

## Article

# Girdle Band Structure in the Diatom Genus *Proschkinia* (Bacillariophyta)—Another Potential Adaptation to Stabilise a Deep Cingulum?

Eileen J. Cox

Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK; e.cox@nhm.ac.uk

**Abstract:** The girdle structure of *Proschkinia* (Bacillariophyta) is described in detail, showing the form of the unusual, channelled bands and how they link together. The significance and potential function of the more complex band structure is discussed in relation to its occurrence in other diatom genera and to other potential stabilising elements. Although some similarities in girdle structure are seen with the diatom genus *Undatella*, there is currently no evidence of a close phylogenetic relationship between these genera. Based on the current molecular data, *Proschkinia* is most closely related to the genus *Fistulifera*, with which it shares a distinctive valve feature, a fistula. Because of the traditional focus on valve morphology, far less is known of the girdle structure within the diatoms, despite its importance for maintaining cell integrity and allowing cell growth. The importance of studying the girdle structure as well as the valve morphology in diatoms in relation to their phylogeny and ecology is stressed.

**Keywords:** cingulum structure; diatoms; SEM; taxonomic characters



**Citation:** Cox, E.J. Girdle Band Structure in the Diatom Genus *Proschkinia* (Bacillariophyta)—Another Potential Adaptation to Stabilise a Deep Cingulum? *Diversity* **2023**, *15*, 734. <https://doi.org/10.3390/d15060734>

Academic Editors: Gabrielle Zammit and L. Elliot Shubert

Received: 21 April 2023

Revised: 26 May 2023

Accepted: 29 May 2023

Published: 2 June 2023



**Copyright:** © 2023 by the author. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Diatoms (Bacillariophyta) are perhaps best known for the possession of characteristic external siliceous cell walls (frustules), on which their identification and classification have traditionally been based [1]. The frustule is an essentially bipartite structure, comprising two valves, each with a series of linking bands (cingulum). The addition of new girdle bands (copulae) to the younger half frustule during vegetative growth allows cell expansion until the next mitosis and cell division. While much attention has been given to the shape and structure of the valves—usually the larger, more elaborate components of the frustule—the cingulum and its copulae have been given less attention. However, not only are they critical to the integrity of the frustule, but the variation in their structure also both provides additional taxonomic characters and reveals the different ways in which diatoms potentially “solve” engineering challenges.

Two recent papers [2,3] described several new species of the diatom genus *Proschkinia* Karayeva, discussing their phylogenetic relationships, but with little detail on the structure of their unusual girdle bands. Both papers show essentially the same phylogenetic trees, in which, within the raphid naviculoid diatoms, *Proschkinia* groups with *Fistulifera* Lange-Bertalot in a larger clade including *Craticula* Grunow; *Stauroneis* Ehrenberg and *Parlibellus harffianus* Witkowski, Ch. Li and X. Yu (other *Parlibellus* E.J. Cox species were part of another clade with *Astartiella* Witkowski, Lange-Bertalot and Metzeltin and *Schizostauron* Grunow). Stating that it required much further study, Round et al. [1] placed *Proschkinia* in its own family, the Proschkiniaceae, with *Craticula* and *Stauroneis* in their (preceding) family Stauroneidaceae (both within the Naviculineae, which also included the Naviculaceae and Pleurosigmataceae). They [1] commented that *Proschkinia* shows “superficial similarities to *Craticula* and *Stauroneis*” but questioned a close relationship due to differences in the raphe and girdle structure. On the other hand, the relationship between *Proschkinia* and *Fistulifera* was first shown in a mitochondria-based phylogeny [4] and then in a study of

*Fistulifera* by Zgrundo et al. [5] that included a phylogenetic analysis based on 18S rDNA. Considering their contrasting valve and girdle morphology, these were surprising results, but both genera share the presence of a fistula, an unusual, isolated pore near the central raphe endings, with a hymenate internal occlusion. Majewska et al. [2] commented that a potential homology between a fistula and the internally occluded stigma of *Didymosphenia* M. Schmidt, based on the mitochondrial tree [4], was not supported by their expanded dataset [2].

In terms of the cingulum structure of *Proschkinia*, Majewska et al. [2] noted the single row of hymenate areolae on the pars interior of the U-shaped bands, but none of their SEMs were at a high magnification. The cingulum structure in raphid diatoms is often relatively simple, comprising relatively few (in most cases), similar, band-like, split rings, which may or may not contain rows of areolae. Thus, in some genera (e.g., *Navicula* Bory *sensu stricto*, *Gyrosigma* Hassall, *Pleurosigma* W. Smith, *Sellaphora* Kützing) the girdle bands lack pores, whereas in others, one or two rows of open (e.g., *Cymbella* C.A. Agardh, *Gomphonema* Ehrenberg, *Oricymba* Jüttner et al., *Cymbopleura* (Krammer) Krammer), hymenate (e.g., *Berkeleya* Greville, *Parlibellus*, *Dickieia* Berkeley ex Kützing, *Amphipecta* Kützing) or cribrate (e.g., *Achnanthes* Bory, *Craspedostauros* E.J. Cox) pores are present. More complex, chambered valvocopulae are found in *Mastogloia* Thwaites and *Aneumastus* D.G. Mann and A.J. Stickle, associated with mucilage secretion in *Mastogloia* [1,6–10]. Hollow tubular girdle bands are a distinctive characteristic of *Undatella* Paddock and Sims and were used to define and discriminate this genus from *Auricula* Castracane [11]. However, despite the interest in cingulum structure shown by some authors [12–18], most studies of raphid diatoms have focussed on the valve structure, and the girdle band details have been poorly documented. The only study that attempted to understand the cingulum of *Proschkinia* [17] showed that most bands were U-shaped in cross-section, with a plain external face, a perforate internal face and an external abvalvar ridge abutting the adjacent band. However, their interpretation was limited by the quality of their micrographs, and more recent observations [19,20] have provided more detail on these intriguing cingula.

The lack of interest in the girdle structure derives not only from the traditional focus on the valve structure for diatom identification and classification but also from the fact that the majority of diatoms are seen in valve view with both LM and SEM. This is particularly the case for raphid diatoms, which tend to lie in valve view even when entire frustules are present. The frustules of *Proschkinia* are unusual in having very deep girdle regions and narrowly lanceolate valves, with frustules usually lying in the girdle view in cleaned preparations. Even then, it is difficult to understand the 3D structure of their cingula unless cross-sectional breaks are found, as shown for *Mastogloia* [7]. However, the use of an embedding and back-etching technique [16,19] makes it possible to see how the gutter-shaped bands fit together with each other and the valve. This paper will present more detailed images of the *Proschkinia* cingula and discuss the potential significance of their structure.

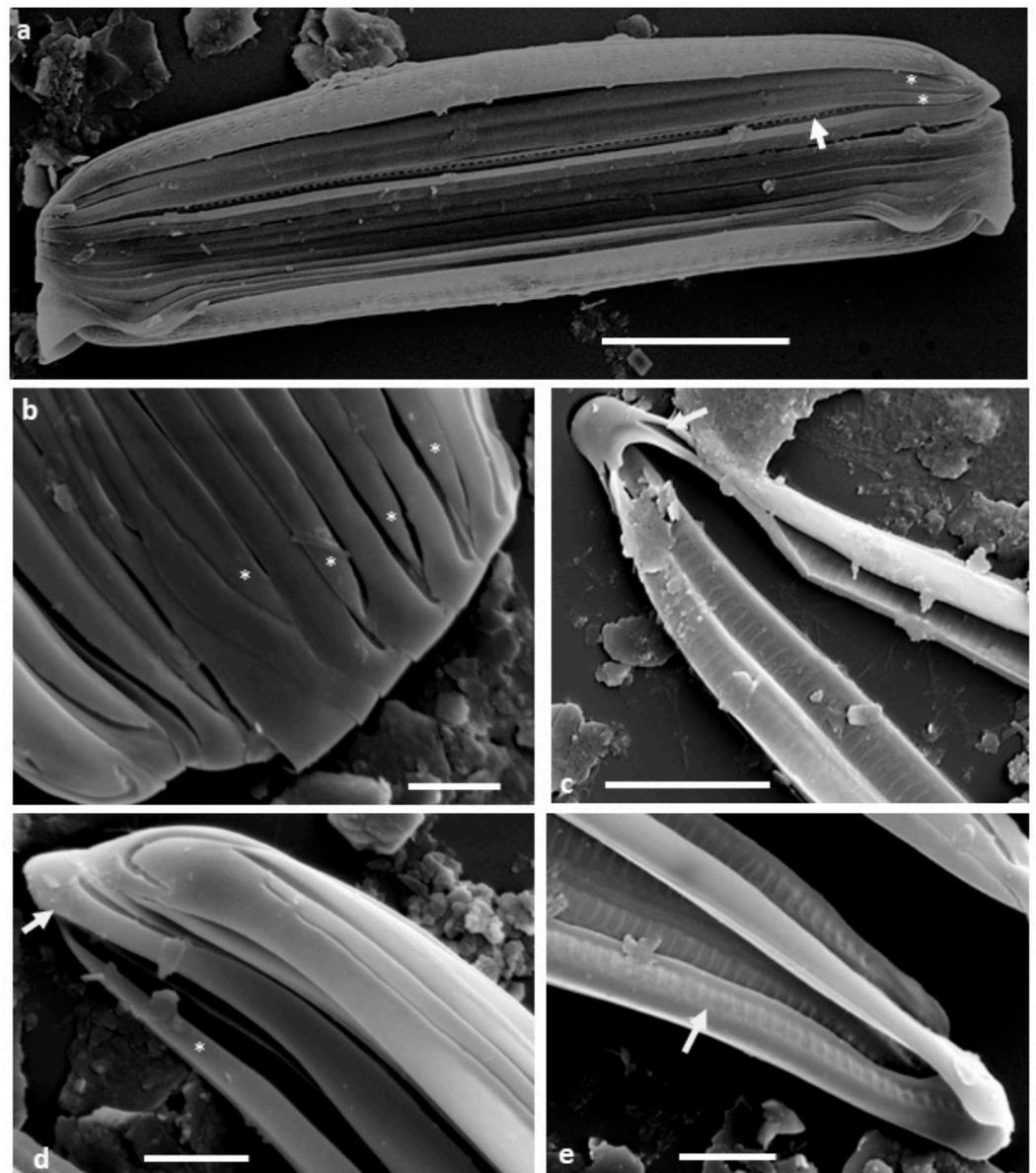
## 2. Materials and Methods

Samples containing specimens of *Proschkinia* species from coastal sediments in the UK were cleaned using heated 50% nitric acid and washed thoroughly in distilled water before mounting on coverslips attached to aluminium stubs or embedding in resin and back-etching, as described in Carr et al. [18]. Scanning electron microscopy on gold/palladium coated material was carried out with a Hitachi S-800 SEM (Hitachi, Tokyo, Japan) or a Philips XL30 field emission SEM (Philips, Eindhoven, The Netherlands).

The terminology follows von Stosch [12]: the valvocopula is adjacent to the valve; there are a number of similar abvalvar copulae following that, with a few, simple band-like pleurae forming the most abvalvar components of the epicingulum.

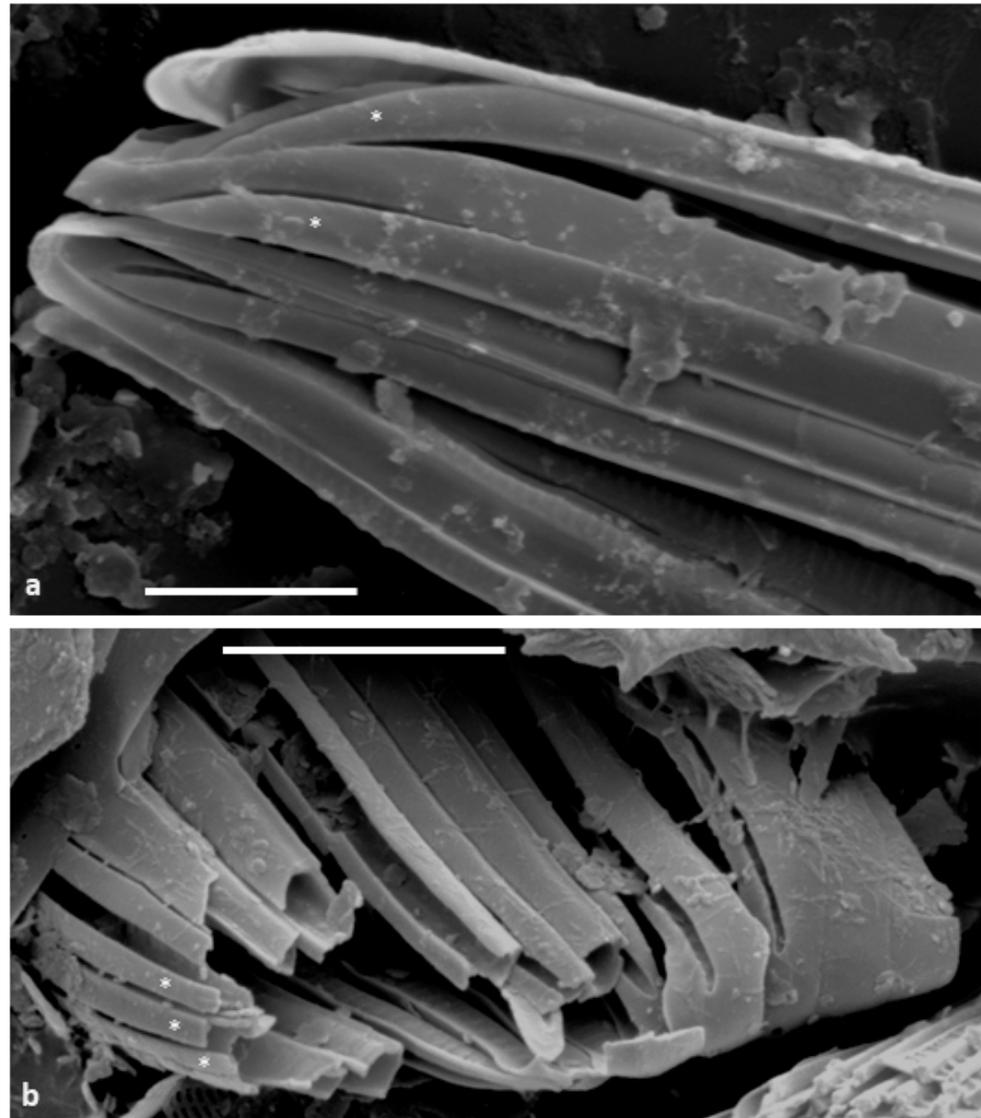
### 3. Results

When the specimens are dried directly on stubs for SEM, they are usually observed in girdle view (Figure 1a) with the valve apices curving down so that the frustule is slightly biconvex, narrower at the apices than the middle. The cingulum appears to comprise narrow, unperforated bands (copulae), sometimes separating from each other, revealing longitudinal grooves particularly in the mid-region (Figure 1a). The individual copulae are split rings, with the tapered open ends alternating and ending slightly short of the frustule apices (Figures 1a,b,d and 2a). At their closed ends, the copulae are simple band-like structures around the frustule apices, slightly broader than the depth of the channel, with the sides of the channel converging as the channel reduces in depth and width (Figures 1c–e and 2a). The tapered open ends of the copulae fit in against the narrowed ends of the channel of the adjacent copula (Figure 1a,b). In isolated copulae, the perforate inner wall of the channel can also be observed (Figure 1c,e).



**Figure 1.** Scanning electron micrographs of *Proschkinia*. (a) Whole frustule of *P. complanata* in girdle view showing the multiple copulae with a plain pars exterior, occasionally opening to reveal the perforate pars interior (arrow). Insertion of open ends of alternate copulae seen well on the right-hand end of the frustule (asterisks). (b) Apex of the girdle region of *P. hyalosira*, showing an alternating

arrangement of copulae, with tapered open ends (asterisks) inserted into grooves on the closed end of the adjacent band. (c) Detail of the closed end of the copula showing how the channelling narrows as the copula curves around the end of the frustule (arrow). (d) Detail of the apex of a *P. hyalosira* valve with valvocopula (arrow) and one copula (asterisk). (e) Detail of the closed end of a *P. hyalosira* valvocopula showing row of hymenate pores (arrow) on the internal surface. The inner surface of the valve is seen below the valvocopula. Scale bars represent 5  $\mu\text{m}$  (a), 2  $\mu\text{m}$  (c) and 1  $\mu\text{m}$  (b,d,e).



**Figure 2.** Scanning electron micrographs of *Proschkinia*. (a) Partial cingulum of *P. hyalosira*, showing alternate bands open at the end of the frustule. Open ends with asterisks. (b) Part of the cingulum showing channelled and simple band-like pleurae (asterisks) from the embedded material. Given the orientation of the channelled copulae, this particular cingulum had probably been disrupted, but the band-like structure of the pleurae is clear. Scale bars represent 2  $\mu\text{m}$ .

The embedded and back-etched material confirms that the copulae are U-shaped (Figures 2a,b and 3a–f); the outer face and base of the U are plain and unperforated (Figures 2b and 3b,e), while the inner face contains square to elongate, hymenate areolae (Figures 2b and 3c,e,f). The copulae open towards their respective valve (Figure 3a–e), with an abvalvar flange on the outer portion overlapping the outer side of the adjacent abvalvar copula (Figure 3a,b,f) and a flat cup-like thickening on the advalvar internal margin abutting the bottom of its advalvar neighbour (Figure 3a,b,f,g). Thus, thanks to

these abutments, the intact cingulum appears to comprise hollow tube-like structures (Figure 3a,c–e). The images of the embedded specimens show that the valve overlaps the valvocopula (Figure 3a,b,e). A few simpler, unchannelled pleurae form the most abvalvar bands (Figures 2b and 3e).

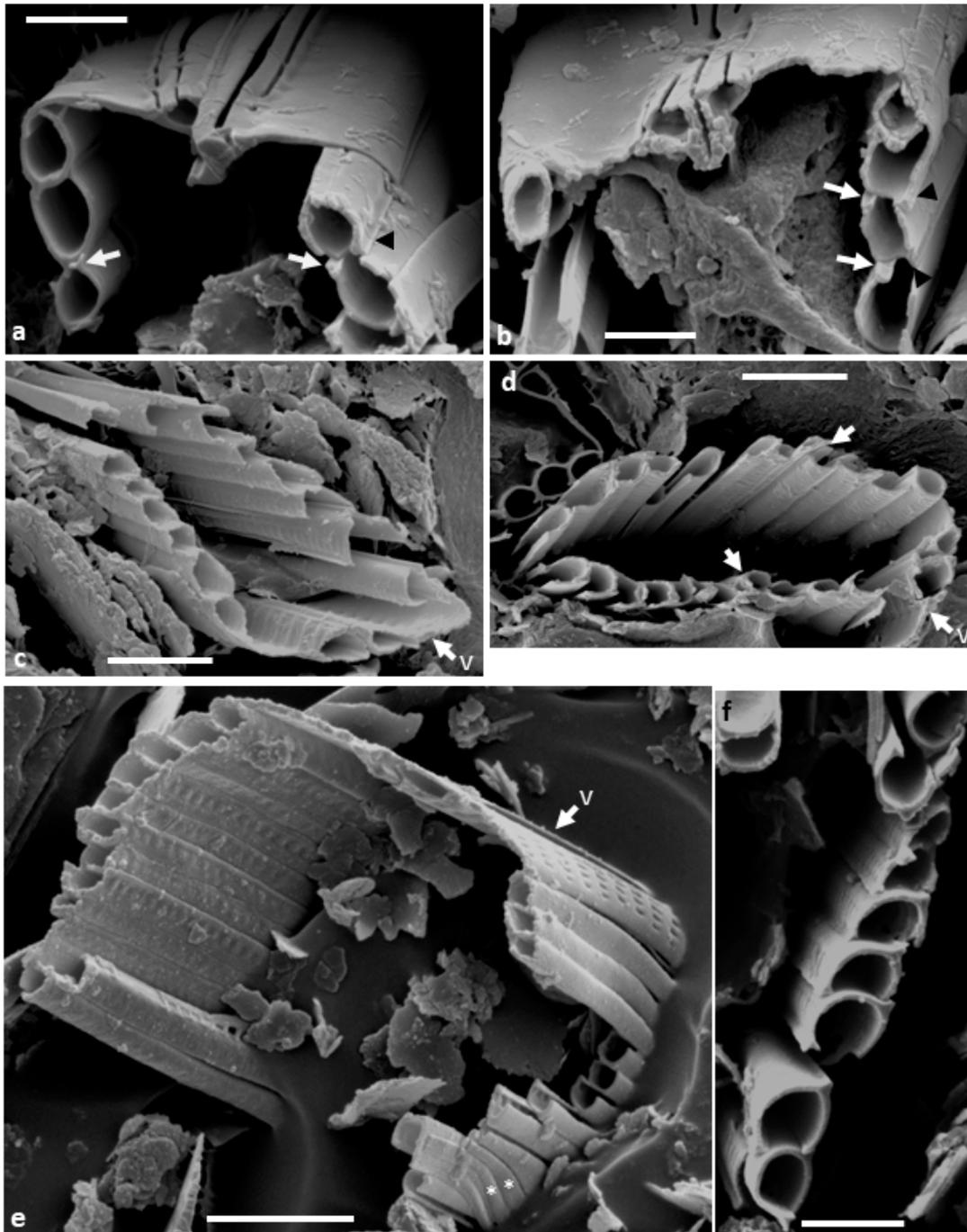
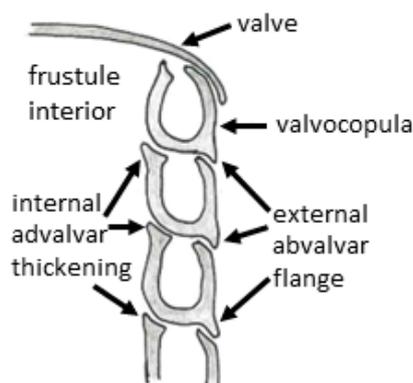


Figure 3. Cont.



g

**Figure 3.** Scanning electron micrographs of the embedded and etched frustules of *Proschkinia* showing cross-sections through the cingula. (a,b). Cross-sections through *P. hyalosira* near the valve centre, showing a valve overlapping the valvocopula and copulae with plain exterior walls. The exterior abvalvar margin forms a ridge that overlaps the next band (arrowheads), while the interior advalvar margin is expanded and butts against the base of its advalvar neighbour (arrows). Figure 1a is adapted with permission from Carr et al. [19]. Copyright year 2008, Muséum National d’Histoire Naturelle, Paris. (c) Section through cingulum showing that the copulae open towards their valve, with a row of hymenate pores on their interior face. (d) Section showing that the orientation of the copulae switches between the epitheca and the hypotheca (arrows indicate change in orientation). (e) Section of *P. complanata* showing that the cingula form smaller channels in an abvalvar direction with unchannelled pleura terminating the epicingulum (asterisks). (f) Detail of copulae showing how adjacent bands abut each other; abvalvar ridges on pars exterior to the right, expanded advalvar pars interior margins to the left. Scale bars represent 2  $\mu\text{m}$  (c,d) and 1  $\mu\text{m}$  (a,b,f). (g) Drawing to show the cross-sectional relationships of the valve, valvocopula and copulae.

#### 4. Discussion

Brugan and Rosowski [17] concluded that the copulae of *Proschkinia* (such as *Navicula complanatoides* Hustedt) were “hollow, forming a semi-tube the length of the frustule”, with unornamented external walls, although they suggested that the internal walls had regularly spaced slits and comb-like edges [7] (p. 267). Most of the above observations confirm many of Brugan and Rosowski’s [17] conclusions but provide more detail on the way in which the copulae interlink, although they contradict their interpretation of copulae having comb-like edges to their pars interior and the lack of overlap between succeeding elements. These interpretations were probably due to artefacts created by the eroded nature of their material [17] (Figure 15) and the way in which the cingulum elements were opening as frustules dried on stubs [17] (Figures 22 and 23). However, even in better prepared material, if seen obliquely [2] (Figure 11), the perforate structure of the pars interior of the valvocopulae can create this impression, although the internal margins of the copulae are always intact and do not abut the valve.

As discussed previously [16,17], the development of more complex copulae in diatoms with deep cingula may be an adaptation to provide strengthening in dynamic littoral environments [11,16,17]. Thus, although only a few genera with deep cingula have channelled, tubular or loculate copulae, others (e.g., *Tabellaria* Ehrenberg, *Grammatophora* Ehrenberg, *Striatella* C.A. Agardh, *Pseudostriatella* Sato et al., *Hyalosira* Kützing, *Hanicella* Lobban and Ashworth) have septa on one or more copulae [1,21–23], which would also reduce the likelihood of cell distortion. These taxa usually form chains of some kind, straight or zig-zag, often attached to a substratum as well as to each other, and are thus susceptible to wave and water movement. Whereas some centric taxa with deep cingula (*Urosolenia* Round and Crawford, *Rhizosolenia* Brightwell) have multiple, imbricate scale-like copu-

lae [1] (pp. 319, 325), these are usually planktonic and therefore unlikely to be subject to the same stresses.

As a benthic motile naviculoid genus, *Proschkinia* is unusual in having such a deep cingulum. (*Parlibellus* cells also have numerous copulae, but their cells are usually only about twice as deep in girdle view as in valve view, with proportionally wider valves [24]). Fresh samples show that *Proschkinia* cells are highly motile, but, whereas most motile taxa remain in valve view when observed under the light microscope, *Proschkinia* cells do not and often seem to “fall over” into girdle view (pers. obs.). This may not, however, be a disadvantage in soft sediments, where they can still move between particles. Their occurrence as epibionts shows that they can also live within biofilms on moving hosts [2] where motility may be less important.

Although Paddock and Sims [11] do not discuss its habit or habitat, as another deep-girdled raphid diatom (with a keeled, sometimes fibulate raphe), *Undatella* is presumably motile and, similar to *Proschkinia*, would be found on benthic sediments. (Original material of *Undatella quadrata* (Brébisson ex Kützing) Paddock and Sims was collected from oyster beds, and Round et al. [1] indicate its habitat as marine, epipelagic.) The numerous hollow copulae of *Undatella* have external advalvar and abvalvar flanges that overlap the adjacent copulae [11] (Figures 22, 23 and 28), thereby linking the elements of the cingulum. Osada [18] (Figures 18, 19, 22, 23, 25 and 26) provides more detailed micrographs of *Undatella* copulae, showing multiple rows of areolae on the inner side of the copulae and plain external surfaces. Short struts from the recurved advalvar margin on the outer surface link across to the pars interior to create the tubular form of the copulae [18] (Figures 17 and 18) but without closing them completely. Paddock and Sims [11] (p. 173) suggest that intermittent linkage between copulae across the cell lumen via short struts (seen as bright dots in LM) [11] (Figures 11 and 47–50) could offer additional strengthening to the frustule, although they do not discuss whether hollow bands could provide strength.

Two other benthic marine diatoms with broad cingula that are usually observed in girdle view (*Entomoneis* Ehrenberg and *Auricula*) have keeled, fibulate and laterally compressed valves. However, unlike *Proschkinia*, their valves have deeper mantles, and therefore, their copulae only contribute approximately one third of their total girdle depth, presumably not requiring additional strengthening to retain their integrity [1] (pp. 632–625), [11] (Figures 8–12).

The chambered valvocopula of *Mastogloia* is involved with the secretion of mucilage around the cell [6,10], and although the valvocopula of *Aneumastus* also has small chambers that open to the exterior [1], there is currently no evidence that it is also associated with mucilage secretion. In both genera, the valvocopulae have small pores opening to the exterior. On the other hand, the pars exterior of *Proschkinia* copulae are plain, without pores, which makes a mucilage secretion function less likely, unless the channels in the copulae widen advalvarly. If this were the case, it could facilitate the growth of epibiontic taxa in biofilms on turtles and other marine animals [2].

The mechanical properties of some chain-forming planktonic diatoms have been explored experimentally [25], and there have been some studies investigating the impact of grazing and nutrients on chain length [26,27]. However, although there has been speculation on the significance of the structural features of the frustules themselves, these derive from structural engineering concepts and have not been tested for microscopic organisms. Thus, it is assumed that the septa on copulae in genera with deep cingula in the Striatellaceae and Grammatophoraceae (both sensu Lobban and Ashworth [21]) act in a stabilising manner, maintaining the valve outline through the cingulum, keeping the sides of the more abvalvar copulae from bulging outwards. Similarly, potentially stabilising septa are present on the copulae at the more inflated head pole of *Licmophora* C.A. Agardh and across (transapical) the cell lumen of some particularly elongated cells with relatively shallow cingula (e.g., *Climacosphenia* Ehrenberg, *Climaconeis* Grunow) [1].

Although the cingulum structure remains relatively poorly understood across the diatoms as a whole, the occurrence of loculate, channelled or tubular copulae is limited to a

few genera, whose phylogenetic relationships have barely been investigated. Although they fall in the same clade in phylogenetic studies, *Fistulifera* lack a deep complex cingulum but share the possession of a fistula with *Proschkinia*. Górecka et al. [28] showed a shallowly U-shaped valvocopula in the monoraphid *Schizostauron*, which sits in a clade with *Astartiella*, sister to the clade containing *Stauroneis*, *Craticula*, *Fistulifera* and *Proschkinia* [3] (S4). However, whereas, similar to *Fistulifera* and *Proschkinia*, *Astartiella* has a fistula, *Schizostauron* does not. *Undatella* with its tubular copulae has not yet been included in any molecular studies but was placed in a different family and order by Round et al. [1]. Neither does current evidence suggest that *Mastogloia* is phylogenetically close to *Proschkinia* [3] (S4). On present evidence, the cingulum structure of *Proschkinia* is unique within the diatoms (albeit with some similarities to that of *Undatella*), whilst the shared possession of a fistula, across otherwise morphologically dissimilar taxa, is intriguingly supported by the molecular phylogenies.

Although genera within some orders, e.g., Cymbellales, Naviculales, share the same copula structure, it is clear that we still have little understanding of the diversity of cingulum structure in the diatoms or of how that variety contributes to frustule stability, let alone any functional role. Comparing *Proschkinia* and *Undatella*, we can see convergent structural developments across major diatom groups in the same environment. However, other genera with similar cell dimensions, also living on marine sediments, have simpler, unchambered bands, e.g., *Auricula*, *Entomoneis* and *Thalassiosiphysa* Conger, suggesting that it is not simply an adaptation for frustule stability. The continued focus on valve structure and cleaned specimens means that we are still missing much information, not only on structural features but also on how the cells are living and interacting in their environment. Brugan and Rosowski [17] asked two interesting questions: “Was the evolution of deep girdles via selection for that trait or the result of selection on a correlated trait?” and “If deep girdles were selected for, what is their adaptive value?”. It seems that over 30 years later, those questions remain unanswered, and we still need to look more closely at all the structural elements of diatoms and consider them in both a phylogenetic context and ecologically.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Data Availability Statement:** No new data were created or analyzed in this study. Data sharing is not applicable to this article.

**Acknowledgments:** SEM images of the embedded specimens were taken by Andrew Carr when working as a volunteer in the NHM. Thanks are due to one of the anonymous reviewers for alerting me to the paper by Osada (2002) [18].

**Conflicts of Interest:** The author declares no conflict of interest.

## References

1. Round, F.E.; Crawford, R.M.; Mann, D.G. *The Diatoms. Biology and Morphology of the Genera*; Cambridge University Press: Cambridge, UK, 1990; 747p.
2. Majewska, R.; Busak, S.; Frankovich, T.A.; Ashworth, M.P.; Sullivan, M.J.; Robinson, N.J.; Lazo-Wasem, E.A.; Pinou, T.; Nel, R.; Manning, S.R.; et al. Six new epibiotic *Proschkinia* (Bacillariophyta) species and new insights into the genus phylogeny. *Eur. J. Phycol.* **2019**, *54*, 609–631. [[CrossRef](#)]
3. Kim, S.-Y.; Witkowski, A.; Park, J.-G.; Gastineau, R.; Ashworth, M.P.; Kim, B.-S.; Mann, D.G.; Li, C.; Igersheim, A.; Płociński, T.; et al. The taxonomy and diversity of *Proschkinia* (Bacillariophyta), a common but enigmatic genus from marine coasts. *J. Phycol.* **2020**, *56*, 953–978. [[CrossRef](#)] [[PubMed](#)]
4. Gastineau, R.; Kim, S.Y.; Lemieux, C.; Turmel, M.; Witkowski, A.; Park, J.G.; Kim, B.S.; Mann, D.G.; Theriot, E.C. Complete mitochondrial genome of a rare diatom (Bacillariophyta) *Proschkinia* and its phylogenetic and taxonomic implications. *Mitochondrial DNA B* **2009**, *4*, 25–26. [[CrossRef](#)] [[PubMed](#)]
5. Zgrundo, A.; Lemke, P.; Pniewski, F.; Cox, E.J.; Latała, A. Morphological and molecular phylogenetical studies on *Fistulifera saprophila*. *Diat. Res.* **2013**, *28*, 431–443. [[CrossRef](#)]
6. Stephens, F.C.; Gibson, R.A. Observations of loculi and associated extracellular material in several *Mastogloia* (Bacillariophyceae) species. *Rev. Algol. Nouv. Ser.* **1979**, *14*, 21–32.

7. Novarino, G. A note on the internal construction of the partectal ring of *Mastogloia lanceolata*. *Diat. Res.* **1987**, *2*, 213–217. [[CrossRef](#)]
8. Novarino, G. Observations on the frustule architecture of *Mastogloia smithii*, with particular reference to the valvocopulae and its integration with the valve. *Diat. Res.* **1990**, *5*, 373–385. [[CrossRef](#)]
9. Paddock, T.B.B.; Kemp, K.-D. An illustrated survey of the morphological features of the diatom genus *Mastogloia*. *Diat. Res.* **1990**, *6*, 73–103. [[CrossRef](#)]
10. Novarino, G.; Muftah, A.R. Observations sur les filaments mucilagineux chez quelques espèces de *Mastogloia* (Bacillariophycées). *Cryptogam. Algol.* **1992**, *13*, 169–179.
11. Paddock, T.B.B.; Sims, P.A. Observations on the marine diatom genus *Auricula* and two new genera, *Undatella* and *Proboscidea*. *Bacillaria* **1980**, *3*, 161–196.
12. Von Stosch, H.A. An amended terminology of the diatom girdle. *Nova Hedwig. Beih.* **1975**, *53*, 1–28.
13. Roth, L.E.; Francisco, D.A. The marine diatom, *Striatella unipunctata*. II. Siliceous structures and the formation of intercalary bands. *Cytobiologie* **1977**, *14*, 207–221.
14. Rosowski, J.R. Valve and band morphology of some freshwater diatoms. II. Integration of valves and bands in *Navicula confervacea* var. *confervacea*. *J. Phycol.* **1980**, *16*, 88–101. [[CrossRef](#)]
15. Fryxell, G.A.; Hubbard, G.F.; Villareal, T.A. The genus *Thalassiosira*: Variations of the cingulum. *Bacillaria* **1981**, *4*, 41–63.
16. Pockock, K.L.; Cox, E.J. Frustule structure in the diatom *Rhabdonema arcuatum* (Lyngb.) Kütz. with particular reference to the cingulum as seen with the scanning electron microscope. *Nova Hedwig.* **1982**, *36*, 621–641.
17. Brogan, M.W.; Rosowski, J.R. Frustular morphology and taxonomic affinities of *Navicula complanatuloides* (Bacillariophyceae). *J. Phycol.* **1988**, *24*, 262–273. [[CrossRef](#)]
18. Osada, K. Fine structure of the marine pennate diatom, *Undatella quadrata* (Brébisson ex Kützing) Paddock & Sims. *Jpn. J. Phycol. (Sorui)* **2002**, *50*, 109–115.
19. Carr, A.; Jones, G.C.; Cox, E.J. An embedding, polishing and etching procedure for examining the 3-D structure of diatoms with SEM. *Cryptogam. Algol.* **2008**, *29*, 285–291.
20. Cox, E.J. Ontogeny, homology and terminology—Wall morphogenesis as an aid to character and character state definition for pennate diatom systematics. *J. Phycol.* **2012**, *48*, 1–31. [[CrossRef](#)]
21. Sato, S.; Mann, D.G.; Matsumoto, S.; Medlin, L.K. *Pseudostriatella* (Bacillariophyta): A description of a new araphid diatom genus based on observations of frustule and auxospore structure and 18S rDNA phylogeny. *Phycologia* **2008**, *47*, 371–391. [[CrossRef](#)]
22. Lobban, C.S.; Ashworth, M.P. *Hanicella moenia*, gen. et sp. nov., a ribbon-forming diatom (Bacillariophyta) with complex girdle bands, compared to *Microtabella interrupta* and *Rhabdonema cf. adriaticum*: Implications for Striatellales, Rhabdonematales, and Grammatophoraceae, fam. nov. *J. Phycol.* **2014**, *50*, 860–884.
23. Lobban, C.S.; Majewska, R.; Ashworth, M.; Bizsel, N.; Bosak, S.; Kooistra, W.H.C.F.; Lam, D.W.; Navarro, J.N.; Pennesi, C.; Sato, S.; et al. Diatom genus *Hyalosira* (Rhabdonematales emend.) and resolution of its polyphyly in Grammatophoraceae and Rhabdonemataceae with a new genus *Placosira*, and five new *Hyalosira* species. *Protist* **2022**, *172*, 125816. [[CrossRef](#)] [[PubMed](#)]
24. Cox, E.J. Taxonomic studies on the diatom genus *Navicula* V. The establishment of *Parlibellus* gen. nov. for some members of *Navicula* sect. *Microstigmaticae*. *Diat. Res.* **1988**, *3*, 9–38. [[CrossRef](#)]
25. Young, A.; Karp-Boss, P.A.; Jumars, P.A.; Landis, E.N. Quantifying diatom aspirations: Mechanical properties of chain-forming species. *Limnol. Oceanogr.* **2012**, *57*, 1789–1801. [[CrossRef](#)]
26. Takabayashi, M.; Lew, K.; Johnson, A.; Marchi, A.; Dugdale, R.; Wilkerson, F.P. The effect of nutrient availability and temperature on chain length of the diatom, *Skeletonema costatum*. *J. Plankton Res.* **2006**, *28*, 831–840. [[CrossRef](#)]
27. Bergqvist, J.P.; Thor, H.; Jakobsen, S.-A.; Wängberg, A.E.; Selander, A. Grazer-induced chain length plasticity reduces grazing risk in a marine diatom. *Limnol. Oceanogr.* **2012**, *57*, 318–324. [[CrossRef](#)]
28. Górecka, E.; Ashworth, M.P.; Davidovitch, N.; Davidovitch, O.; Dąbek, P.; Sabir, J.S.M.; Witkowski, A. Multigene phylogenetic data place monoraphid diatoms *Schizostauron* and *Astartiella* along with other fistula-bearing genera in the Stauroneidaceae. *J. Phycol.* **2021**, *57*, 1472–1491. [[CrossRef](#)]

**Disclaimer/Publisher's Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.