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REVIEW PAPER

A taxonomic review of the genus *Phaeocystis*

Linda Medlin · Adriana Zingone

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Abstract *Phaeocystis* is recognized both as a nuisance and as an ecologically important phytoplankton species. Its polymorphic life cycle with both colonial and flagellated cells causes many taxonomic problems. Sequence variation among 22 isolates representing a global distribution of the genus has been compared using three molecular markers. The ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO) spacer is too conserved to resolve species. The most conserved 18S ribosomal deoxyribonucleic acid (rDNA) analysis suggests that an undescribed unicellular *Phaeocystis* sp. (isolate PLY559) is a sister taxon to the Mediterranean unicellular *Phaeocystis jahnii;* this clade branched prior to the divergence of all other *Phaeocystis* species, including the colonial ones. The internal transcribed spacer (ITS) region shows sufficient variation that some spatial population structure can be recovered, at least in *P. antarctica*. *P. globosa* and *P. pouchetii* have multiple different ITS copies, suggestive of cryptic species that are still able to hybridize. A molecular clock has been constructed that estimates the divergence of the cold water colonial forms from the warm-water colonial forms to be about 30 Ma and the divergence of *P. antarctica* and *P. pouchetii* to be about 15 Ma. A short description of the colonial stage and the flagellated stage for each formally recognized species is provided. Morphological information is also provided on a number of undescribed species. These include the strain Ply 559, consisting of non-colonial cells with peculiar tubular extrusomes, a second non-colonial species from the north western Mediterranean Sea producing a lot of mucus, and a colonial species with scale-less flagellates found in Italian waters. In addition, three flagellated morphotypes with scales different from those of *P. antarctica* were reported in the literature from Antarctic waters. The picture emerging from both molecular and morphological data is that the number of species in the genus is still underestimated and that cryptic or pseudocryptic diversity requires a sound assessment in future research of this genus. Based on all published observations, an emended description of the genus is provided.

Keywords Molecular clock · *Phaeocystis antarctica* · *P. cordata* · *P. globosa* · *P. jahnii* · *P. pouchetii* · *P. scrobiculata* · rDNA analysis

L. Medlin (✉)
Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, Bremerhaven, 27570, Germany
e-mail: lkmedlin@awi-bremerhaven.de

A. Zingone
Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy

Introduction

Phaeocystis Lagerheim is a cosmopolitan bloom-forming alga that is often recognized both as a nuisance alga and an ecologically important member of the phytoplankton (Davidson 1985; Lancelot et al. 1987; Smith et al. 1991; Davidson and Marchant 1992; Baumann et al. 1994; Schoemann et al. 2005; Veldhuis and Wassmann 2005). Its various life forms can make large-scale blooms that are often avoided by fish (Chang 1983) and appear detrimental to the growth and reproduction of shellfish and macrozooplankton (Davidson and Marchant 1992) or are ichthyotoxic (Shen et al. 2004). Massive areas of pollution are created when dissolved organic compounds released by *Phaeocystis* during declining bloom conditions accumulate, foam and then wash onshore (Lancelot et al. 1987). *Phaeocystis* is a major contributor to the global sulphur budget by releasing substantial quantities of dimethylsulfide propionate (DMSP) (Keller et al. 1989; Baumann et al. 1993), which is metabolized to dimethylsulfide (DMS) as the cells are grazed or infected and lysed by viruses. It may play yet another important ecological role with its production of ultraviolet B (UV-B)-absorbing compounds (Marchant et al. 1991; Davidson and Marchant 1992).

Phaeocystis has a polymorphic life cycle with both colonial and flagellated cells (Kornmann 1955; Whipple et al. 2005). The colonial stage, with cells very loosely interconnected and enclosed in a thin skin (Hamm et al. 1999), is most easily recognized, although some species may form mucilaginous colonies or do not seem to have a colonial stage. Thousands of cells can occur in a colony that may reach 2 cm in diameter (Jahnke and Baumann 1987; Verity et al. 1988; Rousseau et al. 1994; Davidson and Marchant 1992). Colony sizes of 3 cm or more have been reported in blooms from China (Shen et al. 2004). The difficulty in assigning a specific name to the colonial stage has caused much taxonomic confusion. Flagellated cells have two parietal chloroplasts and two flagella, which may be equal or unequal in length and heterodynamic. A short haptonema is present between the two flagella, which may or may not have a swollen end. The flagellated cells may be naked or have two layers of different shaped organic scales. Some flagellated cells also produce groups of filaments, which are extruded from the cell and assume a characteristic pattern.

The genus was erected by Lagerheim in 1893 to accommodate the colonial stage of an alga described originally as *Tetraspora poucheti* by Hariot in Pouchet (1892). *Phaeocystis pouchetii* (its correct orthography) occurs in cold waters and in its globular, lobed colonies, cells are arranged in packets of four (see Jahnke and Baumann 1987 for illustrations). *Phaeocystis globosa* was described by Scherffel (1900) from temperate waters and forms spherical colonies with cells arranged homogeneously within the colony (Jahnke and Baumann 1987), whereas older stages can assume distorted pear shapes (Bätje and Michaelis 1986). Early workers separated *P. pouchetii* and *P. globosa* based on different distributions and colonial morphologies until Kornmann (1955) doubted the differentiation between the two species. From his life-cycle studies, he considered that *P. globosa* cell types appeared to be juvenile forms of *P. pouchetii*. Since that report, colony morphology has been judged an unreliable specific character.

Sournia (1988) reviewed the diagnostic features of *Phaeocystis*, and discussed the reliability of the nine valid species published since the last century. He discarded two species from the genus, *P. fuscescens* (Braun) De Toni and *P. giraudyi* (Derbès and Solier) Hamel, because they did not fit the genus and probably not even the class characteristics. The descriptions of four species, two from cold waters, *P. antarctica* Karsten and *P. brucei* Mangin, and two from temperate waters, *P. amoeboidea* Büttner and *P. sphaeroidea* Büttner, were all judged as very superficial. The poor illustrations and unlikely features, including one chloroplast per cell and no haptonema (Büttner 1911), were probably the reasons why the two temperate species have never been mentioned again in the literature. For similar reasons the two Antarctic species were reported rarely and not studied again. As for the two most frequently recorded species, *P. pouchetii* (Hariot in Pouchet) Lagerheim and *P. globosa* Scherffel, they had been studied in more detail yet no element was available to keep them separate. Therefore Sournia