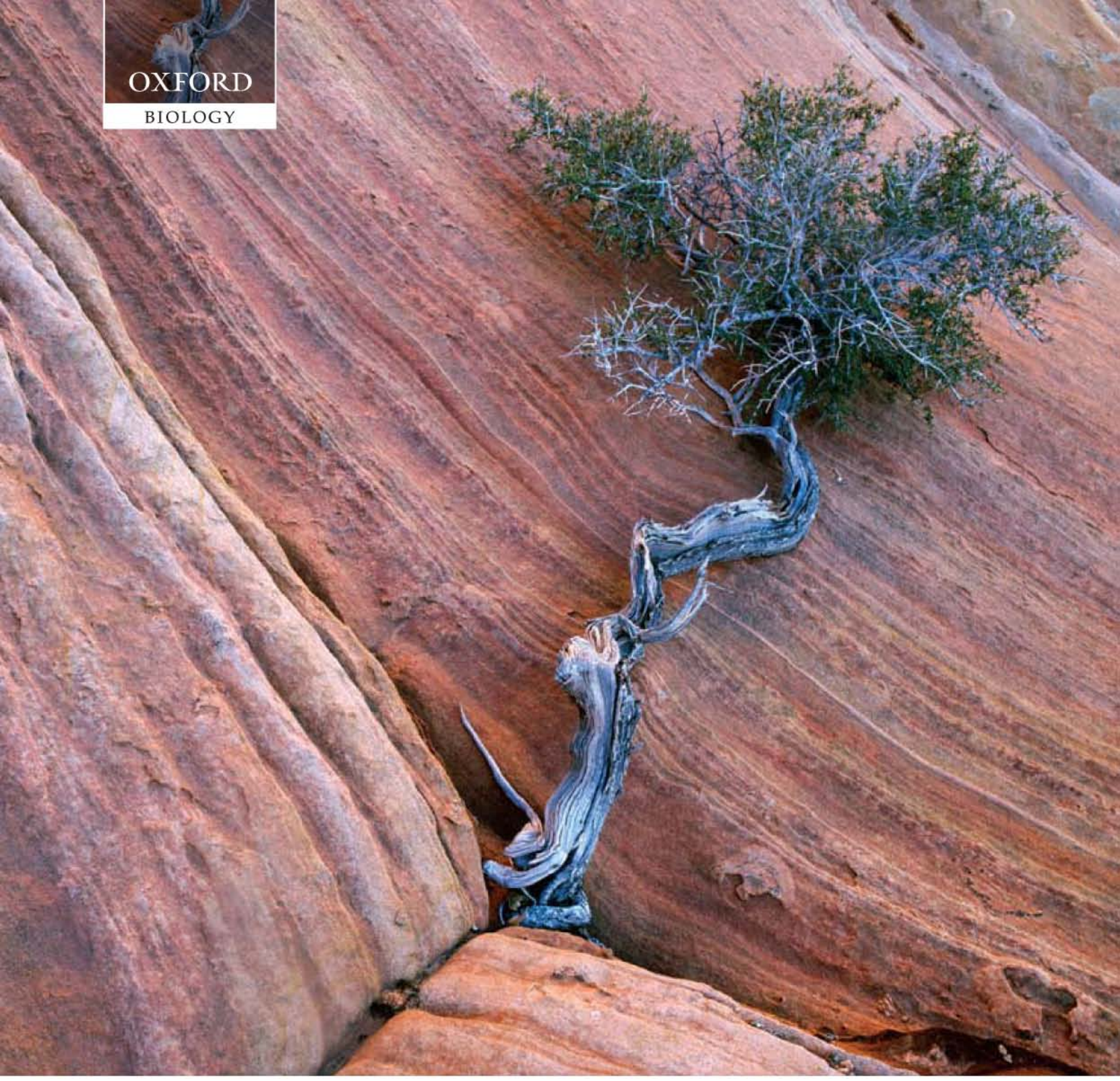

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Haptophyte algae (Haptophyta)

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Abstract

Haptophytes are members of the marine phytoplankton involved in many important biochemical cycles. They possess two smooth flagella and another organelle, called a haptonema inserted between the flagella. The cells are covered by organic scales, which are calcified in one order, the Coccolithales, permitting molecular clock calibration. Time estimates place the divergence of the two classes in the Neoproterozoic, ~800 million years ago (Ma), with order-level diversification occurring in the Phanerozoic, ~340–120 Ma. Selective survival of different orders across major extinction events may be related to the ability of the cells to switch their mode of nutrition from autotrophy to mixotrophy.

Haptophytes (Fig. 1) occur in all seas and are often major components of the nanoplankton (*1, 2*). They are important primary producers, and some species in the genera *Emiliania*, *Gephyrocapsa*, *Phaeocystis*, *Chrysochromulina*, and *Prymnesium* may form extensive blooms with major biogeochemical, ecological, or economic impact. Most species are marine, but a few thrive in freshwater. Most are unicellular, planktonic biflagellates, but palmelloid, coccoid, amoeboid, colonial, and benthic forms also occur (*3*). Nearly all are photosynthetic, but phagotrophy and mixotrophy appears to be common in some genera (e.g., *Chrysochromulina*) (*4*). In most species, at least one stage in their haplo-diplont life cycle possesses two flagella that are similar in form and have no tubular hairs. Between the flagella is a unique organelle, called a haptonema, which differs structurally from the flagellum. Its length varies and it has been secondarily lost in some species. It can coil or bend, but not beat, and can attach to a substratum and may be involved in food handling. Cells are typically covered by one to several layers of organic scales and in the coccolithophorids these are calcified. These are preserved and constitute the feature that leaves a fossil record for calibration of a molecular clock. Species identification within Haptophyta is largely based on scale morphology and often requires electron microscopy.

Two molecular clocks have been made for the haptophytes by Medlin and her coworkers: a strict molecular clock using the Lintree program that averages the rate of evolution across all lineages (*5, 6*) and a relaxed molecular clock (r8s) where the rate of evolution is allowed to vary across the lineages (*7, 8*). Both clocks were calibrated using at least three calibration points from the coccolith fossil record: the character-based constraint of 195 Ma for the emergence of all coccolithophores, and the divergence-based constraints of 64 Ma for the divergence of *Coccolithus* from *Cruciplacolithus* and

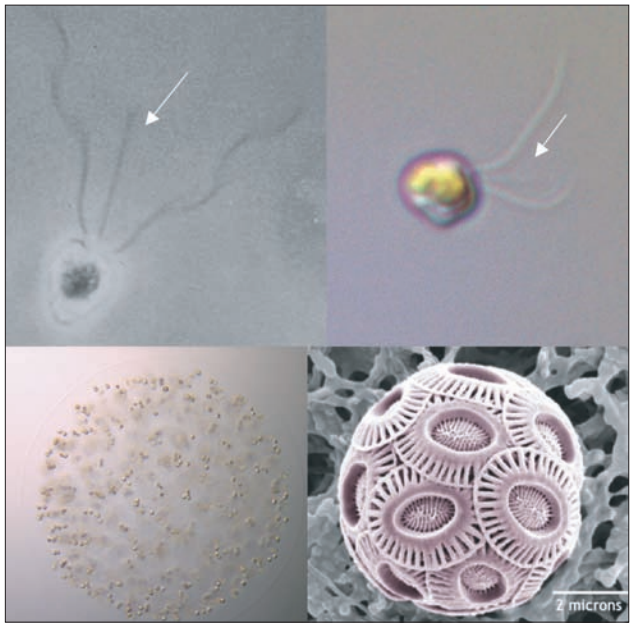

Fig. 1 *Chrysochromulina* (Prymnesiales) with arrow indicating long haptonema (upper left), *Phaeocystis* (Phaeocystales) with arrow indicating short haptonema (upper right), colony of *Phaeocystis antarctica* (lower left), and coccolithophore *Emiliania huxleyi* (lower right). Credits: W. Eikrem (upper left), L. K. Medlin (upper right and lower left), and J. Green (lower right).

L. K. Medlin. Haptophyte algae (Haptophyta). Pp. 123–126 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

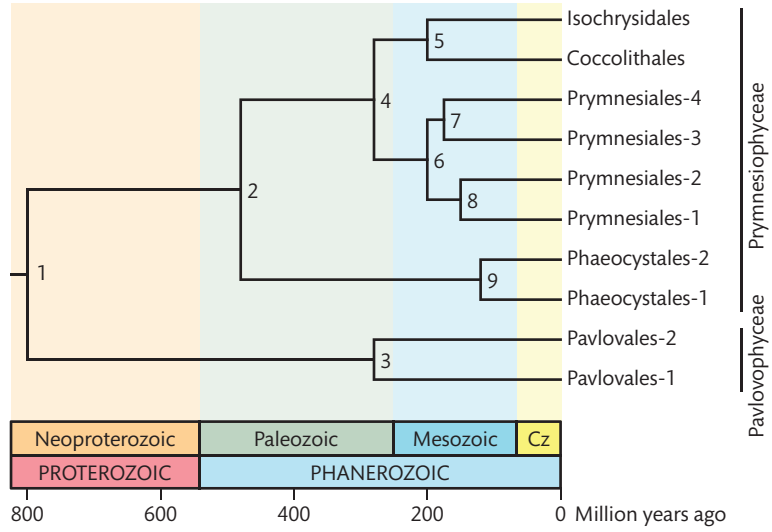

Fig. 2 A timetree of Haptophyta. Divergence times are shown in Table 1. Pavlovales-1 = *Exanthemachrysis* with pigment type A (*15*); Pavlovales-2 = *Pavlova* and *Diacronema* with pigment type B and C (*15*); Phaeocystales-1 = unicellular *Phaeocystis* sp. (*6*); Phaeocystales-2 = colonial *Phaeocystis* sp. (*6*); Prymnesiales-1 = Clade B2 saddle-shaped *Chrysochromulina* sp. including *C. parva*; Prymnesiales-2 = Clade B2 other saddle-shaped *Chrysochromulina* sp.; Prymnesiales-3 = Clade B1 *Imantonia* sp. and OLI clones; and Prymnesiales-4 = Clade B1 round, not saddle-shaped *Chrysochromulina* sp., *Prymnesium* sp., and *Platychrysis* sp. Details of species in each clade are presented elsewhere (*1*). *Abbreviation*: Cz (Cenozoic).

50 Ma for the divergence of Helicosphaeraceae from Pontosphaeraceae. We have constructed a molecular clock from the small subunit ribosomal RNA (SSU rRNA) gene and extrapolated dates for some of the undated nodes where there is no fossil evidence. The SSU rRNA tree appears to be evolving in a clocklike manner as judged by the relative rate tests performed in addition to the use of the Lintree program (*9*). Another molecular clock study of haptophytes has been done, using the SSU and large subunit (LSU) rRNA genes (*10*). Dates for the divergences in that study are slightly older than those found by Medlin and coworkers using a relaxed molecular clock (*8*).

Although not treated in detail here, Haptophyta is a group that diverged from other eukaryotes deep in the Proterozoic, >1200 Ma (*9–11*). The long time period between the origin of haptophytes and the initial divergence (~800 Ma) of the two classes, Pavlovophyceae and Prymnesiophyceae (Table 1, Fig. 2), indicates that many of the early evolutionary branches in this group are extinct, or that they have not yet been sampled (*2*). The Order Phaeocystales diverged from all other Prymnesiophyceae at ~480 Ma and then the Prymnesiales diverged from the Coccolithales plus Isochrysidales at ~280 Ma, and thus this divergence appears to be a late Paleozoic–early Mesozoic event and may be associated with the Permian–Triassic boundary (251 Ma). Modern diversifications in these lineages occurred some time after the lineage origin so many taxa were presumably lost during this time.

Within the Order Phaeocystales, the divergence of the cold water clades from the warm water clades occurs at 30 Ma, when the Drake Passage opened to isolate the Antarctic Continental waters, and dispersal to the Artic occurred across the equator during a cooling trend at 15 Ma, which were separated by a warming trend that then isolated the two polar clades (*6*).

Molecular diversification occurred earlier within the Prymnesiales than within the Coccolithales plus Isochrysidales where most of these latter divergences occurred fairly late in the haptophyte timetree (Fig. 2). The diversification within the Coccolithales plus Isochrysidales occurred predominantly after the Mesozoic–Cenozoic boundary (66 Ma), as predicted by the fossil record. Mesozoic coccolithophores have been intensively studied and at the Mesozoic–Cenozoic boundary an abrupt extinction is documented in the fossil record with ~90% of end-Cretaceous species disappearing (e.g., *12, 13*). Subsequently, there was a major

Table 1. Divergence times among haptophytes.

Timetree		Estimates			
Node	**Time**	**Ref. (*8*) Time**	**Ref. (*9*) Time**	**Ref. (*10*)(a) Time**	**Ref. (*10*)(a) Time**
1	800	800	500	870	1000
2	480	480	200	400	290
3	280	280	–	300	330
4	280	280	–	300	210
5	200	200	–	250	150
6	200	200	–	180	150
7	175	175	–	–	–
8	150	150	–	–	–
9	120	120	–	–	–

Note: The node times in the timetree are based on ref. (*8*). Estimates from ref. (*10*) are based on (a) SSU rRNA and (b) LSU rRNA analyses.

radiation in the early Cenozoic with new clades rapidly diversifying and forming the origins of the modern coccolithophore biota (e.g., *14*).

One novel inference from our molecular tree is that the Mesozoic–Cenozoic boundary extinction does not seem to have affected the Prymnesiales, Phaeocystales, or Pavlovales to the same degree as the Coccolithales. These orders do not have a fossil record so we can only make this statement by comparing the depth of clade diversification. In each of these noncalcifying groups, there are numerous clades/lineages that cross the Mesozoic–Cenozoic boundary (*8*). There is no evidence of major diversification of these clades in the Cenozoic. On this basis, one would expect that the noncalcified haptophytes would have the same rate of extinction as the calcified ones, because no group produces resting stages, although some species have benthic littoral to sublittoral stages as part of their dimorphic life cycle. No haptophytes are known to produce specialized resting cells or zygotes analogous to dinoflagellate cysts or diatom resting spores. There is no evidence of bottlenecking in the noncalcified taxa at this time, as illustrated by the many clades with deeper divergences (Fig. 2).

One possible explanation for this difference in their survival may lie in the mode of nutrition in the haptophyte lineages. The noncalcifying haptophytes are known for their ability to switch between autotrophic and heterotrophic nutrition (*3*). Thus, when nutrients are plentiful, they photosynthesize. However, when the reverse is true, they engulf prey and survive heterotrophically. At the Mesozoic–Cenozoic boundary, it is likely that light quality was reduced and photosynthetic ability was impaired. Therefore, those taxa with either the ability to form resting stages, such as the diatoms and the dinoflagellates, or the ability to switch their mode of nutrition could have an adaptive advantage over those that did not have either of these traits. Coccolithophores are not known to form resting stages, in the strictness sense, and it appears that they are predominantly obligate autotrophs. Thus, at the Mesozoic–Cenozoic boundary, the stress induced by reduced light quantity and quality could have shut down photosynthesis. Cells that could switch nutrition or form resting stages would have had a better chance of survival.

In summary, the haptophytes are a major eukaryotic group of microalgae whose closest relative is unclear. The initial class level divergence occurred in the Neoproterozoic and divergence of the orders appears to be associated with the Permian–Triassic boundary. Because this is a host lineage with a red algal plastid, it is likely that the group radiated at the Permian–Triassic boundary when the ocean chemistry changed to give the red algal plastid an adaptive advantage over host cells with a green algal plastid, which were common in the plankton before the end Permian. There appears to be a selective extinction of the Order Coccolithales at the Mesozoic–Cenozoic boundary where calcified organisms were affected by ocean chemistry, and the uncalcified

lineages likely switched to mixotrophy to take advantage of the poor light conditions at this extinction event.

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