Cryptogamie, Algol., 2009, 30 (2): 125-134

Morphological variability of the marine planktonic diatom *Chaetoceros similis* (Bacillariophyceae)

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(Received 6 October 2008, accepted 24 March 2009)

Abstract – *Chaetoceros similis* is a marine planktonic diatom originally described by Cleve in 1896. It is relatively well-known in the phytoplankton of the North Atlantic Ocean, interior or semi-closed seas in the Northern hemisphere and the North Pacific Ocean. This study investigates its morphological variability based on samples collected during the summer of 2003 in Roscoff, Britanny (France). *Chaetoceros similis* occurred mostly as a solitairy form but sometimes it also formed short chains composed of up to 6 cells. In the chains, the sibling valves of intercalary cells were connected to each other by the valve faces, which were inflated at the centre. The valves had a pattern of costae running from slightly eccentric annuli, and only the terminal valves showed a central rimoportula. All setae, which arose from the valve apices, were straight and directed at an angle of 30-35° with respect to the apical axis; sibling setae in chains did not fuse together. In a few specimens, particularly in the short chains, some teratological forms were seen: one intercalary valve had only one thicker seta at one apex and lacked the other seta at the corresponding apex, but valves with three setae were also found while cells in other shorter chain had only a single terminal seta per valve. This latter morphotype resembled another *Chaetoceros* species, *Chaetoceros throndsenii*. In the short chains, the nature of the cells linked by the inflated valve faces and the lack of fusion of sibling setae may partially explain certain morphological variations in the number and structure of sibling setae.

***Chaetoceros* / Diatoms / Morphology / Plankton / Taxonomy**

Résumé – Variabilité morphologique de la diatomée planctonique marine *Chaetoceros similis* (Bacillariophyceae). *Chaetoceros similis* est une diatomée planctonique marine décrite par Cleve en 1896. L'espèce est relativement bien connue dans le phytoplancton de l'Océan Atlantique du Nord, des mers intérieures et semi-closes de l'hémisphère du Nord et de l'Océan Pacifique du Nord. Ce travail étudie sur sa variabilité morphologique, à partir d'échantillons récoltés pendant l'été de 2003 à Roscoff (Bretagne). Généralement *Chaetoceros similis* est présent comme une forme solitaire mais parfois il forme de courtes chaînes (6 cellules au maximum). Dans les chaînes, les valves-sœurs des cellules intercalaires sont connectées par les faces valvaires qui sont gonflées au centre. Les valves montrent un dessin de costae à partir des annuli légèrement excentriques et une rimoportula centrale dans les valves terminales seulement. Toutes les soies ont leur origine aux apex des valves. Elles sont droites et forment un angle de 30-35° avec les axes apicaux ; dans les chaînes les soies-sœurs ne sont pas fusionnées. Quelques spécimens présentent des formes tératologiques, surtout dans les chaînes. Quelques valves intercalaires ont une seule soie plus grosse sans soie correspondante à l'autre apex. Quelques valves à trois soies sont aussi

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Communicating editor: Diana Sarno

présentes, et quelques cellules dans les chaînes courtes ont une seule soie terminale par valve. Ce dernier morphotype ressemble à une autre espèce de ce genre, *Chaetoceros throndsenii.* Dans les chaînes, la nature des cellules reliées par les faces valvaires gonflées et l'absence de fusionnement des soies-sœurs peuvent contribuer à expliquer la variabilité du numéro et de la structure des soies-sœurs.

***Chaetoceros* / Diatomées / Morphologie / Plancton / Taxinomie**

INTRODUCTION

The diatom *Chaetoceros similis* was originally described in 1896 by Cleve from the plankton of Swedish waters but was also mentioned to occur in Scotland (Cleve, 1896). It is frequently cited in the phytoplankton of the North Atlantic Ocean (Cleve, 1896; Peragallo & Peragallo, 1897-1908; Gran, 1908; Hustedt, 1930; Lebour, 1930; Hendey, 1964; Rines & Hargraves, 1988; Jensen & Moestrup, 1998; Bérard-Therriault *et al.*, 1999; Throndsen *et al.*, 2007), and it also occurs in the Baltic and White Seas (Gogorev *et al.*, 2006), the Black Sea (Axentjev, 1930; Proshkina-Lavrenko, 1955), and the North Pacific Ocean (Gran & Angst, 1931; Cupp, 1943; Chu & Kuo, 1957; Horner, 2002). It has not been recorded in monographs on the genus *Chaetoceros* from the Mexican Pacific waters and the southern Gulf of Mexico (Hernández-Becerril, 1996; Hernández-Becerril & Flores Granados, 1998), nor has it been recorded in the southern hemisphere or the Antarctic Ocean either. Hasle & Syvertsen (1997, p. 210) regarded the species as having a "northern cold water region to temperate?" distribution.

Owing to its characteristic general outline and morphological characters, including the presence of resting spores, it is relatively easy to detect *Chaetoceros similis* during routine phytoplankton surveys and therefore its distribution can be assessed with a high degree of accuracy. The original description mentioned chains of 3 to 5 cells but no solitary forms (Cleve, 1896). Later, a taxonomic variety was proposed for solitary and elongate morphotypes (*Chaetoceros similis* var. *elongata* Axentjev, 1930), while *C. similis* forma *solitarius* Proshkina-Lavrenko (1955) was proposed for solitary morphotypes. No further information on morphological variation is available, although the species has been illustrated using scanning electron microscopy by Gogorev & Makarova (1999) based on specimens from the White Sea, Northwestern Russia, and Gogorev *et al.* (2006) based on specimens from Russian waters which included solitary forms.

The aim of the present study is to investigate the morphological variability of *Chaetoceros similis* using light- (LM), scanning electron (SEM) and transmission electron microscopy (TEM) based on material from Roscoff, Brittany (France).

METHODS

Net (45 µm mesh) and filtered (3 µm filters) samples were collected from the area of Roscoff (ASTAN station: 48° 46' N, 3° 57' W), Brittany, North Atlantic Ocean during the summer of 2003. Conventional methods for studying planktonic diatoms were followed, including acid-cleaning (Simonsen, 1974; Hasle, 1978) and critical point-drying. A Zeiss Axiophot microscope equipped with Nomarski differential interference contrast (DIC), phase contrast and bright field optics was used for LM. Electron microscopy was conducted using a Philips 505 SEM and a Philips 400 TEM.

Morphological terminology follows classical and more recent proposals for diatoms and the genus *Chaetoceros* (Anonymous, 1975; Ross *et al.*, 1979; Rines & Hargarves, 1988; Hernández-Becerril, 1996).

RESULTS

Chaetoceros similis Cleve

= *Chaetoceros pseudosimilis* Cleve-Euler, 1915, p. 44, figs 15 a, b; *Chaetoceros similis* var. *elongata* Axentjev, 1930, p. 129, fig. 19; *Chaetoceros similis* f. *solitarius* Proshkina-Lavrenko, 1955, p. 111, figs 33, 1-4.
Selected references: Cleve, 1896, p. 30, fig. 1; Hustedt, 1930, p. 720, fig. 411; Cupp, 1943, p. 135, figs 90 a, b; Hendey, 1964, p. 130, pl. 15, figs 2, 2a; Rines & Hargraves, 1988, p. 94, figs 222, 223; Gogorev *et al.*, 2006, p. 83, pls. 63, figs 1-9, 64, 4-8; Throndsen *et al.*, 2007, p. 171.

Description of specimens from Roscoff examined here

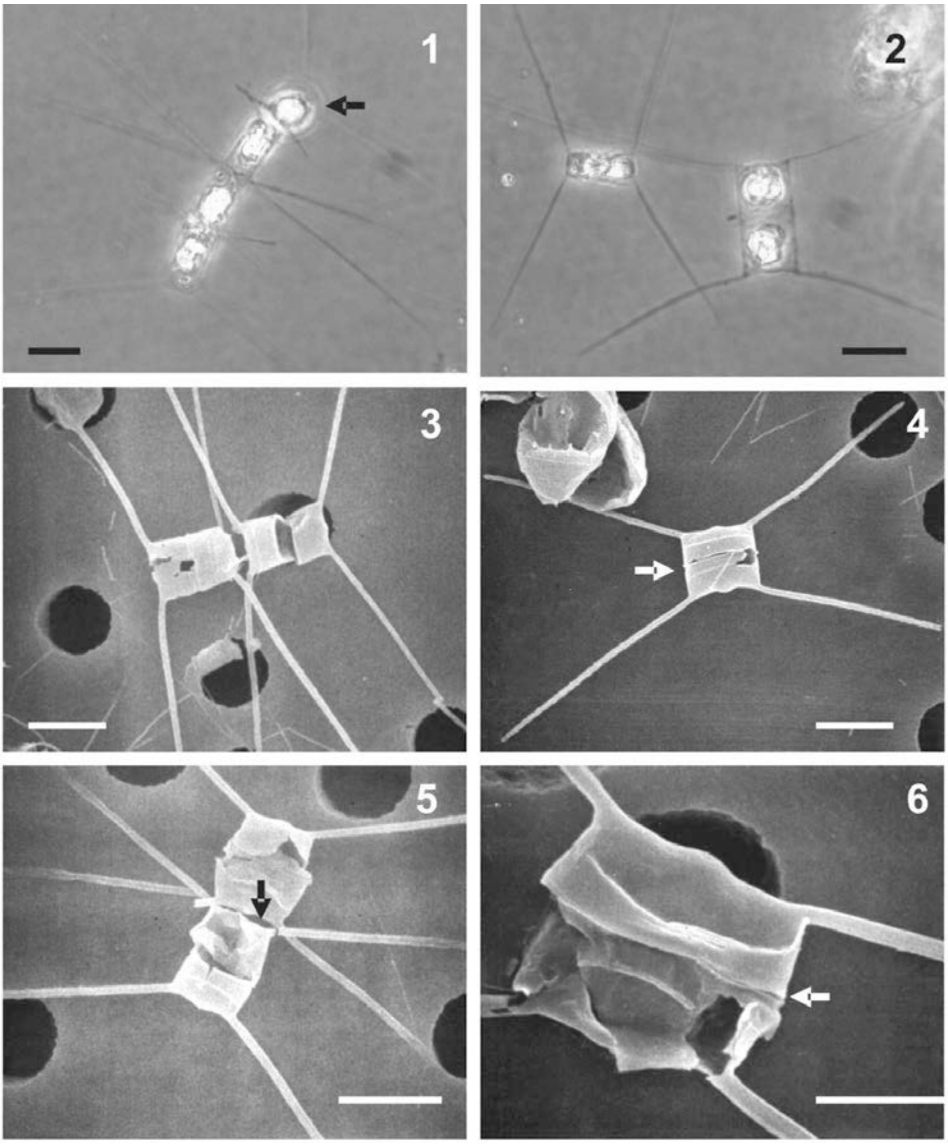
Chaetoceros similis was a frequent and relatively abundant (more than 20% more abundant than other diatoms) species in the Roscoff samples examined here.

Most commonly, *Chaetoceros similis* occurred as a solitary form but it was also found to form short straight chains, usually 2-3 cells long (Figs 1-6) with a few chains containing up to 6 cells. The general outline of the cells in girdle view was rectangular to nearly quadrangular, usually with the apical axis longer than the pervalvar one in single cells, and the opposite in cells within chains (Figs 1-5). Cells were elliptical in valve view (Figs 1, 9, 11). In the chains, the apertures were very narrow and divided into two parts by means of an inflation of the valve face centre (Figs 1, 3, 5, 12, 19). Within chains, the sibling valves of intercalary cells were connected to each other by the valve face, which was inflated at the centre (Figs 1, 5, 8, 12, 19). The valve face was inflated at the centre also in terminal valves (Figs 2, 4, 6, 21). Intercalary valves did not touch or connect at the apices.

The setae which arose from the valve apices were straight and directed diagonally towards the chain ends at an angle of 30-35° with respect to the apical axis (Figs 1-5), whereas the terminal ones ran parallel to the others (Figs 3, 5, 17, 18). The sibling setae were not fused together, and they crossed outside the chain margin (Figs 12, 13, 19). All setae (intercalary and terminal ones) were polyedric with four to six sides and they were perforated by sometimes slightly elongated poroids; they also bore tiny spines at the ridges with a very pointed tip (Figs 13-16).

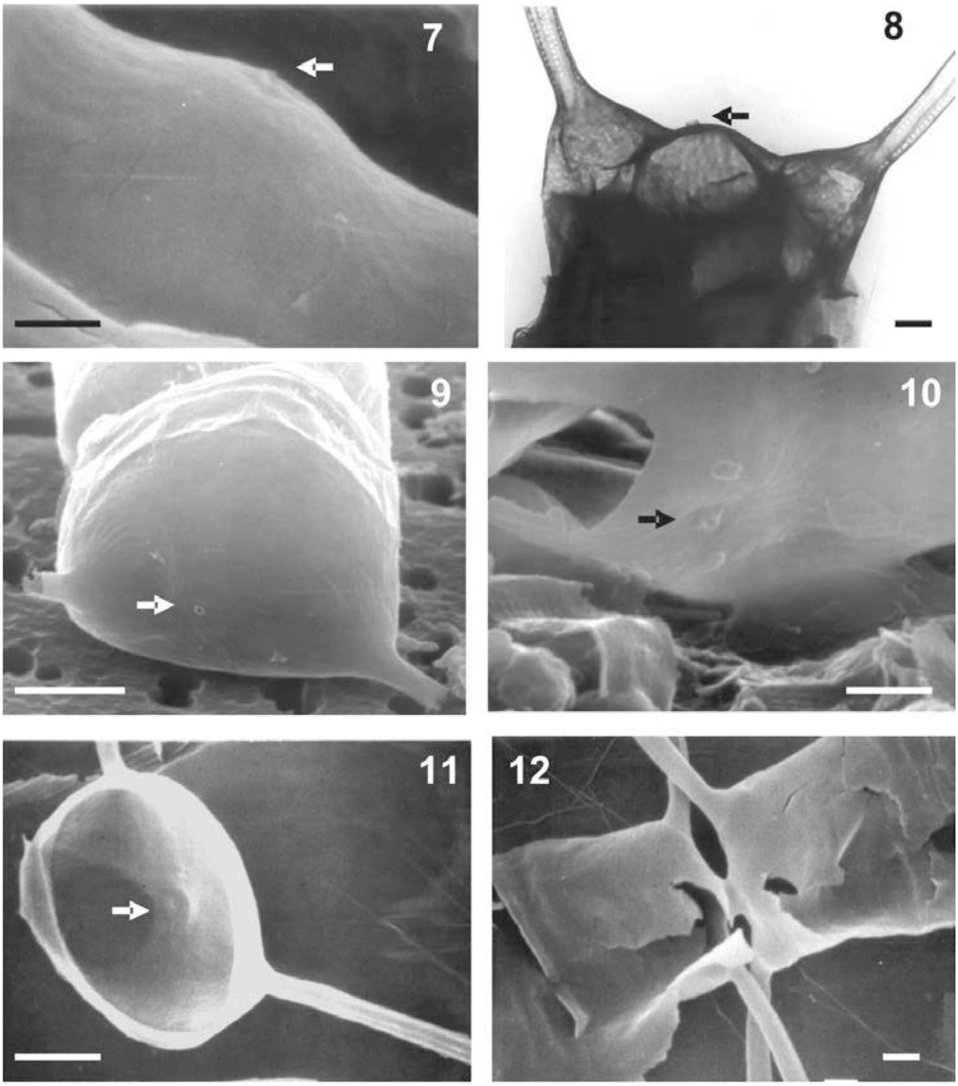
The valves had costae and a distinct, slightly eccentric annulus from which the costae ran (Figs 7, 8). The valve mantle was elevated and clearly separated from the valve face by a rim, with a notch at the suture (Figs 4, 6).

Cingular bands were not studied in detail. There was a slightly eccentric rimoportula, coinciding with the annulus, but in terminal valves only (Figs 7, 11). Externally there was a very short protrusion of the rimoportula and a slit was visible internally (Figs 7-11).

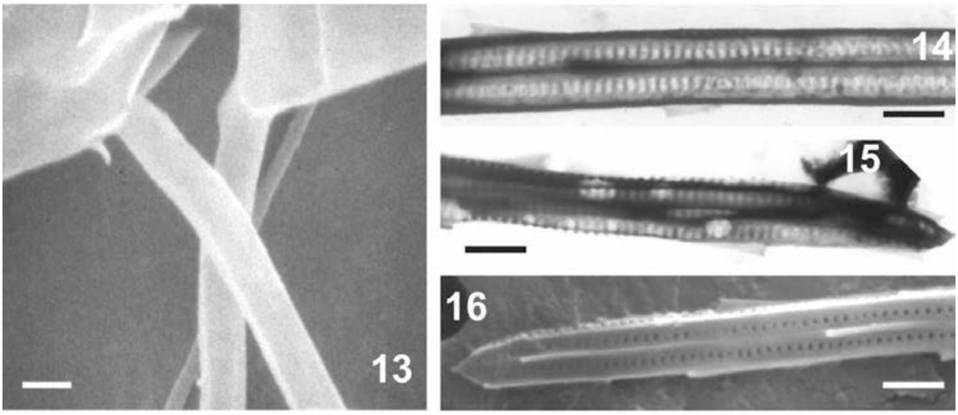


Figs 1-6. *Chaetoceros similis*, LM and SEM. **1.** A short chain (three cells) and another cell in valve view (arrow), LM. **2.** Two solitary cells, right cell possibly dividing, LM. **3.** A chain of two cells, SEM. **4.** A solitary cell showing rim with notch between valve face and mantle (arrow), SEM. **5.** Another chain of two cells, the aperture is arrowed, SEM. **6.** A slightly broken solitary cell showing notch between valve face and mantle (arrow), SEM. Scale bars= 20 µm all except Fig. 6 = 10 µm.

With some reservations (see Discussion below), there appeared to be two chloroplasts per cell (Figs 1, 2). No resting spores were detected, in contrast to previous studies (Cleve, 1896; Hustedt, 1930; Hendey, 1964; Rines & Hargraves, 1988; Jensen & Moestrup, 1998; Throndsen *et al.*, 2007). The size of the specimens was 6.5-13 µm (apical axis) and 8-18 µm (pervalvar axis).



Figs 7-12. *Chaetoceros similis*, SEM and TEM. **7.** Detail of the valve face, showing costae, SEM. **8.** A terminal valve showing costae, TEM. **9.** Another terminal valve, SEM. **10.** Valve face (slightly broken), with the rimoportula detailed, SEM. **11.** Internal view of a terminal valve showing annulus and rimoportula, SEM. **12.** Sibling valves with the valve faces linked together, SEM. Scale bars= 5 µm (Figs 9, 11), = 1 µm (Figs 7, 8, 10, 12). All arrows point to the rimoportula.



Figs 13-16. *Chaetoceros similis*, SEM and TEM. **13.** Two sibling setae rising from the apices of the valves, SEM. **14.** Middle part of a seta, TEM. **15.** Tip of a seta, TEM. **16.** Tip of a seta, showing slightly elongate poroids, SEM. Scale bars= 1 µm.

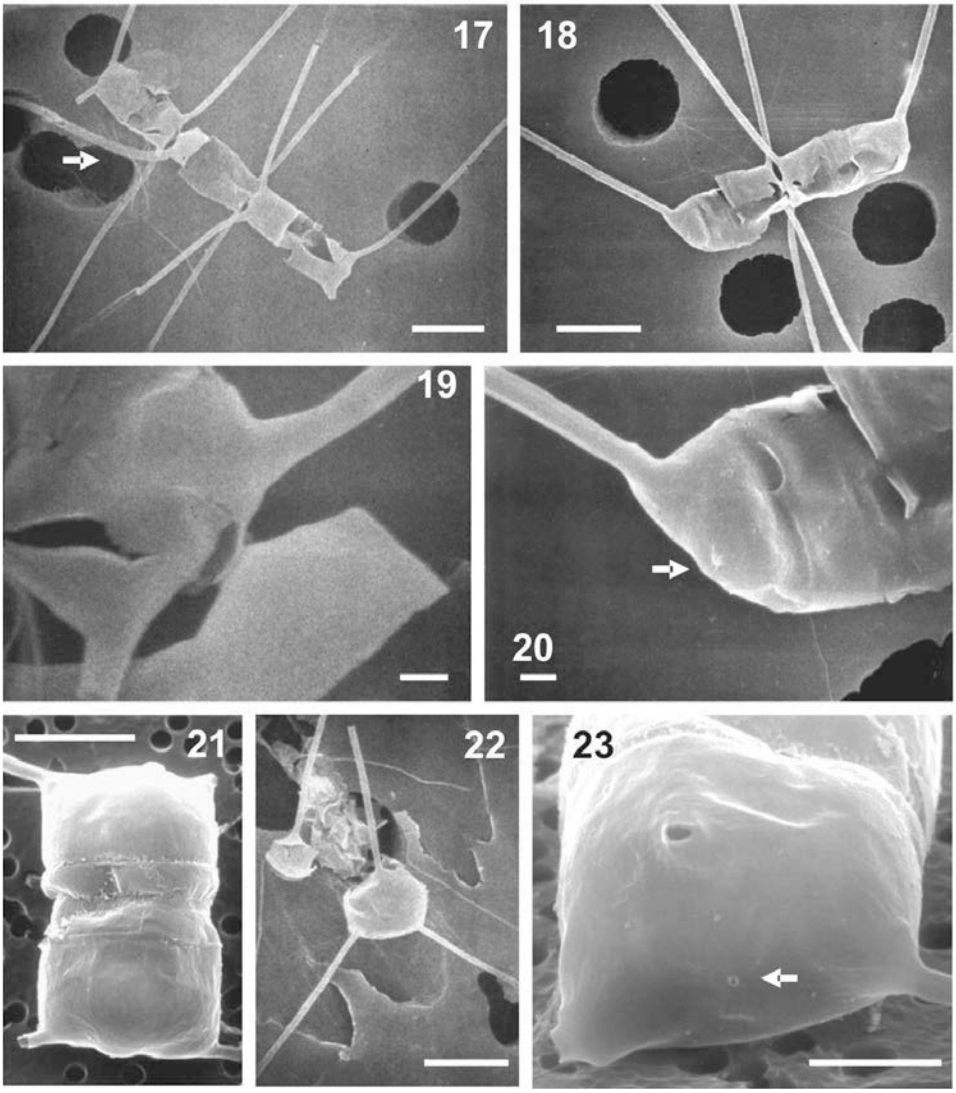
Morphological variability

In addition to the size and shape variation mentioned earlier for *Chaetoceros similis*, a high degree of morphological variation was found, including a few teratological forms. In some specimens, particularly within some short chains, one intercalary valve developed only one thicker seta at one apex and in a different direction to the others, and lacked the other seta at the corresponding apex (Figs 17, 19). In other shorter chains (2 cells per chain) cells had a single terminal seta per valve and both terminal valves lacked the characteristic inflated valve faces (Figs 18, 20). In a solitary cell, one valve had two setae whereas the other one had three (Figs 21, 23). One valve was also found with three setae (Fig. 22).

DISCUSSION

The general morphology of *Chaetoceros similis* has been described in numerous works based on LM observations only (Cleve, 1896; Peragallo & Peragallo, 1897-1908; Gran, 1908; Axentjev, 1930; Hustedt, 1930; Lebour, 1930; Gran & Angst, 1931; Cupp, 1943; Cleve-Euler, 1951; Proshkina-Lavrenko, 1955; Chu & Kuo, 1957; Hendey, 1964; Rines & Hargraves, 1988; Jensen & Moestrup, 1998; Bérard-Therriault *et al.*, 1999; Horner, 2002). Although SEM illustrations were provided more recently (Gogorev & Makarova , 1999; Gogorev *et al.,* 2006), to the author's knowledge TEM observations have been hitherto unavailable.

All the observations made here are consistent with previous descriptions except for the resting spores, which were not detected in this study. The polyedric structure of the setae and the tiny spines and poroids of the setae seen by Gogorev *et al.* (2006) were also observed here. The valves of *C. similis* have costae running from slightly eccentric annuli (as demonstrated in TEM micrographs) and a single



Figs 17-23. *Chaetoceros similis*, SEM. **17.** Chain of three cells, one of the sibling seta is thicker than the others (arrowed). **18.** Chain of two cells, with the two terminal valves lacking one seta. **19.** Detail of intercalary valves, one seta is lacking at the apex of one valve. **20.** Detail of terminal valve, with no inflated valve face and only one seta, the rimoportula is arrowed. **21.** A solitary cell, the upper valve has three setae and the lower one two setae. **22.** One valve with three setae. **23.** Detail of a valve with three setae. The arrow points to the rimoportula. Scale bars= 10 µm (Figs 17, 18, 21, 22), = 5 µm (Fig. 23), = 1 µm (Figs 19, 20).

rimoportula is located on terminal valves only, or in each valve in the case of solitary cells, as is the case in most species of the subgenus *Hyalochaete* (e.g. Evensen & Hasle, 1975; Hernández-Becerril, 1996). These morphological characters also are hithero undocumented.

Only few illustrations available in the literature show chains or cells with two chloroplasts per cell. The specimens studied here appeared to have two chloroplasts per cell although the possibility ought to be borne in mind that chloroplast shape may be lost in fixed cells; one solitary cell appeared to have two possible chloroplasts, but it could also be a cell in division (Fig. 2). The species *Chaetoceros diversicurvatus* V. Goor *emend.* Proshkina-Lavrenko is very similar to *C. similis* in general outline and shape, possible connection of cells by inflated valve faces and the morphology of the setae, although it has only one chloroplast. Future studies may establish whether or not that these two species are actually conspecific.

Another character that was mentioned but not shown (Rines & Hargraves, 1988), is the crossing (not the fusion) of the sibling setae. SEM illustrations by Gogorev *et al.* (2006) clearly show a crossing rather than fusion of these setae. The observations made here confirm this character. Gogorev *et al.* (2006) also illustrated the remanents of mucilage-like material associated with sibling setae, but this material was not seen in the present study.

This lack of fusion raises questions on the nature of cells linked in chains by means of the connection in the inflated valve faces. This may partly explain the morphological variation found in sibling setae (see below). The only other known similar *Chaetoceros* is the species *C. rostratus* Lauder, which forms chains where the cells are connected by a siliceous linking "bridge" emerging from the valve faces (e.g. Hernández-Becerril, 1996). However *C. rostratus* is a more robust species with smaller chloroplasts both in the valves and setae, and with rimportulae on each valve in cells within chains. It also belongs to a distinct subgenus, *Chaetoceros* subgen. *Phaeoceros*.

The original description by Cleve (1896) mentioned chains of 3 to 5 cells, but no solitary forms, although single cells have been widely documented since then (e.g. Rines & Hargraves, 1988; Gogorev *et al.*, 2006). Some new taxa were later proposed for certain morphotypes: *Chaetoceros similis* var. *elongata*, for solitary and elongate morphotypes (Axentjev, 1930) and *C. similis* f. *solitarius*, for solitary morphotypes (Proshkina-Lavrenko, 1955). The present study indicates that solitary and elongate forms may be part of the life history of the species, and therefore it is suggested here to include those taxa as synonyms of *C. similis*. Assmy *et al.* (2008) showed that a considerable morphological variability exists in *C. dichaeta* Ehrenberg (the type species of the genus) but both the solitary and elongated morphotypes all belonged to the same species based on molecular genetic analyses and life cycle studies. *Chaetoceros pseudosimilis* Cleve-Euler (Cleve-Euler, 1951) is considered to be conspecific with *C. similis* (see Gogorev *et al.*, 2006).

Chaetoceros similis has been classified in the Section Brevicatenata Gran, subgenus *Hyalochaete* by Gran (1908), and this classification has also been followed by Hustedt (1939) and Hendey (1964). More recent authors, including Rines & Hargraves (1988), Hasle & Syvertsen (1997), Jensen & Moestrup (1998), Bérard-Therriault *et al.* (1999), and Throndsen *et al.* (2007) did not classify the species in any given Section, although it is quite evident that it belongs in the subgenus *Hyalochaete*. In contrast, Gogorev *et al.* (2006), placed *C. similis* in the Section Similes Ostenfeld *emend.* Gogorev. Among all other species of the subgenus *Hyalochaete*, it is the only one in which sibling cells are linked in chains by the connection of their inflated valve faces.

Biogeographically, *Chaetoceros similis* is considered be a "northern cold water region to temperate?" species (Hasle & Syvertsen, 1997). Its occurrence in interior and semi-closed seas with possibly lower or higher salinities than the open seas, indicates that it may be also tolerant to a wide salinity range. It is referred to as a "neritic" species by Hendey (1964).

Finally, some of the morphotypes found here resemble other, apparently unrelated *Chaetoceros* species. For instance, short chains of *C. similis* with two cells only had one single terminal seta per valve, and both terminal valves were significantly different from the sibling ones. This is reminiscent of *C. throndsenii* var. *trisetosa* Zingone *in* Marino *et al.* (Marino *et al.*, 1991; Aké-Castillo *et al.*, 2004) which, however, is considerably smaller than *C. similis*. Whether or not these morphotypes can be considered as teratological forms may depend on their relative abundance/frequency. One partial explanation for "abnormality", at least in the case of sibling setae, is the lack of fusion in these, because cells are still linked together in the chain thanks to the raised, inflated valve faces, which in fact fuse, therefore the setae may be thicker or they may be present or not. The presence of three setae in single terminal valves is something new for this species (and for almost all species of the genus) and has no simple explanation, at least at the moment. It remains to be established whether or not these morphotypes are a response to a highly fluctuating environment from the point of view of the ecological factors, or whether they represent genetically distinct entities.

Acknowledgements. Special thanks are due to Daniel Vaulot and Anne Cueff for their hospitality and help during my stay at Station Biologique, Roscoff, France, and for sharing samples and data. Thanks are also due to Marina Montresor, Gandi Forlani and Ugo Sacchi for their hospitality and help in processing samples and slides at Stazione Zoologica, Napoli, Italy.

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