The chrysophyte genera *Clathromonas* and *Paraphysomonas* from the Catalan coast (NW Mediterranean Sea)

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Abstract

Water samples were collected from Tarragona port, Catalan coast, in July 2007, in order to study the marine planktonic nanoflagellates. Scale-bearing chrysophytes species observed in the SEM included Paraphysomonas foraminifera Lucas, Paraphysomonas imperforata Lucas, Paraphysomonas cf. vestita (Stokes) De Saedeleer and Clathromonas butcheri (Pennick et Clarke) Scoble et Cavalier-Smith. Clathromonas *butcheri* has two different scales covering the cells: round, inner perforated plate scales, and crown (or basket)-scales with an open meshwork; the round, inner scales predominate over the crown scales. Cells of Paraphysomonas species are covered by one type of scale, with a circular base-plate (perforated or not perforated) and a single spine. In *P. foraminifera* the base-plates are finely perforated and have a mid annulus, and the spines appear straight or curved at the tips, with tips truncate. The other two species have their base-plates unperforated, but scales of P. imperforata showed a characteristic annulus. The morphological variation of the scales (sizes, presence or absence of annulus and thickened marginal rim, and lack of spines) of these species is discussed in the context of morphologic characters of taxonomic value, or the possible development of certain scales structures during the process of maturation.

Key words: Chrysophyceae, *Clathromonas*, Morphology, *Paraphysomonas*, SEM, Taxonomy.

Introduction

Blooms of nanoflagellates are common in harbours and beaches along the Catalan coast; these proliferations are frequently responsible for high levels of chlorophyll *a*, however this plankton fraction has been poorly studied. These nanoflagellates (and also picoflagellates) are represented by many taxonomic groups which may be photosynthetic or heterotrophic, including chrysophytes. Some very important heterotrophic silica-scaled chrysophytes are species of the genus *Paraphysomonas* De Saedeleer, which are major contributors to the microbial loop in brackish and marine ecosystems. Surprisingly, there is no published literature concerning studies of the species and their morphology of this genus (and possible allies) in the Mediterranean Sea.

Members of the genus *Paraphysomonas* include colourless (leucoplasts have been found in several species) and solitary forms, with spherical, ovate or elongate shape, bearing two unequal flagella (one longer with tubular hairs or mastigonemes, the other shorter and smooth), covered by silica scales, and ranging from 3.3 to 26 µm in cell size (Kristiansen and Preisig, 2001; Scoble and Cavalier-Smith, 2013, 2014). The species of the genus are heterotrophic and free-swimming, and occur in soils, and freshwater, brackish and marine environments. The silica-scales have a species-specific morphology, but they are very tiny and have to be studied by electron microscopy. Scoble and Cavalier-Smith (2014) provided a revised diagnosis of the genus *Paraphysomonas sensu stricto* for species with only one type of scale, spine scales, whereas species having 2 or 3 types of scales were assigned to the new genus *Clathromonas* Scoble *et* Cavalier-Smith. There are 63 currently accepted species within *Paraphysomonas*, eleven of which are from marine habitats and may be important predators of bacteria, cyanobacteria and small algae (Kristiansen and Preisig, 2001), although after the revisions and proposals of Scoble and Cavalier-Smith (2014), they recognise only 32 species of *Paraphysomonas sensu stricto*.

The genus *Paraphysomonas* has been considered to be ubiquitous, especially in freshwater (Finlay and Clarke, 1999). It has been included in the Encyclopedia of Chrysophyte genera (Kristiansen and Preisig, 2001), and a brief historical revision of the taxonomy of *Paraphysomonas* has been made, describing the outstanding morphological and molecular diversity within the genus, especially regarding variability of the silica-scales (Scoble and Cavalier-Smith, 2013). Furthermore, Scoble and Cavalier-Smith (2014) studied the details of the silica-scales by transmission electron microscope (TEM) and carried out phylogenetic analysis using SSU rDNA, and proposed the genus *Clathromonas* for species having non spine scales, but basket scales; molecular and morphological data were congruent and support such division (Scoble and Cavalier-Smith, 2014).

Most studies on the cells and scales of these species have been conducted using TEM. In this paper we provide detailed morphological observations of three species of *Paraphysomonas, Paraphysomonas foraminifera* Lucas, *P. imperforata* Lucas, *P. cf. vestita* (Stokes) De Saedeleer, and one former species of the genus, now assigned to the genus *Clathromonas, Clathromonas butcheri* (Pennick *et* Clarke) Scoble *et* Cavalier-Smith, using the scanning electron microscope (SEM).

Material and methods

Water bottle samples were taken from the port of Tarragona, Catalonia, Spain, in the north west Mediterranean Sea (Fig. 1), on 7th July, 2007. The water temperature and salinity at the sampling site were 23.2° C and 37.4, respectively.

Samples were kept alive during transport to the laboratory where they were concentrated by passive filtration (e.g. with no vacuum pump, and filters of 2 μ m mesh), then the concentrated samples (about 20 ml) were fixed with OsO₄ in buffer, until a final concentration of 1%, for 10 minutes. Fixed samples were carefully placed onto filters (5 μ m mesh) with a syringe, dehydrated (five ethanol concentrations, from 20% to 100%), critically point-dried, mounted onto stubs and studied in a Hitachi S-570 SEM.

Terminology for the spines of *Paraphysomonas* follows Scoble and Cavalier-Smith (2013).

Results

Paraphysomonas foraminifera Lucas

(**Fig. 2**)

References: Lucas, 1967, p. 330, text-figs I A-C, pl. I, figs C, E, F; Tong, 1997a, p. 532, fig. 8 f; LeRoi & Hallegraeff, 2006, p. 220, fig. 7.

Non Thomsen, 1975, p. 114, figs 1-5 (*partim Paraphysomonas perforata* Scoble *et* Cavalier-Smith ?); non Bergesch *et al.*, 2008, p. 42, fig. 6B (*Paraphysomonas perforata* Scoble *et* Cavalier-Smith ?).

Description: This species has a typical nano-picoplanktonic cell size. Cells are covered by one type of scale, with a circular, finely perforated base-plate and a single spine, although some plates are spineless (Fig. 2). The base-plates are circular and have an arrangement of seven to eight concentric rings of minute pores and a mid annulus, located between the fourth and the fifth ring of pores (Fig. 2); base-plates are 0.9-0.97 µm in diameter. The spines appear straight or curved and usually taper slightly, with tips truncate, although in few spines their diameter changes abruptly, $0.92-1.2 \ \mu m$ in length. *Paraphysomonas foraminifera* was rare in the samples.

Remarks: When originally describing this species, Lucas (1967) did not mention the presence of an annulus in the base-plates of the scales, but his figure (pl. I, C) clearly exhibits this character. Not many works have shown an annulus in the scales of this species, and we consider that the illustrations provided by Thomsen (1975) (except probably his fig. 3 where an annulus is apparent) and Bergesch *et al.* (2008) do correspond to the newly described species *Paraphysomonas perforata* Scoble *et* Cavalier-Smith (Scoble and Cavalier-Smith, 2014), which has scales with no conspicuous annulus, whereas Vørs (1993, fig. 33) illustrated this species with a scale with no annulus and very different to *P. foraminifera*, as the base-plate is very wide and has many perforations, and the spines are very thin and relatively short. This is a very characteristic marine species.

Another consideration is that the presence of the annulus and the relative size of the pores perforating the base-plate may depend on the "maturity" of the scales.

Paraphysomonas imperforata Lucas

(Figs 7-10)

References: Lucas, 1967, p. 330, pl. I, figs A, B, D; Tong, 1997a, p. 533, fig. 8 c; Bérard-Therriault et al., 1999, p. 320, pl. 146 h, j; LeRoi & Hallegraeff, 2006, p. 221, figs 8 a-f.

Description: Cells found solitary, spherical to ovoid, 4.57-5.42 μ m in diameter, with two conspicuous unequal flagella, one longer (7.1 μ m length), with mastigonemes, and the other shorter and smooth (Figs 7, 8). Spiny scales covering the body of the cells, with the base-plates nearly circular and flat (artificially curved probably because of sample treatment), 0.8-1.02 μ m of diameter, with no perforations, but an evident mid annulus (Figs 9, 10). The spines are usually straight, with some curved close to the tip, slightly taper, but some spines show an abrupt diameter change, 0.8-1.1 μ m length. This species was fairly common in the study area.

Remarks: As in the previous species, in the original description of *Paraphysomonas imperforata*, Lucas (1967) did not specifically mention the presence of an annulus in the base-plates of the scales, although his figure (pl. I, D) shows this structure and he discussed the presence of "an annular fold" (Lucas, 1967, p. 332). This character ("always exhibits an annulus") was also mentioned and illustrated by Scoble and Cavalier-Smith (2014, p. 565, fig. 5F) and it has been also shown by Tong (1997a, b) and LeRoi & Hallegraeff (2006), whereas Vørs (1993) and Bergesch et al. (2008), among others, illustrated scales with no annulus, and Thomsen (1975) occasionally observed this feature "an annular fold" but did not show it.

This is another example where we poorly know the "natural" variation of some key morphological characters, such as the presence (or possible development) of an annulus in the base-plates of the scales, or the presence or absence of a thickened marginal rim, or the range of sizes of the scales.

Paraphysomonas cf. vestita (Stokes) De Saedeleer

(Figs 3-6)

References: Manton and Leedale 1961, pl. 3, figs 13, 14; Takahashi, 1976, p. 39, figs 1-4; Takahashi, 1987, p. 163, figs 10, 11.

Description: Cells solitary, irregularly spherical in shape, 5.8-6.25 μ m in diameter, with two conspicuous and unequal flagella, the longest (10-12 μ m in length), with mastigonemes (1.1-1.4 μ m in length), and the shortest smooth (2.6 μ m in length) (Figs

3, 4). Numerous (more than 100) spiny scales covering the body of the cells (Figs 3, 4), with the base-plates circular and flat (slightly curved most probably because of the sample treatment), 0.54-0.6 μ m in diameter, with no perforations nor an evident mid annulus, but with rimmed margin (Figs 5, 6). The spines are somewhat straight or slightly curved, tapering (Figs 5, 6), 0.9-1.1 μ m in length. This species was fairly common in the study area.

Remarks: Specimens found in this study were tentatively identified as *Paraphysomonas* cf. *vestita*, which is considered a freshwater species (with reports from marine environments), but it most probably belongs to a species recently described from marine habitats (Scoble and Cavalier-Smith, 2014), as *Paraphysomonas hebes* Scoble *et* Cavalier-Smith; most observations and measurements coincide with this species, especially considering that many descriptions of *Paraphysomonas vestita* annotate a rather larger cell size, between 5 and 20 µm (8-26 µm in Preisig & Hibberd, 1982a) in diameter. The descriptions and illustrations of *Paraphysomonas vestita* by Preisig & Hibberd (1982a, p. 401, figs 1 A, C-F) and Marchant & Scott (2005, p. 301, figs 7c, d) include the conspicuous presence of a thickened rim, although Preisig & Hibberd (1982a) stated that the rim "is, in fact, a reflexion of the periphery". Marchant & Scott's (2005) report shows the species again from a marine Antarctic habitat.

Clathromonas butcheri (Pennick et Clarke) Scoble et Cavalier-Smith

(Figs 11-15)

Reference: Scoble and Cavalier-Smith, 2014, p. 581, figs 16A-G.
Additionally references (as *Paraphysomonas butcheri* Pennick *et* Clarke): Pennick and Clarke, 1972, p. 45, figs 1-13; Thomsen, 1975, p. 120, figs 16-19; Takahashi, 1976, p. 41, figs 10-13; Preisig & Hibberd, 1982b, p. 617, figs 11 A-H; Ikävalko & Thomsen,

1996, p. 152, figs 3, 4; Marchant & Scott, 2005, p. 295, figs 7.2 a-e; LeRoi & Hallegraeff, 2006, p. 220, figs 6 a-g; Bergesch *et al.*, 2008, p. 42, fig. 6A. Description: Complete cells were found solitary, with rounded to ovoid shape, cell length of 3.0-3.4 μm, and two conspicuous unequal flagella, the longest (4.9-6.5 μm), with mastigonemes (0.6-0.8 μm long), and the shortest (1.8-2.7 μm) smooth (Figs 11, 12). The cells were covered by two different types of scales (Figs 11-15): round to slightly elliptical, regularly flat, inner perforated plate scales, and basket (or crown)-scales with an open meshwork (Fig. 15); the round, inner scales predominated over the crown scales (Figs 11-14). The plate scales had an arrangement of concentric rings of small pores, most of them have an annulus or thickened structure after the second marginal concentric ring (Fig. 13), although there were some with no annulus (Fig. 14); they are 0.61-0.78 μm in diameter. The crown scales varied slightly in size (0.6-0.81 μm) and also in structure (Fig. 15). *Clathromonas butcheri* was fairly common in the samples.

Remarks: Most illustrations of *Clathromonas butcheri* in the literature (cited in the references, above) show the characteristic perforated plate scales, with rather large pores (or apertures, as stated in the original description by Pennick and Clarke, 1972) arranged in an 11-16 outer ring and an inner ring of 11-12 pores, and an irregular central area. Only LeRoi & Hallegraeff (2006) have provided a wide range of variation of these scales, in which it is possible to find some scales similar to the ones we found in this study, whereas Bergesch et al. (2008) illustrated this species with scales also similar to those of this report, in the two cases with a mid annulus, and Leadbeater (1974) also illustrated this species (pl. V, figs G, H) with plate scales more similar to those showed in this study, but with no annulus. The species *Clathromonas ignivoma* (Preisig *et* Hibberd) Scoble *et* Cavalier-Smith (= *Paraphysomonas ignivoma* Preisig *et* Hibberd)

possesses plate scales very similar to the ones we found in this study for *Clathromonas butcheri*, especially the presence of the thickened structure (or rim) after the second marginal concentric ring (Preisig & Hibberd, 1982b, fig. 9 E).

The structure of the plate scales found in this study differs from the original description, and from many other records of the species, particularly regarding the size and arrangement of the pores (or apertures). We recognise that assignation to the species *Clathromonas butcheri* was tentative, and we debated whether or not to propose a new species, but we took into account the morphological variation of these scales provided by LeRoi & Hallegraeff (2006).

Discussion

Morphology

Most of our observations confirm previous descriptions by many authors regarding the species found here, observations that have been mainly made using TEM (instead of SEM). The only exception should be perhaps the plate scales detected in *Clathromonas butcheri* which were different from the original description (Pennick and Clarke (1972) and many others in the literature (as annotated in the references of this species). In fact, the arrangement of concentric rings of rather small pores (if compared with the pores or apertures originally described) found in the plate scales and the evident annulus (or thickened structure) led us to consider a new species. The work by LeRoi & Hallegraeff (2006) included a wide range of morphological variation of these scales of the species, in which some scales resembled our own findings. We believe that we still have to learn much about the "natural" variability of morphologic characters of the genera *Clathromonas* and *Paraphysomonas*.

It seems that some morphologic characters considered to have taxonomic value may vary within the species, including the thickened marginal rim, mid annulus or simple annulus, and the size of pores (or apertures) in the scales of the species, but also the apparent lack of spines in several scales. Some of these morphological features appear to be key characters for species identification: shape and size of cells, sizes of the two flagella, structure of the scales: plain, perforated or radially ribbed base, presence or absence of mid annulus and thickened margin, presence or absence of inflated spine base, tapered or straight spines, and truncate or pointed tip of spine (Scoble and Cavarlier-Smith, 2013, 2014), but as stated by these authors variability of scales is poorly known.

The species *Paraphysomonas foraminifera* has been described and illustrated in many places by many authors but not all workers have considered the arrangement of pores and the presence of a mid annulus for positive identification (see also references in the corresponding species). The case of *P. imperforata* is also similar, and for *P. vestita* the situation is even more complicated as this species, originally described from freshwater environments, has appeared in reports of practically all over the world (e.g. Finlay & Clarke, 1999), either in freshwater or marine locations. This problem has been also discussed by Scoble and Cavarlier-Smith (2013, 2014).

The use of SEM has proved to be a useful method to observe some details of the morphology of these small and complicated organisms, particularly the complexity of the morphology of the crown (or basket) scales of species of *Clathromonas*, although some details of the tips of the spines in the spiny scales may be viewed in better detail by TEM. Previously, Leadbeater and Barker (1995), Marchant & Scott (2005) and Petronio and Rivera (2010) also showed some details of the species *Paraphysomonas vestita* by SEM.

Additionally, besides microscopical observations (using a combination of LM, TEM and SEM), the use of molecular tools (e.g. Caron et al., 1999) is strongly recommended whenever they are available, from cultures or environmental sequences.

Taxonomy

Although the separation of *Paraphysomonas* and *Clathromonas* appears to be wellsupported, the name *Clathromonas butcheri* (Pennick *et* Clarke) Scoble *et* Cavalier-Smith is found to be "nom. illeg." in ALGAE BASE. The name of the genus *Clathromonas* is apparently superfluous. A new name for the genus should be found and new taxonomic combinations should be made in future.

Distribution

The heterotrophic chrysophyte genus *Paraphysomonas* is ubiquitous in aquatic environments (Finlay and Clarke, 1999), and the same applies to *Clathromonas butcheri*, initially described as *Paraphysomonas* species. In our study we could find some species to be fairly common, like *Paraphysomonas imperforata*, *P*. cf. *vestita* and *Clathromonas butcheri*, whereas *Paraphysomonas foraminifera* was rare. All the species encountered in this study are marine forms, except *Paraphysomonas* cf. *vestita*, which is mainly distributed in freshwater environments (Scoble and Cavalier-Smith, 2014), but usually recorded in marine habitats (e.g. Takahashi, 1987). However, it is surprising that no published literature had been dedicated to the species of these two genera in the Mediterranean Sea (e.g. Finlay and Clarke, 1999).

Paraphysomonas foraminifera has been widely reported from many places around the world, especially in marine environments, but we cannot be certain that all reports belong to this species or to other described (e.g. *Paraphysomonas perforata* Scoble *et*

Cavalier-Smith) or yet undescribed species, due to the range of illustrations showing scales to be variable.

Paraphysomonas imperforata has been recorded in many places around the world, including some freshwater locations, although the species was described as marine, which arises the question if all "natural" morphological variation (particularly sizes and structure of the scales) has been considered in identifying the species or the specimens found may belong to other similar, related species.

Conversely, we should improve the number and detail of the observations to assess the natural distribution of authentic *Paraphysomonas vestita*, for it is considered to be a widely distributed species in freshwater and marine habitats. As demonstrated by Scoble and Cavalier-Smith (2014), there may be many more species superficially resembling *P. vestita*.

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Legends for the figures

Figure 1. Location of the sampling point in the port of Tarragona, Catalan coast, Spain, in the north west Mediterranean Sea.

Figures 2-6. Two species of *Paraphysomonas*, SEM Fig. 2. *Paraphysomonas foraminifera*, scales of the species; the arrow points to the spine changing its diameter abruptly. Figs 3-6. *Paraphysomonas* cf. *vestita*. Figs 3, 4. Two complete cells, showing the unequal flagella and the scales covering the cells. Figs 5, 6. Details of the scales of the species; arrows point to the rimmed margins.

Figures 7-10. *Paraphysomonas imperforata*, SEM. Figs 7, 8. Two different cells covered by scales and showing the longest flagellum. Figs 9, 10. Details of the scales detached from the cells; arrow in Fig. 10 points to a spine changing diameter abruptly.

Figures 11-15. *Clathromonas butcheri*, SEM. Figs 11, 12. Two different cells covered by two different types of scales. Figs 13-15. Details of the two different types of scales, including the base plates and the crown (or basket) scales.







