# *Cocconeis pediculus* EHRENBERG and *C. placentula* EHRENBERG var. *placentula* (Bacillariophyta): Typification and taxonomy

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**Abstract:** The nominate varieties of the monoraphid diatoms *Cocconeis pediculus* EHRENBERG and *C. placentula* EHRENBERG are typified. Discrepancies from common concepts in Ehrenberg's types, habitats and descriptions were discovered which might affect our current understanding of both *Cocconeis* species. To ensure stabilization of names and concepts for these two taxa, epitypes from a location in Berlin close to the *locus typicus* are presented. Monoclonal cultures of these two taxa have been established. Morphological and morphometric data from clones as well as from populations for both taxa are presented. The taxonomy of *C. pediculus* and *C. placentula* var. *placentula* is discussed and evaluated in the context of historical and recent publications.

**Key words**: diatoms, Cocconeis, typification, taxonomy, micro-morphology, morphometrics, monoclonal cultures, populations

### Introduction

In his early compendium book EHRENBERG (1838) described the diatom genus Cocconeis in Latin and French and offered a great deal of information on (his understanding of) the morphology, habitus and habitat of this monoraphid diatom. Since Cocconeis sits like a buckler ("Schild" in German) on filaments or other microalgae, he named it after the insect genus Coccus L. (scale louse or "Schildlaus"). Ehrenberg first described Cocconeis scutellum Ehrenberg and C. undulata EHRENBERG from brackish waters at Wismar on the Baltic Sea (see also ROMERO 1996, DE STEFANO et al. 2008); the first species is the type of Cocconeis and will be typified in a separate publication (HUCK & JAHN, unpubl.). As next two, EHRENBERG listed C. placentula and C. pediculus from freshwater localities in (at his time close to) Berlin. The last two names are C.? clypeus EHRENBERG and C.? finnica EHRENBERG from fossil material; his markings with a "?" point to the fact that Ehrenberg was not sure that these taxa could be assigned to *Cocconeis*. Consequently, shortly after its description C. clypeus was recombined to Campylodiscus clypeus (Ehrenberg) Ehrenberg ex Kützing which was recently typified and published by POULÍČKOVÁ & JAHN (2007).

*Cocconeis placentula* and *C. pediculus* are some of the most common taxa in freshwater bodies and seem to be cosmopolitan. Since their description 170 years ago, their identity and differentiation seem to be clear (for *C. pediculus* see GERLOFF & RIVERA 1979). Uncertainties and difficulties in differentiation focus on Ehrenberg's taxa *C. lineata* EHRENBERG and *C. euglypta* EHRENBERG and their morphological relation to *C. placentula* var. *placentula;* currently *C. lineata* and *C. euglypta* are commonly considered to be infraspecific varieties of *C. placentula*. This paper deals with the typification and taxonomy of *C. pediculus* and *C. placentula* var. *placentula*.

# Material

The following micas in the Ehrenberg Collection at the Museum für Naturkunde, Berlin (BHUPM) have been studied and photographed :

- EC 544205: Trockenpräparate XLII 5 under the name *Cocconeis pediculus* on *Navicula sigmoidea* (≡ *Nitzschia sigmoidea*) (Fig. 4); template for his drawing on Zeichenblatt No 297 (Fig. 3).
- EC 544206: Trockenpräparate XLII 6 under the

name *Cocconeis placentula* on *Lemna minor* root, marked as  $\alpha$  (Fig. 2); template for his drawing on Zeichenblatt No 301 (Fig. 1).

• EC 544301: Trockenpräparate XLIII 1 under the name *Cocconeis placentula* on *Vaucheria* marked as *β*.

The following drawings from the Ehrenberg Collection have been studied and downloaded (http://download. naturkundemuseum-berlin.de/Ehrenberg/) :

- Zeichenblatt No. 297 is his original drawing of *Cocconeis pediculus* (Fig. 3).
- Zeichenblatt No. 301 is his original drawing of *Cocconeis placentula* (Fig. 1); template for his publication (Ehrenberg 1838, pl. 21: fig. 11).

For further details of the Ehrenberg Collection see LAZARUS & JAHN (1998) and JAHN & KUSBER (2004).

Modern material of these two species has been investigated and is deposited at Botanischer Garten und Botanisches Museum Berlin–Dahlem (B):

- Epiphyton, Landwehrkanal, Tiergarten, Berlin [Latitude 52.511 N, Longitude 13.339 E], leg. Wolf-Henning Kusber, 2005–06–11.
  - a. B 40 0040641: slide with dried raw material (Figs 5–9),
  - b. B 40 0040642: slide with  $H_2O_2$  cleaned material,
  - c. B 40 0040643: tube with  $H_2O_2$  cleaned material.
- 2. Monoclonal culture of *C. pediculus*, strain D36\_020, cell isolated from sample No. 1 by Jana Bansemer.
  a. B 40 0040644: slide (epitype) (Figs 10–21),
  - b. B 40 0040645: SEM stub (Figs 22-27, 44),
  - c. B 40 0040646: tube with H<sub>2</sub>O<sub>2</sub> cleaned material.
- 3. Monoclonal culture of *C. placentula*, strain D36\_012, cell isolated from sample No. 1 by Jana Bansemer.
  - a. B 40 0040647: slide (epitype) (Figs 28–36),
  - b. B 40 0040648: SEM stub (Figs 37–43),
  - c. B 40 0040649: tube with  $H_2O_2$  cleaned material.
- 4. Epiphyton, River Spree, Kreuzberg, Berlin [Latitude 52.495 N, Longitude 13.447 E], leg. Oliver Skibbe, 2005–10–29.
  - a. B 40 0040650: slide (population studies) (Figs 45-51),
  - b. B 40 0040651: SEM stub,
  - c. B 40 0040652: tube with  $H_2O_2$  cleaned material.

Light microscopy-pictures at BHUPM were taken with an Olympus DP 50 and at B with a Zeiss Axioplan DIC; for SEM Philips 515 at B was used.

### Observations

### **Cocconeis pediculus** Ehrenberg

Infusionsthierchen 1838: 194, Tafel XXI, fig. XI. Diagnosis: C. testula ovata, dorso valde convexo, semiglobosa, extus et intus laevis. Translation: shell ovate, very convex on the dorsal side and semiglobose, inside and outside smooth.

**Lectotypus** (here designated): EC 544205 (see Fig. 4); compare to Ehrenberg's drawing sheet 297 (Fig. 3) published as pl. 21: fig. 11 in EHRENBERG (1838).

**Locus typicus**: Bei Berlin ("near Berlin", Germany, currently part of the city of Berlin).

EHRENBERG (1838: 194) elaborates: Ich habe diese besondere Art nur auf andren Naviculis beobachtet. *N. librile* und *sigmoidea* sind zuweilen davon ganz bedeckt und kriechen damit herum. Die mittlere Öffnung, auch die Längsfurche des Panzers sind bei dieser und der vorigen Art deutlich. Länge 1/192 Linie; Breite mehr als die Hälfte der Länge; Höhe 1/3 der Länge. Translation: I have seen this species only on other Navicula. N. librile ( $\equiv$ Cymatopleura librile (EHRENBERG) PANTOCSEK) und *sigmoidea* ( $\equiv$  *Nitzschia sigmoidea*) are often completely covered and creep around with them. The middle opening and the longitudinal line of the shell are well visible in this and the former species (C. placentula). Length 12 µm. Breadth more than half of the length; height one third of the length.

**Epitypus** (here designated): Specimen B 40 0040644 (see Figs. 14, 15) from monoclonal strain D36\_020.

Locus epitypicus: Epiphyton, Landwehrkanal, Tiergarten, Berlin, Germany; 11 June 2005, leg. W.-H. Kusber.

Emended species description of Cocconeis pediculus (Figs 10-27, 44, 46, 48, 49): Valve strongly convex, broadly elliptical or somewhat rhombic-elliptical. Raphe valve (RV) with narrow, linear axial area terminating in a small, semicircular hyaline area near the valve ends. Central area small, circular to somewhat irregular in outline. Raphe filiform, proximal endings close, extending into the central area; distal endings straight, terminating at the small, semicircular hyaline area near the valve end. Striae curved and radiate, finely but distinctly punctuate, not reaching the valve margin, but interrupted by a narrow marginal area, continuous around the valve like a rim (wording modified after PATRICK & REIMER 1966: 240). Sternum valve (SV) with a narrow, linear sternum surrounded by a lyrashaped axial area. Striae curved and radiate with distantly placed conspicuous areolae; in LM, the areolae are externally slit-like and are arranged in longitudinally, undulating rows. In the SEM



Figs 1–9: *Cocconeis pediculus* EHRENBERG and *Cocconeis placentula* EHRENBERG var. *placentula*: (1–4) original material, Ehrenberg Collection (BHUPM), (1–2) *Cocconeis placentula*, (1) part of Ehrenberg's drawing sheet Nr. 301, (2) lectotype: EC 544206; dried preparation, (3–4) *Cocconeis pediculus*, (3) part of Ehrenberg's drawing sheet Nr. 297, (4) Lectotype: EC 544205; dried preparation; (5–9) *Cocconeis*, probably *C. pediculus*, on a filamentous green algae; dried preparation of a modern sample from the locus epitypicus; Landwehrkanal, Tiergarten, Berlin (B 40 0040641). Scale bar 50  $\mu$ m (Fig. 2), scale bar 20  $\mu$ m (Fig. 4), scale bar 10  $\mu$ m (Figs 5–9).

	Length µm	Breadth µm	Breadth to length ratio	RV striae [poroids] / 10 µm	SV striae [areolae] / 10 µm	Autecology
Ehrenberg 1838*	12		more than half of length			Living on other diatoms, Berlin
Kützing 1844	28					Epiphytic on freshwater algae especially <i>Cladophora fracta</i> , common in all of Europe
Van Heurck 1885	15–30			16–17		Fresh and brackish waters, very common
Hustedt 1930	15-56	10–37	0.78	16–18		Widespread and common, best developed in brackish water
Patrick & Reimer 1966	11–30	6–20	0.81-0.84	16–20	15–18	Widespread eurytopous species; epiphytic on aquatic plants, not often found in large numbers resistant to moderate organic pollution; alkaliphil, and salt "indifferent"
Lange–Bertalot 1996						Eutraphentic, very common
Krammer & Lange- Bertalot 2004	12–54	7–37	0.70-0.73	16–24 [18–23]	16–24 [10–13]	Cosmopolitan, epiphyte; in inland waters with medium to higher electrolyte content and in brackish coastal waters. The species massively covers green algae and higher plants.
Kobayası et al. 2006	11-56	6-37		16–24 [18–23]	16–24 [10–13]	Attached, weakly pollution tolerant, in ponds and rivers of Japan, in fresh and brackish waters.
Spree population from Berlin B40 0040650	13.5–38.9 Ø 24.3 n=29	11.8–26.5 Ø 18.4 n=29	0.65–0.9 Ø 0.76 n=29	17–23 Ø 20.4 n=14 [23]	17–21 Ø 19.3 n=15 [11]	Sample (2005-10-29): alkaline, eutrophic, low temperature, electrolyte content see below.
Epitype-strain from Berlin B40 0040644	16.6−40.0 Ø 31.0 n=50	13.0–26.0 Ø 22.0 n=50	0.62 - 0.82 0 = 0.72 n = 50	14–22 Ø 16.4 n=25 [23–25]	14–22 Ø 18.3 n=25 [6–10]	Original epiphytic sample (2005–06–10): alkaline, eutrophic, $17^{\circ}$ C, 725 $\mu$ S cm <sup>-1</sup> .
* Ehrenberg's measur	ements probably corr	respond to C. place	entula			

Table 1. Comparison of morphometric data for Cocconeis pediculus.

	Length µm	Breadth µm	Breadth to length ratio	RV striae [poroids] / 10 μm	SV striae [areolae] /10 µm	Autecology
Ehrenberg 1838*	19		more than 2/3 of length			On <i>Vaucheria</i> and roots of <i>Lemna</i> , Berlin
Kützing 1844						In freshwaters on <i>Vaucheria</i> and roots of <i>Lemna</i> at Berlin, Iceland, Falkland Isles, Chile, Mexico
VAN HEURCK 1885**	12.5–35			15-22		Fresh and brackish waters, common
HUSTEDT 1930**	11–70	8-40	0.75	23	25	Periphyton, very common
Patrick & Reimer 1966**	10-70	8-40	69.0	20–23	24–26	Widespread eurytopous species epiphytic on aquatic plants and other objects. More commonly found in circumneutral to alkaline waters (alkaliphil?); apparently salt "indifferent" but not observed in great numbers in slightly brackish waters.
LANGE–BERTALOT 1996						Tolerant, very common
Krammer & Lange–Bertalot 2004**	7.5–98 [all varieties]	8–40 [all varieties]		20–23	24–26 [18–22]	Cosmopolitan, epiphyte; occurring commonly and often in masses; especially var. <i>eugylpta</i> , var. <i>lineata</i> and var. <i>placentula</i> . They live in standing and running waters also on non–living objects such as wood and stones.
Kobayasi et al. 2006**	10-70	8-40		20–23 [18–22]	24-26 [10–12]	Attached, weakly pollution tolerant, occurs often in Japanese rivers.
Spree population from Berlin B40 0040650	10.9–36.2 Ø 19.5 n=62	7.2–25.7 Ø 12.4 n=62	0.57–0.71 Ø 0.64 n=62	22-26 Ø 23.8 n=35 [24-26]	15-25 Ø 22.0 n=27 [6-8]	Sample (2005–10–29): alkaline, eutrophic, low temperature, electrolyte content see below.
Epitype-Strain from Berlin B40 0040644	14.7–33.7 Ø 29.9 n=50	9.7–22.8 Ø 20.1 n=50	0.61–0.73 Ø 0.67 n=50	18–26 Ø 21.5 n=25 [24–26]	18–26 Ø 21.1 n=25 [6–8]	Original epiphytic sample (2005–06–10): alkaline, eutrophic, 17° C, 725 $\mu S\ cm^{-1}.$
* Ehrenberg's measure: ** the concepts of these r	ments probably cc eferences do not c	rrespond to C. per coincide with the t	<i>liculus</i> ype			

Table 2. Comparison of morphometric data for Cocconeis placentula var. placentula

it can be seen that on the SV the areolae differ greatly between the internal and the external side; the internal are like punctae and the external are closed exhibiting a densely punctuate structure (Figs 25, 26, 44). In GERLOFF & RIVERA (1979) the external areolae look quite differently; this can be due either to destruction of the finely punctuate closing structure or they dealt with a different taxon.

The valvocopula shows the typical rhombicelliptical outline with fimbriate margins only in the central part of the valve, never at the poles (Fig. 16, 19, 27). In the SEM it becomes clear that this is a closed band (see also HOLMES et al. 1982).

Morphometric data (for details see Table 1 and Fig. 52, data in parentheses not our own): Length: (11) 13.5–40.0 (56)  $\mu$ m. Breadth: (6) 11.8–26.5 (37)  $\mu$ m. Striae, both valves: 14–22 (24) in 10  $\mu$ m. Punctae: RV poroids, (18–23) 23–25 in 10  $\mu$ m; SV: 6–11 (10–13); has areolae instead of poroids which form 8-20 (Ø 12.2; n=25) in LM visible longitudinal lines across entire valve width. For future studies we recommend to use breadth/ length ratio which is about 0.75 for *C. pediculus*.

# *Cocconeis placentula* Ehrenberg var. *placentula*

Infusionsthierchen 1838: 194. no figure.

Diagnosis: C. testula elliptica plana, margine abrupto, extus et intus laevis. Translation: Shell elliptic, flat, with abrupt margin, inside and outside smooth.

**Lectotypus** (here designated): EC 544206 (see Fig. 2) compare to Ehrenberg's drawing sheet Zbl 301 (Fig. 1).

**Locus typicus**: Bei Berlin EHRENBERG (1838: 194) elaborates: auf Vaucherien und *Lemna* Wurzeln findet sich diese Form zuweilen sehr zahlreich bei Berlin. Ich sah sie auch am *Byssus* des *Mytilus polymorphus*. Länge 1/120 Linie, Breite mehr als 2/3 der Länge; Höhe 1/4 bis 1/5 der Länge. Eine Abbildung konnte nicht mehr gegeben werden. Translation: This form is found very commonly on *Vaucheria* and roots of *Lemna* at Berlin. Length 19 µm. Breadth more than 2/3 of the length, height 1/4 to 1/5 of the length. It was not possible to present a figure.

**Epitypus** (here designated): B 40 0040647 (see Fig. 28 & 29) from monoclonal strain D36 012.

Locus epitypicus: Epiphyton Landwehrkanal, Tiergarten, Berlin. Germany; 11 June 2005, leg.

## W.-H. Kusber.

Emended species description of C. placentula var. placentula (Figs 28-43, 45, 47, 50, 51): Valve elliptical to somewhat linear-elliptical. RV with very narrow axial area; central area small, more or less oval. Raphe filiform; proximal endings close, distal endings straight, terminating at inner hyaline ring. Striae curved radiate, finely punctuate, interrupted near the margin by a short hyaline area. A second hyaline area surrounds the valve close to the margin isolating a short submarginal area with striae of 3-4 poroids. SV with very narrow, linear sternum surrounded by a wide axial area. Striae also curved and radiate, faintly etched as a shallow trough, with distantly placed conspicuous areolae. Areolae are dash-like (or slit-like) and are arranged in longitudinally, undulating rows (wording strongly modified after PATRICK & REIMER 1966: 240). The valvocopula shows the typical elliptical outline and fimbriate margins all around with additional secondary structures (fimbriae 1st and 2nd order according to KRAMMER & LANGE-BERTALOT 2004: 86), here termed double-fimbriated (Figs 35, 42). In the SEM, it becomes clear that the valvocopula is an open band (see also HOLMES et al. 1982). In the SEM it can also be seen that in the SV areolae greatly differ between the internal and the external side (Figs 40, 41, 43); the internal foramen is rounded while the external ones are dash-like which explain the different images that can be obtained by LM when focussing.

We present our own morphometric measurements only because of differing taxonomic concepts in literature (for details and data from other references see Table 2 and Fig. 52): Length: 10.9–36.2 µm. Breadth: 7.2–25.7 µm. Striae, RV: 18–26 in 10 µm; SV: 15–16 in 10 µm. Punctae: RV poroids, 24–26 in 10 µm; SV: 6–8 in 10 µm, has areolae instead of poroids which form 6–10 ( $\emptyset$  8.6; n=25) in LM visible longitudinal lines across entire valve width. For future studies, we recommend using breadth/length ratio which is about 0.65 for *C. placentula* var. *placentula*.

As seen in the morphometrics of Table 2, mainly in the figures of the SV and the autecology, the species concepts by VAN HEURCK (1880–1881, 1885), PATRICK & REIMER (1966) and KRAMMER & LANGE–BERTALOT (2004) differ from the concept of the type of var. *placentula* as shown here.



Figs 10–21. *Cocconeis pediculus*; monoclonal culture, strain D36\_020; epitype slide B 40 0040644. LM: (10–13) four different foci of the same cell, from raphe valve to sternum valve, (14–15) two different foci of the same cell, raphe valve shows fimbriate lines (Fig. 14) and sternum valve (Fig. 15), (16) closed fimbriate valvocopula, (17) sternum valve, (18) slanted cell showing different foci, in front: raphe valve, in back: sternum valve, (19) small closed fimbriate valvocopula, (20–21) small cell with foci on raphe and sternum valve. Scale bar 10  $\mu$ m.



Figs 22–27. *Cocconeis pediculus*; monoclonal culture, strain D36\_020; epitype culture. SEM: (22) raphe valve, external view, (23) raphe valve, internal view; a smaller valve lies on top of a larger raphe valve, (24) two small sternum valves (external view) are assembled inside a large sternum valve (inside view), (25) sternum valve, external view, (26) sternum valve, internal view, (27) the closed valvocopula has fimbriae with frills which are not present at the poles. Scale bars 10 μm.

### Discussion

As deduced from Ehrenberg's explanation of the locus typicus and the substrata as well as his diagnoses, Ehrenberg's type material of these two taxa differ somewhat from current concepts. Searching his type mica (EC 544205) for *Cocconeis pediculus* specimens, it can be seen that *Nitzschia sigmoidea* is covered with small *Amphora* (?) as well as some *Cocconeis* specimens (Fig. 4), these, however, are not identifiable. In addition, on studying his type mica (EC 544206) for *Cocconeis placentula* it became clear that the identifiable specimens probably correspond to our current concept of *C. pediculus* (Fig. 2); most of them cannot be identified though.

Somewhere along the history of diatom

research a re-interpretation of these two taxa must have taken place. It should be kept in mind that Ehrenberg published a figure (EHRENBERG 1838, pl. 21: fig. 11) only for *C. pediculus* but not for *C. placentula* and that both taxa are too small in order to recognize differences such as details of striation and hyaline ring by means of simple light microscopy at his time.

KÜTZING (1844) though presented a figure for each (*C. pediculus*: t. 5: fig. IX; *C. placentula*: t. 28: fig. 13) and probably most importantly a change of habitat for *C. pediculus* (1844: 71): "on fresh water algae especially *Cladophora fracta*, everywhere in Europe" and an extended habitat for *C. placentula* (1844:73): "..., in Iceland, Falkland Isles, Chile and Mexico." Most important, KÜTZING pictured



Figs 28–36: *Cocconeis placentula*; monoclonal culture, strain D36\_012; epitype slide B 40 0040647. LM: (28–29) two different foci of the same cell, raphe valve shows fimbriate lines, and sternum valve, (30) raphe valve with hyaline ring, (31, 34, 36) sternum valves with differently focused punctae or dashes, (32–33) small cell with foci on raphe and sternum valve, (35–36) same cell; open double-fimbriate valvocopula (Fig. 35) still attached to sternum valve. Scale bar 10 μm.

C. pediculus on filamentous algae (t. 5: fig. 9) and C. placentula as an individual valve (t. 28: fig. 13). Since Ehrenberg did not publish a drawing of C. placentula, Kützing referred to Ehrenberg's later published figures (1843; T. 3; 7, 15 and 4, 1, 9.) based on Vera Cruz and New York living materials, respectively, which show only individual valves. On Ehrenberg's original drawing sheet though, which was never published, it is quite clear that he described C. placentula as living on filamentous structures (Fig. 1). This suggests that due to the missing figure in EHRENBERG (1838) at the time of description and to the change of habitat proposed by KÜTZING (1844), C. pediculus took over the concept, at least of the habitat, of Ehrenberg's placentula.

It took another couple of decades until some valve features such as the hyaline ring and number of striae began to play an important role in separating *C. pediculus* from *C. placentula*. VAN HEURCK'S publication (1880–1881, pl. 30; 1885: 133) seems to be the basis for some of our current concepts. Cocconeis pediculus is presented with its typical sternum valve with undulating longitudinal lines, finely "punctuated" RV and the typical fimbriate valvocopula (1880-1881, pl. 30, figs 28-30). These features are undisputed until today and have been shown in a number of papers (HUSTEDT 1930, PATRICK & REIMER 1966, GERMAIN 1981, KRAMMER & LANGE-BERTALOT 2004) and have been investigated even with electron microscopy by modern authors (GERLOFF & RIVERA 1979, HOLMES et al. 1982, ROUND et al. 1990, see also our Figs 22-27). Cocconeis placentula is presented in VAN HEURCK (1880-1881, pl. 30, figs 26, 27) with a hyaline ring on both SV and RV, both valves are densely punctuated. Cocconeis *lineata* (1880–1881, pl. 30, figs 31, 32) is here treated as an independent species but in VAN HEURCK 1885, it is a variety of C. placentula and C. euglypta as its variety (1880-1881, pl. 30, fig.



Figs 37–42. *Cocconeis placentula;* monoclonal culture, strain D36\_012; epitype culture. SEM: (37) raphe valve, external view, (38) raphe valve, internal view, (39) complete frustule with partly broken raphe valve (external view), sternum valve visible (internal view) and a number of girdle bands, (40) sternum valve, external view, (41) sternum valve, internal view, (42) the open valvocopula has double–fimbriae; the band is partly broken. Scale bars 10 μm.



Figs 43–44. *Cocconeis placentula* var. *placentula* (Fig. 43) and *Cocconeis pediculus* (Fig. 44) from epitype cultures; comparison of external sternum valves (SEM). Scale bars 4 µm (Fig. 43), 6 µm (Fig. 44).



Figs 45–51, *Cocconeis pediculus* (Figs 46, 48, 49) and *Cocconeis placentula* var. *placentula* (Figs 45, 47, 50, 51); mixed sample from population studies; Bewuchs, River Spree, Kreuzberg, Berlin (B 40 0040650). LM. Scale bar 10 μm.

33, 34). However, only the RV of VAN HEURCK *C. lineata* var. *euglypta* (1880–1881, pl. 30, fig. 34) shows the *C. placentula*-typical alternating darker and lighter lines between the hyaline ring and the valve edge which is caused by the double-fimbriated valvocopula (Fig. 42; see also HOLMES et al. 1982).

In the following decades, *C. lineata* and *C. euglypta* kept on being treated as varieties of *C. placentula*, and further varieties were described such as var. *pseudolineata* GEITLER (1927) and var. *euglyptoides* GEITLER (1958). In his papers on "Formwechsel", GEITLER (1927, 1932, 1958, 1982) did his studies only on several varieties of *C. placentula* other than var. *placentula*. HUSTEDT (1930) pictured the species and its varieties *euglypta* and *lineata* without naming var. *placentula* explicitly. Some later authors did

not differentiate varieties but subsumed them under C. placentula (GERMAIN 1981, HOLMES et al. 1982, ROUND et al. 1990). This usage of a species epithet, subsuming all varieties, tends to blur the understanding of the nominate variety, here var. placentula, which presents the original concept of the species. Only recently, the nominate variety has been picked up again and a few pictures are presented which are supposed to represent C. placentula var. placentula (i.e., PATRICK & Reimer 1966, Krammer & Lange-Bertalot 2004, KOBAYASI et al. 2006). Specimens pictured by these later authors somewhat resemble VAN HEURCK's concept but differ between each other; i.e. KOBAYASI et al. (2006) explicitly states that this variety has no prominent transverse lines in the SV (compare data in Table 2).

Currently, the one common feature shared by all



Fig. 52. Comparison of morphometric data for *Cocconeis placentula* var. *placentula* and *Cocconeis pediculus* from two clone cultures (epitype strains) and from one natural sample in Berlin (Spree populations).

varieties of *C. placentula* seems to be the hyaline ring in the RV. Additionally, the double–fimbriated valvocopula (HOLMES et al. 1982) also seems to be a feature at least of the nominate variety. However, the number of striae, the shape of the central area, as well as the number and zigzagpattern of the longitudinal lines of areolae in the SV are the main distinguishing features among varieties (ROMERO & DE STEFANO, unpublished observations) or on species rank (MONNIER et al. 2007). In our study of material from the Berlin type locality we did not find any finely punctuated forms (named var. *placentula* sec. VAN HEURCK, sec. PATRICK & REIMER, sec. KOBAYASI et al.); the epitype has SV with rather widely spaced poroids. In fact, the SV of the epitype does not agree with any common current concept of any variety of *C. placentula*, VAN HEURCK'S *C. lineata* var. *euglypta* (VAN HEURCK 1880–1881, pl. 30, fig. 33) and Geitler's var. *euglyptoides* (GEITLER 1958, p.363; fig. 4c–e, 5 a–c, 6–10) coming the closest. Interestingly, the SV of C. placentula var. placentula and C. pediculus are relatively similar: both have dash-like areoalae, longitudinally arranged in a zigzag-pattern, easily discernable with the LM. In the SEM, the internal valve face of the SV look almost similar, but its external valve face differs (Figs 43, 44). Besides the very different raphe valves (RV) and the strikingly different fimbriate valvocopula, only the wider valves of C. pediculus – about 3/4 of the length - can warrant a distinction under LM (Fig. 52). In mixed and treated samples, where all parts of the frustule are separated, it might be difficult to unambiguously identify C. placentula var. placentula if C. pediculus is co-occurring (Figs 45-52). We realized the extent of this problem when we studied monoclonal cultures of C. pediculus and C. placentula var. placentula which were isolated from the same sample.

In this context, we also noticed differences between cultured and natural specimens. Whereas in *C. placentula* var. *placentula* the breadth to length ratio is very similar between clones and population, the specimens of the natural population of *C. pediculus* are generally wider (Fig. 52) and more strongly curved (Fig. 46) than the valves from monoclonal cultures. This might be an effect of the substrate; whereas *C. pediculus* grows naturally epiphytic on filamentous structures (such as *Cladophora*, see also Figs 5–8) which will determine the curvature, the unialgal clones were grown on a flat surface (petri–dish).

In conclusion, we propose to reconcile Ehrenberg's original material with our current taxonomic concept by presenting epitypes of C. pediculus and C. placentula var. placentula. In recent studies of Berlin diatoms (GEISSLER & KIES 2003), we have found that both species often occur together in intermixed populations. Whenever a filamentous substrate is present, this is mainly covered by valves of Cocconeis pediculus (Figs 5-9). A more accurate observation allows to recognize the occurrence of C. placentula, although less abundant. Referring these findings to Ehrenberg's original material, we conclude that although Ehrenberg's identifiable specimens belong to our current concept of C. pediculus, many cannot be identified and it is concluded that some correspond to C. placentula var. placentula. In order to find a solution that does not destabilize the current usage of the names of these two species, we chose a recent

sample from Berlin waters, the type locality, which contains both species; mainly *C. pediculus* and to a lesser degree *C. placentula* var. *placentula*, to serve as raw material for the epitypes of both species. Both taxa – from the same locality – have been brought into culture and their morphological (this paper) as well as molecular data (in prep.) can serve as reference to distinguish other species or varieties in the future.

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