

Protoraphis Simonsen, a newly recorded marine epizoic diatom genus for China

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Abstract

Epizoic diatoms on marine copepods are common in nature and may have a special ecological relationship with their hosts. However, this special ecological group is not well known, and it has only rarely been studied in the China seas. To address this knowledge gap, the species diversity and classification of epizoic diatoms on planktonic copepods were studied with samples collected from the East China Sea. In the present study, a marine araphid diatom genus *Protoraphis* and its type species, *Pr. hustediana*, were observed and identified by light and electron microscopy, thus representing the first record of this genus and its type species in China. This genus is characterized by a median sternum strongly bent to opposite sides and terminate in two transapical grooves at the valve ends. *Protoraphis hustediana* was found to be epizoic on the posterior body appendages and segments of the marine calanoid copepod *Candacia bradyi*. An internal view shows a complex, ear-shaped process that is close to the apical slit field. The ecological habitats and geographical distributions of *Protoraphis* were also discussed, and, together with complementary morphological studies, our results have increased the number of records for marine epizoic diatoms to three genera with three species in China, including *Pseudohimantidium* and *Pseudofalcula*.

Key words: marine epizoic diatom, copepod, *Protoraphis*, newly recorded genus, ear-shaped process

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1 Introduction

In the last few years, the term “epizoic diatom” has been prominent in the taxonomy of marine diatoms, and many articles on this special diatom group have been continuously published (Sar and Sunesen, 2014; Li et al., 2014; Majewska et al., 2017; Frankovich et al., 2018). Most of these studies were carried out on the carapace or neck skin of sea turtles and the exoskeleton of marine copepods (Fernandes and Calixto-Feres, 2012; Donadel and Torgan, 2016; Gárate-Lizárraga and Esqueda-Escárcega, 2018). According to their results, it seemed that epizoic diatoms occurred with greater abundance on vertebrates compared to invertebrates and that distinct differences existed in the morphology of epizoic diatoms on different hosts (Riaux-Gobin et al., 2017a, b). Numerous new diatom taxa, such as species of *Tursiocola* Holmes, Nagasawa & Takano, *Tripterion* Holmes, Nagasawa & Takano, *Chelonicola* Majewska, De Stefano & Van de Vijver, *Poulinea* Majewska, De Stefano & Van de Vijver and *Medlinella* Frankovich, Ashworth & Sullivan, were described from marine turtles and manatees (Frankovich et al., 2015; Majewska et al., 2015; Frankovich et al., 2016; Riaux-Gobin et al., 2017a, b; Frankovich et al., 2018). In contrast, after Hiromi et al. (1985) and Hallegraeff and McWilliam (1990) recognized only six araphid diatom taxa (*Pseudohimantidium pacificum* Hustedt & Krasske, *Falcula hyalina* Takano, *Protoraphis atlantica* Gibson, *Pr. hus-*

tediana var. *hustediana* Simonsen, *Sceptronema orientale* Takano, and *Licmophora unidenticulata* Takano) as epizoic diatoms on marine copepods, no new species or varieties specific to copepods have been reported.

All the araphid diatoms epizoic on marine copepods are highly distinctive, and most are either monotypic or species-poor genera. For example, both *Protoraphis* Simonsen and *Pseudohimantidium* Hustedt & Krasske have clearly visible sigmoid sternum and polar grooves under light microscopy (LM), but they can be easily distinguished by shapes (Simonsen, 1970). *Falcula hyalina*, which was transferred into the new genus *Pseudofalcula* Gómez, Wang & Lin in Gómez et al. (2018), shows two plate-like chloroplasts and arcuate valve views (Li et al., 2014). Although *Pseudohimantidium pacificum* possesses a sickle-like valve, it can be separated from *Pseudofalcula hyalina* (Takano) Gómez, Wang & Lin by its rostrate apices and stalk-forming colony (Rivera et al., 1986; Fernandes and Calixto-Feres, 2012).

Apart from *Pseudohimantidium pacificum* documented sixty years ago and *Pseudofalcula hyalina* found in the mariculture and mangrove waters, only sparse research on epizoic diatoms has been carried out in China (Voigt, 1959; Li et al., 2014). The present study describes a newly recorded epizoic diatom genus, *Protoraphis*, represented by *Pr. hustediana* var. *hustediana* epizoic on *Candacia bradyi* Scott collected from the East China Sea

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during a survey cruise in the autumn of 2016. Morphology and ultrastructure were examined by light and scanning electron microscopy. Biogeography and ecology of *Protoraphis* taxa were also briefly described.

2 Materials and methods

2.1 Sampling

Copepods in this study were collected on October 1, 2016 by a standard zooplankton net (diameter 80 cm, mesh 505 μm) hauled vertically from the open waters in the East China Sea (26°23'58.194"N, 121°27'06.39"E) at a depth of 79 m. Samples were collected from the bottom of the net and immediately preserved in 5% seawater formalin. The East China Sea is located in the western North Pacific between China and Okinawa in the Ryukyu Arc. It is one of the largest continental shelf seas in the world (Jiao et al., 2005; Takayanagi et al., 2006). The area is about $7.5 \times 10^5 \text{ km}^2$, and the average depth is 349 m (Takayanagi et al., 2006). Three main water systems exist in the East China Sea: fresh water input from the Changjiang (Yangtze) River in the west, the Kuroshio Current in the east, and the mixing water system between them (Jiao et al., 2005). Along the shelf, picoplankton and nanoplankton are very common, and the abundance of diatoms depends on the thickness of the mixed surface layer (Takayanagi et al., 2006).

2.2 Methods

Copepods with epizoic diatoms were examined under an inverted microscope (Olympus CKX41, Japan) and then transferred into a tube with Pasteur pipettes. Epizoic diatoms were removed from the infested copepods by ultrasound at 300 W for 25 s, acidized with HCl (36%–38%) at 100°C for 20 min to eliminate organic matter, and then rinsed with distilled water eight to ten times. Cleaned material was mounted on slides and coverslips for LM (Olympus BX51, Japan) and SEM (JEOL JSM-6390LV, Japan) observations, respectively. LM micrographs were taken by a digital camera (Olympus DP71, Japan). Permanent slides were made with Naphrax[®] and deposited in the School of Life Sciences, Xiamen University, China.

Diatom morphological terminology, as presented in Simonsen (1970), Hallegraeff and McWilliam (1990), Sullivan (1993) and Witkowski et al. (2000), was respectively referenced.

3 Results

Based on our observations and reports in the literature (Simonsen, 1970; Hallegraeff and McWilliam, 1990), the diatom of interest among our specimens was identified as *Pr. hustediana* var. *hustediana*, which was epizoic on the planktonic copepod *C. bradyi* collected from the East China Sea. This is the first record of the genus *Protoraphis* for China. Generic and specific descriptions follow.

3.1 *Protoraphis* Simonsen

Simonsen, 1970, p. 383–394, pl. 1; Gibson, 1979a, p. 109–126, Figs 1–18; Hallegraeff and McWilliam, 1990, p. 39–45, Figs 1–13; Sullivan, 1993, p. 161–167, Figs 1–8; Witkowski et al., 2000, p. 74, 75, pl. 26, Fig. 15, pl. 29, Figs 1–3.

3.1.1 Description

Cells attached to the hosts with mucilaginous stalks (Figs 1a–d). Chloroplasts two or four, large, positioned near the middle of the cell (Fig. 1d). Valves clavate to lanceolate, with broadly rounded apices (Figs 1d–f). Sternum narrow, but conspicuous, straight

and median in the middle of the valve, abruptly bent to opposite sides at the ends, terminating in two polar grooves (Figs 1e, f). Transverse striae parallel, composed of rounded, elliptical or rectangular areolae, interrupted by the sternum (Figs 2a, b, e). Apical groove surrounded by a hyaline zone, penetrating the frustule, forming a siliceous rim (basis) and protruding as a series of specific structures internally (Figs 2b–d and 3b–d). Apical slit fields starting on the valve face and going down the mantle with unequal vertical openings (Figs 2a–d). Girdle bands several to numerous, perforated by two rows of rounded or elongate pores per band (Fig. 2f).

3.1.2 Ecology

Protoraphis was established by Simonsen in 1970. Up to now, only two species and one variety have been reported. All taxa inhabit marine environments and most of them are epizoic on copepods, snails or the second stage larva of a barnacle, the *Cyparis* (Foged, 1984; Sullivan, 1993; Gómez et al., 2018).

3.2 *Protoraphis hustediana* var. *hustediana* Simonsen

Simonsen, 1970, p. 383–394, pl. 1; Hallegraeff and McWilliam, 1990, p. 39–45, Figs 1–13; Witkowski et al., 2000, p. 75, pl. 29, Figs 1 and 2; Guiry and Guiry, 2018.

3.2.1 Description

Chloroplasts four, large, positioned close to the middle of the cell (Figs 1b–d). Frustules in girdle view rectangular to slightly inflexed (Fig. 1d). Valves lanceolate, diagonally symmetrical, with broadly rounded apices (Figs 1d–f and 2a). Apical axis 45–129 μm , transapical axis 4–10 μm . Striae uniseriate, composed of rounded areolae (Figs 2a–e). Transverse rows 31 in 10 μm , longitudinal rows 3–4 in 1 μm . Sternum distinct, linear, lying in the median position for almost its entire length, bent to opposite sides at the apices (Figs 1e, 1f and 2a–d). A total of 12–16 vertical openings present in the apical slit fields (Figs 2b–d). A groove (1.1–1.7 μm long) penetrating the valve located in the hyaline zone at the end of sternum, exposing a siliceous structure concave to the valve pole (Figs 2a–d). Internally, margin of groove thickened and developed as an ear-shaped basis (1.3–2 μm long), with a large E-shaped lip protruding from the distal side and a small lamelliform or U-shaped lip projecting from the opposite side (Figs 3b–d). Transapical striae slightly depressed between weakly developed virgae (Fig. 3e). Girdle bands open, with two rows of rounded pores (Fig. 2f).

3.2.2 Ecology

In our material, *Pr. hustediana* var. *hustediana* attached to the hosts with unbranched mucilaginous stalks. They usually occurred as solitary cells or formed short chains by apex-to-apex. It seemed that this taxon preferred to infect the posterior body appendages and segments of the calanoid copepods. All three host copepods in our study were males. Hallegraeff and McWilliam (1990) also reported that the diatom taxon was only epizoic on male calanoid copepods (*C. discaudata* Scott).

3.2.3 Distribution

The diatom species *Pr. hustediana* was first found in the Arabian Sea and Persian Gulf by Simonsen in 1970. Hallegraeff and McWilliam (1990) recorded *Pr. hustediana*, which was recognized as var. *hustediana* in Sullivan (1993), from coastal waters of northwestern Australia. Our copepods infested with diatoms were sampled from open waters in the East China Sea.

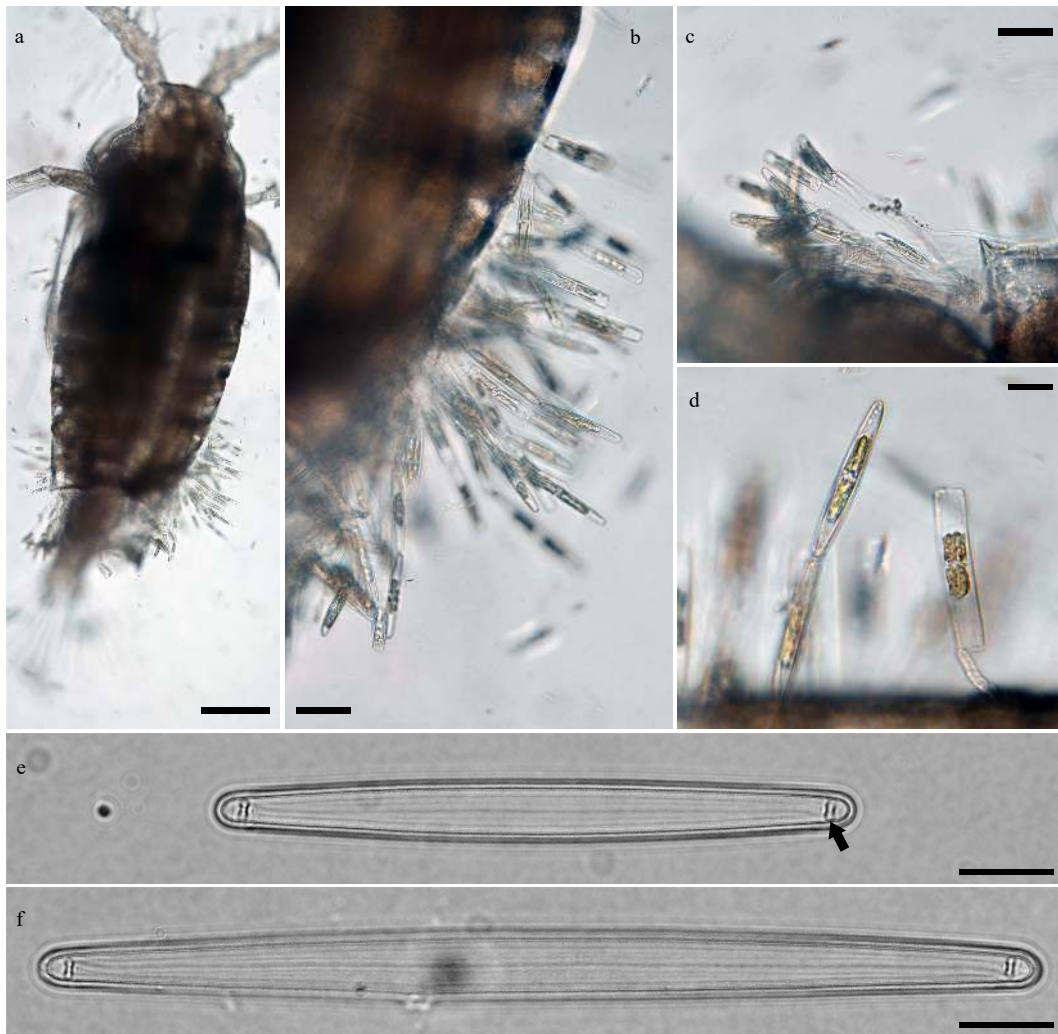


Fig. 1. *Protoraphis hustediana* var. *hustediana* Simonsen. LM. a–c. Living colonies on *Candacia bradyi* Scott; d. cells with chloroplasts, one showing girdle view; and e and f. cleaned frustules showing sternum and polar grooves (arrow). Scale bars: 200 μm (a), 50 μm (b, c); 20 μm (d), and 10 μm (e, f).

4 Discussion

Protoraphis is a distinct araphid diatom genus characterized by its linear valve, sigmoid sternum and transapical grooves at the valve ends. Its type species, *Pr. hustediana*, was first described in Simonsen (1970). After that, Gibson (1979a) reported a new species, *Pr. atlantica*, from the northwestern Atlantic Ocean. In addition, a variety, *Pr. hustediana* var. *nana* Takano, was reported from the northwestern Pacific Ocean (Takano, 1985). Results showed that its transapical groove was shorter than that in the nominate variety and that an internal Y-shaped process was positioned at the groove. The fine structure of *Pr. hustediana* var. *hustediana* was first revealed by Hallegraeff and McWilliam (1990). Considering that the ear-shaped processes located near the apices were complex and specific, the authors hypothesized that the raphe system in raphid diatoms and the grooves in *Pr. hustediana* var. *hustediana* were homologous. *Pseudohimantidium* also displays similar sternum and grooves, but it can be easily distinguished by its scythe-shaped valve and series of rimoportulae at each apex of the valve (Simonsen, 1970; Rivera et al., 1986). Based on these facts, the two genera were merged into the family Protoraphidaceae by Simonsen (1970). So far, although the significance of the groove has not been confirmed,

most studies have recognized that the mucilaginous stalks in Protoraphidaceae taxa are not secreted by this structure (Gibson, 1979a, b; Sullivan, 1993).

Protoraphis has some morphological similarities with *Neosynedra* Williams & Round, *Cyclophora* Castracane and *Lucanicum* Lobban & Ashworth (Table 1). All of these diatoms share somewhat lanceolate or linear valve outlines and structureless valves when observed with light microscope. Since an apical slit field is one of their common features, several studies have reported on this feature, making respective comparisons among these genera (Round et al., 1990; Lobban and Ashworth, 2014; Gómez et al., 2018). The *Protoraphis* taxa differ mainly from *N. provincialis* (Grunow) Williams & Round by their grooves with complex labiate processes and uninterrupted apical slits (Table 1). *Cyclophora* is characterized by the central pseudosepta on the valves and the absence of polar grooves. The general shape of this genus is often constricted in the middle or below the apices (Ashworth et al., 2012). *Lucanicum* is a benthic genus with long chains, while *Protoraphis* can only form short chains or live in a solitary frustule. Like *Neosynedra* and *Cyclophora*, *Lucanicum* also bears a simple rimoportula near each apex (Table 1). The striae of *Lucanicum* are composed of transapically elongated macroareolae,

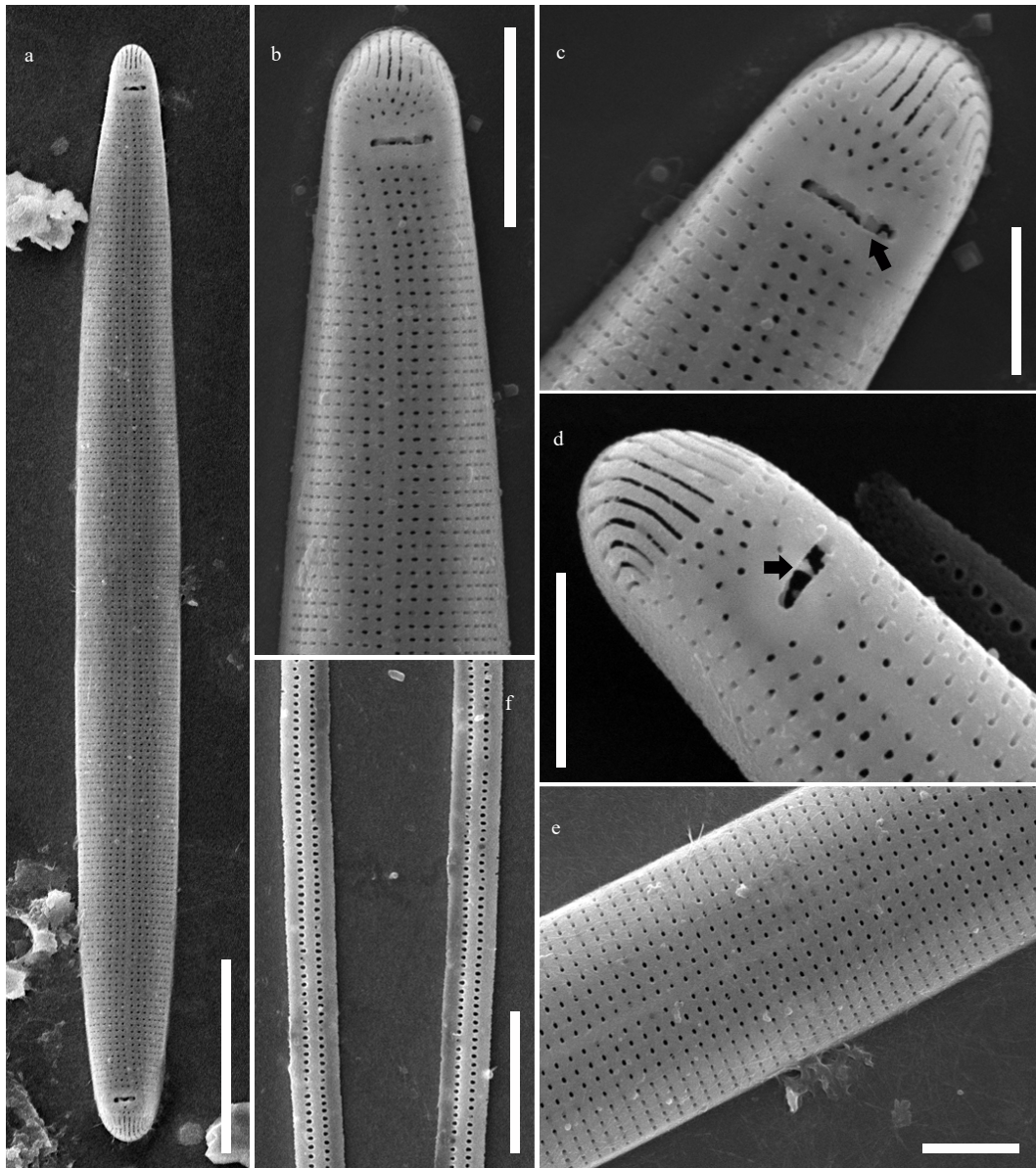


Fig. 2. *Protoraphis hustediana* var. *hustediana* Simonsen. SEM. a–e. External valve view: entire valve (a); valve ends showing apical slit fields and transapical grooves, note the siliceous structure concave to the valve pole (arrows) (b–d); mid-valve with uniseriate striae composed of rounded areolae (e). f. Detail of girdle bands. Scale bars: 10 μm (a), 5 μm (b, f), and 1 μm (c–e).

while areolae in *Protoraphis* are very small (Lobban and Ashworth, 2014). Consequently, critical features of these genera are apparent and easily to be recognized under light and electronic microscopy.

The dimensions and fine structures of the valves in our material are close to those in Hallegraeff and McWilliam (1990) (Table 2). But our SEM images revealed that the U-shaped lip combined with the groove can develop as a lamelliform structure with two spines (Fig. 3b). Compared to the complex ear-shaped labiate process in *Pr. hustediana* var. *hustediana*, a simpler Y-shaped protrusion presents in var. *nana* (Sullivan, 1993). Sullivan (1993) suggested that “all features of valve morphology appear to be identical” in the genus *Protoraphis*. In fact, some slight distinctions in valve morphology are present within the genus, except for the heteropolarity of *Pr. atlantica*. It is clear that the maximum valve lengths in both *Pr. hustediana* var. *nana*

(57 μm) and *Pr. atlantica* (50 μm) are much shorter than valve length in *Pr. hustediana* var. *hustediana* (130 μm). According to Figs 4–8 in Sullivan (1993), the areolae in *Pr. hustediana* var. *nana*, which are similar to those in *Pr. atlantica*, seem to be elliptical or rectangular. However, *Pr. hustediana* var. *hustediana* only has small, rounded areolae based on our results (Figs 2b–e and 3b–e) and those of Hallegraeff and McWilliam (1990). Furthermore, both *Pr. hustediana* var. *nana* (Fig. 4 in Sullivan, 1993) and *Pr. atlantica* (Fig. 4 in Gibson, 1979a) have two rows of elongate pores on the girdle bands, while the bands of *Pr. hustediana* var. *hustediana* are pierced by two rows of rounded pores (Fig. 2f). Therefore, although no internal view of *Pr. hustediana* was shown in Gómez et al. (2018), the taxon seems rather to represent var. *nana* based on their description.

Up to now, *Protoraphis* has been reported from the Arabian and Persian Gulfs, the United States, Japan, Australia, the Carib-

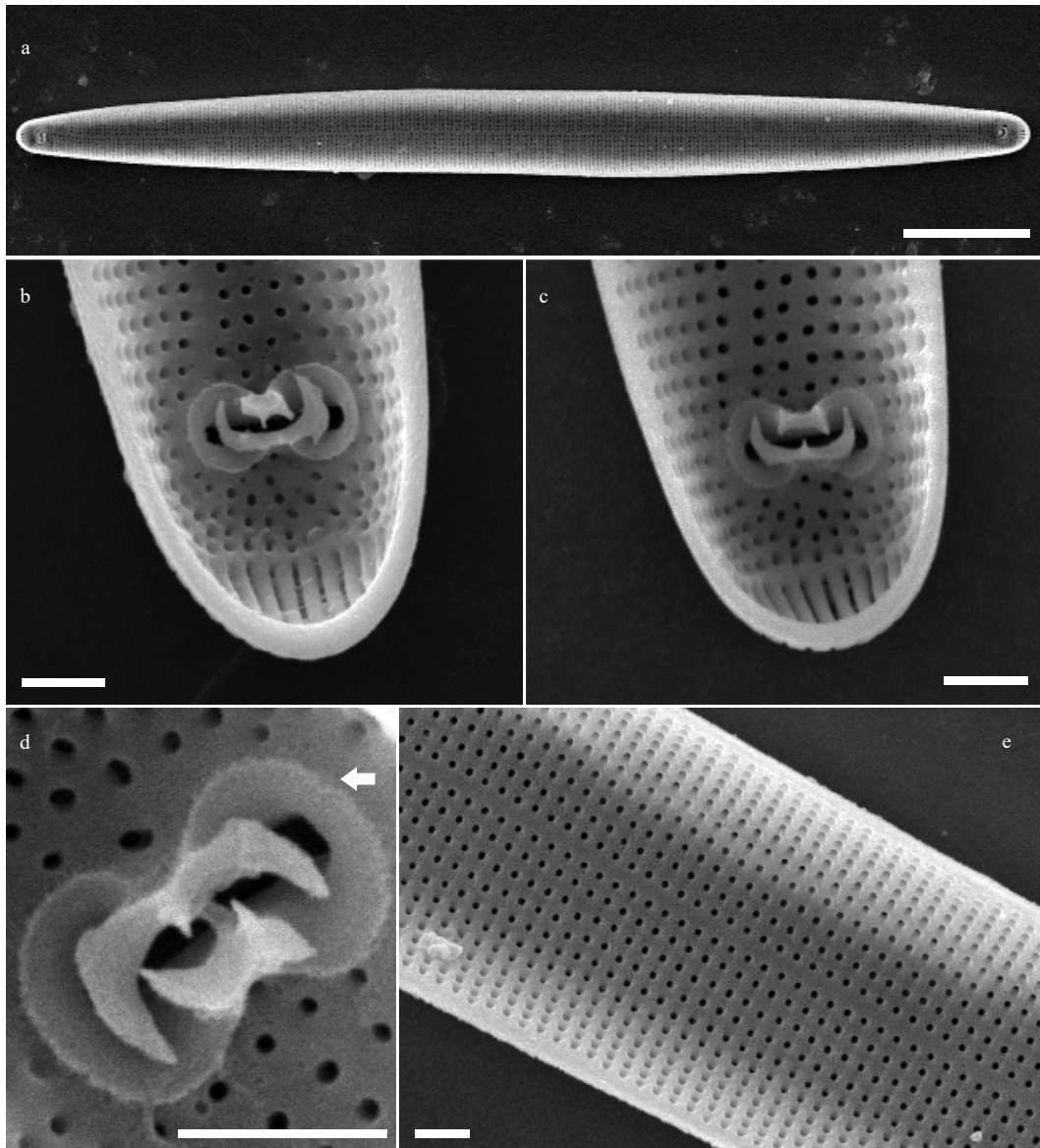


Fig. 3. *Protoraphis hustedtiana* var. *hustedtiana* Simonsen. SEM. Internal valve views. a. Entire valve; b–d. close up of ear-shaped processes located near the apices, and arrow indicating the basis; and e. close up of the valve middle, note the striae forming areolae depressed between the narrow viminae. Scale bars: 10 μm (a), 1 μm (b–e).

bean Sea, Brazil and the East China Sea (Simonsen, 1970; Gibson, 1979a; Foged, 1984; Takano, 1985; Hallegraeff and McWilliam, 1990; Sullivan, 1993; Witkowski et al., 2000; Gómez et al., 2018). This genus distributes mainly in the Indian Ocean, the West Atlantic Ocean and the North Pacific Ocean. Our result enlarges the global distribution of this genus and indicates that *Protoraphis* may be widespread in the world. In the present study, *Pr. hustedtiana* var. *hustedtiana* was observed on the posterior body appendages and segments of planktonic copepods, consistent with the results in Gibson (1979a) and Hallegraeff and McWilliam (1990). *Candacia* Dana seemed to be one of the most common copepod hosts for *Protoraphis*. The occurrence of *Protophis* taxa (except for *Pr. hustedtiana* var. *nana* and *Pr. hustedtiana* f. *latior* Foged) on specific body parts is probably related to the motion of planktonic copepods. As the main appendages for swimming, the first antennae of calanoid copepods are generally longer than those of harpacticoid families, and their strong swing may inter-

fere with the attachment of epizoic diatoms to the anterior body appendages and segments. But harpacticoid copepods are mostly benthic and their first antennae are usually very short. The less swing range of first antennae may have no influence on the attachment diatoms. That may explain why *Pr. atlantica* can be found on the all body segments of harpacticoid copepods (Gibson, 1979a). In some ways, the infestation of *S. orientale* on the harpacticoid copepod *Euterpina acutifrons* Dana confirmed our inference of the first antennae (Skovgaard and Saiz, 2006; Sar and Sunesen, 2014). As for *Pseudofalcula hyalina*, which attaches itself to various parts of *Acartia* Dana by mucilaginous pads (Takano, 1983; Prasad et al., 1989), its smaller cell size and shorter extension may not interfere with movement of the first antennae. Gibson (1979a) insisted that the infestation of *Pr. atlantica* can be related to the mating behavior of copepod hosts. However, neither our observations nor those of Hallegraeff and McWilliam (1990) were based on finding *Pr. hustedtiana* var. *hus-*

Table 1. Comparison of *Protoraphis* with related genera

	<i>Protoraphis</i> 1, 2, 3, 4, 5, 6	<i>Pseudohimantidium</i> 7, 8, 9	<i>Neosynedra</i> 10, 11, 12	<i>Cyclophora</i> 12, 13	<i>Lucanicum</i> 14
Order	Protoraphidales	Protoraphidales	Fragilariales	Cyclophorales	Cyclophorales
Colony	solitary or in short chains	solitary	zig-zag	zig-zag	apex-to-apex into nearly straight chains
Frustule outline	clavate to lanceolate	sickle-shaped	linear or undulate	lanceolate to linear	linear
Chloroplasts	two or four	multiple	four	four to multiple	multiple
Sternum	straight in the middle of the valve, abruptly bent to opposite sides at the ends	principally median, or slightly off-centre, narrow, strongly curved at the apices to form a hook-like shape	straight	straight	straight
Areolae	small, rounded, elliptical or rectangular	small, elliptical or rounded	small, elliptical or somewhat quadrate	small, elliptical or rectangular	elongated macroareolae
Apical slit fields	slits uninterrupted	elongated perforations	slits intermittent	slits intermittent	slits intermittent
Pseudosepta	-	-	-	+	-
Grooves	+	+	-	-	-
Labiata processes	ear-shaped, Y-shaped processes or plicate siliceous bands	rimoportulae	rimoportulae	rimoportulae	rimoportulae
Ecology	epizoic	epizoic	epiphytic/benthic	epiphytic/benthic	benthic

Note: 1 represents Simonsen, 1970; 2 Gibson, 1979a; 3 Hallegraeff and McWilliam, 1990; 4 Sullivan, 1993; 5 Witkowski et al., 2000; 6 present study; 7 Gibson, 1979b; 8 Rivera et al., 1986; 9 Fernandes and Calixto-Feres, 2012; 10 Williams and Round, 1986; 11 Takano, 1988; 12 Round et al., 1990; 13 Ashworth et al., 2012; and 14 Lobban and Ashworth, 2014.

Table 2. Biometric data and morphological features of the *Protoraphis* taxa

	<i>Pr. hustediana</i>				<i>Pr. atlantica</i>
	<i>var. hustediana</i>		<i>var. nana</i>	5	
	1	2			
Valve length/ μm	45–129	40–130	³ 19–57 / ⁴ 32–48	46–112.5	18–50
Valve width/ μm	4–10	5–8	³ 4.5–5.8 / ⁴ 4.5	5–5.5	4–11
Transverse striae in 10 μm	31	32	³ 32 / ⁴ 34–36	30–32	33–40
Areolae	rounded, 3–4 in 1 μm	rounded, no data	⁴ elliptical or rectangular, 4 in 1 μm	-	elliptical to rectangular, no data
Number of apical silts	12–16	12–18	³ 8 / ⁴ 12	-	60 in 10 μm
Groove length/ μm	1.1–1.7	1.5	³ ca. 0.7 / ⁴ 0.6–0.85	-	-
Labiata processes	ear-shaped, 1.3–2 μm long	ear-shaped, 1.6–2 μm long	Y-shaped, no data	-	plicate siliceous band, no data
Girdle bands	two rows of rounded pores	two rows of rounded pores	⁴ two rows of elongate pores	-	two rows of elongate pores

Note: 1 represents the present study; 2 Hallegraeff and McWilliam, 1990; 3 Takano, 1985; 4 Sullivan, 1993; 5 Simonsen, 1970; and 6 Gibson, 1979a.

tediana on female copepods. In our opinion, more specimens from different locations should be examined to confirm if *Pr. hustediana* var. *hustediana* is specific to male individuals, and more *in vitro* experiments should be conducted to explain the relationship between *Pr. hustediana* var. *hustediana* and *Candacia*.

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References

- Ashworth M P, Ruck E C, Lobban C S, et al. 2012. A revision of the genus *Cyclophora* and description of *Astrosyne* gen. nov. (Bacillariophyta), two genera with the pyrenoids contained within pseudosepta. *Phycologia*, 51(6): 684–699, doi: 10.2216/12-004.1
- Donadel L, Torgan L C. 2016. *Falcula hyalina* (Fragilariaceae, Bacillariophyta) from a coastal lagoon, Southern Brazil: an additional approach on its morphology. *Phytotaxa*, 243(2): 185–189, doi: 10.11646/phytotaxa.243.2.10
- Fernandes L F, Calixto-Feres M. 2012. Morphology and distribution of two epizoic diatoms (Bacillariophyta) in Brazil. *Acta Botanica Brasiliica*, 26(4): 836–841, doi: 10.1590/S0102-33062012000400012
- Foged N. 1984. Freshwater and littoral diatoms from Cuba. *Bibliotheca Diatomologica*, 5: 1–243
- Frankovich T A, Ashworth M P, Sullivan M J, et al. 2016. *Medlinella amphoroidea* gen. et sp. nov. (Bacillariophyta) from the neck skin of Loggerhead sea turtles (*Caretta caretta*). *Phytotaxa*, 272(2): 101–114, doi: 10.11646/phytotaxa.272.2.1
- Frankovich T A, Ashworth M P, Sullivan M J, et al. 2018. Epizoic and apochlorotic *Tursiocola* species (Bacillariophyta) from the skin of Florida manatees (*Trichechus manatus latirostris*). *Protist*, 169(4): 539–568, doi: 10.1016/j.protis.2018.04.002
- Frankovich T A, Sullivan M J, Stacy N I. 2015. *Tursiocola denysii* sp. nov. (Bacillariophyta) from the neck skin of Loggerhead sea turtles (*Caretta caretta*). *Phytotaxa*, 234(3): 227–236, doi: 10.11646/phytotaxa.234.3.3
- Gárate-Lizárraga I, Esqueda-Escárcega G M. 2018. *Ditrichocorycaeus*

- anglicus* (Copepoda; Poecilostomatoidea), new basibiont of *Pseudohimantidium pacificum* (Bacillariophyceae) in Bahía de La Paz, Gulf of California. *CICIMAR Océánides* (in Spanish), 33(1): 63–67
- Gibson R A. 1979a. *Protoraphis atlantica* sp. nov., a new marine epizoic diatom. *Bacillaria*, 2: 109–126
- Gibson R A. 1979b. An ultrastructure study of *Pseudohimantidium pacificum* Hust. & Krasske (Bacillariophyceae: Photraphidaceae) with special reference to the labiate processes. *Nova Hedwigia Beihefte*, 64: 147–161
- Gómez F, Wang Lu, Lin Senjie. 2018. Morphology and molecular phylogeny of epizoic araphid diatoms on marine zooplankton, including *Pseudofalcula hyalina* gen. & comb. nov. (Fragilariophyceae, Bacillariophyta). *Journal of Phycology*, 54(4): 557–570, doi: [10.1111/jpy.12760](https://doi.org/10.1111/jpy.12760)
- Guiry M D, Guiry G M. 2018. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org> [2003–09–22/2018–07–15]
- Hallegraeff G M, McWilliam P S. 1990. The complex labiate process of the epizoic diatom *Protoraphis hustedtiana* Simonsen. *Beihefte zur Nova Hedwigia*, 100: 39–45
- Hiroimi J, Kadota S, Takano H. 1985. Diatom infestation of marine copepods (review). *Bulletin of Tokai Regional Fisheries Research Laboratory*, 117: 37–45
- Jiao Nianzhi, Yang Yanhui, Hong Ning, et al. 2005. Dynamics of autotrophic picoplankton and heterotrophic bacteria in the East China Sea. *Continental Shelf Research*, 25(10): 1265–1279, doi: [10.1016/j.csr.2005.01.002](https://doi.org/10.1016/j.csr.2005.01.002)
- Li Xuesong, Chen Changping, Liang Junrong, et al. 2014. Morphology and occurrence of a marine epizoic diatom *Falcula hyalina* Takano (Bacillariophyta) in China. *Algological Studies*, 145–146: 169–179, doi: [10.1127/1864-1318/2014/0158](https://doi.org/10.1127/1864-1318/2014/0158)
- Lobban C S, Ashworth M P. 2014. *Lucanicum concatenatum*, gen. nov., sp. nov., a benthic marine diatom from Guam, and a less restrictive diagnosis for Cyclophorales (Bacillariophyta). *Marine Biodiversity Records*, 7: 1–8, doi: [10.1017/S1755267214000918e90](https://doi.org/10.1017/S1755267214000918e90)
- Majewska R, Kociolek J P, Thomas E W, et al. 2015. *Chelonicola* and *Poulinea*, two new gomphonemoid diatom genera (Bacillariophyta) living on marine turtles from Costa Rica. *Phytotaxa*, 233(3): 236–250, doi: [10.11646/phytotaxa.233.3.2](https://doi.org/10.11646/phytotaxa.233.3.2)
- Majewska R, Van de Vijver B, Nasrolahi A, et al. 2017. Shared epizoic taxa and differences in diatom community structure between green turtles (*Chelonia mydas*) from distant habitats. *Microbial Ecology*, 74(4): 969–978, doi: [10.1007/s00248-017-0987-x](https://doi.org/10.1007/s00248-017-0987-x)
- Prasad A K S K, Livingston R J, Ray G L. 1989. The marine epizoic diatom *Falcula hyalina* from Choctawhatchee Bay, the Northwestern Gulf of Mexico: frustule morphology and ecology. *Diatom Research*, 4(1): 119–129, doi: [10.1080/0269249X.1989.9705057](https://doi.org/10.1080/0269249X.1989.9705057)
- Riaux-Gobin C, Witkowski A, Kociolek J P, et al. 2017a. New epizoic diatom (Bacillariophyta) species from sea turtles in the Eastern Caribbean and South Pacific. *Diatom Research*, 32(1): 109–125, doi: [10.1080/0269249X.2017.1299042](https://doi.org/10.1080/0269249X.2017.1299042)
- Riaux-Gobin C, Witkowski A, Chevallier D, et al. 2017b. Two new *Tur-siocola* species (Bacillariophyta) epizoic on green turtles (*Chelonia mydas*) in French Guiana and Eastern Caribbean. *Fottea*, 17(2): 150–163, doi: [10.5507/fof.2017.007](https://doi.org/10.5507/fof.2017.007)
- Rivera P S, Gonzalez H E, Barrales H L. 1986. Cingulum and valve morphology of *Pseudohimantidium* Hustedt & Krasske (Bacillariophyceae). *Phycologia*, 25(1): 19–27, doi: [10.2216/i0031-8884-25-1-19.1](https://doi.org/10.2216/i0031-8884-25-1-19.1)
- Round F E, Crawford R M, Mann D G. 1990. *The Diatoms. Biology and Morphology of the Genera*. Cambridge: Cambridge University Press, 345–447
- Sar E A, Sunesen I. 2014. The epizoic marine diatom *Sceptronema orientale* (Licmophoraceae, Licmophorales): epitypification and emendation of specific and generic descriptions. *Phytotaxa*, 177(5): 269–279, doi: [10.11646/phytotaxa.177.5.3](https://doi.org/10.11646/phytotaxa.177.5.3)
- Simonsen R. 1970. Protoraphidaceae, eine neue Familie der Diatomeen. *Nova Hedwigia Beihefte* (in German), 31: 377–394
- Skovgaard A, Saiz E. 2006. Seasonal occurrence and role of protistan parasites in coastal marine zooplankton. *Marine Ecology Progress Series*, 327: 37–49, doi: [10.3354/meps327037](https://doi.org/10.3354/meps327037)
- Sullivan M J. 1993. The labiate process of the diatom *Protoraphis hustedtiana* var. *nana* Takano. *Nova Hedwigia Beihefte*, 106: 161–167
- Takano H. 1983. New and rare diatoms from Japanese marine waters—XI. Three new species epizoic on copepods. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 111: 23–35
- Takano H. 1985. A small form of the marine diatom *Protoraphis hustedtiana*, epizoic on a snail. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 117: 31–35
- Takano H. 1988. A bloom of *Neosynedra provincialis* in a maricultural tank. *Diatom* (in Japanese), 4: 17–19
- Takayanagi K, Nishiuchi K, Yokouchi K, et al. 2006. A possible collaboration with China on marine ecosystem research in the East China Sea. *Japan Agricultural Research Quarterly*, 40(1): 59–64, doi: [10.6090/jarq.40.59](https://doi.org/10.6090/jarq.40.59)
- Voigt M. 1959. Nouvelle note concernant le genre *Pseudohimantidium*. *Vie Milieu* (in French), 10: 199–203
- Williams D M, Round F E. 1986. Revision of the genus *Synedra* Ehrenb. *Diatom Research*, 1(2): 313–339, doi: [10.1080/0269249x.1986.9704976](https://doi.org/10.1080/0269249x.1986.9704976)
- Witkowski A, Lange-Bertalot H, Metzeltin D. 2000. Diatom flora of marine coasts I. In: Lange-Bertalot H, ed. *Iconographia Diatomologica*. Ruggell: A. R. G. Gantner Verlag Kommanditgesellschaft, 74–75