



***Hippodonta lange-bertalotii* Van de Vijver, Mataloni & Vinocur sp. nov. and related small-celled *Hippodonta* taxa**

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With 75 figures and 2 tables

Abstract: *Hippodonta lange-bertalotii* Van de Vijver, Mataloni & Vinocur sp. nov. is described from Crater Lake, Deception Island (South Shetland Islands). Present paper reports a detailed morphological description of this species by means of light and scanning electron microscopy. The main diagnostic criteria include the rhombic outline of the valves, the comparatively narrow striae and the presence of two shortened striae delimiting the central area. The adscription of this new species to the genus *Hippodonta* and the differences with related taxa are briefly discussed. Additionally, the morphological variability of the similar *H. pseudacceptata* is examined analyzing the valvar ultrastructure of different populations collected from Western Europe or published in the literature. *Hippodonta pumila* is presented as a heterotypic synonym of *H. pseudacceptata*.

Key words: Bacillariophyceae, *Hippodonta*, new species, synonymy, taxonomy, emended description.

Introduction

The genus *Hippodonta* was established in 1996 (Lange-Bertalot et al. 1996) to gather taxa formerly belonging to *Navicula* sensu lato with generally small and strongly silicified frustules, broad transapical virgae and simple raphe systems. Since no single apomorphies distinguish this genus from other naviculoid taxa, *Hippodonta* is commonly regarded as a polythetic genus (Lange-Bertalot 2001) and its systematic position is still not well resolved. For example, Cox (1999) criticized the establishment of this new genus providing the lack of cytological distinctive features and regarded *Hippodonta* as a subgenus within a broadened concept of *Navicula*. However, Bruder & Medlin (2008) enumerated some additional ultrastructural characters common to all known *Hippodonta*, namely the straight raphe, the absence of internal raphe ribs and the presence of small apical septa, and evidenced the position of this genus as a sister group to *Navicula* sensu stricto based on molecular data.

Within the c. 30 species currently ascribed to this genus, several small-celled forms (up to c. 20 µm length) morphologically around *Hippodonta pseudacceptata* (H. Kobayasi) Lange-Bertalot constitute a rather homogeneous group characterized by rhombic to linear-rhombic outlines, relatively dense striations and comparatively short lineolae, and two shorter striae opposed in the central area. The illustrations in Lange-Bertalot (2001) of *H. avittata* (Cholnoky) Lange-Bertalot (pl. 76, figs 19–22, (?) 23–28), *H. subtilissima* Lange-Bertalot, Metzeltin & Witkowski (pl. 76, figs 47–53) and *Hippodonta* “(?nov.) spec. cf. *subtilissima* (pl. 76, figs 54–58)” (= *H. pumila* Lange-Bertalot, G. Hofmann & Metzeltin, see Metzeltin et al. 2009, pl. 63, figs 21, 22, pl. 255, fig. 9) provide a general overview of these forms, to which the more recent *H. subrhombica* Metzeltin et al. (Metzeltin et al. 2005, pl. 59, figs 31–36) can also be included.

This paper first reports a new taxon found at the South Shetland Islands belonging to this group of *Hippodonta* and discusses the taxonomic position of some closely related species analyzing the valvar ultrastructure of populations collected from different locations in Western Europe through light and scanning electron microscopy. Additionally, we propose an emended description for *H. pseudacceptata* on the basis of the existing discrepancy between the illustrations and the description in the protologue.

Materials and methods

Epilithic diatom samples from France, Portugal and Spain were analyzed using light (LM) and scanning electron (SEM) microscopy. Details of the sampling sites are presented in Table 1. Collected material was treated using hot hydrogen peroxide (H₂O₂ 8M) and diluted HCl (37%), in order to obtain a suspension of clean frustules. The material from the South Shetland Islands was prepared following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H₂O₂ and heating to 80 °C for about one hour. The reaction was completed by addition of KMnO₄. Following digestion and centrifugation (three times 10 minutes at 3700 x g), the resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax®.

LM observations and morphometric measurements were performed using a Leica® DMRX light microscope with 100x oil immersion objective and an Olympus BX51 microscope, equipped with Differential Interference Contrast (Nomarski) optics. Light microscopy photographs were taken using a Leica® DC500 camera and the Colorview I Soft Imaging System. Samples selected for scanning electron microscopy analysis were filtrated through polycarbonate membrane filters with a pore diameter of 1 or 3 µm, mounted on stubs, sputtered with gold (40 nm) with Modular High Vacuum Coating System (BAL–TEC MED 020) and studied with a Leica® Stereoscan 430 i and a JEOL-5800LV, operated at 20 kV.

Table 1. Sampling localities.

Site	Date	Latitude	Longitude	Altitude (m a.s.l.)	Ecological particularities
Crater Lake, Rectangular Lake and Irizar Lake, Deception Island, South Shetland Islands	09/02/2002	62° 58' 37" S	60° 39' 00" W	200	Oligotrophic waters with high electrolyte content
Olmedo, Adaja River, Spain	19/08/2005	41° 17' 21" N	4° 49' 50" W	740	Mesotrophic waters with average electrolyte content
Mogent River, Besòs basin Catalonia	09/05/2001	41° 37' 60" N	2° 27' 16" E	300	Oligo-mesotrophic streams with average electrolyte content
Lamotte, Beuvron River, France	28/07/2009	47° 36' 10" N	2° 01' 32" E	118	Mesotrophic waters with low electrolyte content
Porto de Lagos, Boima Stream, Portugal	17/04/2006	37° 11' 55" N	8° 31' 42" W	72	Mesotrophic waters with low electrolyte content
Chamusca, Tejo River, Portugal	06/07/2006	39° 21' 34" N	8° 28' 51" W	45	Mesotrophic waters with average electrolyte content

Morphological terminology follows Hendeby (1964), Round et al. (1990) and Lange-Bertalot (2001).

Results and discussion

Hippodonta lange-bertalotii Van de Vijver, Mataloni & Vinocur sp. nov. (Figs 1–19)

Descriptio: Valvae rhombicae ad rhombicae-lanceolatae marginibus convexis apicibusque obtuse rotundatis, non-protractis. Longitudo 15–20 μm , latitudo 4.5–5.2 μm . Area axialis angustissima, linearis, numquam dilatans ad aream centralem. Area centralis distincta, formans subfasciam plus minusve expansam striis mediis singulis utroque abbreviatis variabiliter. Raphe filiformis, recta poris centralis parvissimis dense sitis inter se. Fissurae terminales leviter deflexae, curtae. Striae transapicales moderate radiatae prope aream centralem, sed parallelae et paene leviter convergentes ad apices, 14–17 in 10 μm . Areolae non discernendae in microscopio photonico.

Holotype (here designated): BR-4210 (National Botanic Garden, Meise)

Isotypes: PLP-163 (UA, University of Antwerp), BRM-ZU7/78 (Hustedt Collection, Bremerhaven)

Type locality: Crater Lake, Deception Island, South Shetland Islands, sample (coll. Vinocur, coll. date 9/02/2002)

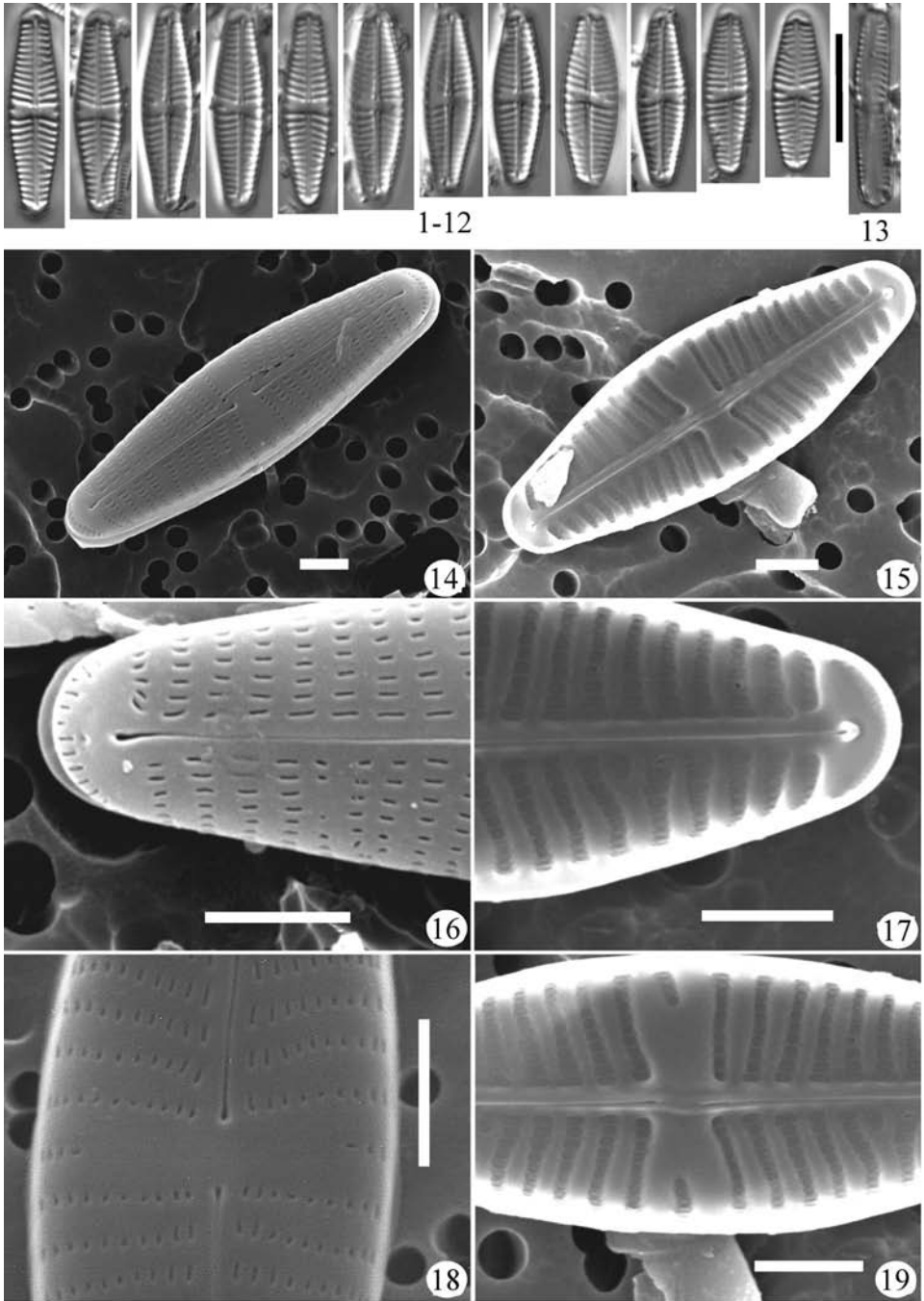
Etymology: The specific epithet commemorates Horst Lange-Bertalot.

LM observations

Valves are rhombic to rhombic-lanceolate with convex margins and obtusely rounded, non-protracted apices (Figs 1–12). Valve dimensions: length 15–20 μm , width 4.5–5.2 μm ($n = 13$). Axial area very narrow, linear, never widening towards the central area. Central area distinct, forming a wedge-shaped subfascia with 1–2 shortened striae bordering the central area (Figs 1–12). Raphe is filiform, straight with very small, rather narrow-standing, proximal pores and distally with weakly deflected, short terminal fissures. Transapical striae moderately radiate near the central area, becoming parallel and even weakly convergent towards the apices, 14–17 in 10 μm . Genus-typical thickened terminal stauros-like areas [sensu Lange-Bertalot et al. (1996)] present (Figs 1–13). Areolae are not discernible in LM.

SEM observations

Striae uniseriate, composed of apically elongated, rather short areolae except for the areolae of the striae bordering the central area being more roundish and less elongated, 40–50 in 10 μm (Figs 14–19). Virgae larger than the striae. Striae in the central area clearly shortened, consisting of only 2–4 areolae (Figs 18, 19). Terminal stauros clearly developed bordered by semicircumpolar, slit-like elongated areolae (Figs 16, 17). External raphe branches slightly undulated with small, drop-like, straight proximal raphe endings (Fig. 18). External distal raphe fissures very short, not expanded but very weakly deflected (Fig. 16). Internally, areolae covered by hymens (Figs 15, 17, 19). Internal raphe rib absent. Raphe terminating distally on small helictoglossae (Fig. 17).



Figs 1–19. *Hippodonta lange-bertalotii* sp. nov. Holotype, Crater Lake, Deception Island, slide BR-4210. Figs 1–13. LM. Scale bar = 10 μ m. Figs 1–12. Valve view. Fig. 13. Girdle view. Figs 14–19. SEM. Valve view. Scale bars = 1 μ m. Figs 14, 16, 18. External view. Figs 15, 17, 19. Internal view. Figs 16, 17. Detail of the apical area. Figs 18, 19. Detail of the central area.

Ecology, distribution and associated diatom flora

So far, *Hippodonta lange-bertalotii* has only been found on volcanic Deception Island (South Shetland Islands) in three lakes (Crater Lake, Rectangular Lake and Irizar Lake), located at the southwestern side of the island. The lakes have a circumneutral to slightly alkaline pH (7.2–7.9). High SO_4^{2-} concentrations (80 to 250 mg. L⁻¹) account for high specific conductance levels (1780–7100 $\mu\text{s}\cdot\text{cm}^{-1}$). Nutrient concentrations, in turn, are low (PO_4^{3-} 0.07 to 0.18 mg.L⁻¹, $\text{NO}_3^- + \text{NH}_4^+ < 0.13$ mg.L⁻¹). The samples are dominated by *Achnanthes muelleri* G. W. F. Carlson, *Brachysira minor* (Krasske) Lange-Bertalot, *Gomphonema* spp., *Navicula gregaria* Donkin, *Nitzschia* spp., *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *P. lanceolatum* (Brébisson) Lange-Bertalot and *Pinnularia* cf. *globiceps* W. Gregory.

Remarks: *Hippodonta lange-bertalotii* clearly belongs to the genus *Hippodonta* based on the uniseriate striae, the presence of the terminal stauros, the raphe structure lacking the typical *Navicula*-type terminal fissures and the internal structure with the thickened raphe rib. Contrary to more typical *Hippodonta*-species such as *H. capitata* (Ehrenberg) Lange-Bertalot et al., the striae are less broad. Based on the combination of morphological features, only a few *Hippodonta* species present some similarities: *Hippodonta subrhombica* Metzeltin et al., *H. subtilissima* Lange-Bertalot et al. and *H. coxiae* Lange-Bertalot.

The most similar taxon is *Hippodonta subrhombica*, described in 2005 from Uruguay, but the latter can be distinguished based on its smaller width (4–4.5 vs 4.5–5.2 μm), the typical rhombic outline (contrary to a more rhombic-lanceolate outline in *H. lange-bertalotii*) and the smaller central area that is much more developed in *H. lange-bertalotii*. *Hippodonta subtilissima* is much smaller (valve width 2.5–3 vs. 4.5–5.2 μm) with areolae that are visible in LM and a valve outline more or less linear-lanceolate. *Hippodonta coxiae* has more elliptical-lanceolate valves, lacks a large central area and has less striae in 10 μm (11–12.5 vs. 14–17 in 10 μm). All other *Hippodonta* species known up to now have broader striae and different valve outlines and dimensions with usually broader valves. These differences justify the description of *H. lange-bertalotii* as a new species.

Redescription of *Hippodonta pseudacceptata*

Hippodonta pseudacceptata (H. Kobayasi) Lange-Bertalot in Lange-Bertalot et al. 1996, p. 263 emend. S. Blanco (Figs 20–74)

Lange-Bertalot, H., D. Metzeltin & A. Witkowski (1996): *Hippodonta* gen. nov. Umschreibung und Begründung einer neuen Gattung der Naviculaceae. – Iconogr. Diatomol. **4**: 247–275.

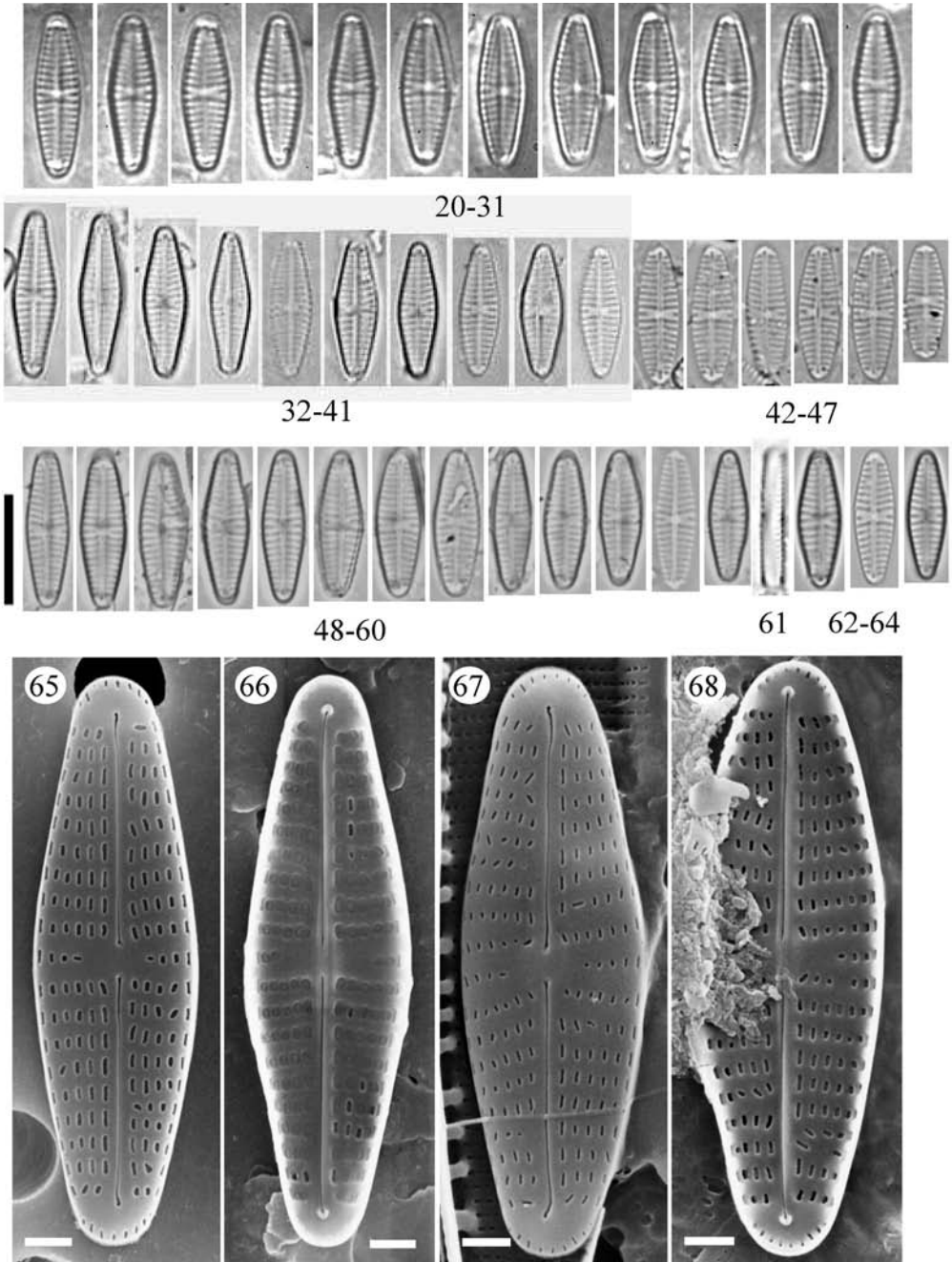
Basionym: *Navicula pseudacceptata* H. Kobayasi in Kobayasi, H. & S. Mayama (1986): *Navicula pseudacceptata* sp. nov. and validation of *Stauroneis japonica* H. Kob. – Diatom **2**: 95–101, p. 96, 97, figs 1–4, 7–12.

Holotype: H. K. T-79 in coll. H. Kobayasi. Type material: K-5385, coll. 18/11/1959.

Type locality: Ishima-gawa Stream, a tributary of Akahira-gawa, tributary of Ara-kawa River (Japan).

Synonyms: “*Hippodonta* (?nov.) spec. cf. *subtilissima*” in Lange-Bertalot 2001, pl. 76, figs 54–58; *Hippodonta pumila* Lange-Bertalot et al. in Metzeltin et al. 2009, p. 57, pl. 63, figs 21, 22, pl. 255, fig. 9, syn. nov.

The morphometric values provided in the protologue do not fit with the corresponding illustrations of this taxon (Kobayasi & Mayama 1986, figs 1–4), since the width of the type specimens (3.0–3.5 μm) fall out of the range of 4–5 μm specified in the original description. This fact and



Figs 20–68. *Hippodonta pseudacceptata*. Figs 20–64. LM. Scale bar = 10 μ m. Figs 65–68. SEM. Scale bars = 1 μ m. Figs 20–60, 62–64. Valve view. Fig. 61. Girdle view. Figs 20–31, 65–68. Adaja River (Spain). Figs 32–41, 61. Mogent River, Besòs basin (Catalonia). Figs 42–47. Tejo River (Portugal). Figs 48–60. Boina Stream (Portugal). Figs 62–64. Beuvron River (France). Figs 65, 67. External valve view. Figs 66, 68. Internal valve view.

Table 2. Morphometric and ecological comparison of *Hippodonta* studied populations. Data gathered from the protologues or measured on original illustrations. n: sample size for measurements. L: valve length, μm . W: valve width, μm . S: striae in 10 μm . P: punctae in 10 μm .

Population	Reference	n	L	W	L/W	S	P	Habitat	Distribution
<i>H. avittata</i>	Bergrivier, South Africa Lange-Bertalot et al. (1996)	4	11.3–14.7	3.7–4.0	3.0–3.7	13.2–13.6	?	Rivers with average to high conductivities	Greenland (fossil), Ireland, Israel?, South Africa, Spain
<i>H. coxiae</i>	Type (Schlitz, Germany)	?	15.0–21.0	4.8–5.4	3.1–3.9	11.0–12.5	c. 30	Meso-eutrophic streams, average conductivity	Germany, Sweden
<i>H. lange bertalotii</i> sp. nov.	Type (Crater lake, Deception Island)	13	15.0–20.0	4.5–5.5	3.3–3.6	14–17	40–50	Maritime Antarctic lakes	Deception Island
<i>H. pseud-acceptata</i>	Type (Ishimagawa River, Japan), protologue	?	6.0–15.0	4.0–5.0	1.5–3.0	16 (18)	c. 50	Meso-eutrophic streams, average conductivity	Cosmopolite? Probably often misidentified (see discussion and Fig. 75)
	Illustrated holotype and isotypes	4	10.0–11.0	3.0–3.5	3.1–3.3	17.0–17.3	c. 50		
	Kyung Pook Prefecture, South Korea	?	12	3.5	3.4	16	?		
	Kwang River, South Korea	?	8.5–9.5	3.0–3.5	2.7–2.8	18–20	?		
	Kase River, Japan	?	10	3	3.3	?	?		
	Lake Walldorf, Germany	?	12.5–14.0	3.6–4.0	3.5	16–18	c. 45		
	Tuul River, Mongolia [as <i>H. pumila</i>]	3	15.3	3.6–4.0	3.8–4.2	18	c. 35		
	Adaja River, Spain	16	13.3–14.7	4.0–4.7	3.1–3.3	15.0–16.4	c. 40		
	Mogent River, Besòs basin, Catalonia	15	10.6–13.4	3.2–4.0	3.3	16–20	28–33		
	Beuvron River, France	4	12.0	3.0–4.0	3.0–4.0	15–17	30		
	Tejo River, Portugal	19	10.0–13.3	3.3–4.0	3.3	17–21	?		
	Boina Stream, Portugal	20	10.2–15.0	3.3–4.7	3.1–3.2	17–21	29–35		

<i>H. subrhombica</i>	Type (La Pedrera, Uruguay)	Metzeltin et al. (2005)	? 14.0–16.6	4.0–4.5	3.5–3.7	14.5–15.5	?	Subtropical creeks	Only known from type locality in Uruguay
<i>H. subtilissima</i>	Type (Jylland, Denmark)	Lange-Bertalot et al. (1996)	? 12.0–15.0	2.5–3.0	4.8–5.0	14–16	30	Slightly saline watercourses	Denmark, Hungary

the finding of several populations outside the type locality (Table 2) providing a more comprehensive overview of its morphological variability, allow the proposal of an emended description of this species:

Descriptio: Valvae elliptico-lineares vel lineares-rhombicae apicibus late rotundatis raro leviter protractis area apicali conspicua hyalina, 10–15 µm longae, 3–5 µm latae. Raphe recta filiformis extremitas raphis punctiformes. Area axialis angusta linearis. Area centralis transapicaliter dilatata rectangularis limitata duabus striis curvis centralis. Striae transapicales uniseriatae leviter radiantes in centro sed parallelae versus apices, 15–21 in 10 µm. Areolae non nisi aspectabiles in microscopio apicaliter raro transapicaliter elongatae electronico longioras ad axem et ad centrum. 72 valvae mensae.

LM observations

Valve outline linear-elliptic (Figs 42–47) to linear-rhombic (Figs 20–41, 48–64), broadly rounded ends, not or only slightly protracted, with a conspicuous hyaline apical area (Figs 20–64). Valve dimensions: length 10–15 µm, width 3–5 µm (n = 72). Raphe filiform, straight. Axial area narrow, linear. Central area is transapically dilated, rectangular, delimited by two shortened central striae (Figs 20–64). Transapical striae slightly radiate at the center, becoming parallel toward the ends, 15–21 in 10 µm (Lee et al. [1995] describe a population with consistently radiate striae at the apices). Areolae not discernible in LM.

SEM observations

Externally, both proximal and distal endings are punctiform. Distal endings not or only slightly undulated and deflected (Figs 65, 67, 69, 73, 74). Internally, raphe branches ending abruptly in the terminal stauros characteristic of the genus (Fig. 71). Striae uniseriate, composed of apically (but sometimes transversally, Fig. 73) elongated areolae, often becoming longer towards the apices (Fig. 69) and the transapical axis (Fig. 68), densely spaced (30–50 in 10 µm). Terminal stauros clearly developed, bordered by semi-circumpolar, slit-like elongated areolae (Figs 65, 67, 69, 73, 74).

Illustrated records

Kobayasi & Mayama 1986, pl. 1, figs 1–4, 7–12, Lee et al. 1992, pl. 6, fig. 90, pl. 12, fig. 166, Lee et al. 1994, pl. 1, fig. 19, Yamakawa 1994, pl. 13, fig. 6, Lange-Bertalot 2001, pl. 76, figs 54–58, Metzeltin et al. 2009, pl. 63, figs 21, 22, pl. 255, fig. 9, Blanco et al. 2010, pl. 50, figs 18–29, pl. 54: figs 1–4.

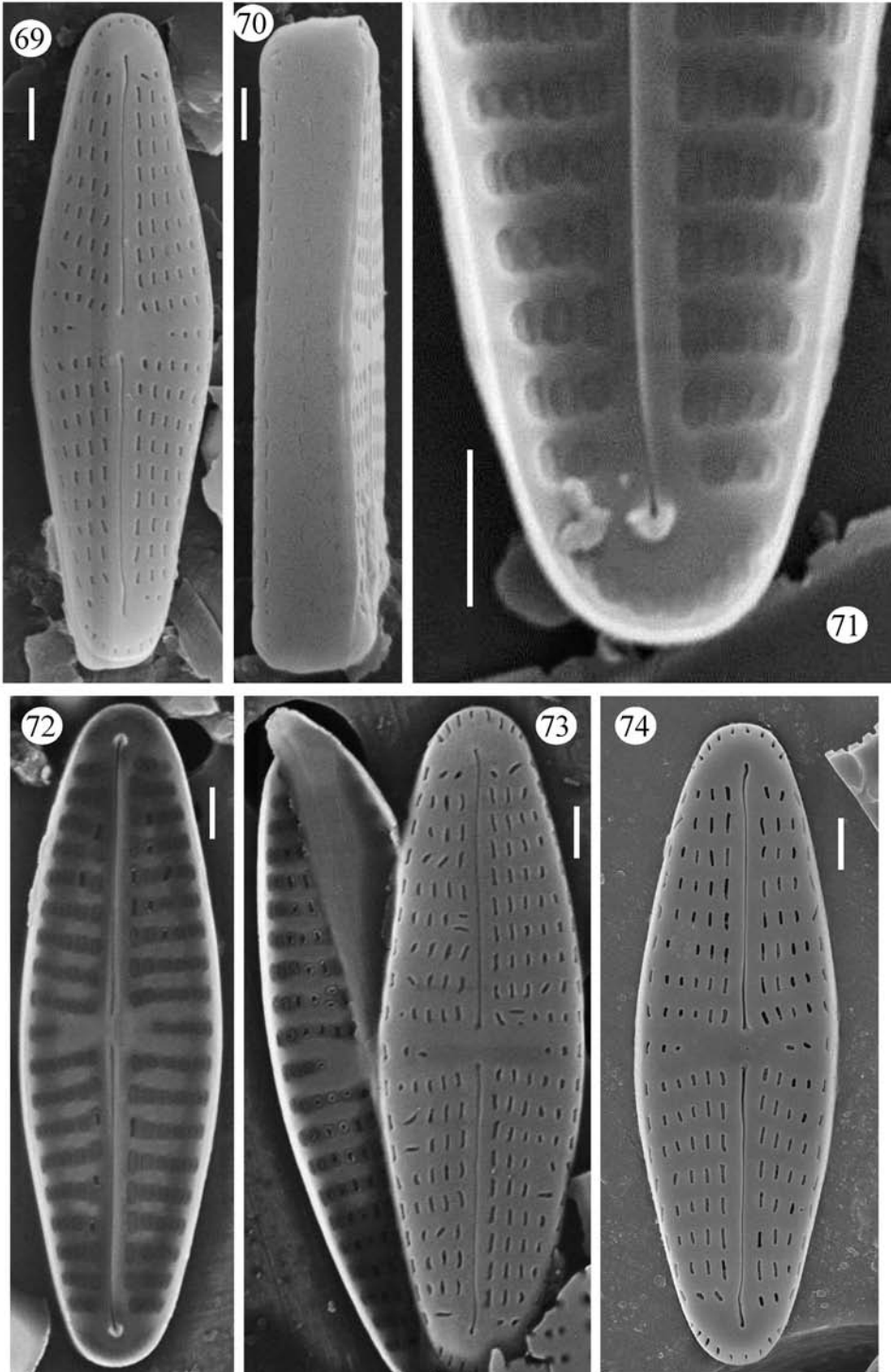




Fig. 75. World distribution map of *Hippodonta pseudacceptata* sensu emend

Distribution and ecology

Adding to citations in France (including the Mediterranean island Corsica: Metzeltin et al. 2009), Portugal and Spain presented on Table 1, *Hippodonta pseudacceptata* (including synonyms) has been recorded so far in Germany (Lake Walldorf: Metzeltin et al. 2009), Japan (Ishima-gawa Stream, Japan: Kobayasi & Mayama 1986, Kase River: Yamakawa 1994, Yura and Kamo Rivers: Ohtsuka & Tuji 1997, Hii River: Ohtsuka 2002), Mongolia (Tuul River: Metzeltin et al. 2009) and South Korea (Kyung Pook Prefecture: Lee et al. 1992, Kwang River: Lee et al. 1994, 1995) (Table 2, Fig. 75). In the Spanish part of the Duero River Basin it appeared in several stations of the Adaja River (Ávila, Donhierro, Valdestillas, Olmedo, Arévalo) and in Toro (Duero River), formerly misidentified as *H. subrhombica* (Blanco et al. 2008). Further records exist in the Tordera Basin (NE Iberian Peninsula). According to Ohtsuka (1998), this species prefers pebbles and sand as substrata to cobbles or plants. In Spain this taxon inhabits meso-eutrophic watercourses with average to moderately high conductivities, often with low relative frequencies within the diatom assemblages. In Portugal it appears always with low abundances, but occurring with a large geographic distribution, being present in the Ribeiras do Algarve, Tejo, Mondego and Douro basins. Despite the few accurate citations collected up to date, the wide geographical occurrence of this taxon is compatible with a sub-cosmopolite or cosmopolite distribution pattern that might be confirmed in the future.

- ◀ **Figs 69–74.** *Hippodonta pseudacceptata*. SEM. Scale bars = 1 μ m. Figs 69–71. Mogent River, Besòs basin (Catalonia). Figs 72, 73. Boina Stream (Portugal). Fig. 74. Beuvron River (France). Figs 69, 74. External valve view. Fig. 70. Girdle view. Figs 71, 72. Internal valve view. Fig. 71. Detail of the apical area. Fig. 73. External and internal valve views of the same frustule.

Remarks: Kobayasi and Mayama (1986) discussed the separation of this taxon from *Navicula acceptata* Hustedt, and evidenced the close morphological similitude of *Hippodonta pseudacceptata* to species around *Navicula perminuta* Grunow in Van Heurck like *N. mendiota* VanLandingham that presumably had led to frequent misidentifications. Other similar *Navicula* taxa share several structural features with these small-celled *Hippodonta*, such as *N. jeffreyae* Hallegraeff & Burford or *N. pargemina* Underwood & Yallop. Lange-Bertalot et al. (2003) suggested indeed the transfer of *N. jeffreyae* to *Hippodonta*, but its evidently deflected terminal raphe fissures (Hallegraeff & Burford 1996, figs 8 d, 8 e) discourage this combination.

On the other hand, the diagnosis of *Hippodonta pumila* (Metzeltin et al. 2009) fits well with the emended description of *H. pseudacceptata* (see above). Both metric and morphological features strongly overlap (Table 2), thus leading to propose *H. pumila* as a later taxonomic synonym of *H. pseudacceptata* that retains the nomenclatural priority. Contrastingly, *H. pseudacceptata* sensu emend. differs from *H. subrhombica* in having more densely spaced striae (15–21 vs. 14.5–15.5 in 10 µm) and from *H. subtilissima* in having a lower average valve length/width ratio (3.0–4.2 vs. 4.8–5.0). Other similar taxa compared in Table 2 are clearly discernible from *H. pseudacceptata* under LM regarding valve shape and size.

Accepting the conspecificity of all studied populations (Table 2), *H. pseudacceptata* exhibits a notable morphological and morphometric variability, with the populations analyzed from Western Europe appearing with consistently sparser areolae (30–40 in 10 µm) than the type (c. 50 in 10 µm). The individuals from Tuul River (Mongolia) illustrated in Metzeltin et al. (2009, pl. 63, figs 21, 22, pl. 255, fig. 7) are significantly larger and broader. However, the different number of specimens studied at each site prevents the calculation of comparable intrinsic ranges for these morphometric parameters and, hence, the eventual obtaining of taxonomic conclusions.

A more precise analysis of the taxonomic relationships between the studied species, including the eventual proposal of new taxa and/or synonymies, will be possible once more SEM-based studies on their types become available.

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