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Cytological characteristics of the Sellaphoraceae

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Chloroplast and pyrenoid structure are described for *Sellaphora*, *Fallacia* and *Rossia* (Sellaphoraceae). All have a single chloroplast per cell, which is basically H-shaped, consisting of two large girdle-appressed plates connected by a central isthmus, though the plates may also bear longitudinal or transverse lobes; one or two invaginated pyrenoids are always present. *Fallacia* chloroplasts are more variable than those of *Sellaphora* but always differ fundamentally from the valve-appressed chloroplasts of the unrelated but superficially similar genus *Lyrella*. Outside Sellaphoraceae, invaginated pyrenoids are uncommon except in the Pinnulariaceae, closely related to the Sellaphoraceae according to molecular data and sharing a similar raphe structure, consistent with the classification of both in the suborder Sellaphorineae. However, invaginated pyrenoids are also found in *Diploneis*.

Key words: diatom, *Diploneis*, *Fallacia*, *Rossia Sellaphora*, Pinnulariaceae, Sellaphoraceae, chloroplast, pyrenoid

Introduction

Several changes to the genera of raphid diatoms were made by ROUND et al. (1990) and set in the framework of a new suite of families and orders. A brief description was provided for each genus, but the format did not allow detailed discussion and more detailed accounts of each new or remodelled raphid genus were planned for separate publication. Few of these have been completed, except for *Sellaphora* (MANN 1989), *Lyrella* (MANN and STICKLE 1993) and *Petroneis* (JONES et al. 2005). Meanwhile, molecular biology has provided new tools to probe relationships at all taxonomic levels (e.g. MANN and EVANS 2007), providing important new insights that quite frequently contradict the ROUND et al. (1990) classification at the family level and above.

Among the new taxa described by ROUND et al. (1990: 657) was the suborder Sellaphorineae, which comprised two families: Sellaphoraceae (*Sellaphora*, *Fallacia*, *Rossia* and *Caponea*) and Pinnulariaceae (*Pinnularia*, *Diatomella*, *Oestrupia* and the extinct genus *Dimidiata*) (ROUND et al. 1990: 128). Small-subunit rDNA (BEHNKE et al. 2004, MEDLIN and KACZMARSKA 2004, SORHANNUS 2007) and *rbc*L gene trees (EVANS et al. 2008) support the view that *Sellaphora*, *Fallacia*, *Rossia* and *Pinnularia*, together with some

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small-celled naviculoid species currently referred to *Mayamaea* and *Eolimna* (both described after 1990), comprise a monophyletic group. As noted by ROUND et al. (1990: 657, 'Sellaphorineae'), the raphe in Sellaphoraceae and Pinnulariaceae exhibits similar characteristics, with internal central endings deflected towards the primary side (except where hidden by extra silica deposition) and external central endings similarly deflected but also expanded. In this paper, we make a preliminary survey of protoplast structure in the Sellaphorineae, as a first step to determine whether any characteristics are autapomorphic for the Sellaphoraceae.

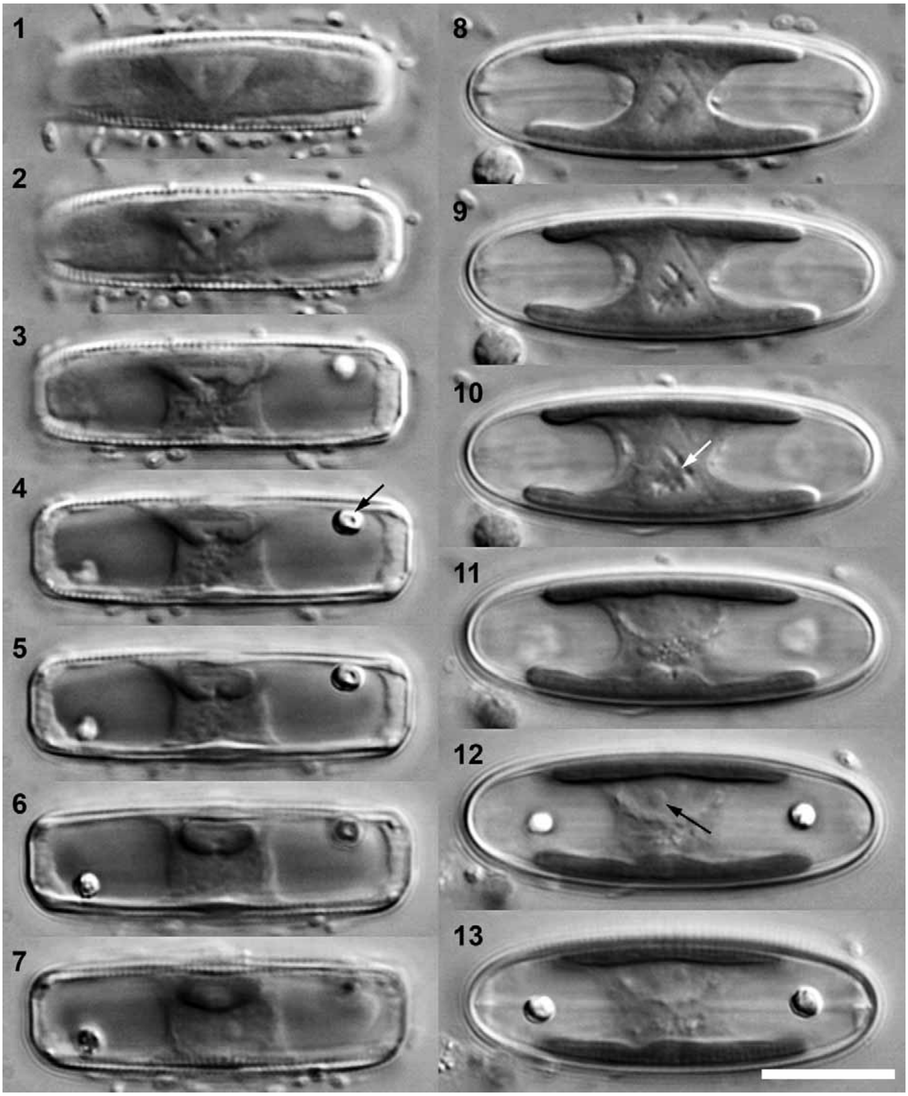
Material and methods

Sellaphorineae are generally epipelic. To obtain freshwater epipelon from shallow (< 1 m) sites, sediment and overlying water were collected using a glass tube as described by ROUND (1953); deeper sediments were sampled using an Ekman grab. For marine species, exposed damp sand was sampled at low tide. Sample preparation was as described by MANN and STICKLE (1993) and MANN and CHEPURNOV (2005). Bright field (BF) and differential interference contrast (DIC) light microscopy (LM: planapochromat lenses, nominal numerical aperture 1.32) were carried out using a Reichert Polyvar 1 photomicroscope and Kodak Technical Pan film, or a Polyvar 2 fitted with a Polaroid DMC2 digital camera. Film negatives were digitized using a Nikon Super Coolscan 5000. Contrast and brightness of digital and digitized images were manipulated in Adobe Photoshop CS2 (http://www.adobe.com/) by global application of the Levels and Curves tools; limited burn-in of the chloroplasts and valve detail in figures 14–28; and use of the Unsharp Mask filter at 60%, 4.5 pixels radius on final-size images at 300 dpi. The observations were made between October 1984 and August 2008, initially by A.J.S. (Figs. 29–43) but after 1986 by D.G.M. (Figs. 1–20, 44–52).

Results

The interphase plastid structure was determined for selected species of *Sellaphora*, *Fallacia* and *Rossia* within the Sellaphoraceae. In order to check whether the characteristics found may occur outside the Sellaphoraceae, we also studied *Pinnularia* and *Diploneis* species, to confirm and extend literature records. Identifications follow MANN et al. (2008) for *Sellaphora*, HUSTEDT (1964) for *Fallacia* (as *Navicula* spp.), and HENDEY (1964) for *Pinnularia*.

***Sellaphora bacillum* (Ehrenb.) D.G. Mann (Figs. 1–13):** Two optical sections of *S. bacillum* cells are provided, in girdle and valve views (Figs. 1–7, 8–13, respectively), to facilitate understanding of chloroplast structure in Sellaphoraceae. Each cell contains a single saddle-like, H-shaped chloroplast (Figs. 8, 9), which lies with its central isthmus against the epivalve. The single large pyrenoid is tetrahedral (here and in most other larger *Sellaphora* species, it is usually close to being a regular tetrahedron) and lies eccentrically within the chloroplast with one vertex projecting through the central isthmus into the opposite chloroplast lobe. The outer edges of the pyrenoid are entire (Figs. 1, 8), but the edge facing the nucleus is penetrated by a branching system of cavities and tubes (Figs. 2–6, 9–11). The nucleus, which lies as a broad cytoplasmic bridge separating the two apical vacuoles is displaced towards the corner of the cell opposite the pyrenoid (Figs. 7, 12). Two prominent spherical volutin granules are present, one in each vacuole (Figs. 5, 6, 13), usually associated with one of the raphe slits.



Figs. 1–13. *Sellaphora bacillum*, living cells (Ashford-in-the-Water, Derbyshire, England). **1–7** – Successive foci of a cell in girdle view (epivalve at the top). The pyrenoid is entire and triangular in surface view (**1**) but penetrated by branching tubular channels (**2–6**) extending from the nucleus (**6, 7**); the cell also contains two prominent volutin granules (**4–6**, arrow). **8–13** – Successive foci of a cell in valve view, from near the epivalve (**8**) to near the hypovalve (**13**). Again, the pyrenoid is entire and triangular in surface view (**8**) and cytoplasmic invaginations become visible in deeper foci (**10**, arrow). The nucleus (with single spherical nucleolus, arrow **12**) lies on the opposite side of the cell from the pyrenoid. Scale bar = 10 µm.

***Sellaphora pupula* (Kütz.) Mereschk. (Fig. 49):** Cell structure in *S. pupula* and its allies (see MANN et al. 2008 for a taxonomic review) is like that of *S. bacillum* (compare figures 8 and 49). The chloroplast is again saddle-like. The observation of this species led MERESCHKOWSKY (1902) to propose the genus. He unaccountably overlooked the prominent, tetrahedral and invaginated pyrenoid. The nucleus is eccentric. *Sellaphora pupula* is the generitype.

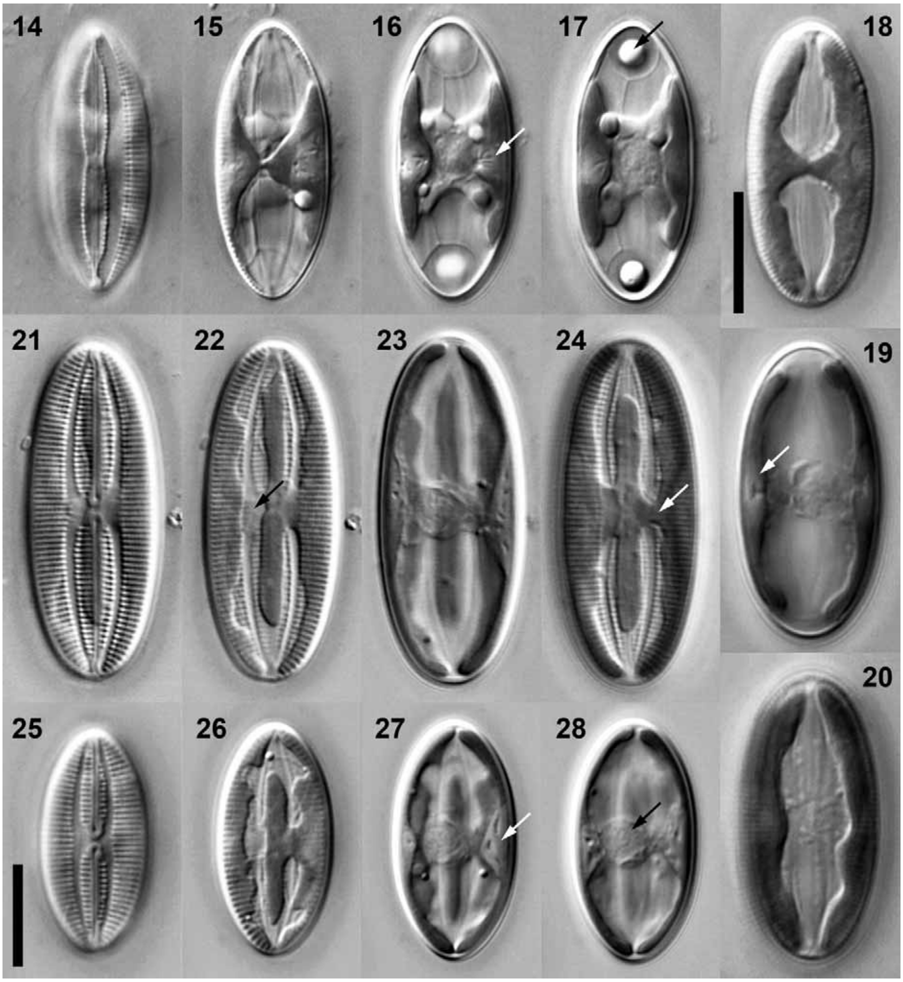
***Rossia* (Figs. 14–17):** *Rossia* valves bear lyre-shaped or linear, lateral areas, in which striae are present but more delicate than elsewhere. The lateral areas also bear small 'pegs', which appear to link to the edge of a very wide conopeum (SIMS and PADDOCK 1979). However, in LM the raphe system does not possess the 'tear-drop' central endings that are characteristic of *Fallacia* (compare figures 14, 21, 25 etc.). *Rossia* was described by VOIGT (1960) and has rarely been reported. The species illustrated here is very similar to '*Navicula hyalinula*' sensu SIMS and PADDOCK (1979) and needs to be transferred to (or described as a new species within) *Rossia*. There is a single H-shaped chloroplast with an extremely narrow connection between the two sides (Fig. 15). Each side contains a slightly angular, invaginated pyrenoid (Figs. 15–17). The nucleus is central, lying in a broad cytoplasmic bridge between the two principal vacuoles. Near each pole, there is a ± spherical compartment of the vacuole surrounding a single large volutin granule (Fig. 17).

***Fallacia pygmaea* (Kütz.) Stickle et D.G. Mann (Figs. 18–20):** There is a single H-shaped chloroplast per cell, whose proximal (Fig. 18) and distal (Fig. 20) margins are plain or slightly undulate. The connection between the two sides of the chloroplast is narrow, but not as fine as in *Rossia.* There is a small cushion-like pyrenoid embedded in the centre of each chloroplast lobe, penetrated by a small, little-branched cavity (Fig. 19). The nucleus was slightly eccentric in the specimens seen (Fig. 19). No volutin granules are present. *Fallacia pygmaea* is the generitype.

***Fallacia forcipata* (Grev.) Stickle et D.G. Mann type I (Figs. 21–28):** *Fallacia forcipata* is a heterogeneous complex and we illustrate four demes here, each with its own chloroplast and frustule morphology (a valve is illustrated for each deme to facilitate future taxonomic revisions). In type 1, the chloroplast has a complex morphology. Essentially, the chloroplast consists of two large, girdle-appressed plates. It is offset with respect to the apical plane, with the isthmus displaced to one side (Fig. 24, arrow; contrast Fig. 18) and the distal margins displaced in the opposite direction (Fig. 22, arrow). The chloroplast isthmus bears two longitudinal extensions beneath the raphe system of the epivalve (Figs. 24, 26), and two similar extensions are formed on the opposite side, by elaboration of the chloroplast margin (Fig. 22). This arrangement persists during size reduction (Figs. 21–24, 25–28). There are two pyrenoids per chloroplast, each flattened, angular and invaginated; they do not extend into the isthmus (Fig. 24). The nucleus is eccentric (Figs. 23, 28). No volutin granules are present.

***Fallacia forcipata* type II (Figs. 29–33):** The chloroplast is simpler than in type I and has a simple or slightly undulate distal margin (compare figures 33 and 20); it is symmetrically placed with respect to the apical plane. Unlike others studied here, it has a very wide isthmus (Fig. 30), accommodating a transversely elongate invaginated pyrenoid (Fig. 31) that is rectangular in valve view. There are two volutin granules, one in each vacuole.

***Fallacia forcipata* type III (Figs. 34–37):** Type III cells (which have strikingly convergent striae at the centre: Fig. 34) have a symmetrically placed chloroplast as in type II, but possess two pyrenoids (Fig. 36), as in type I. The pyrenoids are invaginated and have flat



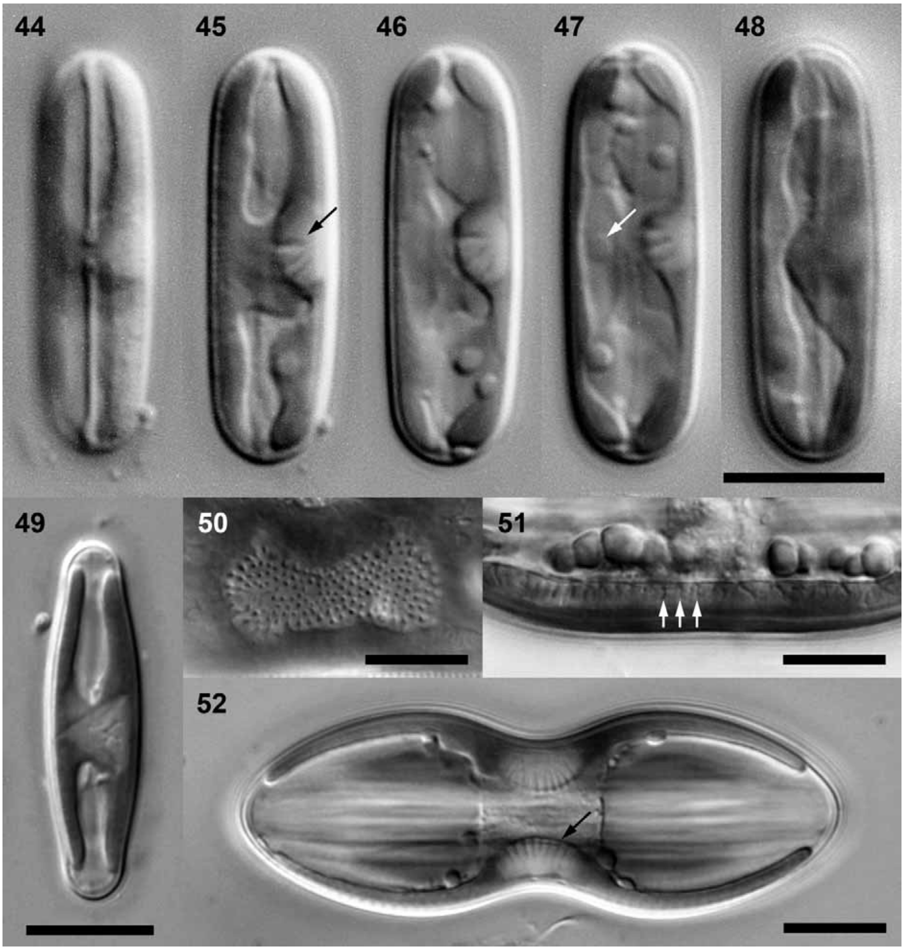
Figs. 14–28. Sellaphorineae, living interphase cells in valve view. **14–17** – *Rossia* valve and successive foci (Portobello Beach, Edinburgh); note the very narrow connection between the two sides of the chloroplast (**15**), the two invaginated pyrenoids (e.g. **16**, arrow), and the two polar volutin granules (e.g. **17**, arrow), each in a special vacuolar compartment. **18–20** – *Fallacia pygmaea* (from a freshwater pond at Ashford-in-the-Water, Derbyshire, England), with a simple H-shaped chloroplast and one small, cushion-like, invaginated pyrenoid (e.g. **19**, arrow) on each side. **21–28** – *Fallacia* cf. *forcipata*, type I: a large (**21–24**) and a small (**25–28**) cell from Portobello Beach, Edinburgh. The longitudinal lobes of the complex chloroplast are connected beneath the epivalve (**24**, arrow) but not beneath the hypovalve (**22**, arrow). Both sides of the chloroplast contain a flat, angular pyrenoid (e.g. **27**, arrow), but the nucleus is nevertheless eccentric (**28**, arrow). Scale bars = 10 µm (use the bar in **25** for all except **18–20**).

tops, rather than the sloping profiles of type I (contrast figures 36 and 23). The chloroplast bears broad lobes alongside the isthmus (Fig. 35) and on the opposite side (Fig. 37); these have no longitudinal extension. The nucleus is eccentric (Fig. 36).

Figs. 29–43. *Fallacia*, living cells in valve view. **29–33** – *Fallacia forcipata*, type II (Cruden bay, near Aberdeen, Scotland), with a relatively simple chloroplast and ± central isthmus (**30**), a single central rectangular pyrenoid and prominent volutin granules (**31**), and eccentric nucleus (**32**). **34–37** – *Fallacia forcipata*, type III (Cruden bay, near Aberdeen, Scotland), with convergent central striae (**34**), central plastid isthmus (**35**), transverse chloroplast lobes (**35**, **37**) and one flat pyrenoid on each side (e.g. **36**, arrow). **38–41** – *Fallacia forcipata*, type IV (Portobello Beach, Edinburgh), with narrow valves (**38**), longitudinal chloroplast lobes (**39**, **41**), eccentric isthmus (**39**), and a single high tetrahedral pyrenoid (**40**, arrow). **42, 43** – Postmitotic *Fallacia forcipata* cells with valve-appressed chloroplasts (Portobello Beach, Edinburgh). Scale bars = 10 μm (use the bar in **43** for all except **42**).

***Fallacia forcipata* type IV (Figs. 38–41):** The principal cytological difference between this and type I is that type IV has only one pyrenoid, which is tetrahedral and lies to one side of the cell (Fig. 40) as in *Sellaphora*. Longitudinal lobes are present beneath the raphe system (Figs. 39, 41).

***Fallacia* cf. *subhamulata* (Grun.) D.G. Mann (Figs. 44–48):** The single H-shaped chloroplast is similar to that of *Sellaphora*, except that the pyrenoid is more rounded (Figs.



Figs. 44–48. *Fallacia* cf. *subhamulata*, living cell in valve view (Threipmuir Reservoir, near Edinburgh), showing the simple H-shaped chloroplast (**45**, **48**), single eccentric, invaginated, cushion-like pyrenoid (**45–47:** arrow in **45**), and eccentric nucleus (**47**, with nucleolus at arrow). **49** – *Sellaphora pupula sensu stricto* (Malham Tarn, N England) with prominent tetrahedral pyrenoid and simple H-shaped chloroplast. **50** – *Pinnularia* cf. *cruciformis* in girdle view (Portobello Beach, Edinburgh): detail of pyrenoid, penetrated by numerous tubular channels. **51, 52** – Marine *Diploneis* species (Portobello Beach, Edinburgh) in which the elongate (**51**) or cushion-like (**52**) pyrenoids are apparently invaginated (arrows). Scale bars = 10 µm.

45–47) with simpler invaginations. The chloroplast was asymmetrically placed with respect to the apical plane in the two specimens photographed (Fig. 48).

***Pinnularia* cf. *cruciformis* (Donkin) Cleve (Fig. 50):** Cells almost always lay in girdle view and possessed two girdle-appressed chloroplasts, each with a single panduriform pyrenoid at its centre (Fig. 50), penetrated by > 100 simple tubular channels.

***Diploneis* spp. (Figs. 51, 52):** Two marine *Diploneis* species apparently had invaginated pyrenoids. The invaginations appeared as simple or branched fine striations.

Cell cycle changes: Although the chloroplast morphologies described above were constant in tens to hundreds of interphase cells examined for each species, major changes in shape and position occur during the cell-cycle. These have been described in detail for *Sellaphora* by MANN (summarized 1989) and involve premitotic translational movement onto the girdle and postmitotic rotation during the development of the new chloroplast isthmuses. Similarly, in *Fallacia*, the chloroplast moves across the cell before cell division to lie beneath the valves with simultaneous simplification of shape (Figs. 42, 43).

Discussion

Some of the observations reported here were used as the basis for the description of *Fallacia* by ROUND et al. (1990: 554), as follows: »Plastid basically H-shaped, consisting of 2 girdle-appressed plates connected by a narrow isthmus lying against the epivalve; there may also be narrow lobes parallel to the raphe, extending out from the isthmus, and from one of the lateral plates. One or two invaginated pyrenoids present.« *Fallacia* chloroplasts have also been described briefly by KUYLENSTIERNA (1989–1990), COX (1996) and SABBE et al. (1999), whose descriptions are consistent with our data, and by KARSTEN (1899: 58, 59), who claimed that *F. pygmaea* and *F. reichardtii* (Grun.) Witkowski, Lange-Bertalot & Metzeltin had two chloroplasts. We believe he was mistaken, because we collected several populations of the *F. pygmaea* species complex from fresh and brackish waters, all of which had a single H-shaped chloroplast, as does the morphologically similar *F. hudsonis* (COX 1996). Cells kept in rough culture, as Karsten's were, often accumulate large amounts of refractile reserve material in the vacuoles, which can obscure fine detail.

Fallacia, *Rossia* and *Sellaphora* therefore share the following cytological characteristics: (1) one chloroplast per cell, (2) chloroplast basically H-shaped, consisting of two large girdle-appressed plates connected by a central isthmus, and (3) pyrenoids invaginated. All *Sellaphora* species studied so far have a simple chloroplast containing a single offset pyrenoid, which is clearly tetrahedral in the larger-celled species (> 10 µm long). *Fallacia* is more variable than *Sellaphora* in chloroplast shape and position (exactly centred with respect to the apical plane or slightly displaced); pyrenoid number (one or two) and shape (regular tetrahedron to flattened rectangular to rounded); and pyrenoid position (usually in the lateral plates but sometimes central). Some *Fallacia* species resemble *Sellaphora* in having a simple chloroplast and a single eccentric pyrenoid (compare figures 44–48 with 49), but the agreement is not exact (e.g. *F.* cf. *subhamulata* has rounded, not strictly polyhedral pyrenoids). The single *Rossia* species examined is unusual among Sellaphoraceae for its extremely narrow chloroplast isthmus, the exactly central nucleus, and the special compartment in each vacuole, containing a volutin granule. Whether this arrangement is typical of other *Rossia* species is unknown (the type of *Rossia* is *R. elliptica* M. Voigt, which is apparently unreported since its discovery).

Fallacia and *Lyrella* were formerly classified together in *Navicula* sect. *Lyratae* because of the presence in both of a lyre-shaped area of plain or only faintly striated silica. The separation of these genera in ROUND et al. (1990), which is supported by *rbc*L data (JONES et al. 2005, EVANS et al. 2008), was based on the presence or absence of a conopeum, the kind of pore occlusion, nuclear behaviour during successive cell divisions, and a »completely different plastid structure and arrangement«. The single *Fallacia* chloroplast occupies the whole of the girdle (except small areas close to the poles) and, as shown here, consists of two large girdle-appressed plates, connected by an isthmus lying against one valve (apparently always the epivalve, as in *Sellaphora*). In *Lyrella*, on the other hand, the chloroplast or chloroplasts lie almost wholly against the valves, leaving the girdle free (MANN and STICKLE 1993, 1997), as in the related genus *Petroneis* (JONES et al. 2005), and the pyrenoids are never invaginated.

The Pinnulariaceae, closely related to the Sellaphoraceae according to molecular data (see Introduction), are not as uniform in cell structure. Some species possess two large girdle-appressed chloroplasts per cell, including *Pinnularia* cf. *cruciformis* (illustrated here) and other marine species (e.g. MERESCHKOWSKY 1901, Pl. 1, Figs. 14, 21, 22; MANN 1996, Fig. 8), and some freshwater species (e.g. HEINZERLING 1908, Pl. 1, Figs. 1, 12; TSCHERMAK-WOESS 1953, Figs. 1, 7; COX 1996, Fig. 22; SCHMID 2003; POULÍČKOVÁ et al. 2007, POULÍČKOVÁ and MANN 2008). Other Pinnulariaceae have H-shaped chloroplasts with an isthmus against one valve (e.g. HEINZERLING 1908, Pl. 1, Fig. 16; TSCHERMAK-WOESS 1953, Figs. 2g, 5, 6; COX 1996, Fig. 26), as in Sellaphoraceae, and the diplastidic *Caloneis amphisbaena* exhibits a transient phase during the cell cycle in which there is a single valve-appressed, H-shaped chloroplast (THALER 1972, Fig. 7e).

Many Pinnulariaceae, both diplastidic and monoplastidic, possess invaginated pyrenoids (TSCHERMAK-WOESS 1953, THALER 1972, MANN 1996, Fig. 8, SCHMID 2001: 10, POULÍČKOVÁ et al. 2007, POULÍČKOVÁ and MANN 2008). The invaginations of the *C. amphisbaena* pyrenoid were studied in thin sections by WALKER et al. (1979), EDGAR (1980) and SCHMID (2001). All shown by EDGAR (1980) contained extensions of the cytoplasm, but SCHMID (2001: 10) states that some are extensions only of the periplastidial compartment, i.e. they are lined by the two inner plastid membranes but not the two outer 'chloroplast endoplasmic reticulum' membranes (unfortunately, membranes are not visible in SCHMID's figures 44 and 45). No other invaginated pyrenoids have been examined ultrastructurally. SCHMID (2001) suggested that this type of pyrenoid represents »significant surface enlargement for localized activity in bi-directional transport phenomena between host and chloroplast (endosymbiont)«, presumably largely in relation to the pyrenoid's function as a key site for carboxylation (e.g. ROBERTS et al. 2007).

Outside the Sellaphorineae, invaginated pyrenoids are very rare. We have not detected them in any other marine or freshwater genera except *Diploneis*, two species of which we illustrate here. S.J.M. DROOP also recorded invaginated pyrenoids in other *Diploneis* species (archived photographs, Royal Botanic Garden Edinburgh) and TSCHERMAK-WOESS (1953) illustrated them in species identified as *Diploneis domblittensis* var. *subconstricta* A. Cleve (in which the invaginations were identical to those shown in our figure 51) and *D. oculata* (Bréb.) Cleve; however, the drawing of the *D. oculata* valve given by TSCHERMAK-WOESS (1953, Fig. 4d) suggests misidentification of *Fallacia pygmaea* or *F. hudsonis*. So far, no molecular data have been published for *Diploneis* species, many of which are difficult to establish in culture (our unpublished observations), and there are few other pointers to a close relationship between the Sellaphorineae and *Diploneis*, apart from the pyrenoid structure. It is not inconceivable, however, that the porous conopea of *Fallacia* (ROUND et al. 1990) and *Rossia* (SIMS and PADDOCK 1979) could be homologous to the outer wall in *Diploneis*. Hence it is unclear whether the invaginated pyrenoids of Sellaphorineae are an autapomorphy for the suborder or symplesiomorphic for a broader grouping including *Diploneis*.

References

BEHNKE, A., FRIEDL, T., CHEPURNOV, V. A., MANN, D. G., 2004: Reproductive compatibility and rDNA sequence analyses in the *Sellaphora pupula* species complex (Bacillariophyta). Journal of Phycology 40, 193–208.

BRUDER, K., MEDLIN, L. K., 2007: Molecular assessment of phylogenetic relationships in selected species/genera in the naviculoid diatoms (Bacillariophyta). I. The genus *Placoneis*. Nova Hedwigia 85, 331–352.

COX, E. J., 1996: Identification of freshwater diatoms from live material. Chapman & Hall, London.

EDGAR, L. A., 1980: Fine structure of *Caloneis amphisbaena* (Bacillariophyceae). Journal of Phycology 16, 62–72.

EVANS, K. M., WORTLEY, A. H., SIMPSON, G. E., CHEPURNOV, V. A., MANN, D. G., 2008: A molecular systematic approach to explore diversity within the *Sellaphora pupula* species complex (Bacillariophyta). Journal of Phycology 44, 215–231.

HEINZERLING, O., 1908: Der Bau der Diatomeenzelle mit besonderer Berücksichtigung der ergastischen Gebilde und der Beziehung des Baues zur Systematik. Bibliotheca Botanica 69, 1–88.

HENDEY, N. I., 1964: An introductory account of the smaller algae of British coastal waters, part V: Bacillariophyceae (Diatoms). H.M.S.O., London.

HUSTEDT, F., 1964: Die Kieselalgen Deutschlands, Österreichs und der Schweiz. In: Dr L. Rabenhorsts Kryptogamenflora von Deutschland, Österreich und der Schweiz, 7 (3: 3), 349–556. Akademische Verlagsgesellschaft, Leipzig.

JONES, H. M., SIMPSON, G. E., STICKLE, A. J., MANN, D. G., 2005: Life history and systematics of *Petroneis* (Bacillariophyta), with special reference to British waters. European Journal of Phycology 40, 43–71.

KARSTEN, G., 1899: Die Diatomeen der Kieler Bucht. Wissenschaftliche Meeresuntersungen, new series (Kiel), 4, 17–205.

KUYLENSTIERNA, M., 1989–1990: Benthic algal vegetation in the Nordre Älv estuary (Swedish west coast). PhD thesis, University of Göteborg.

MANN, D. G., 1989: The diatom genus *Sellaphora*: separation from *Navicula*. British Phycological Journal 24, 1–20.

MANN, D. G., 1996: Chloroplast morphology, movements and inheritance in diatoms. In: CHAUDHARY, B. R., AGRAWAL, S. B. (eds): Cytology, genetics and molecular biology of algae, 249–274. SPB Academic Publishing, Amsterdam.

MANN, D. G., CHEPURNOV, V. A., 2005: Auxosporulation, mating system, and reproductive isolation in *Neidium* (Bacillariophyta). Phycologia 44, 335–350.

MANN, D. G., EVANS, K. M., 2007: Molecular genetics and the neglected art of diatomics. In: BRODIE, J., LEWIS, J. R. (eds), Unravelling the algae – the past, present and future of algal systematics, 231–265. CRC Press, Boca Raton, Florida.

MANN, D. G., STICKLE, A. J., 1993: Life history and systematics of *Lyrella.* Nova Hedwigia 106, 43–70.

MANN, D. G., STICKLE, A. J. 1997: Sporadic evolution of dorsiventrality in raphid diatoms, with special reference to *Lyrella amphoroides* sp. nov. Nova Hedwigia 65, 59–77.

MANN, D. G., THOMAS, S. J., EVANS, K. M., 2008: Revision of the diatom genus *Sellaphora*: a first account of the larger species in the British Isles. Fottea 8, 15–78.

MEDLIN, L. K., KACZMARSKA, I., 2004: Evolution of the diatoms: V. Morphological and cytological support for the major clades and a taxonomic revision. Phycologia 43, 245–270.

MÉRESCHKOWSKY, C., 1901: Études sur l'endochrome des diatomées. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg, Ser. 8, 11, 1–40.

MERESCHKOWSKY, C., 1902: On *Sellaphora*, a new genus of diatoms. Annals and Magazine of Natural History, Ser. 7, 9, 185–195.

POULÍČKOVÁ, A., MANN, D. G., 2008: Autogamous auxosporulation in *Pinnularia nodosa* (Bacillariophyceae). Journal of Phycology 44, 350–363.

POULÍČKOVÁ, A., MAYAMA, S., CHEPURNOV, V. A., MANN, D. G., 2007: Heterothallic auxosporulation, incunabula and perizonium in *Pinnularia* (Bacillariophyceae). European Journal of Phycology 42, 367–390.

ROBERTS, K., GRANUM, E., LEEGOOD, R. C., RAVEN, J. A. 2007: Carbon acquisition by diatoms. Photosynthesis Research 93, 79–88.

ROUND, F. E., 1953: An investigation of two benthic algal communities in Malham Tarn, Yorkshire. Journal of Ecology 41, 174–179.

ROUND, F. E., CRAWFORD, R. M., MANN, D. G., 1990: The diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge.

SABBE, K., VYVERMAN, W., MUYLAERT, K., 1999: New and little-known *Fallacia* species (Bacillariophyta) from brackish and marine intertidal sandy sediments in northwest Europe and North America. Phycologia 38, 8–22.

SCHMID, A. -M. M., 2001: Value of pyrenoids in the systematics of the diatoms: their morphology and ultrastructure. Proceedings 16 International Diatom Symposium, Athens 1–31.

SCHMID, A. -M. M., 2003: Endobacteria in the diatom *Pinnularia* (Bacillariophyceae). I. »Scattered ct-nucleoids« explained: DAP–DNA complexes stem from exoplastidial bacteria boring into the chloroplasts. Journal of Phycology 39, 122–138.

SIMS, P. A., PADDOCK, T. B. B., 1979: Observations and comments on some prominent morphological features of naviculoid genera. Nova Hedwigia 64, 169–191.

SORHANNUS, U., 2007: A nuclear-encoded small-subunit ribosomal RNA timescale for diatom evolution. Marine Micropaleontology 65, 1–12.

THALER, E., 1972: Beitrag zur Entwicklungsgeschichte und zum Zellbau einiger Diatomeen. Österreichische Botanische Zeitschrift 120, 313–347.

TSCHERMAK-WOESS, E., 1953: Über auffallende Strukturen in den Pyrenoiden einiger Naviculoideen. Österreichische Botanische Zeitschrift 100, 160–178.

VOIGT, M., 1960: Some new diatoms from the Far East. Journal of the Royal Microscopical Society, Ser. 3, 78, 92–94.

WALKER, G. K., SICKO-GOAD, L., STOERMER, E. F., 1979: An ultrastructural examination of the pennate diatom *Caloneis amphisbaena*. Microbios Letters 12, 141–152.