



Seven new species expand the morphological spectrum of *Haslea*. A comparison with *Gyrosigma* and *Pleurosigma* (Bacillariophyta)

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Abstract

Seven new *Haslea* species demonstrate that the genus has evolved a richer morphological repertoire than so far reported. *H. feriarum* sp. nov. has a valve contour suggesting an *Amphora*; *H. staurosigoidea* sp. nov. has a sigmoid valve with a pseudostauros; *H. tsukamotoi* sp. nov. and the closely similar *H. meteorou* sp. nov. possess uniquely shaped external central raphe endings and a fully sideways-tilted internal raphe system; *H. clevei* sp. nov. and *H. avium* sp. nov. also have central raphe ending shapes not yet described in the genus; *H. amicorum* shows interrupted longitudinal fissures besides the continuous fissures characteristic of *Haslea*. A survey of the *Haslea* species described, for differentiation of our taxa, led to two conclusions: 1) the data in the protologue of *H. indica* Desikachary & Prema are spurious and 2) “*Navicula*” *duerrenbergiana* Hustedt is here transferred to the genus *Haslea*. The basic *Haslea* morphology is a sandwich-type valve, with a grate-like inner layer (here called **basal layer**) and an outer layer (here called **tegumental layer**) perforated by continuous longitudinal fissures. These two layers are shored by upright longitudinal “bulkheads”, here called **saepes**, seen to be perforated in the valves that permitted their observation. This morphology is closely similar to that of *Gyrosigma* (and *Pleurosigma*). The great variety of central external raphe ending patterns in *Haslea*, *Gyrosigma* and *Pleurosigma* is shown and discussed.

Introduction

The genus *Haslea* was erected in Simonsen (1974:46), based on *Haslea ostrearia* (Gaillon) Simonsen (1974: 47; basionym: *Vibrio ostrearius* (*ostrearia*) Gaillon 1820: 93), to include the fusiform diatoms with straight transapical and apical striae, previously classified as *Naviculae* fusiformes (Hustedt 1961: 34). The similar delicate fusiform species *Navicula gigantea* Hustedt (1961: 40), *Navicula frauenfeldii* (Grunow) Grunow (1877: 179; basionym: *Amphipleura frauenfeldii* Grunow 1863: 14) and *Navicula trompii* Cleve (1900: 932) were logical candidates for inclusion in *Haslea*. More robust naviculoid species such as *Navicula britannica* Hustedt & Aleem (1951: 184) and species with a pseudostauros such as *Navicula crucigera* (W. Smith) Cleve (1894: 111; basionym: *Schizonema cruciger* W. Smith 1856: 74) and *Stauroneis spicula* Hickie (1874: 290) have also been included in *Haslea*. In those cases where such transfer has been based on examination of type material in SEM, the valve exterior displayed continuous longitudinal fissures. For a review of the literature on the genus see Gastineau *et al.* (2014).

Valve shape in *Haslea*, however, is not limited to a lanceolate contour. In the early 1990s, Stuart R. Stidolph (pers. comm.) noted that the taxon named *Gyrosigma nipkowii* Meister (1932: 43) also showed such continuous longitudinal fissures and Poulin *et al.* (2004) presented morphological, biochemical and molecular evidence for its inclusion in the genus *Haslea*. Recently, Talgatti, Sar & Torgan (2014) described another sigmoid *Haslea* with a pseudostauros.

Here we describe *Haslea feriarum* sp. nov., which has an amphoroid valve contour, and *H. staurosigoidea* sp. nov., a markedly sigmoid species with a pseudostauros, illustrating the great variety in *Haslea* valve contour. *H. tsukamotoi* sp. nov., *H. meteorou* sp. nov., *H. clevei* sp. nov., and *H. avium* sp. nov. have external central raphe fissure endings entirely different from the simple homolaterally deflected pattern generally attributed to *Haslea*. In *H.*

amicorum the more peripheral longitudinal fissures are continuous, the more central striae consist of separate areolar fissures. The general morphology of *Haslea* requires an emended description and the rich spectrum of external central raphe ending patterns in *Haslea*, *Gyrosigma* and *Pleurosigma* is surveyed here.

Methods and materials

Methods

Slides and stubs were prepared, examined and photographed in SEM with the usual methods as in Sterrenburg *et al.* (2014). The LM photomicrographs (stacks of 12–22 separate images) were taken with DIC in blue light (420 nm) using a special astrocamera (for a detailed description see Herwig 2011), except for Fig. 11, which was taken with DIC in unfiltered light to show what one may expect to see on routine visual inspection.

The “raphe angle” (Sterrenburg 1991) is the angle subtended between a line through the central portion of the raphe and one through its apical ends.

Materials

The materials are specified under the taxon descriptions. Slide coordinates for the holotype specimens were determined as described in Sterrenburg *et al.* (2012), the benchmarks are marked scribed rings on the slide unless specified otherwise and the holotype specimen is marked with a scribed ring. Material of *Haslea tsukamotoi* (Sterrenburg #724) has also been deposited in the Phycological Herbarium of the Botanical Institute of Sao Paulo (International ID: SP). The collection *Sterrenburg* will eventually be deposited in BRM, the collections *Tiffany* and *Hargraves* are unnumbered.

Valve morphology of *Haslea*

Observations on a population of *Haslea nipkowii* (Meister) Poulin & Massé may serve as an introduction to the valve morphology of *Haslea*, especially since it illustrates how, despite a valve contour very different (sigmoid instead of lanceolate) from that of the species first included in the genus, the general valve morphology of *Haslea* is maintained.

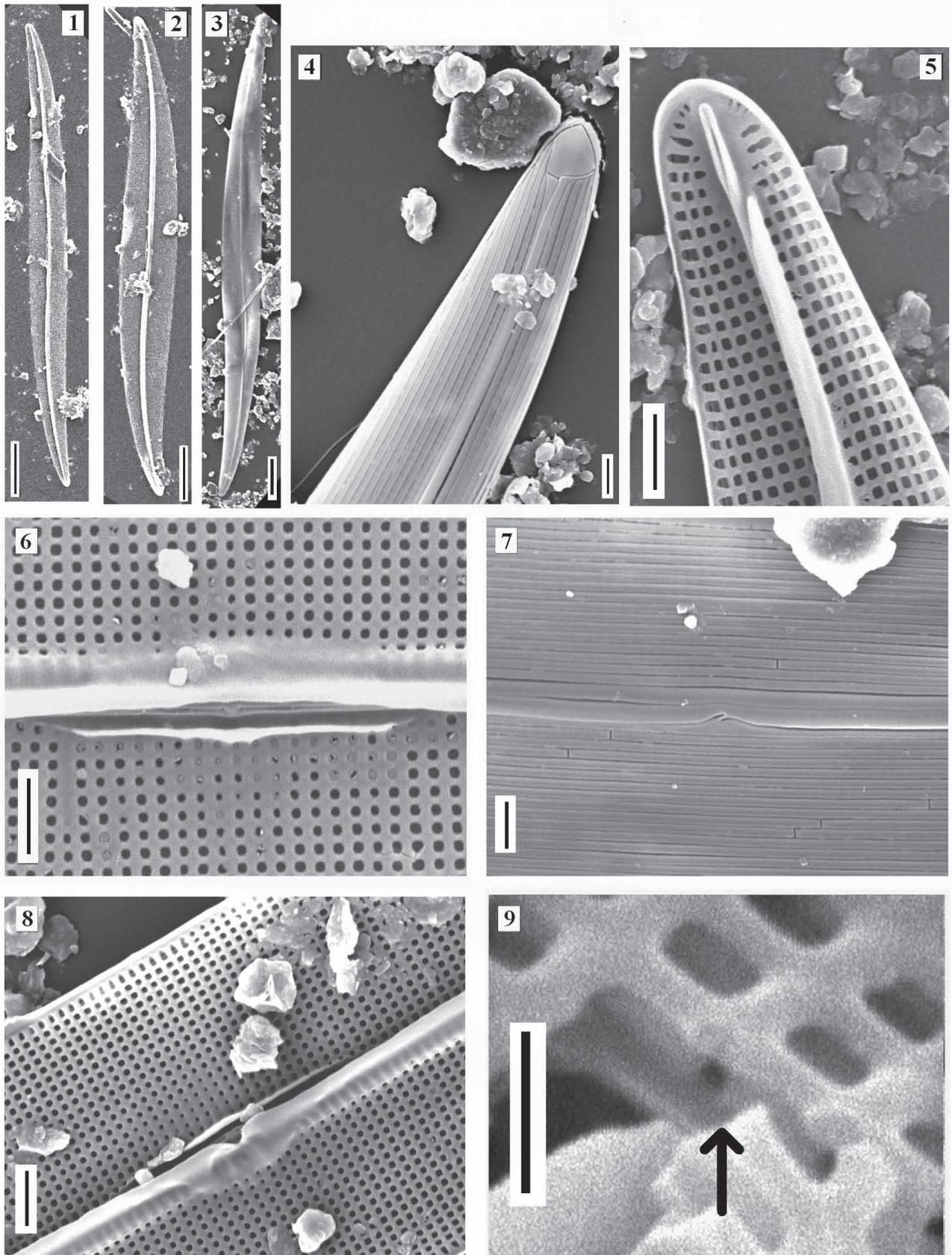
H. nipkowii (Meister) Poulin & Massé (Figs 1–9)

Material:—“Isla Montague, Gulf of California, Mexico, May, 2, 1999, geographic coordinates 31°44’ N, 114°44’ W. In collection *Sterrenburg* #655.

Valve lanceolate-sigmoid (Figs 1–3), 190–290 µm long, 16–22 µm wide, with acute apices and sigmoid raphe sternum. Striae perpendicular, transverse circa 25, longitudinal circa 30 in 10 µm. Axial and central area extremely narrow, inconspicuous in LM. In SEM, the valve exterior, with continuous longitudinal fissures, shows little surface relief (Figs 1, 7). External central raphe endings oppositely deflected and overlapping (Fig. 7), external terminal endings bifurcated (Fig. 4). Internally, a short sharply delineated central bar on one side of the raphe, a very pronounced silica ridge on the other (Figs 6, 8). The latter is almost as long as the raphe ridge and folded sideways over it, only leaving the helictoglossa free (Fig. 5). At the apices, a crescent of tiny pores (microforamina) perforates the margin of the valve (Fig. 5). Internal areolar openings round near the central raphe node, elsewhere more or less square, transverse bars demarcating the areolar openings somewhat broader than the longitudinal (Figs 5, 6, 8). A fractured valve (Fig. 9) is seen to be composed of an internal grate-like layer (top in the figure) and an external layer (bottom in the figure), with an upright “bulkhead” in between. This is not solid but perforated, the perforations (arrow in Fig. 9) are located underneath (in the figure!) the transverse bars demarcating the areolar openings.

In LM the valve shape and striation suggest a *Gyrosigma*, but the tiny central raphe node and extremely narrow central and axial area are not usual in the latter genus (exception: *G. tenuissimum* (W. Smith) Griffith & Henfrey, see Sterrenburg *et al.* 2014). SEM is required for correct generic assignment, however.

Habitat:—littoral estuarine-marine sediment.



FIGURES 1–9. *Haslea nipkowitzii* (Meister) Poulin & Massé. Fig. 1–3. General aspect, bars = 20 μ m. Fig. 4. Apex, exterior, bar = 2 μ m. Note bifurcated raphe ending. Fig. 5. Apex, interior, bar = 2 μ m. Note apical microforamina. Fig. 6. Centre, interior, bar = 2 μ m. Conspicuous raphe ridge, sharply delineated central bar. Fig. 7. Centre, exterior, bar = 2 μ m. Overlapping oppositely deflected raphe endings. Fig. 8. Centre, interior, bar = 2 μ m. Conspicuous raphe ridge, different in shape from that of Fig. 6. Fig. 9. Broken valve, bar = 0.5 μ m. Basal layer (uppermost) and tegumental layer (lower) joined by upright saepes with small perforations (arrow).

Distribution:—observed in the Pacific, Indian Ocean and Mediterranean. Our specimens fully match those of Poulin *et al.* (2004) from the Mediterranean.

The *Haslea* valve structure has been described as follows:

- Round *et al.* (1990: 576): "striae ... overlain by longitudinal strips, many of which are continuous from pole to pole". "External raphe fissures turned to the same side centrally...". "Raphe sternum with a prominent ridge internally on one side of the raphe".
- Massé *et al.* (2001: 625): "...longitudinal strips of silica over the vimines with intervening ("virgae" omitted in original text) forming continuous slits...". "There is a well-defined accessory rib on the primary side of the raphe sternum, which often overlaps the raphe sternum for most of its length". "Externally the raphe fissures are straight for most of their length, slightly expanded at their endings, all endings usually deflected to the same side of the valve."
- Talgatti *et al.* (2014): "...areolae square to rectangular occluded by hymenes internally and externally overlain by longitudinal strips usually continuous from pole to pole and an accessory rib along the raphe-sternum".

These descriptions do not accurately describe the essential point of the *Haslea* valve morphology. The totally different aspect of the external and internal surfaces of the valve, continuous fissures and areolar foramina respectively, implies that these do not represent two surfaces of the same object, because the external continuous longitudinal fissures would then be broken up by the internal transverse ridges demarcating the areolar openings. The valve therefore consists of a sandwich (as in *Pleurosigma* and *Gyrosigma*) of two separate layers: a grate-like inner layer (called **basal layer** here), which generates the diffraction image of perpendicular rows of puncta in the LM, and an external layer (called the **tegumental layer** here) with long continuous fissures, not ordinarily visible in the LM.

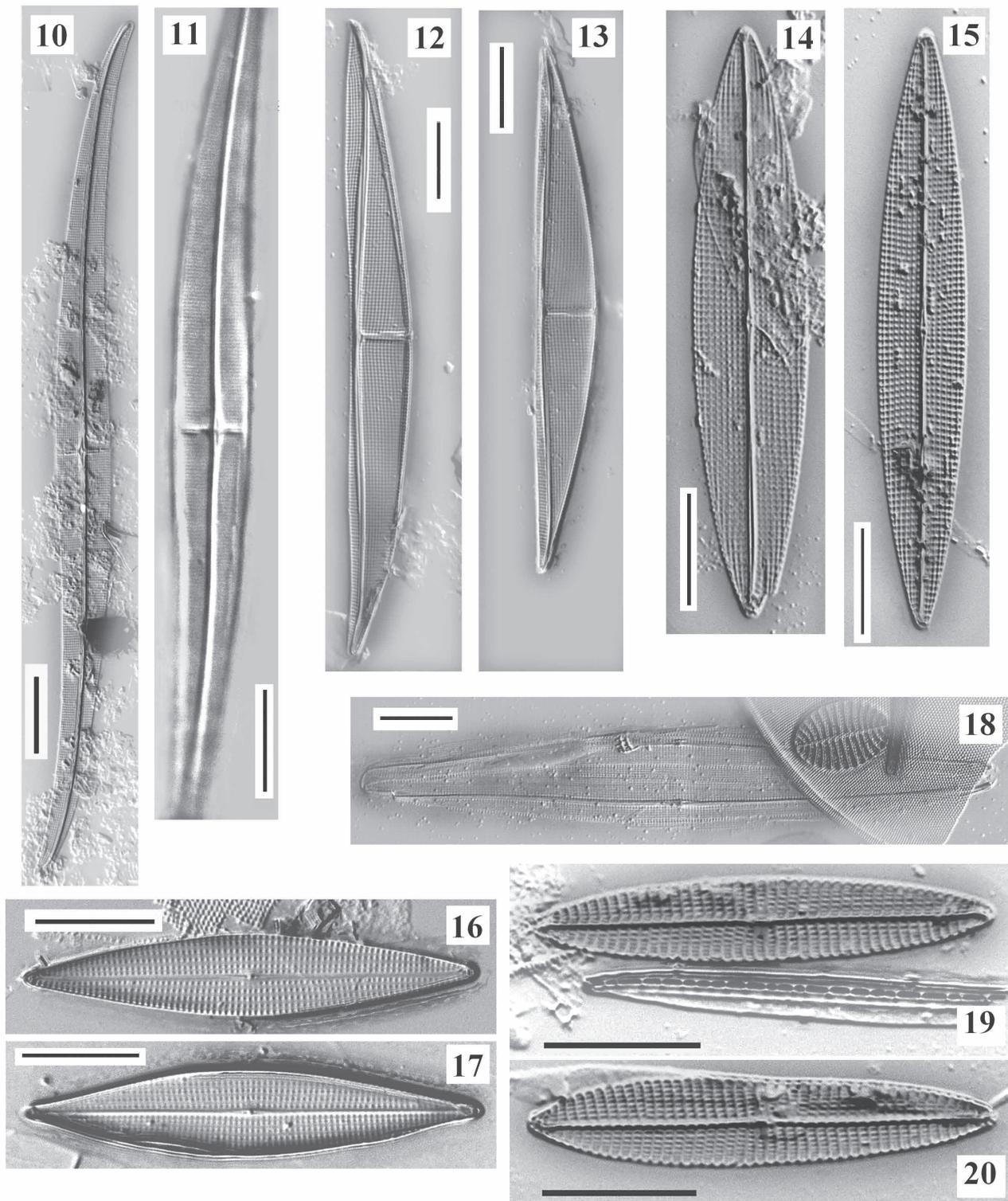
These two layers of the valve sandwich must be shored somehow. In *Haslea* (Cox 1999, Figs 33–44) as in *Pleurosigma* and *Gyrosigma*, the basal layer is the first to be formed in valve morphogenesis, followed by deposition of rows of upright columns for shoring—in three linear systems in *Pleurosigma*, in two perpendicular systems in *Gyrosigma*. The spaces in between the columns may be partially filled in subsequently, but there are no solid partitions, so the valve is not loculate. Finally the tegumental layer is deposited, first as a coarse mesh, the mazes of which are then filled in until only very narrow fissures remain. At the margin, the two valve layers are fused, so that there is a monolayer structure. The entire process has been documented for *Pleurosigma* in Sterrenburg *et al.* (2005). Exactly the same morphology is seen in *H. nipkowii* and will here be demonstrated in other new *Haslea* species, where the two valve layers are also shored by longitudinal rows of columns, the spaces in between being partially filled in, resulting in perforated longitudinal "bulkheads" we call **saepes** (Latin: "fence", plural: saepes) here. The saepes are only visible in SEM, mostly in fragmented valves or specimens permitting an oblique view into their interior, although in some cases they will "shine through" in exterior views of the valve. This is the case in our Fig. 50, for instance, and in Gastineau *et al.* (2014) they are clearly visible (although not mentioned) in Fig. 15.3, which shows 4 images of *H. ostrearea* (Gaillon/Bory) Simonsen, *H. silbo* sp. ined., *H. provincialis* sp. ined. and *H. karadagensis* Davidovich, Gastineau & Mouget. In a fractured valve of *H. nipkowii* the saepes—with small perforations—are clearly seen (Fig. 9, arrow). The process of infilling of the saepes apertures is expressed in various degrees, the apertures may also be large as in two new species we describe here (see further). As shall be shown, during tegumental layer morphogenesis of *Haslea* the external areolar openings are also wide initially, subsequently being filled in until only very narrow slits remain—as happens in *Pleurosigma* and *Gyrosigma*. The continuous silica "strips" of the tegumental layer mentioned in Round *et al.* 1990 are thus the consequence of the underlying morphogenetic phenomenon of continuous longitudinal external fissures perforating the valve surface. These fissures can be interpreted as the result of fusion of the separate external slits present in *Gyrosigma* species. Because of the perforated saepes, the valve interior resembles the "parking-garage" aspect present in *Pleurosigma* (Sterrenburg *et al.* 2005) and *Gyrosigma*.

Haslea species show a much greater variety of features than so far described, as illustrated by the seven new species presented here. All possess a tegumental layer with continuous longitudinal fissures and a basal layer composed of grate-like more or less perpendicularly arranged bars, characteristic of *Haslea*.

Taxon descriptions

Haslea staurosigmoidea Sterrenburg & Tiffany, *sp. nov.* (Figs 10, 11: LM, 21–26: SEM)

Type:—"Itacorubi, Florianopolis, Brasil, August, 21, 1987, leg. de Souza Mosimann", geographic coordinates 27°34' S, 48°29' W. Holotype BRM ZU9/87, slide coordinates 15.0 E, 18.1 S. Isotypes in collection Sterrenburg #596.



FIGURES 10–20. New *Haslea* species, LM images (DIC). All bars = 10 μ m. All except Fig. 11 are stacks of 12–22 separate images.
FIGURES 10, 11. *H. staurosigmoidea* sp. nov. Fig. 10. Holotype, Fig. 11. Isotype, aspect in normal DIC corresponding to what is seen on visual inspection.
FIGURES 12, 13. *H. feriarum* sp. nov. Fig. 12. Holotype. Fig. 13. Isotype.
FIGURES 14, 15. *H. tsukamotoi* sp. nov. Fig. 14. Holotype. Fig. 15. Isotype.
FIGURES 16, 17. *H. meteorou* sp. nov. Fig. 16. Holotype. Fig. 17. Isotype.
FIGURE 18. *H. clevei* sp. nov., holotype, complete frustule.
FIGURES 19, 20. *H. avium* sp. nov. Fig. 19. Holotype, inset: arrow marks continuous fissures. Fig. 20. Isotype.

Valve (Figs 10, 11, 21, 22) delicate, sigmoid with a narrow pseudostauros, 100–120 µm long, 6.5–7.5 µm wide, almost parallel-sided in the middle portion, with acute apices. Raphe sternum central over most of the valve length but becoming eccentric near the apices, curved. Raphe angle circa 7°. Striae perpendicular, transverse circa 30 in 10 µm, longitudinal circa 40 in 10 µm. In LM, axial and central area so narrow that there is no clear hyaline space separating striae and raphe sternum, central raphe node minute. In SEM, the tegumental layer shows little surface relief (Figs 23, 25, 26) and broad marginal zones not perforated by longitudinal fissures. External central raphe endings very approximate and slightly curved either to the same side (Fig. 25) or oppositely (Fig. 26); apical raphe endings more or less straight; (Fig. 23); small apical fissure present (arrow in Fig. 23). Internally, transverse silica ridges (pseudostauros) are present on both sides of the very narrow central raphe node, extending over the full width of the valve, only about 1 interstria wide; the pseudostauros is joined to a longitudinal ridge along the raphe on one side and a long central bar on the other (Fig. 24). Helictoglossa prominent (Fig. 22). Basal layer: transverse bars of the perpendicular grate slightly broader than the longitudinal, foramina more or less square in the central portion (Fig. 24), apically elongated oblong near the apices (Fig. 22).

Etymology:—The specific epithet refers to the sigmoid valve contour and pseudostauros.

Habitat:—Muddy marine-littoral sediment.

Distribution:—Brazil, marine littoral, not rare in the sample. One of us (WEH) has observed diatoms matching *H. staurosimoidea* (in LM!) in the Adriatic Sea.

Observations:—The species resembles a *Gyrosigma* in LM because of its sigmoid contour but the pseudostauros, minute central raphe node (in contrast to the evident round to oval node usual in *Gyrosigma*) and inconspicuous axial and central areas indicated that SEM investigation was necessary, which revealed the *Haslea*-type valve structure. A particularly noteworthy finding is the variability of the central raphe ending deflection, which in the same population was either to the same, or to opposite sides. Saepes not satisfactorily visualized, no fragmented valves found. In LM, this species is readily separated from *H. nipkowii* by the presence of the pseudostauros, in SEM there are additional major differences, e.g. in the shape of the apical and central external raphe fissures. The sigmoid species *H. sigma* Talgatti, Sar & Torgan (Talgatti *et al.* 2014) also has a pseudostauros like *H. staurosimoidea*. The characters separating these two species are given in Table 1.

TABLE 1. Characters separating *H. sigma* and *H. staurosimoidea*.

Character	<i>H. sigma</i>	<i>H. staurosimoidea</i>
Valve contour	Lanceolate sigmoid	More linear sigmoid
Raphe sternum curvature	Straight for about 75% of its length	Curved for about 75% of its length
Raphe angle	Circa 3°	Circa 7°
Length and length-width ratio	55.8–70 µm, circa 9 to 12	100–120 µm, near 14
Accessory apical fissure	Absent	Present
Peripheral longitudinal fissures	Join near apex	Not seen to join
Apical raphe endings	Sharply recurving	Straight
Foramina of basal layer	More or less square throughout	Elongated near the apices

***Haslea feriarum* Tiffany & Sterrenburg, sp. nov.** (Figs 12, 13: LM, 27–32: SEM)

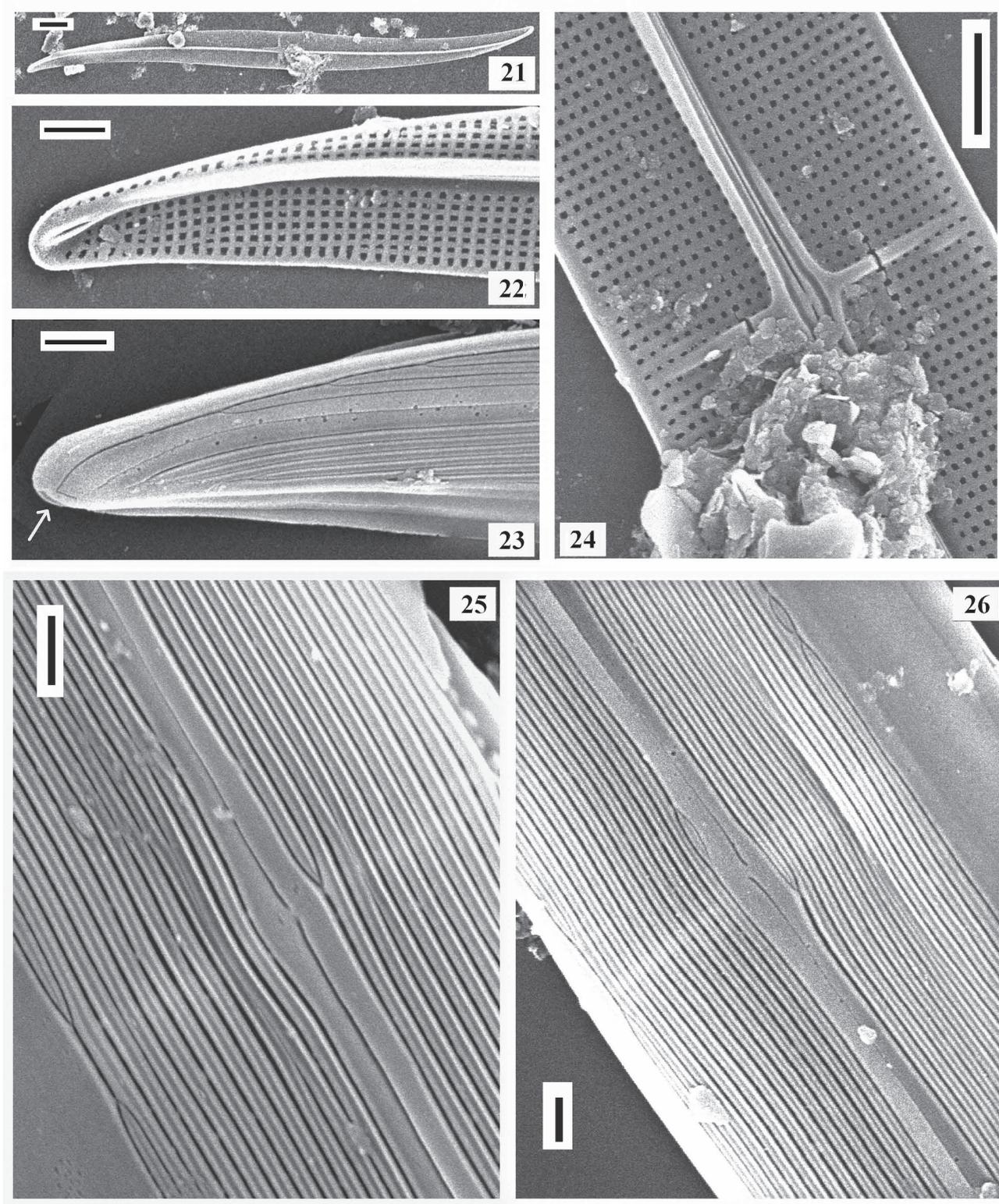
Type:—"Fiesta Island, Mission Bay, San Diego, California, USA, April, 27, 2000", geographic coordinates 32°46' N, 117°13' W. Holotype BRM ZU 5/34, slide coordinates 15.6 E, 9.1 S. Isotypes in collection *Sterrenburg* #657 and collection *Tiffany*.

Valve (Figs 12, 13, 27, 28) with asymmetric crescent-shaped contour as in the genus *Amphora*, 70–90 µm long, 9–15 µm wide, with acute ends and a distinct unilateral stauros-like structure. Raphe situated almost at the periphery of the non-convex valve margin. Striae perpendicular, transverse circa 18–20 in 10 µm, longitudinal circa 20–23 in 10 µm. In SEM, the tegumental layer shows little surface relief (Figs 30, 32). External central raphe fissure endings very approximate and very slightly curved towards the convex half of the valve (Fig. 32). Basal layer: foramina transversely elongated oblong (Fig. 31), a transverse silica ridge (pseudo-stauros) is up to 3 interstriae wide (Fig. 31). The two layers of the sandwich valve are joined by longitudinal upright saepes with small perforations (Fig. 29, inset). The perforations are located underneath (in the figure!) the transverse bars of the basal layer.

Etymology:—The specific epithet refers to the type locality, Fiesta Island.

Habitat:—Muddy brackish to littoral marine sediment.

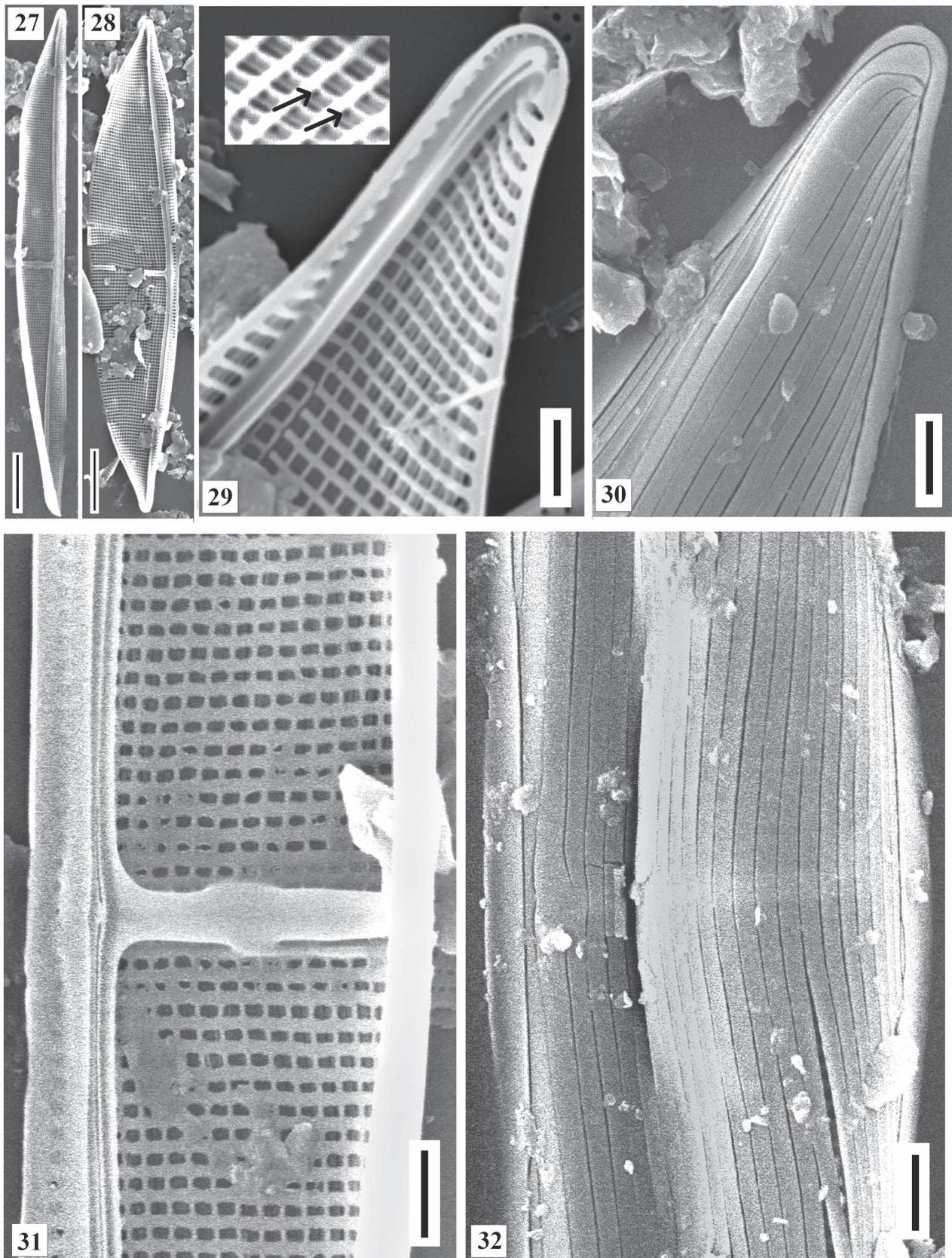
Distribution:—Type locality only, not rare in the sample, but see Observations.



FIGURES 21–26. *H. staurosigmoidea* sp. nov. SEM, isotypes. Fig. 21. General aspect, bar = 5 μ m. Fig. 22. Apex, exterior, bar = 2 μ m. Fig. 23. Apex, interior, bar = 2 μ m. Arrow marks apical pore. Fig. 24. Centre, interior showing pseudostauros, bar = 2 μ m. Fig. 25. Centre, exterior, raphe endings deflected to the same side, bar = 1 μ m. Fig. 26. Centre, exterior, raphe endings oppositely deflected, bar = 1 μ m.

Observations:—Detached valves of *Haslea feriarum* would be labeled as an *Amphora* in routine LM studies and in fact this may have been done. For instance, the reference to *Amphora laevis* Gregory in Hendey (1964:267) contains data similar to those of our species. The differences between these two entities are evident, however. The multiple girdle bands of *A. laevis* clearly illustrated in Gregory (1857: Pl XII, Fig. 74) are typical of *Amphora* but are not seen in any *Haslea* species. On the other hand, the sandwich structure of the valve of *H. feriarum* is typical of *Haslea* but

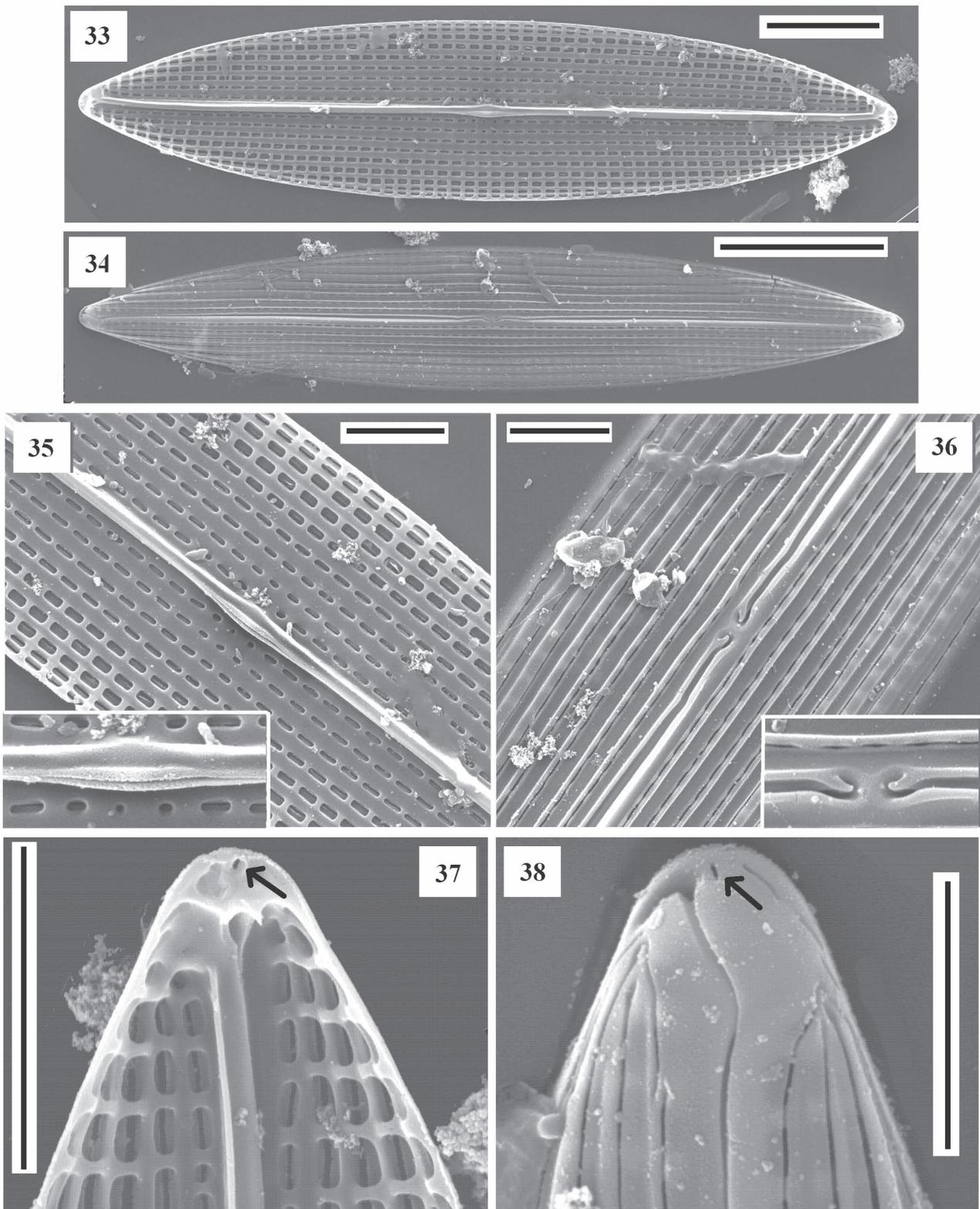
excludes *Amphora*. Specimens matching *H. feriarum* (but only observed in LM!) have been found (FASS) in samples from New Zealand (Leg. Lesley Rhodes) and the Wadden Sea (The Netherlands) but their morphology has not yet been examined in SEM.



FIGURES 27–32. *H. feriarum* sp. nov. SEM, isotypes. Figs 27, 28. General aspect, average and broad specimen. Bars = 10 µm. Fig. 29. Apex, interior, note apical micropores, bar = 2 µm. Inset (2x enlargement): saepes, arrows mark perforations. Fig. 30. Apex, exterior, bar = 2 µm. Fig. 31. Centre, interior, bar = 2 µm. Fig. 32. Centre, exterior, bar = 2 µm.

Haslea tsukamotoi Sterrenburg & Hinz, sp. nov. (Figs 14, 15: LM, 33–38: SEM)

Type:—“Toque-Toque Grande Beach, Sao Sebastiao, Sao Paulo, Brazil, June, 30, 2012, leg. R.Y. Tsukamoto”, geographic coordinates 23°83' S, 45°51' W. Holotype BRM ZU9/88, slide coordinates 13.0 E, 6.1 S., isotypes in collections *Sterrenburg* #724 and (SP) *Herbario Maria Eneyda P. K. Fidalgo, Instituto de Botanica de Sao Paulo* #SP428.775.



FIGURES 33–38. *H.tsukamotoi* sp. nov. SEM, isotypes. Fig. 33. Large specimen, general aspect, interior view, bar = 5 μ m. Fig. 34. Average specimen, general aspect, exterior view, bar = 10 μ m. Fig. 35. Centre, interior, bar = 2 μ m. Inset (2x enlargement): note sideways tilted central raphe node. Fig. 36. Centre, exterior, bar = 2 μ m. Inset (2x enlargement): detail of crook-shaped raphe endings. Fig. 37. Apex, interior, bar = 2 μ m. Note apical pore (arrow). Fig. 38. Apex, exterior, bar = 2 μ m. Note apical pore (arrow).

Valve (Figs 14, 15, 33, 34) robust, lanceolate, 40–55 μm long, 8–9.5 μm wide, with acute ends. Striae transverse slightly radiate, 16–19 in 10 μm , longitudinal finer, 18–21 in 10 μm . In LM, axial and central area so narrow that there is no visible hyaline space separating striae and raphe sternum. In SEM, the tegumental layer shows marked surface relief (Fig. 36). External central raphe fissure endings approximate, forming tiny “crooks” tightly curved over about 270° around a tooth-like projection (Fig. 36 and inset); apical endings undulating, terminating as retrograde hooks (Fig. 38). At the apex a small accessory pore perforates the solid margin of the valve (Figs 37, 38, arrows). Basal layer: foramina apically elongated oblong, becoming about twice as wide near the margin (Fig. 35). The broader peripheral foramina are not reflected as wider puncta spacing in the LM, as the widening of the foramina is at the expense of the width of the longitudinal bars of the basal layer grate. Entire internal raphe fissure and internal central raphe node (which is slightly depressed in the middle) fully tilted sideways (Fig. 35 and inset).

Etymology:—Named after the collector, Dr. Ricardo Tsukamoto.

Habitat:—Wet beach.

Distribution:—Type locality only so far, fairly abundant.

Observations:—The marked difference in width of the median and the more peripheral internal foramina of the basal layer is a special feature in this new *Haslea* species and its internal and external raphe morphology is particularly unusual. The tightly curved “crooks” of its external central raphe endings have not yet been described in *Haslea*, where the fissures are generally described as almost straight or very slightly curved, as they are in *H. feriarum* and *H. staurosimoidea*. Whilst sideways twisting of the internal raphe fissure over most of its length is considered a typical feature of *Haslea* species, at least its central portion is perpendicular to the valve plane in the species previously described, whereas in *H. tsukamotoi* the entire internal raphe system is fully sideways tilted, including the central raphe node. Saepes not satisfactorily visualized, no fragmented valves found.

H. tsukamotoi has much finer striae than *H. howeana* and *H. nautica*; it is longer and has more markedly radiate striae than *H. brittanica*.

***H. meteorou* Hinz & Sterrenburg, sp. nov.** (Figs 16, 17 : LM, 39–46: SEM)

Type:—“SM338 IOE “Meteor” Sta. # 103, 170-0m, 20-12-1964, geographic coordinates 11°27,5’N 53°04,5’E. Holotype BRM SIM 64/43, slide coordinates (benchmark left upper corner of coverslip) 13.2 E, 6.0 S, isotype coordinates 15.0 E, 7.3 S.

Valve (Figs 16, 17, 39, 40) lanceolate, 38–45 μm long, 7–10 μm wide, with acute ends. Striae transverse slightly radiate, 18–20 in 10 μm , longitudinal 14–16 in 10 μm . In LM, axial and central area very narrow. In SEM, the tegumental layer shows little relief (Figs 41, 44). External central raphe fissure endings approximate, tiny “crooks”, tightly curved over about 270° around a tooth-like projection (Figs 44, 46), apical endings undulating and terminate as retrograde depressed hooks (Fig. 41). At the apex 2–3 small accessory pores perforate the solid margin of the valve (Fig. 41, 42). Basal layer: foramina apically elongated oblong, longitudinal bars of the grate much broader than the foramina (Figs 42, 43). Entire internal raphe fissure and central raphe node (which is slightly depressed in the middle) tilted sideways (Figs 43, 45).

Etymology:—The specific epithet, genitive of Greek “meteoros”, refers to the research vessel used by the expedition during which the material was collected.

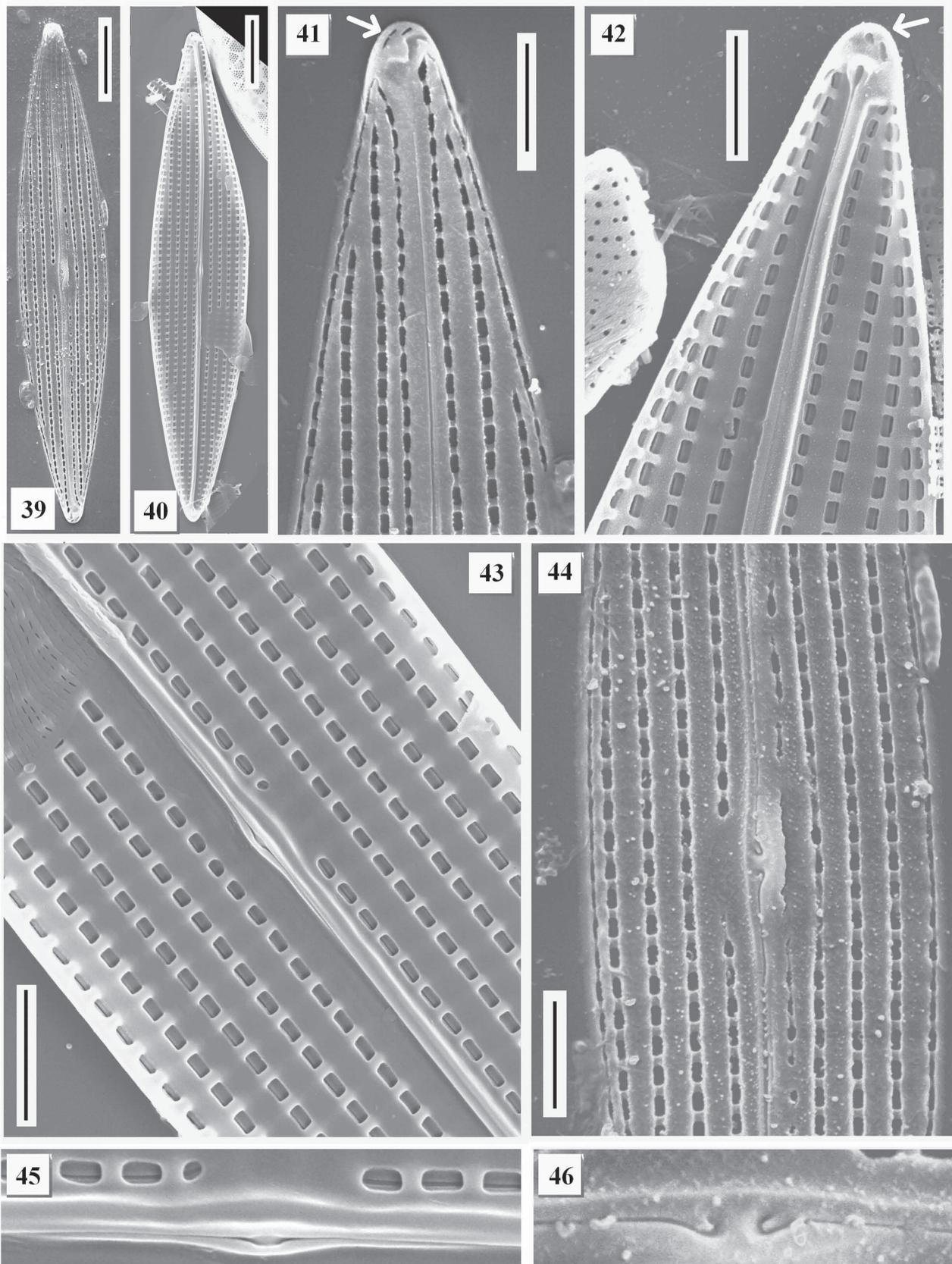
Habitat:—planktonic, marine.

Distribution:—so far known from the type locality only, fairly rare in the sample.

Observations:—In samples of the Meteor expedition discussed in Simonsen 1974, we found specimens resembling *H. tsukamotoi* in the peculiar central external raphe ending shapes and fully tilted central raphe node. There is no marked broadening of the internal areolar foramina near the margin, however, and transverse striation is much finer than the longitudinal, warranting separate taxonomic status. Simonsen (1974) does not describe such specimens under either *Haslea* or *Navicula*. In the specimen of Figs 41 and 44 valve development is not yet complete: infilling has resulted in narrow fissures at the periphery, but has not yet finished in the median portion of the valve. The specimen of Fig. 43 shows the final situation, with very narrow longitudinal fissures. Saepes not satisfactorily visualized, no fragmented valves found.

H. meteorou has much coarser longitudinal than transverse striae, setting it apart in the genus *Haslea*.

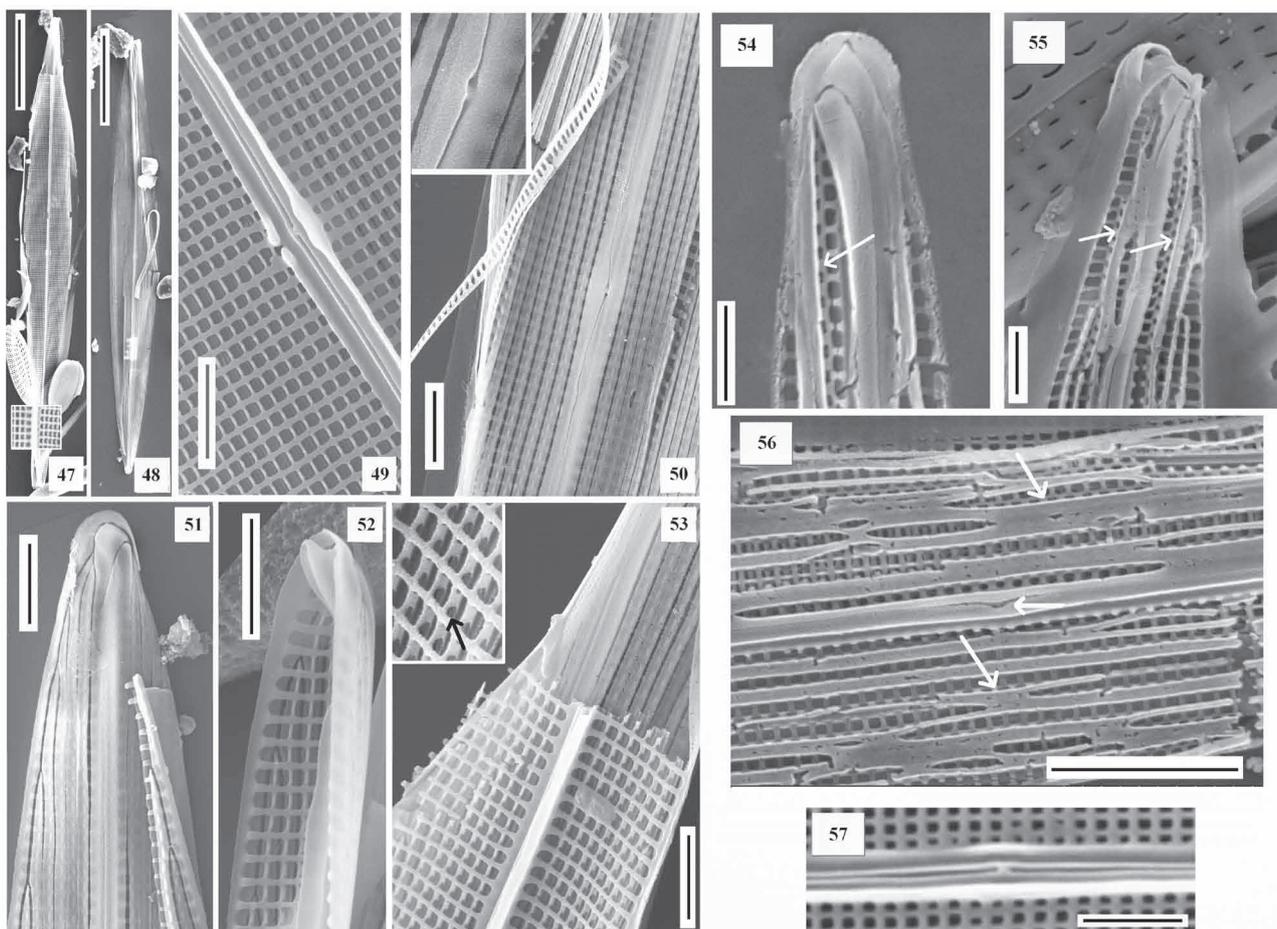
***H. clevei* Hinz, Hargraves & Sterrenburg, sp. nov.** (Figs 18: LM, 47–57: SEM)



FIGURES 39–46. *H. meteorou* sp. nov. SEM, isotypes. Fig. 39. General aspect, exterior, bar = 5 μ m. Fig. 40. General aspect, interior, bar = 5 μ m. Fig. 41. Apex, exterior, bar = 2 μ m. Note apical pores (arrow). Valve morphogenesis not yet complete, fissures to be filled in. Fig. 42. Apex, interior, bar = 2 μ m. Note apical pores (arrow). Fig. 43. Centre, interior, bar = 2 μ m. Fig. 44. Centre, exterior, bar = 2 μ m. Fig. 45. Detail of Fig. 43, 2x enlargement. Note sideways tilted central raphe node. Fig. 46. Detail of Fig. 44, 2x enlargement. Note crook-shaped raphe endings.

Type:—"E251, Finnmark, Maasö, a, P.T. Cleve, 12.1881, von E. Weissflog", geographic coordinates 71°00' N, 24°00' E. Holotype BRM ZU9/89, slide coordinates 10.2 E, 2.3 S. This material is a subsample of Cleve & Möller 312, "Finnmark, Maasö".

Valve (Figs 18, 47, 48) delicate, inconspicuous in LM even with contrast enhancement, slender lanceolate, 85–110 µm long, 10–12 µm wide, apices acute. Striae perpendicular, transverse circa 23, longitudinal circa 30 in 10 µm. Most of the transverse striae are offset, the striae on one side of the raphe ridge aligning with the interstriae on the other (Fig. 47, inset). Axial and central area so narrow as to be inconspicuous in LM. In SEM, the tegumental layer shows little surface relief (Figs 50, 51). External raphe fissures slightly undulating in the centre, central external raphe endings extremely approximate and depressed as two tiny pits so close together that they tend to fuse (Fig. 50 and inset; Fig. 56, horizontal arrow), terminal raphe fissures long and curved (Fig. 51). Internally, the raphe ridge is not markedly twisted sideways (Fig. 49). Central bars highly variable: from an elevated central bar on one side and two elevated small ridges on the other (Fig. 49) to only one vestigial bar (Fig. 57). At the apices, there is a prominent projecting helictoglossa (Fig. 52). Basal layer: foramina practically square, transverse bars of the grate clearly wider than the longitudinal (Figs 49, 57). The two layers of the valve sandwich are joined by longitudinal upright saepes with large perforations (Fig. 53 inset, Figs 54, 55, 56 oblique arrows). These perforations are located underneath (in Fig. 53) the transverse bars of the basal layer grate.



FIGURES 47–57. *H. clevei* sp. nov., SEM. figs 47–53. Type material, Finnmark, Norway. figs 54–57. Material from Florida, USA. SEM. Fig. 47. General aspect, exterior, bar = 20 µm. Inset: detail, magnified 4x, showing offset striae. Fig. 48. General aspect, interior, bar = 20 µm. Fig. 49. Centre, interior, bar = 2 µm. Note vestigial central bar. Fig. 50. Centre, exterior, bar = 2 µm. Inset (2x enlargement): central raphe endings in "pits", almost fused. Fig. 51. Apex, exterior, bar = 2 µm. Fig. 52. Apex, interior, bar = 2 µm. Note prominent helictoglossa. Fig. 53. Interior view of valve where basal and tegumental layer have separated, bar = 2 µm. Inset (2x enlargement): saepes with large perforations (arrow) located underneath the transverse basal layer bars. Figs 54, 55. Apex, exterior, 2 different specimens, bars = 1 µm. Valve morphogenesis not yet finished, longitudinal fissures still to be filled in. Arrows mark perforations in saepes. Fig. 56. Centre, exterior of developing valve, longitudinal fissures still to be filled in. Horizontal arrow marks raphe endings in "pits", oblique arrows mark perforations in saepes. Bar = 3 µm. Fig. 57. Centre, interior. Vestigial central bar, compare with Fig. 49 for variability. Bar = 2 µm.

Etymology:—named after P.T. Cleve, as the sample is part of the collection Cleve & Möller.

Habitat:—littoral-marine sediment.

Distribution:—The type locality is now known as Måsøy, Norway. Rare in the type material, less so in a sample from the Indian River Lagoon, Florida, see under Observations.

Observations:—In several slides of Cleve & Möller 312 examined, no additional specimens have been seen, but the species is so delicate that we may simply have overlooked it. Samples (collection *Hargraves*) from the Indian River Lagoon, Florida, USA, contained specimens matching the type, including the central external raphe endings in “pits” (horizontal arrow in Fig. 56), but the central bars (Fig. 57) are obviously as variable as in *Gyrosigma* and *Pleurosigma*. In several specimens observed (Figs 54–56) valve development is not yet complete: the basal layer and saepes are fully formed, the fissures in the tegumental layer are being filled in. All perforations of the saepes are located on top (in the figure!) of the transverse bars of the basal layer.

The offset of the striae on either side of the raphe ridge has not so far been described in *Haslea* and is not limited to *H. clevei*. It is also evident in *H. salstonica*, see Massé *et al.* 2001: Plate II, figure E, and *H. provincialis* sp. inedit., see Gastineau *et al.* 2014, Fig. 15.3, but is not mentioned in the texts of these publications.

Of the smaller *ostrearia*-like taxa, *H. hyalinissima* superficially resembles *H. clevei*, but the latter is almost double the size of the former and has much coarser transverse striae (23 as against 27–28 in 10 µm). *H. crystallina* also has finer transverse striae (26 in 10 µm) than *H. clevei* and is longer and broader.

***H. avium* Tiffany, Herwig & Sterrenburg, sp. nov.** (Figs 19, 20: LM. 58–64: SEM)

Type:—“Birdrock, La Jolla, California, USA, January, 17, 2003, from *Codium*”, geographic coordinates 32°48’N, 117°16’ W. Holotype BRM ZU9/90, slide coordinates holotype: 4,4 E; 3,4 S, isotype: 4,8 E; 5,3. Isotypes also in collection *Sterrenburg* # 728.

Valve (Figs 19, 20) robust, lanceolate, 38–45 µm long, 6–9 µm wide, with acute apices. Striae transverse slightly radiate, circa 13–15, longitudinal much finer, circa 30 in 10 µm. A few central transverse striae somewhat more radiate and slightly shortened, leaving a tiny more or less oval central area, but this is variable (Figs 19, 59, 64). Axial area extremely narrow, inconspicuous in LM. In SEM, the tegumental layer, with longitudinal fissures that are continuous over most of the valve but sometimes interrupted near the central area, may show marked surface relief (Figs 60, 62, but not in Fig. 63). External raphe fissures often undulating in the middle (Fig. 62, less so in Fig. 63), central endings tightly curving hooks that form depressed pits with tooth-like projections (Figs 62, 63), external terminal endings deeply depressed and retrograde (Fig. 60). Internally, no central bars apparent, one side of the raphe ridge thickened but no pronounced accessory silica ridge paralleling the raphe ridge present (Figs 59, 64). The entire internal raphe ridge, including the central raphe node, tilted sideways (Fig. 64). Basal layer: foramina longitudinally elongated oblong, transverse bars of the grate considerably broader than the longitudinal (Fig. 64).

Etymology:—The specific epithet (genitive, plural of Latin “avis” = bird) refers to the birds of the type locality.

Habitat:—Littoral marine, epiphytic and in sediment.

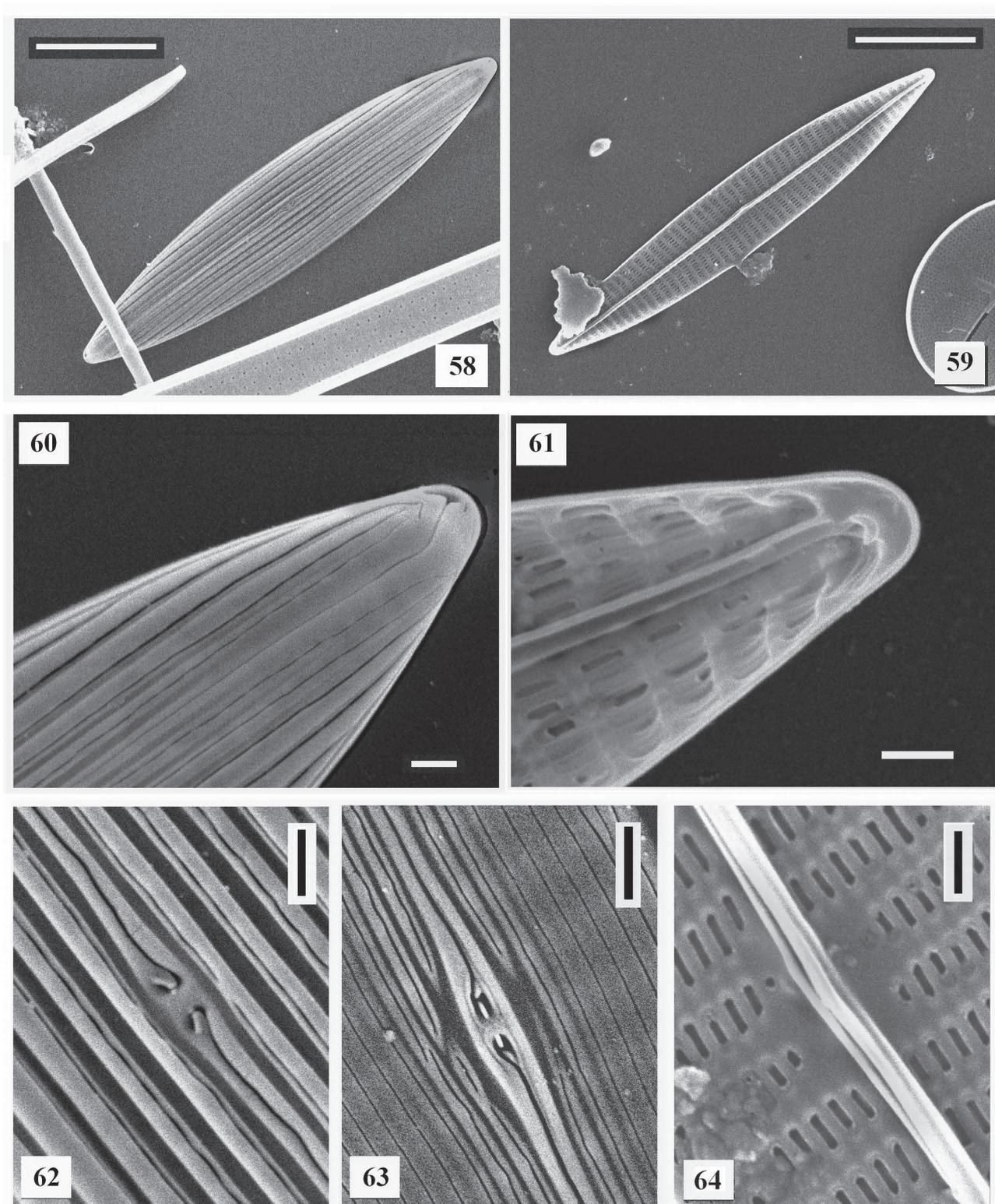
Distribution:—Known from the type locality only, not rare, also in several other samples from the Birdrock locality in collections *Tiffany* and *Sterrenburg*.

Observations:—This species somewhat resembles *H. tsukamotoi* and *H. meteorou* with regard to the marked surface relief of the robust valve, the hook-shaped external central raphe endings with tooth-like projections and the sideways tilted internal central raphe node, but the external central raphe endings and tooth-like projections are very different in shape. Also, the basal layer and striation are clearly different. Saepes not satisfactorily visualized, no fragmented valves found.

In LM, this species may be readily mistaken for one of the *Naviculae sensu stricto* (the “*Lineolatae*”) but the SEM images are decisive. In Fig. 63 the coarse transverse bars of the basal layer grate “shine through” the tegumental layer as ghost images, permitting a transverse stria count in the SEM material. Without this, it would not have been possible to verify that the exterior views of Figs 58, 60 and 62 and the interior views of Figs 59, 61 and 64 are indeed of the same species.

In *H. avium* the longitudinal striae are much finer than the transverse, which excludes a match with *H. britannica*, *H. howeana* or *H. nautica*.

***H. amicorum* Herwig, Tiffany, Hargraves & Sterrenburg, sp. nov.** (Fig. 65 LM, Figs 66–68 SEM)

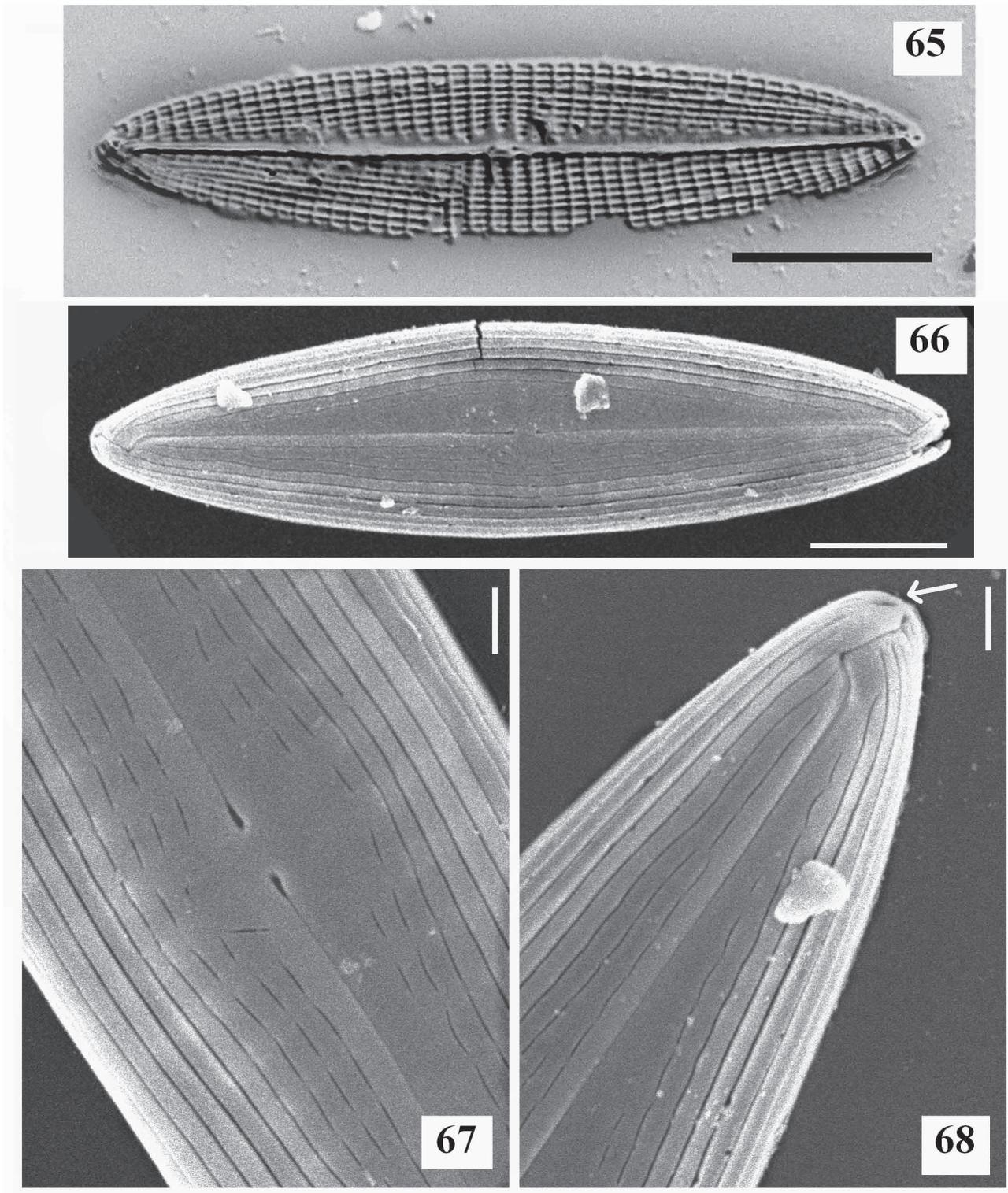


FIGURES 58–64. *H. avium* sp. nov. SEM, isotypes. Fig. 58. General aspect, exterior, bar = 10 µm. Fig. 59. General aspect, interior, bar = 10 µm. Fig. 60. Apex, exterior, bar = 1 µm. Fig. 61. Apex, interior, bar = 1 µm. Figs 62, 63. Centre, exterior showing central raphe endings, bar = 1 µm. Fig. 64. Centre, interior, showing sideways tilted raphe node, bar = 1 µm.

Type:—"Birdrock, La Jolla, California, USA, January, 17, 2003, from *Codium*", geographic coordinates 32°48'N, 117°16' W. Holotype BRM ZU9/90, slide coordinates holotype: 4,3 E; 14,5S. Isotypes in collection *Sterrenburg* # 728.

Valve rather broadly lanceolate, 32–39 µm long, 7.5–8.5 µm wide. Striae transverse radiate, circa 11 in 10 µm, longitudinal strongly curved, circa 22 in 10 µm. Axial and central areas inconspicuous in LM (Fig. 65). In SEM,

the tegumental layer shows continuous longitudinal fissures in the more peripheral portions of the valve, interrupted fissures in the more median portion (Fig. 66, 67). At centre, there is an elliptical field not perforated by external areolar fissures (Fig. 67). Central external raphe fissure elongated droplet-shaped, not deflected (Fig. 67). Apical raphe fissures with V-shaped deflection, ending in depressions (Fig. 68), apical pore present (Fig. 68, arrow). Basal layer with longitudinally elongated oblong foramina (Fig. 65). Saeppes not observed, no fragmented valves found.



FIGURES 65–68. *H. amicorum* sp. nov. Fig. 65. Holotype, LM. Bar = 10 μ m. Fig. 66. Isotype, SEM, general view. Bar = 5 μ m. Fig. 67. Isotype, SEM, exterior view, centre. Note interrupted longitudinal fissures in median portion of valve, continuous fissures towards margin. Bar = 1 μ m. Fig. 68. Isotype, exterior view, apex. Arrow marks apical pore. Bar = 1 μ m.

Etymology:—The specific epithet refers to the spirit of this investigation.

Habitat:—Littoral marine, epiphytic and in plankton.

Distribution:—Known from the type locality (rare) and also observed (rare) in a plankton sample from the Mosquito Lagoon, a tributary of the Indian River Lagoon, Florida, USA.

Observations:—This species is rare in the materials collected and no valves presenting an internal view have been seen. From the LM image, the structure of the basal layer can be derived, however, with foramina that are about twice as long as they are wide. The strongly curved longitudinal striae are a particular feature of this species, which also has a special position in the genus *Haslea* because the more median longitudinal fissures, unlike the more peripheral, are not continuous throughout. Nevertheless, the continuous peripheral fissures and the presence of two separate layers in the valve, as evident from the LM image, warrant assignment to *Haslea*.

In *H. amicorum* the longitudinal striae are much finer than the transverse, which excludes a match with *H. britannica*, *H. howeana* or *H. nautica*.

A review of the literature yielded a species described as a *Navicula* but with the features of *Haslea*. It is here transferred:

Haslea duerrenbergiana* (Hustedt) Sterrenburg, *comb. nov.

Basionym:—*Navicula duerrenbergiana* Hustedt (in Schmidt *et al.* 1934: pl. 393, figs 8–9).

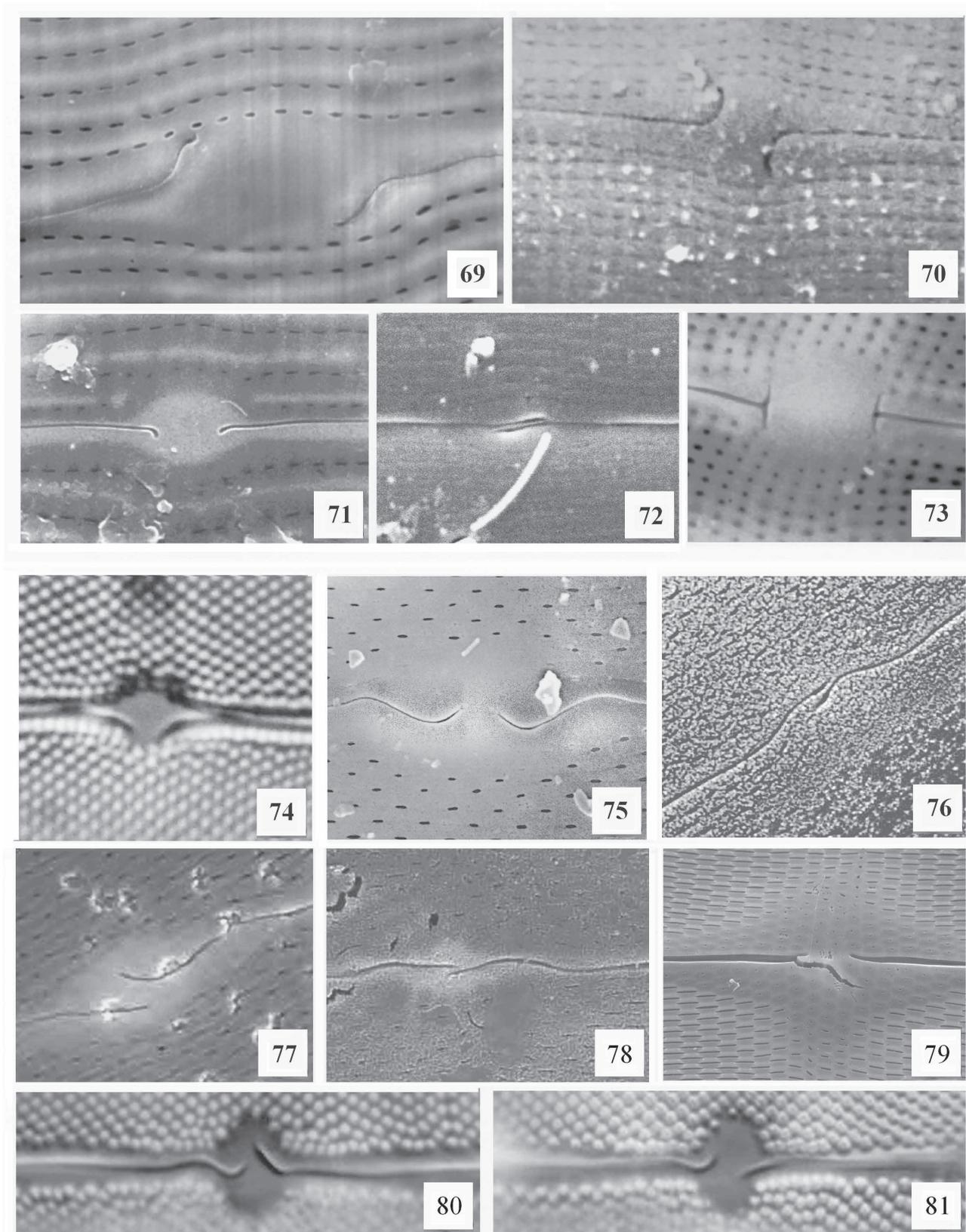
Observations:—The striae are perpendicularly arranged, the axial and central area are extremely narrow and the valve exterior shows continuous longitudinal fissures, see Pl. 26, fig. 6 in Krammer & Lange-Bertalot 1986. These features are all typical of *Haslea*.

The data in the protologue of another taxon from the literature, *H. indica* Desikachary & Prema, are spurious. Desikachary (1988, Pl. 479, fig. 3) shows a broadly lanceolate diatom, one end is capitate and there are two V-shaped transverse hyaline fields on both sides of the central raphe node. All these features are missing from its protologue, which also states that the transverse striae are 10 in 10 µm, the longitudinal “delicate”, meaning much finer. The specimen of plate 479, fig. 3 shows equally fine transverse and longitudinal striae. In other words, the protologue and figure (which does not resemble a *Haslea* in any feature) do not correspond.

Discussion

The genus *Haslea* is obviously highly morphologically diverse. *Haslea feriarum* resembles a chimaera of *Amphora* and *Haslea*, *H. staurosigoidea* resembles a *Gyrosigma* in LM and *H. clevei*, *H. avium*, *H. tsukamotoi* and *H. meteorou* illustrate the great variety in raphe fissure shapes in the genus. It would be difficult to name another genus where valve contour covers such a cornucopian spectrum—especially if one also considers *H. wawriake*—but valve ultrastructure outweighs valve contour as a character in diatom taxonomy. For instance, in the genus *Pleurosigma*, where a sigmoid valve contour has often been regarded as typical, it cannot be considered a generic character, as is evident from the many non-sigmoid *Pleurosigma* species (e.g. Sar *et al.* 2012). In *Haslea* the dominant direction of silica deposition during valve morphogenesis is from proximal to distal (Cox 1999). In *H. feriarum* this silica deposition partially fails unilaterally, leading to “half a *Haslea*” contour.

Several features so far attributed to the genus *Haslea* as a whole are now seen to be highly diverse interspecifically. The “prominent” internal ridge on one side of the raphe mentioned in Round *et al.* (1990) for *Haslea* is not unique to that genus as it is also present in certain *Gyrosigma* species, for instance *G. littorale* (W. Smith) Griffith et Henfrey (Sterrenburg 1992). Neither is it always prominent in *Haslea*—in *H. clevei*, *H. avium*, *H. tsukamotoi* and *H. meteorou* it is not conspicuous. The twisting of the internal raphe fissures shown in Round *et al.* (1990) and Massé *et al.* (2001), for instance, is not unique to *Haslea* either, a good example being *Gyrosigma tenuissimum* (W. Smith) Griffith et Henfrey, see Sterrenburg *et al.* (2014). Again, this feature may not be conspicuous, as in *H. clevei*. In some *Haslea* species, the two outermost longitudinal fissures meet at the apex (see, for instance, Figs 4 and 30), but this is not a generic character as it is not the case in other species, see, for instance, Figs 23, 38 and 60).



FIGURES 69–81. Some central raphe fissure ending shapes in *Gyrosigma* and *Pleurosigma* species. No scale bars added, as not relevant in this context. Fig. 69. *Gyrosigma attenuatum* (Kützing) Cleve. Fig. 70. *G. peisonis* (Grunow) Hustedt. Fig. 71. *G. littorale* (W. Smith) Griffith et Henfrey. Fig. 72. *G. tenuissimum* (W. Smith) Griffith & Henfrey. Fig. 73. *G. obtusatum* (Sullivant et Wormley) Boyer. Fig. 74. *Pleurosigma* aff. *normanii* Ralfs in Pritchard. Fig. 75. *P. elongatum* W. Smith. Fig. 76. *P. frenguellianum* Sunesen, Sterrenburg & Sar. Fig. 77. *P. perlucidum* Sar, Sterrenburg & Sunesen. Fig. 78. *P. patagonicum* (Ferrario & Sar) Sterrenburg & Sar. Fig. 79. *P. indicum* Simonsen. Figs 80, 81. Different shapes seen in a single slide of *P. aff. normanii* Ralfs in Pritchard.

In a paper dealing with species of *Haslea*, Massé *et al.* (2001:626) also discuss some aspects of external central raphe fissure morphology, as follows (verbatim quote): “In *Gyrosigma* and *Pleurosigma* W. Smith, the raphe endings are simpler deflections, although the ends of each slit are usually opposite (*sic*) deflected in *Gyrosigma*. In *Pleurosigma* the central endings turn to the same side, but polar endings are opposite.”

Actually, in these two genera the morphological spectrum of the external central raphe fissures is extraordinarily diverse rather than “simpler” (simpler than what? the preceding paragraph in the paper cited mentions both *Haslea* and *Navicula*). Although in many *Gyrosigma* species the external central raphe endings are oppositely deflected, this presumed stereotyped morphological landscape of opposite deflection is split by a major “Continental Divide” (Sterrenburg 1990, 1993). In one realm, the endings (of various shapes) are abruptly deflected “hooks” and their pattern of deflection is identical on both valves (“isomorphic” species). Fig. 69 illustrates this in *G. attenuatum* (Kützing) Cleve. In the other realm, the endings form small “crooks” and their pattern of deflection is to the convexity of the raphe sternum on one valve of a frustule, to its concavity on the other (“dimorphic” species). Fig. 70 illustrates these crooks in *G. peisonis* (Grunow) Hustedt. These two different iso/dimorphic deflection patterns, with chirality in the dimorphic species (Sterrenburg 1993), are major taxonomic characters. But in addition, the endings in *Gyrosigma* may also be deflected to the same side as in *G. littorale* (W. Smith) Griffith et Henfrey (Fig. 71); they may be long and overlapping as in *G. tenuissimum* (W. Smith) J.W. Griffith & Henfrey (Fig. 72) and may even be undeflected and T-shaped as in *G. obtusatum* (Sullivant et Wormley) Boyer (Fig. 73).

In *Pleurosigma* the spectrum of deflection and shape of the external central raphe endings is also extraordinarily diverse. Deflection may indeed be to the same side, as simple curves (Fig. 74, *P. aff. normanii* Ralfs in Pritchard) but also complex and W-shaped (Fig. 75, *P. elongatum* W. Smith). Alternatively, the endings may be oppositely deflected in various ways: overlapping and extremely closely spaced as in *P. frenguellianum* Sunesen, Sterrenburg & Sar (Fig. 76), overlapping and widely spaced as in *P. perlucidum* Sar, Sterrenburg & Sunesen (Fig. 77), only slightly curved and slightly overlapping as in *P. patagonicum* (Ferrario & Sar) Sterrenburg & Sar (Fig. 78) or practically straight as in *P. indicum* Simonsen (Fig. 79). Finally, there may be marked variation within a species: for instance, in a single population of *P. aff. normanii* Ralfs in Pritchard, some valves show central raphe endings deflected to the same side (Figs 74, 80), others, to opposite sides (Fig. 81).

Likewise, the known variety of raphe ending shapes in the genus *Haslea* has increased as more species have now been examined in SEM: practically straight, dilated and well-separated in *H. ostrearia* (Gaillon) Simonsen; minimally curved, undilated and very approximate in *H. staurosigoidea* and *H. feriarum*; well-separated and with complex curvature in *H. salstonica* Massé, Rincé and Cox, crook-shaped with tooth-like projections in *H. tsukamotoi* and *H. meteorou*, pit-shaped and almost fused in *H. clevei*, depressed pits with tooth-like projections in *H. avium*, oppositely deflected and overlapping in *H. nipkowii*. No generalizing conclusions should be made on either deflection pattern or raphe ending shape in *Haslea*, *Gyrosigma* or *Pleurosigma*, therefore. Central raphe fissure deflection is clearly not useful as a generic distinction and in light of *G. aff. normanii* it may also be questionable as a specific criterion.

The distribution of *H. staurosigoidea* and *H. clevei* is puzzling, the two localities where we have observed these species being almost antipodal—coast of Brazil vs Adriatic and Finnmark vs Florida respectively—but this may simply be a case of the phenomenon that “diatoms are where the diatom collectors are”. To some extent, this also applies to *H. amicum*, which was observed on the West and East coast of the USA.

Generic placement of *Haslea* species in LM may be difficult. The regular more or less perpendicular stria arrangement may be an indication, but is not unambiguous (e.g. confusion with *Gyrosigma* as in the case of *H. nipkowii*) and the transverse striae may be radiate. In *Haslea* the internal central raphe node presents as a tiny linear structure in LM, in contrast to the obvious round to oval node usual in *Gyrosigma*, for instance. Also, the axial and central areas are extremely narrow in *Haslea*, so that in LM there is no evident hyaline space between the striae and the raphe sternum. But again, in *Gyrosigma tenuissimum* (W. Smith) Griffith et Henfrey the central raphe node is also tiny and linear and the axial and central area are also extremely narrow (Sterrenburg *et al.* 2014).

The special optical technique used for the LM figures in this paper reveals far more detail than is visually observed in normal LM work (compare Figs. 10 and 11), where it may be very difficult to separate *H. tsukamotoi*, *H. meteorou* and *H. avium* from taxa in *Navicula sensu stricto* (the “*Lineolatae*”). It is therefore highly probable that several *Haslea* species are still hidden amongst the latter. A good example is *H. avium*: after it had been diagnosed in SEM, selection of the holo- and isotypes in LM was found to be extraordinarily difficult as the material also contains numerous “*Lineolatae*”, which led to a vivid discussion among the authors. For reliable taxonomy of such “*pseudo-Lineolatae*”, type studies including SEM are obligatory, nomenclatural transfer does not equate taxonomy.

Surveying our findings, the morphological spectrum of *Haslea* appears to be as follows:

- Valve contour: fusiform, naviculoid, sigmoid, amphoroid, filiform;
- Central external raphe endings: simple, deflection homolateral, heterolateral and sometimes either in the same species; or alternatively, complex curvature with prominent teeth and pits; from well-separated to very approximate and overlapping;
- Central internal raphe endings present no special features in the specimens we have seen, central bars may be vestigial or absent;
- Raphe ridge: fully tilted sideways, partially tilted or not appreciably tilted;
- Accessory ridge paralleling raphe: from very prominent to inconspicuous;
- Striation not always perpendicular, the transverse may be radiate, the longitudinal strongly curved.
- In many *Haslea* species, the two outermost longitudinal striae meet at the apex, but this is not a generic feature.

At the genus level, there is a common morphological denominator: the *Haslea* species now examined in SEM have a sandwich-structured valve, with grate-like basal layer and a tegumental layer perforated by continuous longitudinal fissures, shored by upright longitudinal bulkhead-like structures we call saepes. In those cases where we have found broken or suitably oriented valves, these saepes were perforated. This sandwich-type valve ultrastructure is typical of the *Pleurosigmataceae* and in the classification proposed by Reid (2012) *Haslea* is placed as a sister clade of the *Pleurosigmataceae* (Fig. 2, p. 54, Fig. 3, p. 57 and Fig. 8, p. 81).

Craticula and *Proschkinia* also have the appearance of longitudinal lines on the external valve surface. These, however, are mere surface relief and not the result of fusion of the external areolar slits as is the case in *Haslea*. Neither *Craticula* nor *Proschkinia* have a sandwich-structured valve and in *Proschkinia* (e.g. *P. bulnheimii*) there are multiple girdle bands, which are not present in *Haslea* species—see the complete frustule of *H. clevei* in Fig. 18.

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