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Medlinella amphoroidea gen. et sp. nov. (Bacillariophyta) from the neck skin of Loggerhead sea turtles (*Caretta caretta*)

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Abstract

Medlinella amphoroidea gen. et sp. nov. is described from the dorsal neck skin of loggerhead sea turtles (*Caretta caretta*). The presence of girdle septa, multiple copulae, and the marine epizoic habitat of *Medlinella amphoroidea* are characteristic features shared with many species in the similar *Tripterion*, *Chelonicola*, and *Poulinea* genera. The semi-lanceolate valve shape, the asymmetric valve face with distinct dorsal and ventral striae, and the volate pore occlusions distinguish *Medlinella* from these genera. *Medlinella amphoroidea* accounted for up to 50% of all diatom valves on the skin of examined loggerhead turtles. Examination of the type slides of *Tripterion kalamensis* and *T. philoderma* for comparative purposes revealed morphological features that were either insufficiently or incorrectly described in the original publications. Our observations confirm that *T. philoderma* lacks septa and therefore does not conform to the genus description of *Tripterion*. The description of cingulum structure in *Tripterion kalamensis* is amended to identify multiple porose copulae that are open at one end. While the description of *Medlinella* creates another monotypic genus within a group of similar marine epizoic genera, we feel the novel character state (volate occlusions) present in this taxon is significant. Clearly, however, further phylogenetic analysis of morphological, or the development of molecular characters in the group of similar genera is required.

Keywords: Epidermal diatoms, *Tripterion*, epizoic, Florida, new species, morphology, SEM

Introduction

A relatively abundant but unknown marine diatom taxon was observed in epizoic samples from the neck skin of loggerhead sea turtles (*Caretta caretta*). The taxon exhibited morphological features that are shared with many of the “marine gomphonemoid diatoms” (Medlin & Round 1986), but also exhibited unique features not present in those genera. Medlin & Round (1986) showed that several marine species previously assigned to the genus *Gomphonema* Ehrenberg (1832: 87) because of the heteropolar cuneate shape of their frustules and valves, and their attachment to the substratum by mucilage stalks, were dissimilar in several other morphological features from the freshwater members of the genus. Medlin & Round (1986) consequently transferred those species to *Cuneolus* Giffen (1970: 90) and three new genera—*Gomphoseptatum* Medlin ex Medlin & Round (1986: 212), *Pseudogomphonema* Medlin ex Medlin & Round (1986: 214), and *Gomphonemopsis* Medlin ex Medlin & Round (1986: 207). These four marine genera and *Gomphonema* were differentiated by a combination of morphological characters including velum type (volate or hymenate pore occlusions), basal pore field presence or absence and morphology, presence or absence and location of septa and pseudosepta, proximal raphe end morphology (deflected, dilated, coaxial, or hooked), external terminal raphe end fissure (curved or none), and morphology of the internal raphe branch fissures (lateral or straight) (see Table 1 in Medlin & Round 1986). Medlin & Round (1986) referred to *Gomphonemopsis*, *Gomphoseptatum*, *Cuneolus*, and *Pseudogomphonema* as the “marine gomphonemoid diatoms” and assigned *Gomphonemopsis*, *Gomphoseptatum* and *Cuneolus* to the Family Rhoicospheniaceae. Round *et al.* (1990) later assigned *Pseudogomphonema* to the

Naviculaceae. A recent cladistics analysis of morphological characters suggested that the Rhoicospheniaceae are polyphyletic (Majewska *et al.* 2015). Though the term “marine gomphonemoid diatoms” has no taxonomic value, it has been useful temporarily in describing a range of similar taxa whose mid-level taxonomic positions (*i.e.*, Family and Order levels) have yet to be determined, or are uncertain. As such, we refer to the “marine gomphonemoids” using quotation marks throughout our following discussions.

TABLE 1. Comparison of morphological characteristics distinguishing the genera *Gomphonema*, *Cuneolus*, *Gomphonemopsis*, *Gomphoseptatum*, *Pseudogomphonema*, *Tripterion*, *Chelonicola*, *Poulinea*, and *Medlinella*.

	Cell shape	Sternum	Velum, areolae	Raphe	Basal pore field	Pseudosepta	Cingulum
<i>Gomphonema</i> ^{1,2,3,4} Ehrenberg 1832	Heteropolar, cuneate in girdle view	Straight, central	Foricula; variously shaped pores, mostly reniform	Straight or slightly sinuous with external distal raphe ends curved, bent, or simple; external proximal raphe ends curved, bent or simple; internal raphe fissure lateral with internal proximal raphe ends hooked to same side	Distinct, separated by silica strip	Present, both poles, small, or absent	Often 4 open, porose copulae
<i>Cuneolus</i> ^{1,2,5} Giffen 1970	Heteropolar, weakly cuneate and slightly bent in girdle view	Straight, central	Hymenes; circular pores (external)	Straight with unequal length raphe branches; external distal raphe ends angular hooked at head pole, T-shaped at foot pole; external proximal raphe ends dilated; internal raphe fissure straight with internal proximal raphe ends hooked to same side	Absent	One, at head pole	Valvocopulae open, porose with septa present at head pole; other copulae open, non-porose
<i>Gomphonemopsis</i> ^{1,4} Medlin 1986	Heteropolar, cuneate in girdle view	Straight, central	Hymenes; transapically elongated pores	Straight with unequal length raphe branches; external distal raphe ends absent, or T-shaped at foot pole; external proximal raphe ends straight, simple, or dilated; internal raphe fissure straight with simple internal proximal raphe ends	Absent, or indistinct with a few, small, and scattered pores	Absent	Where known, 5 open, porose copulae
<i>Gomphoseptatum</i> ¹ Medlin 1986	Slightly heteropolar, cuneate in girdle view	Straight, central	Unknown velum; rounded or transapically elongated pores constricted into sections	Straight with unequal length raphe branches; external distal raphe ends curved to one side; external proximal raphe ends expanded, pore-like; internal raphe fissure lateral with internal proximal raphe ends straight	Distinct, with a cluster of densely packed round pores	One, at foot pole	Valvocopulae open, porose with septa present at head pole; several other copulae open, porose
<i>Pseudogomphonema</i> ¹ Medlin 1986	Heteropolar, cuneate in girdle view	Straight, central	Hymenes; apically elongated slit-like pores	Straight with unequal length raphe branches; external distal raphe ends absent at head pole, hooked at foot pole; external proximal raphe ends expanded, pore-like; internal raphe fissure lateral with straight, simple internal proximal raphe ends	Row of slits at foot pole	One, at foot pole	4 open, non-porose copulae, copulae 2 and 4 reduced to small segments
<i>Tripterion</i> ^{4,6,7,8} Holmes, Nagasawa & Takano 1993	Heteropolar, cuneate in girdle view	Straight, central	Hymenes; circular to transapically elongated pores	Straight to slightly arched with unequal length raphe branches; external distal raphe ends hooked towards same side; external proximal raphe ends expanded, pore-like; internal raphe fissure lateral with straight, or slightly deflected, simple internal proximal raphe ends; internal distal raphe ends slightly deflected towards secondary side, with weakly developed helictoglossae	Indistinct, closer striae	Absent	Valvocopulae open, porose, with or without septa; 2 nd copulae open, porose, with or without septa; younger copulae open, porose without septa

...continued on the next page

TABLE 1. (Continued)

	Cell shape	Sternum	Velum, areolae	Raphe	Basal pore field	Pseudosepta	Cingulum
<i>Chelonicola</i> ⁹ Majewska, De Stefano & Van de Vijver 2015	Slightly heteropolar, slightly cuneate in girdle view	Straight to weakly curved, central	Hymenes; small, rounded pores	Straight to weakly curved; external distal raphe ends deflected to secondary side; external proximal raphe ends weakly deflected towards primary side, slightly expanded; internal raphe fissure lateral with internal proximal raphe ends obscured by silica flap; internal distal raphe ends straight, with weakly developed helictoglossae	Absent	Absent	Valvocopulae open, porose, with septa; 2 nd copulae open, porose, with septa; younger copulae open, porose without septa
<i>Poulinea</i> ⁹ Majewska, De Stefano & Van de Vijver 2015	Slightly heteropolar, slightly cuneate in girdle view	Straight to weakly curved, central	Hymenes; transapically elongated pores	Straight to curved with unequal length raphe branches; external distal raphe ends elongated, unilaterally bent to same side; external proximal raphe ends spatulate, unilaterally weakly deflected; internal raphe fissure lateral with simple internal proximal raphe ends obscured by silica flap; internal distal raphe ends straight, with weakly developed helictoglossae	Absent	Absent	Valvocopulae open, porose, with septa; 2 nd copulae open, porose, with septa; younger copulae open, porose without septa
<i>Medlinella gen. nov.</i> ⁸ Frankovich, Ashworth & M.J. Sullivan	Isopolar, semi-lanceolate in valve view, rectangular in girdle view	Generally straight, asymmetric along the apical axis	Volae; circular to transapically elongated pores	Generally straight; external distal raphe ends hooked towards ventral margin; external proximal raphe ends spatulate, slightly deflected towards ventral margin; internal raphe fissure straight with simple internal proximal raphe ends obscured by a pair of silica knobs; internal distal raphe ends straight, with weakly developed helictoglossae	Absent	Absent	Valvocopulae open, porose, with septa; 2 nd copulae open, porose, with septa; younger copulae open, porose with shallower septa

¹ Medlin & Round 1986, ² Round *et al.* 1990; ³ Cox 2004; ⁴ Fernandes & Sar 2009; ⁵ Giffen 1970; ⁶ Holmes *et al.* 1993a; ⁷ Holmes *et al.* 1993b; ⁸ present study; ⁹ Majewska *et al.* 2015.

Holmes *et al.* (1993a) established the genus *Tripterion* R.W. Holmes, Nagasawa & Takano (1993a: 7), based on specimens that were scraped from the skin of Dall's porpoises (*Phocoenoides dalli*). *Tripterion* [generitype: *T. kalamensis* R.W. Holmes, Nagasawa & Takano (1993a: 8)] was differentiated from similar "marine gomphonemoid" taxa by a different combination of pore field, pseudosepta, septa, central raphe ends, distal raphe ends, and internal raphe fissure characters used by Medlin & Round (1986), and by the structure of the cingulum (1–2 closed and septate copulae in *Tripterion*) (see Table 1 in Holmes *et al.* 1993a). Holmes *et al.* (1993b) described a second *Tripterion* species, *T. philoderma* R.W. Holmes, Nagasawa & Takano (1993b: 130), from the teeth of strap-toothed whales (*Mesoplodon layardii*). Holmes *et al.* (1993b) did not reference the presence of septa in *T. philoderma* and described the presence of four open copulae in the cingulum. These morphological characteristics of the copulae of *T. philoderma* differ from those of the generitype *T. kalamensis*. The open copulae described for *T. philoderma* not only expanded the morphological variation of the genus but also removed that character as a distinguishing characteristic between *Tripterion* and the other marine gomphonemoid genera. It is unclear why Holmes *et al.* (1993b) assigned their second taxon to *Tripterion* and not to other genera in Medlin & Round's (1986) "marine gomphonemoid" group. Fernandes & Sar (2009) noted the confusion regarding the stated differences in the cingulum structure of *T. kalamensis* and *T. philoderma* in the original literature and described the need for more information about the cingulum structure of these taxa in order to make comparisons with other "gomphonemoid" taxa. Fernandes & Sar (2009) transferred *Gomphonema margaritae* Frenguelli & Orlando (1958: 98) to the genus *Tripterion* establishing a third species within the genus, *T. margaritae* (Frenguelli & Orlando *ex* Fernandes & Sar) Fernandes & Sar (2009: 67). *Tripterion margaritae* was observed attached to benthic substrates and also in plankton hauls from the Antarctic Peninsula (Frenguelli & Orlando 1958, Fernandes & Sar 2009). The cingulum of *T. margaritae* is similar to that of *T. kalamensis* with well-developed septa on the valvocopula and the second copula (Fernandes & Sar 2009). Fernandes & Sar (2009) also proposed placing *Tripterion* in the Family Rhoicospheniacea.

Majewska *et al.* (2015) established the monotypic genera *Chelonicola* Majewska, De Stefano & Van de Vijver (2015: 241) and *Poulinea* Majewska, De Stefano & Van de Vijver (2015: 243) from specimens living on olive ridley sea turtles (*Lepidochelys olivacea*) (Majewska *et al.* 2015). *Chelonicola* and *Poulinea* are similar to *T. kalamensis* in the lack of pseudosepta, and the presence of septa on the valvocopulae and second copulae. However, both genera differ from the latter and *T. philoderma* in having a uniform areola size and stria density on the valve face, and small siliceous flaps in the interior central area that obscure the internal proximal raphe ends (Majewska *et al.* 2015). *Chelonicola* and *Poulinea* differ from each other in the structure of the central area, the shape and spacing of areolae, and the number of areolae per stria (Majewska *et al.* 2015). It is interesting to note that with the description of each of these species-poor or monotypic genera, there are few to no characters or features described that are novel to the “marine gomphonemoid group”. Instead, these genera seem to be distinguished by the presence/absence of characters off an “*a la carte*” menu of features found in many raphid pennate lineages (e.g., apical pore fields or siliceous flaps obscuring proximal raphe ends), or spectra of character states which in other genera might separate species (e.g., stria or pore density).

Tripterion kalamensis, *T. philoderma*, *Chelonicola costaricensis*, and *Poulinea lepidochelicola* are epizoic. Little is known about the degrees of host specificity, endemism, and biogeographical distribution of epizoic diatoms. We observed and described an unknown “gomphonemoid” taxon from scrapings of epibiota from the neck skin of loggerhead sea turtles. Scanning electron microscopy revealed this to be a new taxon that is similar to species within the genera *Tripterion*, *Chelonicola*, and *Poulinea* based on shared morphological characteristics. However, significant differences in velum type, valve shape, position of the raphe-sternum, and raphe morphology warrant the establishment of a new genus. We describe this new taxon as *Medlinella amphoroidea* Frankovich, Ashworth & M.J. Sullivan, *gen. et sp. nov.*, and discuss its affinities and differences with *T. kalamensis*, *T. philoderma*, *T. margaritae*, *C. costaricensis* Majewska, De Stefano & Van de Vijver (2015: 242), and *P. lepidochelicola* Majewska, De Stefano & Van de Vijver (2015: 243). We also re-examined specimens of *T. kalamensis* and *T. philoderma* using light microscopy (LM) from the type slides (materials for SEM were unavailable) in order to clear up confusion regarding their cingulum structure. This investigation expands the study of epizoic diatom biodiversity and describes the current ambiguous state of the borders delimiting the “marine gomphonemoid genera”.

Materials and Methods

During an annual survey of sea turtle populations in Florida Bay, June 24–July 1, 2015, epizoic diatoms were opportunistically sampled from loggerhead sea turtles that were captured from the marine waters (salinity *ca.* 38 psu) of western Florida Bay (24° 55' 18" N, 80° 48' 28" W). Dorsal areas of the neck and lateral carapace of the turtles were cleaned for blood collection using cotton-tipped applicators (Fisherbrand, Fishersci.com). Epibiota collected on the cotton-tipped applicators applied to these two areas were sampled separately from individual turtles. Subsequent LM examination revealed an abundance of *Medlinella amphoroidea gen. et sp. nov.* from the neck samples of the 5 individual turtles that have been analyzed so far. The description of *Medlinella amphoroidea* and the identification of co-occurring taxa are limited to these 5 neck samples from 5 individual turtles at the present time because of the higher relative abundances of *M. amphoroidea* in the neck samples.

In the laboratory the cotton tips of the applicators were removed using a razor blade and then oxidized for diatom examination. The cotton fibers of the applicator tip and epizoic organic material were removed by oxidation in 100 ml of boiling 30% nitric acid followed by addition of potassium dichromate when 50 ml of acid remained. Cleaned diatoms were settled from the mixture for a minimum of 6 h and the remaining acid solution decanted. The settled diatoms were rinsed with deionized water. The rinsing/settling/decanting process was repeated six times until the solution reached a neutral pH.

For light microscopy (LM), cleaned diatoms were air-dried on cleaned No. 1 coverslips which were then mounted onto glass slides using Naphrax® (The Biology Shop, New South Wales, Australia). LM analyses were made using differential interference contrast (DIC) and an oil immersion planapochromatic lens (NA = 1.40) on a Nikon E600 microscope (×600 and ×1200 magnification) equipped with a Leica DFC425 digital camera. Diatom morphometrics were determined using Leica Application Suite version 3.7 imaging software. Slides of *Tripterion philoderma* and *T. kalamensis* were examined using Zeiss AXIO Imager.A1 microscope, equipped with DIC optics and Jenoptik ProgRes® SpeedXTcore 5 camera. The relative abundances of individual taxa were determined from the holotype and paratype slides of *Medlinella amphoroidea* by identifying and counting 255–508 diatom valves along arbitrary linear transects.

For comparative purposes, LM images produced from the holotype slide (ANSP! GC 17182a) of *Tripterion philoderma* containing specimens from the teeth of a strap-toothed whale stranded at Milnerton, South Africa in April 1978 were examined. LM images were also produced and examined from the holotype slide (ANSP! GC64443a) and the isotype slide (ANSP! GC64443b) of *T. kalamensis* Holmes, Nagasawa & Takano, containing specimens from the skin of Dall's porpoises collected from various northern Pacific Ocean locations. Measurements for *Tripterion* specimens were obtained using program ProgRes® CapturePro 2.8.8.

For scanning electron microscopy (SEM), subsamples of the cleaned material were dried onto aluminum stubs and sputter-coated with gold or iridium to a thickness of 15 nm. SEM analyses were made with a Zeiss SUPRA 40 VP scanning electron microscope operated at 7 kV. Diatom terminology follows Hendeby (1964), Ross & Sims (1972), Anonymous (1975), and Round *et al.* (1990).

Results

Division Bacillariophyta

Class Bacillariophyceae

Subclass Bacillariophycidae

Order *incertae sedis*

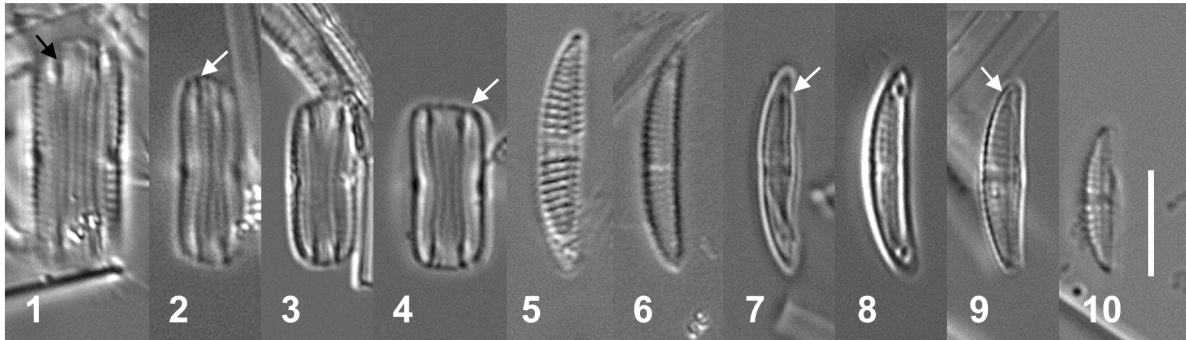
Family *incertae sedis*

Medlinella Frankovich, Ashworth & M.J. Sullivan, *gen. nov.*

Frustules are rectangular in girdle view with bluntly rounded ends and porose girdle copulae (Figs 1–4, 11). Septa are evident on the copulae of whole frustules in girdle view (arrows in Figs 1–4). Septa are also evident in valve view when copulae remain attached to valves (arrows in Figs 7, 9). Valves are isopolar and semi-lanceolate with a convex dorsal margin and a slightly concave ventral margin inflated in the middle (Figs 5–10, 12, 13). The valve face is strongly asymmetric around a narrow axial area, superficially resembling the genus *Amphora* Ehrenberg ex Kützing (1844: 107) with distinct dorsal and ventral striae (Figs 5–10, 12–16). The striae are composed of circular to transapically elongated areolae that are partially occluded by volae (Figs 12–18). Apical pore fields are absent. The raphe-sternum is eccentric and displaced towards the ventral margin (Figs 5, 8–10, 12–16). The raphe is generally straight to slightly arched (Figs 12–16). The external proximal raphe ends are spatulate, weakly deflected towards the ventral margin, and terminate where the fascia extends towards the valve margins (Figs 12, 13, 15). The external distal raphe ends are angularly hooked towards the ventral margin with some variation in the angularity of the bends (Figs 12–16). Small slightly thickened hyaline areas on the primary side of the valves are located near the valve apices adjacent to the distal raphe ends (Figs 12–16, 18). Internally, the raphe is located on a slightly raised and thickened sternum (Figs 19–22, 24). The internal proximal raphe ends are straight, simple, closely spaced, and partially obscured by a pair of small knob-like to flap-shaped structures present at the raphe ends (Figs 19–22). The internal distal raphe ends are straight and terminate on weakly developed helictoglossae (Figs 19–20). Pseudosepta are absent. The cingulum (Figs 11, 25–26) is composed of many bands (up to 12 observed) that are open at one end. The bands of the cingulum (Figs 11, 25–30) are differentiated into three types: the valvocopulae that have septa (Figs 24, 27), the second copulae that have septa at the opposite pole (Figs 26, 28), and additional abvalvarly located copulae (Figs 11, 25, 26, 29, 30) that have shallow, or partially developed septa (arrows in Figs 29, 30). The valvocopula is flanged inward on the pars interior where it attaches to the valve (Figs 25, 27). The flange is expanded as a large tab located in the middle on the dorsal side where it aligns with dorsal side of the internal central area of the valve (Figs 22, 23, 25, 27). The valvocopula septum is located on the pars exterior (Figs 24, 27).

Type:—*Medlinella amphoroidea* Frankovich, Ashworth & M.J. Sullivan, *sp. nov.*

Etymology:—the generic name honors Dr. Linda K. Medlin (Marine Biological Association of the United Kingdom) in recognition of her important research on “marine gomphonemoid diatoms”.



FIGURES 1–10. *Medlinella amphoroidea*. Type population, LM. 1–4. Frustules in girdle view showing size range and morphological variation. Arrows in Figs 2, 4, 7, 9 indicate septa. 5–10. Specimens in valve view showing size range. Scale bar = 5 μm .

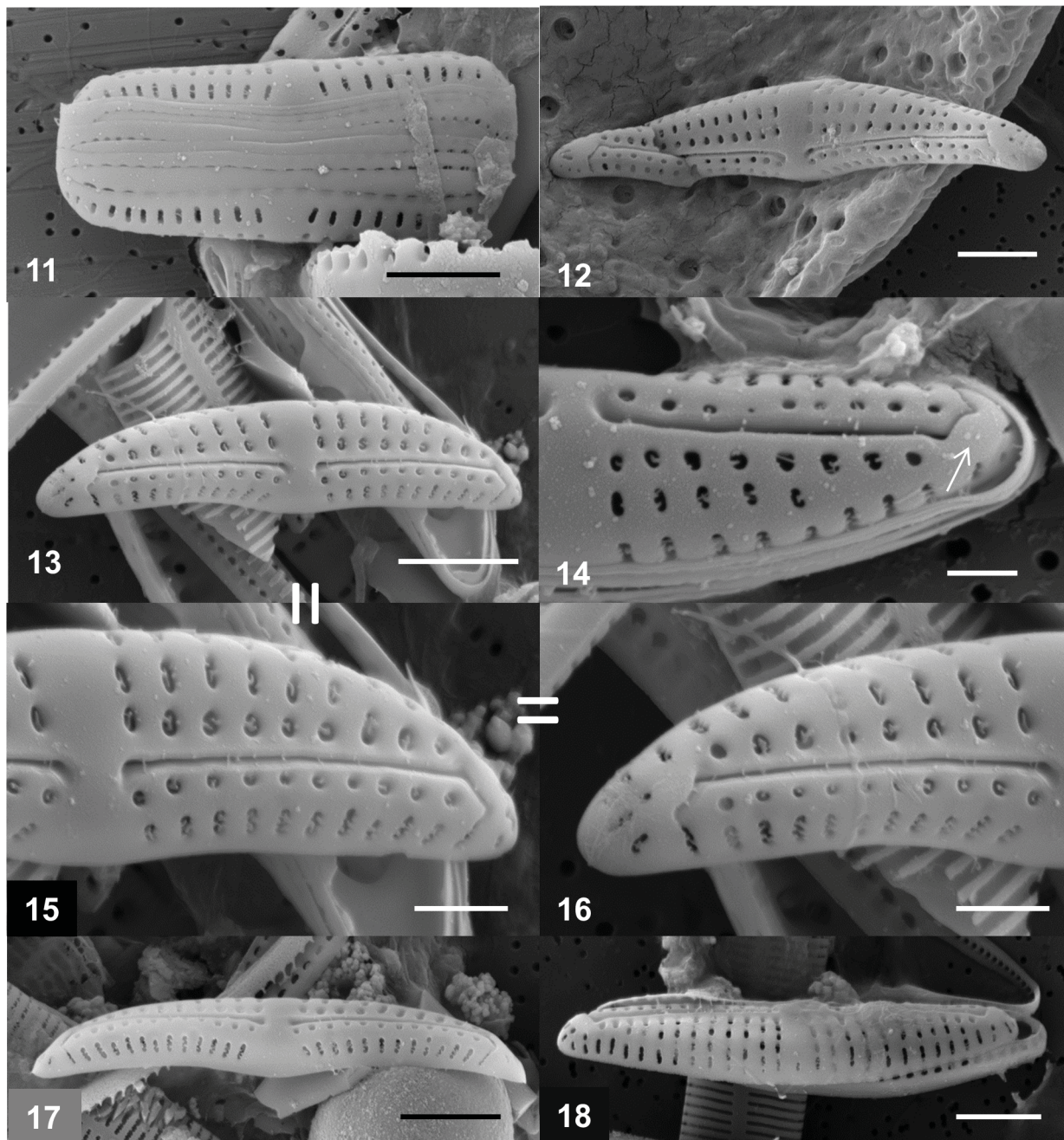
***Medlinella amphoroidea* Frankovich, Ashworth & M.J. Sullivan, *sp. nov.* (Figs 1–26)**

LM morphology: Valve apices are rounded and slightly bent towards the ventral margin (Figs 5–10). Valve morphometrics are as follows: length 7.0–13.0 μm , $n = 19$, width 1.5–2.5 μm , $n = 17$, length-to-width ratio 3.3–6.5, $n = 14$. The dorsal and ventral stria densities are 22–30, $n = 19$, and 26–35 in 10 μm , $n = 10$, respectively (determined from LM and SEM images). The central area is formed by a wide asymmetric rectangular to bow tie-shaped fascia that extends towards the valve margins (Figs 5–10). The septa on the valvocopulae and 2nd copulae extend over *ca.* 1/7 of the frustule length from the apices (Figs 1–4). SEM morphology: Externally, the valve face and mantle have uniseriate transapical striae (Figs 11–18). The dorsal striae are nearly parallel in the valve middle becoming radiate towards the apices, 25–34 in 10 μm , $n = 17$ (Figs 12–16, 18). The dorsal striae continue on to the valve mantle uninterrupted (Figs 12–16, 18) with up to 5 areolae per stria on the valve face and mantle in the middle of the valve adjacent to the fascia (Fig. 18) gradually decreasing to 1 or 2 areolae that wrap around the apices (Figs 12–16, 18). The ventral striae are interrupted at the valve face-mantle transition with a single apical row of smaller circular to oval areolae located on the valve face adjacent to the raphe and a single row of larger transapically elongated areolae located on the valve mantle (Figs 12, 13, 15–17). The ventral striae are strongly radiate in the valve middle becoming parallel and finally convergent at the valve apices, 30–36 in 10 μm , $n = 12$, (Figs 13, 15–18). Smaller areolae are occluded by a single simple or branched vola (Figs 13–16). Wider, transapically elongated areolae are occluded by multiple volae (up to six observed) arranged in an alternate or irregular pattern (Figs 13–16). The central area is large, forming an asymmetric rectangular to bow tie-shaped fascia that extends to the valve margins and is wider on the ventral side (Figs 11–13, 15, 17, 18). Occasionally, shortened striae are present at the dorsal valve margin adjacent to the central area (Fig. 18). The valvocopula and the second copula have a single row of apically elongated pores around the perimeter, pore densities: 28–30 in 10 μm , $n = 5$ (Figs 22–28). The remaining copulae have a single row of slightly smaller pores, 32–45 in 10 μm , $n = 6$ (Figs 11, 25, 26, 29, 30).

Type:—UNITED STATES. Florida: Florida Bay, samples removed from the skin in the dorsal neck area of loggerhead sea turtles *Caretta caretta*, 24° 55' 01" N, 80° 48' 28" W, *B.A. Stacy*, 24 June 2015 (holotype CANA! 124075, illustrated as Figs 1–5, 7–30; paratypes CAS! 223049, illustrated as Fig. 6, ANSP! GC59142, BM! 101808, BRM! ZU10/31. The holotype slide and paratype slides are specimens from separate individual turtles).

Etymology:—refers to the resemblance of the valves of *Amphora* in the valve view.

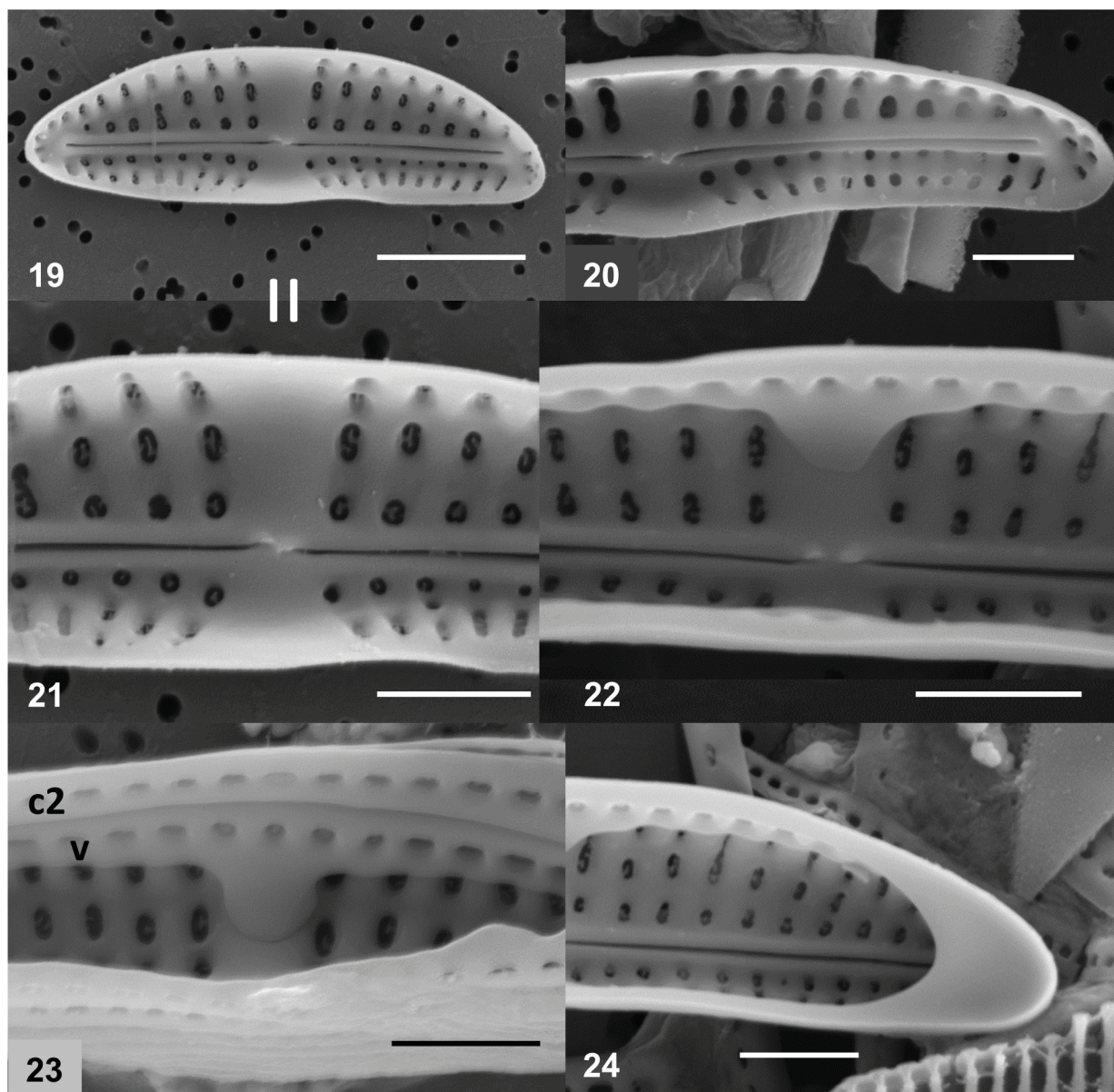
Taxa relative abundances:—Forty-nine taxa from 24 genera were observed from the neck skin of five loggerhead turtles. The relative abundances of the newly described *M. amphoroidea* ranged from 13% to 50%. *Medlinella amphoroidea* was the most abundant taxon in 3 of the samples. *Hyalosynedra cf. laevigata* (Grunow 1877: 166) D.M. Williams & F.E. Round (1986: 316) was the second most abundant taxon comprising 2% to 62% of the valve counts. At the third rank, the most abundant taxon was *Tursiocola denysii* Frankovich & Sullivan ex Frankovich *et al.* (2015: 228), comprising 5% to 43% of the valve count. 5% of the valves remained undetermined at the genus and/or at the species rank. Only four other taxa (*i.e.* *Mastogloia cuneata* (Meister 1937: 268) Simonsen (1990: 134), *Navicula* sp., *Achnanthes* sp., and *Nitzschia* sp. exhibited mean relative abundances >1%). The remaining taxa observed were common benthic forms.



FIGURES 11–18. *Medlinella amphoroidea*. Type population, SEM, external views. 11. Entire frustule in girdle view showing cingulum with 8 copulae visible. Single rows of pores are evident on the copulae. Note that the hypovalve with its attached valvocopula (not visible) is partially collapsed on the left side of the image towards the frustule interior. 12. Broken valve showing shape of longer valves. 13. Whole valve showing orientation of striae, eccentric raphe-sternum, and fascia. 14. Dorsal striae and valve apex showing raphe branch, hyaline area (arrow) on primary side of valve adjacent to the angularly hooked distal raphe end. 15. Detail of central area and valve apex on right side of specimen depicted in Figure 13 showing volate pore occlusions, spatulate and slightly deflected proximal raphe ends, and hooked distal raphe end. 16. Detail of valve apex on left side of specimen depicted in Figure 13 showing angularly hooked distal raphe end that points towards the ventral margin. 17. Whole valve in side view showing orientation of ventral striae and the extension of the fascia onto the valve mantle. 18. Whole valve in side view showing orientation of dorsal striae and a single shortened stria on the valve margin adjacent to the central area. “=” indicate the same specimen. Scale bars: Figs 11–13, 17, 18 = 2 μm , Fig. 14 = 0.5 μm , Figs 15, 16 = 1 μm .

Re-examination of the type slides of Tripterion kalamensis and T. philoderma

Valves of both *Tripterion kalamensis* and *T. philoderma* are heteropolar and clavate with a broadly rounded head pole and a narrower foot pole (Figs 31, 32). For both species, the raphe is straight and the central area is formed by a wide asymmetric bow tie-shaped fascia that terminates at or near the edge of the valve face (Figs 31, 32).



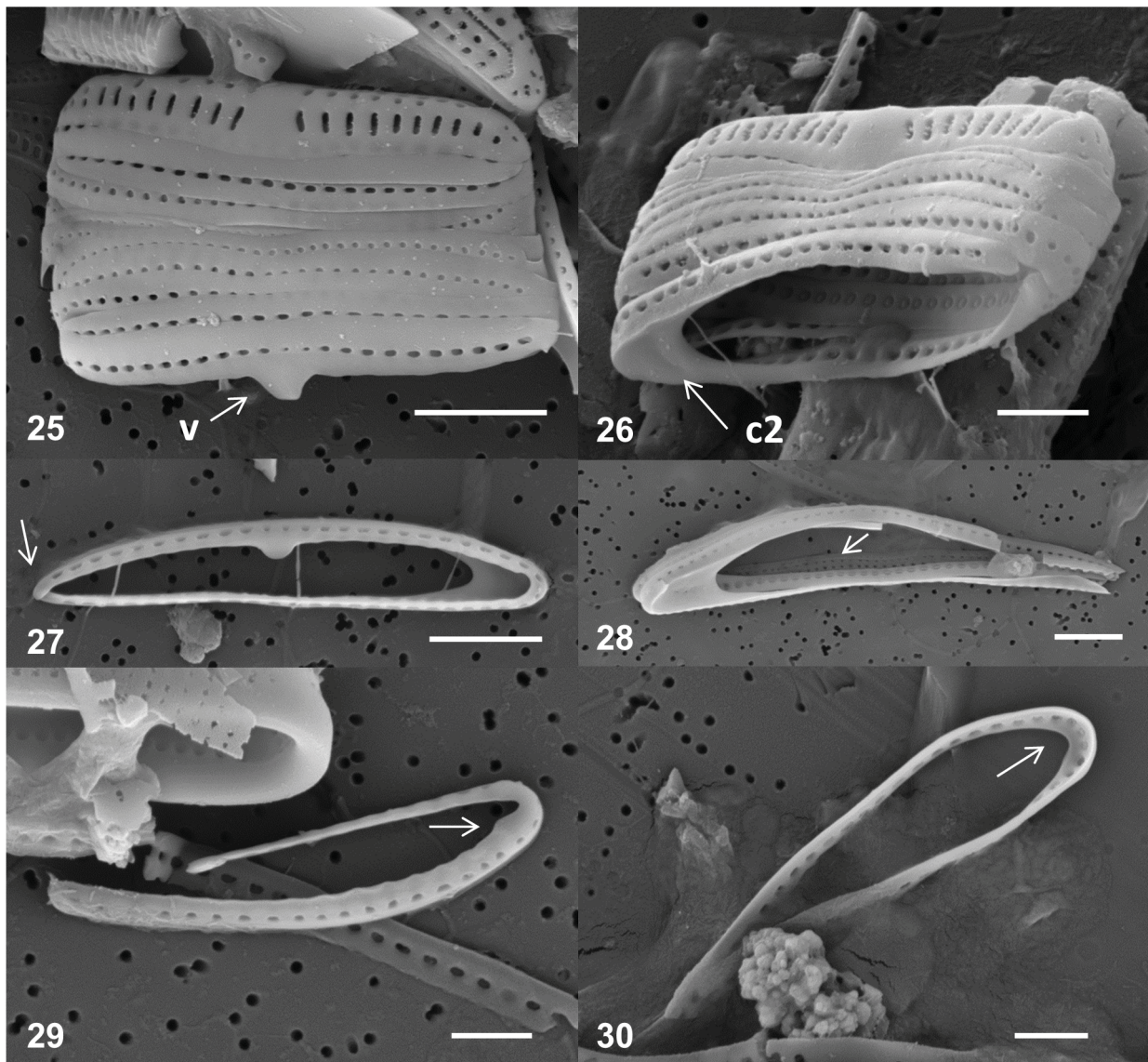
FIGURES 19–24. *Medlinella amphoroidea*. Type population, SEM, internal views. 19. Whole valve. 20. Detail of central area and valve apex showing the raphe located on a slightly raised and thickened sternum. 21. Detail of central area of the valve depicted in Fig. 19. 22. Oblique view of central area of valve with attached valvocopula showing the attachment of the central tab of the valvocopula to the dorsal side of internal central area and a pair of small knob-like to flap-shaped structures present at the internal proximal raphe ends. 23. Oblique view of central area of valve with attached valvocopula (v) and second copula (c2), each with a single row of pores. 24. Valve with attached valvocopula showing detail of pars exterior of valvocopula septum. “=” indicate the same specimen. Scale bars: Fig. 19 = 2 μ m, Figs 20–24 = 1 μ m.

Tripterion kalamensis Holmes, Nagasawa & Takano (Fig. 31)

LM morphology: Valve morphometrics are as follows: length 18.5–34.5 μ m, maximum width 2.5–5.0 μ m, length-to-width ratio 4.9–9.6, n = 78. The transapical striae are radiate in the middle of the valve, 18–24 in 10 μ m, n = 30, becoming parallel at the apices, up to 24 in 10 μ m near the head pole, up to 32 in 10 μ m near the foot pole, n = 30. Our observations of the holotype slide of *T. kalamensis*, the generitype, revealed that the cingulum is composed of multiple copulae that are open at one end (Fig. 31, arrows). This contradicts the original description in Holmes *et al.* (1993a): “Cingulum consisting of one robust closed band, sometimes two (dividing frustules?), with short septa at each pole and bearing a single row of puncta.” We observed many separated single copulae with very short septa and also separated cingula consisting of at least two copulae. We believe the latter is what Holmes *et al.* (1993a) referred to as a “robust” (our emphasis) “closed band”. We offer the following emended description of cingulum structure in *Tripterion kalamensis*:

the cingulum consists of 2–7 porose copulae per frustule that are open at one end with small septa that extend ca. 1/20 of the valve length from the apices.

Type:—BERING SEA. Specimens from the skin of *Phocoenoides dalli* (Dall's porpoise) RCF037-1983, 55° N 174° E, *R.W. Holmes*, 17 April 1989 (holotype ANSP! GC64443a, isotype ANSP! GC64443b).

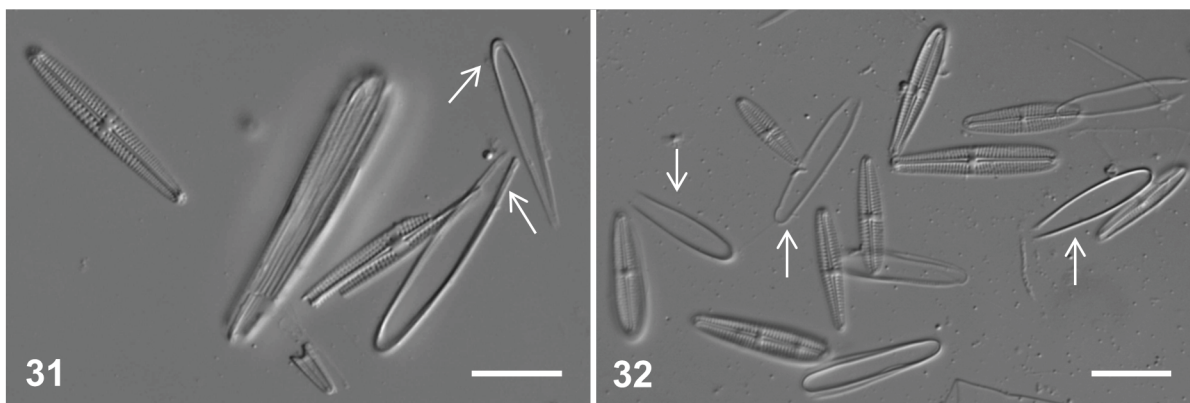


FIGURES 25–30. *Medlinella amphoroidea*. Type population, SEM. 25. Valve with attached cingulum showing central tab (arrow) of valvocopula (v) with 11 additional copulae in side view. 26. Valve with attached partial cingulum in oblique view showing the pars interior of the septum of the second copula (c2). 27. Pars interior of valvocopula showing flanged margin, central tab on the pars interior, and septum located on the pars exterior. Arrow indicates open end of valvocopula. 28. Second septate copula with 2 attached additional copulae. Note smaller pores on copula 3 (arrow). 29. Copula of undetermined order showing partially developed septum (arrow). 30. Copula of undetermined order showing shallow septum (arrow). Scale bars: Figs 25–28 = 2 μ m, Figs 29, 30 = 1 μ m.

Tripterion philoderma Holmes, Nagasawa & Takano (Fig. 32)

LM morphology: Valve morphometrics are as follows: length 8.5–28.0 μ m, maximum width 2.0–4.0 μ m, length-to-width ratio 3.3–7.5, n = 75. The transapical striae are radiate in the middle of the valve, 22–26 in 10 μ m, n = 34, becoming parallel to slightly convergent at the apices, up to 29 in 10 μ m, n = 34. Copulae are open at one end and do not have septa (arrows in Fig. 32).

Type:—SOUTH AFRICA. Milnerton, specimens from the teeth of *Mesoplodon layardii* (strap-toothed whale), 33° 52' S 18° 29' E, *R.W. Holmes*, 6 April 1978 (holotype ANSP! GC 17182a).



FIGURES 31–32. *Tripterion kalamensis* and *T. philoderma*. Type populations, LM, specimens in valve view showing valve and frustule shape, size range, and separated copulae. 31. *Tripterion kalamensis* (holotype slide ANSP! GC64443a), arrows indicate septum on copula (top arrow) and open end of copula (bottom arrow). 32. *Tripterion philoderma* (holotype slide ANSP! GC17182a), arrows indicate lack of septa in separated copulae. Scale bars = 10 µm.

Discussion

The new species, *Medlinella amphoroidea*, is easily recognized using LM and SEM by its amphoroid shape and the presence of septa on the valvocopulae and 2nd copulae. It is unlikely to be confused with any other species in similar genera because of its semi-lanceolate and isopolar valve shape, distinct dorsal and ventral striae organized around an eccentric raphe-sternum, straight internal raphe fissure, and volate pore occlusions (see Tables 1, 2). When examining specimens using LM, the valves of *M. amphoroidea* are more likely to be misidentified as a *Catenula* Mereschkowsky (1903: 97) species or a small *Amphora* species, but careful focusing through valves with attached valvocopulae, or examination of intact frustules in girdle view, will reveal the presence of septa that are not present in *Catenula* or *Amphora* species. The frustule shape of *M. amphoroidea* is also rectangular, while that of *Amphora* species is shaped like “a third of an orange” or sphere (Hendey 1964).

The characters suggested to be most important generic architectural criteria include valve shape, position of the sternum, areolae structure, raphe structure, presence/absence of pore plates, and details of copulae (Round 1996, Cox 2014). *Medlinella amphoroidea* exhibits at least four differences in this list of suggested generic characters for any pair-wise comparison with the similar genera (Table 1). These differences in the set of suggested generic structural features justify the establishment of the new genus *Medlinella*.

SEM examination revealed volate pore occlusions in the areolae of *M. amphoroidea*, a characteristic not observed in any of the other “marine gomphonemoid diatoms”. The shared characteristic of hymenate pore occlusions in *Cuneolus*, *Gomphonemopsis*, *Gomphoseptatum* and *Pseudogomphonema* (Table 1), which differs from the reniform volae [currently known as foricula (Cox 2004)] found in *Gomphonema* (Round *et al.* 1990), was one of the morphological differences used to separate and distinguish the “marine gomphonemoids” from the freshwater genus *Gomphonema* (Medlin & Round 1986). The pore occlusions in *M. amphoroidea* are volate and conform to the original concept of volae—occlusions with narrow points of attachment and irregular branching (Ross & Sims 1972; Cox 2004), while those of *Gomphonema* are foriculate (Cox 2004), suggesting little relationship between *Medlinella* and *Gomphonema*.

The volate pore occlusions, isopolarity of valves and frustules, and the amphoroid shape of *Medlinella amphoroidea* are features not shared with any of the “marine gomphonemoid” genera (Table 1), possibly suggesting a distant relationship between *Medlinella* and the other genera. However, similar valve and cingulum structures in the shared lack of pseudosepta on the valves and the presence of septa on both valvocopulae and 2nd copulae of *M. amphoroidea*, *Tripterion kalamensis*, *T. margaritae*, *Chelonicola costaricensis* and *Poulinea lepidochelicola* (Tables 1 and 2) might suggest closer relationships. The combination of these two character states has been considered a characteristic feature distinguishing *Tripterion* from *Cuneolus*, *Gomphonemopsis*, *Gomphoseptatum* and *Pseudogomphonema* (Holmes *et al.* 1993a; Fernandes & Sar 2009). However, our observations of the holotype slide of *T. philoderma*, the second *Tripterion* species described, confirm that *T. philoderma* lacks septa on the copulae. This makes distinctions between

Tripterion and the other gomphonemoid genera less clear. Cox (2014) has suggested that cingulum construction, including the presence or absence of septa is consistent within taxa. This would suggest that *T. kalamensis*, *T. margaritae*, *Chelonicola* and *Poulinea* are more closely related to each other while *T. philoderma* is more closely related to other taxa. The lack of both pseudosepta and septa in *T. philoderma* may suggest placement of the species in *Gomphonemopsis* but many differences in raphe structure (e.g., lateral versus straight raphe fissure, and strongly hooked versus straight distal raphe ends) between these two taxa make such a transfer problematic.

Medlinella amphoroidea is most similar to *Poulinea lepidochelicola*, sharing a similar cingulum structure, lack of pseudosepta, external central area with fascia, spathulate and deflected external proximal raphe ends, angularly hooked external distal raphe ends, internal flaps of silica on the valve interior that obscure the proximal raphe ends, the relatively large number of copulae, and the epizoic habitat (Table 2). Similarities with *Tripterion* species and *Chelonicola costaricensis* are fewer (Table 2).

TABLE 2. Comparison of morphological characteristics and habitats of *Tripterion kalamensis*, *T. philoderma*, *T. margaritae*, *Chelonicola costaricensis*, *Poulinea lepidochelicola* and *Medlinella amphoroidea*. Characters in **bold** differentiate *M. amphoroidea* from all other taxa in the table.

	<i>Tripterion kalamensis</i>	<i>Tripterion philoderma</i>	<i>Tripterion margaritae</i>	<i>Chelonicola costaricensis</i>	<i>Poulinea lepidochelicola</i>	<i>Medlinella amphoroidea</i>
Length (µm)	17–40	8–28	7–31	6.0–17.5	5.2–10.0	7.0–13.0
Width (µm)	2.5–6.0	2.0–4.5	3.5–7.0	1.7–3.1	1.6–2.8	1.5–2.5
Striae in 10 µm	16–24 in middle of valve; 24–38 near foot pole	21–30 in middle of valve; 26–36 near foot pole	24–28 in middle of valve; 32–34 near foot pole	36–47	25–36	25–34, dorsal striae; 30–36, ventral striae
Stria pattern	Radiate in middle, becoming parallel towards apices, uniseriate	Radiate in middle, becoming parallel to slightly convergent at apices, uniseriate	Radiate, uniseriate	Parallel, uniseriate	Slightly radiate in middle, becoming almost parallel on rest of valve, uniseriate	Dorsal striae are parallel in middle becoming radiate towards apices; ventral striae are radiate in valve middle, becoming parallel and finally convergent at apices.
Areolae	Narrowly elliptical near central area, narrowly oval near foot pole, more circular near head pole	Narrow, transapically elongated	Circular in external view, subrectangular, transapically elongate in internal view	Small, rounded	Transapically elongated	Circular to transapically elongated areolae
Velum	Hymenes	Hymenes	Hymenes	Hymenes	Hymenes	Volae
Apical pore field(s)	Indistinct, few scattered small circular puncta at apices	Absent, but denser striae with elongate areolae predominantly at foot pole	Distinct, several small, circular pores at foot pole	Absent	Absent, but denser areolae at apices	Absent
Valve outline	Clavate with broadly rounded head pole and narrower foot pole	Clavate with broadly rounded head pole and narrower foot pole	Clavate with broadly rounded head pole and narrower foot pole	Clavate with broadly rounded head pole and narrower foot pole	Clavate with acutely rounded apices	Semi-lanceolate with a convex dorsal margin and a straight to concave ventral margin
Symmetry	Heteropolar, head pole longer than foot pole	Heteropolar, head pole longer than foot pole	Heteropolar	Heteropolar	Heteropolar	Isopolar
External central area	Large bow tie-shaped fascia with 1–2 isolated puncta near margin on one valve	Large bow-tie shaped fascia, extending to edge of valve face	Large bow tie-shaped fascia, asymmetric around apical axis, extending to	Very small, indistinct	Small, bow tie-shaped fascia, sometimes with shortened striae towards mantle	Large, asymmetric bow tie-shaped fascia, wider on ventral side
External proximal raphe ends	Straight, expanded, pore-like	Straight, expanded, pore-like	Straight, expanded, pore-like or spathulate	Expanded, pore-like, deflected towards primary side of valve	Spathulate, weakly unilaterally deflected	Spathulate, weakly deflected toward ventral margin

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TABLE 2. (Continued)

	<i>Tripterion kalamensis</i>	<i>Tripterion philoderma</i>	<i>Tripterion margaritae</i>	<i>Chelonicola costaricensis</i>	<i>Poulinea lepidochelicola</i>	<i>Medlinella amphoroidea</i>
External distal raphe ends	Strongly hooked toward the same side of valve	Strongly hooked toward the same side of valve	Angularly hooked toward the same side of valve, T-shaped at some foot poles	Elongated, deflected towards secondary side of valve, continuing onto mantle	Angularly hooked toward the same side of valve, terminate near apices	Angularly hooked toward ventral margin
Internal raphe fissure	Lateral	Not determined	Lateral	Lateral	Lateral	Straight
Internal proximal raphe ends	Straight	Straight	Slightly deflected towards secondary side	Obscured by silica flap	Obscured by silica flap	Obscured by 2 silica flaps
Pseudosepta	Absent	Absent	Absent	Absent	Absent	Absent
Cingulum	2–7 open copulae with 1 row of puncta	4 open copulae, with 1 row of elongate puncta	4 open copulae with 1 row pores	Up to 12 open copulae each with 1 row of apically elongated slit-like pores	Up to 12 open copulae each with 1 row of apically elongated slit-like pores, double row at foot pole	Up to 12 open copulae each with 1 row of apically elongated pores
Septa	Present	Absent	Present at head pole of valvocopulae and foot pole of 2 nd copula	Present at head pole of valvocopulae and foot pole of 2 nd copula, Absent in rest of copulae.	Present at head pole of valvocopulae and foot pole of 2 nd copula, Absent in rest of copulae.	Present on valvocopulae and 2 nd copulae, shallower septa on rest of copulae.
Growth habit	Attached by mucoid stalk at foot pole	Not determined	Attached by bifurcate mucoid stalks at foot pole	Attached by mucoid stalk at foot pole	Attached without a stalk at foot pole	Not determined
Host animal/substrate	Dall's porpoises, skin	Strap-toothed whale, teeth	Epilithic	Olive Ridley sea turtles, carapace	Olive Ridley sea turtles, carapace	Loggerhead sea turtles
Geographic location(s)	Bering Sea, northern California USA, northern Japan	Milnerton, South Africa	Bahía Esperanza, Antarctica	Costa Rica, Pacific coast	Costa Rica, Pacific coast	Florida Bay, Florida, USA
References	Holmes <i>et al.</i> (1993a), present study	Holmes <i>et al.</i> (1993b), present study	Fernandes & Sar (2009)	Majewska <i>et al.</i> (2015)	Majewska <i>et al.</i> (2015)	Present study

The distinguishing morphological characteristics of the “marine gomphonemoid” genera are not well-defined despite several comprehensive attempts using the morphological data available at the time to create order among the genera. The distinguishing criteria are varying combinations of many shared and unshared morphological traits (Table 1), hence our comparison of the current classification scheme to an *à la carte* dinner menu, where a morphological feature can seemingly be selected for a genus along with any other feature available on the menu. A recent cladistics analysis of putative members of Rhoicospheniaceae, including all the “marine gomphonemoid genera” except *Pseudogomphonema*, suggested that the Rhoicospheniaceae is polyphyletic, but indicated a monophyletic clade consisting of the sister genera *Cuneolus*, *Chelonicola*, *Poulinea* and *Tripterion* (Majewska *et al.* 2015). Interestingly, the three genera with species described from epizoic habitats (*i.e.*, *Chelonicola*, *Poulinea*, and *Tripterion*) are within this clade, suggesting the possibility of speciation occurring as a result of isolation and adaptation to the epizoic microenvironment. The importance of this observation and the subsequent speculation is tempered by the possibility that “epizoic” taxa may simply be an artifact of the incomplete sampling of marine benthic environments for diatoms; *Cuneolus* and *Tripterion margaritae* have been described from non-epizoic habitats, after all.

The paucity of species amongst the epizoic genera is a curious trend. It is entirely possible this is also an artifact of poor sampling, both in epizoic and non-epizoic habitats. Does diversification in *Chelonicola*, *Tripterion*, *Poulinea* and *Medlinella* track with the diversification of the large vertebrates that they colonize? Or is the large number of monotypic genera an artifact of diatomists’ interpretation of valve morphology? We feel the volate pore occlusions and dorsiventral valve symmetry of *M. amphoroidea*, found in no other “marine gomphonemoid” genera, would have drastically altered the descriptions of any other existing genus; the simplest option was to create a new genus to house it. It is tempting to hope that DNA sequence data will help to answer these questions by providing a different data source to compare against various morphological interpretations. A DNA sequence-based phylogeny consisting of single species for *Chelonicola*, *Poulinea* and *Medlinella* might not look all that different from the diagram based on morphological characters in Majewska *et al.* (2015). It is uncertain whether the branches of a phylogenetic tree

consisting of these monotypic genera represent intra- or inter-generic genetic variation. Perhaps rather than struggling to isolate and culture epizoic diatoms, that may require something specific from the host that precludes their growth in captivity, a more helpful and hopeful approach would be the continued and mindful sampling of marine vertebrates, and the environments they inhabit, for diatoms.

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