhibiting the properties of true nucleins (cf. Guilliermond, 1926b). Granules giving the Feulgen reaction have also been found (Poljansky and Petruschewsky, 1929; Petter, 1933; Spearing, 1937; Delaporte, 1939, 1940) but their fate during cell division is not clear, and they seem less defined than the nucleoids of bacteria (Robinow 1944, 1945; Klieneberger 1945, 1947).

The differentiation into central and peripheral cytoplasm is wanting in the pigment-free genera *Beggiatoa* (Delaporte, 1939, who gives the older literature) and *Thiothrix* (Fourment, 1926) which otherwise have much in common with certain Myxophyceae. This lack of correspondence must not be overestimated. Fischer's conclusions (1897a, pp. 119 *et seq.*) seem still to be valid. According to him, "the centroplasm is no more than the main body of the protoplast surrounded by the chromoplasm in which are also stored the products of assimilation."

Changes in cell-structure, somewhat comparable to the differences in cell structure between *Oscillatoria* and *Beggiatoa*, are connected with apochlorosis in various algae. The loss of pigments in *Euglena* and other flagellates, for instance, is associated with the destruction of the chromatophores, and the chondriome system also undergoes changes (Pringsheim, 1949). It is therefore not surprising that in apochlorotic Myxophyceae also the loss of pigments is connected with a reduction of the differences between the regions of the protoplast. A similar reasoning can be applied to the storage of reserve substances, which are deposited inside the chromatophore in *Chlamydomonas* but in the cytoplasm in the related chlorophyll-free *Polytoma*. Differences in this respect are likely to occur even between closely related phytotrophic and heterotrophic organisms.

The process of cell division by diaphragm-like ingrowths from the periphery towards the center is similar in both classes. During such division the daughter cells often remain joined by connections, while secondary divisions are in preparation. The parallelism in cell-division may indicate a remote affinity but may equally well be merely superficial.

In the large purple sulphur bacterium *Chromatium* the cell structure (Dangeard, 1909; Guilliermond, 1932; Delaporte, 1940, p. 42; cf., however, Fischer, 1897) resembles that of certain blue-green Algae inasmuch as the pigments are restricted to the outer cytoplasm, while the inner region resembles the centroplasm of Myxophyceae. Although the peculiar, almost homogeneous finely granulate appearance of the cell constituents increases the similarity, Guilliermond's view that *Chromatium* and its allies should be grouped among the Myxophyceae, cannot be accepted (Fritsch, 1945, p. 860), since the presence of flagella in the former is too strong an argument against such a relation. The peripheral location of the pigments in both cases may be due to the same physiological causes without a derivation from a common ancestry.

There are other differences in cell-structure between Bacteria and Myxophyceae. The former have a true cell-wall (Fischer, 1895, 1897b; Benecke, 1912, p. 90; Robinow, 1945), while the cells of Myxophyceae seem to be bounded merely by a differentiated layer of the outer cytoplasm, apart from mucilage (Geitler, 1936, pp. 25 *et seq.*; Fritsch, 1945, pp. 778, 788). Bacteria undergo true plasmolysis in hypertonic solutions. In the Myxophyceae the whole cell shrinks without the protoplasm being detached from the wall (Geitler, 1936, p. 4). Vacuoles filled with cell-sap, such as are found in higher plants and in many Algae and Fungi, are lacking in healthy cells both of Myxophyceae and of Bacteria. The former are suspected of having a gel-like protoplast although this requires substantiation (Fritsch, 1945, p. 771). It remains doubtful whether there is a resemblance in this respect to the Bacteria.

4. Physiological characteristics. Myxophyceae exhibit such varied habits and occur in habitats of such different kinds that no general conclusions regarding their ecological adaptations are possible. Species of blue-green Algae are found wherever living organisms can exist, occurring in marine and freshwater localities, in water rich in organic substances or containing extremely low concentrations of even indispensable inorganic salts. Many are terrestrial and some of them are among the first organisms to colonize barren rock and sand; some can stand high concentrations of brine, acids, hydrogen sulphide, or carbon dioxide. In short, Myxophyceae can adjust themselves to all kinds of extremes, even to the lowest and highest temperatures any organism can endure. Such adaptations are, however, found only in certain species or groups of species. Little is known of the capacity of the majority of Myxophyceae to accommodate themselves to their environment, nor what role competition may play in the predominance of certain forms in special habitats.

In this connection motility, dealt with in the next section, and resting stages are no doubt important. Among the latter the spores (akinetes) of Nostocaceae (*Nostoc*, *Anabaena*, *Cylindrospermum*) are noteworthy. They withstand drying and can germinate after long periods of inactivity. They can also survive heating almost to boiling point and cooling to −60 C. In all these respects their power of resistance contrasts with that of the vegetative cells of the same species which are even more susceptible than those of non-sporulating Myxophyceae (Glade, 1914).

Many Myxophyceae remain alive without multiplication for long periods of nutritional deficiency despite the absence of morphologically discernible adaptations. This was observed in cultures of *Synechococcus parvus* n.sp., *Merismopedia glauca*, *Oscillatoria formosa*, *Pseudanabaena catenata*, and *Phormidium faveolarum*. When the medium becomes nitrogen deficient the cells bleach out by reduction of the chlorophyll content (Magnus and Schindler, 1912; Pringsheim, 1913; Boresch, 1913) but on addition of nitrate recover their original hue even after many months. Such faintly colored trichomes are often found in nature, and there is every reason to assume that the phenomenon is the same. Although such growths may have long ceased to multiply they can still be used to start cultures, indicating that Myxophyceae are able to survive unfavorable conditions in this way. There is also evidence that numerous species can withstand desiccation in the vegetative state.

A comparison with Bacteria with respect to these properties is difficult. Except in really barren habitats Bacteria are also found everywhere, but little is known about those species which do not occur in dense populations and fail to multiply in routine bacteriological media. Certain Bacteria are adapted to all the extremes mentioned above for Myxophyceae. Some (e.g., Sarcina) are able to resist drying, others survive in an active state without much change or visible adaptation if the conditions of multiplication, e.g., in water devoid of nutrient substances, are lacking. Bacteria can also produce spores, though these are of a different morphological nature (cf. p. 54); they are still more resistant than those of Nostocaceae. Spores are produced both by aerobic and anaerobic Bacteria. Some of the nitrogen-fixing species sporulate, without any obvious relation to ecological conditions.

In popular descriptions and in textbooks emphasis is generally laid on the impressive chemical activity of Bacteria in relation to disease or the decompositon and fermentation of organic substances. Nothing of the kind occurs among Myxophyceae. In this respect the former approach more nearly to the Fungi, while Myxophyceae resemble the Algae, in correspondence with the possession of assimilatory pigments. The anaerobic fermentation, which is supposed to lead to the production of gas vacuoles in certain Myxophyceae (Canabaeus, 1928, p. 25, following a suggestion of Kolkwitz) has still to be proved experimentally. Even if colorless Myxophyceae (cf. p. 61) are included so that photosynthesis does not come into consideration, there is still a great divergence between the two classes in fermentative activity.

Actually only a relatively small number of Bacteria are conspicuous by their parasitism or the performance of large-scale chemical transformations, but it is just this minority which has provided the material for most bacteriological investigations. The great achievements thus attained must not distract attention from the fact that a large proportion, possibly the great majority of Bacteria, are very economical in their nutritional requirements and thus escape the attention of the bacteriologist.

Among Myxophyceae there are, on the other hand, a considerable number that live in an environment providing a rich supply of organic substances. Such forms are found in the mud of polluted waters, both marine and freshwater, on dead animals, feces, seaweeds, rotting wood, within the tissues of flowering plants (*Gunnera*, *Cycas*), or associated with other cryptogams (*Azolla*, *Blasia*, Lichens). Little is known of the biochemical, especially enzymatic, properties of these specialized forms, but there is some evidence that pigmented Myxophyceae, inhabiting spaces within the tissues of other plants, are able to multiply in the dark, if provided with sugar and organic nitrogen compounds (Pringsheim, 1917 Harder, 1917); certain free living species have been treated in a similar way without positive results (Pringsheim, 1913, and unpublished experiments). More species of Myxophyceae will probably be found to benefit from organic compounds in the substrate, although the mere presence of such substances should never be regarded as indicating that the organisms present are adapted to a heterotrophic or mixotrophic mode of nutrition, as has repeatedly been done (Pringsheim, 1913).

Fixation of elementary nitrogen has been established in various, otherwise unrelated microörganisms. Among Bacteria it takes place in *Azotobacter*, *Clostridium*, and *Rhizobium*, and in other endobiotic species. The fact that nitrogen fixation shows no relation to systematic position suggests that it may still be found in other organisms, perhaps in a less efficient form. This is also true of nitrogen fixation among Myxophyceae (Beijerinck, 1901) which so far has been established only in species of Nostocaceae (for references, see Fogg, 1942; Fritsch, 1945, pp. 871/72). This need not be a mere coincidence, but, owing to the difficulty of obtaining bacteria-free cultures, few Myxophyceae have so far been isolated in pure culture, and most of these have been lost. The pervading mucilage is generally inhabited by bacteria and much patience is necessary to eliminate these epiphytes (Pringsheim, 1946a, p. 94).

One special method of nutrition has long been regarded as the peculiar property of Bacteria, viz., chemo-autotrophy, or the utilization of chemical energy derived from the oxidation of inorganic compounds. Bacteria, which oxidize ammonia, nitrite, hydrogen, sulphur, hydrogen sulphide and other compounds of sulphur, are known to reduce carbon dioxide and to convert the organic substances thus synthesized into body-building material. *Beggiatoa*, the first organism recognized as living chemo-autotrophically (Winogradsky, 1887), is not, however, a 'sulphur bacterium', but a colorless member of Myxophyceae (cf. p. 63). This and the related genus *Thiothrix* have been shown to be autotrophic also in pure culture (Keil, 1912). The former, like many autotrophic bacteria, is also able to live on organic substances (Cataldi, 1940; and my own observations).

To sum up, there is no unbridgeable gap between Bacteria and Myxophyceae in physiological respects, but these classes have no feature in common which is not also found in other organisms. Of the two, certain Bacteria alone appear to have acquired an intensive biochemical activity and thus to consume an amount of material not required by organisms that live more economically.

5. Movement. Lower organisms exhibit two kinds of locomotion, swimming, and creeping or gliding. The mechanisms of both are still hypothetical. Swimming permits free movements through the water, while gliding requires a solid body or at least the surface film of the water as a substratum. The two modes of locomotion are mutually exclusive so that very few organisms (i.e., certain Flagellata, cf. p. 88) exhibit both, either simultaneously or at different stages of their life cycle.

So far as they possess active movement at all, Bacteria swim and Myxophyceae glide. The locomotion of Bacteria is brought about by flagella, as has been known since these organs were discovered in *Spirillum volutans*. The reasons for regarding the movements of Bacteria as caused by flagella were, for instance, discussed by Migula (1900, I, p. 110), and have never been challenged since.

Pijper (1940, 1946, 1947), however, has attempted to substitute for the concept of flagellar locomotion in Bacteria an undulating movement of the flexible body, the 'so-called flagella' being regarded as trailing strands of mucilage. In order to reduce the danger of confusion Pijper's views must be discussed here. Views analogous to his are to be found in the older literature. Nägeli (1849) believed that the flagella of algal swarmers were without significance for their movement. Van Tieghem (1879) tried to explain the movements of bacteria as being due to protoplasmic contractions, the flagella being superfluous appendages, an opinion which Hüppe and de Bary were inclined to accept.

In larger cells, like flagellates and the zoospores of algae, the flagella have long been recognized as organs of locomotion. Those of bacteria, already detected with the help of photographs by Koch (1877), were established as regularly present in motile forms by Löffler's (1889) method which was more extensively applied by Fischer (1895). These discoveries put an end to doubts as to the means of movement in bacteria.

In view of much evidence Pijper's contradictory theory is not convincing. There is no reason why the mechanism of swimming in bacteria should differ fundamentally from that of other flagellate cells. Their flagella are not strands of mucilage, but well-defined cell organs with specific antigenic properties. They can be seen as distinct threads not only in preparations stained in various ways and in electron micrographs, but also in the living organism. In large bacteria, such as *Spirillum volutans* and *Chromatium okenii* their active beating can be demonstrated. With the help of darkground illumination bell-shaped rotation figures can be observed and their reversal watched when the cells change the direction of their movement. Various species possess a definite number of flagella, with a characteristic arrangement and of a definite length. After division the newly formed ends of the daughter rods bear shorter flagella. Flagella are present only in motile species but are found in all of them and are confined to the motile stages. If they merely represented mucilage strands it should be possible to find motile bacteria devoid of such structures.

Pijper also fails to prove that bacteria possess a mechanism which could replace flagellar action. His own photographs (1946, pl. XLVII, fig. 20) show that, contrary to his statements, bacterial cells do not change their shape during movement. The slight curvatures seen in the photographs remain remarkably constant and reappear in the same shape after every rotation. The undulation of the body which is supposed to drive the bacterial cell through the water, does not exist. Many problems connected with flagellar movement remain unsolved, but there is little promise in Pijper's approach.

The evolution of flagella is entirely obscure. Since 'amoebae' are no longer regarded as mere lumps of protoplasm nor as the most primitive organisms, there are no grounds for interpreting flagella as modified pseudopodia. There are, moreover, organisms in which ameboid and flagellated organization exist side by side without apparent morphological relation between pseudopodia and flagella. Like those of flagellates, the flagella of bacteria are cytoplasmic organs connected through holes of the cell-wall with the surface of the protoplast ? (van Iterson, 1947, fig. 11; Kingma-Boltjes, 1948, p. 279).

No true bacterial organism (i.e., excluding colorless Myxophyceae and Myxobacteria) exhibits gliding movement. Winogradsky (1888) and Cholodny (1926, pp. 7, 10, 14) claim that the filaments of *Leptothrix* creep out of the old sheaths and form new ones, but this gliding movement is only a matter of conjecture. Special investigations directed to that end failed to provide confirmation of such movements either in liquid media or on agar (Pringsheim 1949a, p. 461). On the other hand such bacteria, as *Proteus vulgaris* and *Bacillus sphaericus*, which move over the surface of agar plates, appear to use flagella as the means of locomotion. M.

Gliding movement is characteristic of Myxophyceae, and no flagellate stages have ever been observed. The movements of *Oscillatoria* and *Beggiatoa* are generally familiar, although not completely elucidated (Fritsch, 1945, pp. 800–804), but the extent and frequency of locomotion among Myxophyceae are greater than often realized.

Stanier and van Niel (1941, p. 449), after enumerating the characteristics common to true Bacteria and Blue-green Algae, say: "One major difference, however, is the complete absence of flagellar motility in the Myxophyta, whose representatives are either immotile or exhibit creeping motility. It is among the Chroococcales, the most primitive assemblage of the Myxophyta, that we find forms closely resembling the Eubacteriales. A *Chroococcus* sp., for example, would be indistinguishable from a *Micrococcus* sp. if it were to lose its photosynthetic pigments." The general argument in this paragraph is sound. It was already hinted at by Benecke (1912, pp. 31/32) and is repeated, for example, by Dubos (1945, p. 11), although he does not mention its origin. The conclusion, though, that such primitive Myxophyceae have perhaps developed from Eubacteria (cf. p. 49) could with greater probability be reversed.

It does not seem, however, that the Chroococcaceae are generally immotile. Stanier and van Niel (1941, p. 452) mention Jahn's (1924, p. 102) claim to have found creeping motility in (unidentified) unicellular Blue-green Algae, although they state that this requires substantiation. A number of other instances of movement in Chroococcaceae have become known. Fritsch (1945, p. 800) believes it to be not uncommon. Geitler (1925, p. 110; 1936, p. 57) characterizes the movement of *Synechococcus* as slow and irregular; in the smaller species, which are more bacteria-like in appearance, it is said to be barely distinguishable from Brownian movement. It is not altogether certain whether *Synechococcus elongatus* Naeg. with rod-shaped, narrow cells (cf. Geitler, 1936, p. 20, fig. 11, a–c) differs from *Pelogloea* Lauterb., and whether the two species of the latter (Lauterborn, 1915), supposed to be Green Bacteria (cf. p. 80), are not mere modifications.

In order to obtain young vigorous cells these small forms were grown in soil-water cultures (Pringsheim, 1946b). Slow, swinging movements were observed in *Synechococcus elongatus* Naeg., *Chroococcus turgidus* (Kütz.) Naeg. var. *nigricans* n.var., *Chroococcus sabulosus* (Menegh.) Hansg., and *Aphanocapsa rivularis* (Carn.) Rabenh., their rapidity depending to a large extent on the condition of the cells. When multiplication ceases the movements slow down considerably and may cease to be observable.

It remains doubtful if there are completely immotile Myxophyceae. Gliding stages seem to occur widely in multicellular genera, where they play a role somewhat parallel to that of swarmers of other algae. Unicellular propagation stages were called planococci by Borzi (1914), who observed their slow irregular movements, in a number of hormogonales. In a similar way unicellular stages of Rhodophyceae exhibit gliding movements, for instance *Porphyridium cruentum* (Vischer, 1935; Pringsheim, 1949a) and spores and spermatia of other species (Fritsch, 1945, pp. 429, 433, 597, etc.).

Of colonial Myxophyceae, *Merismopedia* (Niklitschek, 1934, p. 212) and *Holopedia* (Lund, 1942) are known to show active movement. The entire, tabular or foliose, colonies, when buried in mud, creep slowly out of it or move towards a better illuminated region. This can be inferred from observations in cultures; when their position is altered by turning the tubes through an angle the colonies move towards brighter regions. *Holopedia* readily dissolves into pairs of slightly curved rod-shaped cells which move still more quickly, so that their translocation can easily be observed. The movement is an interrupted one, with a tendency for attachment by one end, while the other swings round, i.e., similar to that described by Geitler (1925, p. 110; 1935, p. 57). It is characteristic that the movement appears to be undirected over short distances. Whether there is really only dissipation or perhaps also phototaxis, as in *Porphyridium*, remains to be decided.

The same kind of gliding movement was observed in pairs of spherical cells belonging to *Aphanocapsa*, as well as in *Tetrachloris inconstans* Pascher (Geitler and Pascher, 1925, p. 456), the nearest approach to a 'green bacterium' which I could examine. The cells of this minute form, 1.2 to 1.5 μ in diameter and arranged in diplococcus-like pairs, have a faint greenish tinge while larger groups appear bluish-green. Their shape and behavior resembles that of *Aphanocapsa*, but the movement of *Tetrachloris* is more lively.

Other Myxophyceae also exhibit phenomena which can scarcely be explained without assuming active locomotion. How can the social habit of epiphytic genera like *Dermocarpa*, *Clastridium*, and *Chamaesiphon*,[3] the branched colonies of the last and the net-shaped aggregates of *Pelodictyon* be understood without the assumption of motility? In *Chamaesiphon incrustans* (?) growing epiphytically on *Rhizoclonium hieroglyphicum*, the characteristic myxophycean movement could actually be observed, in detached vegetative cells as well as in the spores.

Gliding movements thus occur, not only in the Oscillatoriaceae and in the hormogonia of all the Hormogonales, but also in many Chroococcaceae, in Chamaesiphonales and Cyanochloridinae. Although Geitler (1936, p. 57) is of the opinion that the movement of unicellular stages is different in its nature from that of filamentous ones, there is in view of the existence of unicellular and multicellular hormogonia some possibility of its being essentially the same. There is thus little probability that colorless Myxophyceae would be indistinguishable from Bacteria, although a few debatable cases may still perhaps be found. Colorless Bacteria, parallel to the Chroococcaceae, like *Micrococcus*, *Sarcina*, etc. are different by their gram-positivity, and the gram-negative bacteria *Gonococcus* and *Meningococcus* are also not likely to be apochlorotic members of Myxophyceae, while true colorless members of the latter have been discovered and recognized as such by their gliding movements (see following chapter).

III. COLORLESS MYXOPHYCEAE

1. Chamaesiphonaceae and Oscillatoriaceae. The few colorless Myxophyceae so far known belong to all three of the main series, into which Geitler (1925) divides the class: Chroococceae, Chamaesiphoneae and Hormogoneae, or to three of Fritsch's five orders, viz. the Chroococcales, Chamaesiphonales and Nostocales. The colorless Chroococcales will be described in section (*4*) below. It is as yet not possible strictly to follow the classification of Myxophyceae when dealing with colorless forms.

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[3] *Ankistrodesmus* and *Echallocystis*, it is true, may have a similar habit.

A pigment-free *Chamaesiphon*, described by Scherffel (1907; cf also Geitler, 1925, p. 151) is somewhat dubious. According to Geitler (1925, p. 148; 1932, p. 428) Scherffel's *C. hyalinum*, 'which may not be a blue-green alga at all', is faintly colored like *C. macer*, the bluish-green tinge of which is only recognizable in dense aggregates. Such very faintly pigmented species are not uncommon among Myxophyceae. Bavendamm (1924, p. 45) mentions another "colorless *Chamaesiphon*" without giving any description of it.

Among Oscillatoriaceae there are several forms with so little pigment that individual filaments may appear to be colorless. The minimum amount of chlorophyll sufficient to support adequate photosynthesis is not known, so that it is not justifiable to conclude that such forms are heterotrophic or mixotrophic. Moreover, Myxophyceae tend to bleach when the medium becomes deficient (Magnus and Schindler, 1912; Pringsheim, 1913; Boresch, 1913). *Pseudanabaena catenata* Lauterb. and *Oscillatoria formosa* Bory, for instance, look almost colorless in old exhausted cultures, although the trichomes are still motile. They soon recover their blue-green tint and multiply again when nutrient salts are added. Lauterborn (1915, p. 435) and Geitler (1925, p. 38; 1936, p. 8) record pale yellowish Myxophyceae which inhabit mud rich in hydrogen sulfide and which they regard as constituting a special ecological group. *Pseudanabaena catenata* and *Oscillatoria formosa* are supposed to belong to this group (Lauterborn, l. c., p. 437; Geitler, 1925, p. 372). As they are blue-green when in a healthy state, it is possible that the others would also turn blue when supplied with proper nutrients.

Species with a very pale bluish color are *Lyngbya endophytica* Elenkin and Hollerbach (Geitler, 1925, p. 402) inhabiting algal mucilage, and *Oscillatoria decolorata* West, stated to lead a saprophytic existence in stagnant ditches (Bhâradwâja, 1940, p. 204). *O. beggiatoiformis* (Grun.) Gom. is not colorless like *Beggiatoa*, but faintly blue-green. *O. angusta* Koppe (1924), again from oxygen-free mud (gyttja) is described as really colorless; but Geitler (1925, p. 365) questions the absence of pigments. Almost colorless is also *O. profunda* Kirchner from the bottom of a deep lake, and likewise *O. koprophila* Skuja (1948, p. 46) from a similar habitat. *O. beggiatoides* Arzichowsky (1902; cf also Kolkwitz, 1909, p. 153), which is described as colorless, and stores sulfur, is supposed to be a link between *Beggiatoa* and *Oscillatoria*. How it differs from *Beggiatoa* could not be ascertained as the paper was not accessible (cf. Bavendamm, 1924, p. 104).

In none of the instances of almost pigment-free species of *Oscillatoria* is the issue quite clear, owing to the lack of culture experiments. There is, however, no doubt as to the existence of chlorophyll-free Myxophyceae. *Beggiatoa*, when it lives saprophytically, is barely distinguishable from an apochlorotic *Oscillatoria* (cf. section *2*, below), while *Spirulina albida* Kolkwitz (1909, p. 137), which, like other Spirulinas, differs only in its spirally shaped body, is certainly chlorophyll-free and saprotrophic. Geitler (1925, p. 346) at first regarded *S. albida* as a very dubious form, but finding it later (1932, p. 927) on slides exposed in a stream, accepted it as a true heterotrophic member of Myxophyceae (so also 1942, p. 34). The trichomes were colorless and showed not the slightest tint even when massed. In a recent letter he again expresses doubts regarding its taxonomic position. Apochlorotic Myxophyceae are not given much prominence in Geitler's books, and he tends to deny their existence.

Spirulina albida is not rare in England, occurring in the surface film of waters where the bottom is covered with black mud. It was twice cultured as a unialgal strain for nearly a year in a mixture of soil with a little organic matter but, although it was often subcultured, I was not successful in growing it free from bacteria. This was achieved by Dyar (1947) who found that on agar with sterile blood it multiplies and glides over the surface, freeing itself from contaminating organisms so that pure cultures were obtained. Dyar calls the organism *Spirochaeta plicatilis* Ehrbg., but her description and figures show clearly that it is *Spirulina albida*, and by her courtesy I was able to establish its complete identity with the material studied earlier.

The relation of *Spirulina* to *Spirochaeta*, which has repeatedly been discussed will be dealt with later (cf. p. 82). Here it suffices to mention that *Spirulina albida* is 0.8 to 1.2 μ wide, successive coils being 3 to 6 μ apart, and 2 μ wide, while *Spirochaeta plicatilis* is about 0.3 μ wide, the coils being close together and about 1 μ wide. *Spirochaeta plicatilis* is unicellular, while *Spirulina albida*, like other Oscillatoriaceae, consists of a number of cells, into which it disintegrates when injured.

The kind of movement is also different. *Spirulina albida*, like other members of its genus, has a certain degree of rigidity, although it bends slowly and slightly to and fro when entangled between detritus, as is often the case in its natural habitat. When mounted on a slide it commences after some time to glide in an almost straight line over the glass surface, meanwhile rotating on its axis. *Spirochaeta plicatilis* also rotates during movement, but does not keep a straight line, turning in various directions without apparent cause (cf. also p. 83).

2. Beggiatoaceae. When Bhâradwâja (1940, p. 204), in his review of the relations between Myxophyceae and thread-bacteria, states that 'heterotrophic colorless forms in the blue-green algae are not known to occur with certainty', he does not take the Beggiatoaceae into consideration because he believes their cell structure to be fundamentally different from that of the Oscillatoriaceae (l.c., p. 205). This opinion cannot be accepted (cf. p. 54).

The presence of sulphur droplets in the cells of *Beggiatoa* and Winogradsky's (1887) demonstration, more precisely confirmed by Keil (1912), that *Beggiatoa* can live without organic substances, have produced such an impression on biologists that the 'sulphur bacteria' were regarded as falling outside the range of other colorless organisms. This group was henceforth grouped together with others likewise oxidizing hydrogen sulfide and storing the sulfur inside their cells, like *Thiothrix*, *Thioploca*, many purple bacteria and certain colorless unicellular organisms (*Achromatium*, *Thiospirillum*, *Thiovulum*, etc. as Thiobacteriales (Bergey, 1926, p. 402)). The latter are, however, a conglomeration of taxonomically unrelated forms, and the discovery of sulfur also in pigmented Myxophyceae (Hinze, 1903b; Nakamura, 1937) shows that the sulfur organisms are a biochemical group like the iron organisms (Pringsheim, 1946b) and not a taxonomical unit.

Beggiatoa was in fact long ago recognized as a pigment-free relative of *Oscillatoria.* Vaucher described it under the name *Oscillatoria alba* as long ago as 1803. Cohn (1871/72, p. 186) included *Beggiatoa* and *Leptothrix* (syn. *Thiothrix*) as colorless subgenera of *Oscillatoria.* Van Tieghem (1880) states that certain Oscillatoriaceae (e.g., *Beggiatoa* and *Thiothrix*) lack chlorophyll. The name 'Sulphur Bacteria' (Winogradsky 1887, 1888) created confusion, although Solms-Laubach (1901) criticizes Wettstein for including *Beggiatoa* among the bacteria in opposition to the view then generally accepted.

It is, however necessary to consider whether the striking similarity is merely superficial and the result of convergent evolution, or whether a true relationship can be proved by other resemblances.

The little there is of differentiation in *Oscillatoria* is evident also in *Beggiatoa.* It is provided by the biconcave cells and the different end-cells of the filaments. Only the calyptra covering the tip in many species of the former genus is lacking in the latter. According to Geitler (1925, p. 338), 'The Oscillatoriaceae are probably not as little specialized as they seem. Their organization is complicated by segmentation, rhythmical growth and spiral symmetry of the cells.' The trichomes are slightly constricted at intervals, and the segments thus defined are of the same length as actively moving hormogonia. Each segment probably contains the descendants of a single cell (Geitler, 1932, p. 907, and own observations; cf. also *Caryophanon* p. 74 for comparison).

As observed in several species when actively growing, cell-division is not evenly distributed over the length of an Oscillatoria-trichome. Regions with short, evidently young, dividing cells alternate with others in which the cells enlarge but do not divide. The maximum length of the cells is reached only after several divisions, mostly the third (Geitler, 1932, p. 231). Owing to these morphological complexities and the great variety of forms Geitler (1925, p. 349) apparently believes that *Oscillatoria* is a relatively young and highly derived genus (although on page 36 of the same book he ascribes a great age to it), while 'the Beggiatoaceae by their simple cell-organization and their autotrophic nutrition belong to the most primitive plants' (Geitler, 1934, p. 191).

Actually it seems that the trichome organization is the same in *Beggiatoa* as in *Oscillatoria.* According to Hinze (1901, p. 373) 'Cell-division is markedly intercalary in *Beggiatoa mirabilis*; . . . in a relatively long filament, for instance, nearly a quarter of the cells are dividing almost simultaneously. Usually several adjacent cells, sometimes two, oftener three, divide at the same or nearly at the same time; during this period neighboring cells elongate and divide soon afterward . .' . The analogy is perfect and, as my own observations show, the smaller species of *Beggiatoa* behave in the same way as *B. mirabilis.* There is also in *Beggiatoa* a wide range of closely related forms, differing essentially only in their dimensions so that this genus might likewise be regarded as being in full evolutionary development, while the faculty of living chemo-autotrophically has nothing to do with primitivity.

The movements have been studied in both genera by competent investigators without producing a better explanation of their mechanism than has been obtained for other gliding organisms. The name *Oscillatoria* refers to the oscillating movements of the terminal part of the filaments. The oscillating appearance under the microscope is due to the optical projection of a conical circulation complicated by the friction between slide and slip which forces the tip to describe a narrow ellipse instead of a circle. It is the same in *Beggiatoa.*

Oscillatoria exhibits translocatory movements only when some part of the trichome is in contact with a solid body or the air-water surface. Forward movement is generally accompanied by rotation, and there is a certain relation between the two (Correns, 1897, p. 141), although some change of place can occur without rotation which seems to be lacking in certain species (Hansgirg, 1883) and in hormogonia (Harder, 1918). I have observed a faintly blue *Oscillatoria* and a narrow *Beggiatoa* moving to and fro without alteration of the slight, irregular undulation of the filaments and without rotation. The delicate mucilage sheath (Niklitschek, 1934) becomes visible in material mounted in fine suspensions (Correns, 1897, p. 146) and on agar, where it can be stained with safranine (Pringsheim, 1913, p. 67). The surrounding mucilage supposed to be lacking in *Beggiatoa* has been detected by Keil (1912, p. 362), and this removes the last morphological difference. In all these respects there is therefore complete agreement between *Oscillatoria* and *Beggiatoa* (cf. Kolkwitz, 1897, p. 463/64; and also own observations).

The trichomes both of *Oscillatoria* and *Beggiatoa* possess a certain degree of elasticity and straighten after having been bent. On the other hand they are also pliable, circumventing obstacles with which they come in contact during forward gliding. There is no spontaneous flexibility, bending resulting from resistance and disappearing with it (Kolkwitz, 1897, p. 461).

Small particles adhering to the filaments of *Oscillatoria* travel along the surface, at some places in one and at other places in the opposite direction. They thus form dense accumulations at certain points on the filaments. These accumulations are not static but change their positions. The direction of movement of the particles may reverse in any part of the filament (Correns, 1897, p. 144). The same can be said of *Beggiatoa* (Keil, 1912; and own observations). The phenomenon just discussed is no doubt in some way related to the still unsolved problem of the mechanism of movement.

In *Oscillatoria* rhythmic waves of contraction are commonly accepted as the chief cause of locomotion, as first suggested by Engelmann (1879, p. 55) and more clearly by Schmid (1923, p. 383). For *Beggiatoa* a similar view has been propounded by Benecke (1912, p. 150), and Ullrich (1926, 1929) demonstrated the existence of such waves in *B. mirabilis.* Other hypotheses that have been brought forward (cf. Fritsch, 1945, p. 802) are not very helpful. Even the contractile wave theory does not satisfactorily explain all the phenomena. Periodic contractions cannot well be the cause of the gliding movements of unicellular Myxophyceae (cf. p. 61), nor of those of few-celled or one-celled hormogonia, which Geitler (1935, p. 57) believes to be of a different nature. Contractile waves have not at present been demonstrated in hormogonia at all (Fritsch, 1945, p. 803). Nor does the theory explain the role of mucilage-secretion which seems to be closely related to some still unknown mechanism concerned in the gliding of these organisms. Such a connection is suggested by the same phenomenon occurring in other gliding organisms. Myxobacteria (Jahn, 1924, p. 33), *Porphyridium* (Vischer, 1935, pp. 79/80), *Vitreoscilla* (cf. p. 71), as well as diatoms and amebas (e.g., *Naegleria Gruberi*; own observations) leave similar muclilage-tracks behind them, when moving over an agar surface. The importance of such residua and the contact with the substratum obtains support through observations that the direction of movement of gliding organisms is influenced by slight tensions in the agar (Stanier, 1942b, 1947b), as well as by their own previous mucilage-exudations.

It remains to compare the method of reproduction. In *Beggiatoa* and in numerous species of *Oscillatoria* the trichomes can grow to great lengths. Under unknown circumstances they break up into shorter units, called hormogonia, which exhibit lively movements and, by cell division and extension, again form long filaments. Their length is not related to the commencement of hormogonium formation. An improvement in nutritive conditions, after an interruption in development caused by a deficiency, seems to induce the onset of the reproduction phase.

Hormogonia are produced by active changes in the trichomes and develop specially shaped end-cells which artificially formed fragments are unable to produce. The injury resulting from mechanical fragmentation is often fatal, and short pieces of trichomes cannot be used for starting cultures. Even long filaments do not generally survive local lesions (Omelianski, 1904, p. 228; Cataldi, 1941). This indicates an intimate interrelation between the cells, such as is lacking in most other filamentous algae. The thread of an *Oscillatoria* or other similar member of Nostocales can be interpreted as an imperfectly septate derivative of a unicellular individual (Fritsch, 1942, p. 141; cf. also Crow, 1922, p. 85). The regions of dividing and enlarging cells, which can be distinguished in the trichomes, seem to be derived from one original cell. These are also the filamentous units which are transformed into hormogonia.

Beggiatoa again behaves like *Oscillatoria*. The filaments divide into portions which have the value of hormogonia and move actively (Winogradsky, 1888; Benecke, 1912, p. 205).

The great variation in width of the threads of *Beggiatoa* (Winogradsky, 1888; Klas, 1937) is remarkable. Winogradsky (l.c., p. 610) maintains that the species, which differ only in the diameter of the cells, are perfectly constant, but there is considerable variability in clone cultures. The definition of species in *Beggiatoa* is therefore still dubious (Bavendamm, 1924, p. 106). The situation is similar in certain species of *Oscillatoria*. In *O. princeps*, for instance, the variation in dimensions is far greater than one would expect in a well-defined species.

While there is thus striking resemblance between *Beggiatoa* and certain Oscillatorias, except in pigmentation and sulfur content, some authorities lay great stress on differences in the structure of the protoplast (cf. p. 54). Fischer

(1897) and Guilliermond (1926a) failed to find in *Beggiatoa* the differentiation into outer and inner protoplasm seen in many pigmented Myxophyceae, in spite of the employment of various staining methods. Guilliermond, who regards the central body as a primitive nucleus, says in regard to *Beggiatoa* (l.c., p. 581): 'on ne retrouve donc rien analogue à un noyau, ni au corps central des Cyanophycées.' Although an analogous conclusion of Bütschli's (1896, 1902) had already been disproved by Fischer (1897, p. 8), Guilliermond (l.c., p. 580) decides that the cytological structure of *Beggiatoa*, despite its general similarity to *Oscillatoria*, shows that it belongs to the Bacteria. Migula (1900, p. 40) states that '*Beggiatoa* follows *Oscillatoria* closely, even in its internal structure (existence of central body), so that the two genera can scarcely be separated', without giving the authority for his statement. Guilliermond's results have been confirmed by Petter (1933) and Delaporte (1939, p. 764); and Fritsch (1945, p. 860) summarizes the position in the words, 'The facts above detailed suggest the possibility that these types belong to a plurality of evolutionary lines diverging from a remote ancestry, from which the Myxophyceae also arose.'

In my opinion the loss of pigments may have been accompanied by a loss of differentiation within the cytoplasm (cf. p. 54), so that such a difference between *Beggiatoa* and *Oscillatoria* is not irreconcilable with their affinity. Skuja (1948 p. 46; cf. p. 62) has, however, observed a colorless species, referred by him to the latter genus, in which the central body is recognizable.

Thioploca is similar to *Beggiatoa*, except that the filaments are aggregated to form bundles enclosed within a common sheath. The analogy to *Hydrocoleus* and *Microcoleus* among pigmented Myxophyceae is obvious. The hormogonia of *Thioploca* enlarge into trichomes within the sheath without much movement. Lauterborn (1907), who discovered the genus, found the trichomes full of sulfur droplets and showing a bluish tint. Wislouch (1912) described a second species, having a faint bluish-green color, but only when the sulfur content was high. This does not suggest that the color is due to pigmentation as in the Myxophyceae, but rather that it might be due to some optical effect. Kolkwitz (1912), who was unable to detect any color in an otherwise identical organism, reports that 'the trichomes were as colorless as those of *Beggiatoa alba* present in the same preparation.' Both also presented the same appearance in dark-ground illumination, without any sign of fluorescence.

3. Thiotrichaceae. Thiothrix is customarily placed close to *Beggiatoa*, with which it shares the mode of nutrition and the storage of sulfur droplets in the cells (Winogradsky, 1888; Keil, 1912). It inhabits running water, where *Beggiatoa* would be washed away, being attached to a solid substratum by a basal holdfast. The absence of motility and the differentiation between base and apex, which is lacking in *Beggiatoa*, would in certain groups be regarded as sufficient for the establishment of a separate family. *Thiothrix* is therefore classed here as a representative of the Thiotrichaceae.

Reproduction is brought about by the detachment from the free ends of the trichomes of short lengths which give rise to new growths after attachment to some substratum. Winogradsky (1888) and Wille (1902, p. 259) describe gliding movement of these reproductive bodies, but the formation of true hormogonia could not be confirmed by more recent observations. Keil (1912, p. 363) observed plenty of these hormogonia-like structures, but failed to find active movement, and I was equally unsuccessful. The capacity for gliding movement is, however, easily disturbed by changed conditions, and the settlement of young filaments is scarcely explicable without motile reproductive stages. True hormogonia may therefore well occur in *Thiothrix*.

If so, its nearest relatives must be sought among the pigmented Myxophyceae. Migula (1900, p. 40) does not include *Thiothrix* in the Beggiatoaceae, but in the Chlamydobacteriaceae; but the similarity between *Thiothrix* and *Leptothrix*, which ranked for some time as synonyms, is only superficial since the latter possesses flagellate reproductive stages (cf. p. 78). No blue-green alga, parallel to *Thiothrix*, seems to be known. The nearest approach is constituted by attached species of *Lyngbya*. The formation of few- or one-celled hormogonia from the ends of the filaments does not seem to have been observed in this genus, but it occurs in other Myxophyceae.

4. Achromatiaceae. The forms included in this family, the type of which is *Achromatium oxaliferum* Schewiakoff, are unicellular, deposit sulfur droplets and exhibit a peculiar movement. There are a number of genera: *Achromatium* Schewiakoff 1893, *Modderula* Frenzel 1897, *Hillhousia* West and Griffiths 1909, 1913, *Thiophysa* Hinze 1903, and Nadson 1914. Some of these names, perhaps even all, seem to be synonyms. *Achromatium* may, however, represent the freshwater and *Thiophysa* the salt water species. *Thiovulum* and *Thiosphaerella*, sometimes placed close to *Achromatium*, are flagellate and do not therefore belong to the family.

The name Achromatiaceae seems to have been used first by Buchanan 1918 (Bergey's Manual, 1926, p. 402) for an assemblage of unrelated forms, including for instance *Thiospira* Wislouch 1914 which is morphologically a typical flagellate *Spirillum*. The same confusion is found in Buchanan's contribution to Bergey's Manual of 1939 (p. 910). Moreover, the author maintains that 'Cell division (in *Achromatium*) resembles the constriction of flagellates rather than the fission characteristic of bacteria', forgetting that in the Coccaceae cell division is generally of this type.

As a more natural classification, the family Achromatiaceae is here restricted to non-flagellate organisms showing gliding movements, and constitutes the unicellular parallel to the Beggiatoaceae. The first organism of this group to be observed was interpreted as a stage in the life cycle of *Beggiatoa mirabilis* (Cohn, 1867), with which it was associated. This form was marine, and Kolkwitz (1909) refers it to *Thiophysa*.

The practice of certain authors to regard flagellate, and non-flagellate, gliding species as near related, or even as belonging to the same genus, must be abandoned. Ellis (1932), for instance, at one place (p. 116) speaks of cilia in *Thiovolum* and at another place of its being devoid of cilia (p. 125), while the authors of *Hillhousia* erroneously describe it as having peritrichous flagella, whereas sulfur bacteria have polar flagella, if at all; this latter mistake is repeated by Buchanan (in Bergey, 1939, p. 910), although the character of the movement could not be explained on this basis. Lauterborn's (1915, p. 413) *Achromatium mobile* (syn. *Macromonas* Utermöhl and Koppe; *Microspira* Gicklhorn) is described as possessing a polar flagellum but, although it was found in company with *Achromatium oxaliferum*, it cannot be grouped in the same genus with this gliding organism which has no flagella.

In *Achromatium* there is a considerable range of sizes. Bersa (1920, p. 233) found the length to be between 9 and 75 μ, with all intermediate lengths represented, the usual dimensions being 30 to 40 μ long and 10 to 18 μ broad. The cells of Nadson's (Ellis, 1932; Nadson and Wislouch, 1923?) *Achromatium gigas* even reach a length of 102 μ, while Bavendamm (1924) records small individuals, as short as 3 μ. The occurrence of forms showing a wide range of widths is one more parallel to *Beggiatoa.*

Achromatium, in its movements and morphological features, resembles *Synechococcus* in the family Chroococcaceae among Myxophyceae. Stanier and van Niel (1941, p. 453/54) rightly say: 'it is tempting to compare them (i.e., *Achromatium*) with such members of the Myxophyta as *Synechococcus aeruginosus,* to which they might well be related in the same manner as *Beggiatoa* is to *Oscillatoria.*' Both forms are cylindrical with rounded ends and divide by median constriction. *Synechococcus aeruginosus* is the largest species, being about 60 μ long and 40 μ wide. The habitats occupied by the two genera are, however, very different, so that a direct transformation of *Synechococcus* into *Achromatium* cannot have taken place.

The movement of *Achromatium* has been described by Schewiakoff (1893), Zacharias (1903a), and Virieux (1912, 1913) as spasmodic, slow, rolling, changing its direction irregularly, jerky, interrupted,—in short a very different kind of movement from that of flagellate bacteria, indicating that it does not belong to the Bacteria, to which it was so often relegated. The movements of *Synechococcus* are described in the same way, almost with the same words (cf. Geitler, 1925, p. 110; 1936, p. 57). According to Virieux (1913, p. 267; West and Griffiths 1913, p. 83) and my own observations *Achromatium* adheres to the slide by a thin mucilaginous exudation, and the same has been observed by me in *Synechococcus elongatus* n. var. *parva.*

Virieux (1912, p. 279/80) records that, in addition to division of cells into two, the formation of large numbers of endospores takes place in *Achromatium.* This method of spore production is known in many Myxophyceae, for instance in *Aphanothece,* a genus similar to *Synechococcus* (cf. Fritsch, 1945, p. 810), but not in any member of the Bacteria.

Thiophysa, with the marine or brackish-water species *T. volutans* Hinze and *T. macrophysa* Nadson, appears to be related to *Achromatium,* although it is difficult to assess this on the little information available. It is still more difficult to say anything definite about *Thiovulum Mülleri* Warming (syn. *Achromatium Mülleri* (Warming) Migula (cf. Molisch, 1912, p. 55)) and *Thiosphaerella amylifera* Nadson, which Ellis (1932, p. 116) groups among the Achromatiaceae. The ellipsoid cells of *Thiovulum majus* (Hinze, 1913, p. 198) are stated to be covered with flagella 0.7 μ thick and to exhibit a movement which is more rapid than that of *Achromatium*. The 'flagella' appear to be bacteria like those described in *Hillhousia* by West and Griffiths (1913, p. 83).

5. Vitreoscillaceae. As stated above, *Beggiatoa alba* can live heterotrophically without depositing sulfur and cannot then be distinguished from a colorless *Oscillatoria*, although the existence of such species is not established beyond doubt. Geitler, in his various synopses, says little about pigment-free members of Myxophyceae, and other authors do not mention them at all, whereas, according to Fritsch (1945, p. 871) 'there can be no doubt that colourless Myxophyceae occur in a free state in nature'.

There are, in fact, numerous colorless, filamentous, gliding organisms, which are by no means rare and are easily demonstrated, so that it is difficult to understand how they have escaped notice. They live in a variety of habitats and are almost regularly present amidst floating masses of filamentous blue-green algae; other species live in cow dung, in the mucilage of various organisms (e.g., *Ophrydium*, accompanied by *Oscillatoria amphibia*), and between débris in the surface scum of stagnant waters, particularly those with a bottom of black mud. Seven species, one marine, have so far been isolated in pure culture, although in many cases attempts to culture such organisms have failed. While all have distinctive features of their own, some are similar to a colorless *Oscillatoria* or a sulfur-free *Beggiatoa*, so that they were suspected of belonging to the latter genus until the inability to deposit sulfur from hydrogen sulfide had been established.

It is proposed to include these organisms in the new family Vitreoscillaceae, with *Vitreoscilla beggiatoides* as the type. Four of the species, that have been cultivated possess cylindrical threads, while the others are more or less constricted between the cells so that the trichomes are moniliform. Most of the species tend to break up into short lengths (hormogonia) more readily than *Beggiatoa alba*, and only in one of them do the filaments reach a great length under favorable circumstances.

The length of the trichomes and the degree of constriction are so variable, even in one and the same strain, that distinct genera cannot be established, although some of the forms not yet grown in culture differ more profoundly. The various species seem to be confined to certain habitats, but the chief characters are furnished by the width and length of the cells, the tendency to fragment into short lengths, the rapidity of movement and the cultural behavior and appearance. Other differentiating features may be found by more detailed physiological and cytological investigations.

The cells have a low refractive index, rather like that of Myxobacteria, so that the small, narrow species are not readily observed under low power. The cells are gram negative, but stain well with bacterial dyes and vital stains. Old or unhealthy growths contain fat and volutin, while those in vigorous development appear optically almost empty. They possess nucleoid structures not very different, as far as investigated, from those of Bacteria. Cell-division takes place by diaphragm-like ingrowth of the cell wall, much as in Myxophyceae and Bacteria. Hormogonia are initiated by certain constrictions deepening to form circular grooves, so that the descendants by division from one original cell are eventually separated from others. The frequency of such fragmentation varies within the same species with the conditions of growth, as does also the length of the cells.

These organisms, which earlier biologists would probably have regarded as Bacteria, differ from them essentially in their gliding movements. These also facilitate their separation from other microörganisms during the preparation of pure cultures. The trichomes of *Vitreoscilla* escape from aggregations of other organisms which cannot move over an agar surface, so that the technique of their isolation is the same as that devised by Cataldi (1940) for *Beggiatoa*. *Vitreoscilla beggiatoides*, the first species grown in pure culture, was, however, purified by washing by the pipetting method.

Four species were isolated from cow-droppings on plates of dung-agar, but the pure cultures grew better on other media. The remaining 3 species were isolated using an agar medium with neutralized yeast extract. Relatively low concentrations of proteid substances, ranging from 0.05 to 0.3% were found to be most suitable, not only to obtain pure cultures, but also to maintain them in a healthy state. None of these organisms seems to live in heavily polluted water. Although not specially delicate, they do not stand competition very well.

The gliding habit determines the nature of the growths on agar, most species producing wavy, curly, or spiral colonies on media of not too high a nutritive value. On rich media drop-like colonies, resembling those of many bacteria, are formed. In the former case single filaments project and start growths on free portions of the agar surface. The projecting strands gradually become wider as the trichomes elongate and glide past one another, forming outgrowths and twirls. A characteristic feature is the production of new colonies, at a distance from the original growth, from individual trichomes which leave tracks behind them as they glide forward. Such secondary colonies cannot be formed by organisms lacking the capacity for gliding movement, although the growths may otherwise be strikingly similar owing to the possession of long threads by the organisms concerned. This is so, for instance, in *Bacillus mycoides*, *Lineola longa* (Pringsheim and Robinow, 1947), and *Sphaerotilus natans* (Pringsheim, 1949a), three bacteria which, though not closely related, all produce spirals and curls but show always a connection with the place of inoculation.

All the species of *Vitreoscilla* resemble *Beggiatoa* in being able to live on peptone, beef extract, yeast extract and the like. Sugar produces no favorable effect, and that of acetate is not very pronounced. This group therefore seems, like the majority of heterotrophic microörganisms, to have no specific biochemical properties, but to utilize compounds formed in the bacterial decomposition of proteins. None of them seems to be able to hydrolyze genuine proteins. Casein is not dissolved, nor is gelatine liquefied.

In liquid media growth occurs only with concentrations of nutrient substances even lower than in agar media. A suitable solution contains 0.04% yeast extract, 0.04% Bacto tryptone, 0.02% beef extract, and 0.02% sodium acetate. Mixtures are on the whole better than single substances. A medium composed of 0.1% yeast extract and 0.1% Bacto tryptone needs the addition of soil extract, this mixture being the best so far tested. Multiplication is never as luxuriant as on agar, but the trichomes appear healthier and more like the original material, and show pronounced motility, seen especially well at the margin of small hanging drops on a fat-free cover-slip.

Apart from the species grown in pure culture, only a few others presenting characteristic features have so far been distinguished. It is doubtful whether they should all be included in the genus *Vitreoscilla*. A few are described below.

The specific name of *Vitreoscilla flagellum* refers to the lively movements of its narrow trichomes (about 0.3 μ wide) which almost give the impression of a flagellum of *Euglena*. Cells could not be distinguished. The length of the trichomes varies greatly, the shortest not exceeding 10 μ, while the longest are so much curved and entangled that they cannot be measured, although certainly more than 100 μ long. This species was found frequently among filamentous Myxophyceae, such as *Oscillatoria amphibia*. It resembles *Vitreoscilla marina*, but is narrower and confined to fresh water.

V. stricta was found in a pond with water fowl and in a pool polluted by cattle, both containing iron organisms and a multitude of pigmented flagellates. This species is characterized by its rigid trichomes which during the lively gliding movements bend only when caught between obstacles and straighten out immediately when they become free. In the marked elasticity of the trichomes, which are about 1 μ wide, it differs from other species of the genus, as well from *Beggiatoa*, but only in degree. The cylindrical cells were full of small granules.

An organism found only as a few individuals, though in various places between debris and algae may be named *Bactoscilla flexibilis*. The generic name refers to the fact that the short trichomes are composed of a number of rods, about 0.5 μ wide, apparently separated by empty interspaces. The peculiar feature of this genus is the slow, though pronounced bending, during which the individual rods remain straight. The structure is therefore comparable to that of *Lineola articulata* n.sp. (unpublished); but while this filamentous bacterium swims with the help of peritrichous flagella, *Bactoscilla* is a gliding organism. In both forms, it is the invisible matter constituting the hinge-like joints that bends. This is similar, though far less evident, in other members of the Vitreoscillaceae, for instance in *Vitreoscilla moniliformis*, the widest species of all, as well as occasionally in *V. paludosa*, but, owing to the shortness of the cells, not quite certain. The occurrence of such a mechanism, although obscure in its physical nature, renders a general application of the contractile wave theory still more difficult.

Certain yet smaller filamentous forms, to be grouped in the same genera or in a third one, *Microscilla*, are only mentioned here to illustrate the range of unknown organisms still to be described. They may possibly have some relation to the Myxobacteria, to which, as filamentous members, they may form a transition.

IV. ORGANISMS WHOSE AFFINITY WITH BACTERIA AND MYXOPHYCEAE IS DISPUTED

1. Caryophanon and Oscillospira. Caryophanon was discovered and isolated by Peshkoff (1940). It is the largest bacterium ever grown in pure culture, and for this and other reasons of considerable interest. Peshkoff's title 'Phylogenesis of two microbes *Caryophanon latum* and *C. tenue*, organisms which are intermediate between Blue-green Algae and Bacteria' explains why some space must be devoted to a discussion of these organisms.

Although most of the features stated to be characteristic of the genus could be corroborated by an investigation of *C. latum*, Peshkoff's cytological data were found to be incorrect, and his views as to taxonomic relations had to be refuted (Pringsheim and Robinow, 1947). It is curious that Peshkoff (l.c., p. 615/16) although admitting that *Caryophanon* is a 'typical bacterium . . . owing to its peritrichate flagella and some other features', believes that 'the type of its nucleal apparatus suggests its direct relationship to the Blue-green Algae.' In actual fact it is, just as in *Oscillospira*, the appearance of the trichomes which suggests a similarity to the Myxophyceae and not the nature of the cell-contents.

Peshkoff devoted much attention to the nuclear apparatus but, owing to an unmethodical use of various fixing and staining methods, he misapprehended the cellular and nuclear organization. As nuclei of *Caryophanon* he describes various structures which cannot well be identical, to wit (1) Denser regions in the living organism and arranged in a row within the filaments are interpreted as nuclei, hence the generic name. They are also shown in some of his photographs of stained preparations, where they appear as elongate structures placed transversally, or as V-, H-, and X-shaped bodies. They probably comprise the whole or nearly the whole of the protoplast, which is repeatedly cut into by penetrating cross-walls during the process of cell division. (2) In certain captions to the colored figures in the first publication (1940) rings are described as nuclear structures; these seem to be in part nucleoid bodies deformed by unsuitable preparation and in part developing cross-walls. (3) The beaded structures, lining the inner surface of the outer walls in one of the photographs, are again of a different nature, probably a cytoplasmic granulation in the ridges flanking inwardly progressing cross-walls. (4) There are indications that Peshkoff has also seen the true nucleoids which, as in other bacteria, are better demonstrated by Giemsa staining after hydrolysis (Pringsheim and Robinow, 1947). None of these structures much resembles the Feulgen-positive granules described in the few Myxophyceae so far investigated (Poljansky and Petruschewsky, 1929; cf. also p. 54).

Peshkoff is also wrong in ascribing a non-cellular organization to *Caryophanon*. It seems that the absence of cross-walls, the existence and mode of formation of which can be demonstrated in *Caryophanon* more readily than in most other bacteria, was suggested to him by earlier studies (1938) of the cell structure of a bacterium, obviously misshapen by 'involution'. It is not clear why the lack of cross-walls is regarded as a feature by which *Caryophanon* approaches the Myxophyceae, since the trichomes of the latter are always composed of numerous cells.

Peshkoff does not mention the peculiar morphological structure of *Caryophanon*, either in the Russian text or in the English summary, as a feature relating it to certain Myxophyceae, although chains of discoid cells like those constituting the body of *Caryophanon*, so common in Oscillatoriaceae, were not known in any bacterium; moreover the breaking up of the filaments into short lengths is reminiscent of the hormogonia of Myxophyceae, while filamentous bacteria were believed to dissolve into single cells.

These rather striking resemblances do not, however, appear to be of taxonomic importance. The shortness of the cells of *Caryophanon* can be correlated with their extraordinary width (2.5 to 3.2 μ) and indicates a tendency opposed to the formation of over-large cells, a tendency which can also be recognized in *Oscillatoria*, if the shapes of cells in species with different widths are compared. As a rule the narrow species have elongate, the wide ones short cells, a rule already recognized by Gomont (Geitler, 1936, p. 25).

The hormogonia of Myxophyceae are short lengths of filament which are characterized by the capacity for movement (Fritsch, 1945, p. 804). Up to the time of Peshkoff's publications, such structures were unknown in Bacteria, and they differ of course in *Caryophanon* from those of Myxophyceae in that movement is effected by flagella. Another difference is afforded by the absence in *Caryophanon* of any indication of a life-cycle as there is in *Oscillatoria* where periods of vegetative growth alternate with such of hormogonia production. When growth is undisturbed in *Caryophanon*, the trichomes develop constrictions which appear at regular intervals and steadily deepen until that first formed and situated approximately at equal distances from the ends divides the trichome into two. No *Oscillatoria* seems to be provided with such marked constrictions indicating at an early stage the place of fragmentation; but the alternation in this genus between portions exhibiting cell-division and others exhibiting elongation shows that there is another kind of periodicity in *Oscillatoria*, the formation of hormogonia being initiated by external factors and commencing with the death of certain cells. This divergence in organization is best explained on the assumption that the similarities between *Caryophanon* and certain Myxophyceae are superficial and due to convergent evolution, rather than to a common origin, while the difference between *Caryophanon* and other bacteria has become less marked since we know that bacterial rods are often composed of several cells (Robinow, 1944). They then divide in essentially the same way as *Caryophanon* trichomes (cf. also Bisset, 1949).

Peshkoff's recognition of *Caryophanon* as a form intermediate between Bacteria and Myxophyceae cannot be accepted. There are no intermediate forms; the two classes are independent. Peshkoff (1940, p. 616) attempts 'to find out what bacteria-like organisms described in scientific literature could be classified as the nearest relations to *Caryophanon*.' In this connection he mentions as closely related *Oscillospira*, which is dealt with below, and *Pontothrix* (Molisch, 1912), a member of Chlamydobacteriaceae. The polar flagella on the swarmers of the latter (cf. p. 78) show that it is widely removed from the peritrichous bacteria *Caryophanon* and *Oscillospira*.

Organisms of the Oscillospira group have frequently been described, usually as colorless parasitic Myxophyceae. It is difficult to assess the taxonomic relationship between the forms observed by the various authors. They are: *Arthromitus intestinalis* Valentin (1836), *Entomitus batrachorum* Collin (1912/13), *Oscil-*

lospira Guilliermondi Chatton and Pérard (1912/13), *Oscillatoria caviae* Simons (1920), *Simonsiella Mülleri* Schmid (1922), *Anabaeniolum brumpti* Langeron (1923), *Anabaeniolum Langeroni* and *A. longum* Nadson and Krassilnikov (1928), *Oscillatoria cyprini* Léger and Bory (1932), and *Dactylococcopsis echini* Mortensen and Rosenvinge (1934). Grassé (1924) recognized three genera: *Oscillospira* Chatton and Pérard, *Entomitus* n.g. (syn. *Arthromitus* Collin) (?) and *Simonsiella* (Schmid), but there may be more synonyms. A relationship with the Myxophyceae was already assumed by Chatton and Pérard.

All members of the group inhabit the intestines of animals, and occur in a great variety of them, especially in the rumen of ruminants and the cecum of rodents, but some are found in batrachians and others in the human mouth. Morphologically they are characterized by the possession of filaments composed of a limited number of discoid cells with approximately hemispherical end cells, cell-divisions being accomplished by diaphragm-like ingrowth of the wall. In certain instances (e.g., *Oscillospira*, Delaporte, 1934) endospores have been found, but these seem to be rather erratic in their occurrence. Grassé (1924), who found them in all the members of the group investigated, believes they are universal. Some authors record motility, while others do not mention it or failed to observe movement. Reproduction is effected by fragmentation into short lengths, in a way similar to that in *Caryophanon.*

While Harder (1920), Pascher (1921), Schmid (1922), Canabaeus (1929) and others, who were well acquainted with Myxophyceae, follow Chatton and Pérard and Simons in regarding *Oscillospira* and its relatives as apochlorotic members of this class, Geitler (1925, 1936), Bhâradvâja (1940), and Fritsch (1945, p. 871) doubt their assignability to the Myxophyceae.

Pascher (1921) speaks of the group as parasitic Oscillatoriaceae and points to 'the quite analogous occurrence of colorless Oscillatoriaceae in the dead bodies of Rotatoria and Cladocera' which he repeatedly found filled with colorless filaments sometimes even occurring in the live animals. According to him almost or completely hyaline Myxophyceae also live in the mucus of other organisms (cf. pp. 62, 70). He constructs a (rather artificial) evolutionary series, commencing with normal blue-gree forms and passing through faintly pigmented to colorless Myxophyceae, as was already done by Simons (1920, p. 363). Pascher's views do not seem to be based on personal knowledge of *Oscillospira* or similar organisms, and there is no evidence that the transformation of chlorophyll-containing into apochlorotic organisms has ever gone this way.

Geitler (1925, p. 338; 1932, p. 909; 1936, p. 1) rejects the idea that these organisms are Myxophyceae. According to him they '. . . have a certain resemblance to *Oscillatoria* and have therefore been described as such. The occurrence of peculiar, large, refractive, not readily stainable structures, which are probably spores, and the quick movements observed in certain forms are against grouping them among the Myxophyceae. They are provisionally to be referred to the Bacteria.'

Actually there is little that speaks in favor of a close relationship between the Oscillospiraceae and the Myxophyceae, except a superficial resemblance in Oscillospira to certain species of *Oscillatoria* with short discoid cells. As pointed out above, this characteristic is also found in *Caryophanon*, whose similarity to *Oscillospira* was already recognized by Peshkoff (1940, p. 616) and resulted in a similar error. There are in fact scarcely any pigmented Myxophyceae that resemble *Oscillospira*, the filaments of the former generally being much longer and lacking endospore-formation (cf. also Bhâradvâja 1940, p. 204), while the kind of movement is also different.

In his first paper Simons (1920, p. 361) described the movement of his *Oscillatoria caviae* as resembling that of *Oscillatoria* and *Beggiatoa*, but later (1922, p. 503) he points out that the speed of movement considerably surpasses that of any *Oscillatoria*, and this should have warned him as to the difference. I failed to observe motility in ordinarily mounted preparations from the rumen of sheep and the cecum of guinea pigs, although *Oscillospira* was often present in enormous numbers. The movement was therefore suspected to be affected by access of air. Robinow and I (1947, p. 274) observed motility only in sealed preparations where it was similar to that of *Caryophanon* in cow dung. This suggested the presence of flagella, which Robinow was able to demonstrate.

Mr. Frank Baker of the Rowett Research Institute, Bucksburn, Aberdeenshire (private communication; cf. also Baker, 1933, 1943) was kind enough, in response to my request, to test our observations on a rich material. By working with a warm stage and sealing the cover-glass with wax, he regularly obtained free swimming by healthy trichomes from the rumen of sheep and cattle and the cecum of guinea pigs. He informed me also of the occasional occurrence of spores in material from these sources. Mr. Baker believes that the Oscillospira-like organisms from ruminants and rodents are 'generically, if not specifically, identical... in view of: (1) the very similar internal organization of the filaments; (2) the formation of hormogones and (3) of spores; (4) the formation within the filaments of a substance giving a blue-mauve reaction with iodine.' The variation in width of the trichomes is probably due to the fact that they taper markedly towards one or both ends, so that hormogonia of different diameters are produced.

Oscillospira is therefore a bacterium, resembling *Caryophanon* in its short trichomes composed of wide discoid cells and provided with peritrichous flagella, but differing in (1) the still greater diameter of 3 to 7.5 μ, compared with 2.5 to 3.2 μ in the latter; (2) the anaerobiotic characteristics;[4] (3) the starch-like reserve substance 'granulose', resembling that of *Clostridium* and several small organisms associated with *Oscillospira*; (4) the spore formation. The ovoid spores are peculiar in that they are too large to be accommodated by single cells, so that several break down to for a spore chamber. The spores appear to be of the same type as in bacteria, not like the ordinary spores (akinetes) of Myxophyceae.

Although all the organisms of the Oscillospira-group have a similar appearance, their affinity is not in every case established. For instance one form recorded as frequently occurring in the human mouth (Miller, 1892; Fellinger, 1924) may

[4] There are, however, indications of aerobic growth on agar plates (Simons, 1922, p. 509; Hocquette, 1933), and of occurrence in the mouths of mammals (Simons, 1922, p. 508).

perhaps be different. Delaporte (1934) demonstrated a nucleal reaction in bodies situated in the center of the cells of several forms, but further cytological and cultural investigations are required to clarify the situation.

2. Chlamydobacteriaceae. The supposed relationship between the Chlamydobacteriaceae and certain Myxophyceae has a long history and is linked with the names of some of the best microbiologists. It is still supported at the present day, although there is little substance in it.

Cohn (1870–71, p. 118) compares the filaments of *Frenothrix* to colorless Oscillatoriaceae. Migula (1904–07, p. 129) believes that of the Bacteria the Chlamydobacteriaceae are nearest to the Myxophyceae. Kolkwitz (1909, p. 76) places colonial and filamentous Bacteria and Myxophyceae with a similar cell arrangement side by side. He compares *Sphaerotilus* and *Cladothrix* with *Scytonema*, *Clonothrix* with *Rivularia*, and *Crenothrix* with *Chamaesiphon*. None of these pairs of forms are really parallel in their morphological structures. Passing over the intermediate period, Bhâradwâja (1940, p. 203) may be mentioned as repeating similar arguments in more recent years. The resemblance between *Cladothrix* and *Crenothrix* and certain Myxophyceae is also mentioned by Fritsch (1945, p. 860) who, however, abstains from drawing rash conclusions.

The view of a similarity between Chlamydobacteriaceae and certain Myxophyceae is based on (1) the presence of sheaths around the trichomes; (2) the propagation by short lengths of filament; (3) the 'false' branching of *Cladothrix* which is also found in many Myxophyceae; (4) the erroneous belief that trichomes of *Leptothrix* creep out of their sheaths and form new ones. Such gliding movements could not be observed, either in microscopical preparations or on agar plates (Pringsheim, 1949a, p. 459); (5) the deposition of ferric and manganic compounds on the surface of certain Myxophyceae, as in the Chlamydobacteriaceae.

Owing not so much to such parallels, but merely because of the true filamentous habit, although this is found in many other bacteria, the Chlamydobacteriaceae have been coupled with the Beggiatoaceae as Trichobacteria or Desmobacteria in most systems of classification of bacteria (cf. p. 7). This practice is misleading and has been abandoned by Stanier and van Niel (1941, p. 455/56), although they maintain the suggestion that '*Clonothrix fusca* is probably a colorless blue-green alga whose counterpart might be found in the myxophytal genus *Rivularia*.' If the writers have in mind *Clonothrix fusca* Roze (1896), for which its author asserts a bluish tint and consequently describes it as a member of the Myxophyceae, then we are not dealing with a colorless organism. If, however, they are thinking of a form identical with or very similar to *Cladothrix*, such as Schorler's (1904) *Clonothrix fusca*, then there is scarcely much similarity with *Rivularia*. Regarding *Sphaerotilus*, *Leptothrix*, and *Crenothrix* Stanier and van Niel are more cautious. It is not clear, however, why they believe that 'the morphological characteristics of *Crenothrix* are so outstandingly different from those of the other two genera'. Although it seems that *Crenothrix* does not produce swarmers like *Sphaerotilus*, and although its conidia are formed by division along three planes instead of one, these are not very important differences. The reproductive stages of *Sphaerotilus* may also be non-motile, and longitudinal divisions may occur

(Pringsheim, 1949a). Moreover, non-motile aplanospores are produced under certain circumstances in place of swarmers by many algae.

There is, however, a blue-green alga which is really strikingly similar to *Crenothrix* but for the color: *Letestuinema Bourrellyi* (Hortobágyi, 1947). It shares with *Crenothrix* the lack of heterocysts and hormogonia and propagates with the help of spores which are produced within an apically widening sheath by transverse and longitudinal division. They round up before being discharged. Nothing about motility is known.

Even those characteristics of Chlamydobacteriaceae which most recall those of Myxophyceae are, in fact, on closer inspection rather unlike. (1) The sheaths of Chlamydobacteriaceae are very thin and tough, and the cells of older threads are often separated from one another. This is not so in any member of Myxophyceae; (2) while the hormogonia of the latter are well-defined portions of filaments originating by separation at prepared places, the Chlamydobacteriaceae reproduce by irregular fragmentation into short lengths. Moreover, the hormogonia of Myxophyceae exhibit gliding movements, while the reproductive cells or cell-aggregates of Chlamydobacteriaceae are either motionless or, in the possession of flagella, resemble swarming bacterial rods; (3) the false branching of *Cladothrix* is not so well defined as that of Rivulariaceae and Scytonemataceae. There are neither heterocysts, nor necridia. The branching of *Cladothrix* may be suppressed altogether when the sheaths are either too soft to hold the parts together or too rigid for cells to break through and to give origin to branches.

Too much weight may therefore not be given to the similarities which really all depend on one feature, the enclosure of the trichomes in sheaths which has developed by parallel but independent evolution in the two groups. The Chlamydobacteriaceae are true Bacteria, more nearly related to the Spirillaceae than, for instance, are *Corynebacterium* or *Mycobacterium*, or probably even *Bacillus*.

3. Photosynthetic Bacteria. There are many bacteria-like organisms of minute size which possess pigmented protoplasm and whose relation to true Bacteria and to Myxophyceae has some bearing on the problems discussed in this review. Their color is green, yellowish green, blue-green, brown, red, or purple. While the Purple Bacteria or Rhodobacteria and the brown Phaeobacteria are closely related (van Niel, 1944), those with a more or less green shade belong to various unrelated groups.

a. Green Bacteria. The designation 'Green Bacteria' has merely a descriptive value. The earlier records (Perty, 1852; van Tieghem, 1880; Engelmann, 1882) can scarcely be adjudged since diagnoses, measurements and figures are lacking. Dangeard (1895), and in part also Ewart (1897), possibly mistook small Chlorophyceae for green bacteria. Zopf (1882), Cohn (1897, p. 494) and Schmidle (1901) refer such organisms to the Algae. Benecke's (1912, p. 243) statement that blue-green Spirillas bearing flagella have been observed has not been substantiated. Baas-Becking (1925, p. 630) found a minute green coccus and a green streptococcus-like organism, which he believes to be identical with Ewart's *Streptococcus varians*. He succeeded in growing the latter on peptone agar, though not in pure culture; and he concludes that it is aerobic.

Green Bacteria were, however, for the most part found associated with organisms adapted to a high concentration of hydrogen sulfide (Szafer, 1911; Skene, 1914; van Niel, 1931), such as Purple Bacteria and Myxophyceae, or in mud and stagnant water rich in organic matter, or as symbionts on the surface or within the body of various small organisms.

Geitler and Pascher (1925, p. 451) published a fairly comprehensive treatment as an appendix to the Myxophyceae and proposed to change the older name of Chlorobacteriaceae (Lauterborn, 1915, p. 425) into Cyanochloridinae. According to them the bacterial nature of these organisms has not been proved in a single case. They admit that they represent a non-homogeneous assemblage, the majority of whose members are not blue-green but yellowish. This does not preclude an affinity with the Myxophyceae, which is highly probable in many cases.

Van Niel (1931, p. 73) subjects Pascher's (1914) and Geitler and Pascher's (1925) descriptions of numerous symbiontic and free-living Green Bacteria, as well as their grouping as Cyanochloridinae near to the Myxophyceae, to severe criticism. He himself found only one species which he isolated in pure culture and which he believes to be identical with *Chlorobium limicola* Nadson (1906, 1912), as well as with the greenish rods belonging to Lauterborn's (1915) *Chlorochromatium aggregatum*, and even with Pascher's *Cyanarcus hamiformis*, *Chroostipes linealis* and certain other Cyanochloridinae.

Although Pascher may sometimes have been rash in naming occasional discoveries, van Niel's distrust goes too far (Pringsheim, 1932a). He underestimates the importance of morphological investigations. Moreover several of these minute organisms do not possess the yellowish to olive-green hue of the green sulfur bacteria, but are blue-green like true Myxophyceae, as in Pascher's *Cyanarcus* and *Chroostipes* (Geitler and Pascher, 1925, p. 116). I myself observed the blue-green color in several bacteria-like organisms which I studied in cultures. How vague the description of color may be, is shown by Geitler and Pascher's (l.c., p. 460) diagnosis of a form similar to *Chlorochromatium* as 'gelbgrün mit einem ausgesprochenen Stich ins blaugrüne' (yellowish green with a distinctive blue-green tinge), a contradiction in itself.

The pigments of Green Bacteria have only been investigated by Metzner (1922), who discovered a new green pigment bacterioviridin, differing from chlorophylls a and b, as well as from the bacteriochlorophyll of Purple Bacteria. The pigments will probably be the most suitable features upon which to base a classification and, until more Green Bacteria have been investigated from this point of view, no definite statements as to the taxonomic position of most species can be made. In this connection it is significant that the yellowish color, regarded as characteristic of the Cyanochloridinae by Geitler and Pascher, is also met with in several true Myxophyceae. In the latter, contrary to Geitler's (1925, pp. 346, 362) opinion, it does not always constitute a specific feature but represents a state of nutrition (cf. p. 62), although some species may perhaps be more readily influenced in their pigmentation by nutritional deficiency than others. There is no doubt, as my cultures have shown, that minute, bacteria-like forms behave in this respect like larger Myxophyceae.

Until a better knowledge of Green Bacteria has been obtained, they may tentatively be placed in three groups: (1) Small unicellular Myxophyceae, 0.5 to 1 μ wide, usually referred to the Chroococcaceus genera *Synechococcus*, *Rhabdoderma*, *Dactylococcopsis*, *Cyanarcus*, *Chroostipes*, etc.; (2) Cyanochloridinae (Chlorobacteriaceae in Lauterborn's sense), such as *Tetrachloris*, *Pelogloea*, *Streptococcus varians* Ewart; (3) Green Sulphur Bacteria (in van Niel's sense), showing relation to the Purple Bacteria, e.g., *Chlorobium* Szafer, *Chloropseudomonas* Czurda and Maresch.

(1) The first group certainly does not belong to the Bacteria, since gliding movements are known in some of them (cf. p. 60), and the pigmentation seems to be the same as that of other Myxophyceae, with capacity of reversible bleaching under adverse conditions. Individual cells may not betray their color, owing to their small size, and may then easily be mistaken for true bacteria. It is only when these small forms are massed in large numbers that they can be identified by their blue-green hue fading to yellow. Some of them aggregate to form distinctive colonies.

(2) The Cyanochloridinae may still be nothing else than small Myxophyceae. Geitler and Pascher (l.c., p. 451) refer to a central colorless and a peripheral pigmented part of the cells and state that the yellowish forms are connected through intermediate shades with distinctly blue-green ones. These are features characteristic of Myxophyceae. The color of dense populations of organisms identified as *Pelogloea* and *Tetrachloris* is definitely blue-green.

(3) The Chlorobacteriaceae (Lauterborn in part) or Green Sulphur Bacteria (van Niel) share the habitat and certain characteristics with the Purple Bacteria. Attention was first drawn to them by Szafer (1911) and Nadson (1912). Skene (1914), who found them only in fresh water, grew them in cultures. Bavendamm (1924) found it difficult to exclude green bacteria from his enrichment cultures of Purple Bacteria. Van Niel (1931, p. 27) isolated Green Sulphur Bacteria also from sea water; they appear as a green sediment with a greyish tinge. According to him (1944, p. 61), they contain a chlorophyll-like pigment which is 'most certainly not identical with either the bacteriochlorophyll of Purple Bacteria or chlorophylls a and b', a statement apparently only based on Metzner's investigation (cf. p. 79).

The only species of Chlorobacteriaceae so far thoroughly investigated is the *Chlorobium limicola* of van Niel (1931, p. 66), who inclines to the belief that all Green Bacteria belong to it (1931, p. 72), but this is unlikely to be correct. Even if little weight is given to earlier statements, there are distinct differences between the form studied by van Niel and *Chloropseudomonas* Czurda and Maresch (1937, p. 123). The former is non-motile, and strongly polymorphic (l.c., p. 65), while even single individuals are green; the latter is always rod-shaped, motile with the help of polar flagella, and colorless individually though olive-green (not greyish) when massed. They seem also to differ physiologically.

The variability of van Niel's *Chlorobium* is remarkable. It exhibits coccoid forms, long rod- to club-shaped cells, loosely or closely wound spiral structures and large ellipsoidal or spherical shapes. This polymorphism surpasses that of every other microörganism and should be confirmed by thorough scrutiny. It is not stated whether all the various forms represented in van Niel's fig. 8 (1931, p. 65), were simultaneously found or, if not, under what conditions they were produced.

While groups (1) and (2) may have to be merged, especially as Lauterborn's *Pelodictyon* could scarcely form nets without gliding movement, which would show it to be a member of the Myxophyceae, group (3) is definitely not related to either of the others.

b. Purple and Brown Bacteria. The differences in color between purple, red, and brown bacteria are insignificant, changes being observed even in the same strain (van Niel, 1944, p. 4), so that all these organisms can be treated under the designation of Purple Bacteria. The storage of sulphur in the cells is also not quite as distinctive a feature as was previously believed (van Niel, 1931).

At first sight Purple Bacteria seem to afford little evidence of affinity to Myxophyceae, but a few aspects must be discussed. The possession of photosynthetic pigments, not contained in specially differentiated protoplasmic bodies (plastids), is common to both classes. The appearance of the cytoplasm of the large Purple Bacteria (e.g., *Chromatium okenii*) recalls that of certain Myxophyceae (e.g., *Chroococcus turgidus*) in its fine punctuation and apparent homogeneity and differs from that of other small organisms. Fischer (1897a) failed to demonstrate a central body like that of Myxophyceae in *Chromatium,* while Dangeard (1909) claims to have seen it, although he states that the pigments are diffused throughout the cytoplasm. This also seems to be so in *Chroococcus.* (Acton, 1914, p. 451; Geitler, 1936, p. 6).

These similarities would not amount to much, if all Purple Bacteria possessed flagella. Van Niel (1944, pp. 17, 81) shows convincingly that the polar flagellation of the motile forms, combined with the absence of spores and the gram negative character, admits of a reference of these forms to the Pseudomonadaceae (Kluyver and van Niel 1936). This involves abandoning the family Rhodobacteriaceae and separating certain non-flagellate Thiorhodaceae (Purple Sulphur Bacteria) from the others, although this conclusion was not drawn by van Niel. This author has recently raised the group, of which *Pseudomonas* is the type, to the rank of an order, the Pseudomonadales (van Niel, 1944, p. 82) with which one may well agree. This order is divided into the two families Pseudomonadaceae and Spirillaceae. The inclusion of the sulphur-containing forms in the Pseudomonadales is tacitly assumed by van Niel (l.c., p. 81), although no system of classification is given for the order.

The flagellate Purple Bacteria would apparently belong in part to the Pseudomonadaceae, in part to the Spirillaceae, each including sulfur-depositing species, as well as others which do not deposit sulfur. The Thiorhodaceae, however, comprise genera which cannot be included in the Pseudomonadales. Lauterborn (1915, p. 427) gives a table showing the morphological parallelism of certain colorless, red, yellowish green and blue-green microörganisms. The similarity between the colorless *Lampropedia,* the red *Thiopedia,* and the blue-green *Merismopedia* is striking, and so is that between the red genera *Thiodictyon* and *Pelo-*

chromatium on the one hand, and the yellowish green *Pelodictyon* and *Chlorochromatium* on the other. As in *Pelodictyon* (cf. p. 81), the arrangement of the cells in *Thiodictyon elegans* (Winogradsky, 1888, p. 80; cf. also Bavendamm, 1924, p. 124; Ellis, 1932, p. 169) is scarcely possible without the assumption that the cells can glide over one another. These organisms form net-like colonies of rod-shaped cells, originating by a gradual orientation from a dense primary aggregate. Under unfavorable circumstances the nets again contract into compact masses of cells. Reproduction of the colonies is effected by division or by breaking up into small, slowly moving cell aggregates.

It is not known whether the tabular colonies of *Thiopedia rosea* (Winogradsky, 1888, p. 85; photograph in Pringsheim, 1932a, p. 481) move like those of *Merismopedia* (cf. p. 60), but Winogradsky states that the cells of the former can scatter—perhaps in the same way as those of *Holopedia*? Another genus of Thiorhodaceae, *Amoebobactor*, of which three species have been recorded (Winogradsky, 1888, p. 71; cf. also Skene, 1914; Lauterborn, 1915, p. 424; Bavendamm, 1924, p. 122; Ellis, 1932, p. 168) seems likewise to exhibit gliding movements. According to Winogradsky the cells of the colonies are joined by invisible protoplasmic strands, although Lauterborn (1915) could find no indication of them. The cells are described as globular or ovoid and as capable of altering their shape (Ellis, 1932, p. 168). The colonies slowly change their appearance as the cells become closely approximated or separate from one another. Movement due to elastic threads seems to be merely a hypothesis of Winogradsky's, but there is also no real evidence of ameboid movement. It is more likely to be of the same mysterious nature as that of other gliding organisms.

If the occurrence of gliding movements in *Thiopedia*, *Thiodictyon* and *Amoebobacter* be confirmed by further observations, there would be two independent groups of Purple Bacteria, viz., I. Rhodopseudomonadaceae with the subfamilies Athiorhodeae and Thiorhodeae, differing in the deposition of sulfur outside or inside the cells, and in the ability of the latter to live autotrophically; II. Amoebobacteriaceae, sharing with the Thiorhodaceae the storage of sulfur, but awaiting investigation as regards their pigmentation and mode of nutrition. The latter family would perhaps be related to the Cyanochloridinae.

The Purple Bacteria would thus appear as a mere physiological group comprising unrelated forms, although they are not spread over the whole of the Bacteria, as Molisch (1907, p. 26) suggested would be the case if they were not defined as a natural group characterized by its pigmentation.

4. Spirochaetae. Cohn (1853, p. 132) says: 'Just as the colorless *Spirochaeta plicatilis* was found to correspond to the blue-green *Spirulina*, although living only in putrid infusions, so, by investigating fermenting fluids, other forms are encountered which, though unpigmented, have their nearest relations among the algae.' The parallelism between *Spirulina* and *Spirochaeta* has often since been discussed, without finding many advocates. The differences, apart from that of pigmentation, customarily stressed are: (1) *Spirochaeta* is unicellular, *Spirulina* multicellular; (2) *Spirochaeta* has an axial cord, *Spirulina* lacks it; (3) *Spirochaeta* is flexible, *Spirulina* rigid; (4) some *Spirochaetae* swim freely, while *Spiru-*

lina, when moving, always adheres to some solid surface. Most of these matters cannot be fully discussed, because the investigation of these small organisms, and particularly of the delicate spirochaetes, has not so far yielded sufficient evidence (Topley and Wilson, 1946).

The multicellular structure of some of the smaller species of *Spirulina* is not conclusively established. The neutral red stain used for this purpose does not give clear results. A filament may display a row of chambers without being multicellular in the strict sense. The distinction between *Spirulina* without, and *Arthrospira* with cross-walls is in doubt. The grouping of the smaller species as (*Eu-*)*Spirulina*, and the wider ones as *Arthrospira* suggests that the recognition of cross-walls depends on the width of the trichomes (Schmid, 1921; Crow, 1927). Moreover a cellular organization has not the same significance in Myxophyceae as it has in other algae (cf. pp. 53, 66).

Dyar (1947, p. 491; fig. 17, p. 489) has demonstrated axial cords in *Spirulina* and gives reasons for regarding them as artefacts. They are moreover not always found in *Spirochaeta*, not even in electron micrographs (Morton and Anderson, 1942; van Thiel and van Iterson, 1947), so that some at least of the older claims seem to be founded on misinterpretation.

Flexibility is an important characteristic which must be discussed in some detail. In its relation to gliding movement, it is not only an essential distinction between *Spirochaeta* and *Spirulina* (Zuelzer, 1910; 1911, p. 45), but also has some bearing on the general question of possible relationship between Bacteria and Myxophyceae. Although frequently mentioned in this connection it does not seem that flexibility has ever been properly defined. If it meant merely liability to change of shape as a result of external forces, it would be identical with pliability which is inherent, though in various degrees, in any physical body. *Spirillum*, for instance, is supposed to be rigid, but long spirals are easily deformed by traction (Hama, 1933, pp. 137/38). Zacharias (1903 b) describes a large *Spirillum* (*Pseudospirillum uliginosum*) as flexible, while Swellengrebel (1909, p. 548) and Meirowsky (1914, p. 61) sometimes observed in *Spirillum* flexibility like that of *Spirochaeta*. Such spiral organisms, apart from their pliability, show also a certain degree of elasticity. 'The spirals of *Spirulina* can be drawn out until the thread is almost straight, but take on their previous form, when the tension is released' (Fritsch, 1945, p. 788).

If therefore the description of an organism as flexible is to have any significance, it can only mean that the body is especially liable to alter its form, either as a result of outer mechanical influences, or owing to the operation of internal forces. The second alternative which is apparently that assumed by most writers, not only on spirochaetes, but also on motile Myxophyceae, should be termed active flexibility.

Oscillatoria and *Beggiatoa*, for instance, give the impression that their trichomes are markedly flexible. When a mass of trichomes is transferred to a drop of water under the microscope, the loops and tangles caused by the surface tension of the water commence to straighten out, with the tips of the trichomes radiating in all directions, their curved ends exhibiting the well-known rotation. Threads still in close proximity creep along one another and between particles of débris, apparently evading obstacles and following an outward path by active flexible movement. On closer inspection, however, it is clear that the straightening out of curvatures and loops is caused by elasticity, while bending to evade obstacles is due to passive pliability, as already stated by Correns (1897) and Kolkwitz (1897).

It seems to have been overlooked that the flexibility of *Spirochaeta* may perhaps be brought about by the same causes. The body is much narrower and much quicker in its movements. It turns in various directions at frequent intervals; the movement is characteristic for its restlessness and accompanied by strong bending or often even coiling; but that does not necessarily mean that its flexibility is really 'active'. Changes in direction may be caused by differences in external friction or by minute obstacles, and not by unequal internal forces operating on different sides. The unpredictable 'lashings about', which have impressed many observers, may be the result of the impact of imperceptible external impediments on an organism whose shape is readily transformed, and which partly adheres to the glass or other substrata. The difference in behavior, e.g., between *Spirulina* and *Spirochaeta* would then merely be such of degree and not of the nature of the movement, and mainly due to differences in width and rigidity. As an illustration one may compare the mechanical properties of a narrow, elastic, closely coiled wire with those of a wider, less closely coiled one. The former would easily bend in any direction, even through the impact of a stream of air, which would apparently not affect the latter.

While such a conception would not account for the gliding itself, it would help to explain the differences in the mode of motility of the two organisms. The question of course arises whether there is never any doubt as to the reference of a certain specimen to one or other genus. The decision is mostly easy, although *Spirulina* and *Spirochaeta* have so much in common that a general and fundamental difference is difficult to define, and this similarity is demonstrated by the existence of forms of doubtful affinity.

Lagerheim (1892) described two species of *Glaucospira* which, he thought, rendered the relation between *Spirulina* (Gomont) and *Spirochaeta* (Ehrbg) a certainty. These forms possess the characteristics of *Spirochaeta*, but are blue-green. They have narrow coils and form secondary spirals, so characteristic of spirochaetes. The organisms show lively to and fro movements, while, without apparent reason, the direction of movement suddenly becomes irregular, with almost spasmodic bending to different sides 'like a wounded snake'. That is just what is observed in *Spirochaeta*.

Dobell (1912) suspects that the bluish tint was the result of poor optical equipment, but this is not likely to be so. Such delicate organisms, the coils being only 2 μ wide, could scarcely show color individually, so that Lagerheim must have judged it by that of massed cells. However that may be, Skuja (1939, p. 48) describes an organism which he regards as identical with that of Lagerheim, although it is colorless. It is stated to exhibit the kind of movement characteristic of *Spirochaeta* so that it is not altogether clear how it is distinguished from that genus. The description and figure (pl. I, fig. 5) show a form very similar to *Spirulina tenuissima.* No final judgement is possible until Lagerheim's and Skuja's forms are found again. A colorless *Spirulina,* with narrow coils, has already been found by van Tieghem (1880) who describes it as hyaline without being a *Spirochaeta.*

5. *Myxobacteria.* The Myxobacteria resemble many Eubacteria in shape and size, while their movements show some similarity to those of Myxophyceae. Those Myxobacteria that were first discovered differ from both groups in producing peculiar fruiting bodies. Stanier and van Niel (1941, p. 464) in their discussion of bacterial classification, refer the Myxobacteria, together with the Eubacteria and the Spirochaetae, to the Schizomycetae which removes them rather far from the Myxophyta (Myxophyceae). Jahn (1924, p. 104) regards the Myxobacteria as apochlorotic Myxophyceae, a suggestion which does not seem to have been taken seriously by most authorities, although there is much that speaks in favor of this view.

The facts enumerated by Jahn in support of a relationship between Myxobacteria and Myxophyceae are few. He mentions as common to both the softness of the cell wall, the lack of a defined nucleus, the storage of glycogen, and the kind of movement which he regards as most important. *Oscillatoria* is considered unsuitable for comparison, because here the motion of large multicellular trichomes leads to a special organization which is also indicated by their rotation. This is lacking in the Myxobacteria, but also in the hormogonia of *Nostoc, Anabaena* and *Cylindrospermum* (Harder, 1918). For Jahn the decisive fact is the existence of forms intermediate between Myxobacteria and Myxophyceae, namely small unicellular blue-green species he found on moist soil and whose movements he describes as very similar to those of Myxobacteria. According to him such Myxophyceae repeat the kind of movement, the mucilage-exudation and the colony-formation of Myxobacteria. He was unfamiliar with the non-fruiting forms which show still greater similarity with certain Chroococcaceae. Geitler (1925, p. 172) rejects Jahn's view because no swarm-formation is found in the relevant Myxophyceae, although closer observation may still reveal it, while Stanier and van Niel (1941, p. 452) regard Jahn's claim to have observed creeping movements in unicellular blue-green algae, if substantiated, as providing strong support for his hypothesis. Such movements have in fact been repeatedly recorded, also by the present writer (cf. p. 60) so that there is no doubt as to the correctness of Jahn's statement. Microcyst formation, which is probably found in all Myxobacteria, but is lacking in Myxophyceae, is, however, another reason against a close relation between the two groups.

Soriano (1945) restricts the order Myxobacteriales to those Myxobacteria which possess fruiting bodies, while the non-fruiting forms, together with the Beggiatoaceae, are classed in the new order Flexibacteriales, which comprises the two families Flexibacteriaceae and Cytophagaceae. This classification is unnatural in two respects. The structure of the vegetative cells and the formation of microcysts are common both to the fruiting and non-fruiting Myxobacteria, while in the Beggiatoaceae the structure and arrangement of the cells is different and microcysts are lacking. Soriano's separation of the cellulose-attacking Myxobacteria as the family Cytophagaceae from the remainder, the Flexibacteriaceae, lays far too much stress on a physiological feature of doubtful significance. Where, for instance, should one then class Stanier's (1947a) chitin-destroying *Cytophagas?* Stanier (p. 313) rightly says: 'if these organisms really comprise as large and varied a group as appears to be the case . . . careful thought should be given to the selection of significant, mutually exclusive differential characters.' He also emphasizes the difficulty arising from the complexity of biochemical properties in an attempt to use them for taxonomic purposes. A Cytophaga may be able to decompose cellulose but also to live on glucose.

A closer affinity of the Myxobacteria may exist to the Vitreoscillaceae than to unicellular Myxophyceae (cf. p. 70). Some species of *Vitreoscilla*, in the readiness with which they dissociate into short filamentous fragments and single gliding cells, as well as in their low refraction, seem to be more like Myxobacteria than like *Beggiatoa.* They might even, in spite of the absence of microcysts, be regarded as filamentous counterparts of the Myxobacteriaceae, as the Oscillatoriaceae are the filamentous counterparts of the Chroococcaceae, provided that additional evidence in support of this view were furnished by further investigation.

In this connection it is of interest that there are organisms resembling Myxobacteria but capable, like many Eubacteria, of forming multicellular trichomes; they have been isolated in pure culture. Garnjobst (1945) obtained such a Myxobacterium, which she called *Cytophaga columnaris*, from diseased fish; this grows well on peptone agar and in liquid media, is strictly aerobic and produces a carotene pigment which turns blue with sulphuric acid. It utilizes neither glucose nor lactose. The filaments may attain a length of more than 150 μ, forming almost mycelium-like colonies on agar (p. 124, fig. 5); microcysts were not found. Stanier (1947a, p. 314) proposes the name of *Flexibacter* for myxobacterial forms capable of growing in the absence of carbohydrates, and *Cytophaga* for those requiring them. Garnjobst's species should then be called *Flexibacter columnaris.* Stanier is probably right in not attaching much importance to the presence or absence of microcysts.

I have repeatedly isolated a similar organism on agar plates with 0.05% yeast extract from decaying plant residues and from cow dung. It exhibits two growth forms, sometimes spreading like a mycelium from the place of inoculation, at other times being denser with fringed edges and closely resembling *Cytophaga* as shown by Stanier's photographs (1947a, p. 310). The spread over the agar is readily influenced by small differences in moisture. The filamentous strands on agar are composed of thin rods which separate in mounting a preparation, while the appearance of turbidity in liquid media is due to the presence of irregularly bent filaments reaching 50 μ in length and exhibiting the slow, interrupted, hesitating movements characteristic of Myxobacteria, as well as of unicellular pigmented and colorless Myxophyceae and of Vitreoscillaceae.

In its nutritive requirements and the production of an orange pigment this common organism resembles *Flexibacter columnaris*, but it differs from it in its apparent non-pathogenic character and in producing microcysts. Since the latter were only found in a few old liquid cultures, they may have been overlooked by Garnjobst, although microcysts are stated to be lacking in a number of other Myxobacteria (Garnjobst, 1945, p. 126) and were never found in the Vitreoscillaceae.

These filamentous Myxobacteria share with the Vitreoscillaceae the gliding movement, the low refraction, the appearance of the growths on agar, the kind of nutrition, and in part the production of carotenes. Whether they are really nearly related can only be established by further investigation.

V. DISCUSSION

From the consideration of facts given in this review, it emerges that there is no affinity between Bacteria and Myxophyceae. A similar opinion was expressed long ago by Chodat (1909, p. 135): '... il devient de moins en moins probable que ces deux classes (Schizomycètes et Schizophytes) soient réellement parentes.... Les deux groupes se ressemblent probablement bien plus en vertu de phénomènes de convergence, que grâce à une réele affinité naturelle.' While this view was based on the differences in cell structure (cf. p. 54), Geitler (1934, p. 185) seems to be impressed mainly by morphological differences when he says: 'Da die positiven Übereinstimmungen im feineren Zellbau andererseits nicht sehr gross sind, lässt sich auch die Auffassung der Blaualgen als eigener Pflanzenstamm (Cyanophyta) vertreten.' He is of the opinion, however, that the Trichobacteria may possibly have a closer affinity to Myxophyceae than other Bacteria, a point of view discussed above (p. 77). It does not lead us any further to admit that the two classes may perhaps have an extremely remote common ancestry because even of this there is no real evidence.

The denial of any relation between Bacteria and Myxophyceae applies to the bulk of the former, which are called Eubacteria in treatises dealing with the classification of the class. It may be doubted, however, whether the Eubacteria constitute a natural group, and their subdivision into three or more independent classes will probably become necessary. None of these would serve as a bridge to the Myxophyceae, although the Myxobacteria have the gliding movement in common with them; but they have nothing to do with true bacteria.

The reasons for and against an affinity between Myxobacteria and Myxophyceae have been discussed in detail (p. 85). The evidence speaks against a close relationship, but a common origin is quite possible. It is indicated by the kind of movement which suggests a similar cell organization. Moreover Myxobacteria and Myxophyceae are connected by way of the Beggiatoaceae and the Vitreoscillaceae. Certain of the latter show resemblances to Myxobacteria, while others are more like Beggiatoaceae and may therefore prove to be apochlorotic Myxophyceae. The Vitreoscillaceae seem, however, to be a natural group differing from the majority of the Myxobacteria in their pronounced filamentous habit, and in the absence of the microcysts characteristic of the latter.

These considerations bring one to the borderline of mere speculation, but one may be tempted to sketch, though only in dim outlines, two very large groups, that of the gliding and that of the swimming organisms, neither of which can be postulated as more ancient than the other. The former include the Myxophyceae, the Myxobacteria, the Vitreoscillaceae, the Spirochaetae, while Rhodophyceae, Desmids and Diatoms, which also exhibit gliding movements brought about in different ways, do not belong here in view of their advanced cell-organization. The only classes containing members exhibiting both swimming and gliding movements, are the Chrysophyceae and the Euglenineae, and it is obvious that they have nothing in common with the Myxophyceae. Gliding movement in general presupposes a special cellular organization, namely soft membranes differing from the cell walls of Algae and Bacteria, and filaments with interconnection of cells by way of the septa, which are not true cross-walls and permit coordination between the cells, but resulting in death when part of a trichome is injured.

Swimming organisms possess flagella (or cilia) and the presence of these organs of locomotion cannot in general be regarded as a taxonomic character, since they are found in groups with no obvious affinity to one another: Bacteria, Spirochaetae(?), Chrysophyceae, Xanthophyceae, Phaeophyceae, Diatoms, Chloromonadinae, Euglenineae, Chlorophyceae, Charophyta, Bryophyta, Pteridophyta, Gymnospermae, Myxomycetes, Phycomycetes, and Flagellata of doubtful affinity, as well as Ciliata and most other animals including Mammalia. Unless one assumes a polyphyletic origin for flagellar locomotion, all the Flagellata and their descendants must be derived from remote common flagellate ancestors, from which the Bacteria, most Algae and Fungi, and other plants, as well as animals have descended, or alternately the Bacteria might stand near the origin of the majority of living organisms. There is, however, no clear connection between flagellate Bacteria (Holoplastideae) and other flagellate organisms (Euplastideae), such as Flagellata, Ciliata, etc., while the evolution of various classes of Algae from flagellates is widely accepted.

For the time being there is insufficient basic knowledge, even of relatively restricted groups like the Myxobacteria, Vitreoscillaceae and Myxophyceae on the one hand, and of the true Bacteria on the other, to justify the utilization of the mode of locomotion on a broad scale as a diagnostic character for taxonomic purposes, for which it might well become useful in future. The scanty evidence available for assessing relationship could probably be supplemented by cytological details brought to light by improved staining methods, and with the help of the electron microscope, as well as by better biochemical characterization of the nature of the relevant cell constituents, cytoplasmic, nucleoproteid, etc., including serological tests. The latter have been somewhat discredited by their uncritical application in certain quarters to problems of taxonomy. Far-reaching conclusions cannot be expected to be trustworthy, if the same technique is applied for large groups as has proved to be valuable in the comparison of closely related forms. Modern methods of extracting specific proteins and other compounds of high molecular weight may eventually afford the clue to the problems above indicated.

While a near affinity between true Bacteria and Myxophyceae cannot be accepted, there still remains the problem of the relation between pigmented and non-pigmented forms of comparable organization. This involves the question which bacteria-like organisms should be considered as apochlorotic Myxophyceae and which as Bacteria. It is possible too that present-day Bacteria include apochlorotic Myxophyceae which still await detection although this is so far only a hypothesis.

When two sets of organisms differ in the presence or absence of photosynthetic pigments, but are otherwise similar in all essential respects, the phenomenon is usually explained as due to a phylogenetic connection between the two. Pigment can either have been lost or have been acquired, after the principal characteristics of the organisms had become fixed. The pigments of the chlorophyll-group possess complex chemical structures and, together with other pigments, form a photosynthetic system which is mostly located in special parts of the cytoplasm. The whole mechanism is too complicated to have developed more than once in the same way. The Purple Bacteria and the Green Sulphur Bacteria (cf. p. 80) differ in this respect from the majority of photosynthetic organisms, and this indicates that they belong to an independent line of evolution.

By contrast loss of the photosynthetic apparatus can easily be supposed to have occurred in various instances, provided that the organisms concerned were able to survive the change in nutrition, owing to their possession of other means of acquiring food.

In considering the general relation between Bacteria and Myxophyceae the question whether colorless or pigmented forms of similar construction are primary can only be put if the organisms in question are clearly related. It can therefore only be propounded with regard to those 'Bacteria' which can be definitely recognized as apochlorotic Myxophyceae, i.e., *Beggiatoa*, *Thioploca*, *Thiothrix*, *Achromatium*, *Vitreoscilla*, etc.

Benecke (1912, p. 243), when discussing the relation between certain Bacteria and Myxophyceae, leaves the question of origin open: 'Which are the more primitive, colorless bacteria or pigmented algae, is a question about which one can dispute to one's heart's content, as nothing certain is known.' Stanier and van Niel (1941, p. 450) say: 'Thus is seems at least possible that the primitive blue-green algae of the *Chroococcus* type have developed from the Eubacteriales as a second photosynthetic line' (apart from the Purple Bacteria). Even if the possibility of such an affinity were accepted there is in the data they give little evidence of the direction of the evolution.

Van Niel (1944, pp. 80 *et seq.*), in attempting to determine the taxonomic position of Purple Bacteria, cites the relation between Flagellata and Algae and their colorless counterparts, as a parallel to that between pigmented and unpigmented Bacteria. The Purple Bacteria are, he states, 'polarly flagellate' (cf., however, p. 81), 'they fall . . . in the morphological family of the Pseudomonadaceae, and represent the pseudomonas, vibrio, and spirillum types, resembling completely the non-photosynthetic members of these tribes.' He includes therefore all pigmented bacteria in the order Pseudomonadales. Since the transformation 'from pigmented to non-pigmented forms' (of algae) 'but not the opposite, has been experimentally achieved, it appears more logical to consider the purple bacteria as the progenitors of the corresponding non-photosynthetic bacteria' (so already Delaporte, 1940).

There are some more conclusions which were not drawn by van Niel. If photosynthetic bacteria are more primitive than colorless ones, they must have acquired their pigments before morphological diversity had developed. The main evolution of the pigment-free Pseudomonadales, up to the Chlamydobacteriaceae, would have taken place after the loss of pigments, and they would not be related in any way to the rest of the true Bacteria which must have had a different origin. The gap would be so wide as to split the 'Eubacteria' into two groups which would better be considered as independent classes of the same status as the Myxobacteria for instance and might be called Bacillales and Pseudomonadales. The resemblance between the two would be the result of convergent evolution. The Bacillales are less homogeneous than the Pseudomonadales; the position of the Coccaceae remains undecided owing to doubts on their homogeneity, while the Myxobacteriales are again an independent class.

Van Niel's conclusion as to the origin of colorless bacteria is based on a comparison with what is known to occur in other groups. The direction of evolution in these is indicated by the scattered occurrence of unpigmented forms among a majority possessing a functioning photosynthetic apparatus (Pringsheim, 1941, p. 193). Apochlorosis has clearly originated here and there in a small number of taxonomic groups which, by virtue of their special modes of nutrition, were able to survive the loss of assimilatory pigments.

The same conclusion can be drawn for colorless Myxophyceae. That is the answer to Benecke's question, while the one propounded by Stanier and van Niel remains open until unicellular colorless forms are found, which in conformity with their concept, are bacteria-like, non-motile, coccoid and gram negative, and which may be suspected with some justification to be derived from Chroococcaceae, although they are not recognized with certainty as such any more. Whether, e.g., a four-celled 'colorless *Chroococcus*' mentioned without details by Bavendamm (1924, p. 45) belongs here, cannot be ascertained. Members of the Achromatiaceae would not be of this nature, since they are recognizable as apochlorotic Myxophyceae by their kind of movement. *Gonococcus* and *Meningococcus* are probably too far modified by parasitism to come into question. The great majority of Coccaceae can be ruled out because they are gram positive. There is therefore no indication that any member of the true Bacteria has originated from Myxophyceae.

VI. SUMMARY

I. The theory of an affinity between Bacteria and Myxophyceae has recently been revived by regarding the former as an apochlorotic offshot of the latter, an interesting but controversial proposition.

II. In order to clarify the position, certain aspects of bacterial taxonomy are revised. By using all available means of recognizing natural relationships the Bacteria can be divided into a number of independent classes, none of which could have evolved from Myxophyceae.

III. This conclusion is founded on a review of the various characteristics of the Myxophyceae and a comparison of them with those of the Bacteria. Morphological similarities appear more probably to have originated by convergence and afford no evidence of descent from a common ancestry. The pigmentation, where present, is different; the cytological and physiological characteristics are not altogether comparable; motile Bacteria swim freely, while Myxophyceae glide along solid surfaces. Some so-called Bacteria, which do not display the usual characteristics of true Bacteria, can be shown actually to be pigment-free Myxophyceae.

IV. Apochlorotic Myxophyceae, which are reviewed in some detail, are more numerous than is generally believed. Among accepted Myxophyceae there are very few apochlorotic species and these in part are doubtful, but *Beggiatoa* in all its characteristics shows a close relation to *Oscillatoria*, while *Thiothrix* and *Achromatium* can also be recognized as colorless Myxophyceae. A number of other pigment-free forms have been discovered (and some of them grown in pure culture) which, by their gliding movements and other features, can justifiably be grouped among apochlorotic Myxophyceae.

V. Other bacteria-like organisms which, for one reason or another, have been suspected of being related to Myxophyceae, are discussed in this connection. Certain green and purple bacteria, spirochaetes, and myxobacteria have at least the characteristic of gliding movement in common with Myxophyceae, while the remainder belong to the Bacteria proper.

VI. The type of movement as a taxonomic character is discussed and supplemented by other features so that some progress towards a more natural classification is reached. Problems connected with the direction of evolution from pigmented to colorless organisms are discussed.

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