

## Complicated family relationships, or about taxonomic problems in the family Pyrenomonadaceae (Cryptophyceae)

by

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### Abstract

Cryptophytes, to which the Pyrenomonadaceae family belongs, are interesting organisms that occur almost all over the world and they are an important element of trophic chains in many ecosystems. The development of research methods and techniques, including electron microscopy and molecular studies, allowed for a better understanding of taxonomic relationships in this group of organisms. The Pyrenomonadaceae family currently includes three genera: *Rhodomonas*, *Rhinomonas*, and *Storeatula*, but their validity is being debated in the light of the latest data. The state of knowledge and the problems faced in the taxonomic revision of this family of cryptophytes are summarized in this article.

**Key words:** Algae, cryptophytes, Pyrenomonadaceae, *Rhodomonas*, *Rhinomonas*, *Storeatula*, taxonomy, dimorphism

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## 1. Introduction

Cryptophytes are a relatively small but widespread group of organisms considered either algae or protists due to the fact that they include both photoautotrophic and heterotrophic species. Photosynthetic species have chlorophyll *a* and *c*<sub>2</sub> and highly modified biliproteins, phycoerythrin or phycocyanin. They are found worldwide in various types of water bodies, from saltwater oceans to freshwater puddles (e.g. Borics et al. 2003, Hoef-Emden & Archibald 2017, Javornický & Hindák 1970, Klaveness 1988, Kugrens et al. 1999, Lane & Archibald 2008, Lepistö & Holopainen 2003). They are an important component of aquatic ecosystems because they are a food source for many planktonic organisms (Brown et al. 1997, Sheng et al. 2010, Yih et al. 2004).

These microscopic organisms are unicellular flagellates (Fig. 1), whose size varies depending on the species, ranging from about 3 µm in the representatives of the genus *Hemiselmis* to about 50 µm in *Cryptomonas curvata* (campylomorphic form, which is one of the alternative morphotypes in *Cryptomonas* species, as described by Hoef-Emden & Melkonian 2003). The asymmetrical shape of the cell and the peculiar way of moving with the help of two flagella of different lengths usually makes it easy to distinguish cryptophytes from other planktonic organisms. They also have a gullet or a furrow (or a combination of both), which is lined with coiled, ribbon-shaped organelles, called ejectosomes that are ejected under mechanical or chemical stimulus (Morrall & Greenwood 1980). Cryptophytes are characterized by a unique and complex cell structure, with a vestigial endosymbiont nucleus (nucleomorph), making them the focus of studies on the evolution of organisms (Curtis et al. 2012, Douglas et al. 2001, McFadden 2017, Tanifuji & Archibald 2014, Zauner et al. 2019). Cryptophyte cells are surrounded by a periplast, a proteinaceous structure that envelopes the cell membrane. The outer layer of the periplast (surface periplast component, SPC) can be made up of fibrils, individual plates or rosette-like scales, while the inner periplast (inner periplast component, IPC) is smooth or made up of plates of various shapes (polygonal, hexagonal or rectangular).

## 2. Taxonomic identification of cryptophytes

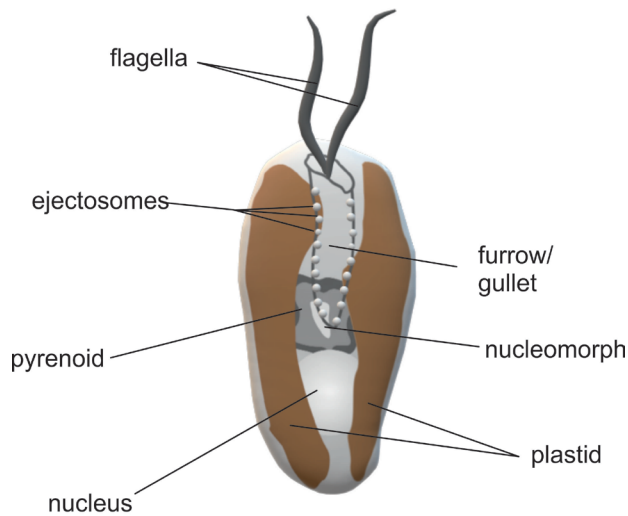
Since cryptophytes were first described by Ehrenberg (1831), about 200 different taxa have been reported (Guiry & Guiry 2022, Hoef-Emden et al.

2002). However, their number is probably severely underestimated (although at the genus level the taxa number might be reduced as a result of the problems discussed in this paper), and the systematics of this group has changed and continues to change with the development of research methods and techniques. Initially, cryptophytes were identified and described solely on the basis of morphological features visible by light microscopy. One of the first scientists to propose a classification system for cryptophytes was Pascher, who distinguished groups of cryptophytes based on their ability to move and the position of their flagella (Pascher 1913). Later, cryptophytes were classified based on various factors, such as nutrition type (Pringsheim 1944), the presence of a furrow or gullet (Butcher 1967), or ultrastructural features visible using electron microscopy, such as the presence of a nucleomorph, its position, flagella attachment, or periplast type (Kugrens et al. 1999, Novarino & Lucas 1993, Santore 1984). A summary of all of the classification systems was prepared by Novarino (2012).

The study of cryptophytes advanced with the use of molecular methods for taxonomic purposes, as it became clear that relying solely on morphological and ultrastructural traits was insufficient for species characterization. Phylogenetic analyses revealed that clonal cultures with diverse morphologies could have identical or nearly identical DNA sequences, whereas morphologically similar cultures could represent different species genetically (Deane et al. 2002, Hoef-Emden et al. 2002, Marin et al. 1998). The discovery of dimorphism in some members of this group further complicated the already uncertain taxonomic classification of cryptophytes (Altenburger et al. 2020, Hill & Wetherbee 1986, Hoef-Emden 2007, Hoef-Emden & Melkonian 2003, van den Hoff et al. 2020).

Throughout the years, the understanding of the phylogenetic relationships and species affiliation of cryptophytes was organized using integrative taxonomy (Dayrat 2005), which combines microscopic techniques like light and electron microscopy with molecular analysis. Currently, the following clades are distinguished within the cryptophyte group: *Cryptomonas*, *Chroomonas/Komma/Hemiselmis*, *Rhodomonas/Rhinomonas/Storeatula*, *Guillardia/Hanusia*, *Geminigera/Plagioselmis/Teleaulax*, *Proteomonas sulcata*, *Falcomonas daucoides*, *Urgorri complanatus*, *Goniomonas*, *Hemiarma marina*, *Baffinella frigidus* (see summary in Łukaszek 2017). However, not all the listed clades contain monophyletic genera, as exemplified by the *Rhodomonas/Rhinomonas/Storeatula* clade, namely the family Pyrenomonadaceae.



**Figure 1**

A model of a cryptophyte cell

### 3. "Red" cryptophytes – family Pyrenomonadaceae

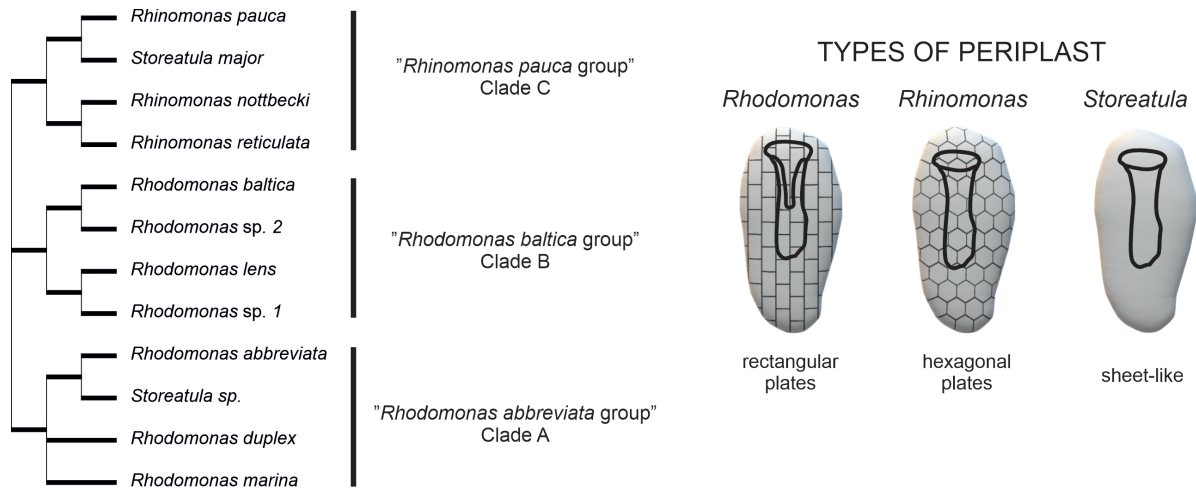
The Pyrenomonadaceae family includes three genera: *Rhodomonas* Karsten (syn. *Pyrenomonas* Santore), *Rhinomonas* Hill et Wetherbee and *Storeatula* Hill (Clay 2015, Clay et al. 1999, Guiry & Guiry 2022). They are widely distributed but mostly found in marine environments, with only a few species occurring in freshwater. These algae play a crucial role in the food chain in many aquaculture systems, being a direct source of food for bivalves, and the larval and juvenile stages of fish and crustaceans. They are also used for feeding, or enriching the cultures of copepods, rotifers or *Artemia*, which in turn are the main food in the cultures of many marine larval stage species (e.g. Brown et al. 1997, Koski et al. 1998, Seixas et al. 2009, Tremblay et al. 2007). They are considered a particularly valuable food due to the content of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) in their cells (Nogueira et al. 2021, Oostlander et al. 2020, Peltomaa et al. 2018, Seixas et al. 2009).

Common features that distinguish the Pyrenomonadaceae family include the presence of a specific type of biliprotein – Cr-phycoerythrin 545, a bilobed plastid with a pyrenoid in a starch envelope and a nucleomorph "submerged" in the pyrenoid space (see Fig. 1).

### 4. Taxonomic problems concerning the family Pyrenomonadaceae

The first of the genera belonging to the Pyrenomonadaceae family is *Rhodomonas*, which was first used by Karsten (1898) to describe *Rhodomonas baltica*, a red-coloured marine cryptophyte. Since then, nearly 30 taxa have been assigned to the genus (Guiry & Guiry 2022), both marine and freshwater. However, over time, with the development of research methods, it became apparent that cell colour was not a reliable taxonomic trait (Pringsheim 1944, 1968), and the validity of maintaining the taxon and its name was debated for years to come (Butcher 1967; Hill & Wetherbee 1989; Novarino 1991, 2003; Pringsheim 1944; Santore 1984). For example, Butcher (1967) proposed a new classification system for cryptophytes that was based on furrow/gullet morphology, rejecting cell colour as a taxonomic trait. Later studies showed that biliprotein type (rather than cell colour) was the reliable diagnostic criterion (Glazer & Wedemayer 1995, Hill & Rowan 1989, Hoef-Emden 2008), and Butcher's classification was revised, but it still causes some confusion in naming the cultures of these organisms (especially in older literature or culture collections). Santore (1984) argued that the name *Rhodomonas* should be withdrawn because it refers to the red colour of the cells, and the description of the genus does not contain details to critically distinguish representatives of this taxon, so he proposed a new genus *Pyrenomonas* (Santore 1984). A few years later, Hill and Wetherbee (1989) revised the genus *Rhodomonas* again, based on light and electron microscopy, highlighting several defining features such as the presence and varying lengths of furrow/gullet, rectangular plates in the IPC (Fig. 2), a pyrenoid surrounded by a distinctive starch sheath, thylakoids that do not penetrate the pyrenoid matrix, and a nucleomorph located in the periplastidal space. Both names have since appeared in the literature, but function as synonyms. Two other taxa in the Pyrenomonadaceae family, namely *Storeatula* and *Rhinomonas*, share similar ultrastructural features to *Rhodomonas*, except for IPC. *Rhinomonas* is distinguished by an IPC composed of hexagonal plates, while *Storeatula* has a smooth IPC, with both genera lacking a furrow (Fig. 2) (Clay et al. 1999).

Similar to the rest of the cryptophytes group, molecular research has brought new insights into the classification of the Pyrenomonadaceae family. Early phylogenetic analyses showed that different clonal cultures of cryptophytes, characterized by unique types of periplast, do not form separate clades (e.g. Deane et al. 2002, Hoef-Emden et al.

**Figure 2**

Schematic phylogeny of the Pyrenomonadaceae family after Majaneva et al. (2014) showing that it comprises three clades with a mixture of genera with ultrastructural differences in the inner periplast component.

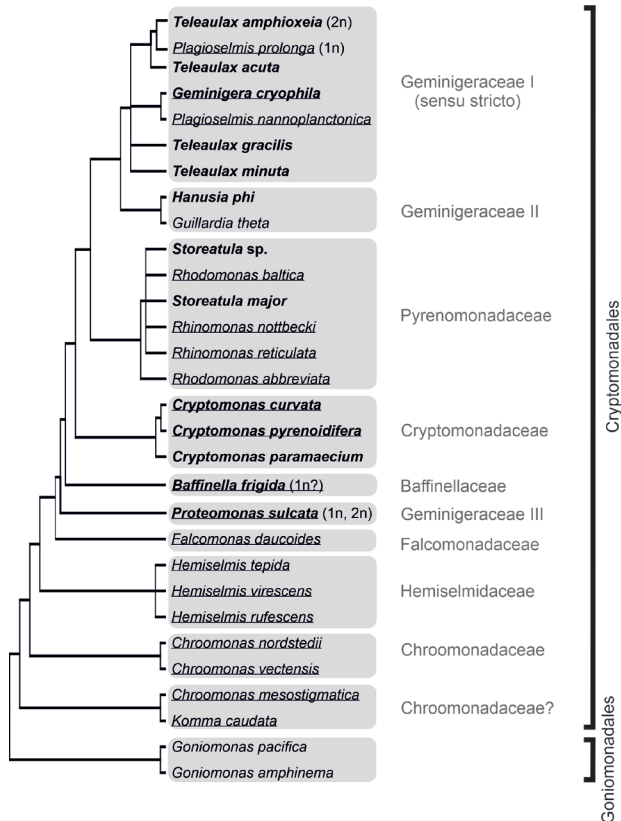
2002). Phylogenies confirmed the monophyly of the Pyrenomonadaceae family, but the most abundant genus *Rhodomonas* grouped also with representatives of *Rhinomonas* and *Storeatula* (Deane et al. 2002, Hoef-Emden et al. 2002, Lane et al. 2006, Novarino & Lucas 1993, Shalchian-Tabrizi et al. 2008).

Majaneva et al. (2014, 2016) conducted a phylogeny of the Pyrenomonadaceae family upon discovering a new species, *Rhinomonas nottbecki*. The analysis found the *Rhinomonas* clade to be monophyletic, but the genus *Rhodomonas* to be paraphyletic, split into two clades, the *R. baltica* and *R. abbreviata* groups. Notably, sequences of *Storeatula* appeared in both the *Rhinomonas* and *R. abbreviata* clades (Fig. 2), as previously noted by Deane et al. (2002), Hoef-Emden et al. (2002), Lane et al. (2006), and Shalchian-Tabrizi et al. (2008). Majaneva et al. (2014) suggested that difficulties in classifying taxa in this group may have arisen from three factors: reliance on questionable morphological characters, insufficient sequencing for phylogenetic analyses, and potential dimorphism. During their work, the authors utilized molecular data to confirm morphological differences and included more taxa in the phylogenetic analysis. However, the occurrence of dimorphism remains only a hypothesis.

The phenomenon of two morphotypes in the life cycle was first documented in the cryptophyte *Proteomonas sulcata* by Hill & Wetherbee (1986). In clonal cultures of this organism, two distinct cell types were observed and described as haploid and diploid forms, based on microspectrophotometric measurements of their DNA content. The haploid cells were smaller and had an IPC composed of hexagonal plates, while the diploid cells were larger,

with a smooth IPC. Similarly, during a revision of the genus *Cryptomonas*, cultures were discovered in which there were cells with two types of periplast, as well as a number of pairs of alternative morphotypes with the same sequences of DNA fragments that were analysed (Hoef-Emden 2007, Hoef-Emden & Melkonian 2003). As a result, Hoef-Emden & Melkonian (2003) proposed to name the forms with plated periplast as cryptomorphs, while those with a smooth periplast type as campylomorphs (the names of the morphotypes were adapted after the previously described genera *Cryptomonas* and *Campylomonas* respectively). Recent studies also show the occurrence of dimorphism in cryptophytes of other genera as well. For *Geminigera cryophila*, previously described as having a sheet-like IPC, a cryptomorph with plated IPC was found (confirmed with morphological, chemical, and molecular evidence; van den Hoff et al. 2020). *Plagioselmis prolunga* was found to be the haploid form (plated IPC) of diploid *Teleaulax amphioxeia* (sheet-like IPC; Altenburger et al. 2020). It is also suspected that *Baffinella frigida* might be dimorphic, as the described species had plated IPC, and identical small subunit DNA sequences to another cryptophyte strain, that had twice as much DNA as *B. frigida* (though the IPC of the strain was not examined; Daugbjerg et al. 2018). Phylogenetic relationships among the cryptophytes and their morphotypes that have been described so far are presented in Figure 3. Based on these observations it can be hypothesized that in the dimorphic life cycles of cryptophytes, the morphotype that has sheet-like IPC is a diploid stage, whereas the morphotype with plated IPC is haploid, as speculated already by Altenburger et al. (2020) for different genera.



**Figure 3**

Schematic phylogeny of cryptophytes based on Altenburger et al. (2020) and Daugbjerg et al. (2018). Taxa with a plated inner periplast component (IPC) are underlined, taxa with sheet-like IPC are in bold, and taxa with dimorphic strains or pairs of both morphotypes identified are in bold and underlined. 2n and 1n refer to the ploidy of the cells. The tree was prepared with Mesquite software (Maddison & Maddison, 2023) and turned into graphic form with CorelDRAW Graphics Suite (Version 24.3.0.571, © Corel Corporation).

It is likely that pairs of morphotypes of a single species will be described in the Pyrenomonadaceae family in the future. Majaneva et al. (2014) suggested that their study results may indicate the presence of dimorphism in the family, as the holotypes of the two genera *Rhinomonas* and *Storeatula* (i.e. *Rhinomonas pauca* and *Storeatula major*) appear to be very closely related. Similar results were previously reported by Hoef-Emden et al. (2002) and Lane et al. (2006). The grouping of representatives of *Rhinomonas* and *Rhodomonas* with a plated periplast type with *Storeatula* with a smooth periplast type, may indicate the presence of a potential dimorphic life history of

these algae, where the genus *Storeatula* would be an alternative morphotype for the genera *Rhinomonas* and *Rhodomonas*.

Also interesting are recent reports of a newly discovered species of *Rhodomonas* with a smooth periplast, namely *Rhodomonas storeatuloformis* (Khanaychenko et al. 2022). The morphological features of *R. storeatuloformis*, i.e. smooth IPCs and the absence of a furrow at the gullet, would indicate that the species belongs to the genus *Storeatula*, but phylogenetic analyses unambiguously grouped the taxon among the genus *Rhodomonas*. The results presented in these publications once again show that using only morphological and ultrastructural characters for identification in the cryptophyte group is insufficient.

So far, several taxonomic revisions have been made taking into account all the mentioned taxonomic complications occurring in the group of cryptophytes and they have been carried out for the genus *Cryptomonas* (Hoef-Emden & Melkonian 2003, Hoef-Emden 2007) and *Chroomonas* (Hoef-Emden 2018). They can serve as an excellent example of how to proceed with the taxonomic revision of the cryptophyte genus, bearing in mind the various complexities involved in classifying these fascinating organisms.

## 5. Summary

Cryptophytes belonging to the family Pyrenomonadaceae are undoubtedly an interesting and ecologically important group of organisms whose taxonomic relationships within the family remain largely unexplained. Given the data suggesting the presence of dimorphism in this family, a taxonomic revision of the Pyrenomonadaceae should take into account not only morphological features in combination with molecular data, but also cell ploidy studies using clonal cultures of these algae.

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