

**CHROMISTA REVISITED: A DILEMMA OF OVERLAPPING  
PUTATIVE KINGDOMS, AND THE ATTEMPTED  
APPLICATION OF THE BOTANICAL CODE OF  
NOMENCLATURE**

**Will H. Blackwell**

Biological Sciences, The University of Alabama, Tuscaloosa, AL  
35487, USA

**ABSTRACT**

It was many centuries before it was realized that all organisms were not either plants or animals, and many more years before it was understood that the catch-all kingdom “Protista”—proposed to include predominantly unicellular, “non-plants” and “non-animals”—was heterogeneous and phylogenetically inadequate, encompassing both related and unrelated organisms. The probable unity of a particular group of protists—viewed as chromophytous algae or pseudofungi (and related protozoal forms), and often exhibiting a characteristic heterodynamic flagellar pattern—was gradually understood; these became separated from Protista, and recognized by various kingdom, subkingdom, phylum, or subphylum names. At kingdom level, two names and groupings—Chromista and Stramenopiles—have competed, among others, for these typically heterokont protists, in a partial overlay of descriptive information. Stramenopiles have the “tighter” circumscription, by virtue of *definition* based on the occurrence of unique, composite, tubular, flagellar hairs. Acceptance of Stramenopiles (as a more clearly monophyletic group) was beginning to hold sway over the more diverse Chromista (with its less obviously related major sub-groupings). However, recent evidence from plastid evolution has suggested that the larger, yet still generally monophyletic, assemblage of (mostly) heterokont protists—the Chromista—remains viable as a putative kingdom, much in the original sense of Cavalier-Smith (1981, 1986). Although the matter is still equivocal, the present paper notes a return to usage of the kingdom name Chromista—representing an assemblage including not only stramenopilous organisms, but also plastid-related groups, i.e., haptophytes and cryptomonads. The naming of chromistans has fallen by tradition mainly under the botanical code of nomenclature, which, as the other

major eukaryotic code (the zoological code), contains little regulation at kingdom level. Difficulty in properly establishing kingdoms, such as Chromista, or Straminipila, might be alleviated if a unified code of (biological) nomenclature were developed, with guidelines for determining/composing kingdom names. As a further point of present code deficiency, supra-kingdom ranks (to which yet larger groupings such as “Chromalveolata” might be assigned) are not recognized in existing, formal codes (botanical, zoological, or bacteriological)—a situation that could also be changed through code unification. It is important to examine current, proposed, *ad hoc* naming schemes in context of present nomenclatural codes (one of the points of this paper). It would be gratifying if systematists that produce future encompassing taxonomies (major eukaryotic schemata), and those involved with the development of a future code (or codes) of nomenclature, could work in consort toward the goal of improved, stable systems of classification—systems not only modern and biologically accurate, but nomenclaturally appurtenant as well. *Phytologia* 91(2): 191-225 (August, 2009).

**KEY WORDS:** Chromalveolata, Chromista, codes of nomenclature, code unification, complex plastids, Domain, endosymbiosis, heterodynamic flagella, Heterokonta, holophyletic, Kingdom, monophyletic, Ochrata, Pseudofungi, Stramenopila, Straminipila, supergroup, Supra-kingdom, tubular mastigonemes, tubular mitochondrial cristae.

---

Botanical nomenclatural regulation is lax at ranks above Family, especially for names not automatically typified—consider Articles 16 and 17, *International Code of Botanical Nomenclature* (ICBN), McNeill et al. (2006). Nomenclature at these “higher” levels can be confusing. At the rank of Class, three different terminations for names are suggested (Recommendation 16A.3, ICBN), depending on the “kind” of “plant” in question. This can result in rather closely related plant groups—e.g., liverworts, compared with their probable relatives, the charophytes (cf. Niklas, 1997; Blackwell, 2003)—having quite different sounding Class names. At Division/Phylum level, although name-terminations are reduced to two (i.e., for “plants” vs. “fungi”), the dual usage in botany now—i.e., Division *or* Phylum (Recommendation 16A.1)—is in itself confusing. At Kingdom level,

there are essentially no *Code* instructions on how to name these major groups. There are, for example, no guidelines for kingdom name terminations. By convention, such names often end in “a”—e.g., Animalia, Archaeobacteria, Biliphyta, Monera—but this is not uniformly followed, e.g., Fungi, Plantae, Viridiplantae. Jeffrey (1971) proposed that the suffix “-biota,” implying neither plant, nor animal, nor fungus (nor bacterium, for that matter), be used as a standard, “neutral” ending for kingdom names; however, this proposal was not widely adopted.

There is, in fact, a paucity of nomenclatural regulation by the botanical code and (particularly) by the zoological code of higher categories such as Phylum (Division), Class, and even Order. In the case of the botanical code, such “weak regulation” has been attributed to the belief that these “upper groups” are too unstable or uncertain in delimitation (cf. Gledhill, 1989) for application of rigorous nomenclature—such as the principle of priority, or the type method (with the exception of automatically typified names, cf. Article 16.2, ICBN, 2006; but even this does not clearly apply to Kingdom). The dearth of rules and recommendations at the level of Kingdom, however, is perhaps more of an historical artifact. Until the mid-nineteenth century, it was believed that there were just plant and animal kingdoms—hence, no need for detailed regulation of names of kingdoms (because the matter was non-controversial). This changed, though, when authors such as Hogg (1860) and Haeckel (1866) recognized, additionally, a “protocist” (or “protist”) kingdom for (mostly) unicellular organisms, not clearly plant or animal. While some later authors (e.g., Copeland, 1956; Whittaker, 1959) continued to emphasize (and increase the recognition of) kingdoms, others (e.g., Christensen, 1958) came to believe that Kingdom was a relatively meaningless, perhaps artificial, grouping category, and recommended removal of *Regnum* (Kingdom) from the botanical code. Christensen’s proposal (1958) did not gain favor, however, and the ICBN (2006) still recognizes “Kingdom” (Article 3.1)—even though specific rules for “regulating” this category remain absent.

By mid-twentieth century, the number of kingdoms generally accepted had risen to five (cf. Whittaker, 1969). More recently, six to nine kingdoms have often been recognized (cf. Edwards, 1976; Cavalier-Smith, 1981, 1987, 1993, 2004; Corliss, 1994; Blackwell and

Powell, 1995, 1999; Blackwell, 2004). With proliferation of kingdoms came the additional complication of the supra-kingdom category, "Domain" (Woese et al., 1990)—a rank not sanctioned by codes of nomenclature. In any case, more kingdoms or kingdom-level groups are presently recognized than there are codes of nomenclature (There are three major organism-based codes, discussed below). Several different kingdoms, or parts of kingdoms, are under the umbrella of the botanical code alone (cf. Blackwell and Powell, 1999; Blackwell, 2008)—e.g., Fungi, Myxomycetes (these being Protozoa, cf. Corliss, 1991), Cyanobacteria, and most Stramenopiles (cf. Blackwell and Powell, 1999)—in addition to plants, obviously the intended objects of this code. It may be controversial which code should control the nomenclature of a given group of organisms, e.g., Cyanobacteria—in this case, the botanical or the bacteriological code (cf. Blackwell, 2008).

So, questions remain: Were the kingdoms that we now recognize properly established, based on both biology and nomenclature? If not, how should they be established? Is it possible to determine if a given kingdom name is technically accurate and properly applied? Is, for example, the kingdom name-termination appropriate?—On what basis is this decided? And, under which code of nomenclature should each putative kingdom be "governed?" Cavalier-Smith (1978) and Corliss (1983) initially raised questions concerning possible nomenclatural consequences of creating multiple kingdoms of organisms, a situation readdressed by Blackwell and Powell (1999), and that pertains here. These sorts of questions do not necessarily have ready answers, nor will I seek to deal with all such questions here (and certainly not for all kingdoms). What I wish to address is a special confusion concerning two proposed kingdoms—Chromista and Stramenopila—that have similar, yet clearly non-identical, circumscriptions; i.e., they are descriptively over-lapping. I give, subsequently, particular consideration to determination of the usage and best application of these particular names and groupings, and to the various complications that are attendant.

### **CHROMISTANS, STRAMENOPILES, AND THE BOTANICAL CODE**

The case in point here, Chromista vs. Stramenopiles, is which kingdom and name to recognize? In addressing this question, it should be decided under which code the nomenclature of these groups should fall. Organisms recognized variously as chromistans and stramenopiles are neither plants nor animals (cf. Patterson, 1989; Cavalier-Smith, 1987; Keeling, 2004). Historically, however, the naming of the majority of the membership of either alleged kingdom has been in accordance with the botanical code (cf. Blackwell and Powell, 1999); thus, this question is decided (for now), by precedent, in favor of the ICBN. Although this decision is perhaps more clear-cut with Stramenopiles, it is nonetheless true that, since the Chromista are also largely characterized by chromophytous algal (e.g., chrysophytes, xanthophytes, phaeophytes, diatoms) and by pseudofungal lineages (e.g., Oomycetes), cf. Cavalier-Smith (1989), their nomenclature generally forfeits to the botanical code as well (further discussed below). To a lesser extent, some members of “both” putative kingdom groups have been named under the zoological code (e.g., certain amoeboid or colonial chrysophytes).

We are saddled at present with the situation of having two separate eukaryotic codes, botanical and zoological, plus the bacteriological or prokaryotic code—hence, three major organismal codes (and, in addition, a code for viruses, and a specialty code for cultivated plants). In hindsight, it is apparent that none of these codes is a good fit (in biological context) for the naming of organisms considered herein (chromistans/stramenopiles). Furthermore, since the three main codes were each conceived (more or less independently) to facilitate nomenclature of members of the plant, animal and bacterial kingdoms respectively, the nomenclature in each code (with some exception in the bacteriological code) effectively starts *below* the level of kingdom. The naming procedure for the category of kingdom is substantially neglected in the botanical code, and even more so in the zoological code. If, however, there were a unified code (cf. Cavalier-Smith, 1978; Patterson, 1986; Corliss, 1990; Blackwell and Powell, 1999; Blackwell, 2008), the question of which code should cover which kingdom (e.g., Chromista) need not be asked, since nomenclature of all

organisms (regardless of their “biology”) would be under one code, and rules would doubtless be in place for kingdom names.

But since there is as yet no accepted unified code, the nomenclatural default in the case of all eukaryotes (regardless of relationships) is, at present, to either the botanical code or the zoological code. Whereas some organisms considered to be Chromistans (and Stramenopiles), such as the more protozoal representatives (e.g., the primitive Bicoecids), have often fallen under the zoological code, the majority are (as indicated) still under the governance of the botanical code—since most chromistal/stramenopilous organisms, accurately or not, have typically been referred to as either “algae” or “fungi” (“groupings” traditionally covered by the botanical code). In the case of “fungi,” however, it should be noted that none of the “chromistal fungi” are actual Fungi, but rather are “Pseudofungi”—e.g., Oomycetes, Hyphochytriumycetes, and the more protozoan-like Labyrinthulids—these pseudofungi being relatively unrelated to true Fungi (Cavalier-Smith, 1986, 1989; Alexopoulos et al., 1996; Blackwell and Powell, 2000) and more closely related to types of (alveolate) Protozoa, such as ciliates, dinoflagellates, and apicomplexans (cf. Cavalier-Smith et al., 1995; Van de Peer and De Wachter, 1997; Keeling, 2004). Nonetheless, pseudofungi continue to be “covered” (as do true fungi) by the botanical code—evidenced, for example, by the reference to Oomycetes in item number 7 of the Preamble (ICBN, 2006). “Algae,” no longer considered a cohesive phylogenetic construct (cf. Van den Hoek et al., 1995, p. 9), are still also generally treated, operationally, as “plants” by the ICBN. It remains equivocal whether the nomenclature of certain groups of organisms (in the Chromista) such as the Pedinellids (cf. Patterson, 1989) and Silicoflagellates (cf. Tappan, 1980)—difficult to pigeonhole as “algae” vs. “protozoa”—should be considered, presently, under the botanical or the zoological code.

In opting at the present time primarily for the botanical code, based on overall membership of assemblages considered here, it might be assumed that we would thereby know what rules to follow in establishing the appropriate kingdom (Chromista or Stramenopila, or other competing names/groupings subsequently discussed). But since there essentially aren't any “kingdom rules” per se—being as which

name came first is largely irrelevant (priority is not binding at kingdom level, as extrapolated by comparing Principle IV with Article 11, ICBN)—and since none of these names, arguably, is really a typified name (see later discussion, however, concerning Chromista)—such decisions boil down more to a matter of informed preference than code “legality.” This preference is informed, mainly, by asking biologically based questions, such as: Which grouping is the most monophyletic (pertinent, if one is striving for phylogenetic nomenclature, cf. de Queiroz and Gauthier, 1992; de Queiroz, 1997, 2006; Cantino, 2000)? Even though a *PhyloCode* has not been formally endorsed by any official, international nomenclatural congress (other than, perhaps, that of those promoting the *PhyloCode*, cf. de Queiroz, 2006), it would nonetheless seem logical that at kingdom level we would wish to recognize a group that is phylogenetically inclusive (holophyletic)—with the caveat that all included sub-groups are not going to be equally related. If such can be determined, then, armed with this “phylogenetic knowledge,” we would perhaps next seek to assess which name is descriptively most appropriate, given the “special biology” of the group that it is desired to recognize. After answering biological questions, one would presumably want to determine how properly to compose this name, including the proper name-ending. Again, in these matters, there is no effective counsel from the ICBN at kingdom level. This seems ironic, if not a full-blown “Catch-22,” in that one is bound into the botanical code for guidance for naming, but there is virtually no guidance (in the case of kingdoms). Cavalier-Smith and Chao (1996) alluded to inconsistencies (confusion, or lack of instruction as the case may be) in the botanical code concerning the establishment of names at higher ranks. As suggested (e.g., Blackwell, 2008, and above), such situations could be addressed more forthrightly if there were a unified code of nomenclature, with clear rules for naming higher categories—including kingdoms.

### **DISTINCTION OF PROPOSED KINGDOMS: CHROMISTA VS. STRAMINIPILA**

Whereas Chromista and Stramenopiles, both, are now rather well-known and often accepted names/groupings, usage of the name Chromista is slightly longer standing—and Chromista is the more inclusive grouping. The kingdom Chromista was formally proposed by

Cavalier-Smith (1981), who subsequently (1986, 1989) provided more thorough expositions. The original Latin diagnosis by Cavalier-Smith (1981) emphasized: tubular mitochondrial cristae, chloroplast endoplasmic reticulum (complex plastids, with extra envelope membranes), and the presence of tubular mastigonemes (tubular "hairs") on at least one flagellum (cilium). The expansive content of kingdom Chromista (Cavalier-Smith, 1986, 1989) encompassed three presumably related phyla: **I.** Cryptophyta or "Cryptista" (the cryptomonads or cryptophyceans); **II.** Heterokonta: including, **A.** the "Ochrista" or chromophytous algae, such as chrysophytes, synurophytes, pedinellids, dictyochophytes (silicoflagellates), xanthophytes (tribophytes), eustigmatophytes, raphidophytes, phaeophytes, and bacillariophytes; **B.** "Pseudofungi," i.e., the Oomycetes, Hyphochytriomycetes, and the somewhat more protozoan-like labyrinthulids and the related thraustochytrids; and **C.** certain "protozoa," such as the bicoecids (or bicosoecids) which Cavalier-Smith (1986) first recognized as a group, lacking plastids, under the Ochrista; and, finally, **III.** Haptophyta or "Haptomonada" (the prymnesiophytes, which include the stratigraphically significant coccolithophorids). As discussed below, the grouping which came to be known as "Stramenopiles" (Patterson, 1989) is generally equivalent to phylum II (Heterokonta) of Cavalier-Smith's "Chromista."

The (usually) two flagella of heterokont chromistan motile cells are heterodynamic, with quite different actions or "beats" (cf. Sleight, 1989). Tubular mastigonemes (typically tripartite, flagellar hairs)—sometimes known as "retronemes" (a more specific, functional term), because these generate a reversal of flagellar thrust (Cavalier-Smith, 1986, 1989; Round, 1989)—are found on the more anterior of the two subapical or lateral flagella (or on the only flagellum in some cases). These distinct, composite (three-tubulate) mastigonemes were determined to be often associated with a distinct organization of the flagellum-to-basal-body ultrastructure, viz. the "transitional helix" (cf. Patterson, 1989; Preisig, 1989). Such heterokont Chromista are, as indicated, known as "Stramenopiles"—in reference to the tubular mastigonemes (cf. Patterson, 1989). Photosynthetic representatives of Chromista typically have chlorophylls "a" and "c," but not "b" (Cavalier-Smith, 1986; Jeffrey, 1989). More than one form of chlorophyll "c" may be present (Jeffrey, 1989). Distinctive carotenoids

frequently occur (Bjørnland and Liaaen-Jensen, 1989), imparting often (not exclusively) a golden-brown pigmentation to the plastids.

Additional groups of stramenopilous (heterokont) algae, that is, groups added to the list of Ochrista (or chromophytous Chromista) since Cavalier-Smith's treatments (1986, 1989), include phaeothamniophytes, bolidophytes, and pelagophytes (see e.g., Blackwell and Powell, 2000, p. 71). Horn et al. (2007) proposed Synchronophyceae as a new class for an amoeboid "heterokontophyte" with a peculiar plastid complex. Relationships of certain other groups—such as the opalinids and the proteromonads—to Chromista have been postulated, but are equivocal (discussed in Blackwell and Powell, 2000). Regardless, there is no question that the Chromista (*sensu* Cavalier-Smith, 1986) are a diverse assemblage, including forms ranging from diminutive golden algae, diatoms, and large brown algae, to water molds, slime-nets (labyrinthulids), and related "protozoa" (see website: <http://www.ucmp.berkeley.edu/chromista/chromista.html>). A preliminary cladistic analysis of Chromista was presented by Williams (1991), supporting relationships among heterotrophic (including pseudofungal) and autotrophic (chromophytous algal) members.

The Kingdom (Regnum) name "Chromista" (Cavalier-Smith, 1981) apparently stems *in part* from the Division (apparent Class) name, "Chromophycées" (Chadefaud, 1950)—cf. Christensen (1989). Other related names, though, are more directly equivalent to Chadefaud's name, such as "Chromophyta" (Christensen 1962, 1989). Christensen (1989) formally proposed Division Chromophyta, including a Latin diagnosis (emphasizing the *absence* of chlorophyll *b*). Cavalier-Smith (1986) had earlier, however, validated Chromophyta as a Subkingdom name (Latin diagnosis high-lighting the tubular mastigonemes and tubular mitochondrial cristae). Subkingdom Chromophyta (name meaning "colored plant") represents a difficult concept, in that—being "above" phylum Heterokonta in Cavalier-Smith's classification—it includes both chromophytous algae (which typically have colorful plastids) and pseudofungi (which lack plastids, and therefore often lack pigment or special color as well). According to Cavalier-Smith (1986), Subkingdom Chromophyta is typified by genus *Chromophyton*. There is indeed a "chrysophyte" genus name *Chromophyton* Woronin (Bot. Zeit. 38: 625, 1880), cf. *Index Nominum*

*Genericorum*. However, it is not clear in the ICBN (2006) that automatic typification applies to Subkingdom and Kingdom level (see, for example, Article 16.2); nor is it clear, even if it did, that “Chromophyta” would be the correct name-form based on *Chromophyton* (see Christensen, 1989, but compare his view with Articles 10.7 and 16.4). In any case, the nomenclatural propriety of Chromophyta (be it considered a divisional or a subkingdom name) does not directly affect the legitimacy of Cavalier-Smith’s kingdom name Chromista—especially if Chromista is viewed as primarily a descriptive name (Article 16.1), viz. “colored protists.”

Seemingly more pertinent to the question of whether Chromista should be the kingdom name recognized is that, prior to Cavalier-Smith’s (1981) Chromista, Jeffrey (1971) had proposed a similar (if somewhat more polyphyletic) Kingdom, the “Chromobiota.” Jeffrey (1982), however, later modified this to a more monophyletic, Subkingdom grouping, the “Chromobionta”—inserting an “n” into the name—a grouping more or less equivalent to phylum Heterokonta of kingdom Chromista (cf. Cavalier-Smith, 1986). But, Jeffrey provided no Latin diagnosis for either name, Chromobiota or Chromobionta, leaving them (technically) nomenclaturally invalid (cf. Article 36.1, 36.2). Regardless, since priority is only a recommendation above the rank of Family (Recommendation 16B, even this not clearly applying to Kingdom), and since names (in specific reference here to subkingdom names) have no necessary priority outside of their original ranks (Article 11.2), there is no obligation (for one reason, or another) to employ Jeffrey’s (or Christensen’s, see above) name(s) at Kingdom level. Hence, the Kingdom name Chromista may be recognized, and attributed to Cavalier Smith (1981), with no requirement to reference other, perhaps similarly intended, names. Again, whether one can argue (spuriously, I believe) that Kingdom “Chromista” is an automatically typified name, based on the stated typification of Subkingdom Chromophyta by Cavalier-Smith (1986)—see paragraph above—is a matter of debate. However, this point is relatively moot to name selection, given the lax position of the ICBN on priority at higher levels (especially kingdom). Specific rules for naming Kingdoms (and Subkingdoms) would be a helpful addition to the botanical code—or better still, to a future, unified code of biological nomenclature.

In consideration of the fact that Chromista, as outlined by Cavalier-Smith (1986), constitutes a diverse assemblage, somewhat vaguely defined—the name seeming to emphasize the “algal” or plastid-bearing representatives more than the “fungal” members—Patterson (1989) suggested that “core chromophytes” (primarily the heterokont assemblage of chromophytous algae), along with related pseudofungal and “protozoan” representatives, be recognized (informally, at the time) by a more uniformly appropriate name, “Stramenopiles.” Patterson (1989) coined this name (meaning, literally, “straw hairs”) emphasizing the distinctive, lineage-defining, tubular flagellar hairs (i.e., the composite, tubulate mastigonemes) possessed by members of this group. A more precise group is thus suggested by the name Stramenopiles than is the case with the more inclusive Chromista, although the overlap of these two large groupings is very substantial. As has been indicated, Stramenopiles correspond to the phylum Heterokonta (Cavalier-Smith, 1986) of kingdom Chromista. Haptophytes and Cryptomonads (both groups included in the Chromista, cf. Cavalier-Smith, 1986) are excluded from Stramenopiles (*sensu* Patterson, 1989, and later publications, e.g., Blackwell and Powell, 2000). “Algal” representatives of Stramenopiles—the ochristal heterokont groups (goldens, browns, xanthophytes, diatoms, pelagophytes, eustigmatophytes, etc.) listed previously—have informally been referred to as “stramenochromes” (Leipe et al., 1994)—acknowledging the tubular mastigonemes as well as the often colorful plastids. There appears to be no comparable (“strameno-”) designation for pseudofungal or “protozoan” members of this heterokont grouping.

Ultrastructural studies on Chromista (particularly Stramenopiles)—such as of the flagellar apparatus and transition zone, as well as the flagellar hairs—proved useful in establishing relationships of member groups, among (and between) Ochrista (chromophytous algae) and Pseudofungi (e.g., Hibberd, 1979; Moestrup, 1982; Beakes, 1989; Cavalier-Smith, 1989; Patterson, 1989; Preisig, 1989; O’Kelly, 1989; Owen et al., 1990a,b; Andersen, 1987, 1991). Molecular confirmation of the “unity” of Stramenopiles (or organisms that would come to called such) was established, among others, by Gunderson et al. (1987), Ariztia et al. (1991), Bhattacharya et al. (1992), Leipe et al. (1994), Wee et al. (1996), and Honda et al.

(1999). Based on morphological and molecular information, the Stramenopiles came to be viewed as a kingdom or kingdom-like category (i.e., a “crown” group) by Leipe et al. (1994), Blackwell and Powell (1995, 1999), Alexopoulos et al. (1996), Van de Peer and De Wachter (1997), and Sogin and Silberman (1998). The name “Stramenopile” (originating, as indicated, with Patterson, 1989) found its way into textbooks of phycology (e.g., Lee, 1999), and Stramenopiles were recognized in selected biological diversity texts, e.g., Barnes (1998). In their introductory college biology textbook, Campbell et al. (1999) put forward this group as a “candidate kingdom,” employing a formalization of the name, “Stramenopila.” Alexopoulos et al. (1996) had earlier made use of “kingdom Stramenopila” in correctly asserting that organisms morphologically, nutritionally and ecologically thought of as “fungi” actually encompass more than one kingdom—Fungi, Stramenopila, and various Protist groups (or Fungi, Chromista, and Protozoa, cf. Beakes, 1998). Blackwell and Powell (2000) presented a detailed consideration of (and support for) the phylogenetic integrity of the overall stramenopilous assemblage. Ideas on the filiation of the numerous member groups of Stramenopiles are found in Sogin and Patterson (1995, Tree of Life Web Project) and Blackwell and Powell (2000). Some authors have continued to use the name Stramenopiles (Reyes-Prieto et al., 2007), while others (e.g., Baldauf et al., 2000) recognized the stramenopile grouping, but employed other names—in this latter case the generally equivalent category, Heterokonta, of Cavalier-Smith (1986).

In spite of the recognition mentioned above, it was apparently not until the book, *Straminipilous Fungi*, published by Dick (2001), that Stramenopiles were formally proposed (Latin diagnosis presented) as a Kingdom—viz., kingdom “Straminipila.” Dick’s circumscription appears primarily to include pseudofungal organisms (By whatever names employed, it is these that are enumerated)—although he spoke (pursuant to the diagnosis) of “coevolutionarily linked endosymbiont characters,” including plastid and chlorophyll features, in seeming reference to “algal” representatives. Dick does note in introductory discussion that “biflagellate fungi” and chromophyte algae, as well as labyrinthulids for example, are unified by the “straminipilous flagellum”—i.e., the anterior “tinsel” flagellum of previous discussion, bearing composite, tubular mastigonemes. It is plausible that Dick

intended to include chromophytous algae (and bicoecids) by his statement in the diagnosis concerning “organisms that originally possessed, or evolved to possess” such features as heterokont flagella and straminipilous scales. In any case, it seems a little strange that Dick refers to straminipilous “fungi,” since, as he himself notes, these are not true fungi. As for nomenclatural detail, indication by Dick of the holotype of kingdom Straminipila, as phylum Heterokonta Cavalier-Smith [1986], is unnecessary since “Straminipila” is a descriptive, not a typified, name (cf. Article 16.1, ICBN)—and the type method does not otherwise apply above the rank of Family (compare Articles 7.1 and 16); requirement for citation of type for validation purposes is, in fact, primarily at genus level or below (Article 37). Dick’s spelling of the name of this kingdom is unique, viz. “Straminipila.” He not only altered the spelling to “Straminipila” (from, presumably, “Stramenopila”), he listed his name (alone) as author of the kingdom (regnum). This assignment of authorship by Dick (to himself) is technically correct, although, as has been indicated, Patterson (1989) originated the informal name (and the concept of) “Stramenopiles,” and others (as mentioned), prior to Dick, used the name Stramenopila. Dick’s alteration of the connecting vowel in the name (from “o” to “i”) is appropriate (cf. Stearn, 1983, p. 269). However, there was nothing incorrect about the spelling of the second syllable of the name “Stramenopila” (based on Latin, *stramen*), as given in the kingdoms listed by Alexopoulos et al. (1996) and Campbell et al. (1999)—although, these were, of course, not intended as formal kingdom proposals (no Latin diagnoses provided). If *stramen*, a noun, is (in the name Straminipila) employed adjectivally (cf. Stearn, 1983, p. 267), i.e., deriving from *stramineus* (cf. Simpson, 1968), then Dick’s spelling (Stramin-i-pila) would be acceptable. Dick (2001), however, indicated the etymological derivation to be from *stramen* [the noun]—this being equivalent to Patterson’s (1989) original usage. But, even if one accepts Dick’s kingdom, name and spelling, Straminipila, it would not seem inappropriate to cite authorship as Patterson ex Dick (cf. Article 46), since Patterson (technicalities aside) generated the name basis and originated the construct of what would become this “kingdom.” And, if kingdom Straminipila is recognized (regardless of spelling), it should be rendered convincingly more inclusive (i.e., formally emended, cf. Recommendation 47A)—in the sense of Stramenopiles as circumscribed, for example, by Patterson (1989), Leipe et al. (1994)

and Blackwell and Powell (2000)—so that “chromophytous algal” and “protozoan” member groups are definitively included (listed, and accorded equal importance to the “pseudofungal” representatives emphasized by Dick, 2001). This suggested inclusiveness is especially pertinent given recent evidence of (not plastids but) plastid-associated genes in Oomycetes (cf. Tyler et al., 2006; Bailey, 2008; Sanchez-Puerta and Delwiche, 2008), indicating further relationship of algal and pseudofungal representatives of stramenopiles. However, formal emendation becomes truly important only if Straminipila is selected as the kingdom to best represent heterokont chromistans—rather than simply recognizing this group as, for example, phylum Heterokonta of kingdom Chromista (Cavalier-Smith, 1986). If accepted, “Stramenipili”—the first half of the name based on the Latin noun, *stramen* (straw), and the second half based on the Latin noun, *pilus*, *pili* (hair, hairs), cf. Simpson (1968)—might be a preferable spelling (to Dick’s “Straminipila”), and more comparable to Patterson’s original, informal “Stramenopiles.” Such orthographic changes are permitted (if justifiable) by the ICBN without invalidation of the standing name, authorship or date of publication (cf. Articles 32.7 and 60.1), i.e., the validating author would still be Dick (2001). And, recall (first paragraph of text following Key Words), there is no rule (cf. ICBN) that kingdom names must end in “-a.” The ending, “pili” (of Stramenipili) is not only permissible, it would unambiguously satisfy the requirement that the name be treated as a noun in the plural (Article 16.1). However, such points concerning spelling (as those concerning emendation) fade in significance if Straminipila (Dick) is not favored as a kingdom over Chromista.

It might be assumed that the name Straminipila (or Stramenopila, or Stramenipili—depending on interpretations of etymology and orthography) should be selected for the kingdom in question, because of the relatively cohesive phylogenetic circumscription of this group (cf. Patterson, 1989; Leipe et al., 1994; Blackwell and Powell, 1999, 2001; Blackwell, 2004). Stramenopiles are restricted to organisms that are actually “heterokont,” implying the presence of composite (usually three-parted), tubular mastigonemes on the more forward of two flagella (or the only flagellum in some cases). Such unique flagellar appendages are considered lineage-defining (cf. Leipe et al., 1994; Blackwell and Powell, 2000). Recent evidence has

indicated that tubular mastigonemes of stramenopiles (Yamagishi et al., 2007, studying *Ochromonas*) are not only structurally but compositionally different from those of the simple mastigonemes of green algae, such as *Chlamydomonas*. In the interest of avoiding semantic confusion, proteins composing tubular mastigonemes (the mastigonemes, of course, externally attached to flagella) appear to be unrelated to tubulin proteins of actual microtubules (of which flagella, and certain other cytoskeletal elements, are composed). But, regardless of the seeming distinctiveness of Stramenopiles, there are complications. In the more broadly cast kingdom, Chromista, additional groups are included and must be considered—viz., the cryptomonads and the haptophytes—even if these have been placed in different phyla, or in some cases subkingdoms, from heterokonts (Cavalier-Smith, 1986, 1989). Pursuant to Cavalier-Smith's initial expositions, certain authors have apparently found haptophytes and cryptomonads to be relatively unrelated to the heterokont assemblage (i.e., to Stramenopiles)—see, for example, Daugbjerg and Andersen (1997) concerning haptophytes, and Van de Peer and De Wachter (1997) regarding cryptomonads. This viewpoint (including the consideration that "Chromista" was possibly too broad of a construct) would seem to support recognition of a separate kingdom Straminipila (as by Dick, 2001) for truly heterokont organisms. Other authors (e.g., Bhattacharya and Medlin, 1995; Cavalier-Smith, 2002), however, have appeared to indicate a degree of relationship between heterokonts (stramenopiles), cryptophytes and haptophytes—and if this is so, a kingdom Straminipila would perhaps be too limiting, and a broader construct (Chromista) would be favored. So, how does one decide whether major chromistal groups are substantially related?

The monophyly of the pseudofungal groups of chromistans has not (in recent times) been substantially in question (cf. Blackwell and Powell, 2000). Now, in consideration of "algal" representatives, information has come to light to suggest that there was a common, eukaryote/eukaryote (i.e., "secondary") endosymbiosis—involving a red algal endosymbiont—connecting (through common plastid ancestry) the cryptomonad, haptophyte and heterokont "algae"—cf. Cavalier-Smith (1992, 2002), Delaney et al. (1995), Delwiche (1999), Palmer (2003), Bhattacharya et al. (2004), Keeling (2004), Li et al. (2006), and Reyes-Prieto et al. (2007). Possibly, more than one such

major secondary (or even a tertiary) endosymbiotic event was involved (Sanchez-Puerta and Delwiche, 2008). But in any event, the general consensus of references cited above (among others) suggests that the diverse “algal” (i.e., plastid-containing) representatives of the Chromista (*sensu* Cavalier-Smith, 1986) are also, broadly, monophyletic (that is, with regard to origin of their plastids, i.e., involving the same, an identical, or a very similar, secondary endosymbiosis). The kingdom Chromista, as conceived by Cavalier-Smith (1981, 1986, 1989), thus represents not only a larger grouping of organisms (than Straminipila), but possibly one that can still be viewed (by some measures at least) as monophyletic as well (Cavalier-Smith, 2002)—even if not as obviously (clearly definably) monophyletic as the Stramenopiles. In other words, based on recent knowledge of plastid evolution (e.g., Keeling, 2004; Reyes-Prieto et al., 2007), it is not unreasonable to consider the Chromista as the more holophyletic—if plainly the circumscriptively looser and phylogenetically more diverse—of the two assemblages (Chromists and Stramenopiles). Therefore, if putative holophylysis (at least in the sense of containing a greater number of paraphyletic groups, cf. Bhattacharya et al., 1992; Schuh, 2000) is the guideline for kingdom selection, the nod would seem to go, for now, to Chromista (over Straminipila); however, the matter cannot be considered finally settled.

### **IF NOT STRAMINIPILA, IS CHROMISTA THE BEST REMAINING OPTION?**

If deciding not to use the name Straminipila (or a related spelling) for this assemblage—because it is not the most encompassing group—then is one left with Cavalier-Smith’s (1981) name Chromista, with its attendant broad circumscription? Perhaps so, but there are additional problems. The name “Chromista” is without universal applicability of meaning, even within the heterokont assemblage. “Chrome” (Greek/Latin: *Chroma*, *Chromus*) implies the presence of color or pigment; principally, it came to connote the “brown” line of algae (Round, 1989), as distinct from “green” or “red” algae. However, as noted by Cavalier-Smith (1986) and Round (1989), not all members of Chromista are pigmented. Pseudofungi, such as Oomycetes and hyphochytrids, and pseudofungal/protozoan representatives such as labrynthulids (as well as the “more protozoan” bicoecids), are without

actual plastids (even though plastid genes may be present in Oomycetes, cf. Bailey, 2008). Also, the name “chrome” is vague in meaning (simply, “color”)—not precise given the various hues encountered in representative chromophytous algal groups (brown, golden, golden-brown, reddish-brown, yellow-green, almost grass green, and even other hues). And, any suggestion of “Protista” in the name Chromista (viz. “chrome-ist” abridging “chrome-protist”) is superannuated, since the hodgepodge “protist” or “protocist” kingdom (Haeckel, 1866; Whittaker, 1969; Margulis, 1981; Corliss, 1984) is no longer phylogenetically tenable (Cavalier-Smith, 1987, 1993; Corliss, 1994; Blackwell and Powell 1995, 2001). However, a name such as Chromista is not to be rejected because it is not compellingly descriptively appropriate (Article 51, ICBN, 2006). For that matter, the meaning of “Chromista” is not entirely inappropriate, being applicable generally to the chromophytous algal representatives (although there are colorless chrysophytes, e.g., as investigated by Belcher and Swale, 1972). Furthermore, usage of the name Chromista (in the sense of Cavalier-Smith, 1986, 1989) has been steadfastly inclusive of rather diverse groupings that continue to seem suitable for inclusion (on plastid evidence, for example, cf. Keeling, 2004). Before finally accepting this kingdom name, however, it should be asked if other legitimate, descriptively appropriate names are available for use?

A kingdom name that preceded Cavalier-Smith’s (1981) Chromista was Ochrobionta (Edwards, 1976). Edward’s “Ochrobionta” is loosely equivalent to the “Ochresta” (recognized later by Cavalier-Smith, 1986), and to “Ochrophyta” (Cavalier-Smith, 1997)—viz., “Ochrophytes” (Graham and Wilcox, 2000). In other words, Ochrobionta (Edwards) is composed mainly of what would come to be viewed as the chromophytous algal component of kingdom Chromista (including though, in Edward’s view, cryptophytes in addition to ochristal chromophytes). The kingdom name Ochrobionta, however, would not now be considered acceptable for several reasons. For one thing, “Ochrobionta” was not validly published (no Latin diagnosis). Secondly, organisms belonging to the pseudofungal group of heterokont chromistans were not covered by Edward’s construct (Ochrobionta). As a third point, dinoflagellates (“Pyrrhophyta”) were included in Ochrobionta by Edwards—not a desirable placement (as presently understood), since dinoflagellates, regardless of ultimate

potential (multiple) plastid connections (cf. Keeling, 2004), are probably not as immediately related to chromophytous algae of the Chromista as they are to (other) Alveolate Protozoa (cf. Cavalier-Smith et al., 1995; Hausmann and Hülsmann, 1996; Blackwell and Powell, 2001; Yoon et al., 2005). Finally, Edwards (1976) spoke of “a preponderance of carotenoids over chlorophylls” in members of his Ochrobionta, seeming to downplay the role of chlorophyll which is still the primary photosynthetic pigment in these organisms—and, some chromophytes are indeed decidedly greenish in coloration, especially certain members of the Xanthophyceae (a fact which Edwards, 1976, acknowledged). A proposed kingdom mentioned previously, Chromobiota Jeffrey (1971), though similar to Edward’s Ochrobionta, did include some pseudofungi (i.e., as presently known). However, Jeffrey’s Chromobiota is otherwise beset with the same circumscriptive and nomenclatural problems as Edward’s “kingdom”—e.g., inclusive of dinoflagellates, lacking Latin diagnosis. Edward’s (1976) apparently partially patterned his kingdom (Ochrobionta) after Jeffrey’s (1971) Chromobiota.

As for other “kingdom” name possibilities, a perhaps more serious candidate, Heterokonta, would appear to be available, and some recent authors (e.g., Baldauf et al., 2000) have employed this name. The name “Heterokonta” is descriptively applicable to the distinct, heterodynamic flagella—one forwardly directed pleuronematic (“tinsel” or “hairy”) flagellum (bearing tubular, reverse-thrusting mastigonemes), and one, sometimes trailing, smooth, whiplash flagellum (with a more typical flagellar motion)—of heterokont chromistan groups that are biflagellate (the majority), cf. Moestrup (1982), Cavalier-Smith (1986), Van den Hoek et al. (1995). However, there are problems. “Heterokonta” was formally established—Latin diagnosis focusing on tubular mastigonemes of the anterior flagellum of heterokonts: “algal,” “pseudofungal,” etc.—as a Phylum (Division) name by Cavalier-Smith (1986), not a Kingdom name. And, as pointed out, a name does not have priority outside its own rank (Article 11.2, ICBN)—even if we allow that priority carries any force at these upper ranks (kingdom, subkingdom, phylum, subphylum, etc.)—although a given descriptive name may in fact be used at different ranks (Article 16.1). Earlier, Cavalier-Smith (1978) had informally (no Latin diagnosis) suggested “Heterokonta” as a kingdom name—but for a

heterogeneous assemblage, including not only chromophytous algae and Oomycetes, but also chytrids (which are true fungi), Myxomycetes (i.e., slime molds, which are Protozoa), and Foraminifera (also Protozoa); yet, this unwieldy grouping did not include cryptophytes (which are usually considered to be chromistans). Subsequent to better understanding, Cavalier-Smith (1986) abandoned Heterokonta as an overly diverse kingdom concept, in favor of the more circumspect divisional usage of the name (i.e., for a grouping generally equivalent to what would subsequently be termed Stramenopiles, cf. Patterson, 1989; Leipe et al., 1994; Blackwell and Powell, 2000). Later, perplexingly, Cavalier-Smith (cf. 1995, 1997) “raised” Heterokonta to “infrakingdom” (= subkingdom?, cf. Article 4.2). In further complication, Cavalier-Smith’s (1986) phylum Heterokonta, though well-defined phylogenetically, is readily confused with the pre-existing (much older) name Heterokontae (cf. Luther, 1899; Pascher, 1925; Fritsch, 1935). Heterokontae, in the sense of these latter authors, is generally equivalent to the algal Class, Xanthophyceae (Tribophyceae, cf. Ott, 1982); the name (“Heterokontae”) thus applies primarily to only a limited subset of Heterokonta (*sensu* Cavalier-Smith, 1986).

Another (somewhat older) version of the phylum name “Heterokonta” (Cavalier-Smith, 1986) is “Heterokontophyta” (Van den Hoek, 1978)—likewise used as a phylum name (or seemingly so) by several authors (e.g., Moestrup, 1982, 1992; Van den Hoek et al., 1995; Horn et al., 2007; Sanchez-Puerta and Delwiche, 2008). “Heterokontophyta” has been applied more to algal than pseudofungal representatives of heterokonts. Cavalier-Smith and Chao (1996), however, pointed out that the name Heterokontophyta was questionably validly published, and favored use of Ochrista instead—It should be noted, though, that Ochrista (Cavalier-Smith, 1986) was published as a subphylum (subdivisional) name, not a phylum (division) name. Regardless, Lee (1999) used Heterokontophyta, *de facto*, in general correspondence to subphylum Ochrista of Cavalier Smith (1986). No matter the exact previous rank, name permutation, or usage employed, a pragmatic problem with a potential *kingdom* Heterokonta (or Heterokontophyta) is that not all chromistans are morphologically “heterokont,” as the term is precisely defined—implying not just flagella of (often) unequal length, but two structurally and functionally different flagella on the same cell (cf. Van den Hoek et al., 1995,

glossary, re: “heterokont zoids”). “Heterokonta” was formally founded on this flagellar distinction (including the presence of tubular mastigonemes on the forward flagellum, cf. Cavalier-Smith, 1986). “Heterokonta” is, as a consequence, not an inclusive enough category for the entire chromistan assemblage. For example, Haptophytes usually have two, similar, “apical,” whiplash flagella, plus a “haptonema” (a central, superficially “flagellum-like,” sometimes coiled, appendage—cf. Sleight, 1989; Van den Hoek et al., 1995). Haptophytes are *not* Heterokonts, yet they still appear to qualify as Chromistans (based on knowledge of plastid evolution, cf. Bhattacharya et al., 2004; Keeling, 2004). “Heterokonta” (*sensu* Cavalier-Smith, 1986) thus constitutes, even in broadest usage, too narrow of a kingdom concept to encompass all chromistans, as historically and presently recognized.

In final analysis, “Chromista” (as conceptualized by Cavalier-Smith, 1981, 1986, 1989) remains the most applicable name for the over-all group of heterokont *and potentially related* organisms discussed herein as a kingdom (Reference the listings in the first and third paragraphs of the preceding section: “Distinction of Proposed Kingdoms...”). The main consideration that might alter future acceptance of kingdom Chromista is not the appropriateness of the name, or the potential “challenge” of other competing names, but rather the question of the degree of relationship of the somewhat disparate, major member (chromistal) groups, that continue to be included (discussed below).

### **CONCLUDING POINTS, CURRENT VIEWS, AND CONCERNS (Not only Kingdoms and their delimitation, but “Supergroups”)**

Though not representing an overwhelming consensus, the balance of currently available information indicates that the kingdom name Chromista Cavalier-Smith (1981; see also 1986, 1989) is the best option for proper application to, and implicit circumscription of, the presumed reasonably holophyletic assemblage of chromophytous algal, pseudofungal, and related primitive protozoal organisms discussed herein (see again, “Distinction of Proposed Kingdoms...” section, listings in first and third paragraphs). The Stramenopiles (as delineated, for example, in Patterson, 1989; Leipe et al., 1994; and Blackwell and

Powell, 2000) are probably best viewed, presently, as constituting a major phylum of kingdom Chromista. It is possible (if one so wished) to use the kingdom name Straminipila Dick (2001)—by whatever spelling (discussed previously)—as a phylum (division) name, rather than Heterokonta Cavalier-Smith (1986), since priority generally does not apply above family rank (Article 11.1, ICBN, 2006), and since descriptive names (such as Straminipila) may be used, unchanged, at different ranks (Article 16.1). The suggested endings, “-phyta” or “-mycota,” for divisional names in the botanical code are, in the case of Straminipila (or Heterokonta, for that matter), not only inappropriate, but constitute merely a recommendation (16A.1)—firm rules for properly establishing a name such as this are lacking. Again, in these instances, one could wish for a unified code with well-reasoned, unambiguous rules for names of “higher” ranks. In any case, though, the possibility still exists that Straminipila Dick (2001), if emended to be more clearly defined and formally inclusive—e.g., as concerns chromophytous heterokont (i.e., certain “chromophytous algal”) groups—could eventually be accepted as a kingdom-level category, perhaps even replacing the more heterogeneous Chromista. However, this replacement would come to bear only if seemingly authenticated relationships of non-stramenopilous chromistan groups to stramenopiles are *not* sustained (see discussions in Harper et al., 2005 and Sanchez-Puerta and Delwiche, 2008). But, should future evidence indicate that cryptomonads and haptophytes (prymnesiomonads) are no longer tenable as members in an assemblage containing stramenopiles (i.e., within the Chromista), these groups would possibly revert to temporary systematic placement in the “catch-all” kingdom Protozoa (cf. Blackwell and Powell, 2001).

Some recent authors have indeed adopted (or re-adopted, as the case may be) usage of “Chromista” in the sense of a kingdom name (e.g., Bhattacharya et al., 2004; see also the website: <http://www.ucmp.berkeley.edu/chromista/chromista.html>). Given the “super-groups” of organisms now recognized (Cavalier-Smith, 1999; Palmer, 2003; Bhattacharya et al., 2004; Keeling, 2004; Parfrey et al., 2006), Chromista (as compared with the more restrictive grouping Stramenopiles) is the kingdom which appears more broadly suited (further discussed below) for membership within the supra-kingdom grouping, Chromalveolata (cf. Cavalier-Smith, 1999; Adl et al., 2005;

Reyes-Prieto et al., 2007)—an assemblage encompassing not only chromists, but also the related alveolate protozoa, i.e., dinoflagellates, ciliates and apicomplexans (cf. Bhattacharya and Medlin, 1995; Hausmann and Hülsmann, 1996; Blackwell and Powell, 2001; Cavalier-Smith and Chao, 1996; Cavalier-Smith, 2002).

Relationships between certain Chromists and Alveolates (still somewhat equivocal, cf. Sanchez-Puerta and Delwiche, 2008) were established, among others, by Cavalier-Smith et al. (1995), Van de Peer and De Wachter (1997), and Sogin and Silberman (1998)—a connection (based partly on plastid genetics, cf. Cavalier-Smith, 2002; Keeling, 2004) that has, so far, generally held up under scrutiny (Adl et al., 2005; Parfrey et al., 2006). However, such a phylogenetic relationship is perhaps one that is chimaeric (cf. Corliss, 1994; Cavalier-Smith, 2002; Parfrey et al., 2006), not necessarily taking the composite organism (“holobiont,” cf. Mindell, 1992) into account. Recent evidence (Harper et al., 2005; Sanchez-Puerta and Delwiche, 2008), including evidence from genes *additional* to those involved with plastids, supports a closer relationship of alveolate protozoa with heterokont members of the Chromista (i.e., with stramenopiles) than with either of the other putative chromist groups: haptophytes (prymnesiomonads) or cryptomonads (cryptophytes)—see also Adl et al. (2005). Among chromistan organisms, thus, there may be only a distant overall (host-cell?) relationship between stramenopiles (true heterokonts) and either cryptomonads or haptophytes. On the other hand, there is some evidence of relationship between these chromistan groups: for example, the tubular flagellar hairs of cryptophyceans are similar (although bipartite, rather than tripartite) in morphology to those of true heterokonts (Moestrup, 1982; Cavalier-Smith, 1989); also, there is possibly a sibling relationship between cryptomonads and haptophytes (Sanchez-Puerta and Delwiche, 2008); and, some relationship of large-subunit (28S) cytoplasmic ribosomal RNA was indicated between chromophytous algae [stramenopiles] and haptophytes (Perasso et al., 1989). In any case, considering evidence pro and con, the recognition of Heterokonta, Cryptophyta, and Haptophyta as quite distinct phyla—yet these encompassed *within* the Chromista (Cavalier-Smith, 1986, 1989)—can be viewed as an assessment (by Cavalier-Smith) that was probably on target. As pointed out by Harper et al. (2005) and Sanchez-Puerta and Delwiche (2008),

more data is needed before final establishment of membership of the Chromalveolata (and final re-establishment of the Chromista, in my view). Both support and doubt have been expressed concerning the “chromalveolate hypothesis” (see Palmer, 2003; Adl et al., 2005; Harper et al., 2005; Li et al., 2006; Sanchez-Puerta and Delwiche, 2008)—i.e., concerning whether this very large grouping can truly be viewed as (even generally) monophyletic. Nonetheless, inclusion of Chromists and Alveolates in a common super-group is for the time-being reasonable (Adl et al., 2005; Yoon et al., 2005; Li et al., 2006), and comparable to inclusion of Fungi and Animalia in the Opisthokonts (Unikonts). Both “supergroups,” Chromalveolata and Opisthokonta, are arguably tenable based on selected morphological and molecular grounds (cf. Keeling, 2004; Adl et al., 2005; Parfrey et al., 2006; Reyes-Prieto et al., 2007).

Given the above, the final question on the propriety of kingdom name selection (e.g., Chromista) concerns how well the kingdom fits (including considerations of phylogeny) with other kingdoms (or kingdom components) in the context of larger, super-group assemblages now recognized (e.g., Keeling, 2004; Adl et al., 2005; Parfrey et al., 2006)—Amoebozoa, Opisthokonta, Rhizaria, Archaeplastida (Plantae), Chromalveolata, and Excavata. In the case of the super-grouping pertinent to the present paper—Chromalveolata (grouping Chromista with Alveolata)—the fit would appear to be relatively good, given improved, if still controversial, knowledge (especially plastid information, cf. Cavalier-Smith, 2002; Bhattacharya et al., 2004; Keeling, 2004; Reyes-Prieto, 2007) of phylogenetic relationships among major subgroups of these organisms. If it is eventually determined (see discussion in Adl et al., 2005; Harper et al., 2005; Sanchez-Puerta and Delwiche, 2008), however, that haptophytes and cryptomonads are sufficiently phylogenetically distant from alveolates (and stramenopiles) to be marginalized or even excluded from the “Chromalveolata,” then a new supra-kingdom name may need to be formulated (based on a more restricted grouping). This new name could possibly derive from a combination of the names Straminipila (representing a more precise circumscription than Chromista) and Alveolata, since truly heterokont organisms (stramenopiles) and certain alveolates appear substantially related (Van de Peer and De Wachter, 1997; Baldauf et al., 2000; Keeling, 2004; Harper et al., 2005; Reyes-

Prieto et al., 2007)—although the extent of their monophyly is not completely resolved (Sanchez-Puerta and Delwiche, 2008).

As evident from discussion, some recent authors (e.g., Keeling, 2004; Adl et al., 2005; Parfrey et al., 2006) have utilized quasi-formal “Supergroups” (six in total, see above) *instead* of Kingdoms. Adl et al. (2005) considered these largest groups “similar to traditional ‘kingdoms’”—however, they are not (as may be judged from Table 1 in Adl et al., 2005; and Figs. 1, 2 and 3 in Parfrey et al., 2006). Rather, such super-groups are *inclusive of* kingdoms, among other (not necessarily coequal) groupings; e.g., the super-group Opisthokonta includes Fungi, Metazoa (animals), Choanomonads, and Mesomycetozoa. Use of six supergroups in the sense of kingdoms (Adl et al., 2005), and a contemporaneous recognition of six (actual) kingdoms (Cavalier-Smith, 2004), is potentially confusing (different names are typically used for supergroups vs. kingdoms). Parfrey et al. (2006) made a limited attempt to sort the matter out. Possibly, future codes of nomenclature should serve not only to establish rules for naming kingdoms, but should take supra-kingdom assemblages into account as well. Kingdom and Supra-kingdom categories should be clearly distinguished. In point of fact, however, no supra-kingdom ranking (super-group category) is presently covered (or “allowed,” depending on one’s point of view) by any official code of nomenclature. A related question (scarcely raised to date) is, whether such “super-groups” should be called “Domains”?—as previously applied by Woese et al. (1990) to the most major prokaryotic groupings, Archaea and Bacteria—a question (re: the six largest eukaryotic clusters) for nomenclaturists of eukaryotes to decide. There are other options (in addition to “Domain”) for the appellation of supergroups (e.g., “Empire,” “Super-kingdom,” “Supra-kingdom”). Almost any option would seem preferable to the current designation of each of these largest assemblages by the informal, non-rank-identifiable term, “supergroup” (Parfrey et al., 2006). Regardless of which rank-category-name is ultimately selected, nomenclatural consistency would be desirable for such supervening taxonomic categories.

With continued emphasis on kingdom and supra-kingdom categories, it does not seem that we (as taxonomists) are necessarily proceeding just in the direction of “rankless” classifications (cf.,

Hibbett and Donaghue, 1998), toward a systematics of (only?) clades, not formal, named, taxonomic ranks. Whether stated or de facto, largely formal, hierarchical taxonomic systems still generally hold sway. Adl et al. (2005) indicated that the eukaryote cluster-group system they employed is “nameless” and (although they asserted the inherence of a “ranked systematics”) is a system “without formal rank designations”—i.e., a system “not [formally] constrained...” However, the vast majority of the taxonomic groups, including the six main clusters, in Adl et al. (2005) bear what appear to be formal names—three of six main cluster names stemming from works of Cavalier-Smith. Significantly, traditional formal names (for what might be known to some as phyla, classes, orders, families, etc.) continue to be used under the main cluster names (Adl et al., 2005)—de facto signifying particular ranks, even though ranks are not explicitly stated. The reference by Adl et al. is useful and comprehensive. However, the (rank-unidentified) name mix can be confusing, requiring that one search the context of particular names (helpfully, sources are provided). In some cases, perplexingly, names of different ranks are apparently considered to be at a comparable taxonomic level, e.g., *Schizocladia*, Synurales and Xanthophyceae (see Adl et al., 2005, p. 429).

The systematic descriptive enumeration of Adl et al. (2005) is unquestionably a valuable compilation; yet, it is not (I believe) the optimal, ultimate systematic approach to the higher level classification of eukaryotes. Though divided orderly into six clusters (of uncertain, though one would assume the *same*, “formal” rank), it is otherwise much of an “information-board presentation,” with items pasted from zoological, botanical, mycological, and protistological taxonomy. It would seem that, rather than attempting to piece together an *ad hoc* phylogenetic system such as Adl et al. (2005)—some potential nomenclatural pitfalls in *ad hoc* systems discussed in Blackwell (2002)—it would be prudent in the long run to take the trouble to render consistent the formal, upper-level nomenclature of eukaryotes, modifying not only the naming scheme employed but codes of nomenclature as well (an effort involving two at least partially different groups of workers—evolutionary systematists and nomenclaturists). In other words, the most desirable approach would be that of bringing both taxonomic/evolutionary schemata and nomenclatural codes into accord. If present codes of nomenclature are ill-tuned to the task, it

logically follows that efforts to rebirth a formal *BioCode* might be appropriate, given the perceived need by some (cf. Cavalier-Smith, 1978; Corliss, 1983, 1990; Patterson, 1986; Blackwell and Powell, 1999; Blackwell, 2008) for code reform. The *BioCode* draft (Greuter et al., 1996—minor revision done in 1997) did not meet with success, and was not adopted. It is pointless to debate its merits here; however, the draft *BioCode* did at least purport to add the rank “domain” (above kingdom) to existing ranks (of the botanical code). Perhaps future *BioCode* efforts (cf. Hawksworth, 2007), no matter what form the document might take, could give detailed consideration to kingdom, subkingdom, and supra-kingdom nomenclature—addressing what ranks should be recognized, and how names appropriate to these ranks should be formed. By so doing, perhaps a mechanism could be provided through which the most comprehensive clades, e.g., “crown clades” (cf. de Queiroz and Gauthier, 1992), could be formally recognized as “crown taxa” (cf. Van de Peer and De Wachter, 1997). If a future version of the *BioCode* does not prove to be the answer to supra-familial nomenclatural problems, development of a unified biological code of nomenclature (even if it be, initially, a minimal or “skeleton” code) should nonetheless be pursued, hopefully to the eventual outcome of acceptance by all factions involved. If, in the process, it is desired to accommodate particular elements of the unofficial *PhyloCode* (cf. Cantino, 2000; de Queiroz, 2006) in a new, formal, unified code of biological nomenclature—thereby enhancing the “phylogenetic capability” of nomenclature, while maintaining sound nomenclatural practice and eliminating undesirable competition between these two possible future codes—this would seem a reasonable and appropriate way to proceed.

### ACKNOWLEDGEMENTS

I thank Dr. Juan M. Lopez-Bautista (University of Alabama) and Dr. Heather A. Owen (University of Wisconsin – Milwaukee) for their thoughtful reviews of this manuscript—extremely valuable in manuscript revision. I also thank Dr. Martha J. Powell (University of Alabama) for critical reading of the manuscript, and for help with formatting the paper for publication.

## LITERATURE CITED

- Adl, S. M., A. G. B. Simpson, M. A. Farmer, R. A. Andersen, O. R. Anderson, J. R. Barta, S. S. Bowser, G. Brugerolle, R. A. Fensome, S. Fredericq, T. Y. James, S. Karpov, P. Kugrens, J. Krug, C. E. Lane, L. A. Lewis, J. Lodge, D. H. Lynn, D. G. Mann, R. M. McCourt, L. Mendoza, Ø. Moestrup, S. E. Mozley-Standridge, T. A. Nerad, C. A. Shearer, A. V. Smirnov, F. W. Spiegel and M. F. J. R. Taylor. 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *J. Eukaryot. Microbiol.* 52: 339-451.
- Alexopoulos, C. J., C. W. Mims and M. Blackwell. 1996. *Introductory mycology*, 4<sup>th</sup> edition. John Wiley & Sons, Inc., New York, Chichester, Brisbane, Toronto and Singapore.
- Andersen, R. A. 1987. Synurophyceae Classis Nov., a new class of algae. *Amer. J. Bot.* 74: 337-353.
- Andersen, R. A. 1991. The cytoskeleton of chromophyte algae. *Protoplasma* 164: 143-159.
- Ariztia, E. V., R. A. Andersen and M. L. Sogin. 1991. A new phylogeny for chromophyte algae using 16S-like sequences from *Mallomonas papillosa* (Synurophyceae) and *Tribonema aequale* (Xanthophyceae). *J. Phycol.* 27: 428-436.
- Bailey, C. 2008. Oomycetes among algae. Annual meeting of the Phycological Society of America, Abstracts, p. 20.
- Baldauf, S. L., A. J. Roger, I. Wenk-Siefert and W. F. Doolittle. 2000. A kingdom-level phylogeny of eukaryotes based on combined protein data. *Science* 290: 972-977.
- Barnes, R. S. K. (Editor). 1998. *The diversity of living organisms*. Blackwell Science, Oxford and London.
- Beakes, G. W. 1989. Oomycete fungi: Their phylogeny and relationship to chromophyte algae. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Beakes, G. W. 1998. Relationships between lower fungi and protozoa. *in* *Evolutionary Relationships among Protozoa*. G. H. Coombs, K. Vickerman, M. A. Sleight and A. Warren, eds., Kluwer Academic, Dordrecht, Boston and London.

- Belcher, J. H. and E. M. F. Swale. 1972. The morphology and fine structure of the colourless colonial flagellate *Anthophysa vegetans* (O. F. Müller) Stein. *Brit. Phycol. J.* 7: 335-346.
- Bhattacharya, D. and L. Medlin. 1995. The phylogeny of plastids: A review based on comparisons of small-subunit ribosomal RNA coding regions. *J. Phycol.* 31: 489-498.
- Bhattacharya, D., L. Medlin, P. O. Wainright, E. V. Ariztia, C. Bibeau, S. K. Stickel and M. L. Sogin. 1992. Algae containing chlorophylls *a* + *c* are paraphyletic: Molecular evolutionary analysis of the Chromophyta. *Evolution* 46: 1801-1817.
- Bhattacharya, D., H. S. Yoon and J. D. Hackett. 2004. Photosynthetic eukaryotes unite: Endosymbiosis connects the dots. *BioEssays* 26: 50-60.
- Bjørnland, T. and S. Liaaen-Jensen. 1989. Distribution patterns of carotenoids in relation to chromophyte phylogeny and systematics. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Blackwell, W. H. 2002. One-hundred-year code déjà vu? *Taxon* 51: 151-154.
- Blackwell, W. H. 2003. Two theories of origin of the land-plant sporophyte: Which is left standing? *Bot. Rev.* 69: 125-148.
- Blackwell, W. H. 2004. Is it kingdoms or domains? Confusion & solutions. *Amer. Biol. Teacher* 66: 268-276.
- Blackwell, W. H. 2008. "Anabaena," "Anabaina," and codes of nomenclature: A review of the feasibility of name correction, and a possible direction for the future. *Phytologia* 90: 324-354.
- Blackwell, W. H. and M. J. Powell. 1995. Where have all the algae gone, or, how many kingdoms are there? *Amer. Biol. Teacher* 57: 160-167.
- Blackwell, W. H. and M. J. Powell. 1999. Reconciling kingdoms with codes of nomenclature: Is it necessary? *Syst. Biol.* 48: 406-412.
- Blackwell, W. H. and M. J. Powell. 2000. A review of group filiation of stramenopiles, additional approaches to the question. *Evol. Theory & Rev.* 12(3): 49-88.
- Blackwell, W. H. and M. J. Powell. 2001. The Protozoa, a kingdom by default? *Amer. Biol. Teacher* 63: 483-490.

- Campbell, N. A., J. B. Reece and L. G. Mitchell. 1999. *Biology*, 5<sup>th</sup> edition. Benjamin/Cummings (Addison Wesley Longman), Menlo Park, California.
- Cantino, P.D. 2000. Phylogenetic nomenclature: Addressing some concerns. *Taxon* 49: 85-93.
- Cavalier-Smith, T. 1978. The evolutionary origin and phylogeny of microtubules, mitotic spindles and eukaryote flagella. *BioSystems* 10: 93-114.
- Cavalier-Smith, T. 1981. Eukaryote kingdoms: Seven or nine? *BioSystems* 14: 461-481.
- Cavalier-Smith, T. 1986. The kingdom Chromista: Origin and systematics. *Prog. Phycol. Res.* 4: 309-347.
- Cavalier-Smith, T. 1987. The origin of eukaryote and archaeobacterial cells. *Ann. New York Acad. Sci.* 503: 17-54.
- Cavalier-Smith, T. 1989. The kingdom Chromista. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Cavalier-Smith, T. 1992. The number of symbiotic origins of organelles. *BioSystems* 28: 91-106.
- Cavalier-Smith, T. 1993. Kingdom Protozoa and its 18 phyla. *Microbiol. Rev.* 57: 953-994.
- Cavalier-Smith, T. 1995. Zooflagellate phylogeny and classification. *Cytology (St. Petersburg)* 37: 1010-1029.
- Cavalier-Smith, T. 1997. Sagenista and Bigyra, two phyla of heterotrophic heterokont chromists. *Arch. Protistenkd.* 148: 253-267.
- Cavalier-Smith, T. 1999. Principles of protein and lipid targeting in secondary symbiogenesis: Euglenoid, dinoflagellate, and sporozoan plastid origins and the eukaryote family tree. *J. Eukaryot. Microbiol.* 46: 347-366.
- Cavalier-Smith, T. 2002. The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *Int. J. Syst. Evol. Microbiol.* 52: 297-354.
- Cavalier-Smith, T. 2004. Only six kingdoms of life. *Proc. Roy. Soc. Lond., B*, 271: 1251-1262.
- Cavalier-Smith, T. and E. E. Chao. 1996. 18S rRNA sequence of *Heterosigma carterae* (Raphidophyceae), and the phylogeny of heterokont algae (Ochrophyta). *Phycologia* 35: 500-510.

- Cavalier-Smith, T. E. E. Chao and M. T. E. P. Allsopp. 1995. Ribosomal RNA evidence for chloroplast loss within Heterokonta: Pedinellid relationships and a revised classification of ochristan algae. *Arch. Protistenkd.* 145: 209-220.
- Chadefaud, M. 1950. Les cellules nageuses des algues dans l'embranchement des Chromophycées. *Comptes Rendus Hebdomadaire, Acad. Sci. Paris* 231: 788-790.
- Christensen, T. 1958. Regnum and subregnum? *Taxon* 7: 270.
- Christensen, T. 1962. Alger. *in* Botanik, Bd. 2, Systematisk Botanik, Nr. 2. T. W. Böcher, M. Lange and T. Sørensen, eds., Munksgaard, Copenhagen.
- Christensen, T. 1989. The Chromophyta, past and present. *in* The Chromophyte Algae: Problems and Perspectives. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Copeland, H. F. 1956. The classification of lower organisms. Pacific Books, Palo Alto, California.
- Corliss, J. O. 1983. Consequences of creating new kingdoms of organisms. *BioScience* 33: 314-318.
- Corliss, J. O. 1984. The kingdom Protista and its 45 phyla. *BioSystems* 17: 87-126.
- Corliss, J. O. 1990. Toward a nomenclatural protist perspective. *in* Handbook of Protoctista. L. Margulis, J. O. Corliss, M. Melkonian and D. J. Chapman, eds., Jones and Bartlett, Boston.
- Corliss, J. O. 1991. Introduction to the Protozoa. *Microscopic Anatomy of Invertebrates* 1: 1-12.
- Corliss, J. O. 1994. The place of the protists in the microbial world. U.S. Federation for Culture Collections, *Newsletter* 24(3): 1-6.
- Daugbjerg, N. and R. A. Andersen. 1997. Phylogenetic analyses of the *rbcL* sequences from haptophytes and heterokont algae suggest their chloroplasts are unrelated. *Mol. Biol. Evol.* 14: 1242-1251.
- Delaney, T. P., L. K. Hardison and R. A. Cattolico. 1995. Evolution of plastid genomes: Inferences from discordant molecular phylogenies. *in* Chrysophyte Algae: Ecology, Phylogeny and Development. C. D. Sandgren, J. P. Smol and J. Kristiansen, eds., Cambridge University Press, UK.
- Delwiche, C. F. 1999. Tracing the thread of plastid diversity through the tapestry of life. *Amer. Nat.* 154 (Suppl.): S164-S177.

- de Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* 15(2): 125-144.
- de Queiroz, K. 2006. The *PhyloCode* and the distinction between taxonomy and nomenclature. *Syst. Biol.* 55:160-162.
- de Queiroz, K. and J. Gauthier. 1992. Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* 23: 449-480.
- Dick, M. W. 2001. *Straminipilous Fungi: Systematics of the Peronosporomycetes including accounts of the marine straminipilous protists, the plasmodiophorids and similar organisms.* Kluwer Academic, Dordrecht, Boston and London.
- Edwards, P. 1976. A classification of plants into higher taxa based on cytological and biochemical criteria. *Taxon* 25: 529-542.
- Fritsch, F. E. 1935. *The structure and reproduction of the algae*, Vol. 1. Macmillan, New York and Cambridge University Press, UK.
- Gledhill, D. 1989. *The names of plants*, 2<sup>nd</sup> edition. Cambridge University Press, Cambridge, UK.
- Graham, L. E. and L. W. Wilcox. 2000. *Algae*. Prentice Hall, Upper Saddle River, NJ.
- Greuter, W., D. L. Hawksworth, J. McNeill, M. A. Mayo, A. Minelli, P. H. A. Sneath, B. J. Tindall, R. P. Trehane and P. K. Tubbs. 1996. Draft *BioCode*: Prospective international rules for the scientific names of organisms. *Bull. Zool. Nomencl.* 53: 148-166. (Minor revision of this "draft" was done in 1997)
- Gunderson, J. H., H. Elwood, A. Ingold, K. Kindle and M. L. Sogin. 1987. Phylogenetic relationships between chlorophytes, chrysophytes, and oomycetes. *Proc. Natl. Acad. Sci. USA* 84: 5823-5827.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen*. Berlin, G. Reimer.
- Harper, J. T., E. Waanders and P. J. Keeling. 2005. On the monophyly of chromalveolates using a six-protein phylogeny of eukaryotes. *Int. J. Syst. Evol. Microbiol.* 55: 487-496.
- Hausmann, K. and N. Hülsmann. 1996. *Protozoology*, 2<sup>nd</sup> edition. Georg Thieme, Stuttgart and New York.
- Hawksworth, D. L. 2007. *Index Fungorum to Species Fungorum and the BioCode*. Mycological Society of America Annual Meeting (2007), Published Abstracts: p. 71.

- Hibberd, D. J. 1979. The structure and phylogenetic significance of the flagellar transition region in the chlorophyll *c*-containing algae. *BioSystems* 11: 243-261.
- Hibbett, D. S. and M. J. Donoghue. 1998. Integrating phylogenetic analysis and classification in fungi. *Mycologia* 90: 347-356.
- Hogg, J. 1860. On the distinctions of a plant and an animal, and on a fourth kingdom of nature. *Edinburgh New Philosoph. J., n.s.,* 12: 216-225.
- Honda, D., T. Yokochi, T. Nakahara, S. Raghukumar, A. Nakagiri, K. Schaumann and T. Higashihara. 1999. Molecular phylogeny of labyrinthulids and thraustochytrids based on the sequencing of 18S ribosomal RNA gene. *J. Eukaryot. Microbiol.* 46: 637-647.
- Horn, S., K. Ehlers, G. Fritzsche, M. C. Gil-Rodriguez, C. Wilhem and R. Schnetter. 2007. *Synchroma grande* spec. nov. (Synchromophyceae class. nov., Heterokontophyta): An amoeboid marine alga with unique plastid complexes. *Protist* 158: 277-293.
- Jeffrey, C. 1971. Thallophtyes and kingdoms—a critique. *Kew Bull.* 25: 291-299.
- Jeffrey, C. 1982. Kingdoms, codes and classification. *Kew Bull.* 37: 403-416.
- Jeffrey, S. W. 1989. Chlorophyll *c* pigments and their distribution in the chromophyte algae. *in* The Chromophyte Algae: Problems and Perspectives. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Keeling, P. J. 2004. Diversity and evolutionary history of plastids and their hosts. *Amer. J. Bot.* 91: 1481-1493.
- Lee, R. E. 1999. *Phycology*, 3<sup>rd</sup> edition. Cambridge University Press, Cambridge, UK.
- Leipe, D. D., P. O. Wainright, J. H. Gunderson, D. Porter, D. J. Patterson, F. Valois, S. Himmerich and M. L. Sogin. 1994. The stramenopiles from a molecular perspective: 16S-like rRNA sequences from *Labyrinthuloides minuta* and *Cafeteria roenbergensis*. *Phycologia* 33: 369-377.
- Li, S., T. Nosenko, J. D. Hackett and D. Bhattacharya. 2006. Phylogenomic analysis identifies red algal genes of endosymbiotic origin in the chromalveolates. *Mol. Biol. Evol.* 23: 663-674.
- Luther, A. 1899. Über *Chlorosaccus*, eine neue Gattung der Susswasseralgen, nebst einigen Bemerkungen zur Systematik

- verwandter Algen. Bih. Kgl. Svensk. Vetensk. Handl. 24, Afd. 3, No. 13: 1-22.
- Margulis, L. 1981. How many kingdoms? Current views of biological classification. *Amer. Biol. Teacher* 43: 482-489.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema and N. J. Turland (Editors). 2006. ICBN: International Code of Botanical Nomenclature (Vienna Code). Adopted by the Seventeenth International Botanical Congress, Vienna, Austria (July, 2005). Gantner, Verlag; Koeltz Scientific Books, Koenigstein, Germany.
- Mindell, D. P. 1992. Phylogenetic consequences of symbioses: Eukarya and Eubacteria are not monophyletic taxa. *BioSystems* 27: 53-62.
- Moestrup, Ø. 1982. Flagellar structure in algae: A review, with new observations particularly on the Chrysophyceae, Phaeophyceae (Fucophyceae), Euglenophyceae, and *Reckertia*. *Phycologia* 21: 427-528.
- Moestrup, Ø. 1992. Taxonomy and phylogeny of the Heterokontophyta. *in* Phylogenetic Changes in Peroxisomes of Algae. Phylogeny of Plant Peroxisomes. H. Stabenau, ed., University of Oldenburg Press, Oldenburg.
- Niklas, K. J. 1997. The evolutionary biology of plants. University of Chicago Press, Chicago and London.
- O'Kelly, C. J. 1989. The evolutionary origin of the brown algae: Information from studies of motile cell ultrastructure. *in* The Chromophyte algae: Problems and Perspectives. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Ott, D. W. 1982. Tribophyceae (Xanthophyceae): Introduction and bibliography. *in* Selected Papers in Phycology II. J. R. Rosowski and B. C. Parker, eds., Phycological Society of America, Lawrence, Kansas.
- Owen, H. A., K. R. Mattox and K. D. Stewart. 1990a. Fine structure of the flagella apparatus of *Dinobryon cylindricum* (Chrysophyceae). *J. Phycol.* 26: 131-141.
- Owen, H. A., K. D. Stewart and K. R. Mattox. 1990b. Fine structure of the flagellar apparatus of *Uroglena americana* (Chrysophyceae). *J. Phycol.* 26: 142-149.
- Palmer, J. D. 2003. The symbiotic birth and spread of plastids: How many times and whodunit? *J. Phycol.* 39: 4-11.

- Parfrey, L. W., E. Barbero, E. Lasser, M. Dunthorn, D. Bhattacharya, D. J. Patterson and L. A. Katz. 2006. Evaluating support for the current classification of eukaryotic diversity. *PLoS Genetics*: 2: 2062-2073.
- Pascher, A. 1925. Heterokontae. Die Susswasser-flora Deutschlands, Oesterreichs und Der Schweiz 11: 1-118.
- Patterson, D. J. 1986. The actinophryid heliozoa (Sarcodina, Actinopoda) as chromophytes. *in* *Chrysophytes: Aspects and Problems*. J. Kristiansen and R. A. Andersen, eds., Cambridge University Press, Cambridge, New York, and Melbourne.
- Patterson, D. J. 1989. Stramenopiles: Chromophytes from a protistan perspective. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Perasso, R., A. Baroin, L. Hu Qu, J. P. Bachelier and A. Adoutte. 1989. Origin of the algae. *Nature* 339: 142-144.
- Preisig, H. R. 1989. The flagellar base ultrastructure and phylogeny of chromophytes. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Reyes-Prieto, A., A. P. M. Weber and D. Bhattacharya. 2007. The origin and establishment of the plastid in algae and plants. *Ann. Rev. Genet.* 41: 147-168.
- Round, F. E. 1989. The chromophyte algae—problems and perspectives. A summarizing view. *in* *The Chromophyte Algae: Problems and Perspectives*. J. C. Green, B. S. C. Leadbeater, and W. L. Diver, eds., Clarendon Press, Oxford, UK.
- Sanchez-Puerta, M. V. and C. F. Delwiche. 2008. A hypothesis for plastid evolution in chromalveolates. *J. Phycol.* 44: 1097-1107.
- Schuh, R. T. 2000. *Biological systematics: Principles and applications*. Comstock Publishing Associates/Cornell University Press, Ithaca and London.
- Simpson, D. P. 1968. *Cassell's Latin dictionary*, 5<sup>th</sup> edition. MacMillan, New York.
- Sleigh, M. A. 1989. *Protozoa and other protists*. Arnold/Routledge, London and New York.
- Sogin, M. L. and D. J. Patterson. 1995. Stramenopiles. Version 01 January 1995 (under construction). <http://tolweb.org/Stramenopiles/2380/1995.01.01> *in* *The Tree of Life Web Project*, <http://tolweb.org/>

- Sogin, M. L. and J. D. Silberman. 1998. Evolution of the protists and protistan parasites from the perspective of molecular systematics. *Int. J. Parasitol.* 28: 11-20.
- Tappan, H. 1980. The paleobiology of plant protists. W. H. Freeman, San Francisco.
- Tyler, B. M., S. Tripathy, X. Zhang, P. Dehal, R. H. Y. Jiang., A. Aerts and F. D. Arredondo. 2006. *Phytophthora* genome sequences uncover evolutionary origins and mechanisms of pathogenesis. *Science* 313: 1261-1266.
- Van de Peer, Y. and R. De Wachter. 1997. Evolutionary relationships among the eukaryotic crown taxa taking into account site-to-site rate variation in 18S rRNA. *J. Mol. Evol.* 45: 619-630.
- Van den Hoek, C. 1978. *Algen: Einführung in die Phykologie*. George Thieme, Stuttgart, Germany.
- Van den Hoek, C., D. G. Mann and H. M. Jahns. 1995. *Algae: An introduction to phycology*. Cambridge University Press, Cambridge, UK.
- Wee, J. L., J. M. Hinchey, K. X. Nguyen, P. Kores and D. L. Hurley. 1996. Investigating the comparative biology of the heterokonts with nucleic acids. *J. Eukaryot. Microbiol.* 43: 106-112.
- Whittaker, R. H. 1959. On the broad classification of organisms. *Quart. Rev. Biol.* 34(3): 210-226.
- Whittaker, R. H. 1969. New concepts of kingdoms of organisms. *Science* 163: 150-160.
- Williams, D. M. 1991. Phylogenetic relationships among the Chromista: A review and preliminary analysis. *Cladistics* 7: 141-156.
- Woese, C. R., O. Kandler and M. L. Wheelis. 1990. Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eucarya. *Proc. Natl. Acad. Sci. USA* 87: 4576-4579.
- Yamagishi, T., T. Motomura, C. Nagasato, A. Kato and H. Kawai. 2007. A tubular mastigoneme-related protein, OCM1, isolated from the flagellum of a chromophyte alga, *Ochromonas danica*. *J. Phycol.* 43: 519-527.
- Yoon, H. S., J. D. Hackett, F. M. Van Dolah, T. Nosenko, K. L. Lidie and D. Bhattacharya. 2005. Tertiary endosymbiosis driven genome evolution in dinoflagellate algae. *Mol. Biol. Evol.* 22: 1299-1308.