Research Article

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A new species of *Craspedostauros* (Bacillariophyceae) from the west coast of Sweden, with taxonomic and ecological notes on *Craspedostauros laevissimus*

https://doi.org/10.1515/bot-2023-0065
Received August 18, 2023; accepted December 5, 2023;
published online January 5, 2024

Abstract: Since its separation from *Stauroneis* in 1999, several new species of *Craspedostauros* were discovered in a variety of habitats and geographic locations, adding morphological and phylogenetic data to the investigations of the genus. In a survey of littoral diatoms of Sweden, both on the west and east coasts, two epiphytic stauros-bearing species were encountered and assigned to *Craspedostauros* following the characteristic features of this genus, including the possession of a stauros narrower than the central area and cribrate areolae. One species is described as new to science; *Craspedostauros lateralis* sp. nov., and the other is of uncertain identity but bears morphological similarity to *C. laevissimus*. *Caspedostauros lateralis* is a marine epiphytic species found in the west coast of Sweden, off Gothenburg city. Based on light and electron microscopy, a detailed description of the morphological and ultrastructural features of these species is given and a comparison of the distinguishing characters with allied species is discussed. Some ecological data and the occurrence of associated species on the host macrophyte are provided.

Keywords: brackish water; epiphytic diatoms; marine; morphology; taxonomy

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1 Introduction

Although the study of Swedish diatoms extends for more than a century and a half, yet we do not have an estimate on how many species exist in the extensive aquatic habitats of the country. Diatom investigation in Sweden seems to have initiated by the work of Cleve (1895) on the freshwater species occurring in Lule Lappmark in the northern regions of the country. Brackish water diatom in the Baltic coast of Sweden received more attention and were investigated along the whole coastal line (Snoeijs 1993; Snoeijs and Balashova 1998; Snoeijs and Kasperoviciene 1996; Snoeijs and Potapova 1995; Snoeijs and Vilbaste 1994). Most of the diatom works in the country, however, were oriented towards freshwater taxa with less attention to littoral diatoms (Cleve-Euler 1951–1953; Foged 1980; Håkansson 1989; Hustedt 1924, 1942; Miller 1964; Van de Vijver and Lange-Bertalot 2008a, 2010, 2012a). Taxonomic reports on the marine diatoms of the west coast of Sweden are rare and seem to have been started by Edsbagge (1968) who investigated diatoms of the Skagerrak and Kattegat seas bordering Norway and Denmark. Aleem (1973) produced a list of 189 species of benthic diatoms from mudflats to the west of Gothenburg city. Two new species of *Tabularia* D.M. Williams *et* Round and one species of *Entomoneis* Ehrenberg occurring on the West coast of Sweden were described by Snoeijs and Kuylenstierna (1991) and Al-Handal et al. (2020) respectively.

Craspedostauros E.J. Cox was erected for species previously placed in *Stauroneis* Ehrenberg and characterized by having a stauros on the internal hyaline central area which always form a fascia, cribrate areolae, proximal raphe endings terminating with continuous or separate helictoglossae in the valve interior, and two chloroplasts encompassing a central pyrenoid (Cox 1999). Other features which might not be specific to the genus include a raphe positioned on a distinct sternum and curved external distal raphe endings. The cribrate areolae have 4–7 peripheral pores and none to multiple central pores. Although with few described taxa (15 species), *Craspedostauros* is widely distributed from Antarctica to the Mediterranean, inhabiting brackish water and marine environments (Convey et al. 2000; Cox 1999; Sabbe et al. 2003; Zidarova et al. 2022). During the last five years, eight *Craspedostauros* species were described as new to science from various geographic locations: *Craspedostauros alyoubii* Sabir *et* Ashworth (marine, Saudi Arabia, Ashworth et al. 2017), *Craspedostauros paradoxus* Ashworth *et* Lobban (marine, Guam, USA, Ashworth et al. 2017), *Craspedostauros alatus* Majewska *et* Ashworth (marine, epizoic, Long Island Beach, USA, Majewska et al. 2018), *Craspedostauros legouvelloanus* Majewska *et* Bosak (marine, epizoic, Kosi Bay, South Africa, Majewska et al. 2020), *Craspedostauros macewanii* Majewska *et* Ashworth (marine, epizoic, Durban, South Africa, Majewska et al. 2020), *Craspedostauros ineffabilis* Trentin et al. (marine, Ross Sea, Antarctica, Trentin et al. 2022), *Craspedostauros zucchellii* Trentin et al. (marine, Antarctica, Trentin et al. 2022) and *Craspedostauros confusus* Zidarova et al. (marine, Livingston Island, Antarctica; Zidarova et al. 2022). Additionally, several of the older *Stauroneis* species which have not yet been typified or critically examined might belong to *Craspedostauros*.

In samples collected from various regions of the extensive Swedish coastline, two species of *Craspedostauros* were observed with morphological features different from the documented species of the genus and described here. The first; *Craspedostauros lateralis* sp. nov. is a marine epiphytic species found in Saltholmen, west of Gothenburg, and the second; *C.* cf. *laevissimus* is a brackish water epiphytic species encountered in Grisslehamn, north of Stockholm, the Baltic coast of Sweden. Both species were assigned to *Craspedostauros* based on having features typical of this genus including the raised stauros on the internal hyaline central area which reach valve margins (facia), the cribrate areolae with peripheral and central pores, and a junction line between valve face and mantle. These two species are compared with most similar taxa of the genus and some ecological data are provided.

2 Materials and methods

The macrophyte material upon which the present species were found comes from two different locations along the coastal line of Sweden. *Craspedostauros lateralis* was collected from Saltholmen, on the west coast of Gothenburg city, Sweden (57° 39′ 32″ N, 11° 50′ 21″ E), on 14th October 2019. The area is a marine rocky shore connected to the Skagerrak Sea, which in turn receives water from the North Sea. *Craspedostauros* cf. *laevissimus* was collected from Grisslehamn (60° 46′ 32″ N, 18° 49′ 51″ E), on the Baltic coast of Sweden. Grisslehamn is a small fishing port located 114 km north of Stockholm. The whole area forms chain of large rocks spread over hundreds of meters. The water between these rocky islets is rather shallow and mixed with freshwater coming from small rivers and streams. Collection of macrophyte material was carried out on 22nd May 2019 from various locations in the area.

At both locations, the macrophytes, mostly phaeophytes and rhodophytes, attached to rocks and sediment, were collected by hand from 30 to 50 cm depth and kept in plastic bags inside a cool box. Both species were found epiphytic on two pheophytes: *Mesogloia* sp. C. Agardh and *Desmarestia* sp. Lamouroux. To free attached diatoms, parts of the macrophytes were shaken in a 50 ml glass jar containing deionized water. About 20 ml of the aliquots containing diatom frustules were boiled in 35 % hydrogen peroxide, a powerful oxidizing agent, for 15 min. After cooling in room temperature, the samples were rinsed few times with deionized water. One milliliter of the clean material was left to dry on a cover slip in ambient temperature. The coverslips with dry diatom cells were heated at 150 °C to insure adhering of the frustules and then mounted in Naphrax. Part of the clean aliquots containing diatoms were preserved in 4 % glutaraldehyde for future investigation.

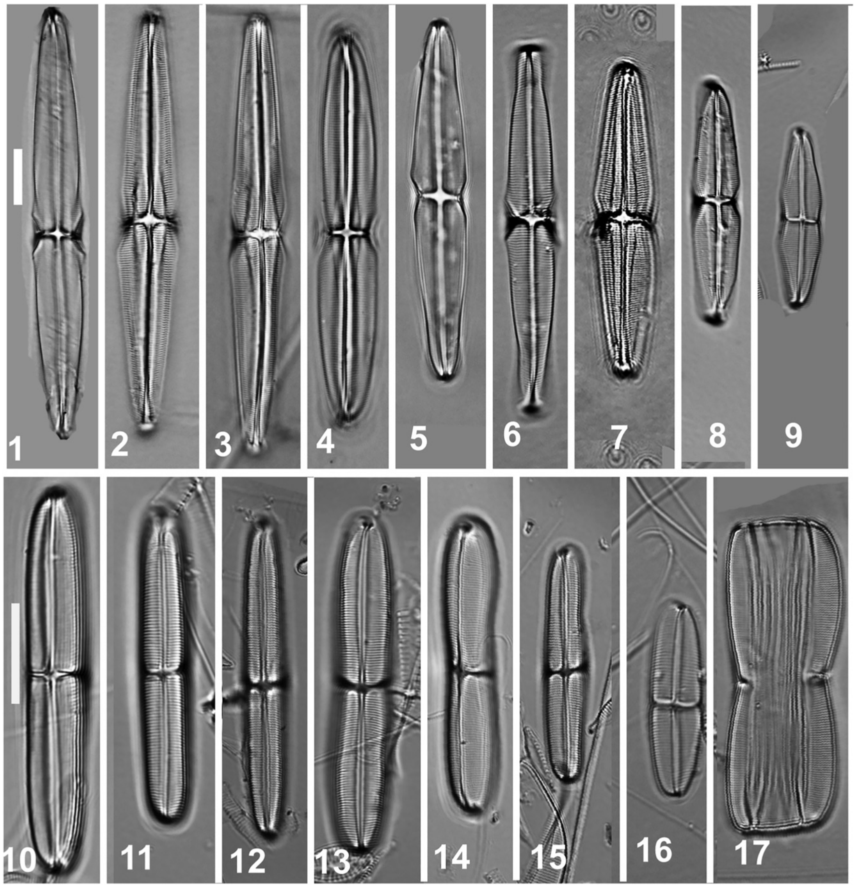
Light microscopy (LM), morphometric measurements and imaging of the species were made under a Zeiss Axiomager 2 microscope equipped with differential interference contrast (DIC) objectives and a Canon Powershot 14 digital camera (Department of Biological and Environmental Sciences, University of Gothenburg, Sweden). For the scanning electron microscopy (SEM), 0.2 ml of the cleaned diatom material were dried on aluminium stubs, coated with gold palladium, and examined in a Zeiss Ultra 55 FEG SEM (Chalmers University, Gothenburg, Sweden). The relative abundance of the new species and the associated diatom taxa was estimated by counting 400 valves in the mounted slides. Diatoms other than the new species were counted only when constituting more than 2 % of the total diatom assemblages in the samples. Terminology used in the present work follows Ross et al. (1979), Round et al. (1990), and Cox (1999).

3 Results

The diatom assemblages on two brown macrophytes collected from a brackish water habitat on the Baltic Sea and a marine environment on the west coast of Sweden, contained two species of *Craspedostauros*. These two species and the associated diatom taxa are described in the following.
Division **Bacillariophyta** Karsten
Class **Bacillariophyceae** Haeckel
Order **Mastogloiales** Mereschkowsky
Family **Mastogloiaceae** D.G. Mann
Genus ***Craspedostauros*** E.J. Cox

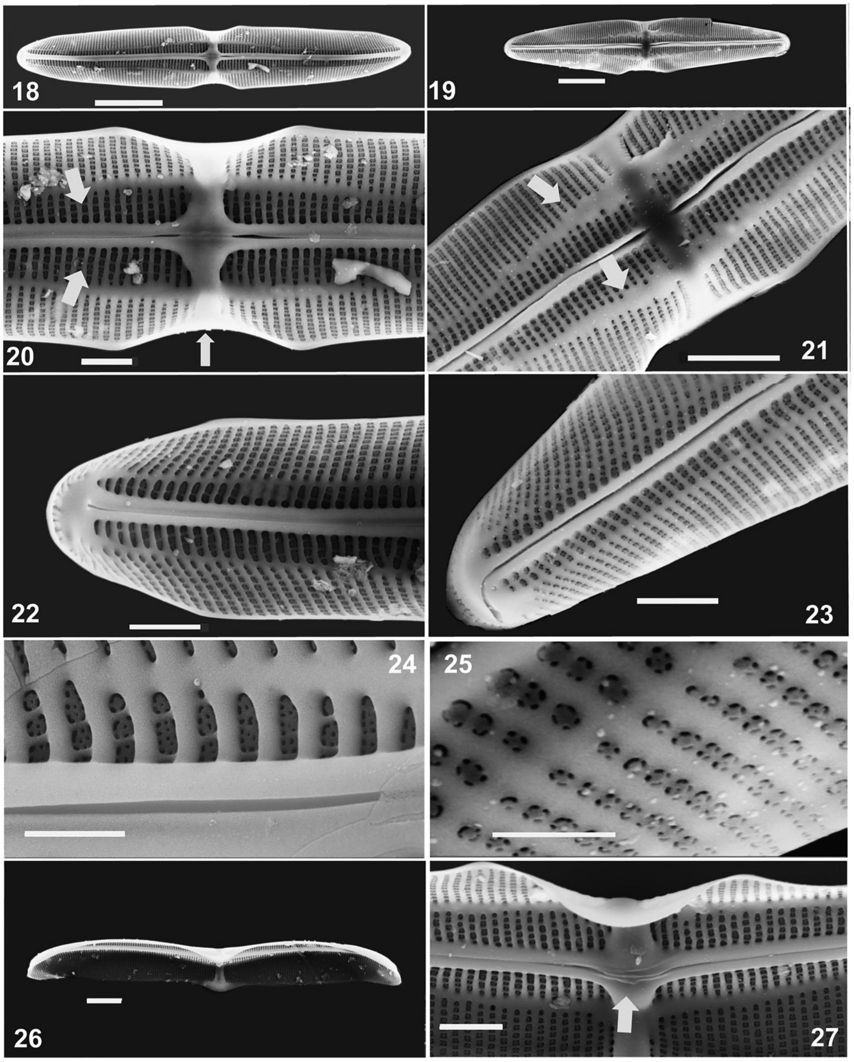
Craspedostauros lateralis **Al-Handal, Ashworth and A. Wulff sp. nov.** (Figures 1–9, 18–27)

Description: *Light microscopy (LM) observations* (Figures 1–9): Valves are linear to linear-lanceolate with a triangular constriction in the middle (Figures 1 and 3). Valve margins are gradually tapering to rounded apices. Smaller valves appear narrowly elliptic (Figure 8). Valves are 34–81 µm long and 8.5–10 µm wide in mid-valve (n = 35).



Figures 1–17: Light micrographs of *Craspedostauros lateralis* sp. nov. and *C.* cf. *laevissimus* of different sizes. (1–9) *Craspedostauros lateralis*. (1–8) Showing the distinct constriction of the valve and the shape of the stauros. (9) A small valve with elliptic outline. (10–17) *Craspedostauros* cf. *laevissimus*. (10–12) Valves with parallel margins. (13, 14) Valves with slightly inflated valve halves. (15) Valve with slightly swollen at the centre. (16) Small elliptic valve. (17) Frustule in girdle view showing constriction and cingular bands. Scale bars = 10 μm.

The axial area is very narrow and linear. The central area is narrow, appearing as a laterally dilated diamond and forming fascia reaching the constricted valve margin. Raphe is faintly visible in LM, particularly near the central area, due to valve curvature. Striae discernible in LM, 19–25 in 10 μm (Figures 6 and 8). The junction line between valve face and mantle is either invisible or appear as a very narrow line on both sides of the valve (Figure 7). *Scanning electron microscopy (SEM) observations* (Figures 18–27): Externally, the valve face is weakly undulate with a gradually bending mantle. The stauros and fascia are extended at the constricted part of the valve to form a distinctive silica flap (Figure 27). The valve poles at the distal raphe ending are devoid of striae except on the apical part of the mantle where few rows of areolae are seen (Figure 23). The axial area is very narrow and straight (Figure 19). The central area is narrow and transversely elongated, slightly raised above valve face which forms a facia reaching valve margin (Figure 21). The raphe is filiform and slightly undulating towards the central area but becoming straight on the rest of the valve (Figures 21 and 23). The proximal raphe endings are straight and elongated (Figure 21), the distal endings are bent at 90° angle (Figure 23). There are two irregular, linear lanceolate hyaline areas marking the junction line between valve face and the mantle (Figure 21, arrows). These are wide around the central area and becoming very straight and narrow towards the apices. The valve part between the hyaline areas and the axial area is slightly depressed (Figures 21 and 25). The striae are uniseriate, parallel at the centre and convergent near the apices (Figure 23). The cribrate areolae are larger on both sides of the axial area, 48–50 in 10 μm, slightly becoming smaller towards the lateral hyaline areas (Figures 21, 23, and 25). Cribra are formed of 4–5 small peripheral pores (Figure 25), central pores are absent. Internally, the area between the junction lines is depressed and formed of elongated areolae (Figures 22 and 24). These elongated areolae resulted from combing 2–4 adjacent quadrangular areolae (Figure 24). The central area widens transversely and apically at the valve margin forming a spectacular triangular fascia (Figure 20, arrow). The stauros is distinct and occupies the middle part of the central area between the junction lines (Figure 20). The central part of the stauros is dome-like helictoglossa which is interrupted by a blunt groove connecting the raphe proximal endings (Figure 27, arrow). The distal raphe endings are weakly bent and terminate on a shallow helictoglossae (Figure 22).



Figures 18–27: Scanning electron micrographs of *Craspedostauros lateralis* sp. nov. (18) Valve in internal view. (19) External side of the valve. (20) Middle part of the valve interior showing the depressed areas on both sides of the axial area (arrows) and the characteristic triangular constriction of the valve which is an extension of the central area (fascia). (21) The two irregular hyaline areas (arrows) which form the junction line between valve face and the mantle. (22) Internal side of the valve pole exhibiting the distal raphe ending. (23) External side of the valve pole with the curved distal raphe ending. (24) Elongated areolae on both sides of the axial area with numerous cribral pores. (25) External openings of the areolae with 4–5 peripheral cribral pores. (26) Valve in girdle view. (27) Internal side of the valve showing the folded marginal silica flap and the dome-like central helicoglossa (arrow). Scale bars: 18, 19, 26) 8 μm; (20, 21, 22, 23, 27) 2 μm; (24, 25) 0.8 μm.

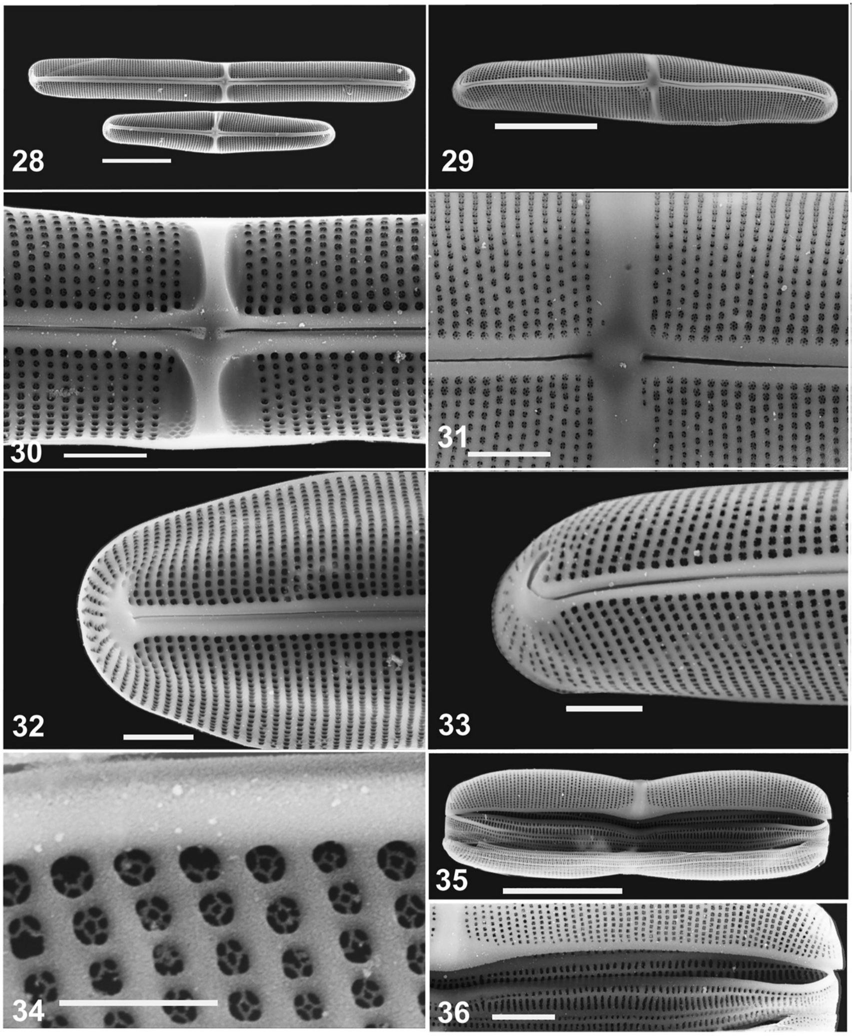
Holotype: Permanent slide containing frustules of *C. lateralis* sp. nov. are deposited in the Botanischer Garten und Botanischer Museum (BGBM), Berlin, Germany under accession B 40 0046319. Holotype illustrated in Figures 1–8. Phycobank registration http://phycobank.org/103978.

Type locality: Saltholmen, west coast of Sweden (57° 39′ 32″ N, 11° 50′ 21″ E).

Etymology: The epithet refers to the lateral hyaline areas on both sides of the axial area.

Ecology: *Craspedostauros lateralis* is a marine species, found epiphytic on the brown macrophyte *Mesogloia* sp. attached to rocks. Temperature at time of collection was 10.5 °C and salinity 27 psu. It was a rare species, constituted 0.8 % of the total diatom community epiphytic on *Mesogloia* sp. Other diatom taxa found associated with *C. lateralis* were *Achnanthes brevipes* C. Agardh (12.6 %), *Tabularia fasciculata* (C. Agardh) D.M. Williams and Round (11.3 %), *Entomoneis paludosa* (W. Smith) Reimer (6.2 %), *Haslea spicula* (Hickie) Bukhtiyarova (3.4 %), *Amphora* spp. (2.5 %), *Nitzschia sigma* (Kützing) W. Smith (1.8 %), *Surirella* sp. (1.1 %), and several other taxa small taxa of *Navicula* and *Nitzschia*.

Differential diagnosis: The marginal hyaline areas differentiate *C. lateralis* from other taxa sharing similar narrow and constricted valves. This feature is not always visible in LM and *C. lateralis* might be confused with related species such as *C. amphoides* (Grunow *et* A. Schmidt) E.J. Cox and *C. macewanii* Majewska *et* Ashworth. It can be distinguished from *C. amphoides* by having larger valves (34–85 μm compared to 28–45 μm), from *macewanii* by its stria density (30–32 compared to 28–31 in 10 μm) and from *C. amphoides* by having larger valves and denser striae. Ultrastructural differences with related taxa are discussed below.



Figures 28–36: Scanning electron micrographs of *Craspedostauros* cf. *laevissimus*. (28) Internal side of two valves with different outline and size. (29) External side of the valve exhibiting weakly inflated central part and a slight undulation of valve face. (30) Valve interior showing the stauros occupying the middle part of the central area, and the simple elongated proximal raphe endings. (31) External central area with the elongated proximal raphe endings. (32) Internal valve pole showing raphe distal ending and striae spreading around all valve apex. (33) External valve pole with the curved raphe distal ending. (34) Rounded areolae with cribral pores, note the equal size pf peripheral and central pores. (35) Frustule in girdle view. (36) Enlarged part of the frustule showing a cingular band with numerous longitudinal rows of variable sized elongated areolae. Scale bars: (28, 29, 35) 10 μm; (30, 31, 32, 33, 36) 2 μm; (34) 1 μm.

***Craspedostauros* cf. *laevissimus* (West *et* G.S. West) Sabbe** (Figures 10–17, 28–36)

Description: *Light microscopy (LM) observations* (Figures 10–17): The frustules are rectangular in girdle view, constricted on the pervalvar axis, with slightly convex margins and several cingular bands (Figure 17). The valves are linear to linear-lanceolate with broadly rounded apices, 21–58 μm long and 5.0–6.4 μm wide (n = 23). Larger valves either with parallel margins (Figures 11 and 12) or rarely slightly irregular (Figures 13 and 15). Smaller valves are elliptic (Figure 16). The axial area is linear and very narrow. The central area is narrow, transversely expanded to the valve margins forming bow tie-shaped (Figures 10–16). The raphe is filiform and straight. The raphe proximal endings are straight, distal endings are bent. Striae are very fine, parallel, 28–32 at mid-valve and 33–40 in 10 μm towards apices. *Scanning electron microscopy (SEM) observations* (Figures 28–35): Externally, the valve face is convex, gradually curving into a wide mantle (Figures 32 and 34). Valve surface is slightly undulated between the mid-valve and poles and is more visible internally (Figure 32). The axial area is narrow, follows valve curvature and widening at the apices into a transverse triangle (Figures 29 and 33). The central area is rectangular, transversely dilated, with straight margins (Figure 31). Middle part of the central area is elevated and rounded (Figure 31). The raphe central endings are elongated, weakly bent to the same direction (Figure 31). Distal raphe endings are curved and hooked, terminated shortly before the mantle (Figure 33). The striae are parallel to weakly radiate in the middle, becoming slightly convergent near the apices and continue around the apical part of the mantle (Figures 31 and 33). The areolae are 55 in 10 μm. Areolae openings are square near the axial area, becoming slightly elongated towards valve margins (Figure 33). Internally, the axial area is linear and straight slightly raised over valve plane (Figure 30). The stauros is narrow and bow tie-shaped, raised on a wider rectangular hyaline fascia (Figure 30). The raphe is straight, the central endings are weakly bent to the same direction and terminate on a shallow helictoglossae (Figure 30). The distal endings are straight and terminate on a very shallow helictoglossae (Figure 32). The cribrate areolae are rounded and slightly decreasing in size towards valve margin (Figure 34). Cribra are composed of four, very rarely 5–7, peripheral pores and a single central one. The pore openings are almost similar in size (Figure 34). On the cingular bands there are several rows of elongated and rounded areolae (Figure 36).

Ecology: *Craspedostauros* cf. *laevissimus* was found in a brackish water habitat, epiphytic on the brown macrophyte *Desmarestia* sp., constituted 1.8 % of the diatom assemblages on this host. Water temperature at time of material collection was 12.3 °C and salinity 4.9 psu. Several other diatom taxa associated with *C. lateralis* including *Diatoma moniliforme* (Kützing) C. Agardh (23 %), *Diatoma tenuis* C. Agardh (16.5 %), *Tabularia fasciculata* (12 %), *Gomphonema* sp. (5.3 %), *Rhoicosphenia abbreviata* (C. Agardh) Lange-Bertalot (5.1 %), *Cocconeis* sp. (4.1 %), *Achnanthidium* sp. (1.9 %), beside other very small *Nitzschia* spp. and *Navicula* spp. which constituted less than 2 %. Several macrophytes as well as benthic samples were collected from the study area and the surrounding region but *C. lateralis* was only found on *Desmarestia* sp.

4 Discussion

The two *Craspedostauros* species described in this study were encountered in different environments and in quite distant locations. *Craspedostauros lateralis* is a marine species found in the west coast of Sweden, which receives water from the North Sea, while *C.* cf. *laevissimus* is a brackish water taxon occurred in the Baltic Sea coast, northeast of Sweden. Both species were assigned to *Craspedostauros* for having typical features of the genus including possession of cribrate areolae with a particular shape and arrangement of cribra, and a distinctive stauros located on the central area (Cox 1999). A morphological comparison between these two species and the related taxa of the genus is given in Table 1.

The two irregular, linear-lanceolate hyaline areas marking the junction line between external valve face and mantle seem to be specific features of *C. lateralis* and has not been similarly reported in all other known species of the genus. Although these hyaline areas are best seen in SEM (Figure 21), it can be visible in LM as a very narrow ridge between valve face and mantle (Figures 7 and 8). In LM, *C. lateralis* bear similarity to *C. alatus* (Majewska et al. 2018, figures 22–25, 2020, figures 7d, e) where both species share the same valve outline with triangular constriction in the middle. The latter species, although with similar stria density, is distinctly smaller where its length does not exceed 37 µm compared to 81 µm in *C. lateralis*. SEM examination also reveals several distinguishing features that make these two species apart. The junction lines of *C. alatus* are very narrow and linear, appearing as a ridge between valve face and mantle whereas that of *C. lateralis* is wider, lanceolate, and irregular. Areolae of *C. alatus* are square to elongated, with up to 16 cribral pores in contrast to mostly rounded areolae of *C. lateralis* that possess 4–5 pores (Table 1). The most distinguishing feature of *C. alatus* is the presence of prominent wing-like silica occlusions of the distal raphe ends, a feature that is missing in our new species. The ecology of these two species is different, *C. alatus* is an epizoic taxon found on carapaces of the green turtle *Chelonia mydas* L, though the NCMA strain was collected from the plankton while *C. lateralis* is an epiphytic species living on a brown macrophyte.

Regarding valve size and outline, *C. lateralis* is among the largest species of the genus which might all appear similar in LM, these include *C. australis* E.J.Cox (1999: L. 35–78 µm, W. 4–6 µm), *C. neoconstrictus* E.J.Cox (L. 140–110 µm, W. 5–7 µm), *C. alyoubii* (L. 83–105 µm, W. 6–10 µm), *C. paradoxus* (L. 88–85 µm, W. 6.5–9 µm) and *C. laevissimus* (West *et* G.S. West) Sabbe (L. 49–98 µm, W. 8–9.5 µm). The Antarctic *C. australis* has no or very shallow valve constriction but possesses nearly similar stria density (35 in 10 µm), the areolae are square with four cribral peripheral pores (Cox 1999). The other Antarctic species, *C. neoconstrictus* has longer and narrower valves, with lighter stria density (25 in 10 µm). The areolae are of the same size and have six cribral pores (Cox 1999). The planktonic and warm water species *C. alyoubii* differs by having slenderer and longer valves with very shallow constriction. The striae are denser (40 in 10 µm), composed of square areolae with 4–5 cribral pores (Ashworth et al. 2017). The equatorial *C. paradoxus* (as *C. paradoxa* Ashworth et al. 2017), possesses elongated valves with a shallow constriction. The striae are denser (36–40 in 10 µm) formed of square areolae with 4–5 cribral pores. All the above species exhibit ultrastructural variations that are only visible in SEM such as stauros structure, raphe endings, helictoglossa shape, cribra number and

Table 1: Comparison of the morphological features of *Craspedostauros lateralis* and *C.* cf. *laevissimus* to some similar species of the genus.

Feature		***Craspedostauros lateralis***	***C.* cf. *laevissimus***	***C. alatus***	***C. neoconstrictus***	***C. alyoubii***	***C. laevissimus***	***C. britannicus***	***C. australis***
Valve	Outline	Linear to linear-lanceolate, rarely elliptic, constricted in the middle	Linear-lanceolate, small valves elliptic	Linear to linear-lanceolate, slightly constricted	Linear to narrowly lanceolate, constricted	Linear, slightly constricted	Linear-lanceolate, slightly constricted	Linear to narrowly lanceolate	Narrowly linear
	Length (µm)	34–85	21–58	20–37	40–110	83–105	35–88	14–60	35–70
	Width (µm)	8.5–10	5.0–6.4	3–5	5–7	6–10	4.8–7.8	5–6	4–6
	Apices	Rounded	Broadly rounded apices	Bluntly rounded	Rounded	Rounded	Broadly rounded to cuneate	Rounded	Bluntly rounded
Internal central area		Narrow, bow-tie shaped	Rectangular fascia with narrow stauros	Rectangular fascia with narrow stauros	Expanded fascia in a ligulate fashion	Narrow, trans-versely elongated	Narrow stauros, in wider hyaline area	Narrow, weakly bow-tie shaped	Narrow, bow-tie shaped
Junction line		Distinct, narrowly linear lanceolate, irregular	Absent	Linear, very narrow	Indistinct	Indistinct	Absent	Absent	Absent
Striae	Arrangement	Parallel at the center, convergent near apices	Parallel at the center, convergent near apices	Parallel	Parallel	Parallel	Parallel, slightly radiate near the central area	Parallel, or weakly rectangular near the central area	Parallel
	Density in 10 µm	19–25	28–32, mid-valve, 33–40 towards apices	26–28	ca 25	40	26–28	24	35
Areolae	Shape	Square to rounded	Square near the axial area, elongated near the margin	Variable	Square, similar in size	Quadrate	Square to rounded	Rounded	Square, similar in size
	In 10 µm	48–50	55	nd	nd	nd	nd	nd	nd
	Peripheral cribra	4–5	4–5, equal in size	Highly variable	6	4	4 or more	4–5	4
	Central cribra	1 or absent	1	Variable	Variable	Rarely one	One, small	1 or absent	Absent
Raphe	Shape	Straight, undulating near the center	Straight	Straight	Straight	Straight	Filiform, straight to slightly undulate	Straight	Straight
	External prox-imal endings	Expanded	Elongated, slightly deflected	Weakly expanded, slightly deflected	Very slightly expanded	Covered by flasps of silics	Slightly expanded	Weakly expanded, curved	Expanded
	Distal endings	Curved	Curved	Curved	Curved	Covered by flasps of silica	Bent to the same side	Bent to hooked	Bent
	Internal prox-imal endings	Expanded, connected by a groove	Bent	Elongated on weakly constricted rectelevatum	Slight helictoglossae	Long helictoglossae	Double helictoglossae	Double helictoglossae	Silica knob
	Distal endings	Weakly bent, shallow helictoglossae	Straight, shallow helictoglossae	On prominent helictoglossae	Slight helictoglossae	Broad helictoglossae	Terminate in small double helictoglossae	Weakly bent	Shallow helictoglossae
Ecology		Brackish, epiphytic	Marine, epiphytic	Epizoic	Brackish to marine, epipelic	Marine, planktonic	Antarctic, freshwater	Marine, intertidal	Brackish to ma-rine, intertidal
Reference		Present study	Present study	Majewska et al. (2018)	Cox (1999)	Ashworth et al. (2017)	Sabbe et al. (2003)	Cox (1999)	Cox (1999)

nd: not detected.

arrangement. A list of structural differences between *C. lateralis* and other taxa with related valve size is given in Table 1.

Craspedostauros cf. *laevissimus* bear similarities to *C. laevissimus* but differ in having some features that make its correct identity uncertain. The present specimens possess complete rows of striae around the valve poles (Figures 32 and 33), while specimens of *C. laevissimus* examined by Zidarova et al. (2022) exhibit only scattered areolae surrounding valve poles. This feature is not clearly shown in the type material examined by Van de Vijver et al. (2012b). *Craspedostauros* cf. *laevissimus* valves from the Swedish population exhibited two outline morphologies: the larger valves are linear with parallel margins and a very shallow constriction (Figure 28) while the smaller valves are narrowly elliptic with no constriction in the middle (Figure 29). This disparity is similar to that illustrated in the valves of the *C. laevissimus* (Zidarova et al. 2022, figures 2–18, 29–47) as well as *C. alatus* (Majewska et al. 2018, figures 7 and 9 vs. figures 26–28), and may be an artifact of the weakening of the valve away from the stauros. In the internal valve side of *C. laevissimus*, there are two longitudinal rows of areolae bordering the axial area and formed of enlarged square to rectangular areolae with up to seven cribral pores, a feature that is not seen in *C.* cf. *laevissimus*. Cribral pores of *C.* cf. *laevissimus* are large, composed of four peripheral pores and a single central one, all are of the same size (Figure 34), compared to smaller and irregular pores, in terms of size and number, of *C. laevissimus*. Cribral pores, however, may not be a species-specific feature and may vary in relation to environmental conditions, and variation in the number of cribral pores on a valve has been documented in other *Craspedostauros* species (Ashworth et al. 2017; Majewska et al. 2020). With regard to the girdle elements, according to Sabbe et al. (2003), there are two rows of areolae on the cingular bands (though these were not illustrated), whereas in *the* Swedish population several alternating rows of elongated and rounded areolae were observed, as well as bands with two rows of areolae (Figure 36). Zidarova et al. (2022, figures 39 and 45) illustrated several cingular bands in their two of their specimens, which appear to have two rows of areolae.

Craspedostauros laevissimus is an interesting Antarctic species, documented with a wide range of morphological and structural variations. It has first been described as *Tropidoneis laevissimus* West et West (1911), and then transferred to *Craspedostauros* by Sabbe (in Sabbe et al. 2003). Up to date, it has only been reported in Antarctic diatoms assemblages, from freshwater habitats, saline lakes, and marine environment (Bishop et al. 2020; Kellogg and Kellogg 1987; Ko-Bayashi 1963; Sabbe et al. 2003; Van de Vijver et al. 2012b; Zidarova et al. 2022). The valve outline of this species varies almost in all records. Valves of the type material were linear with valve length up to 98 µm (West and West 1911). Different valve outlines were observed in different geographic locations and were linear-lanceolate with cuneate to rounded apices (maximum length 66 µm) in Larsemann Hills and Rauer lakes (Sabbe et al. 2003). Elliptic lanceolate valves with length up to 42 µm were found in Livingston Island (Zidarova et al. 2022). Small elliptic valves (21 µm long) were observed in the present study. Such variations are also observed in stria density and cribral pores structure (Table 1).

The present record of *C.* cf. *laevissimus* is the first outside Antarctica, which expands the environmental preferences of this species. According to Van de Vijver et al. (2012b), *C. laevissimus* is an Antarctic endemic species that has not been reported from regions outside the continental Antarctica. However, this does not seem to be a valid explanation of a restricted distribution of Antarctic diatoms. A good example is *Psammothidium abundans* (Manguin) Bukhtiyarova et Round which has long been considered Antarctic endemic (Oppenheim 1994; Sabbe et al. 2003) but later found widely distributed in the freshwater of Sweden (Van de Vijver et al. 2008b). Endemism of marine benthic diatoms is not well understood, with so much of the world's coasts yet to be examined for diatoms. A species considered as Antarctic endemic may occur elsewhere but has not yet been observed, not yet been dispersed in any other geographic region.

The distribution of *Craspedostauros* in Sweden inland and coastal water is not known. The only documented species was *Craspedostauros neoconstrictus* E.J. Cox reported by Cleve-Euler (1953) as *Stauroneis constricta* Ehrenberg from Lysekil and Malmö shores, on the west coast of the country. Several species illustrated as *Stauroneis* in Cleve-Euler (1953) may belong to other genera that were erected in later years, including *Stauroneis bottnica* (Cleve) Cleve-Euler (1953, figure 959), *Stauroneis perlucens* Østrup (Figure 936) and *Stauroneis gregorii* Ralfs (figure 950). This is also true for *Stauroneis* taxa described from other places; *Stauroneis carinata* Heiden illustrated in Simonsen (1992, pl. 39, figures 1–5) clearly exhibits a stauros raising above the internal central area which expands to the valve margin, as well as a junction line between the valve and mantle, which are features characteristic to *Craspedostauros*. Since identification of *Craspedostauros* species is based mainly on the structure of the stauros and the cribrate areolae with a certain number of pores, only SEM examination of the type material of those taxa, if persist, will reveal their proper specific identity.

Acknowledgments: We are grateful to Mr. Mikael Hedblom, Department of Biological and Environmental Sciences, University of Gothenburg, for his help in sample collection and transport from Grisslehamn. Our gratitude to Dr Stefan Gustafsson, Chalmers University, Gothenburg, Sweden for assisting with the SEM.
Research ethics: Not applicable.
Author contributions: All authors have participated in the writing and morphological analysis and have accepted responsibility for the entire content of this submitted manuscript and approved submission.
Competing interests: The authors declare no potential conflict of interest regarding this article.
Research funding: This work is part of a project funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) as part of the project 2017-00850.
Data availability: Not applicable.

References

Al-Handal, A.Y., Mucko, M., and Wulff, A. (2020). *Entomoneis annagodhei* sp. nov., a new marine diatom (Entomoneidaceae, Bacillariophyta) from the west coast of Sweden. Diatom Res. 35: 269–279.

Aleem, A.A. (1973). Contribution to the study of littoral diatoms on the west coast of Sweden. Bot. Mar. 16: 193–200.

Ashworth, M.P., Theriot, E.C., Jansen, R.K., Lobban, C.S., Witkowski, A., Sabir, M.J., Hajarah, N.H., Sabir, J.S., Jansen, R.K., and Baeshen, M.N. (2017). Molecular and morphological investigations of the stauros-bearing, raphid pennate diatoms (Bacillariophyceae): *Craspedostauros* E.J.Cox, and *Staurotropis* Paddock, and their relationship to the rest of the Mastogloiales. Protist 168: 48–70.

Bishop, J., Kopalová, K., Kohler, T.J., Van de Vijver, B., Roberts, D., McMinn, A., and Gibson, J. (2020). A re-investigation of lake sediment diatoms from the Vestfold Hills, Antarctica, using an updated, fine-grained taxonomy. Diatom Res. 35: 231–254.

Cleve, A. (1895). On recent freshwater diatoms from Lule Lappmark in Sweden. Kong. Sven. Vet.-Akad. Hand. 21: 1–45.

Cleve-Euler, A. (1953). *Die Diatomeen von Schweden und Finnland*. Teil III. Monoraphideae, Biraphideae. Kong. Sven. Vet.-Akad. Hand. 4: 1–255.

Convey, P., Lewis Smith, R.I., Hodgson, D.A., and Peat, H.J. (2000). The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating. J. Biogeogr. 27: 1279–1295.

Cox, E.J. (1999). *Craspedostauros* gen. nov., a new diatom genus for some unusual marine raphid species previously placed in *Stauroneis* Ehrenberg and *Stauronella* Mereschkowsky. Eur. J. Phycol. 34: 131–147.

Edsbagge, H. (1968). Zur ökologie der marinen angehefteten diatomeen. Botanica Gothoburgensia 6: 1–139.

Foged, N. (1980). Diatoms in Öland, Sweden. Bibl. Phycol. 49: 1–193.

Håkansson, H. (1989). Diatom succession during middle and late Holocene time in Lake Kragenholmssjön, Southern Sweden. Nova Hedwigia 48: 143–166.

Hustedt, F. (1924). Die Bacillariaceen-Vegetation des Sarekgebiets. Naturwiss. Untersuch. Sareksgeb. In Schwed. Lappl. 3: 525–626.

Hustedt, F. (1942). Diatomeen aus der Umgebung von Abisko in Schwedisch-Lappland. Arch. Hydrobiol. 39: 82–174.

Kellogg, D.E. and Kellogg, T.B. (1987). Diatoms of the McMurdo Ice Shelf, Antarctica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 60: 77–96.

Ko-Bayashi, T. (1963). Variations on some pennate diatoms from Antarctica. Jpn. Antarct. Res. Exped. (JARE) 1956–1962 Sci. Rep. Ser. E Biol. 18: 1–20.

Majewska, R., Ashworth, M.P., Bosak, S., Goosen, W.E., Nolte, C., Filek, K., Van de Vijver, B., Taylor, J.C., Manning, S.R., and Nel, R. (2020). On sea turtle-associated *Craspedostauros* (Bacillariophyta), with description of three novel species. J. Phycol. 57: 199–218.

Majewska, R., Ashworth, M.P., Lazo-Wasem, E., Robinson, N.J., Rojas, L., Van de Vijver, B., and Pinou, T. (2018). *Craspedostauros alatus* sp. nov., a new diatom (Bacillariophyta) species found on museum sea turtle specimens. Diatom Res. 33: 229–240.

Miller, U. (1964). Diatom flora in the quaternary of the Göta river valley (Western Sweden). Sver. Geol. Unders. 44: 1–83.

Oppenheim, D.R. (1994). Taxonomic studies of *Achnanthes* (Bacillariophyta) in freshwater maritime Antarctic lakes. Can. J. Bot. 72: 1735–1748.

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R., and Sims, P.A. (1979). An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia 64: 513–533.

Round, F.E., Crawford, R.M., and Mann, D.G. (1990). *The diatoms. Biology and morphology of the genera*. Cambridge University Press, Cambridge.

Sabbe, K., Verleyen, E., Hodgson, D.A., Vanhoutte, K., and Vyverman, W. (2003). Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. Antarct. Sci. 15: 227–248.

Simonsen, R. (1992). The diatom types of Heinrich Heiden in Heiden and Kolbe 1928. Bibl. Diatomol. 24: 1–99.

Snoeijs, P. (1993). *Intercalibration and distribution of diatom species in the Baltic Sea*. Baltic Marine Biologist Publication 16a. Opulus Press, Uppsala, Sweden.

Snoeijs, P. and Balashova, N. (1998). *Intercalibration and distribution of diatom species in the Baltic Sea*. Baltic Marine Biologist Publication 16e. Opulus Press, Uppsala, Sweden.

Snoeijs, P. and Kasperoviciene, J. (1996). *Intercalibration and distribution of diatom species in the Baltic Sea*. Baltic Marine Biologist Publication 16d. Opulus Press, Uppsala, Sweden.

Snoeijs, P. and Kuylenstierna, M. (1991). Two new diatom species in the genus *Tabularia* from the Swedish coast. Diatom Res. 6: 351–365.

Snoeijs, P. and Potapova, M. (1995). *Intercalibration and distribution of diatom species in the Baltic Sea*. Baltic Marine Biologist Publication 16c. Opulus Press, Uppsala, Sweden.

Snoeijs, P. and Vilbaste, S. (1994). *Intercalibration and distribution of diatom species in the Baltic Sea*. Baltic Marine Biologist Publication 16b. Opulus Press, Uppsala, Sweden.

Trentin, R., Moschin, E., Lopes, A.D., Schiaparelli, S., Custódio, L., and Moro, I. (2022). Molecular, morphological and chemical diversity of two new species of Antarctic diatoms, *Craspedostauros ineffabilis* sp. nov. and *Craspedostauros zucchellii* sp. nov. J. Mar. Sci. Eng. 10: 1–21.

Van de Vijver, B. and Lange-Bertalot, H. (2008a). *Cymbella amelieana* sp. nov. a new large *Cymbella* species from Swedish rivers. Diatom Res. 23: 511–518.
Van de Vijver, B., Kelly, M., Blanco, S., Jarlman, A., and Ector, L. (2008b). The unmasking of a sub-Antarctic endemic: *Psammothidium abundans* (Manguin) Bukhtiyarova et Round in European rivers. Diatom Res. 23: 233–242.
Van de Vijver, B., Jarlman, A., and Lange-Bertalot, H. (2010). Four new *Navicula* species (Bacillariophyta) from Swedish rivers. Cryptogam. Algol. 31: 355–367.
Van de Vijver, B., Jarlman, A., Haan, M., and Ector, L. (2012a). New and interesting diatom species (Bacillariophyceae) from Swedish rivers. Nova Hedwigia 141: 237–254.
Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson, J., Verleyen, E., Vyverman, W., and Sabbe, K. (2012b). Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. Fottea 12: 149–169.
West, W. and West, G.S. (1911). Freshwater algae. In: Murray, J. (Ed.). *British Antarctic expedition 1907–9*, 1 Biology. William Heinemann, London.
Zidarova, R., De Haan, M., Ivanov, P., Hineva, E., and Van de Vijver, B. (2022). The genus *Craspedostauros* E.J. Cox (Bacillariophyta) on the coasts of Livingston Island, Maritime Antarctica. Phytotaxa 572: 1–24.

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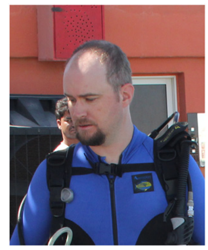

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