

## Revision of *Amphora holsatica* (Bacillariophyceae)

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Material chosen as the lectotype of *Amphora holsatica* Hustedt and others of the type series has been examined using light and electron microscopy, and a more comprehensive concept of *A. holsatica* was established through an expansion of its description. In light of this new description comparisons with the related *A. pseudoholsatica* Nagumo & Kobayasi and *A. holsaticoides* Nagumo & Kobayasi were conducted. Although specimens described as *A. pseudoholsatica* show slight differences with *A. holsatica* in morphometric data, the morphology and the slope of the mantle, as well as the presence of a flap-like rib at the junction of the mantle and valve face in the former, allow us to delimit these two taxa. The specimens described as *A. holsaticoides* differ from *A. holsatica* in length and in stria density. They also exhibit subtle differences in morphology of the ventral striae, slope of the dorsal mantle and morphology of the central area, conopeum and raphe slit. These differences are considered sufficient to justify the maintenance of *A. holsaticoides*. *A. subholsatica* Krammer was also included in this analysis because the author compared it with *A. holsatica* in the protologue of the species. Morphometric parameters and valve morphology of *A. subholsatica* are, however, more similar to those of *A. acutiuscula* Kützing, with which it may be conspecific.

**Key words:** *Amphora holsatica*, subgenus *Halamphora*, taxonomy, type material, ultrastructure

### Introduction

The difficulties in determining species of the subgenus *Halamphora* without the aid of the electron microscope have been demonstrated (Archibald & Schoeman, 1984; Sala *et al.*, 1998; Clavero *et al.*, 2000). These problems are due to the similarity in valve outline and dimensions of these taxa and to the poor knowledge of their valve morphology.

*Amphora holsatica* Hustedt was described in 1925 and placed within the subgenus *Halamphora*. Simonsen (1987) examined the syntype slides and chose one as a lectotype. Because this analysis was carried out with light microscopy, the resolution was insufficient to visualize details of dorsal and ventral striae, conopeum and valve mantle, presence or absence of costae on the valve face or at the boundary of the valve face and mantle, etc. It is thus necessary to study the type material of this species by electron microscopy for an accurate determination of the above-mentioned characters.

Using light, scanning and transmission electron microscopy, Nagumo & Kobayasi (1990) examined *A. holsatica* specimens from Japan and compared them with others from one of the syntype slides, which were photographed using the light microscope. The authors pointed out that the species had frequently been misidentified due to the limited resolution of the light microscope and due to the scarce information given in the protologue. Although they had no information about fine details of the valve morphology from the type material of *A. holsatica*, they erected *A. pseudoholsatica* Nagumo & Kobayasi and *A. holsaticoides* Nagumo & Kobayasi. Both have uniseriate striae and similar valve dimensions to *A. holsatica*. More recently Krammer (1997) erected *A. subholsatica*, which is a species similar to *A. holsatica*, *A. pseudoholsatica* and *A. holsaticoides*. Considering that Nagumo & Kobayasi (1990) and Krammer (1997) did not have any information on the ultrastructure of the type material of *A. holsatica*, the comparison of the three new species with the latter was necessarily superficial and speculative.

In this paper, we provide light and scanning electron microscopic data on the specimens from lectotype material of *A. holsatica* in order to establish its specific limits, to provide a more

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comprehensive description of the taxon and to compare it with allied species.

## Materials and methods

The materials used in this research correspond to those from which the lectotype of *Amphora holsatica* was taken, i.e. E 3691, slide 144/15 from Oldesloe, I,5 Holstein, collected on 15 July 1922, deposited in the Hustedt Collection at the Alfred Wegener Institut für Polar- und Meeresforschung in Bremerhaven. In order to obtain morphometric data for the highest number of specimens, we considered those photographed by Simonsen (1987), and several specimens in the same slide or in materials from the same series. Photomicrographs were obtained with an Axioplan D 7082 light microscope, (LM) with either bright field or with Normarski differential interference contrast optics.

Specimens of sample E 3691 were prepared for scanning electron microscopy (SEM) according to Ferrario *et al.* (1995) and the microphotographs were obtained with an ISI-DS 130 scanning electron microscope.

For comparison of *A. holsatica* with the related taxa *A. pseudoholsatica* Nagumo & Kobayasi, *A. holsaticoides* Nagumo & Kobayasi and *A. subholsatica* Krammer, we used the protologue of each species (Nagumo & Kobayasi, 1990; Krammer, 1997).

Areolae and striae were measured according to Anonymous (1975) and the terminology used is that of Ross *et al.* (1979) and Cox & Ross (1980). For details about the construction of the frustule in the genus *Amphora* and the morphology of the valves in different views, Schoeman & Archibald (1979) and Round *et al.* (1990) should be consulted.

## Results

### *Amphora holsatica* Hustedt

**Light microscopy** The frustule is elliptic to widely lanceolate with ends broadly protracted into subrostrate to truncate poles (Fig. 1). The valvar planes of both valves are at variable angles, from extremely obtuse to almost plane (Figs 1, 2). The girdle is broad and convex in dorsal view of the frustule, and narrower and almost flat in ventral view (Figs 2, 3). The girdle bands are numerous with conspicuous subrectangular punctae (Figs. 1, 3).

The valves are semilanceolate with a convex dorsal margin, and the ventral margin is straight sometimes with a slight central inflation (Fig. 5). Dorsal striae are distinctively punctate (Figs 2, 5); ventral ones are hardly visible and easily confused with the areolae of the girdle bands because these may remain fastened to the ventral valve surface. (The specimen illustrated in Simonsen (1987) pl. 132, fig. 11 is the only one that undoubtedly shows the ventral striae (right valve).) In our materials

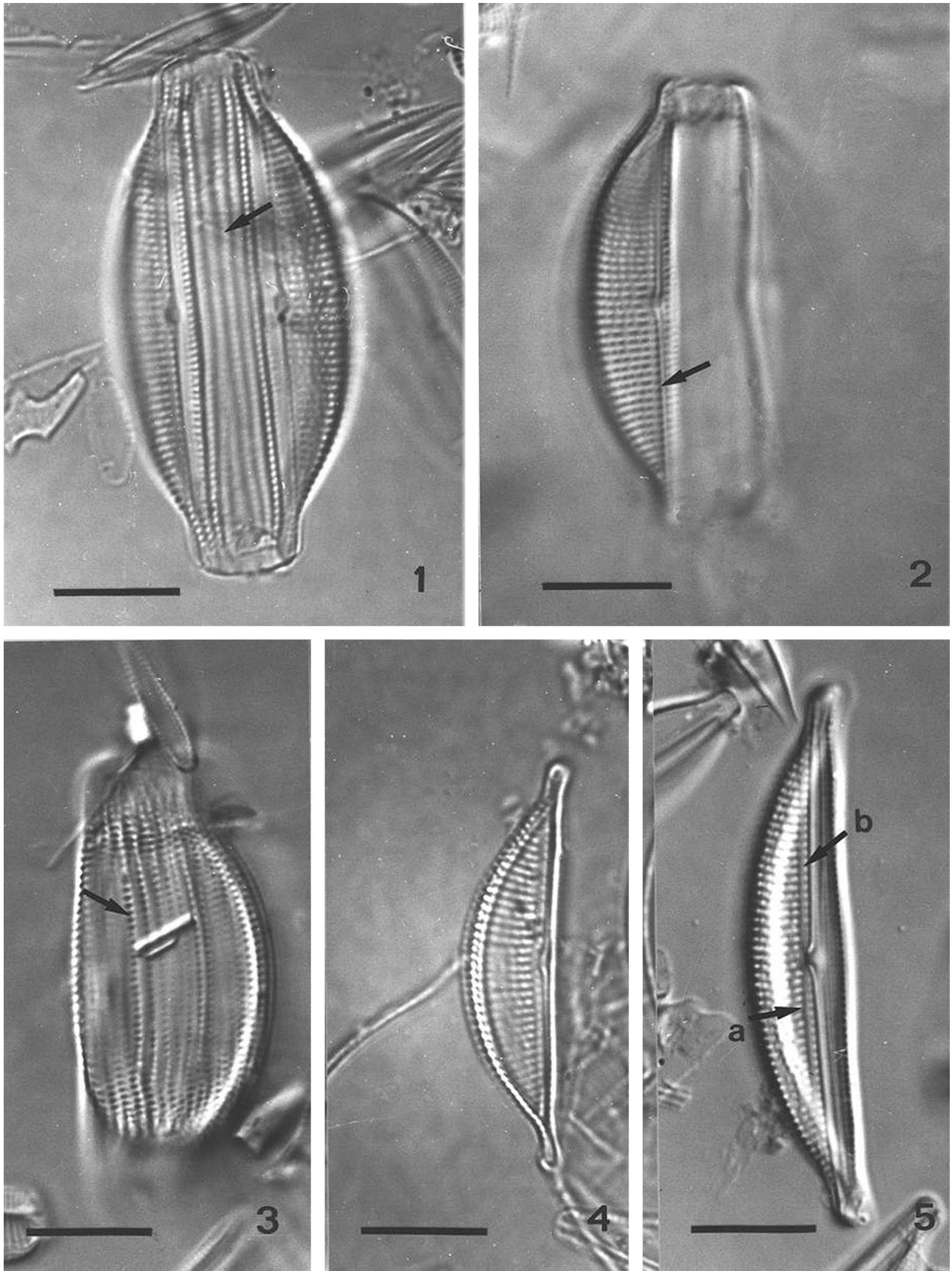
none of the specimens photographed with light microscopy (LM) show the ventral striae clearly. The raphe is simple, filiform and located near the ventral margin, with the proximal ends gently curved toward the dorsal side (Fig. 5). The conopeum is slightly visible as a line crossing the proximal ends of the dorsal striae (Figs 2–5).

**Scanning electron microscopy** With SEM, the general characteristics of the frustule (Fig. 6) and valves (Figs 8, 9) as seen with LM are confirmed, but some features were revealed for the first time. The valve face has a plain zone, which curves gently to the dorsal side into a high and oblique valve mantle (Figs 10, 11) and more abruptly to the ventral side into a shallow mantle (Figs 12, 13). Along the transition between the dorsal valve face and mantle there is no costa interrupting the striae (Figs 10, 11).

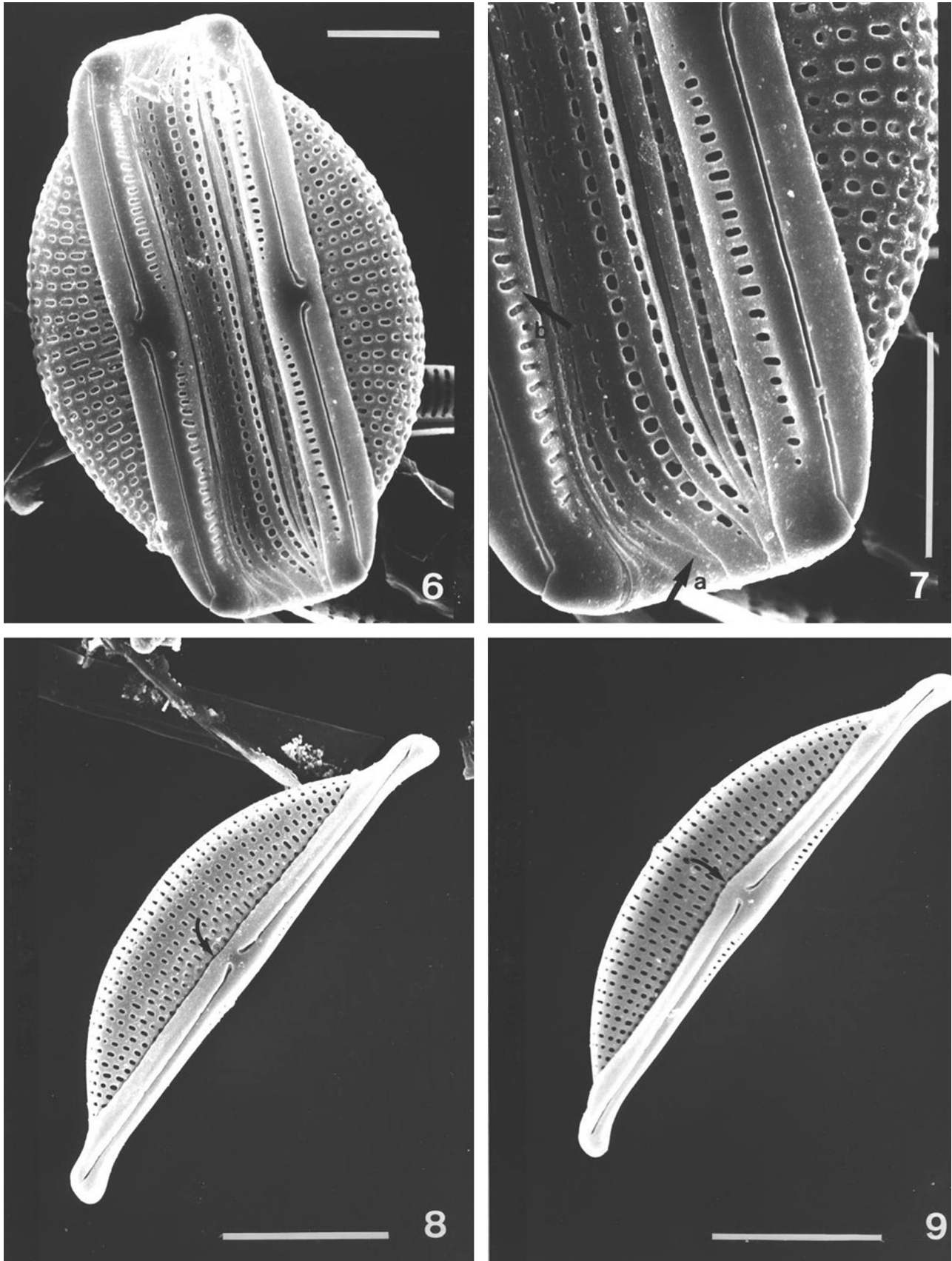
The dorsal striae are uniseriate with transapically elongated areolae that occasionally alternate with small circular ones. Since the areolae may have different sizes, the density of areolae may vary within the same valve. From an internal view, the valve shows that the first areola of each stria is different in shape from the others because it is wider than it is long (Figs 12, 13). These areolae are arranged in an ordered row parallel to the raphe and interrupted at the central area. Externally this row of areolae is not visible because it lies under the conopeum, but it may be observed with LM (Fig. 5).

The ventral striae are more dense and consist of only a single row of small linear to circular areolae, which are not uniform in shape, size, or even in arrangement. They are radial at the centre and convergent towards the ends, lie in the junction of valve face and mantle, and are interrupted at the central area (Figs 6, 7).

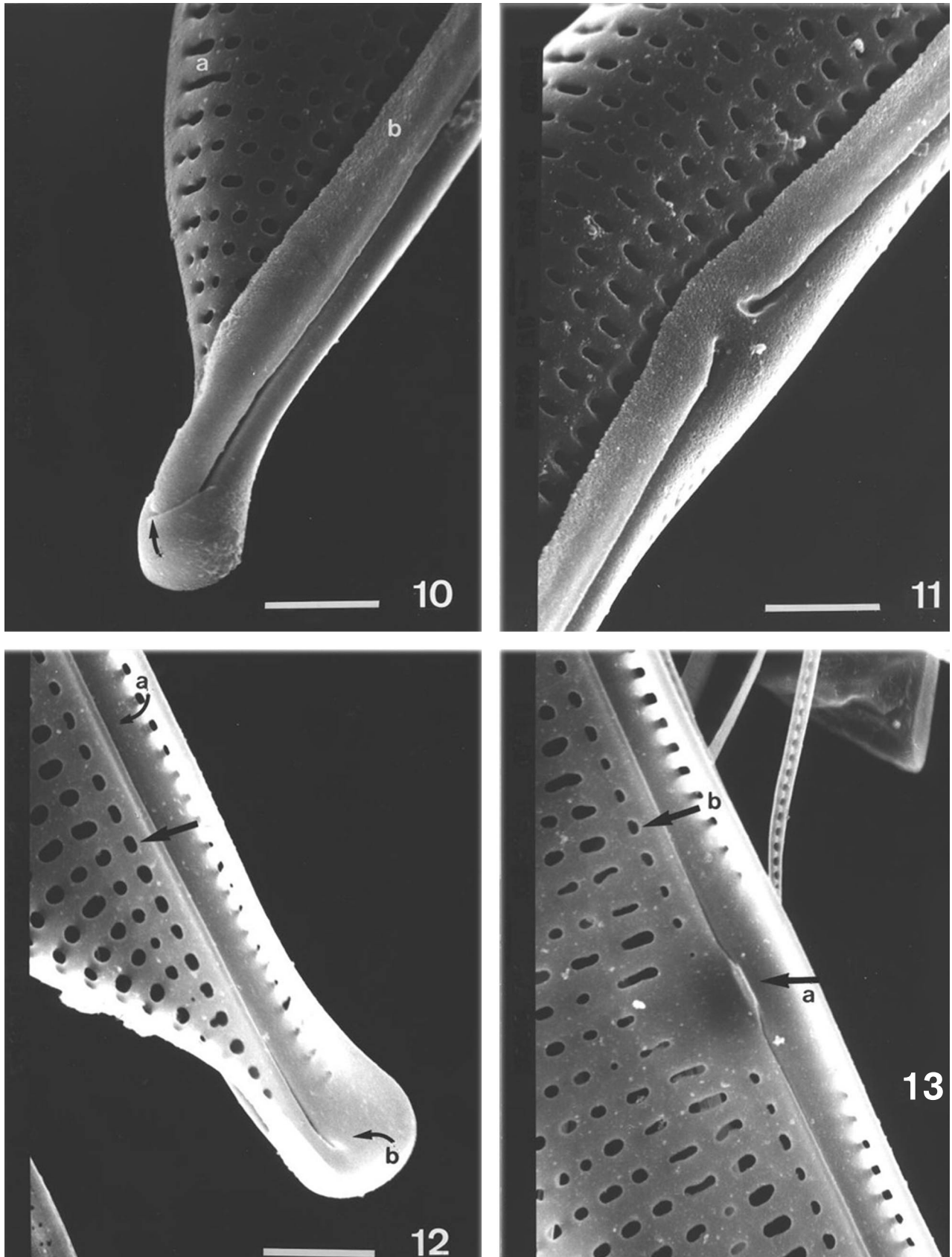
The raphe lies near the ventral margin and both branches of the raphe are straight or almost straight, forming a wide obtuse angle (Fig. 9) or a 180° angle (Fig. 6). Internally the axial area is distinct and narrower on the dorsal side of the valve than on the ventral side. The central area is asymmetric, orbicular on the dorsal side, and wider where it reaches the margin at the ventral side of the valve. (Figs 12, 13). Internally the raphe opens along the ventral edge of an axial rib (Fig. 12). At the central nodule both branches end under a tongue-like expansion (Fig. 13) and at the poles they end in poorly developed helictoglossae (Fig. 12). Externally the proximal fissures of the raphe are dilated in central pores, dorsally bent (Fig. 11) and the terminal fissures are dorsally deflected (Fig. 10). The conopeum is well developed to the dorsal side of the valve, straight with a little low-cut neckline or widening at the centre



**Figs 1–5.** *Amphora holsatica* type material: light micrographs. Figs 1, 2. Frustules in ventral view. Note the different angles at which the valves lie. Fig. 1. Note the punctate girdle bands (arrow). Fig. 2. Note the dorsal punctate striae and the conopeum as a dark line (arrow). Fig. 3. Same specimen as in Fig. 2 at a different level of focus; note the punctate girdle bands (arrow). Fig. 4. Valve showing only the dorsal side due to the tilt at which it was photographed. Fig. 5. Valves showing dorsal and ventral sides. Note the dorsal punctate striae, the conopeum as a dark line (arrow a) and a row of areolae near the raphe (arrow b). Scale bars represent 10  $\mu\text{m}$ .



**Figs 6–9.** *Amphora holsatica* type material: scanning electron micrographs. Fig. 6. Frustule in ventral view, showing girdle bands and ventral striae. Fig. 7. Details of the frustule in ventral view showing the punctate girdle bands open at one end (arrow a) and the ventral areolae occluded by internal hymens (arrow b). Fig. 8. External valve view of a cell showing the dorsal striae with transapically elongated areolae that alternate with circular ones, the conopeum slightly concave at the valve centre (arrow) and raphe branches at nearly a 180° angle. Fig. 9. Another specimen photographed at a different tilt. Note the distribution of the ventral striae; the conopeum slightly convex at valve centre (arrow) and raphe branches at an obtuse angle. Scale bars represent: Figs 6 and 7, 5  $\mu\text{m}$ ; Figs 8 and 9, 10  $\mu\text{m}$ .



**Figs 10–13.** *Amphora holsatica* type material: scanning electron micrographs. Fig. 10. External valve view showing details of the dorsal mantle (a), conopeum (b) and terminal raphe fissures dorsally deflected (arrow). Fig. 11. Valve view of the specimen in Fig. 10 at higher magnification, showing details of the dorsal mantle, conopeum and central raphe fissures that are dorsally bent. Fig. 12. Internal valve view of a pole, showing details of the raphe (arrow a), helictoglossa (arrow b) and axial area; dorsal and ventral striae. Note the row of areolae adjacent to the axial area (arrow c). Fig. 13. Internal valve view of the central region showing details of the axial and central areas, tongue-like expansion between the proximal raphe ends (arrow a) and the row of areolae adjacent to the axial area (arrow b). Scale bars represent 2  $\mu\text{m}$ .

and with the ends embracing the valve poles (Figs 6–11).

Girdle bands are open at one end and are punctate (Figs 6, 7). The structure of the individual bands of the girdle was not clear, and the determination of the exact number of cingular elements is impossible because they are hidden or overlapped by others.

The morphometric data are as follows: length, 26–45  $\mu\text{m}$ ; width of the frustule, 15–25  $\mu\text{m}$ ; width of the valve, 7–9  $\mu\text{m}$ ; dorsal striae in 10  $\mu\text{m}$  at the centre, 11.5–15, at the poles, 13–18; ventral striae in 10  $\mu\text{m}$ , 16–22; valve areolae in 10  $\mu\text{m}$ , 12–16; band areolae in 10  $\mu\text{m}$ , 15–18.

The measurements given in our study fit within the range given in the protologue by Hustedt (1925), except in the number of ventral striae per 10  $\mu\text{m}$  (Table 1). The density of ventral striae given by Hustedt is lower than ours and coincides with the density of the band areolae. This subtle difference could be attributed to the difficulty of distinguishing ventral striae and band areolae with LM.

In the material from sample E 3691 we also found a smaller and narrower taxon with a greater number of dorsal and ventral striae, with uniseriate striae having more areolae per 10  $\mu\text{m}$  and with a greater density of areolae in the girdle bands (Table 1). Besides the differences in morphometric parameters, this taxon is similar to *A. holsatica* in general appearance and in the type of striae but it differs in the ventral central striae having more than one areola and in the conopeum being widened at the ends (Fig. 14). Considering these differences in dimensions and fine structural



**Fig. 14.** *Amphora* sp. found in type material of *Amphora holsatica*. Scale bar represents 5  $\mu\text{m}$ .

morphology, we believe that this specimen is not conspecific with *A. holsatica* and we include it in this paper to point out the coexistence of two taxa in the lectotype material.

## Discussion

In sample E 3691 we found several specimens similar in valve outline, dimensions, general appearance and fine structural morphology; thus we can assume that all belong to the unique taxon, *A. holsatica* Hustedt. Several of the specimens have a wider range in some morphometric parameters than those described by Hustedt (1925) and for this reason we extend the ranges given in the protologue. The most important differences are the density of dorsal and ventral striae at the valve centre, when compared with the density of areolae of the dorsal striae and with the density of areolae in the girdle bands. In Table 1, we show the morphometric data from the protologue, from specimens presented in Simonsen (1987, pl. 132, figs 11–16) and from specimens examined in our study.

SEM analysis of type material resulted in a more comprehensive concept of *Amphora holsatica* Hustedt, which we used to compare with related taxa. We found subtle differences between the morphometric data of the type material and those given by Nagumo & Kobayasi (1990) for specimens described as *Amphora holsatica*. However, when we measured the untilted specimens in figs 3–5 of Nagumo & Kobayasi (1990) we found that the densities of striae and areolae are lower than in their description (Table 2). These differences could be explained as measurements from photographs taken with different tilts being artificially higher due to perspective. Comparing the data obtained by us from the specimens photographed in Nagumo & Kobayasi (1990) with those obtained on type material, it is clear that there are no morphometric differences. Moreover, both materials agree in the frustule and valve outline, the angle of the valves, the morphology of the ventral girdle, the type of dorsal and ventral striae, the morphology and width of the conopeum, the angle built by the raphe branches, the shape and inclination of the proximal and distal fissures and the size of the helictoglossae. In light of these comparisons, we have shown that the specimens described by Nagumo & Kobayasi (1990) are conspecific with *A. holsatica*. The objections of Krammer (1997) about the identity of the materials from Japan are thus refuted.

*Amphora pseudoholsatica* Nagumo & Kobayasi is morphometrically close to *A. holsatica*, with little difference in valve length and breadth and the

**Table 1.** Morphometric data of the type material of *A. holsatica* in the literature and in this study

Species	Author	Length	Width			Dorsal striae in 10 $\mu\text{m}$			Ventral striae in 10 $\mu\text{m}$	Valve areolae in 10 $\mu\text{m}$	Girdle band areolae in 10 $\mu\text{m}$	Girdle bands in 10 $\mu\text{m}$
			F	V	P	C	P					
<i>Amphora holsatica</i>	Hustedt (1925)	30–45	15–25	–	–	15	–	13–15	13	15	10	
	Simonsen (1987)	30.5–43	18	7–9	11.5–15	13–15	–	16–20	12–16	15–16	–	
	LM this study	34.5–45	–	7.5–9	13–15	14–16	–	–	$\geq 14$	$\geq 16–18$	–	
<i>Amphora</i> sp.	SEM this study	26–36	17.5	7.6–8.4	14–15	14–18	–	16–22	(10)12.5–16	16–20	–	
	LM and SEM this study	16.5–19.5	7.7	3–3.6	22–24	–	36	23–25(31)	40	–	–	

–, no data; F, frustule; V, valve; C, centre; P, poles; LM, light microscopy; SEM, scanning electron microscopy.

**Table 2.** Morphometric data of *A. holsatica* and other similar species discussed in the text

Species	Author	Length	Width			Dorsal striae in 10 $\mu\text{m}$			Ventral striae in 10 $\mu\text{m}$	Valve areolae in 10 $\mu\text{m}$	Band areolae in 10 $\mu\text{m}$	Bands in 10 $\mu\text{m}$
			F	V	P	C	P					
<i>Amphora holsatica</i>	This study	26–45	15–25	7–9	11.5–15	13–18	–	16–22	12–16	15–18	–	
	Nagumo & Kobayasi (1988)	32–54	–	8–10	14–17	–	–	–	18	–	–	
<i>A. pseudoholsatica</i>	Nagumo & Kobayasi (1990)	23–53	–	<b>8–9</b>	<b>13–15</b>	–	–	<b>19</b>	<b>12–13</b>	–	–	
	Nagumo & Kobayasi (1990)	45–71	–	6–8	15	–	–	17	13–15	–	–	
<i>A. holsaticoides</i>	Nagumo & Kobayasi (1990)	45–71	<b>21.5</b>	<b>6–8</b>	<b>11–14</b>	–	–	<b>17–18</b>	<b>11–15</b>	<b>21</b>	–	
	Krammer (1997)	20–38	–	8–9	11	–	–	14	13–15	–	–	
<i>A. subholsatica</i>	This study	26–45	–	<b>7.5–9</b>	<b>10–12</b>	–	–	<b>14–16</b>	–	–	–	
	Nagumo & Kobayasi (1990)	32–54	13–25	5.3–6	14–18(20)	14–18(20)	–	22–24	18	23–26	14–16	

–, no data; F, frustule; V, valve; C, centre; P, poles.

Data in bold letters were obtained from untilted specimens in Nagumo & Kobayasi (1990).

density of areolae in the girdle bands (Table 2). Nevertheless, the delimitation of the species is clear when the fine structural morphology of the valves is analysed since there are some differences with *A. holsatica*. The valve face of *A. pseudoholsatica* is depressed at the centre, the valve mantle is perpendicular and delimited by a flap-like marginal ridge, and the mantle areolae are arranged differently from those on the valve face.

*Amphora holsaticoides* Nagumo & Kobayasi is another species that is related to *A. holsatica*. After comparing the range of dimensions in the type material of *A. holsatica* and that of *Amphora holsaticoides* in Nagumo & Kobayasi (1990), we found noticeable differences in length and few differences in the density of ventral and dorsal striae (Table 2). These authors pointed out that *Amphora holsaticoides* differs from *A. holsatica* by a thin silica strip on the dorsal side of the raphe slit. However, we found other subtle differences. The ventral striae are less transapically elongated, the dorsal mantle is more perpendicular, the central area is expanded only ventrally and the conopeum widens to embrace the poles and makes a low-cut neck at the ends. Though the morphometric and morphological differences may be enough to delimit these species, more specimens of the type series of *A. holsaticoides* should be analysed to establish the degree of variability of the diagnostic features.

Krammer (1997) erected *Amphora subholsatica*, and pointed out that it differs from *Amphora holsatica*, *Amphora pseudoholsatica* and *Amphora holsaticoides* in morphometric data and frustule structure. Besides the subtle differences mentioned by Krammer (1997), we found that *Amphora subholsatica* also differs from the other three species discussed above in the morphology of the dorsal striae. Considering this character, the specimen of *Amphora subholsatica* shown by Krammer in the protologue (pl. 205, fig. 10) resembles *Amphora acutiuscula* in Archibald (1983: 34–36, figs 490–492). The materials described in Archibald (1983) show that each stria is composed of a single row of areolae extending about a half to two-thirds of the way from the dorsal margin to the raphe, after which the striae are composed of two rows of small circular pores. In addition to the morphology of the striae, both species are similar in general appearance and morphometric parameters. From our point of view these taxa seem to be conspecific; nevertheless a careful examination of several specimens from the type material of both species is necessary to establish whether they are the same taxonomic entity.

Based on the fine structural morphology of the type material of *Amphora holsatica* and the analysis of allied species, we conclude that *A. pseudoholsa-*

*tica* is clearly different from *A. holsatica* and that *A. holsaticoides* may be considered a different species, but closely related to *A. holsatica*. *A. subholsatica* is less closely related to *A. holsatica* than to *A. acutiuscula*, and needs further examination to establish its identity accurately.

Our results, those of Archibald & Schoeman (1984), Sala *et al.* (1998) and those of Clavero *et al.* (2000) indicate that more detailed electron microscopic studies of the type materials of the species in the subgenus *Halamphora* are necessary to avoid taxonomic confusion. At present, we are analysing the type material of other species of this subgenus, such as *A. tumida* Hustedt, *A. schoederii* Hustedt and *A. subturgida* Hustedt, deposited in the Hustedt Collection.

#### *Emended diagnosis*

#### *Amphora holsatica* Hustedt

*Light microscopy* Frustule elliptic to widely lanceolate with ends broadly protracted into subtruncate to truncate poles. Valvar planes of both valves at variable angles, from extremely obtuse to almost plane. Girdle broad and convex in dorsal view of the frustule, and narrower and almost flat in ventral view. Girdle bands numerous with conspicuous subrectangular punctae. Valves semi-lanceolate with a convex dorsal margin, ventral margin straight sometimes with a slight central inflation. Dorsal striae distinctively punctate. Ventral striae hardly visible. Raphe filiform, located near the ventral margin, with the proximal ends gently curved towards the dorsal side. Conopeum slightly visible as a line crossing the proximal ends of the dorsal striae.

*Scanning electron microscopy* Valve face with a plain zone that gently curves to the dorsal side. Dorsal mantle high and oblique, ventral mantle shallow. Dorsal striae uniseriate with transapically elongated areolae, occasionally alternating with small circular ones. Internally the first areola of striae form a row parallel to the raphe that is discontinuous at the central area. Ventral valve with a single row of small linear to circular areolae radial at the centre and convergent to the ends. Raphe near the ventral margin, branches straight or almost straight, forming a wide obtuse or a 180° angle. Axial area distinct in internal view. Central area asymmetric, orbicular at dorsal valve side, reaching the margin at ventral side. Internal raphe branches running along an axial rib. Proximal raphe ends reaching a tongue-like expansion of the central nodule, distal raphe ends finishing in poorly developed helictoglossae. External proximal fissures dilated in central pores, dorsally bent,

terminal fissures dorsally deflected. Conopeum well developed to the dorsal valve side, straight with a little low-cut neckline or widening at the centre and ends embracing the valve poles. Girdle bands punctate, open at one end.

Morphometric data: length, 26–45  $\mu\text{m}$ ; frustule width, 15–25  $\mu\text{m}$ ; valve width, 7–9  $\mu\text{m}$ ; dorsal striae in 10  $\mu\text{m}$  at the centre, 11.5–15, at the poles, 13–18; ventral striae in 10  $\mu\text{m}$ , 16–22; valve areolae in 10  $\mu\text{m}$ , 12–16; band areolae in 10  $\mu\text{m}$ , 15–18.

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