Biology and systematics of heterokont and haptophyte algae[1]

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In this paper, I review what is currently known of phylogenetic relationships of heterokont and haptophyte algae. Heterokont algae are a monophyletic group that is classified into 17 classes and represents a diverse group of marine, freshwater, and terrestrial algae. Classes are distinguished by morphology, chloroplast pigments, ultrastructural features, and gene sequence data. Electron microscopy and molecular biology have contributed significantly to our understanding of their evolutionary relationships, but even today class relationships are poorly understood. Haptophyte algae are a second monophyletic group that consists of two classes of predominately marine phytoplankton. The closest relatives of the haptophytes are currently unknown, but recent evidence indicates they may be part of a large assemblage (chromalveolates) that includes heterokont algae and other stramenopiles, alveolates, and cryptophytes. Heterokont and haptophyte algae are important primary producers in aquatic habitats, and they are probably the primary carbon source for petroleum products (crude oil, natural gas).

Key words: chromalveolate; chromist; chromophyte; flagella; phylogeny; stramenopile; tree of life.

Heterokont algae are a monophyletic group that includes all photosynthetic organisms with tripartite tubular hairs on the mature flagellum (discussed later; also see Wetherbee et al., 1988, for definitions of mature and immature flagella), as well as some nonphotosynthetic relatives and some that have secondarily reduced or lost tripartite hairs. Brown seaweeds, diatoms, and chrysophytes are commonly known members of the group. Haptophyte algae are a monophyletic group that includes all photosynthetic organisms with a haptonema, as well as some nonphotosynthetic relatives, and some that have secondarily lost the haptonema. The haptonema, from which the group derives its name, is a microtubule-supported appendage that lies between two approximately equal flagella (for review, Inouye and Kawachi, 1994). The coccolithophores and genera such as *Pavlova* and *Isochrysis* are commonly known members of the group. Representatives of heterokont algae and haptophytes are shown in Figs. 1–24. Until 1992, haptophytes were included or closely aligned with heterokont algae, but a nuclear small subunit ribosomal RNA (SSU rRNA) analysis indicated they are distantly related (Bhattacharya et al., 1992). Recent molecular studies, based on other genes, have now indicated that heterokont and haptophyte algae may be more closely aligned than the SSU rRNA data indicated (Yoon et al., 2000a, b; Harper and Keeling, 2003; Ryall et al., 2003).

Historical perspective—Brown seaweeds were referred to in early Chinese (ca. 3000 BC), Greek (e.g., Theophrastos, ca. 300 BC), and Japanese (ca. 500 AD) writings, and knowledge of brown seaweeds likely predated recorded history. In early human history, brown seaweeds were used for human and animal food, medicinal purposes, and dyes. Most other heterokont algae are microscopic, although mats of macroscopic *Vaucheria* (Xanthophyceae) may have been known but not recorded in historical works.

The first modern scientific report is the description of *Fucus*

(Phaeophyceae) by Linnaeus (1753), and shortly thereafter, microscopic chrysophytes (currently = *Oikomonas*, *Anthophysa*) were described by Müller (1773, 1786). The history of heterokont algae was recently discussed in detail (Andersen, 2004), and four distinct periods were identified. The discovery period (1753–1882) is that era in which brown algae were described as plants, and microalgae were described as infusoria and treated as animals. Perhaps the most significant publication of the era was the two-part publication of Ehrenberg (1838) that contained his light microscopic observations. The first synthesis period (1882–1914) began when brown algae and microalgae were first integrated and phylogenetic relationships were discussed (Rostafinski, 1882; Correns, 1892; Klebs, 1893a, b; Lemmermann, 1899; Blackman, 1900), but the period ended when these two groups were once again separated (Pascher, 1914). The floristic period (1914–1950) was dominated by the description of many species. There was a nearly complete absence of evolutionary discussion, for the primary reason that the light microscope was unable to resolve characters for determining relationships (Fritsch, 1935). The second synthesis period (1950–2002) began with and was dominated by evolutionary and phylogenetic relationships (e.g., Chadefaud, 1950; Bourrelly, 1957; Taylor, 1976; Leipe et al., 1996; Daugbjerg and Andersen, 1997a, b). Transmission electron microscopy provided a wealth of new and phylogenetically informative data (e.g., Dodge, 1973; Hibberd, 1976; Taylor, 1976; Andersen, 1987), and biochemical studies were also initiated (e.g., Strain, 1951; Quillet, 1955; Archibald et al., 1963; Ragan and Chapman, 1978; Smestad-Paulsen and Myklestad, 1978; Bjørnland and Liaaen-Jensen, 1989; Jeffrey, 1989). Cladistic analysis brought new ways for analyzing evolutionary relationships (e.g., Hibberd, 1979; Lipscomb, 1989; Andersen, 1991; Williams, 1991; Sorhannus, 2001), and molecular systematics added powerful new data sets (e.g., Gundersen et al., 1987; Leipe et al., 1994, 1996; Guillou et al., 1999b; Moriya et al., 2002; Goertzen and Theriot, 2003). Discoveries led to descriptions of many new taxa, including several classes: Eustigmatophyceae (Hibberd and Leedale, 1970), Dictyochophyceae (Silva, 1980), Synurophyceae (Andersen, 1987), Coscinodiscophyceae and Fragilariophyceae (Round et al., 1990), Chrysomerophyceae (Cavalier-Smith et al., 1995),

Bolidophyceae (Guillou et al., 1999a), Pelagophyceae (Andersen et al., 1993), Phaeothamniophyceae (Bailey et al., 1998), Pinguiophyceae (Kawachi et al., 2002b), and Schizocladiophyceae (Kawai et al., 2003). The sequencing of the *Thalassiosira pseudonana* genome, initiated in 2002, was thought to be the start of a new period, but it is too early to define this period.

The first record of haptophyte algae might begin with Ehrenberg (1836), who discovered that chalk was composed of tiny crystallites that he considered to be formed by precipitation rather than biological activity (see Green and Jordan, 1994; Siesser, 1994). In the mid 1800s, a series of articles were concerned with the biological origin of coccoliths and coccospheres (Huxley, 1858; Wallich, 1860, 1861; Sorby, 1861; Carter, 1871; Wyville-Thomson, 1874), and the matter was resolved in 1898 when Murray and Blackman described and illustrated a dividing cell inside the coccosphere (see Green and Jordan, 1994; Siesser, 1994). The first description of the haptonema was by Scherffel (1901) when he described *Phaeocystis*, but he considered the haptonema to be a third flagellum. Pascher (1910, 1913, 1914) placed golden microalgae with two equal flagella into order Isochrysidales, class Chrysophyceae, and this included not only organisms we recognize today as haptophytes but also some of Synurophyceae and Chrysophyceae. Additional taxa were described in the years following Pascher's classification (e.g., *Prymnesium*, *Chrysochromulina*; Carter, 1937; Lacky, 1939), and with the advent of electron microscopy, many additional species were described (e.g., Parke et al., 1955; Manton and Leedale, 1969; Manton and Leadbeater, 1974). Electron microscopy also demonstrated the unique structure of the haptonema (Parke et al., 1955), unusual features of the Golgi apparatus (Manton, 1967), and ultrastructural differences between haploid and diploid phases of the life cycle (e.g., Parke and Adams, 1960). These differences led Christensen (1962) to propose a separate class, Haptophyceae, which he made approximately equal to Chrysophyceae, Xanthophyceae, Phaeophyceae, etc. Hibberd (1976) provided additional support for the separation of Haptophyceae, Cavalier-Smith (1986, 1989) divided Haptophyta into two classes, and most recently, Edvardsen et al. (2000) summarized the classification of Division Haptophyta, including several nomenclatural proposals to bring classification in accord with the IBCN.

Currently recognized classes—The taxonomic class is the primary currency for classifying heterokont algae. In large part, this stems from an inadequate understanding of phylogenetic relationships. Thus, some workers lump all classes into a single division, Heterokontophyta (e.g., Hoek, 1978; Hoek et al., 1995), whereas others raise classes to division level (e.g., Corliss, 1984). There are currently 17 recognized classes, and, except for the three diatom classes, all classes are listed in Tables 1–3. Diatoms are currently classified in Coscinodiscophyceae (centric diatoms), Fragilariophyceae (araphid pennates), and Bacillariophyceae (raphid pennates; Round et al., 1990). However, diatom classification will change soon because the two pennate classes form a monophyletic group, whereas centric diatoms form two clades (e.g., Medlin et al., 1996). Haptophyta are recognized as a division divided into two classes, Pavlovophyceae and Prymnesiophyceae (Cavalier-Smith, 1998; Edvardsen et al., 2000).

Ecology—Heterokont algae are found in almost all environments where life exists, but the occurrence varies widely among the classes. The ecological literature is extensive and impossible to summarize here; the references listed later are good sources for additional information. Bolidophyceae, Chrysomophyceae, Pelagophyceae, Pinguiophyceae, and Schizocladophyceae are only known from marine environments (Billard, 1984; Guillou et al., 1999a; Andersen and Preisig, 2002b; Kawachi et al., 2002b; Kawai et al., 2003). Phaeophyceae are almost exclusively marine organisms, but five freshwater genera are known (Bold and Wynne, 1985). Synurophyceae are probably restricted to freshwater, although a couple of dubious marine occurrences have been reported (Andersen and Preisig, 2002a). Chrysophyceae, Phaeothamniophyceae, and Xanthophyceae are predominately freshwater organisms, although a substantial number of xanthophytes are terrestrial (Ettl, 1978; Reith, 1980; Starmach, 1985; Kristiansen and Preisig, 2001; Hibberd, 1990b; Ettl and Gaertner, 1995; Bailey et al., 1998; Preisig and Andersen, 2002). Dictyochophyceae occur in both marine and freshwater habitats (Moestrup, 1995; Moestrup and O'Kelly, 2002), and Eustigmatophyceae occur in freshwater, marine, and terrestrial habitats (Hibberd, 1990a). Raphidophyceae are sharply divided into two groups, marine genera with fucoxanthin–violaxanthin type pigments, and freshwater genera with heteroxanthin–diatoxanthin type pigments (Table 2; Heywood, 1990; Potter et al., 1997; Heywood and Leedale, 2002). Finally, diatoms are found in all common habitats supporting life (Round et al., 1990). Regarding haptophytes, they are predominately marine, but several freshwater species are well known (Green and Leadbeater, 1994).

Diatoms are widely used as indicator species in paleoecological studies (for review, see Stoermer and Smol, 1999). Silica-scaled algae are also good indicator species (e.g., Siver, 1991; Smol, 1995). Heterokont and haptophyte classes contain toxic or harmful species. A number of diatoms are harmful to marine life, and domoic acid from *Pseudo-nitzschia*, concentrated in shellfish, has killed humans (see Fryxell and Hasle, 2003 for review). *Aureococcus* and *Aureoumbra* (Pelagophyceae) form coastal blooms that are harmful to marine invertebrates (Cosper et al., 1989; Buskey et al., 1997; Bricelj et al., 2001). *Chattonella* and *Heterosigma* (Raphidophyceae) are well-known fish killers (Okaichi, 1989; Hallegraeff and Hara, 2003). Also, *Chrysochromulina*, *Prymnesium*, and *Phaeocystis* (Prymnesiophyceae) are known to kill fish or be harmful to marine life (Moestrup and Thomsen, 2003).

A number of flagellate heterokont and haptophyte algae are mixotrophic, usually by phagocytosis, and many utilize organic molecules. The "biflagellate" Chrysophyceae, for which *Epipyxis* is the model system, may all be phagocytotic, and they have a sophisticated capturing mechanism that involves microtubules of the flagellar apparatus. Bacteria captured by flagella are pressed into a feeding basket near the flagellar bases at the anterior end of the cell (Andersen and Wetherbee, 1992; Wetherbee and Andersen, 1992). Phagocytosis also occurs in the haptophytes, in which *Chrysochromulina* is the model organism (Kawachi et al., 1991; Inouye and Kawachi, 1994). The haptonema captures food particles, wraps around the cell, and then particles are engulfed at the posterior end of the cell.

Cell biology—Chloroplasts and their pigments—The chloroplast structures of all heterokont algae and haptophytes share some features (Dodge, 1973). The chloroplast is surrounded
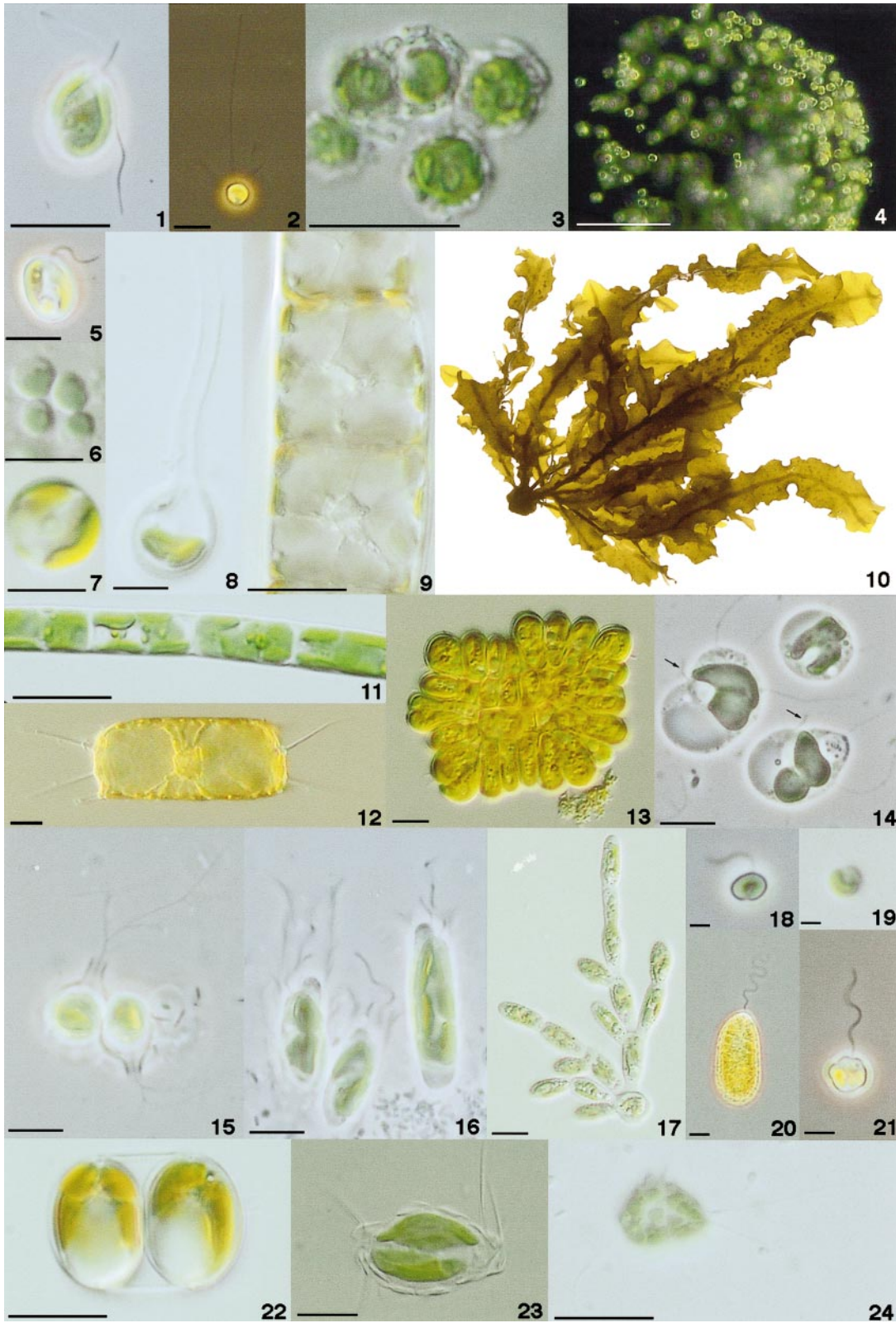
by the chloroplast endoplasmic reticulum, and thus four membranes separate the stroma from the cytosol. Each chloroplast lamella consists of three adpressed thylakoids. Finally, although not strictly a chloroplast feature, the photosynthetic carbohydrate storage product is a β-1,3-linked glucan of small molecular size (20–50 glucose residues), which for osmotic reasons is stored in a vacuole outside the chloroplast.

Distinguishing features include the presence of a girdle lamella, which is a saclike three-thylakoid structure that encloses all other (sheet type) lamellae. Most heterokont classes (Eustigmatophyceae excepted) have a girdle lamella, but it is absent in Haptophyta (Table 1). In most heterokont classes as well as haptophytes, the outer membrane of the chloroplast endoplasmic reticulum is continuous with the outer membrane of the nucleus. The inner chloroplast endoplasmic reticulum is considered to be either the remnant plasmalemma of an ancient endosymbiotic event or derived from the outer nuclear envelope as well (by an out-folding model). Some heterokont algae lack a chloroplast endoplasmic reticulum–nuclear envelope continuity, and these include those diatoms with multiple chloroplasts, raphidophytes and synurophytes. A relationship with symbiotic bacteria occurs in the lumen of the chloroplast endoplasmic reticulum of the diatom *Pinnularia* (Schmid, 2003a, b). The bacteria are blocked from passing down the lumen of the endoplasmic reticulum to the nucleus. The bacteria also cause, or at least occupy, invaginations in the plastid, giving it an irregular margin.

Not all species have chloroplasts. Leucoplasts (unpigmented plastids) are present in some chrysophytes, e.g., *Paraphysomonas* and *Spumella* (Mignot, 1977; Preisig and Hibberd, 1982a, b, 1983). Recently, Sekiguchi et al. (2002) described the presence of leucoplasts in two colorless pedinellids, *Pteridomonas* and *Ciliophrys* (Dictyochophyceae), and they also amplified and sequenced the *rbcL* gene from these organisms. This provided clear evidence that the colorless taxa were derived from photosynthetic ancestors, falsifying an earlier hypothesis that the pigmented forms arose from colorless ancestors via an endosymbiotic event (Cavalier-Smith et al., 1995). A taxonomic reevaluation of pedinellids was subsequently published (Sekiguchi et al., 2003). Leucoplasts may be entirely absent in some heterokonts, e.g., *Picophagus* (Chrysophyceae; Guillou et al., 1999b), but recent cautions indicate that remnants of plastids may remain (Harper and Keeling, 2003). Colorless diatoms, especially *Nitzschia*, are known (Lewin and Lewin, 1967), but whether or not they have leucoplasts is unclear. Finally, *Sphaeropsis pascheri* Schiller (Chrysophyceae) was described as having cyanelles (Schiller, 1954); however, this light microscopic work has not been verified using electron microscopy or molecular techniques. This is apparently the only report of a cyanelle-bearing heterokont alga, and there are no reports of cyanelles in haptophytes.

Many heterokont swimming cells as well as some Pavlovophyceae have an eyespot that is located within the chloroplast or associated with it (e.g., Dodge, 1973; Green, 1980). Eyespots are part of the photoreceptor apparatus (also called the eyespot apparatus), shielding light so that the other elements can more precisely determine the direction of light (Foster and Smyth, 1980). In a wide variety of heterokont and haptophyte algae, one flagellum possesses an autofluorescent substance (flavin and pterin-like in brown algae) that plays a role in phototaxis (Müller et al., 1987; Kawai and Inouye, 1989; Kawai et al., 1996). In the typical case (most heterokont algae, Pavlovophyceae), the eyespot lies just inside the chloroplast in the area immediately adjacent to the mature flagellum. Eustigmatophytes have a large eyespot located outside the chloroplast but adjacent to the mature flagellum; this unusual eyespot is the basis of the class name. For a recent review, see Kawai and Kreimer (2000).

Brown algae produce two types of swimming cells, asexual zoospores and male (and sometimes female) gametes. Kawai et al. (1990, 1991) showed that swimming cells have phototactic responses to photosynthetically active wavelengths. Iken et al. (2001) described five different swimming patterns for *Hincksia* by employing computer-assisted motion analysis. The patterns were associated with finding suitable attachment sites for settlement or with positive or negative reactions to certain environmental stimuli.

Chloroplasts function primarily for photosynthesis, and heterokont and haptophyte algae have a wide variety of light-harvesting pigments, many of which are photosynthetically active. Characterization of pigments has advanced dramatically in the past 50 years, and new techniques as well as more critical characterization of molecules have been significant. Nevertheless, pigment scientists have not always kept abreast of taxonomic changes, and relatively few organisms in each class have been critically studied (e.g., Jeffrey and Vesk, 1997). A summary of chloroplast pigments, by taxonomic class, is shown in Table 2, but the reader should keep in mind the limited taxon sampling. All heterokont and haptophyte algae, except Eustigmatophyceae, have one or more types of chlorophyll *c*, but variability and diversity probably exceeds that shown. These algae are rich in carotenoids, giving them a golden or brown color (Eustigmatophyceae, Xanthophyceae, some Raphidophyceae excepted). In addition to other roles (e.g., ultraviolet light protection, photosynthetic quenching), one or more photosynthetically active carotenoids are usually present (e.g., Alberte and Andersen, 1986; Porra et al., 1997).

Cell coverings—Heterokont algae have a wide range of cell coverings. Bolidophytes are naked flagellates (Guillou et al., 1999a); diatoms have siliceous frustules (Round et al., 1990); chrysomerophytes have cell walls (Billard, 1984); chryso-

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Figs. 1–24. Haptophyte and heterokont algae. Figs. 1–4. Haptophyte algae. **1.** *Prymnesium* (Prymnesiophyceae). Scale bar = 10 μm. **2.** *Chrysochromulina* (Prymnesiophyceae). Scale bar = 10 μm. **3.** *Emiliania* (Prymnesiophyceae). Scale bar = 10 μm. **4.** *Phaeocystis* (Prymnesiophyceae). Scale bar = 10 μm. **5.** *Pavlova* (Pavlovophyceae). Scale bar = 5 μm. Figs. 6–24. Heterokont algae. **6.** *Nannochloropsis* (Eustigmatophyceae). Scale bar = 1 μm. **7.** *Pinguiococcus* (Pinguiophyceae). Scale bar = 5 μm. **8.** *Polypodochrysis* (Pinguiophyceae). Scale bar = 5 μm. **9.** *Pylaiella* (Phaeophyceae). Scale bar = 10 μm. **10.** *Dictyopteris* (Phaeophyceae). Scale bar = 1 cm. **11.** *Tribonema* (Xanthophyceae). Scale bar = 10 μm. **12.** *Odontella* (Bacillariophyta). Scale bar = 10 μm. **13.** *Phaeoplaca* (Chrysophyceae). Scale bar = 10 μm. **14.** *Chrysamoeba* (Chrysophyceae). Arrows = flagellum. Scale bar = 5 μm. **15.** *Lagynion* (Chrysophyceae). Scale bar = 5 μm. **16.** *Epipyxis* (Chrysophyceae). Scale bar = 5 μm. **17.** *Phaeothamnion* (Phaeothamniophyceae). Scale bar = 10 μm. **18.** *Pelagomonas* (Pelagophyceae). Scale bar = 1 μm. **19.** *Aureococcus* (Pelagophyceae). Scale bar = 1 μm. **20.** *Chattonella* (Raphidophyceae). Scale bar = 10 μm. **21.** *Pseudopedinella* (Dictyochophyceae). Scale bar = 5 μm. **22.** *Halodiscus* (Bacillariophyta). Scale bar = 10 μm. **23.** *Mallomonas* (Synurophyceae). Scale bar = 10 μm. **24.** *Rhizochromulina* (Dictyochophyceae). Scale bar = 10 μm.

TABLE 1. Chloroplast features of the heterokont and haptophyte algae. The eyespot of eustigmatophytes is located outside the chloroplast. Genophore type refers to the arrangement of plastid DNA (ring of DNA, scattered granules of DNA).

	Girdle lamella	Plastid-nucleus membrane connection	Eyespot	Genophore type
Heterokont algae				
Bacillariophyta	+	±	−	ring
Bolidophyceae	+	+	−	ring
Chrysomerophyceae	+	+	+	ring
Chrysophyceae	+	+	+	ring
Dictyochophyceae	+	+	−	scattered
Eustigmatophyceae	−	+	+ (outside)	ring
Pelagophyceae	+	+	−	scattered
Phaeophyceae	+	+	±	ring
Phaeothamniophyceae	+	+	+	ring
Pinguiophyceae	±	+	−	scattered
Raphidophyceae	±	−	−	scattered
Schizocladophyceae	+	+	+	ring
Synurophyceae	+	−	−	ring
Xanthophyceae	+	+	±	ring
Haptophyta				
Pavlovophyceae	−	+	+	scattered
Prymnesiophyceae	−	+	−	scattered

Note: + = present; − = absent; ± = present or absent.

phytes have cell walls, organic loricas, organic or silica scale cases, gelatinous coverings, and completely naked cells (Starmach, 1985; Kristiansen and Preisig, 2001; Preisig and Andersen, 2002); dictyochophytes have silica skeletons, organic scales, or naked cells (Moestrup, 1995; Moestrup and O'Kelly, 2002); eustigmatophytes have cell walls (Hibberd, 1990a); pelagophytes have cell walls, thecae, gelatinous coverings, and naked cells (Andersen and Preisig, 2002b); phaeophytes have cellulosic cell walls impregnated with alginates and often interconnected via plasmodesmata (Bisalputra, 1966; Pueschel and Stein, 1983); phaeothamniophytes have cell walls (Bailey et al., 1998); pinguiophytes have mineralized loricas, gelatinous coverings, or naked cells (Kawachi et al., 2002a, b, c);

raphidophytes are naked cells (Heywood, 1990; Heywood and Leedale, 2002); *Schizocladia* has cell walls without cellulose but impregnated with alginates (Kawai et al., 2003); synurophytes have bilaterally symmetrical silica scales glued together to form a highly organized scale case (Ludwig et al., 1996); xanthophytes have predominately cell walls, some with H-shaped overlapping sections, as well as plasmodial and naked forms (Hibberd, 1990b).

Although silica frustules of diatoms have long been studied for taxonomic purposes (e.g., Hustedt, 1928), new technology has allowed scientists to investigate the nonsiliceous components of the cell wall. Higgens et al. (2003) used atomic force microscopy to study the topology and properties of the mu-

TABLE 2. Chloroplast pigmentation of heterokont and haptophyte algae.

	Chlorophylls	Fuc	19′-hex	19′-but	Diato-dino	Viola	Hetero	Vauch
Heterokont algae								
Bacillariophyta	a, $c_{1,2}$ (c_3)	+	+	−	+	−	−	−
Bolidophyceae	a, c_{1-3}	+	+	−	+	−	−	−
Chrysomerophyceae	a, $c_{1,2}$	+	−	−	−	+	−	−
Chrysophyceae	a, $c_{1,2}$	+	+	−	−	+	−	−
Dictyochophyceae	a, $c_{1,2}$	+	−	−	+	−	−	−
Eustigmatophyceae	a	−	−	−	−	+	−	+
Pelagophyceae	a, $c_{1,2}$	+	(+)	+	+	−	−	−
Phaeophyceae	a, $c_{1,2}$	+	−	−	−	+	−	−
Phaeothamniophyceae	a, $c_{1,2}$	+	−	−	+	−	+	−
Pinguiophyceae	a, $c_{1,2}$	+	−	−	−	+	−	−
Raphidophyceae-FW	a, $c_{1,2}$	±	−	−	+	−	+	+
Raphidophyceae-Mar	a, $c_{1,2}$	±	−	−	−	+	−	−
Schizocladophyceae	a, c (type ?)	+	?	?	?	?	?	?
Synurophyceae	a, c_1	+	−	−	−	+	−	−
Xanthophyceae	a, $c_{1,2}$	−	−	−	−	+	+	+
Haptophyta								
Pavlovophyceae	a, c_{1-3}	+	+	+	+	−	−	−
Prymnesiophyceae	a, c_{1-3}	+	+	+	+	−	−	−

Notes: Fuc = fucoxanthin; 19′-hex = 19′-hexanoyloxyfucoxanthin; 19′-but = 19′-butanoyloxyfucoxanthin; diato-dino = pigments of the diatoxanthin; diadinoxanthin cycle; viola = pigments of the violathanin; antheraxanthin; zeaxanthin cycle; hetero = heteroxanthin; vauch = vaucherioxanthin; + = present; − = absent; ± = present or absent; ? = unknown.

TABLE 3.   Features of the flagellar apparatus of the heterokont and haptophyte algae.

	Tri-H	# flagella	TH	Flagellar beat	Lateral hairs	mt roots	Green flagellum	Parafag-ellar rod	Striated root
Heterokont algae									
Bacillariophyta	+	1,0	0	pulls	−	0	−	?	−
Bolidophyceae	+	2	0	pulls	−	0	?	−	−
Chrysomerophyceae	+	2	6 ↑	pulls	−	4	?	−	?
Chrysophyceae	+	2	4–6 ↑	pulls	+	2–4	+	−	+
Dictyochophyceae	+	1	0–2 ↓	pulls	−	0	−	+	−
Eustigmatophyceae	+	2,0	6 ↑	pulls	−	4	−	−	+
Pelagophyceae	±	2,1,0	0–2 ↓	pulls	−	0	−	+	−
Phaeophyceae	+	2	0	pulls	−	4	+	−	−
Phaeothamniophyceae	+	2	6 ↑	pulls	−	4	+	−	+
Pinguiophyceae	±	2,1,0	0,2 ↓	pulls, none?	−	3,4	±	−	+
Raphidophyceae	+	2	0	pulls	−	?	−	−	?
Schizocladophyceae	+	2	6 ↑	pulls	−	?	+	−	?
Synurophyceae	+	2,1	6–9 ↑	pulls	+	2	+	−	+
Xanthophyceae	+	2,0	2 × 6 ↑	pulls	−	4	+	−	+
Haptophyta									
Pavlovophyceae	−	2	0	pulls	−	2	−	−	−
Prymnesiophyceae	−	2	0	pushes, breast pull	−	4	+	−	−

Notes: Tri-H = tripartite tubular hairs; TH = transitional helix; mt roots = microtubular roots. Arrows (↑; ↓) indicate the position (distal, proximal) of the transitional helix with respect to the major transitional plate. + = present; − = absent; ± = present or absent; ? = unknown.

cilage layer that coats diatom frustules. They found two different types of mucilage nanostructure on two benthic species, and on a third species they demonstrated the complete absence of a mucilage layer. They also measured the adhesive-binding properties and elasticity properties of the polymer chains that make up the mucilage. Silicification in diatoms occurs in silica deposition vesicles that are shaped into the form of the final valve or girdle band (Simpson and Volcani, 1981; Schmid, 2003a, b). Silica scales and siliceous cysts of synurophytes and chrysophytes as well as the siliceous skeleton of *Dictyocha* (Dictyochophyceae) are also formed in silica deposition vesicles (Schnepf and Deichgräber, 1969; Mignot and Brugerolle, 1982; Beech et al., 1990; Moestrup and Thomsen, 1990; Preisig, 1994). Despite the unusual nature of siliceous wall coverings as well as the similar silicification processes found among diatoms, chrysophytes, *Dictyocha*, and synurophytes, only Chrysophyceae and Synurophyceae appear to be closely related (see phylogeny section).

Parmales, a poorly known group of heterokont algae not discussed elsewhere in this paper, are tiny marine phytoplankters that are characterized by relatively large silica plates surrounding the protoplasm (Booth and Marchant, 1987, 1988; Kosman et al., 1993; Bravo-Sierra and Hernández-Becerril, 2003). The silicification process is not known for Parmales, but presumably it involves silica deposition vesicles. Parmales are known only from field samples, and their classification remains an enigma. They have been nominally classified in Chrysophyceae, but the lack of distinctive ultrastructural features, apparent absence of flagellate stages, no knowledge of photosynthetic pigments, and absence of gene sequences make an informed classification impossible.

Brown seaweeds (Phaeophyceae) include kelps, the largest and most structurally complex of heterokont algae. Of heterokont algae, they most resemble plants with regard to cell walls. Adjacent cells are often interconnected via plasmodesmata (Bisalputra, 1966; Pueschel and Stein, 1983), a feature not found in other heterokont algae. Biochemical studies provided evidence of intercellular transport, such as movement from the leafy fronds to the meristematic region (e.g., Cabello-

Pasini and Alberte, 2001). Important cell wall features that distinguish Phaeophyceae and Schizocladophyceae are the presence of cellulose and plasmodesmata in the walls of brown algae but the absence of both in *Schizocladia* (Kawai et al., 2003). Like brown algae, however, *Schizocladia* contains alginates that impregnate its (unknown) cell wall fibers.

Haptophytes also have a variety of cell coverings. Benthic stages of some have cell walls, coccolithophorids have calcified scales (usually mineralized onto organic scales) that are termed coccoliths, some have only organic scales, a silica-scaled prymnesiophyte was recently reported, some are surrounded by gelatinous material, and others are naked (see Green and Leadbeater, 1994; Winter and Siesser, 1994).

Flagellar apparatus—The typical swimming cell of heterokont algae has two flagella, a long immature flagellum and a short mature flagellum (Table 3). It is the marked and nearly consistent nature of these two flagella that defines the term heterokont. The control of flagellar length in heterokonts is unknown, but it may be similar to that for green algae (see Beech, 2003, for review). An immature flagellum is produced de novo during cell division, and the previous immature flagellum is transformed into a mature flagellum by a process termed flagellar transformation (e.g., Wetherbee et al., 1988). Thus, each typical cell has a longer immature flagellum bearing tripartite hairs and a shorter mature flagellum (see later for exceptions).

In heterokont algae, orientation of flagella on biflagellate cells varies greatly, from cells with two forward-directed flagella to those with one forward-directed flagellum and one trailing flagellum. Sometimes, but not always, orientation of basal bodies matches that of flagella. Mismatched direction occurs, for example, in zoospores of brown algae (basal bodies at 90°, flagella at 180°) and flagellate cells of Raphidophyceae and some Synurophyceae (basal bodies nearly parallel or 0°, flagella at 180°).

Flagellated vegetative cells of Bolidophyceae, Chrysophyceae, and Raphidophyceae as well as most vegetative cells of Synurophyceae and *Phaeomonas* (Pinguiophyceae) have two

typical flagella (e.g., Hibberd, 1976; Andersen, 1989; Heywood, 1990; Guillou et al., 1999b; Honda and Inouye, 2002). Similarly, flagellated zoospores or sperm of Chrysomerophyceae, Eustigmatophyceae, Phaeophyceae, Phaeothamniophyceae, Schizocladophyceae, and Xanthophyceae as well as some Pelagophyceae have two typical flagella (e.g., Billard, 1984; O'Kelly, 1989; Hibberd, 1990a, b; Lobban et al., 1995; Andersen et al., 1998b; Kawai et al., 2003). Conversely, the flagellate sperm of the diatoms as well as armored vegetative cells of Dictyochophyceae and some *Mallomonas* species (Synurophyceae) have only a single, immature flagellum, i.e., they lack a mature flagellum although they possess a mature basal body (e.g., Manton and von Stosch, 1966; Beech and Wetherbee, 1990a, b; Moestrup and Thomsen, 1990). Of these, the diatom sperm are noteworthy in that the flagellum axoneme has a $9 + 0$ microtubular arrangement; in all other heterokonts, the flagellum has a typical $9 + 2$ arrangement (Manton and von Stosch, 1966; Heath and Darley, 1972). In *Pelagomonas* (Pelagophyceae), only the immature flagellum is present, and no remnant of the mature flagellum basal body is present (Andersen et al., 1993). A paraxonemal rod lies between the axoneme and immature flagellar membrane of some Dictyochophyceae, *Pelagomonas* (Pelagophyceae), and possibly diatom sperm (Heath and Darley, 1972; Zimmermann et al., 1984; Moestrup and Thomsen, 1990; Andersen et al., 1993; Sekiguchi et al., 2003). Paraxonemal rods are absent in other heterokont algae, but a similar rod is present in some dinoflagellates. In *Glossomastix* (Pinguiophyceae), the single flagellum was designated the mature flagellum, with the accompanying basal body identified as immmature (O'Kelly, 2002). In *Polypodochrysis* (Pinguiophyceae), a similar situation was found, but mature and immature structures were not identified (Kawachi et al., 2002c). In some members of Chrysophyceae, diatoms, Eustigmatophyceae, Pelagophyceae, Phaeothamniophyceae, and Xanthophyceae, flagellate stages are unknown.

The typical heterokont swimming cell has tripartite tubular hairs (= mastigonemes) arranged in two rows along the immature flagellum. The flagellum beat is sinusoidal, the hairs reverse the thrust of the flagellum, and therefore the beating flagellum pulls the cell forward (Sleigh, 1974, 1989). Members of Chrysophyceae and Synurophyceae have lateral fibers on the central shaft of the tripartite hair (e.g., Bouck, 1972; Andersen, 1989), but such lateral hairs are absent in all other heterokont algae. It may be worth noting that *Hemiselmis* (Cryptophyceae) also has short and long lateral filaments on its bipartite hairs (Bouck, 1972). In *Pelagomonas* (Pelagophyceae), hairs are bipartite, lacking the basal portion, but nevertheless, the hairs reverse thrust and swimming direction is unchanged (Andersen et al., 1993). There are no tripartite hairs on the emergent flagellum (whether designated mature or immature) of flagellate eggs of *Laminaria angustata* Kjellman (Phaeophyceae; Motomura and Sakai, 1988) or the zoospores of *Glossomastix* and *Polypodochrysis* (Pinguiophyceae); pinguiophyte zoospores glide along the substrate in amoeboid fashion (O'Kelly, 2002; Kawachi et al., 2002c). However, *Phaeomonas* (Pinguiophyceae) has typical tripartite tubular hairs on its immature flagellum (Honda and Inouye, 2002). The terms stramenopiles and stramenochromes have been applied to heterokont algae and their relatives (Patterson, 1989; Leipe et al., 1996), with both terms referring (strameno = straw) to tripartite flagellar hairs as a synapomorphic character. Stramenochromes is equal to heterokont algae, whereas stra-

menopiles includes heterokont algae, öomycetes, labyrithulids, thraustochytrids and certain biflagellate protozoa. The bipartite hairs of *Pelagomonas* and the hairless flagella of *Glossomastix* and *Polypodochrysis* are presumed to be derived conditions.

Flagella (or flagellum) are putatively "anchored" in the cell with various structures that are generally referred to as the flagellar root apparatus. In broad terms, the flagellar root apparatus consists of microtubular roots, striated roots, and a complex transitional region. Because of considerable variability among heterokont algae, it is difficult to designate a typical organization (Andersen, 1991).

Microtubular roots are found in swimming cells of all classes, except diatoms, Dictyochophyceae, and *Pelagomonas* (Pelagophyceae; Andersen, 1991; Andersen et al., 1993; Moestrup, 1995; Sekiguchi et al., 2003). These are designated R_1–R_4 (Andersen, 1987). The R_1 root typically consists of two to four microtubules and associated dense materials. It attaches to the basal body of the immature flagellum, and when viewed from the cell anterior, forms a clockwise arc around the anterior of the cell. In most groups, the arc consists of approximately 180 degrees (Andersen, 1991), but in Synurophyceae, R_1 forms a complete loop of 360 degrees (Andersen, 1985, 1989). In most organisms (Eustigmatophyceae excepted, see Santos and Leedale, 1991), R_1 nucleates numerous cytoskeletal microtubules that extend out and putatively form structural support for the cell (see Andersen, 1991). In some organisms (e.g., brown algae or phaeothamniophytes), a special set of cytoskeletal microtubules termed the bypassing rootlet, extend from the R_1 root past the basal bodies and into the central region of the cell (O'Kelly, 1989; Andersen et al., 1998b). The R_2 root typically consists of one to two microtubules that originate on the side opposite the immature basal body (with respect to the R_1 root) and probably terminates at or near the arc of the R_1 root (Andersen, 1991). This root is not always present. The R_3 root consists of approximately five to seven microtubules arranged in a trough or flat arrangement, and a layered structure is typically associated with microtubules. The R_3 root extends from the mature basal body and, when viewed from the cell anterior, curves in a counterclockwise arc (see Andersen, 1991). The length, curvature, and path for R_3 vary widely. For example, in the brown algal zoospores of *Laminaria*, the R_3 is short (O'Kelly, 1989), whereas in the phagotrophic chrysophyte *Epipyxis*, the R_3 forms a long, complex looping structure that is involved in the engulfing of bacteria (Andersen and Wetherbee, 1992). The R_4 microtubular root arises along the mature basal body opposite the R_3 root. The R_4 root is short, extending slightly away from but parallel to the mature basal body before terminating. Like the R_2 root, the R_4 root is apparently absent in many heterokont flagellates that possess microtubular roots.

A special striated flagellar root, also termed a rhizoplast, is found in swimming cells of Chrysophyceae, Eustigmatophyceae, Phaeothamniophyceae, Pinguiophyceae, Raphidophyceae, Synurophyceae, and Xanthophyceae (e.g., Hibberd, 1976, 1990a, b; Heywood, 1990; Andersen, 1991; Andersen et al., 1998b; Kawachi et al., 2002b). One end of this striated root lies along the nuclear envelope, and the other end is typically attached to proximal end of the immature basal body. However, in Synurophyceae, it attaches to both basal bodies (Andersen, 1985, 1989; Beech and Wetherbee, 1990b). The nucleus is positioned some distance from the basal bodies, and the striated root is probably contractile.

There has been no report of a rhizoplast-type striated root

in Bolidophyceae, diatoms, Dictyochophyceae, Pelagophyceae, Phaeophyceae, or Schizocladophyceae. Some Dictyochophyceae have a striated band that extends from the immature basal body to the nucleus, but because the nucleus is positioned against the basal bodies, it is unclear if this is a homologous structure (e.g., Koutoulis et al., 1988; Sekiguchi, 2003).

The transitional region of the flagellum, that area where the basal body connects to the flagellum, is also variable among heterokont algae (Preisig, 1989). A major transitional plate is found in all heterokont flagella, and in a few instances, a second transitional plate occurs. The major plate is located inside the nine pairs of microtubules so that it is distal to the third microtubule of the basal body triplets and proximal to the central two microtubules of the flagellar axoneme. There is a transitional helix above the major transitional plate in Chrysomerophyceae, Chrysophyceae, Eustigmatophyceae, Phaeothamniophyceae, Pinguiophyceae, Schizocladophyceae, and Synurophyceae; a double transitional helix occurs above the plate in Xanthophyceae. There is a transitional helix between major and minor plates in Dictyochophyceae, Pelagophyceae, and Pinguiophyceae. There is no report of a transitional helix of any kind in Bolidophyceae, diatoms, Phaeophyceae, and Raphidophyceae.

Haptophyte algae are biflagellate, but they completely lack tripartite tubular hairs. Pavlovophyceae sometimes have knob scales on the immature flagellum; these scales appear to reverse the thrust of the flagellum, thereby causing the cells to swim forward. Prymnesiophycae lack even knob scales, and when their flagella beat with a sinusoidal wave, the cells are pushed backward. However, these organisms can also beat their flagella using the ''breast stroke'' action, similar to the green alga *Chlamydomonas*, and with this flagellar beat pattern, the cell swims forward.

The microtubular flagellar roots of haptophytes resemble those of heterokont algae. Typically, Prymnesiophyceae have four microtubular roots that correspond to heterokonts with regard to origin and general path through the cell. Pavlovophyceae differ in that the immature flagellum lacks microtubular roots. The unique structure of haptophytes is the haptonema, a microtubule-supported appendage that extends forward between the two flagella. The function of the haptonema includes the capture of prey particles in mixotrophic and heterotrophic species (Kawachi et al., 1991), attachment to surfaces, and various other poorly documented roles (Inouye and Kawachi, 1994). A fibrous root extends from the immature basal body in *Pavlova*, but fibrous roots are apparently absent in Prymnesiophyceae. The transitional region of haptophytes contains one or more transitional plates, but typical heterokont-like transitional helices are absent. *Pleurochrysis* (Prymnesiophyceae) has a helix, but its structure is different (Beech and Wetherbee, 1988).

Mitosis—Mitosis is known only for a few heterokont and haptophyte algae, and these few examples vary considerably. In diatoms (see Green, 1989, for references) and most Chrysophyceae (e.g., *Ochromonas*, *Poterioochromonas*, *Uroglenopsis*; Slankis and Gibbs, 1972; Bouck and Brown, 1973; Schnepf et al., 1977; Tippit et al., 1980; Andersen, 1989), the nuclear envelope disperses during prophase. Spindle microtubules attach to either basal bodies (diatoms) or the striated flagellar roots (Chrysophyceae). However, in *Hydrurus* (Chrysophyceae), the nuclear envelope remains largely intact, with

openings at the poles (Vesk et al., 1984). *Pelagococcus* (Pelagophyceae; Vesk and Jeffrey, 1987), *Synura* (Synurophyceae; Andersen, 1989), and most Phaeophyceae (see Green, 1989, for references) behave similarly to *Hydrurus*. *Vaucheria* (Xanthophyceae) has an intact nuclear envelope at metaphase, and spindle microtubules form completely within the nuclear envelope (Ott and Brown, 1972). *Vacuolaria* (Raphidophyceae) is perhaps the most unusual situation, in which the nuclear envelope of daughter cells forms inside the dispersing old mother nuclear envelope (Heywood, 1990; Heywood and Leedale, 2002). Mitosis has not been reported for Bolidophyceae, Chrysomerophyceae, Dictyochophyceae, Eustigmatophyceae, Phaeothamniophyceae, Pinguiophyceae, and Schizocladophyceae. Among haptophytes, mitosis has been described for *Pavlova* (Pavlovophyceae) as well as for *Emiliania*, *Chrysochromulina*, *Imantonia*, *Isochrysis*, *Pleurochrysis*, and *Prymnesium* (Prymnesiophyceae; Manton, 1964; Stacey and Pienaar, 1980; Hori and Inouye, 1981; Hori and Green, 1985a, b, c; Green and Hori, 1988; Green et al., 1989). The spindle is U- or V-shaped in *Pavlova* but is straight in Prymnesiophyceae. In general, the nuclear envelope disperses during prophase but is often replaced with rough ER during metaphase; see Green (1989) and Hori and Green (1994) for further details.

Other ultrastructural features—All heterokonts and haptophytes have mitochondria with tubular cristae (Taylor, 1976; Stewart and Mattox, 1980). Heterokont algae have typical Golgi bodies, and in most classes (Dictyochophyceae excepted), Golgi bodies are anterior to the nucleus, with cis-cisternae adjacent the nuclear envelope (e.g., Hibberd, 1976). Haptophytes typically have Golgi bodies that are anteriorly adjacent the nucleus, but they are oriented at 90° so that the cis-trans axis lies parallel to the nuclear envelope (e.g., Manton, 1967). Furthermore, cisternae are unusually inflated. Brown algae often contain numerous vesicles of phenolic-type compounds, and these structures are referred to as physodes. Mucocysts are common in Raphidophyceae (Heywood, 1990; Heywood and Leedale, 2002), and various mucosal vesicles occur in some members of Chrysomerophyceae (Billard, 1984) and Chrysophyceae (e.g., Hibberd, 1970; Mignot, 1977; Andersen, 1982). Haptophytes are characterized by a peripheral endoplasmic reticulum, which lies just beneath the plasmalemma in most areas of the cell (flagellar region excluded; e.g., Hibberd, 1976; Beech and Wetherbee, 1988). It has been suggested that the peripheral endoplasmic reticulum of haptophytes is homologous to alveoli of ciliates, amphiesmal vesicles of dinoflagellates, the inner membrane complex of apicomplexans, the periplast of cryptophytes, and possibly mucosal structures of heterokont algae (Daugbjerg and Andersen, 1997b; Cavalier-Smith, 2002; Andersen, 2004). If these are truly homologous structures, they would be a synapomorphic character for chromalveolates.

Phylogenetic relationships—Phylogenetic relationships of heterokont algae are still largely unresolved. Light microscopy provided few characters that could be used, and the one dominating relationship, Pascher's (1914) division Chrysophyta (classes Bacillariophyceae sensu lato, Chrysophyceae and Xanthophyceae) was quickly demolished when electron microscopy reached widespread use. Cladistic analyses were attempted (e.g., Hibberd, 1979; Lipscomb, 1989; Andersen, 1991; Williams, 1991), but these suffered from a lack of

knowledge of homologous structures. Molecular phylogenetic analyses have made some progress. An early study showed that a heterokont alga was related to an öomycete fungus (Gundersen et al., 1987), bringing further support to a growing consensus that photosynthetic and nonphotosynthetic heterokonts formed a clade (e.g., Cavalier-Smith, 1986). Another early study showed that Xanthophyceae and Phaeophyceae were closely related, as were Chrysophyceae and Synurophyceae; however, the two clades were unrelated (Ariztia et al., 1991). These molecular data provided perhaps the final evidence that Pascher's Chrysophyta was not a natural group. A total evidence approach, using ultrastructural, biochemical, and molecular data, showed that Dictyochophyceae and Pelagophyceae were closely related to each other but distantly related to Chrysophyceae in which species of the former two classes were once classified (Saunders et al., 1995). Furthermore, this study indicated that these classes may be related to diatoms, forming a clade of organisms with reduced flagellar apparatuses. One subsequent total evidence analysis also provided support for this idea (Sorhannus, 2001). To date, molecular phylogenetic analyses including most or all heterokont algal classes have been based on either the 18S rRNA or the *rbcL* gene. Other genes have been examined, e.g., the fucoxanthin/chlorophyll photosystem-I- and -II-binding proteins (Caron et al., 1996; Green and Durnford, 1996), the alpha-tubulin gene (Keeling and Doolittle, 1996), large subunit (LSU) rRNA gene (Van der Auwera and De Wachter, 1996; Ben Ali et al., 2001), the GAPDH gene (Fast et al., 2001; Harper and Keeling, 2003), plastid *psaA*, *psbA*, 16S rRNA, *rbcL* and *tufA* genes (Medlin et al., 1997; Yoon et al., 2002a, b), and the type II fatty acid synthetase gene (Ryall et al., 2003). However, in all cases, taxon sampling was limited, omitting most heterokont algal classes and often including only one to three taxa for classes that were studied.

Two recent studies have combined these more extensively sampled genes (SSU rRNA, *rbcL*; Sorhannus, 2001; Goertzen and Theriot, 2003), and the Sorhannus study also included partial LSU rRNA, ultrastructural, and biochemical data. From these two studies, as well as many other studies that separately examined SSU rRNA and *rbcL* sequences, a few consensus relationships can be identified. Three two-class clades, Chrysophyceae/Synurophyceae, Dictyochophyceae/Pelagophyceae, Bolidophyceae/diatoms, are always recovered. However, there is weak support (e.g., <50% bootstrap values) and no consensus regarding relationships among these pairs of classes. Phaeophyceae and Xanthophyceae are closely related, but when taxa of Chrysomerophyceae, Phaeothamniophyceae, and Schizocladophyceae are added, the Phaeophyceae/Xanthophyceae relationship is weakened or disrupted (e.g., Bailey et al., 1998; Kawai et al., 2003). Eustigmatophyceae, Pinguiophyceae, and Raphidophyceae have no clear relationship among themselves or with other heterokont classes (e.g., Potter et al., 1997; Andersen et al., 1998a; Kawachi et al., 2002b). Figure 25 illustrates a phylogenetic tree constructed from a combined analysis of SSU rRNA and *rbcL* genes from heterokonts, haptophytes, alveolates, cryptophytes, and rhodophytes. This tree is poorly resolved when compared to trees from a *rbcL* gene only analysis (not shown), but the nonphotosynthetic taxa cannot be included in the *rbcL* analysis.

The two classes of haptophyte algae have a sister relationship in phylogenetic analyses (e.g., Edvardsen et al., 2000), but the relationship of Haptophyta to other protists is unresolved in SSU rRNA and *rbcL* phylogenetic analyses. How-
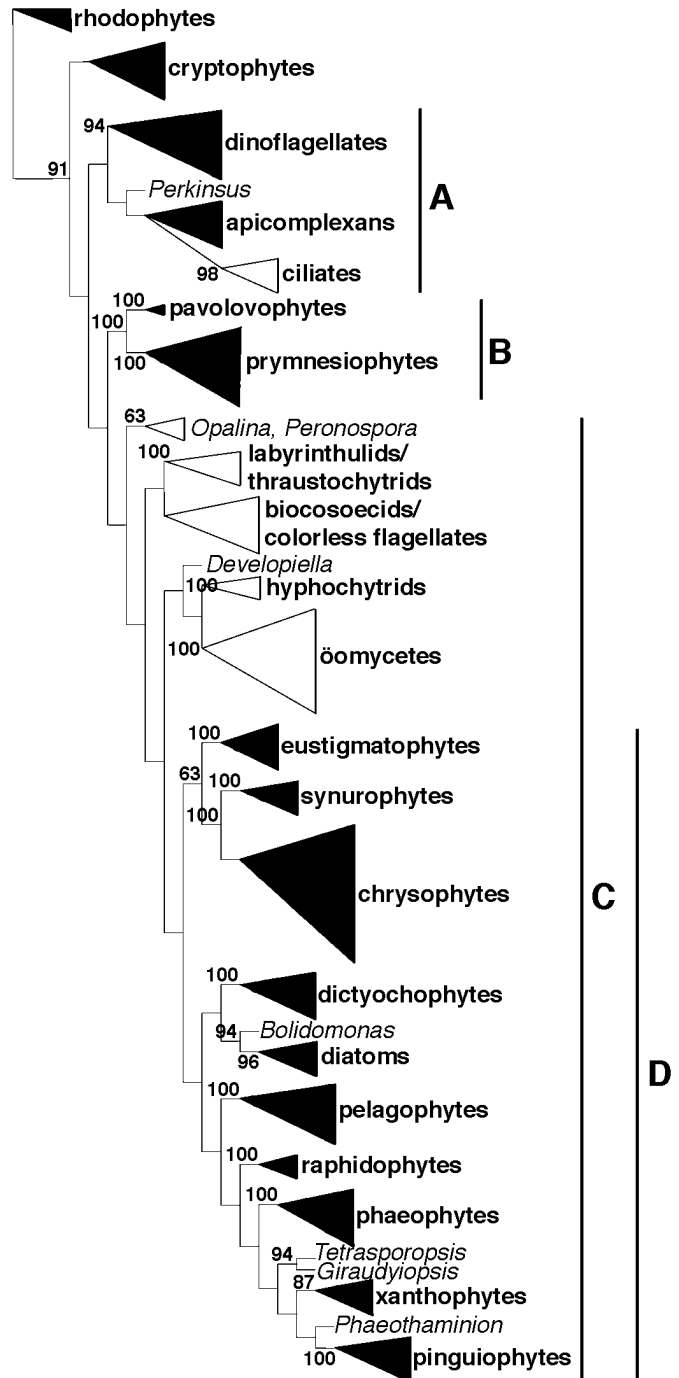

Fig. 25. Single most parsimonious tree (one of three) from a mixed (nucleotide and amino acid) TNT (Tree Analysis using New Technology, version 1.0, by Goloboff, Farris and Nixon, website: http://www.cladistics.org/downloads/webtnt.html) analysis of the concatenated SSU rRNA and *rbcL* genes. Most SSU rRNA sequences were obtained in an aligned form from the European Ribosomal RNA Database (website: http://www.psb.ugent.be/rRNA/index.html); a few additional taxa (e.g., Pinguiophyceae and Phaeothamniophyceae) were added and aligned by eye. The *rbcL* genes were primarily obtained from GenBank; a few Chrysophyceae were from our laboratory. The *rbcL* gene was converted from nucleotides to amino acids. 1000 bootstrap replicates were conducted and the percentage support is shown for all nodes with >50% support. A = alveolate taxa, B = haptophyte taxa, C = all heterokont taxa, and D = heterokont algae. Triangle height is proportional to number of taxa. Solid triangles represent groups with taxa known to possess plastids.

ever, recent studies using other genes, albeit with limited taxa and few classes, are beginning to support a chromalveolate assemblage. That is, Cryptophyceae, Haptophyta, alveolates (dinoflagellates, ciliates, apicomplexans), and heterokont algae are perhaps related, but the branching order is still unclear (e.g., Fast et al., 2001; Yoon et al., 2002a, b; Harper and Keeling, 2003; Ryall et al., 2003). The geological time for the origin of the chromalveolates was placed at 1300 million years ago (Yoon et al., 2004).

Nonpigmented heterokonts are close relatives of heterokont algae, but no details are provided here. Blackwell and Powell (2000) provided an excellent review. Some nonpigmented flagellates are described by Moestrup (2002) and Patterson (2002).

Unity and diversity—Heterokont and haptophyte algae share the following features: mitochondria with tubular cristae; an extraplastidal carbohydrate storage product consisting of short β-1,3-linked glucan chains; a plastid with three adpressed thylakoids internally and two endoplasmic reticulum membranes externally; photosynthesis predominating; most organisms with chlorophylls *a* and *c*. These features are also shared by a number of other protist groups and therefore cannot be considered synapomorphic characters. Heterokont algae are united only by the presence of tripartite tubular hairs on the immature flagellum. This feature is shared with nonphotosynthetic heterokonts and perhaps the bipartite hairs of cryptophytes. Unifying morphological characters define heterokont algal classes, but establishing homologous characters has been difficult, restraining efforts to establish phylogenetic relationships among classes. Molecular analyses, based upon one to a few genes, have indicated some phylogenetic relationships, but considerably more molecular and morphological advances will be required before consensus is reached on their broad phylogenetic relationships. Similarly, the pendulum continues to swing regarding opinions about the relationship between haptophyte and heterokont algae. The uncertain phylogenetic relationships for other related protistan groups (e.g., alveolates, cryptophytes, cercozoans) confound the problem.

Despite our limited knowledge about their phylogenetic relationships, the heterokont algae are certainly a large and diverse group of living organisms. There are many species of diatoms, with estimates of up to a million or more species yet to be described (Round et al., 1990). Heterokont algae range in size from eustigmatophyte and pelagophyte picoplankters (~1 μm) to brown algal kelp (100 m in length). Cell coverings include cellulosic walls, glass walls, organic and mineralized scales, organic and mineralized loricas, and gelatinous substances. The flagellar apparatus is highly variable, to the point that homologous structures are difficult to establish. Similarly, haptophyte algae are diverse, although more fossil species are known than living species. Conversely, Schizocladophyceae contains a single species, and Bolidophyceae, Chrysomerophyceae, Eustigmatophyceae, Pinguiophyceae, and Raphidophyceae have fewer than 25 described species. At present, it is unclear whether these classes are ancient and consist of a few remnant species or if they are newly evolved groups that have not yet radiated.

Although studies in nuclear genes have been initiated (e.g., Fast et al., 2001; Yoon et al., 2002a, b; Harper and Keeling, 2003; Ryall et al., 2003; Yoon et al., 2004), a greater use of multiple nuclear genes in a wide range and large number of photosynthetic and nonphotosynthetic heterokonts and hapto-

phytes is necessary for a better understanding of their evolutionary relationships. This task will require substantial work because there are many classes of heterokont algae, and the nonalgal heterokonts are equally challenging. Phylogenetic relationships of heterokont and haptophyte algae are fertile ground that has been barely scratched, and much exciting work remains in this diverse group.

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