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A brackish diatom, *Pseudofrustulia lancea gen. et sp. nov.* (Bacillariophyceae), from the Pacific coast of Oregon (USA)

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Abstract

Light and electron microscope observations show that a brackish diatom taxon should be classified as a new species of a new genus; *Pseudofrustulia lancea gen. et sp. nov*. We propose separating *Pseudofrustulia* from other similar genera such as *Frickea*, *Frustulia*, *Amphipleura*, *Muelleria*, and *Envekadea* on the basis of its thickened axial ribs, raphe endings, axial costae, morphology of helictoglossa, size of striae on valve surfaces, and areolae on the inner side between its axial ribs and raphe. Girdle bands may be another diagnostic feature for the separation of *Pseudofrustulia* from related taxa, but more detailed observations using SEM images are required to determine if bands are diagnostic.

Keywords: *Pseudofrustulia lancea*, brackish diatom, Washington, Oregon

Introduction

Benthic diatoms are important primary producers on surface sediments in intertidal environments and show higher diversity than planktonic floras (McIntire & Overton 1971, Moore & McIntire 1977). Several researchers have described brackish benthic diatom assemblages from estuaries along the coasts of Washington and Oregon (McIntire & Overton 1971, McIntire 1973, Riznyk 1973, Main & McIntire 1974, Moore & McIntire 1977, Amspoker & McIntire 1978, Sawai & Nagumo 2003, Sawai *et al*. 2016). Recent floral and ecological diatom studies in this region have focused on providing modern baseline data to apply in paleoenvironmental reconstructions (Nelson & Kashima 1993, Hemphill-Haley 1995, Sherrod 1999).

One of such brackish diatom species in these later studies, which in this paper we introduce as *Pseudofrustulia lancea gen. et sp. nov*., has a confused taxonomic classification. Photographs and illustrations in Giffen (1970) and Archibald (1983), apparently similar to this taxon, were identified as *Frustulia interposita* var. *incomperta* (Lewis 1865: 18) Cleve (1894: 123). Their reports referred to Cleve (1894) who had followed the taxonomic revision of the genus *Frustulia* Rabenhorst (1853: 50) by De Toni (1891) and considered *Navicula incomperta* Lewis in Lewis (1865: 18) as a synonym. However, in studies published after De Toni (1891) and Cleve (1894), descriptions, illustrations, and photographs of the taxon do not match the descriptions in the original report of Lewis (1865), especially the size of the valves and their densities of striae and areolae. These inconsistent descriptions suggest that the recent concept of *Frustulia interposita* var. *incomperta* is different from the original one and that the recent usage of *F. interposita* var. *incomperta* is illegitimate. Perhaps the main reason for this taxonomic confusion is that the identifications were based only on text descriptions and hand-drawn illustrations. Here, we use light microscope (LM) and electron microscope (EM; scanning electron microscope [SEM] and transmission electron microscope [TEM]) images to examine the valve morphology of this brackish diatom and amend its taxonomy by proposing its transfer to a new genus.

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Materials and methods

The Astoria study site is in a tidal marsh bordering the mouth of the Lewis and Clark River where it flows into Youngs Bay, southwest of the city of Astoria, Oregon. Vascular plants in the sampled marsh mostly consist of a high-to-middle marsh community dominated by *Schoenoplectus americanus*, *Juncus arcticus*, *Stellaria humifusa*, and Cyperaceae spp. Samples were collected by scraping the upper few millimeters of surface sediment near stems of Cyperaceae spp.

The Alsea Bay site, on the central Oregon coast, is on the eastern shore of the 2-km-wide bay, which is protected from the sea by a sand spit with low dunes. Salt marshes that are tens to hundreds of meters wide fringe the bay's eastern shore and the lower Alsea River. Samples for diatoms were collected from high and middle marsh environments, where vascular plants communities are characterized by *Argentina egedii*, *Carex lyngbyei*, *Juncus arcticus*, *Triglochin maritima*, and *Salicornia virginica*.

Samples were bleached as described by Nagumo & Kobayasi (1990). For LM study, a drop of treated sample was placed on an inverted coverslip and the coverslip was fixed to a glass slide. For EM study, a drop of distilled water was placed on a glass slide and washed specimens were then transferred to the droplet.

Description

Division **Bacillariophyta**
Class **Bacillariophyceae**
Order **Naviculales**
Family **Amphipleuraceae**

Pseudofrustulia **Sawai et Nagumo, *gen. nov.***

Valves lanceolate. Striae uniseriate. Raphe with helictoglossae at the distal ends, with a nodule at the proximal ends, enclosed between two internal ribs. Distal part of the internal ribs fused with helictoglossae, independent from the raphe and the proximal nodule. Areolae are poroids, present on the inner side of the valve between the axial ribs and raphe. Valvocopula opening. Notched features in the middle of valvocopula. Pleura perforated.

Type:—*Pseudofrustulia lancea* Sawai et Nagumo.

Etymology:—the genus epithet is composed of the ancient Greek word "*pseudo*" with the meaning of "resembling to," and *Frustulia*.

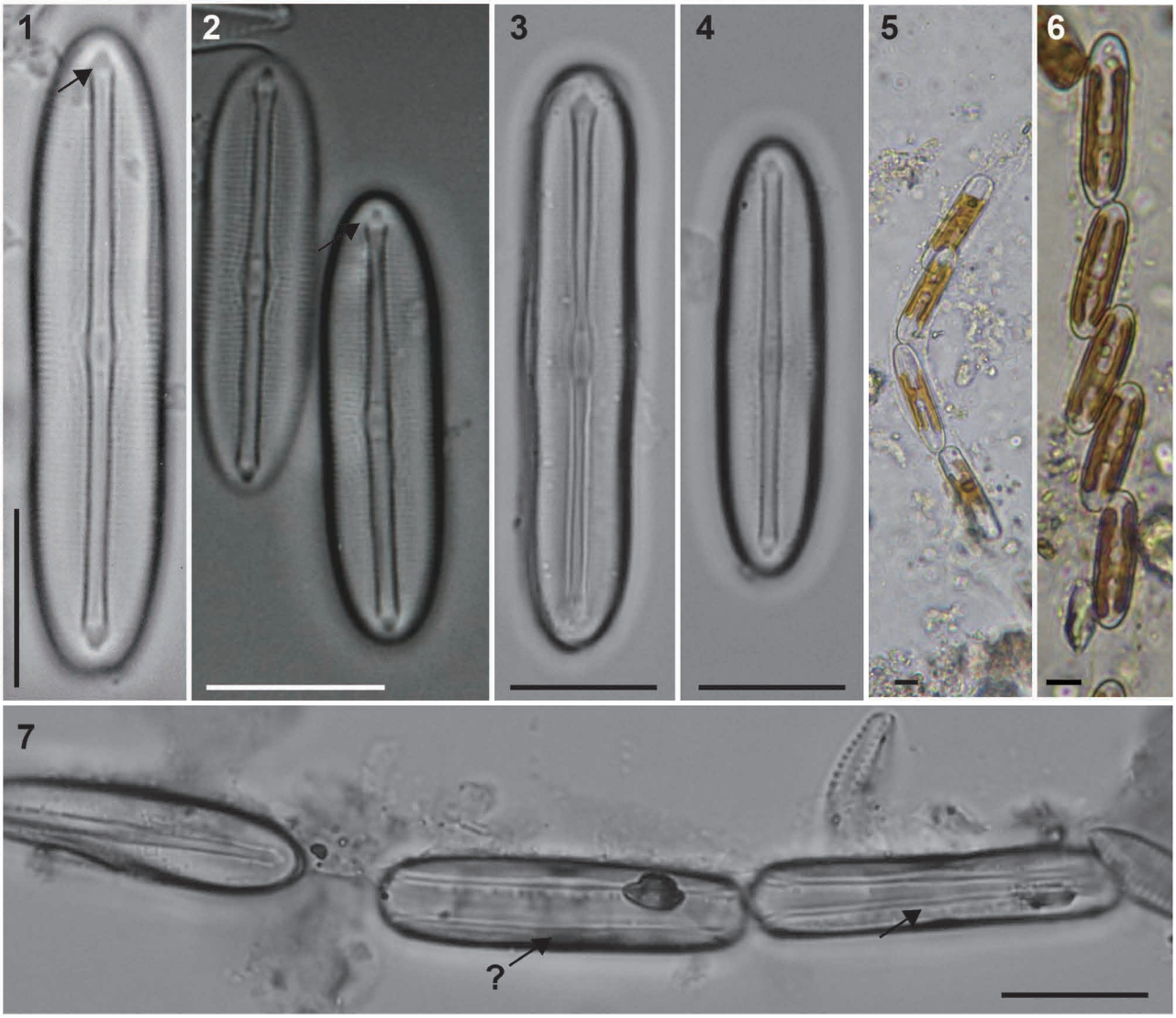
Pseudofrustulia lancea **Sawai et Nagumo, *sp. nov.* (Figs. 1–23)**

A single H-plastid per cell (Figs. 5, 6). Living specimens forming colonies with mucilage tubes (Figs. 5–7). Living specimens gliding within the mucilage tubes. Valves lanceolate-elliptic with rounded apices (Figs. 1–4); length 20 to 70 µm, width 7 to 12 µm. Striae punctate, parallel, about 30–45 in 10 µm (Figs. 5–10). Areolae about 35–40 in 10 µm (Figs. 10–13). The areolae are poroids, occluded internally by vela with fine pores (Figs. 17, 18). Raphe straight between two internal axial ribs (Figs. 14–16), with a nodule at the proximal ends (Figs. 15, 16), enclosed by rounded rib-like structures (helictoglossae) at the distal ends (Figs. 14, 15). The two internal ribs are parallel, or slightly curved at the central area, along the axial area (Fig. 15). Ribs expanded, separated around proximal raphe ends (Fig. 15). Valvocopula opening fimbriated, with a series of slits (Figs. 19–23). The proximal area of the valvocopula with spines in a notch (an arrow in Figs. 7 and 23). Pleura doubly perforated (Figs. 21, 22).

Type:—U.S.A. Oregon: Alsea Bay, 44° 26' 10" N, 124° 01' 32" W, sample collected from the upper few millimeters of surface sediment on the salt marsh (holotype ANSP GC65229, shown in Fig. 4; isotype ANSP GC65230).

Etymology:—the specific species name "*lancea*" is derived from the spearhead-shaped feature around the distal ends of raphe on LM images (arrows in Figs. 1 and 2).

Ecology:—this species is found on surface sediments in the high salt marsh. Salinity range is approximately from 0 to 10 ppt. Relative abundance of *Pseudofrustulia lancea* and accompanying species in a sample from Alsea Bay: *Pseudofrustulia lancea* (25.1 %), *Frustulia vulgaris* (2.9 %), *Gyrosigma eximium* (12.7 %), *Nitzschia scalpelliformis* (4.2 %), *Nitzschia sigma* (9.3 %), *Tryblionella debilis* (3.4 %), *Tryblionella levidensis* (2.6 %).



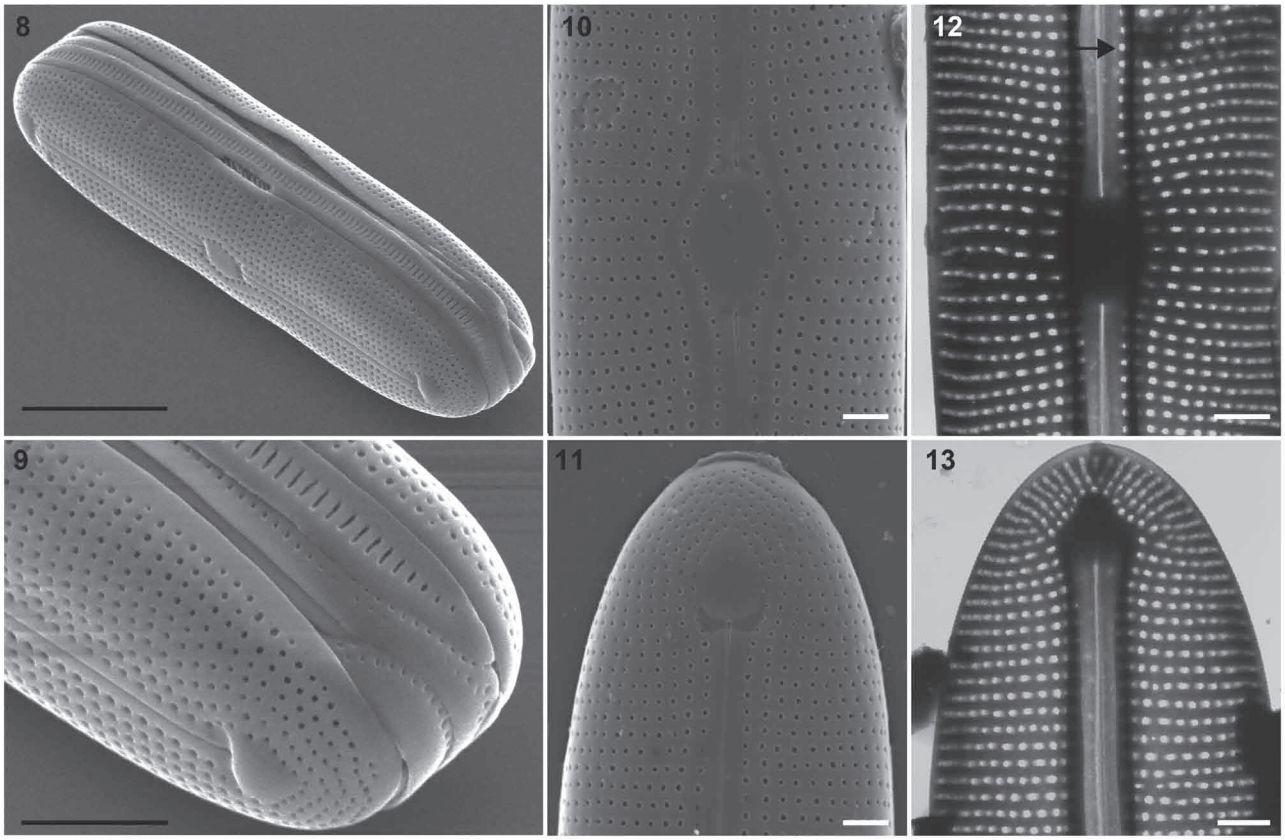
FIGURES 1–7. *Pseudofrustulia lancea*. Light microscopy (LM), holotype and other specimens. 1–3. Treated materials. In distal area, a spearhead-like triangle feature is recognized (arrows in Figs 1–2). 3. Specimen from holotype slide. 4. Holotype. 5–6. Living valves showing H-shaped plastids and colony structures in the mucilage tube. 7. Girdle views (two on the right), specimens from holotype slide. Arrows indicate the notched feature. All scale bars = 10 µm.

Observations and Discussion

In this study, as a result of comparison with other genera of the same family Amphipleuraceae, *Pseudofrustulia* is proposed as a new genus. This new genus can be distinguished from the other related taxa with SEM imagery, but with difficulty using LM. *Pseudofrustulia* is distinguished from *Frustulia*, *Frickea* Heiden (1906: 264), *Amphipleura* Kützing (1844: 103), *Envekadea* Van de Vijver *et al.* in Gligora *et al*. (2009: 136), and *Muelleria* Frenguelli (1945: 172) mainly by the structure of the axial ribs along the raphe, differences in raphe features, the helictoglossa, and the positions of the areolae on the inner side of the valve. Previous studies also have used these morphological features to distinguish taxa within the Amphipleuraceae (Round *et al*. 1990, Spaulding & Stoermer 1997, Gligora *et al*. 2009, Van de Vijver *et al*. 2010). Girdle bands may also be important in differentiating *Pseudofrustulia* from related taxa (Ross & Sims 1978, Round *et al*. 1990, Spaulding & Stoermer 1997, Gligora *et al*. 2009, Van de Vijver *et al*. 2010). *Pseudofrustulia* is considered to be a monotypic genus at present.

The most distinctive feature of *Pseudofrustulia* is a pair of thickened ribs along the raphe in internal view and their relations with the helictoglossae and the central nodule (Fig. 24). In the internal view of the valves of *Pseudofrustulia*, a central nodule, the helictoglossae, and thickened axial ribs are well developed. Although similar structures are common

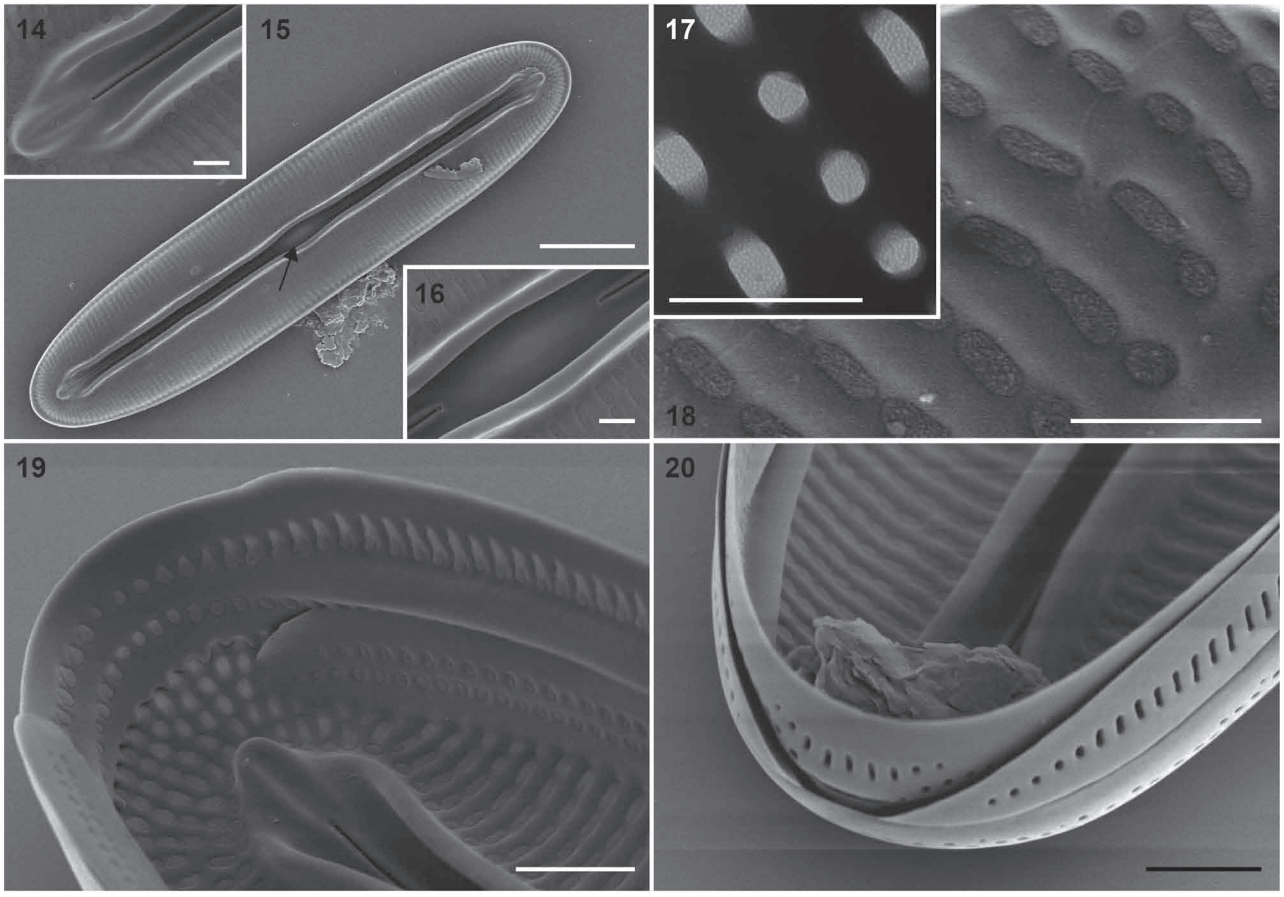
in some related taxa from the genera *Frustulia*, *Amphipleura*, *Muelleria* and *Envekadea*, structure morphology and their relative positions on the valve differ (Fig. 24). For example, *Envekadea metzeltinii* Lee *et al*. (2013: 17) has a central nodule, helictoglossae and developed ribs in internal view (Lee *et al*. 2013). However, its helictoglossae are much smaller than those of *Pseudofrustulia*, and the internal ribs of *Envekadea metzeltinii* are fused, forming a rounded tray at their distal ends. The rounded tray encloses the helictoglossae (Lee *et al*. 2013). Some typical species of *Frustulia* (Graeff *et al*. 2012) have features similar to those of *Pseudofrustulia* in an internal valve view, but the internal ribs are fused with a central nodule and the helictoglossae. *Frickea* and *Muelleria* also have internal ribs, but their ribs are separated from the central nodule and the helictoglossae (Round *et al*. 1990, Spaulding & Stoermer 1997, Spaulding *et al*. 1999, Van de Vijver *et al*. 2010, Bahls 2014) (Fig. 24).



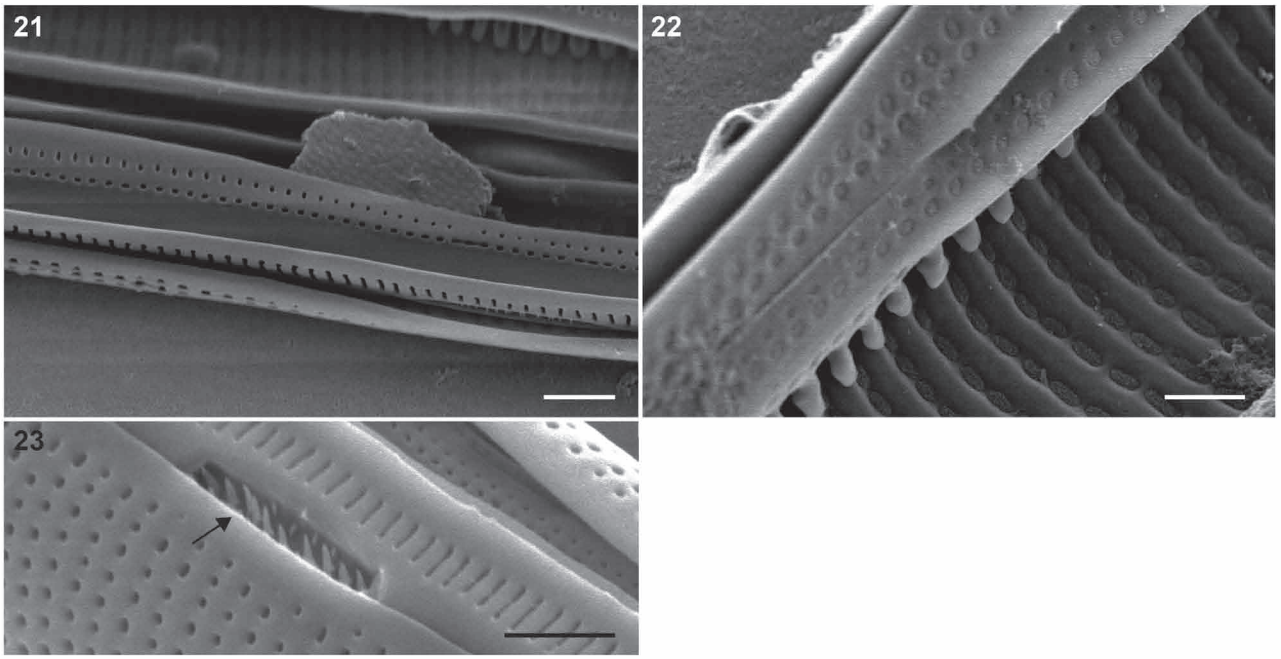
FIGURES 8–13. *Pseudofrustulia lancea*. Scanning (8–11) and transmission (12–13) electron microscopy (SEM, TEM) images. 8. Full view of the frustule. Central area of the valve edge has a notched feature. 9. Close-up view of the apical area of the valve. 10–13. SEM and TEM images of close-up views of the valve surface in proximal (10, 12) and distal (11, 13) areas. Scale bars = 5 µm (8), 2 µm (9), 1 µm (10–13).

Another distinctive feature in the valve morphology of *Pseudofrustulia* is the presence of areolae on the inner side of the valve between the axial ribs and the raphe (arrows in Fig. 12); other related taxa have no areolae in such positions except for *Frickea* (Round *et al*. 1990). These differences in valve structure are visible only on TEM imagery because *Pseudofrustulia* and similar genera have well-developed axial costae on the inner side of their valves (Ross & Sims 1978).

The morphology of the raphe may also help to differentiate related taxa from *Pseudofrustulia*, but raphe morphology is probably less important than other features in the concept of other genera. *Pseudofrustulia* has a simple, straight raphe at the proximal and distal endings, in both external and internal views. Similarly, *Amphipleura* has short but simple raphe features in both external and internal views (Cox 1975, Round *et al*. 1990). In contrast, *Envekadea* and *Muelleria* are characterized by oppositely deflected or unilaterally deflected and branched raphes in external view, respectively (Van de Vijver *et al*. 2010, Lee *et al*. 2013) (Fig. 24). These differences appear to be one of several unique diagnostic features used to identify a specific genus, but the features vary even among species in the present *Frustulia*. For example, *Frustulia* is generally thought to have raphe with T-shaped endings in proximal and distal areas in external view (Round *et al*. 1990), but simple external raphe fissures are also illustrated in *Frustulia* by Silver and Baskette (2004) and in *Frustulia* by Lange-Bertalot (2001; *F. spicula* Amossé 1932: 8). *Frustulia creuzburgensis* (Krasske 1927: 271) Hustedt (1957: 256), *F. capitata* Graeff et Kociolek (2011: 50), *F. latita* Graeff et Kociolek (2011: 52), and *F. soror* Graeff et Kociolek (2011: 54) have deflected raphes at their proximal ends (Graeff & Kociolek 2011).



FIGURES 14–20. *Pseudofrustulia lancea*. Scanning (14–16, 18–20) and transmission (17) electron microscopy (SEM, TEM) images. 14–16. Internal views of the frustule. 17–18. Poroid areolae are occluded internally by vela. 19–20. Valvocopula are open and have a series of slits or pores. Scale bars = 0.5 μm (14, 16–18), 5 μm (15), 1 μm (19, 20).



FIGURES 21–23. *Pseudofrustulia lancea*. 21. Close-up view of valvocopula and pleura having a series of slits and perforations. 22. Fimbriated valvocopula in internal view. 23. A close-up view of the notched feature. Scanning electron microscopy (SEM). Scale bars = 1 μm (21, 23), 0.5 μm (22).

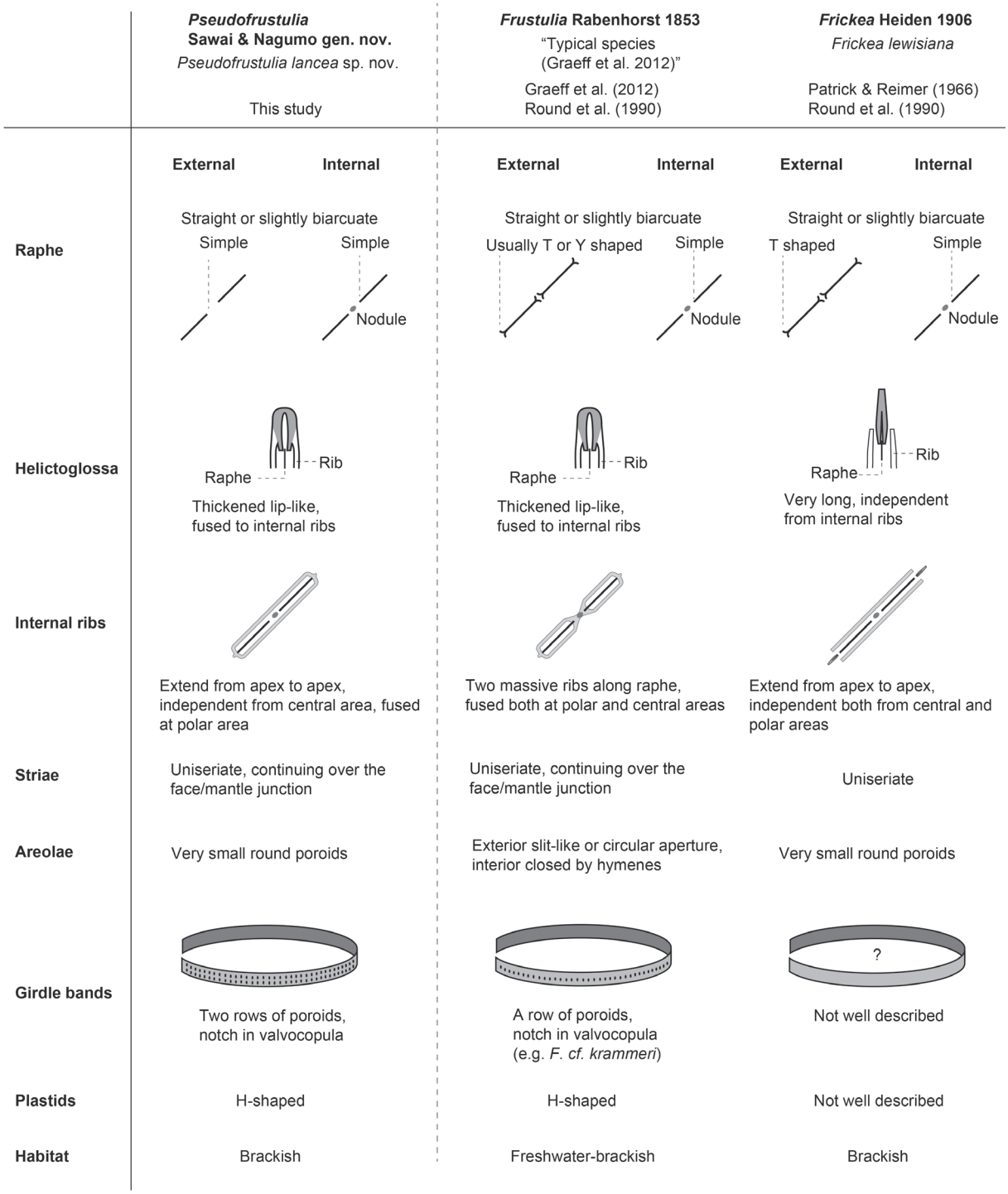


FIGURE 24. Generalized sketches comparing features of *Pseudofrustulia lancea* and other related taxa. Note that this figure does not completely show the possible variation in morphology within this genus. The morphology of the raphe ends in *Frustulia* varies (Kociolek *et al*. 2011) and *Envekadea vanlandinghamii* and *E. pseudocrassirostris* lack developed costae (Gligora *et al*. 2009).

Although only a few examples have been published, the girdle bands of *Pseudofrustulia* are likely a diagnostic feature that can be used to characterize and distinguish this genus from related taxa. Valvocopula of *Pseudofrustulia* are open type, and characterized by a series of slits or perforations (Figs. 19–23). The proximal area of the valvocopula has a feature like an opened window with spikes (Figs. 8 and 23). *Frustulia creuzburgensis* and *F*. cf. *krammeri* have very similar features, namely notches on their valvocopula (Kociolek *et al*. 2011, Graeff *et al*. 2012). In contrast to *Frustulia creuzburgensis*, valvocopula on *Envekadea* do not have any perforations or notches (Gligora *et al*. 2009). To properly compare the details of girdle bands among related taxa, more comprehensive studies using EM imagery will be necessary.

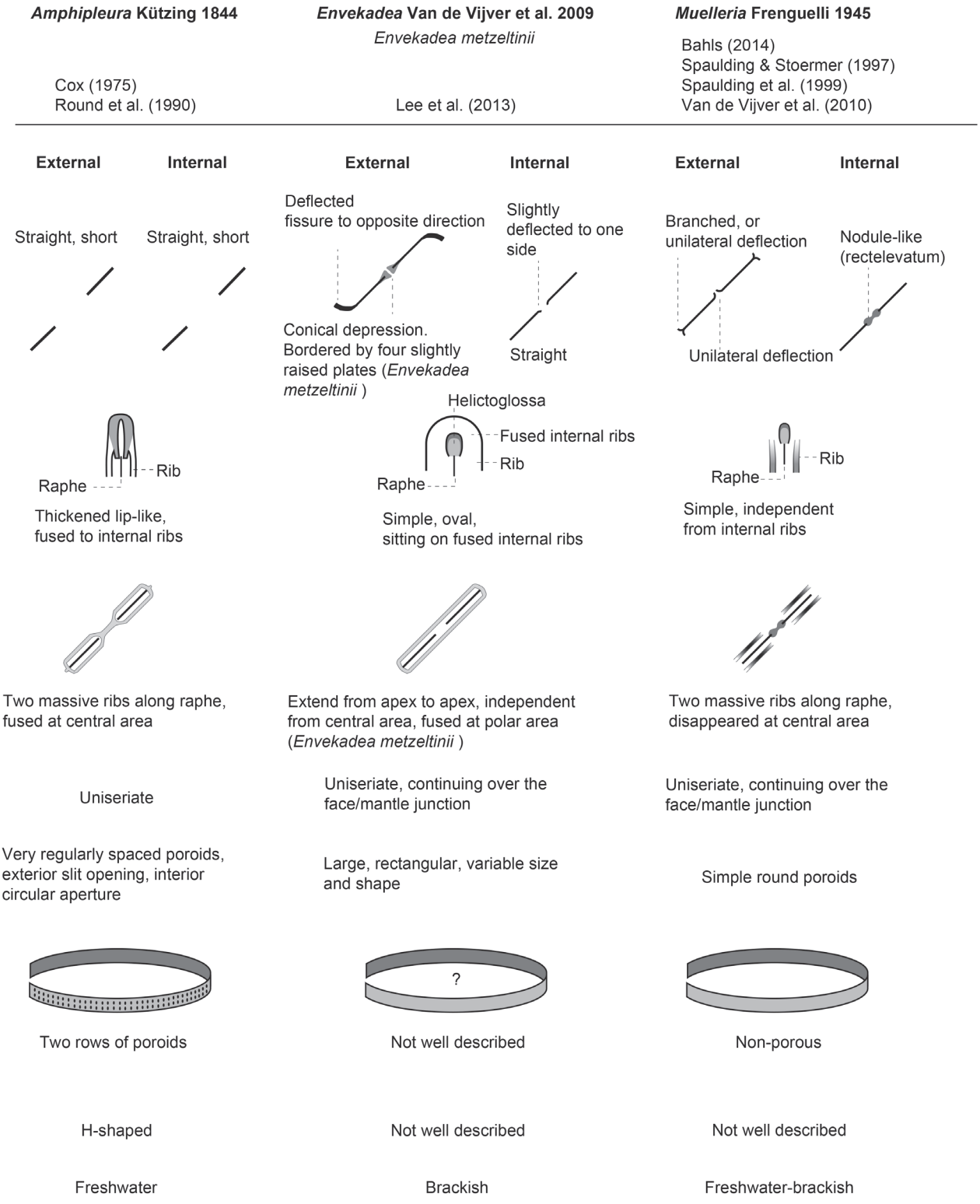


FIGURE 24. (Continued) Generalized sketches comparing features of *Pseudofrustulia lancea* and other related taxa. Note that this figure does not completely show the possible variation in morphology within this genus. The morphology of the raphe ends in *Frustulia* varies (Kociolek *et al*. 2011) and *Envekadea vanlandinghamii* and *E. pseudocrassirostris* lack developed costae (Gligora *et al*. 2009).

We propose *Pseudofrustulia lancea* to be a monotypic species of *Pseudofrustulia*. As mentioned above, the morphologies of specimens in our samples are similar to those in Giffen (1970) and Archibald (1983). Both papers identified them as *Frustulia interposita* var. *incomperta* (formerly *Navicula incomperta*). Their identifications however are incorrect because their descriptions and illustrations differ from the original descriptions by Lewis (1865). Lewis (1865) showed that the size of his *Navicula incomperta* valves was about 150 µm, whereas our specimens range from

20 to 70 µm. Stria and areola densities of *Navicula incomperta* are about 28 in 10 µm and 22–24 in 10 µm, whereas they range between 30 and 45 µm, 35–40 in 10 µm in our specimens, respectively. This is different from the original concept of *N. incomperta*. We conclude that *Pseudofrustulia lancea* differs from the original *Navicula incomperta* sufficiently to be considered a different species.

Pseudofrustulia lancea may be important as an ecological indicator of present and paleo-environments. *Pseudofrustulia lancea* is very abundant at some sites in Washington and Oregon. As observed previously along the Pacific coast, brackish diatom assemblages reflect changes in environmental gradients across salt marshes (Riznyk 1973, McIntire 1973, 1978, Whiting & McIntire 1985, Nelson & Kashima 1993, Hemphill-Haley 1995, Sherrod 1999). We did not observe *Pseudofrustulia lancea* in samples from tidal flats, but this species is abundant in the narrow range of the high-to-middle marsh. This narrow elevational range suggests that this species may be a reliable indicator of former high and middle marshes, if found in high abundance as fossils in sediment.

By proposing *Pseuodfrustulia* as a new genus, our study provides new insights into the taxonomic problems of *Frustulia sensu lato*. There has been much discussion as to how to separate taxa within *Frustulia* in the last few decades. Round *et al*. (1990) offered detailed definitions of valve morphology features (*e.g*., flat valve face, a shallow valve mantle, and longitudinal ribs fusing with helictoglossae and central nodule) to classify *Frustulia*, whereas Lange-Bertalot (2001) simply defined *Frustulia* as possessing longitudinal ribs. The diagnosis by Lange-Bertalot (2001) is probably the most inclusive, but this broad definition makes it difficult to distinguish from the other genera of the family Amphipleuraceae (Graeff *et al*. 2012, Reid & Williams 2007). At present, the definition by Round *et al*. (1990) can be used to separate many *Frustulia* species, although there are still some taxa whose morphology do not fit this definition. For example, *Frustulia creuzburgensis* (Krasske) Hustedt, *F. submarina* Hustedt (1936: 406) and *F. neomundana* Lange-Bertalot & U. Rumrich in Rumrich *et al*. (2000: 135) do not have longitudinal ribs fusing with the helictoglossae or central nodule (Simonsen 1987, Kociolek *et al*. 2011, Graeff & Kociolek 2011). Additionally, as mentioned above, the shapes of the raphe endings vary in some species of *Frustulia* (Fig. 24). We do not have enough data to discuss the phylogenetic relationships within *Frustulia sensu lato*, However, as Graeff *et al*. (2012) recognized "typical *Frustulia* and the others" based on raphe sternum systems, similar features may allow *Frustulia* to be separated into typical *Frustulia* (*Frustulia sensu stricto*) and other species to be separated based on longitudinal rib structures.

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