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Bacteria, algae, and phycobionts: maintaining useful concepts and terminology

William B. SANDERS

Abstract: The assertion that the blue-greens ('cyanobacteria') are bacteria and not algae has led to alternative concepts for both of the latter terms. *Bacteria* is now often used to designate the prokaryote kingdom, that includes the blue-greens, while in other contexts it means specifically those prokaryotes that are not blue-greens. The term *algae*, on the other hand, has no biosystematic implications; it encompasses many phylogenetically independent lineages characterized by oxygen-evolving photosynthesis. The algal status of the blue-greens is therefore not compromised by their classification among the bacteria. Current lichenological terminology, however, reflects the view that the blue-greens are not algae, thereby diverging from the concept of algae employed in phycology. The purpose and utility of terms that group organisms according to structural, functional and ecological criteria are insufficiently appreciated. These concepts do not compete with phylogenetic/biosystematic classifications, but rather complement them.

Key words: algae, bacteria, blue-green algae, chlorobiont, chlorolichen, cyanobacteria, cyanophyte, cyanolichen, cyanoprokaryote, lichen, moneran, phaeobiont, phaeolichen, phycobiont, phycolichen, photobiont, terminology, xanthobiont, xantholichen

Introduction

Some terms relating to lichen algae were recently discussed by Lange & Wagenitz (2003, 2004), who argued against using *phycolichen* to denote lichens with eukaryotic algal symbionts. That usage was supposed to contrast with *cyanolichen*, which refers to lichens whose photosynthetic symbionts are prokaryotic blue-green algae (=cyanophytes, =cyanophyceans, =cyanobacteria). Lange & Wagenitz (2003, 2004) showed that *phycolichen* was used with very different meanings previously, and therefore recommended an alternative term, *chlorolichen* (=lichen with chlorophyte phycobiont), as a more suitable complement to *cyanolichen*. Their well-justified recommendation need only be supplemented here by pointing out that not all lichens with eukaryotic algal symbionts are chlorolichens. Also included are one *phaeolichen* (*Verrucaria tavaresiae*, with phaeophycean phycobiont *Petroderma maculiforme*; Wynne 1969; Moe 1997; Peters & Moe 2001; Sanders et al. 2004) and four reported *xantholichens* (*Verrucaria funckii*, *V. laevata* and Chilean *V. maura* with xanthophycean phycobiont *Heterococcus caespitosus*, and *Staurothele clopimoides* with *Xanthonema montanum*; Zeitler 1954; Parra & Redón 1977; Tschermak-Woess 1988; Pereira 1992).

There is, however, another reason, of broader significance, why *phycolichen* is an unsuitable complement to *cyanolichen*. Many biologists, and particularly phycologists, understand the prefix *phyco-* to include rather than exclude the blue-greens. The term *algae* and the field of phycology encompass the blue-greens traditionally as well as currently, as is evident from the most recent phycology courses, textbooks and treatises (Bold & Wynne 1985; van den Hoek *et al.* 1995; Lee 1999; Graham & Wilcox 2000; John *et al.* 2002; Wehr & Sheath 2003). Because *algae* refers to a diverse and highly

W. B. Sanders: Centro de Ciencias Medioambientales, C.S.I.C., Calle Serrano 115 bis, 28006 Madrid, Spain; and the University Herbarium, University of California, Berkeley, USA.

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polyphyletic assemblage with no taxonomic status, inclusion of the blue-greens in this concept is in no way incompatible with their well-known relationship to the bacteria. However, the promotion of the term *cyanobacteria* (Stanier & Cohen-Bazire 1977) and the use of *Bacteria* with taxonomic rank (Cavalier-Smith 1998; Boone & Castenholz 2001) have given rise to alternative definitions of *bacteria* and *algae* that confuse biosystematic and bio-ecological concepts. It is important to examine the recent history and divergent usage of these terms in order to properly evaluate their implications and utility.

'Bacteria'

When Stanier & Cohen-Bazire (1977) declared that the blue-greens—'cyanobacteria'—were *bacteria* and not *algae*, they were interpreting both the latter terms as biosystematic categories. They believed their statement to follow from the evidence of relationship between the blue-greens and the bacteria. To those authors, this relationship meant that the blue-greens must themselves be considered bacteria—and therefore not algae. A proposal to treat the blue-greens under the bacteriological nomenclatural code was presented shortly thereafter (Stanier *et al.* 1978). A number of biologists raised objections to the redefined concepts of *bacteria* and *algae* implicit in Stanier & Cohen-Bazire's (1977) declaration, and questioned the practicality of treating the blue-greens under the bacterial code (Lewin 1976; Bourrelly 1979; Geitler 1979; Golubic 1979; Kondratieva 1982). There was no disagreement, however, about the biosystematic relationship of the blue-greens and the bacteria. Indeed, Lewin (1976) noted that this relationship was elucidated more than a century ago by Cohn (1875), who classified these organisms together as 'Schizophytae'. In the twentieth century, many authors recognized the prokaryotes (blue-greens and bacteria) as an independent kingdom, known until recently as Monera (Copeland 1938; Whittaker 1969).

With their distinct terminological viewpoint, Stanier & Cohen-Bazire (1977) asserted that ''continued use of the common names blue-green algae and cyanophytes perpetuates a false impression about the biological nature of cyanobacteria''. They did not specify what this false impression might be. Although the term *algae* may once have had taxonomic status, modern sources have long emphasized that *algae* denotes a structural/ecological grade and not a biosystematic entity. The term *algae* implies nothing about phylogeny; the same can be said of the suffix '-phyte', which is applied to all other major groups of algae regardless of phylogenetic affinities. Rather than misleading, the terms *blue-green algae* and *cyanophyte* convey no information at all about such relationships, and that is undoubtedly what Stanier & Cohen-Bazire (1977) found objectionable. At the time, two synonymous terms for the members of this kingdom were well-established: *prokaryote* and *moneran*. These terms even figure in standard English dictionaries (e.g., Merriam-Webster 2000). This situation might have logically suggested the term 'cyanoprokaryote' (Kondratieva 1982) or 'cyanomoneran' to indicate the biosystematic affinities of the blue-greens. However, Stanier & Cohen-Bazire (1977) instead asserted that the blue-greens were *bacteria*, a term employed for a biologically different type of prokaryote. Their usage of *bacteria* has become widespread, but it has not replaced the previous meaning; both concepts now share the same term, depending on the context and the user.

To many biologists, *bacteria* suggests mainly heterotrophic prokaryotes that lack oxygen-evolving photosynthesis. Stanier & Cohen-Bazire (1977) argued that because the bacteria encompass such highly diverse organisms, the concept can be defined satisfactorily only if the blue-greens are included. However, as Lewin (1976) pointed out, to include the blue-greens merely reduces *bacteria* to a synonym of prokaryote, losing a distinct concept while gaining nothing but

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duplication.[1] This would not be disadvantageous if the previous sense of *bacteria* were obsolete or expressed by another term. But observation of usage shows that *bacteria* is still needed and employed to distinguish those prokaryotes that are *not* blue-greens.

When we refer, for example, to the photosynthetic *bacteria* (as opposed to the photosynthetic *prokaryotes*), we mean organisms distinct from the blue-greens. The photosynthetic purple sulphur, purple non-sulphur, green sulphur and filamentous gliding bacteria fix light energy without chlorophyll *a*, without oxidation of water, and without generation of oxygen (Imhoff 2001; Overmann 2001; Pierson 2001). In these key features they differ thoroughly from the blue-greens and all other algae as well as higher plants. Their distinct photosynthetic pigments are called *bacteriochlorophylls* with the implicit distinction of bacteria from the blue-greens (which have chlorophyll *a* instead). The differences between the photosynthetic bacteria and the blue-greens are highly significant. The advent of oxygen-generating photosynthesis in an ancestral blue-green transformed the primeval terrestrial atmosphere and profoundly altered the entire course of biological evolution (Kondratieva 1982).

Another example is relevant to lichenology. There has been some discussion of what role, if any, might be played in the lichen symbiosis by the not-blue-green bacteria that are sometimes observed on or within the thallus (e.g., Jacobs & Ahmadjian 1971). Clearly, these organisms must not be confused with the cyanobionts. Some authors (see Millbank & Kershaw 1973) debated the significance of the 'nitrogen-fixing bacteria' reported in association with certain cephalodiate lichens; they did *not* mean the blue-green algal symbiont, so the distinction was an essential one. Yet how can we now unambiguously distinguish the former from the latter if our terminology equates both with bacteria? What else can we call them? Non-cyano-bacteria? Bacteria *sensu stricto*? Such cumbersome phrases are not being employed. In these contexts, *bacteria* is not meant to include the blue-greens; it is used in the bio-ecological sense it had before being assigned biosystematic status.

[1]Here it must be mentioned that many bacteriologists are currently recognizing the 'Archaea' as a prokaryotic Domain separate from the *Bacteria* (see Boone & Castenholz 2001). In this interpretation, *Bacteria* and *Prokaryota* are no longer synonyms. However, other biologists (Mayr 1990; Cavalier-Smith, 1998) reject this view, recognizing the two groups as *Eubacteria* and *Archaebacteria*. Stanier et al. (1978) and Cavalier-Smith (1998) explicitly synonymize *bacterium* with *prokaryote*.

'Algae'

The delimitation and usage of the term *algae* is not affected by the taxonomic placement of its member organisms. Consider, for example, the 'ochrophytes'—the heterokont, straminipilous algae such as the browns (e.g., kelps and rockweeds), diatoms, chrysophytes, and xanthophytes (Graham & Wilcox 2000). These classic algae have been placed in a distinct kingdom that also includes many non-algal, heterotrophic organisms such as the oomycetes, hyphochytrids, and labyrinthulids (Kingdom *Chromista* or *Straminipila*; Cavalier-Smith 1998; Dick 2001). Yet no one is claiming that the ochrophytes are not algae; their algal status is clearly not affected by their biosystematic affinities with non-algal organisms. The blue-greens should not be treated any differently. The significant differences between prokaryotes and eukaryotes are appropriately represented in biosystematic classification (Mayr 1990), but not in the concept of *algae* (Geitler 1979). The algae are defined by their distinct mode of nutrition and morphological grade. They are the oxygen-evolving photosynthetic organisms[2] that are not embryophytes ('land plants').

The one distinctive feature that the algae (and embryophytes) share is a fundamentally homologous photosynthetic apparatus. Although it is repackaged into distinct organelles (plastids) in eukaryotic algae, its range of diversity transcends the frontier between prokaryotes and eukaryotes. The

[2]All algal lineages show this mode of nutrition. However, most also include species that have become secondarily heterotrophic or myxotrophic, or that might possibly be primitively so (e.g., dinoflagellates).

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rhodophytes or red algae, for example, are unquestionably eukaryotic, yet their photosynthetic apparatus more closely resembles that of certain blue-greens than those of most other eukaryotic algae. Their thylakoids are evenly and individually spaced rather than stacked, chlorophyll *b* and *c* are absent, and phycobilin accessory pigments are present within phycobilisomes on the thylakoids (Graham & Wilcox 2000). Even more reminiscent of the blue-greens is the photosynthetic apparatus of the glaucophyte algae. Their primitive chloroplast is so similar to certain blue-greens that until fairly recently it was considered to be an autonomous, endosymbiotic 'cyanelle' (van den Hoek *et al*. 1995). Among the prokaryotes, on the other hand, the photosynthetic apparatus of the 'prochlorophytes' resembles that of eukaryotes: it has chlorophyll *a* and *b* and stacked thylakoids, like chlorophyte plastids. The range of diversity in the photosynthetic apparatus highlights the utility of considering prokaryotic and eukaryotic algae together.

Although the eukaryotic algae are highly polyphyletic with respect to their nuclear genome, the endosymbiotic origin of the plastid unites prokaryotic and eukaryotic algae in a complex evolutionary reticulum. One could argue that this gives a certain phylogenetic basis to the broad concept of algae, even though it cannot provide a biosystematic framework. It is now widely accepted that the first eukaryotic chloroplast arose by endosymbiotic incorporation and subsequent modification of an oxygen-evolving, photosynthetic prokaryote. Whether extant plastids ultimately descend from one or more primary endosymbiosis events is not fully clear (Delwiche & Palmer 1997). In any case, there is substantial evidence that descendents of those original photosynthetic eukaryotes were repeatedly reincorporated in later endosymbioses, converting them into the secondary and even tertiary plastids of many other major groups of algae (Palmer & Delwiche 1996). This means that eukaryote plastids are not homologous, but the photosynthetic apparatus that they and the blue-greens contain ultimately is. The blue-greens provided the one characteristic element that unites all these diverse lineages; it is therefore difficult to justify a concept of algae that excludes them.

'Phycobionts'

Scott (1957) coined two extremely handy and self-explanatory terms to designate the lichen symbionts: *mycobiont* and *phycobiont*. But introduction of the term *cyanobacteria* with the claim that these organisms are not algae led to the conclusion that they could not be considered phycobionts. Ahmadjian (1982) proposed the new term *photobiont* to replace Scott's *phycobiont*, on the grounds that the blue-greens ''. . . are not algae *per se* but actually bacteria''. This statement simply reiterated the viewpoint of Stanier & Cohen-Bazire (1977) without addressing the terminological objections raised by Lewin (1976), Bourrelly (1979), Geitler (1979) and Kondratieva (1982). The definition of algae was not discussed. As has been shown, renaming the prokaryote kingdom *Bacteria* (a biosystematic concept) may make the blue-greens *bacteria* in this new sense, but has no relevance to their status as algae. It is the other, bio-ecological sense of *bacteria* (prokaryotes lacking oxygenic photosynthesis) that is indeed incompatible with algal status. The confusion of these distinct usages of *bacteria* illustrates the disadvantages of assigning a new meaning to a term whose previous meaning is still needed and used.

Lichenologists widely adopted *photobiont* without debate. More unfortunate was the accompanying proposal that the original term *phycobiont* be applied in a restricted sense to encompass only eukaryotic algal symbionts (Ahmadjian 1982). This usage competes with the inclusive sense of *phycobiont* employed previously in the literature as well as currently by a number of authors who continue to follow the phycologist's concept of algae. The adoption of *photobiont* engendered further changes, such as replacement of *phycosymbiodeme* by *photosymbiodeme* (Ott 1988) and *phycomorph* by *photomorph* (Laundon 1995). Meanwhile, phycologists

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continue to treat the blue-greens as algae and are unlikely to change the name of their field of endeavour from phycology to photology. The lichenological literature is following a divergent concept of *algae*, based on declarations unaccompanied by critical discussion of this term.

Some of the above observations were made in a previous commentary (Sanders 2000) arguing in favour of the original *phycobiont* (Scott 1957). Among the published responses, one lichenologist agreed with many of the arguments but expressed concern that reversing terminology would be too destabilizing (Brodo 2000). This, of course, is a very important consideration. At the same time, it should also be recognized that the inconsistencies in current usage do not promote terminological stability either. Discussions of *bacteria* in the lichen thallus do not refer to the cyanobionts; *photosynthetic bacteria* and *nitrogen-fixing bacteria* are not meant to include blue-greens; and *algae* and *phyco-* currently encompass the blue-greens in phycology but not lichenology. Proliferation of the blue-green *Anabaena* in a eutrophic lake is still called an algal bloom; indeed, to call it a bacterial bloom could be ecologically misleading, even if sanctioned by bacterial systematists. These usages are needed to express biologically meaningful ideas, and are unlikely to disappear. In permitting concepts with different purposes to compete for the same designating terms, we have travelled halfway down a dubious terminological road, and it may now be equally inconvenient to continue to the end or to turn back.

Perspective

These terminological conflicts need not arise. We must recognize that while some traditional terms for grouping organisms are not based on phylogeny and have no biosystematic status, they are not necessarily obsolete or in need of modification. In notable cases their utility is readily observed. Nor should such groupings compete with phylogenetic/biosystematic classification. There is widespread agreement among biologists that systematics should reflect phylogeny, even if there is some controversy about exactly how this should be done (Grant 2003). Ambiguities arise when concepts with different purposes are forced to compete for control of the same designating term. This can be avoided simply by choosing or coining other terms to recognize phylogenetic/biosystematic groupings. For example, if kingdoms and other higher taxa were given names such as *Prokaryota*, *Eumycota* and *Metaphyta*, this would avoid confusion with the non-phylogenetic, biological concepts meant by *bacteria*, *fungi*, and *plants*. These concepts are widely used by biologists as well as the general public, and their utility has not been extinguished by the important advances in our phylogenetic understanding. It should be noted that the most up-to-date phycology, mycology and botany courses and texts each encompass a diverse, polyphyletic group of organisms. As long as the phylogenetic affinities of member organisms are appropriately emphasized, this is by no means an undesirable situation. Such groupings are not merely vestiges of tradition; they embody important structural, functional and ecological themes that merit consideration and study. It is precisely these common biological themes that make elucidation of contrasting phylogenies interesting and relevant. Without this biological-ecological context and the language that expresses it, phylogenetic reconstruction would have little purpose or significance. The two viewpoints are the complementary sides of the same coin of evolution, and we need both if we are to continue to formulate and resolve biologically meaningful questions.

Conclusions and Suggestions

Bacteria and blue-green algae have long been thought of as two different kinds of prokaryotes, the latter distinguished by oxygenic photosynthesis. However, inclusion of both within a biosystematic concept designated *Bacteria* has meant that there is

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no longer an unambiguous term to refer specifically to the prokaryotes that are not blue-greens. The algae encompass phylogenetically distinct lineages that share an oxygen-evolving photosynthetic apparatus. Because *algae* has no biosystematic implication, the relationship of the blue-greens to the bacteria cannot be considered grounds for excluding them from the algae. Since phycology and phycologists continue to include the blue-greens, the term *phycobiont* (Scott 1957) should logically include them as well. Use of *phycobiont* (*sensu* Ahmadjian 1982) to mean exclusively eukaryotic algal symbionts (i.e., as a complement to *cyanobiont*) creates ambiguity and should be avoided; the term *chlorobiont* is far more suitable for that purpose in most cases. In those exceptional cases cited above, *phaeobiont* and *xanthobiont* may be used where necessary. The viewpoints implicit in the different terminology in use should be considered critically. It is hoped that reflection on the broad themes in diversity of organisms will lead to greater appreciation of traditional bio-ecological groupings as useful complements to phylogenetic/biosystematic classification.

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