

**“ANABAENA,” “ANABAINA,” AND CODES OF  
NOMENCLATURE: A REVIEW OF THE  
FEASIBILITY OF NAME CORRECTION, AND A POSSIBLE  
DIRECTION FOR THE FUTURE**

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**ABSTRACT**

Spanning the better part of two centuries, two spellings, “*Anabaena*” and “*Anabaina*,” have competed as the name of a well-known genus of filamentous “blue-green algae” (Cyanobacteria). The orthographic form “*Anabaena*” has been generally favored, but “*Anabaina*” has been defended as well. Although “*Anabaina*” was proposed first (Bory, 1822), “*Anabaena*” is indicated (botanical code, conservation) as the spelling employed in the starting-point publication of those Oscillatoriales with heterocysts (Bornet and Flahault, 1886)—an assemblage largely equivalent to the Nostocales, as presently recognized. Since, according to the botanical code, valid publication of a name can date only from the official nomenclatural starting-date of the group to which it belongs, it might be assumed that “*Anabaena*” is the spelling to be selected. However, it can be shown that “*Anabaena*” is in error and, also, is not a conserved spelling. The name should be returned to the original spelling, “*Anabaina*”—maintaining authorship, under present code structure, in accordance with the starting-point document, viz., *Anabaina* Bory ex Bornet & Flahault. If not acceptable under the botanical code, proposed changes of cyanobacterial names (such as *Anabaina*) could be effected if their nomenclature were transferred from the botanical code to the bacteriological code. However, the case of *Anabaina* invokes larger questions of nomenclatural governance of different kingdoms, putative kingdoms, or parts of kingdoms—Bacteria *pro parte* (i.e., Cyanobacteria), Protozoa *pro parte* (e.g., “Myxomycetes”), Oomycetes (and a number of other Stramenopiles), and Fungi—by the botanical code (an instrument obviously intended for naming members of the plant kingdom). In the long-run, problems of nomenclature involving such “code-misplaced

groups” could probably be resolved with greatest equanimity through development of a unified code for naming all organisms. *Phytologia* 90(3): 324-354 (December, 2008).

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As may be surmised from systematically oriented botany textbooks (e.g., Brown, 1935; Pool, 1940; Smith, 1953; Cronquist, 1961; Raven et al., 1999; Nabors, 2004), *Anabaena* has long been a familiar name for a significant cyanophycean genus—a genus of perhaps 100 species (Van den Hoek et al., 1995; Komárek et al., 2003), although the exact number is uncertain in a group lacking typical sexual reproduction (compare Geitler, 1932; Desikachary, 1959; Drouet, 1978; Anand, 1980; Van den Hoek et al., 1995). *Anabaena*, considered now a member of the Nostocales (Van den Hoek et al., 1995; Graham and Wilcox, 2000), is distinguished from *Nostoc*: by retention of motility of trichomes in the “adult” stage (Kantz and Bold, 1969); by generally less contorted trichomes that do not occur in firm, macroscopic colonies (Prescott, 1962); and, by a sometimes differently patterned relationship of “vegetative cells,” akinetes, and heterocysts (cf. Wilcox et al., 1973; Bold and Wynne, 1985).<sup>1</sup> Also, *Anabaena* is not prone to form the bulbous, hormogonial packets (incipient colonies) characteristic of species of *Nostoc* (cf. Lazaroff, 1973; Komárek et al., 2003). *Anabaenopsis*, a genus similar to *Anabaena*, is distinguished by short filaments, with heterocysts on both ends of the trichome (Smith, 1950). The terminal heterocysts of *Anabaenopsis* arise from a pair of intercalary, incipient heterocysts (formed by asymmetric divisions of two adjacent vegetative cells); the heterocysts separate, leaving one at each end of the trichome (Smith, 1950; Komárek et al., 2003). Heterocysts of *Anabaena*, by contrast, are typically intercalary (Smith, 1950), sometimes specifically positioned along the trichome (Graham

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<sup>1</sup> The term “heterocytes” is preferred to “heterocysts” by some, since these cells are not strictly cysts—D. A. Casamatta, personal communication.

and Wilcox, 2000). The genus *Pseudanabaena* (see Desikachary, 1959; Anagnostidis and Komárek, 1988; Komárek et al., 2003), while resembling *Anabaena* and certain other nostocalean genera, lacks cell differentiation (heterocysts absent); relationships of *Pseudanabaena* to oscillatoriacean (non-heterocystous) forms have been elucidated—cf. Graham and Wilcox, 2000, p. 104 (adapted from Wilmotte, 1994); and Casamatta et al. (2005).

*Anabaena* is frequently an important component of blue-green algal blooms in plankton of freshwater ponds and lakes (Round, 1965), especially during hot, dry conditions of late summer. These blooms may significantly affect trophic conditions, and even water toxicity (Paerl, 1988). Specifically, species of *Anabaena* are known to play a role in nitrogen and phosphorus metabolism in such bodies of water (cf. Moss, 1980; Fogg and Thake, 1987; Graham and Wilcox, 2000). Related to occurrence in phytoplankton, *Anabaena* species exhibit phototactic orientation (Barsanti and Gualtieri, 2006)—varying position in upper layers of water with the aid of gas vacuoles (cf. Bold and Wynne, 1985; Lee, 1999). Buoyancy and rate of photosynthesis may be adjusted to varying light quantity (Kromkamp, 1990; Lee, 1999; Graham and Wilcox, 2000). Although high light intensity can result in temporary photo-inhibition in *Anabaena* (Kromkamp, 1990), biosynthesis of superoxide dismutase may be induced—in *Anabaena* and various planktonic cyanophytes (some studied in marine environments)—scavenging photo-produced molecular oxygen, and enhancing light tolerance (Miyake and Asada, 2003).

In spite of the apparently satisfactory taxonomic and ecological knowledge and distinctiveness of *Anabaena*, and several other major cyanophytes, systematic and culture/habitat delimitation of a number of genera (and species) of heterocystous filamentous blue-green alga—i.e., the formal taxonomic framework in which the genus *Anabaena* resides—remains a matter of debate (cf. Geitler, 1932, 1942; Smith, 1950; Tiffany and Britton, 1952; Desikachary, 1959; Prescott, 1962; Burrelly, 1970; Drouet, 1978; Rippka et al., 1979; Giovannoni et al., 1988; Komárek and Anagnostidis, 1989; Whitton, 2002; Komárek et al., 2003). This is not to say that progress in understanding the phylogeny of heterocystous groupings has not been made (see Rippka et al., 1979; Van den Hoek et al., 1995; Graham and Wilcox,

2000; Gugger and Hoffmann, 2004; Henson et al., 2004). However, the detailed systematics of cyanophyte genera is beyond the scope of the present paper, which focuses primarily on *Anabaena*.

To make a potentially lengthy introduction relatively short, and pertinent to the presentation here, there appears to be little question that *Anabaena* is a well-established name for a distinct, legitimate, large and important genus of the systematically and environmentally significant group, the Cyanophyta (Cyanobacteria or Cyanoprokaryotes). Furthermore, *Anabaena*, unlike some “algal” genera, has received considerable taxonomic attention (e.g., Fritsch, 1949; Anand, 1980; Stulp and Stam, 1985; Hiroki et al., 1998). Thus, there could surely be no real nomenclatural dispute here—at least regarding the propriety of the generic name, *Anabaena*—or, could there? As seen below, there is controversy indeed. As will also become evident, questions concerning *Anabaena* nomenclature call forth the larger issue of how problems involving the naming of entire “code-misplaced” groups, such as the “blue-green algae,” might ultimately be resolved.

### THE SPELLING OF “ANABAENA”: IT SHOULD BE “ANABAINA”

It may be surprising to some that Appendix III of the *International Code of Botanical Nomenclature* (ICBN, McNeill et al., 2006) lists *Anabaena* as a “conserved name.” In other words, it was deemed necessary to “save” the phycological name *Anabaena*—but, from what? Unlike the majority of the 11 conserved blue-green-algal generic names, *Anabaena* is not expressly protected against another algal name (homonymic or not). According to the *Code*, the cyanophycean name *Anabaena* (valid publication date noted as 1886) is conserved, specifically, against an earlier (1824), identically spelled name, *Anabaena* A. Jussieu, applying to an angiosperm genus. This earlier homonym (cf. Article 14.10, ICBN), referring to a Brazilian member of the Euphorbiaceae, is renamed *Romanoa* (cf. Mabblerley, 1987). In the 19<sup>th</sup> century, *Trichormus* Allman was used for a time (Ralfs, 1850) as a replacement name for *Anabaena* (blue-green algae), in part because of potential confusion with the euphorbiaceous homonym. But, because of conservation, the seemingly entrenched

cyanophyte generic name, spelled “*Anabaena*,” is in any case secure, is it not? Well, in spite of the apparent edict of the ICBN, perhaps not.

A majority of phycological authors seemingly considered “*Anabaena*” an assured name, and spelling, for this familiar genus of blue-green algae (e.g., Fritsch, 1945; Smith, 1950; Tiffany and Britton, 1952; Desikachary, 1959; Round, 1965; Morris, 1967; Chapman, 1968; Prescott, 1968; Bourrelly, 1970; Fogg et al., 1973; Pentecost, 1984; South and Whittick, 1987; Paerl, 1988; Trainor, 1988; Van den Hoek et al., 1995; Lee, 1999). However, Bold and Wynne (1985) and Graham and Wilcox (2000), while adopting the spelling “*Anabaena*,” noted that the name is also sometimes spelled “*Anabaina*”—an “i” replacing the “e” in the name. Neither of these latter author-pairs, though, explained why one spelling is preferable to the other. A minority of authors employed “*Anabaina*” as the correct spelling of the name (Drouet, 1978; Humm and Wicks, 1980; Silva et al., 1987, 1996). Humm and Wicks (1980, p. 162), in fact, asserted (without explanation) that the spelling “*Anabaena*” is “an error,” and “not available for conservation”—obviously, a rationale for selecting “*Anabaina*.” So, who is correct? Is it “*Anabaena*” or “*Anabaina*,” and what is the basis for deciding?

According to the botanical code, Bornet and Flahault are the validating authors of the name *Anabaena*, because certain groups of blue-green algae are among those “plants” with a later starting date for nomenclature than Linnaeus (1753). The starting point for filamentous cyanophytes with heterocysts, such as *Anabaena*, is taken as Jan. 1, 1886, a consensus date for publication of the four parts of Bornet and Flahault’s “Révision des Nostocacées hétérocystées” (see Article 13, ICBN). Thus, valid publication of *Anabaena* is considered to date only from 1886. Yet, Bory (de Saint-Vincent) originated this generic name more than 60 years earlier in the *Dictionnaire* (1822); Bory, however, spelled the name “*Anabaina*.” Consistent with Articles 46.6 and 46.7, the *Code* (Appendix III) cites authorship of *Anabaena* as, Bory ex Bornet & Flahault (1886). The *Code*, however, makes no mention of the initial spelling of the name by Bory, viz. *Anabaina*. Because of the starting point rule (Article 13), citation of authorship of *Anabaena* could simply be Bornet & Flahault (1886). But, since Bornet and

Flahault ascribed the name to Bory, it is appropriate to cite authority of *Anabaena* (regardless of spelling) as Bory ex Bornet & Flahault, 1886.

In reviewing various phycological works, authorship for *Anabaena* and other “algal” genera is often omitted (e.g., Fritsch, 1945; Morris, 1967; Pentecost, 1984; Trainor, 1988; Van den Hoek et al., 1995; Dillard, 1999; Lee, 1999; Graham and Wilcox, 2000; Barsanti and Gualtieri, 2006). When writers bothered to provide name authority, *Anabaena* authorship is typically indicated merely as “Bory” or “Bory 1822” (cf. Smith, 1950; Tiffany and Britton, 1952; Desikachary, 1959; Prescott, 1962, 1968; Cocke, 1967; Burrell, 1985; Bold and Wynne, 1985). Drouet (1978) also cited “Bory” as the author of “*Anabaina*,” in this case utilizing Bory’s spelling of the name. Relatively few authors (e.g., Anand, 1980; Whitton, 2002; Komárek et al., 2003) mentioned the authority of Bornet and Flahault (1886), even though, by application of the later starting point rule (Article 13), Bornet and Flahault established validation of the generic name.

Problems of nomenclature of *Anabaena* run deeper still. *Anabaena oscillarioides*, the “type” of *Anabaena* (cf. Geitler, 1942), is traced to Bornet and Flahault (1886), who attributed the name to Bory. Bory did not employ the epithet “*oscillarioides*” in 1822, but apparently did in 1831 (see Drouet, 1978). Bory (1822) used the name *Anabaina pseudo-oscillatoria*. In further complication, Fries (1835) published a different spelling of *oscillarioides*, viz. “*oscillatorioides*.” Drouet (1978) noted the type of “*Anabaina*” as *A. pseudo-oscillatoria*, yet listed *A. pseudo-oscillatoria* as a synonym of *A. oscillarioides*. It would appear, thus, if *A. oscillarioides* were not the name used in the starting point document (Bornet and Flahault, 1886), that *A. pseudo-oscillatoria* would be the legitimate type instead. The nomenclature of *Anabaena* at both genus and species levels is caught into whether or not one accepts a designated starting point (ICBN, Article 13) for nostoclean naming.

To return to the main point—authorship and spelling of the generic name *Anabaena*—the crux of the problem is this: When Bornet and Flahault attributed *Anabaena* to Bory, they did not employ Bory’s spelling, *Anabaina*. The question becomes, should the spelling in the starting point document (Bornet and Flahault, 1886)—allegedly “*Anabaena*,” i.e., as adopted by the botanical code—be retained? Or,

should a change be made to Bory's original spelling, *Anabaina*, since Bory provided a description of the genus (cf. Articles 32 and 41.2), and since he is usually given credit for this name in any case. One might assume that the ICBN is the ultimate arbiter in such matters, and that this genus should continue to be referenced by the more familiar name, "*Anabaena*." However, this indeed may not be the correct answer.

It is plausible to debate both sides of this spelling issue. A minor spelling glitch does not obviate Bornet and Flahault's validation of *Anabaena* or, necessarily, acceptance of their spelling of the name (cf. Article 60.2, ICBN). Furthermore, if one wishes to change a spelling, such as *Anabaena*, there are caveats: Article 60.1 states that "the original spelling of a name or epithet is to be retained, except for the correction of typographical or orthographical errors...." Article 60.3 cautions that "the liberty of correcting a name is to be used with reserve...." In other words, altering the spelling of an established name is not something done casually. A potential change of spelling of *Anabaena*, or any other putatively valid name, hinges ultimately on whether it can be shown that the validating authors made what may be construed as an actual mistake (as interpreted from Articles 60 and 61). In the usual situation, perhaps, one cannot conclusively demonstrate an error, especially since generic names may be composed essentially from any source (Article 20.1). However, in the case of *Anabaena*, inaccuracy can be demonstrated, a conclusion apparently also reached by Humm and Wicks (1980). In fact, there are two embedded mistakes—explained below.

Bornet and Flahault (1886)—who attributed *Anabaena* to Bory (1822)—were assuming no credit for authorship of this genus. In using Bory's generic name, Bornet and Flahault should have used Bory's spelling "*Anabaina*"—but they did not (using *Anabaena*, instead). However, they made no reference to any problem with the name as Bory spelled it. Bory's name, *Anabaina*, is based on two Greek roots: "*ano-*" meaning "upward," and "*baino-*" meaning to "pass" or "go" (Brown, 1956). Graham and Wilcox (2000) offered a reasonable approximation of the meaning of "*anabaina*," as "to rise"—fitting for a planktonic organism. It is certainly a more noble etymological derivation than that of the genus name, *Nostoc*, meaning, loosely, "snot," or else something the equivalent of the part of the anatomy from

which such emanates, i.e., “nostril” (Potts, 1997). In any event, there is no problem with the Greek origin of the two parts of the name *Anabaina*—such (dual Greek origin) is common in botanical nomenclature (Stearn, 1983)—and, the name is appropriately latinized (i.e., the ending and connecting vowel). Bornet and Flahault nonetheless changed the spelling in a limited, but crucially different, way. The first person to alter the spelling, however, was Fries (1835), who indeed used the spelling “*Anabaena*.” But, there is no evidence that Fries’ orthographical variant (cf. Article 61) influenced Bornet and Flahault. And, there is a small but significant difference in Bornet and Flahault’s spelling, versus that of Fries.

Bornet and Flahault not only spelled the name *Anabaena*—erroneously substituting “e” for “i” in Bory’s name (*Anabaina*)—they employed a ligature (second mistake), in which the “a” and “e” are abutted, viz. “æ” (in “*Anabæna*”). It is plausible that Bornet and Flahault used this ligature (æ) to suggest that the two vowels (originally “a” with “i”) be pronounced together—that is, as a single vowel sound (in effect, a transformed, classical Latin diphthong). Whether this was intended to simulate the sound of /e/, /i/, or /a/ is difficult to say with certainty (cf. Brown, 1956; Hendricks, 1962; Stearn, 1983). In any case, utilization of ligature amounts to further orthographic mutation. The *Code* indicates (Article 60.6) that ligatures of “ae” and “oe”—viz. æ, œ—are not permissible. Thus, if Bornet and Flahault’s name, “*Anabæna*,” is adopted, a correction is in order, and there are two possibilities: Usually, as understood from Article 60.6 (ICBN), the ligature would simply be unhinged—“æ” becomes “ae.” However, the situation with *Anabaena* is special, in that Bornet and Flahault (1886) were attempting to base their spelling on a previous, accepted name. Since this previous name (*Anabaina* Bory, 1822) was spelled with a separated “a” and “i”—which Bornet and Flahault were probably trying to unitize (phonetically) with a ligature—it is a more reasonable adjustment just to return *Anabaena* to the original, intended spelling of the name, “*Anabaina*.”

The argument that the spelling of *Anabaena* cannot be changed because it is a *nomen conservandum* in the botanical code (ICBN, 2006) is moot, for two related reasons: In the first place, *Anabaena* (Cyanophyceae) is conserved, in effect, only against



*Anabaena* (Euphorbiaceae), cf. Appendix III—not, specifically, against other generic names (including “algal” names). One cannot cogently argue, in this case, that *Anabaena* is automatically conserved against another particular generic name based on the same type (viz. *Anabaina*) since, as discussed above, *Anabaena* is simply a misspelling of *Anabaina*; in other words, these represent the *same* name (Note 1, Article 14.4). Secondly, whereas *Anabaena* Bornet & Flahault is a *nomen conservandum*, it is not among names that are *orthographia conservanda* (cf. Art. 14.11 and App. III, pp. 158, 172). This latter point is especially telling. If the spelling can be shown to be in error (see above), *Anabaena* (Cyanophyceae) is no more protected from correction than a non-conserved name. The technically correct spelling for this well-known nostocaceous genus should be *Anabaina*, and there is no “legal” reason not to make this change. Whereas the name originated with Bory (1822), the *Code* is nonetheless correct, in that, if one accepts the later starting point rule, authorship should be Bory ex Bornet & Flahault (1886). But even this could become subject to debate, as discussed in the next section.

One point more, before concluding this first section: If it is the case that *Anabaena* is returned to the proper spelling, *Anabaina*, an interesting possibility is raised as a consequence—this being, that conservation against the earlier homonym, *Anabaena* (Euphorbiaceae), may no longer be necessary since, due to the one-letter change of spelling, the cyanophyte name would no longer be (precisely) a later homonym. This could be interpreted as essentially “freeing up” *Anabaena* A. Jussieu (Euphorbiaceae) in nomenclatural competition against the *nomen novum*, *Romanoa*, which has seemingly replaced it. It will, however, be for others to decide if Bory’s original spelling, *Anabaina* (Cyanophyceae), and *Anabaena* Jussieu (Euphorbiaceae) are still to be viewed as homonyms. The ICBN is unclear on such a question. Compare, for example, the somewhat different messages of Article sections 53.1 and 53.3. The botanical code should be clarified as to whether spellings must be identical, or merely very similar, for names to qualify as homonyms.

**IS IT A QUESTION, EVENTUALLY, OF EITHER SWITCHING CODES OR CODE CHANGE?**

Nomenclature of Cyanobacteria (= Cyanophyta = blue-green algae)—including “*Anabaena*”—is controlled by the *International Code of Botanical Nomenclature*. “Justification” for this control is found in item 7 of the Preamble of the ICBN (McNeill et al., 2006) which states that the rules and recommendations of this code apply to “all organisms traditionally treated as plants....” Indeed, there is historical precedent, in that the Cyanophyceae (Myxophyceae) were placed in the plant kingdom in older textbooks of botany (e.g., Brown, 1935; Pool, 1940; Smith et al., 1953). Appreciation of blue-green algae as prokaryotic organisms (viz., bacteria) accrued during the 1960s and early 1970s (see review by Stanier, 1977). The various editions of the botanical code since the mid-1970s are outmoded in continuing to recognize Cyanobacteria as “algae”—not because they do not fit within the polyphyletic, ecological form/function grouping, “algae” (cf. Blackwell and Powell, 1995; Graham and Wilcox, 2000), i.e., within an assemblage of primary producers with relatively simple, often similar, thallus structure (cf. Guttman, 1999)—but because of the implication that, as “algae,” they are treated, de facto, as “plants.” Even green algae (among algae, most closely related to plants) are often no longer included in the plant kingdom *sensu stricto* (cf. Graham and Wilcox, 2000), although certain kinds of green algae, i.e., Charophytes, are clearly in the lineage leading to “higher” plants (Embryophytes), cf. Niklas (1997), Graham and Wilcox (2000), Blackwell (2003). In any event, nomenclaturally, the Cyanobacteria (dealt with, operationally, as “plants” by the botanical code) are a “code-misplaced group”—along with other groups such as Oomycetes, Fungi, and slime molds (and certain other protists)—meaning, that improved knowledge of the biology of these organisms indicates that they should no longer be placed in the plant kingdom (see, for example, Purves et al., 1998; Guttman, 1999). Therefore, one would think, their nomenclature should no longer be governed by the botanical code (cf. Blackwell and Powell, 1999). Nonetheless, the ICBN (McNeill et al., 2006) continues to oversee the naming of these organisms, given the concession in Article 45.4 allowing recognition of names validated under a “pertinent non-botanical code....” In regard to this latter point, some (Friedmann and Borowitzka, 1982; Hoffmann, 2005) suggested the possibility of a

converse recognition of names by the bacteriological code, published in accordance with the botanical code.

As might be surmised from the previous section, some might conclude (contrary to the conclusion I reached) that the name "*Anabaena*" cannot be changed (to "*Anabaina*"), since it is conserved in the botanical code, and seemingly further bound in perpetuity by the starting-point document for heterocystous blue-green algae. If the botanical code is viewed as intractable in permitting such a name change, yet the change is desirable, what options are available? At the moment, there are none perhaps; however, there are eventual possibilities (discussed subsequently) by which such name problems could be resolved—perhaps efficacious in achieving lasting solutions. Since this present paper deals specifically with the naming of blue-green algae, I will limit focus mainly to this group. Informed nomenclatural decision-making ultimately requires proper understanding of the biology of the organisms in question. Our biological understanding of blue-green algae has been greatly enhanced in recent decades. Not only are blue-greens, cytologically, bacteria, they comprise a significant group of true bacteria, viz. the Cyanobacteria (cf. Stanier and Cohen-Bazire, 1977; Olsen et al., 1994; Blackwell & Powell, 1995; Snyder and Champness, 2003). They are distinct among Eubacteria by virtue of their chlorophyll-*a*-associated, oxygenic photosynthesis (cf. Margulis and Schwartz, 1988). As is well known currently, from introductory (and even popular) biological literature, the cells of Cyanobacteria are definitively prokaryotic (Sagan and Margulis, 1988; Purves et al., 1998; Byrd & Powledge, 2006; Cain et al., 2007)—as are other bacteria—not eukaryotic as cells of plants and animals (which contain distinct, membrane-bounded organelles). Beyond the fact that cyanophytes are bacteria, the phylogeny of blue-greens and relationships to other prokaryotes are increasingly well understood (cf. Campbell & Reece, 2005). Blue-greens "constitute a phylogenetically coherent grouping within...Eubacteria" (Van den Hoek et al., 1995, p. 39); see also Graham and Wilcox (2000, p. 103), adapted from Olsen et al. (1994); and Ayala (2007, p. 81), adapted from Woese (2000). Furthermore, Cyanobacteria are considered to be included within the gram-negative assemblage of Eubacteria, i.e., the Gracilicutes (cf. Margulis, 1993; Barnes et al., 1998). In short, the general relationships of Cyanobacteria are no longer in doubt.

Knowledge of phylogenetic relationships within Cyanobacteria is also being clarified, particularly among filamentous forms—e.g., Van den Hoek et al. (1995); Graham and Wilcox (2000, p. 104), adapted from Wilmotte (1994); Gugger and Hoffmann (2004); Henson et al. (2004); and Casamatta et al. (2005).

If blue-green algae are not plants, and they are bacteria, why do they remain under the aegis of the botanical code? Logically, some (e.g., Stanier et al., 1978) have argued that nomenclature of blue-green algae (Cyanobacteria) should be transferred from the *International Code of Botanical Nomenclature* (ICBN) to the *International Code of Nomenclature of Bacteria* (ICNB). Stanier (1977, p. 79) based this proposal on the premise that “the largest evolutionary discontinuity among contemporary organisms lies at the cellular level,” distinguishing “eukaryotes and prokaryotes.” According to Stanier et al. (1978), this major distinction, of prokaryotes (including Cyanobacteria) from eukaryotes, should be observed by codes of nomenclature, as it is in biology textbooks. Gibbons and Murray (1978b) suggested formalizing the name, *Cyanobacteriales* Stanier in Gibbons and Murray (1978a), under the bacteriological (i.e., prokaryotic) code. Other workers (e.g., Lewin, 1976, 1979), however, have favored maintaining the status quo—retention of control of blue-green “algal” nomenclature by the botanical code—because of potential nomenclatural confusion, and possible development of dual nomenclatures (undue proliferation of synonymy), if governance of naming of blue-greens is shifted to the bacteriological code. I note, in passing, that some workers have, to an extent, seemed to downplay the over-riding importance of the prokaryote/eukaryote dichotomy (e.g., Woese, 1981; Woese et al., 1990; Olsen et al., 1994; Woese, 2000)—this in relation to the increasing importance assigned to molecular/biochemical differences between Archaea (= Archaeobacteria) and Bacteria (= Eubacteria). I do not underestimate the importance of the three-domains viewpoint (Archaea, Bacteria, Eucarya) espoused by Woese et al. (1990). The concept of three domains is now well-known, and accepted in a number of modern biology textbooks (e.g., Campbell and Reece, 2005; Johnson, 2006). However, this construct does not, in my view, transcend the significance that both “bacterial” groups (Archaea and Bacteria) are structurally prokaryotic—vastly different in cell complexity vs. eukaryotes—and that both are nomenclaturally covered,

without distinction, by the bacteriological code—It would seem foolish to suggest that there should be separate codes for naming Archaeobacteria and Eubacteria, when they can scarcely be told apart, except by biochemical means. In biological terms, Cavalier-Smith (1987) suggested that sequence homology between these two prokaryotic groups may be greater than initially supposed, a statement basically re-enforced by Carroll (2006). Brinkmann and Philippe (1999, p. 817) indicated at least a limited support for “the monophyly of prokaryotes” (i.e., a sister-group relationship of Archaea and Bacteria). See also Margulis and Schwartz (1988) and Blackwell and Powell (1995) for an interpretation differing from Woese et al. (1990).

I return to the main point of this section, the nomenclatural placement of the cyanobacterial grouping of Eubacteria, i.e., the blue-green bacteria. Whitton (2003, p. 25) stated that “the blue-greens are anomalous in that they are currently treated by some authors under the conventions of the International Code of Botanical Nomenclature, while others treat them under the International Code of Bacteriological Nomenclature.” Whereas it is true that in recent times a limited number species of Cyanobacteria have been named under the bacteriological code (mentioned in Oren, 2004)—or the “code of nomenclature of prokaryotes,” as some prefer to call it (cf. Oren and Tindall, 2005)—formal governance of Cyanobacteria (though not other bacteria) remains, statedly, with the botanical code (ICBN, 2006, page 2: statement 7 and footnote 2). The overwhelming majority of Cyanobacteria have been validly published using the botanical code, and some cyanobacterial taxa continue to be named under this code, e.g., Řeháková et al. (2007). Names among Cyanobacteria suggesting bacterial affinity—e.g. *Gloeobacter* (Rippka et al., 1974), a form lacking thylakoids—are historically most uncommon (Gibbons and Murray, 1978b). Contributing to this scarcity, no doubt, is the fact that the bacteriological code contains no explicit statement of inclusion of Cyanobacteria—only brief mention in the Preface (Lapage et al., 1992) of consideration given to the matter at the Congress for Microbiology in 1978. Nonetheless, discussions on further integrating the naming of Cyanobacteria into the bacteriological code, or facilitating cyanobacterial nomenclature, jointly, under the botanical and the bacteriological codes, have recently been put forward by cyanobacterial systematists (Oren, 2004; Oren and Tindall, 2005; Hoffmann, 2005).

Hoffmann (2005) outlined recommendations for unifying the nomenclature of Cyanophyta/Cyanobacteria (under the ICBN and the ICNB), including, allowance of greater flexibility of the type method under the bacteriological code. Needed presently, in seeking further resolution, is to inveigle both bacterial and botanical systematists to become more involved (perhaps in consort) with these ideas and suggestions for future code-governance of Cyanobacteria. In part, the point of my present paper (written from the viewpoint of involvement with botanical nomenclature) is to address such concepts. I agree that cyanobacterial nomenclature should be phased more effectively into the bacteriological naming system or, at least, into a system of naming that all systematists (including microbiologists) can possibly agree upon.

Arguments based on presumed nomenclatural disruption (Lewin, 1976, 1979)—should blue-greens be transferred to the bacteriological code—are not compelling. It is not clear that serious nomenclatural problems (e.g., discarding names) would arise pursuant to transfer; it is likely that existing (blue-green algal) names would continue to be used in most cases (see Oren and Tindall, 2005, on this point). Also, dual nomenclatures (should such develop for blue-greens) already exist in biological classification—for certain “ambiregnal protists,” e.g., euglenoids and dinoflagellates (cf. Corliss, 1995; Blackwell and Powell, 1999)—without causing substantial difficulty. Concern over possible nomenclatural upset begs the significant question of relationships of major groups of organisms—My opinion on this issue, however, does not constitute endorsement of phylogenetic nomenclature at all systematic levels, i.e., a “*PhyloCode*” (compare, for example, Blackwell, 2002; vs. Cantino, 2000)—Among other problems, it is unlikely that the complete phylogenetic information (i.e., for all known species, of all “categories” of organisms) required to underpin such a “total” system will ever become available. There is, on the other hand, scant reason for codes of nomenclature to ignore basic biological knowledge, resulting in maintenance of improper code placement of entire groups of organisms (case-in-point, the Cyanobacteria). A quote from Sneath (2005) is pertinent in this regard: “Nomenclature is determined by taxonomy, not the reverse.”

In light of unequivocal knowledge of blue-greens (Cyanobacteria) as prokaryotes (Stanier and Cohen-Bazire, 1977;

Gibbons and Murray, 1978a,b; Fox et al., 1980; Krogmann, 1981), it is puzzling that some authors (e.g., Bold & Wynne, 1985; Bold et al., 1987) persisted in recognizing the “Cyanophyta” as “algae”—not because they do not fit within the loose, morpho-ecological construct of “algae” (as previously discussed), but because of the implication that they are somehow more like plants than they are like bacteria. In evidence of their putative algal (i.e., “botanical”) nature, Bold and co-authors cited the plant-like, oxygenic (chlorophyll-*a*-utilizing) photosynthesis of “blue-green algae”—albeit minus chlorophyll *b*, unless the Prochlorophyta are included in the cyanophytes (compare, for example, Krogmann, 1981; Bold and Wynne, 1985; Rowan, 1989; Van den Hoek et al., 1995; Lee, 1999; Graham and Wilcox, 2000). However, it should simply be understood, in this regard, that a free-living cyanobacterium was the source of chloroplast origin through an ancient endosymbiosis that eventually diverged into three basal lineages: glaucocystophytes, green, and red lineages (Van den Hoek et al., 1995; Delwiche, 1999; Palmer, 2000; Bhattacharya et al., 2004; Keeling, 2004). Primary plastids, resultant of original endosymbiosis, are generally considered monophyletic (Moreira et al., 2000; Bhattacharya et al., 2004; Keeling, 2004; Reyes-Prieto et al., 2007), although Delwiche (1999) cautioned concerning the certainty of such a conclusion. Regardless, green algae, and ultimately plants, are a product of primary endosymbiosis, cf. Giovannoni et al. (1988), Stackebrandt (1989), Sitte and Eschbach (1992), Olsen et al. (1994), Blackwell and Powell (1995), Van den Hoek et al. (1995), Barnes et al. (1998), Graham and Wilcox (2000), Larkum and Vesk (2003), Snyder and Champness (2003), Blackwell (2004), Keeling (2004)—while euglenoids and chlorarachniophytes are derived (from the green-algal lineage) by separate, secondary endosymbioses (McFadden and Gilson, 1995; Lee, 1999; Keeling, 2004). Whereas present red algae are the result of primary endosymbiosis (Bonen and Doolittle, 1976; Moreira et al., 2000; Keeling, 2004), evolutionary lines believed to be related to the red lineage developed subsequently through a major, secondary endosymbiosis (e.g., cryptomonads and the different chromistan algal groups), and even by tertiary endosymbioses (various dinoflagellates), cf. Whatley and Whatley (1981); Cavalier-Smith (1986); Maier (1992); Blackwell and Powell (1995); Chesnick et al. (1997), Delwiche (1999); Bhattacharya et al. (2004); Keeling (2004); Reyes-Prieto et al. (2007).

Messages from the discussion above, most pertinent to the point of this paper, are: 1) There is no doubt of the ultimate connection of Cyanobacteria to chloroplasts (whether simple or complex) of all “algal” and plant groups. Plastids are cell organelles descended from cyanobacterial endosymbionts which were once free-living microbes (Delwiche, 1999). 2) However, the well-established relationships between plastids and cyanophyte-cells notwithstanding, the differences between, for example, green-algae/plants (Viridiplantae), on one hand, and Cyanobacteria on the other, must still be judged to be enormous. This major distinction represents (in spite of plastid lineage) the “quantum” cellular divide between present-day eukaryotic and prokaryotic organisms (cf. Stanier, 1977; Margulis, 1993). As Barnes et al. (1998, p. 3) noted, “unlike the Eukarya, the Prokarya [including Cyanobacteria] did not evolve by symbiogenesis.” The structural arrangements of both cell and genome are strikingly different in eukaryotes and prokaryotes—lacking compartmentalization (of function) in prokaryotes (cf. Avers, 1976; Alberts et al., 1989; Campbell and Reece, 2005). 3) Regardless of massive biological evidence to the contrary (and a clear understanding that blue-green “algae” are actually bacteria, i.e., definitely prokaryotic), it is nonetheless the status quo—nomenclatural regulation, and de facto treatment, of Cyanobacteria as “plants” by the botanical code (not explicit inclusion by the bacteriological code)—that continues to hold sway (ICBN, 2006, p. 2).

But, the argument need not be over. Taxonomic considerations of groupings of bacteria have, on occasion (e.g., Trüper & Imhoff, 1999; Oren, 2004), continued to include Cyanobacteria in discussion—implying that code governance of this group is not resolved. In comparing codes, it can be noted that the botanical code (ICBN, 2006) operates by a generally strict, historical method of name priority (exceptions by conservation allowed), within the context of a formal, somewhat complex, starting-point system—dating from 1753 to 1900, depending on the taxonomic group (cf. Article 13, ICBN). Though stately endorsing the principle of name priority, and allowing name conservation as well, the code for bacteria (ICBN, 1992) functions now (more pragmatically, if more arbitrarily, than the botanical code) by one, much more recent starting-point (Jan. 1, 1980; see Rule 23a, Note 3)—this in connection with approved name-lists (document developed



by Skerman et al., 1980); see discussion of “approved lists” of bacterial names in Sneath (2005). Since the botanical code has continued to usurp the prerogative for inclusion of cyanophytes, the bacteriological code—though professing application to all bacteria—has not typically (i.e., with relatively few exceptions) been invoked to validate cyanobacterial names. However, contrary to Lewin’s (1979) belief, if the botanical code relinquished control of the naming of Cyanobacteria, it could be a fairly simple matter, under the bacteriological code, to add names of cyanobacterial genera to new listings for taxa (in issues of *IJSEM* = *International Journal of Systematic and Evolutionary Microbiology*). If such name-addition occurred, existing names for blue-greens, as mentioned, would probably be employed. However, the bacteriological code would not be obliged to honor names (or spellings, or authorities) putatively conserved by the botanical code, since these codes are autonomous (with the exception of avoiding use of identical names for different kinds of organisms). As a case in point, *Anabaina* Bory (1822) could be recognized by the bacteriological code (name lists) as the correct citation for the genus it represents—not *Anabaena* Bory ex Bornet & Flahault (1886)—thereby resolving this particular dilemma.

Transference of blue-green algal nomenclature from the botanical to the bacteriological code could possibly solve the problem for Cyanobacteria, and would be more reflective of the biology of these organisms (as prokaryotes). But, such an approach is not without potential problems. The bacteriological code indicates (Rule 18a) that “the type” of a bacterial species or subspecies should be a strain in pure culture. The requirements for deposition of such type strains are now even more stringent (cf. Tindall et al., 2006). One may surmise from Kantz and Bold (1969) and Baker and Bold (1970) difficulties of achieving axenic cultures of some cyanophyceans, or adequate growth in such cultures. With rewording of the rules, though, special allowance could be made for the “purity” of cyanobacterial strains deposited as type material. Or, preserved (even frozen) specimens (of Cyanobacteria) could be designated as acceptable in the bacteriological code, as under the botanical code (Article 8, ICBN, 2006). In fact, a component of one of the recommendations in Hoffmann (2005), for “unification” of cyanobacterial nomenclature (under both codes), was to provide a statement in the bacteriological code permitting “botanical

types” for Cyanobacteria—this, in essence, had been suggested earlier in Friedmann and Borowitzka (1982). If a few points, such as this, could be resolved, Cyanobacteria could find at last a more appropriate nomenclatural home, indicative of the true nature of their biology.

However, a mechanism for “reselecting” the appropriate name for certain organisms (including Cyanobacteria) could be achieved as well if the *three*, present, major kingdom-based codes (botanical, bacteriological, and zoological) were reconstituted as a “unified code” (cf. Corliss, 1990; Spamer and Bogan, 1997; Blackwell and Powell, 1999) for “all” biological kingdoms (Blackwell, 2004). Less well known, perhaps, there are also separate codes for viruses and for cultivated plants (cf. Spamer and Bogan, 1997). If, though, one code of nomenclature, with one set of rules, could be established for all organisms (how to consider viruses being debatable), then the problem of nomenclatural regulation of any “misplaced” group could finally have a uniform forum for resolution. Also, a consolidated code could provide a venue for more permanent solutions than simply shifting groups between existing codes. Earlier efforts aimed at producing a *BioCode* (Greuter et al., 1996) did not meet with success; the draft document resembled the botanical code too closely to be acceptable to those involved with zoological nomenclature (see mention in Spamer and Bogan, 1997; Blackwell and Powell, 1999; Blackwell, 2002). However, there is no insuperable reason not to try again. In fact, efforts to develop an acceptable *BioCode* may be reinvigorated (Oren, 2004; Hawksworth, 2007). New attempts at code unification may become associated with the development of accepted name lists (as with the present bacteriological code), cf. Hawksworth (2000, 2007). If so, it would be well if these lists—destined, considering all organisms, to become extraordinarily extensive—remain open to modification, should preferable (more correct) names or spellings become manifest.

Yet another approach—in light of improved understanding of phylogeny of major groups of organisms—would be to establish a separate code for each kingdom of organisms (discussed in Corliss, 1990, 1993; Blackwell and Powell, 1999). Not only would plants, animals, and bacteria have their own codes, but other kingdoms such as Fungi (cf. Margulis, 1981; Kendrick, 1992), Chromista (i.e., “Stramenopiles,” cf. Cavalier-Smith, 1989; Blackwell and Powell,

2000) and even Protozoa (Cavalier-Smith, 1993; Blackwell and Powell, 2001) would as well. Such “nomenclatural partitioning” is, in fact, how the code for bacteria came into being. Bacteria, because they were once thought of as “fungi” (i.e., “Schizomycetes”), were for many years prior to 1958 (when the first edition of the bacteriological code was published) simply “covered” by the botanical code (cf. Lapage et al., 1992; Sneath, 2003)—as the Cyanobacteria remain today. By a similar token, nomenclature of viruses was umbrelled by the bacteriological code (i.e., in 1958), but subsequently transferred to the International Congress of Virology (cf. Sneath, 2003). So, some precedent exists for code (name-governance) proliferation, to match better understanding of the delimitation of the most major groups of organisms. However, the problem with this approach (potentially, a code for each kingdom) is that it has been standard practice, recently, that seven, eight, or even nine kingdoms of organisms are recognized (discussed in Cavalier-Smith, 1993; Blackwell & Powell, 1995, 1999; Blackwell, 2004), compared to the five recognized by Whittaker (1969), Margulis (1981), and Margulis and Schwartz (1988). A multiple-code approach (to keep pace with kingdoms recognized) could eventually prove more cumbersome, and uneven, than the current three-kingdom code system. And, at what point could we be sure that we are finished establishing, or at least proposing, “new” kingdoms (or new delimitations of major groups of organisms)? Leedale (1974) once suggested that there are, possibly, as many as 19 kingdoms. Clearly, the number of kingdoms has been debatable, and remains so (cf. Blackwell, 2004). It is worth mentioning, in this context, that the idea of establishing a special “Cyano-Code,” dealing specifically with Cyanobacteria, has generally been dismissed (cf. Oren and Tindall, 2005; also, Hoffmann, 2005).

Hence, it is doubtful that code-proliferation, to match recognized kingdoms—“Kingdom” being the “highest” grouping or rank or organisms (because “Domain,” cf. Woese et al., 1990, though putatively “greater” than Kingdom, is not a category recognized by codes of nomenclature, cf. Blackwell, 2004)—will provide a satisfactory, long-term solution. Such an approach would result in unduly complicated nomenclatural governance. Another extreme approach, that of establishing “rankless” systems of classification (e.g., Hibbett and Donoghue, 1998), likewise does not provide a reasonable alternative when there is still so much need to render order from chaos

in classification—And, when there can be little doubt that classifications are inherently hierarchical (Blackwell, 2002).

It appears, thus, that the possibility of attaining one code for naming all organisms has become the “holy grail” of biological nomenclature. If code unification could be achieved, obviously we would no longer need worry about which code should cover exactly which groups of organisms (Blackwell and Powell, 1999), or how appropriate the inclusion of the nomenclature of a given group in a particular code really is. Cyanobacteria would, for example, hold as unquestioned a place in a unified code as any other group. However, the difficulty is to bring various factions (botanists, bacteriologists, mycologists, zoologists, protistologists, cyanobacteriologists, etc.) involved—each with a particular nomenclatural viewpoint and history—into agreement on the multitude of specifics involved in developing a “consensus code.” So far, attempted code “harmonizations” have met with very limited success (cf. Corliss, 1990; Blackwell and Powell, 1999; Hawksworth, 2000)—due to the numerous minor (and sometimes major) differences between existing codes of nomenclature. As one example of disparity among codes, the bacteriological code mandates, in effect, registration of new names—in this case, currently, publication (or validation, if published elsewhere) in one designated journal, *IJSEM* (mentioned previously), cf. Sneath (2003, 2005), Tindall et al. (2006). The zoological code rejected name registration (cf. Spamer and Bogan, 1997). Registration was initiated in the botanical code and then withdrawn (cf. Hawksworth, 2000). The viral code requires name registration (Spamer and Bogan, 1997). However, regardless of many examples of discordance, all codes have the same general objective—promoting proper naming of the entities and groups they “oversee.” And, probably, virtually all nomenclaturists, professedly or not, would wish to see the process of nomenclature simplified, and unified into an unambiguous set of rules—applicable to the naming of all organisms—that could be “universally” agreed upon. But, regardless of similar goals, and wishes, it remains clear that “the devil is in the details.”

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