



Research Article

Observations on the marine benthic diatom *Halamphora yundangensis* W.W.Wu et al., a species originally described from China, in the Mediterranean Region

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Abstract – During light and scanning electron microscope observations of marine benthic diatoms on various substrates in the eastern Adriatic Sea and the western Black Sea, we discovered a peculiarly structured amphoroid diatom species. The species was characterised by semi-elliptic to semi-lanceolate valves with distinctly protracted capitate to occasionally rostrate apices, a dorsal valve side crossed by transapical slits, a wide dorsal marginal ridge, biseriate dorsal striae internally, and usually lacking ventral striae externally, except for one or two poroids at the apices. Following a search in the literature, this taxon could only be identified as *Halamphora yundangensis*, a recently described species from the southeastern coasts of China. Here we present the first verified observation of this species in the Mediterranean Region. After thorough analyses of the observed populations in scanning electron microscopy and a literature overview, we provide an emended description of the species, and additional information enabling/justifying its separation from similar taxa occurring in the Mediterranean Region. Notes on the ecology and distribution of the species based on the new observations are also given.

Keywords: Adriatic Sea, Bacillariophyta, Black Sea, diatom diversity, Europe, morphology

Introduction

Halamphora yundangensis W.W.Wu, C.P.Chen & Y.H.Gao in Wu et al. (2020: p. 210) was described as an epiphyte on green “leafy” seaweeds (i.e., *Ulva lactuca* Linnaeus) from the saltwater Yundang Lake located near Xiamen, southeastern China. This is a shallow, alkaline, artificial lagoon connected to the South China Sea, and due to the urbanization of the Xiamen area, subjected to eutrophication, chemical pollution, algal blooms and changes in salinity (Wang et al. 2020 and references therein). The species, *Halamphora yundangensis*, possesses a unique combination of features distinguishing it from other *Halamphora* taxa. When observed in scanning electron microscope (SEM), it shows a broad dorsal marginal ridge, a large, flat, unornamented area along the valve face/mantle junction, and dorsal striae appear externally as transapical

slits crossing the valve face, continuing onto the mantle after the wide marginal ridge (Wu et al. 2020). In contrast to all other *Halamphora* taxa studied in SEM, the valves of *H. yundangensis* observed by Wu et al. (2020) from the type population in China lacked ventral striae, apart from one to three poroids at the apices. Later, on hermit crabs from the coasts of Xiaodeng Island in southeastern China, valves similar in morphology to *H. yundangensis* were discovered by Huang et al. (2023a). These valves presented ventral striae, as a row of small, single areolae on the ventral side (Huang et al. 2023a, b). Based on the presence of ventral striae, Huang et al. (2023a, b) recognised the observed taxon as a new variety of *H. yundangensis* (“var. *foramina*”, *nomen nudum*), not validly published under Article 29 and Article 38.1 of the International Code for Botanical Nomenclature (Turland et al. 2025).

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During a survey of the marine benthic *Halamphora* flora in diatom samples from the Adriatic Sea, the northernmost arm of the Mediterranean Sea, and from the Black Sea, the latter a marginal sea to the Mediterranean Sea, we discovered valves with morphology similar to that of *H. yundangensis*. The valves usually lacked ventral striae, with the exclusion of one or two poroids at the apices, but sometimes the ventral side was ornamented by a short row of irregularly spaced, single, small, rounded areolae externally and by “ghost” striae internally. Following light microscopy (LM) and scanning electron microscopy (SEM) observations and comparisons with the type of *H. yundangensis* in Wu et al. (2020), we could only identify the observed valves as belonging to the latter species. Here we present the first verified record of *H. yundangensis* in Europe, more specifically from the Mediterranean Region. The species was found living both epizoically on the carapace of an injured loggerhead sea turtle admitted for recovery at the Sea Turtle Rescue Center of Aquarium Pula, Croatia, and as an epiphyte on various macroalgae from off the coast of Verudela, Croatia, the Northern Adriatic Sea. A few valves were also discovered on plexiglass substrates placed near the western coast of the Black Sea in Bulgaria.

After its description in 2020, *H. yundangensis* has also been reported outside China from the Revillagigedo Archipelago in the Eastern Pacific Ocean (Siqueiros Beltrones et al. 2021) and from coral reefs in Indonesia (Risjani et al. 2021). A single record exists from the western Mediterranean Sea near Spain (Pérez Burillo 2022). However, in all these studies the species was identified based solely on LM observations, which are often not sufficient for the correct separation of small *Halamphora* taxa (Levkov 2009, Stepanek and Kociolek 2018, Pottiez et al. 2025). From the Revillagigedo Archipelago, Siqueiros Beltrones et al. (2021) illustrated two very similar valves in LM: the valve shown on their figure 26j was reported as *H. yundangensis*, but the valve illustrated on their figure 26k, likely belonging to the same taxon, was identified as *H. coffeiformis* (C. Agardh) Levkov (as *coffaeiformis*). The latter species has been largely misinterpreted, and past reports of it often included other and different taxa (Archibald and Schoeman 1984, Levkov 2009). In addition, from the estuary of the Indian River in Florida, USA, Navarro (1982: Pl. XX, Figs. 5–7) illustrated a taxon very similar to *H. yundangensis* in SEM. However, they misidentified and reported this taxon as *Amphora costata* W. Smith (currently *Halamphora costata* (W. Smith) Levkov), a little known, but larger and coarsely striated species from the marine coasts of Northern Europe (Smith 1853, Levkov 2009). These observations suggest that *H. yundangensis* might be another species hidden within the records of *H. coffeiformis* or other *Halamphora* taxa in the Mediterranean Region. Finally, during the literature overview we discovered that the external dorsal structure of *H. yundangensis* in SEM is very similar to that of *H. cejudoe* Álvarez-Blanco and S. Blanco (2014: p. 54), a taxon described from the Mediterranean Sea, but overlooked by Wu et al. (2020) when comparing *H. yundangensis* with

other taxa. Hence, with the lack of recently developed marine benthic diatom floras for the studied areas, we felt it necessary to share our findings and observations. Along with the clear separation from *H. cejudoe* and a few other morphologically similar taxa present in the Mediterranean Region, we provide additional information concerning the unique morphology of *H. yundangensis* and its ecology.

Material and methods

Samples for the study originate from the Croatian (eastern) coast of the Adriatic Sea and the Bulgarian (western) coast of the Black Sea. The following samples, slides and stubs, kept in the BR Collection, Meise Botanic Garden, Belgium, are included in the study:

1. Sample TB225: diatom sample from the carapace of a loggerhead sea turtle superficially cleaned of barnacles and macroalgae. The injured turtle had been rescued northeast of Korčula Island (42°58' N, 16°53' E), Croatia, on 17. 07. 2021, and was then admitted to the Sea Turtle Rescue Center of Aquarium Pula. Sample collected after the turtle had spent one month in a recovery tank at the Center, coll. L. Kanjer, 16. 08. 2021. Slide BR-4915, stub BR-4916.

2. Sample ENV10: diatoms on young thalli of various macroalgae, Verudela, Istria Peninsula, Adriatic Sea (44°50'00" N, 13°49'27" E), coll. L. Kanjer, 27. 02. 2022. Slide s.n., stub s.n.

3. Sample ENV14: diatoms from brown spots on young red calcifying macroalgae (Corallinales), Verudela, Istria Peninsula, Adriatic Sea (44°50'00" N, 13°49'27" E), coll. L. Kanjer, 27. 02. 2022. Slide s.n., stub BR-4873.

4. Sample C3.3: biofilm on artificial substrate (plexiglass) submerged at 3 m below sea surface for a period of 25 days, Sozopol Bay, Bulgaria, Black Sea (42°25'05" N, 27°41'20" E), coll. R. Zidarova & P. Ivanov, 30. 08. 2020. Slide BR-4880, stub BR-4881.

Sampling methods are given in detail by Pottiez et al. (2025) and Zidarova et al. (2022, 2023, 2025). Environmental parameters (water temperature, salinity, pH) were measured during sampling in the Black Sea using a HI98194 Multi-parameter field meter (Hanna Instruments), and are summarised in Zidarova et al. (2023, see Tab. 1 therein). Parameters of the water in the tank housing the turtle in Pula were also taken upon sampling, using Multifunction pH Meter PCE-PHD 1 (PCE Instruments).

For LM analyses, samples were treated either by the method of van der Werff (1955), or by the method described in Hasle and Fryxell (1970), after pretreatment with a few drops of concentrated HCl to dissolve carbonates. Slides were prepared with Naphrax® and studied at 1000x magnification (N.A. 1.30) using an Olympus BX51 light microscope, equipped with Differential Interference Contrast (DIC) optics and Olympus digital imaging system. For SEM observations, a small amount of the pretreated samples was filtered through polycarbonate membrane filters (Whatman™) with a pore size of 2 µm or 5 µm. After airdrying, pieces of

the filters were affixed on aluminium stubs, coated with a platinum/palladium layer of 20 nm, and studied using a JEOL-JSM-7100F field emission SEM at Meise Botanic Garden (Belgium). Identification of the species is based on the recent work by Wu et al. (2020), where it was described. The European populations are compared to both the type of the species in Wu et al. (2020) and the observations of Huang et al. (2023a, b) on similar populations from China. For the description of the morphological features of the species, we followed Levkov (2009) and Stepanek and Kociolek (2018).

Results

Table 1 shows the morphological comparisons between the European populations of *H. yundangensis*, its type population from China (Wu et al. 2020: p. 210, Figs. 1–25), and the population identified as a variety of the latter from China (Huang et al. 2023a, b).

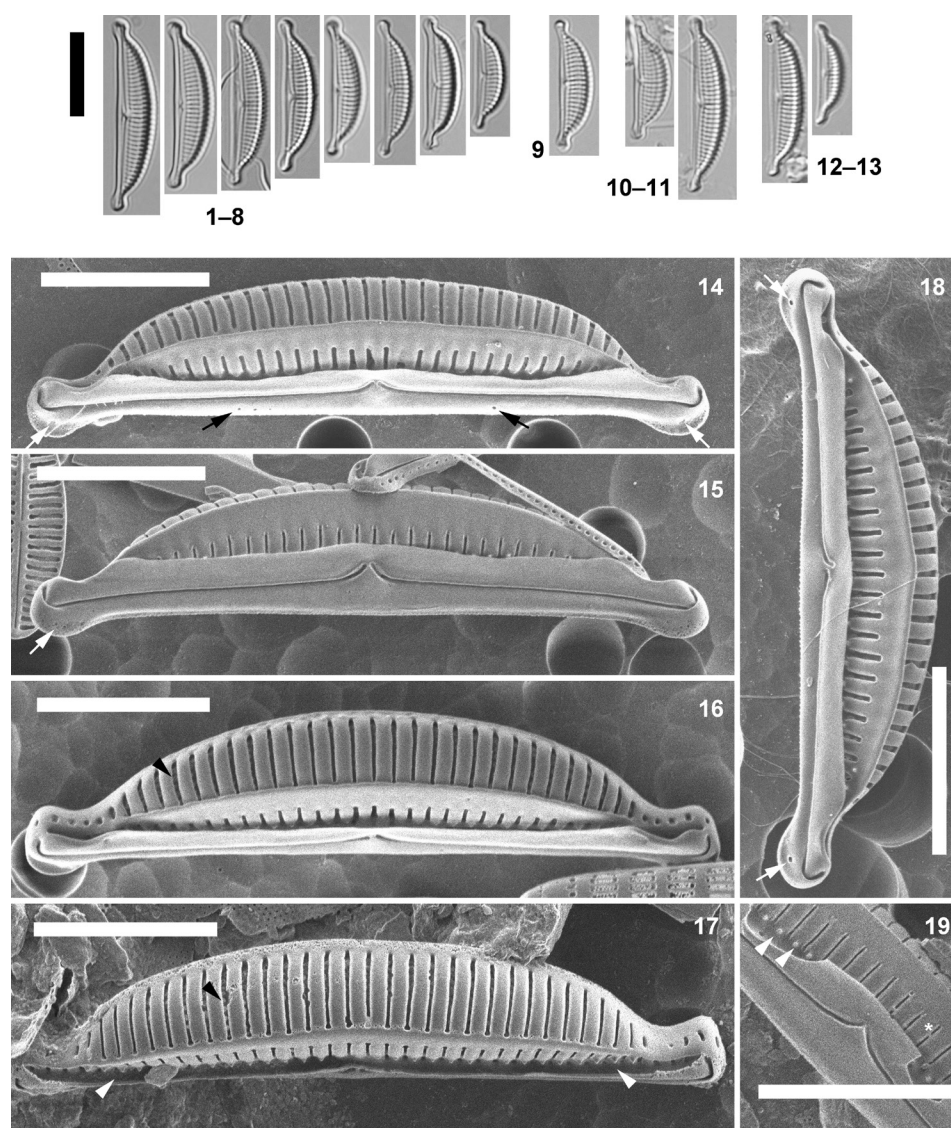
Valves from the European populations are illustrated here in LM on Pl. 1 (Figs. 1–13) and in SEM on Pl. 1 (Fig. 14–19) and Pl. 2 (Figs. 20–23). All valves observed in the samples from both the Adriatic Sea and the Black Sea fit well the type of *H. yundangensis* in Wu et al. (2020) in valve outline, being semi-elliptic to semi-lanceolate with capitate to rostrate protracted apices (Pl. 1: Figs. 1–13, Tab. 1 here;

Wu et al. 2020: Figs. 1–12). The European populations are, however, mostly on the smaller side of the range of dimensions given for the type population: length 11.0–28.0 µm and width 3.0–4.5 µm vs length 13.0–39.0 µm and width 3.5–5.5 µm in the type population (Tab. 1). The dorsal stria densities of the type population and the European populations are also comparable: 17–21 dorsal striae in 10 µm were reported for the type, and 18–22 dorsal striae in 10 µm were present in both the Adriatic Sea and the Black Sea populations (Tab. 1). No morphological differences could be found among the different populations from Europe and Asia in the external structure of the dorsal valve side and striae, dorsal marginal ridge, raphe ledge, external and internal central raphe endings and terminal fissures (Pl. 1: Figs. 14–19 here; Wu et al. 2020: Figs. 13, 17–20). Both the type of *H. yundangensis* from China and its European populations also present small papulae-like structures under the raphe ledge (Pl. 1: Figs. 17, 19, white arrows). The latter, although not mentioned in the original description of the species, are visible in the original illustrations of it (Wu et al. 2020: Figs. 15, 18).

Regarding the ventral striae, the European populations usually lack them (Pl.1: Figs. 15, 18), but occasionally possess a short row of small rounded areolae on the ventral side externally (Pl. 1: Fig. 14, black arrows) and “ghost” striae internally (Pl. 2: Fig. 21). Based on this feature, they take an

Tab. 1. Morphological comparisons between the different populations of *Halamphora yundangensis*, and comparisons with *Halamphora coffeiformis* and other similar taxa present in the Mediterranean Region. Entries marked with an asterisk (*) represent author interpretations based on published figures.

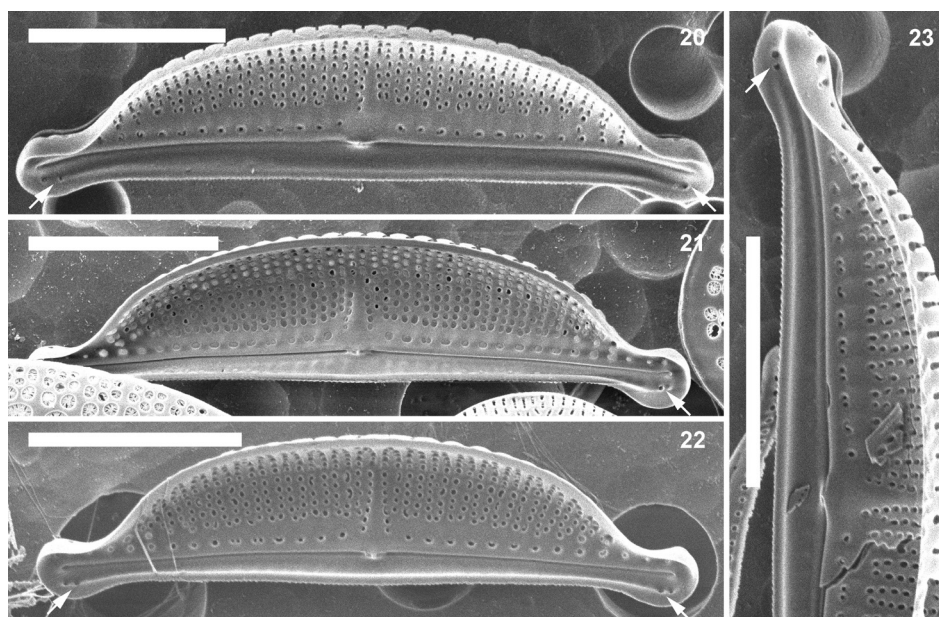
Feature/taxon	<i>H. yundangensis</i>	<i>H. yundangensis</i> (type)	<i>H. yundangensis</i> var. <i>foramina</i> (invalid)	<i>H. cejudoeae</i> (type)	<i>H. coffeiformis</i> (type and other populations)	<i>H. tenuicostata</i> (type)
reference	this study	Wu et al. 2020	Huang et al. 2023b	Álvarez-Blanco and Blanco 2014	Archibald and Schoeman 1984, Levkov 2009, Stepanek and Kociolek 2018 (all as <i>coffeaeformis</i>)	Stepanek and Kociolek 2018 (as <i>tenuicostata</i>)
valve outline	semi-elliptic to semi-lanceolate	semi-elliptic to semi-lanceolate	semi-lanceolate*	semi-lanceolate	semi-lanceolate	semi-elliptic
valve apices	protracted capitate to rostrate	protracted capitate to rostrate	protracted capitate*	subcapitate	protracted capitate, rostrate to subrostrate	protracted capitate to subcapitate
valve length, µm	11.0–28.0	13.0–39.5	12.0–16.2	16.0–33.0	14.0–55.0	23.0–30.0
valve width, µm	3.0–4.5	3.5–5.5	3.7–4.3	3.8–5.5	3.5–7.5	4.5–5.0
dorsal striae in 10 µm	18–22	17–21	21–24	16–19	(16)17–24(26)	17–19
slits dorsally externally	present	present	present*	present*	absent	absent
dorsal striae internally	biseriate	biseriate	biseriate*	biseriate	biseriate	biseriate
ventral striae in 10 µm	usually absent, “ghost” striae (if present) ca 30	absent	27–28	20–22	21–36	30–31
dorsal marginal ridge	wide	wide	wide*	wide*	thin	thin
poroids at the apices	present, 1–2	present, 1–3	present*	absent	absent	absent
semi-stauros	present	n/a	n/a	absent	absent	absent
axial silica band	present	present*	present*	absent	absent	present



Pl. 1. LM views (Figs. 1–13) and SEM external views (Figs. 14–19) of *Halamphora yundangensis* from the Adriatic Sea and the Black Sea: 1–8 – LM views of valves observed on the carapace of a loggerhead sea turtle (Adriatic Sea, sample TB225, slide BR-4915). 9–11 – LM views of valves from samples from macroalgae off the coast of Verudela, Adriatic Sea (Fig. 9 from sample ENV10, s.n., Figs. 10–11 from sample ENV14, s.n.). 12–13 – LM views of two valves from artificial substrates at Sozopol Bay (Black Sea, sample C3.3, slide BR-4880). 14–15 – SEM external views valves observed on the carapace of a loggerhead sea turtle (Adriatic Sea, sample TB225, stub BR-4916). White arrows on Figs. 14–15 indicate the poroids at the apices, black arrows on Fig. 14 indicate the several small areolae on the ventral side. 16–17 – SEM external views of the mantle of valves from the Adriatic Sea (Fig. 16, stub BR-4916) and the Black Sea (Fig. 17, stub BR-4881). Black arrowheads on Figs. 16–17 show the external openings of the areolae inside the slits, white arrowheads on Fig. 17 indicate the papulae-like projections under the raphe ledge. 18 – SEM external view of a valve from the thalli of red calcifying algae (Adriatic Sea, sample ENV14, stub BR-4873). 19 – SEM detail from the central part of a valve from the Black Sea externally showing the dorsally bent central raphe endings (sample C3.3, stub BR-4881). White arrowheads on Fig. 19 indicate the papulae-like projections under the raphe ledge, asterisk points to the occasional interruption of the slits. Scale bars = 10 µm (Figs. 1–13) and 5 µm (Figs. 14–19). LM – Light microscopy, SEM – Scanning electron microscopy.

intermediate position between the type population lacking any ventral striae (Wu et al. 2020), and the second population from China that was recognised by Huang et al. (2023a) as a variety of *H. yundangensis* due to the presence of ventral striae. Further, the ventral striae in the valves reported as *H. yundangensis* var. *foramina* by Huang et al. (2023a) from China, are represented by a single row of small areolae on the ventral side, ranging around 27–28 in 10 µm (Huang et al. 2023b). This number is comparable to the number of the “ghost” striae (ca 30 in 10 µm) present on the ventral side of

the valves internally in the European populations (Pl. 2: Fig. 21, Tab.1). Therefore, in our opinion, the valves recognised as *H. yundangensis* var. *foramina* by Huang et al. (2023a, b) should be considered to be *H. yundangensis*. Moreover, the valve dimensions given by Huang et al. (2023b) for their variety (length 12.0–16.2 µm, width 3.7–4.3 µm) are also in the range of those of the European populations (length 11.0–28.0 µm, width 3.0–4.5 µm), and of the type population of *H. yundangensis* (length 13.0–39.0 µm, width 3.5–4.5 µm) (Tab. 1). Dorsal striae in all populations are also similarly



Pl. 2. SEM internal views of *Halamphora yundangensis* (Figs. 20–23) from populations on a loggerhead sea turtle's carapace (Figs. 20, 23, Adriatic Sea, sample TB225, stub BR-4916) and on macroalgae (Figs. 21, 22, Adriatic Sea, samples ENV10, s.n., and ENV14, stub BR-4873, respectively). White arrows indicate the poroids at the apices. Scale bars = 5 µm. SEM – Scanning electron microscopy.

spaced (17–21 in 10 µm in the type in Wu et al. 2020; 18–22 in 10 µm in the European populations reported here), however, they are slightly denser in the small valves presenting ventral striae, 21–24 in 10 µm (Huang et al. 2023b) (Tab. 1).

Minor differences were observed among the populations in the inner structure of the valves. All populations have biseriate striae internally, but in the type population from China the biseriate dorsal striae internally are composed of smaller areolae (Wu et al. 2020: Figs. 21–25), whereas the European populations show larger areolae with narrower virgae internally (Pl. 2: Figs. 20–23). All populations also have an axial silica band internally, but the areolae separated by the axial silica band near the raphe internally are usually larger in the European populations (Pl. 2: Figs. 20–23 here; Wu et al. 2020: Figs. 21, 25). In the European populations, sometimes, two small adjacent areolae are present in this row (Pl. 2: Fig. 23), whereas all valves illustrated from the type population from China have a single areola along the entire length of the row (Wu et al. 2020: Figs. 21–25). Wu et al. (2020) also did not mention a thickening in the central part of the valves internally (see the central part of the valves from the European populations on Pl. 2: Figs. 20–23). However, in the Chinese population areolae of the first striae near the valve center are similarly more spaced (Wu et al. 2020: Figs. 21, 24), as in the European populations (Pl. 2: Figs. 21–23), suggesting that a small thickening is present. Finally, in the European populations the first rows of areolae at the valve center internally are sometimes longer (Pl. 2: Figs. 21, 22) than those of the type population (Wu et al. 2020: Figs. 21, 24). Nevertheless, at present, we do not find the minor differences observed internally sufficient for the morphological separation of the European populations as another taxon.

Following the observations on the populations of *H. yundangensis* from the Adriatic Sea and the Black Sea and their comparisons with the type of the species in Wu et al. (2020) and the second population from China (Huang et al. 2023a, b), below we provide an emended description of the species, including the following features: the slightly larger range of valve dimensions and dorsal stria numbers; the occasional presence of ventral striae externally and “ghost” striae on the ventral side internally; the papulae like-structures under the raphe ledge; the semi-stauros-like thickening in the middle of the dorsal side of the valves internally. In addition, we further discuss the dorsal slit-like stria structure of the species.

***Halamphora yundangensis* W.W.Wu, C.P.Chen & Y.H.Gao emend. Pottiez, Zidarova, P. Ivanov, Kanjer & Bosak**

References: Wu et al. (2020: p. 210, Figs. 1–25), Huang et al. (2023a, b)

Pl. 1 (Figs. 1–19) and Pl. 2 (Figs. 20–23)

Light microscopy description (Pl. 1: Figs. 1–13):

Valves semi-elliptic to semi-lanceolate. Dorsal margin with coarsely jagged outline (Pl. 1: Figs. 1–3, 11, 12), moderately convex, in the middle slightly flattened, forming small “shoulders” before the apices. Apices distinctly protracted capitate, in smaller valves protracted rostrate (Pl. 1: Fig. 13). Ventral margin straight, sometimes slightly inflated in the middle (Pl. 1: Figs. 1, 12). Valve dimensions: length 11.0–39.5 µm, 3.0–5.5 µm, up to 5.5 µm. Raphe very close to the ventral margin, straight to weakly arched. Central raphe endings slightly enlarged, bent to the dorsal side (Pl. 1: Figs. 4, 13). Raphe ledge as a thin line running parallel to

the raphe (Pl. 1: Figs. 2, 7). Dorsal striae not punctate, parallel in the middle, becoming slightly radiate towards the apices, usually ca 20 in 10 μm , but ranging 17–24. Dorsal marginal ridge as a thin line near the dorsal margin (Pl. 1: Figs. 1, 9). Ventral striae not visible.

Scanning electron microscopy description (Pl. 1: Figs. 14–19 and Pl. 2: Figs. 20–23):

Valves heavily silicified. Externally, dorsal valve face flat, crossed by thin transapical slits, occasionally interrupted (Pl. 1: Fig. 19, asterisk). On the valve face, slits parallel in the middle, radiate at the apices (Pl. 1: Figs. 14, 15). A prominent, wide dorsal marginal ridge present at the valve face/mantle junction (Pl. 1: Figs. 15, 18), interrupting the slits that continue onto the mantle (Pl. 1: Figs. 16, 17). Raphe ledge moderately wide, following the valve outline: slightly expanded in the valve middle, at the constriction at apices pinched, at the apices once again widened, and not narrowed at the ends (Pl. 1: Figs. 15, 18). Under the edge of the raphe ledge, on the virgae between the slits, small papulae-like structures present (Pl. 1: Figs. 17, 19, white arrowheads). Raphe almost straight. External central raphe endings bent towards the dorsal side, closely positioned (Pl. 1: Figs. 15, 19). External distal fissures strongly hooked to the dorsal side, slightly enlarged (Pl. 1: Fig. 18), finishing under the end of the raphe ledge (Pl. 1: Figs. 16, 17). Internally (Pl. 2: Figs. 20–23), valves with thickened central part into a weakly developed semi-stauros dorsally, separating the dorsal striae in the valve middle. Internal central raphe endings finishing onto small, protruded, fused central helictoglossae (Pl. 2: Figs. 20–23). Distal raphe endings internally terminating onto small helictoglossae. Dorsal striae clearly biseriate, composed of two rows of rounded areolae internally (Pl. 2: Figs. 20–23). Externally, areolae discretely open into the slits' foramina (Pl. 1: Figs. 16, 17, black arrowheads). Ventral striae usually absent externally (Pl. 1: Figs. 15, 18, 19), occasionally, a row of a few, irregularly spaced, rounded areolae present on the ventral side (Pl. 1: Fig. 14, black arrows), areolae 27–28 in 10 μm . Internally, ventral striae usually absent, but "ghost" striae possibly present on the ventral side, ca 30 in 10 μm (Pl. 2: Fig. 21). Axial silica band running along the length of the valve internally, near the raphe separating a row of single (Pl. 2: Figs. 20, 21), or of a series of two adjacent, rounded to elliptic areolae (Pl. 2: Fig. 23). Row of areolae near the raphe interrupted in the valve center (Pl. 2: Figs. 20–23). One to three poroids with rounded external and internal openings present at the apices (Pl. 1: Figs. 14, 18 and Pl. 2: 20–23, white arrows). Occasionally, poroids at the apices with very small openings externally, only faintly visible (Pl. 1: Fig. 15, white arrow).

Ecology and associated diatom flora:

The largest population of *H. yundangensis* in the studied area was found on the carapace of an injured loggerhead sea turtle admitted for recovery at the Sea Turtle Rescue Center of Aquarium Pula in summer (sample TB225). The turtle had been residing for a month inside an individual recovery

tank when the sample containing *H. yundangensis* was taken. The sea water in the tank, as measured upon sampling, was weakly alkaline (pH of 7.9) with a temperature of 21.5 °C and salinity of 34.3. The sample was dominated by *Halamphora kolbei* (Aleem) Álvarez-Blanco & S. Blanco and *Tabularia* spp., and contained several other *Halamphora* taxa, such as *H. bosakiana* Pottiez, M. de Haan & Zidarova, *H. capitata* (R. Hagelstein) Álvarez-Blanco & S. Blanco, and *H. cf. isumiensis* J. Stepanek, Mayama & Kociolek. Small populations of *H. yundangensis* were also present during winter in the Northern Adriatic Sea, where it was living epiphytically on various macroalgae, including calcifying red seaweeds. In the Black Sea, the species was observed only occasionally in the biofilm formed on plexiglass substrates during summer months near the western coast of the sea. There it was accompanied by various small-celled *Halamphora* and *Nitzschia* Hassall taxa. The measured environmental parameters at the sampling site in the Black Sea during the sampling period showed weakly alkaline waters (mean pH 8.3) with a temperature of ca 26 °C and salinity of 17–18 (Zidarova et al. 2023, see Tab. 1 therein).

Discussion

With its dorsal valve side structure and the usual absence of ventral striae, *Halamphora yundangensis* is difficult to confuse in SEM. The absence of ventral striae is uncommon in amphoroid diatoms, but it has been observed in some *Amphora* Ehrenberg ex Kützinger taxa, such as *Amphora aliformis* J. Stepanek, Mayam & Kociolek (Stepanek et al. 2015). According to Stepanek et al. (2015), in *A. aliformis* ventral virgae are initially formed during early valve development but are later filled. This may also be the case in *Halamphora yundangensis*, considering the "ghost" striae observed internally (Pl. 2: Fig. 21), as well as the occasional row of poroids ornamenting the ventral surface in some valves externally (Pl. 1: Fig. 14 and Huang et al. 2023a, b).

Along with the usual absence of ventral striae, the presence of one or a few poroids at the apices is another unusual feature of *H. yundangensis* (Pl. 1: Figs. 14, 18 and Pl. 2: 20–23, white arrows here; Wu et al., 2020: Figs. 20, 22–23 therein). To our knowledge, in the genus *Halamphora* such apertures on the ventral side of the valves had not been reported in any other taxon. Apertures at the apices, known as portulae, had been observed particularly in *Amphora micrometra* Giffen, a species doubtfully positioned within the genus *Amphora* (Ács et al. 2011, Zidarova et al. 2023). More recently, valves presenting portulae at the apices were identified by López-Fuerte et al. (2024) as *Halamphora adumbratoides* J. Stepanek & Kociolek. The latter has a morphology very similar to that of *A. micrometra*, but was originally described as a species without any portulae (Stepanek and Kociolek 2018). However, the portulae in the populations identified as either *A. micrometra* or *H. adumbratoides* are located on the dorsal side of the valves, contrary to the poroids in *H. yundangensis*, located on the ventral side of the valves. Among amphoroid diatoms, two

Amphora species, *A. aliformis* (in Stepanek et al. 2015) and *A. commutata* Grunow (in Sato et al. 2013), present pores at the apices on the ventral side. In both taxa these apertures are occluded internally by sieve plates (Stepanek et al. 2015). We did not observe any occlusions in *H. yundangensis* (Pl. 2: Figs. 20–23). The former two *Amphora* taxa also show unique structures among other amphoroid diatoms, and we doubt that there is any relation between these taxa and *H. yundangensis*, even if they present pores at the apices ventrally.

Wu et al. (2020) provided a comprehensive comparison of *H. yundangensis* with a number of amphoroid taxa from the genera *Amphora* and *Halamphora*. They found the dorsal structure of its valves similar to that of several *Amphora* taxa bearing slits on the valve face and mantle, including *A. ovalis* (Kützing) Kützing, *A. eximia* J.R.Carter, *A. pseudoeximia* Levkov, and *A. mongolica* Østrup. However, as noted by Wu et al. (2020: p. 215), all these taxa also have a narrower dorsal marginal ridge and uniseriate, not biseriate, striae internally. Therefore, their structure is not exactly homologous to that of *H. yundangensis*. Based on our observations on the European populations of *H. yundangensis* in SEM and the illustrations in Wu et al. (2020), the striae externally in *H. yundangensis* are not simple slits, but they have a rather complex structure. The slits seem to be formed in between bold, thickened virgae on the valve face and mantle, which, with their edges, shade the openings of areolae externally (Pl. 1: Figs. 16, 17, black arrowheads). Virgae merge at the dorsal margin into the broad marginal ridge, and then continue onto the mantle (Pl. 1: Figs. 16–18). This way, the valves of *H. yundangensis* externally look like double-layered thick “shells” with slits. Regarding the dorsal marginal ridge and external dorsal stria structure, *H. yundangensis* is very similar to *H. cejudoe*, a taxon discovered in the western Mediterranean Sea near El Mojon, Murcia, Spain (Álvarez-Blanco and Blanco 2014). As in *H. yundangensis*, its dorsal valve side possesses a wide, distinct dorsal marginal ridge, slits on the valve face and on the valve mantle externally, and biseriate striae internally (Álvarez-Blanco and Blanco 2014: Pl. 79, Figs. 1–5). Areolae of its biseriate striae are sometimes also visible externally, located just under the edge of the slits (Álvarez-Blanco and Blanco 2014: Pl. 79, Figs. 3, 4), as in *H. yundangensis* (e.g. Pl. 1: Figs. 16, 17 here; Wu et al. 2020: Fig. 18).

Halamphora cejudoe and *H. yundangensis* have similar valve outlines, and they also have comparable dimensions: length 16.0–33.0 µm and width 3.8–5.5 in *H. cejudoe*, overlapping with the range in *H. yundangensis* from all known populations (length 11.0–39.0 µm, width 3.0–5.5) (Tab. 1). They both also have comparable dorsal stria numbers, however, striae are denser in *H. yundangensis* (17–24 in 10 µm in all populations of *H. yundangensis*, vs 16–19 in *H. cejudoe*, Tab. 1). In LM, these two taxa can be separated by: 1) the valve apices, that are distinctly protracted capitate or rostrate in *H. yundangensis*, but only weakly, smoothly protracted subcapitate in *H. cejudoe*, and 2) the always present ventral striae, only 20–22 in 10 µm in *H. cejudoe*, vs 27–30 in 10 µm,

if present, in *H. yundangensis* (Tab. 1). In SEM, the two taxa are easily differentiated by: 1) the usually absent ventral striae and the presence of one or a few poroids at the apices in *H. yundangensis*, as well as by 2) the axial silica band internally, a feature present in *H. yundangensis*, but absent in *H. cejudoe* (Tab. 1). Further, unlike *H. yundangensis*, *H. cejudoe* lacks any semi-stauros or unilateral thickening in the central area internally, but possesses prominent virgae between the two rows of areolae and distinct, fused central helictoglossae (Álvarez-Blanco and Blanco 2014: Pl. 79, Figs. 1, 5).

Halamphora coffeiformis, a species with biseriate dorsal striae composed of small rounded poroids, as defined in Archibald and Schoeman (1984) and later in Levkov (2009) and Stepanek and Kociolek (2018), is only slightly similar to *H. yundangensis*. The similarities between them include the valve outline, and their range of dimensions and dorsal stria density (Tab. 1). In LM, *Halamphora coffeiformis* can be differentiated by its smoothly arched dorsal margin lacking “shoulders” before the apices, as well as by the arched raphe (Archibald and Schoeman 1984: Figs. 1–34, 45, 46, 49, 50, 61–66, Levkov 2009: Pl. 94, Figs. 20–27, Pl. 99, Figs. 15–23, Stepanek and Kociolek 2018: Pl. 45, Figs. 1–8). In SEM, due to the complex structure of *H. yundangensis*, the two taxa cannot be confused.

In LM, in valve outline, dimensions and dorsal stria numbers, *H. yundangensis* is also comparable to *H. tenuicostata* J. Stepanek & Kociolek (2018: p. 42, as *tenuicostata*) (Tab. 1), a species described from Florida, USA, and recently also recorded in the Adriatic Sea (Zidarova et al. 2025). The main difference in LM between the two taxa is the more smoothly arched dorsal valve margin in *H. tenuicostata* and its visible ventral striae in LM (Stepanek and Kociolek 2018: Pl. 45, Figs. 9–12). Finally, due to the robust dorsal structure, the dorsal margin of *H. yundangensis* often appears distinctly and coarsely jagged in LM (Pl. 1: Figs. 1–3). A coarsely jagged dorsal margin in LM is also present in the similarly structured *H. cejudoe* (Álvarez-Blanco and Blanco 2014: Pl. 34, Figs. 3, 6), but not in *H. coffeiformis* and *H. tenuicostata* (e.g. Stepanek and Kociolek 2018: Figs. 1–8 and 9–12).

With the small number of records of *H. yundangensis* so far, little is known about its ecology. Originally, *H. yundangensis* was described from circumneutral to slightly alkaline waters with a temperature of ca 15 °C and moderately high salinity (30–31, Wu et al. 2020). Its presence in the more saline waters of the Adriatic Sea during winter, as well as in the less saline warm waters of the Black Sea during summer, suggests that it has broader temperature and salinity tolerances. In conclusion, *H. yundangensis* is a brackish/marine diatom species, present year-round in the temperate zones.

The currently known and verified distribution of *H. yundangensis* includes isolated locations in two quite distantly located regions, the southern Chinese coasts and the Mediterranean region. The records of this taxon from Indonesia (Risjani et al. 2021) and the Eastern Pacific Ocean (Siqueiros Beltrones et al. 2021) suggest it may have a wider

distribution, but these records still need to be verified. It is at present unclear if the species is indeed native to China and whether it has been transported among the different distant locations. Little is known about the dispersal capabilities of marine benthic diatoms and the vectors for their transportation between continents, such as ship transport or ship maintenance procedures, for instance. The recent discovery and establishment of the Pacific large-celled diatom species *Diademoides luxuriosa* (Greville) K.-D. Kemp & Paddock on the well-studied coastline at Edinburgh, Scotland, indicate that the long-distance dispersal and new introduction of marine benthic diatom species is possible (Mann 2025). *Halamphora* species, in particular, were reported as excellent biofoulers and dominant diatom species on ships' hulls (Park et al. 2025 and references therein). Experimentally, Park et al. (2025) also demonstrated that some *Halamphora* species present in unfiltered water from in-water hull cleaning can remain viable for at least 21 days, and once released into the water column, they may reattach to substrates in the new environment. However, there is no evidence that this is the case with *H. yundangensis*. In the Black Sea, the species was found near a small local port accommodating mostly small pleasure craft and local fishing boats that do not cover large distances. There are no specific ship maintenance services at the port, apart from basic pleasure craft maintenance (RZ, *pers. observ.*). Loggerhead sea turtles, on whose carapaces the largest population of *H. yundangensis* was observed in the Adriatic Sea, could serve as a possible vector for diatom species dispersal (Van de Vijver et al. 2020). In the Black Sea, however, loggerhead sea turtles are extremely rarely seen, though the number of records seems to increase (see Zinenko et al. 2021 for summary of the data). Nevertheless, the presence of *H. yundangensis* in samples collected during two different seasons from different localities and substrates in the Adriatic Sea and the Black Sea shows that the species is established there, and it could have been long present, but overlooked or misidentified.

Finally, most of the species are usually described based on a single population from a single locality of a given region. When species are only recently described, as in the case of *H. yundangensis*, until enough data for their distribution is collected, we can only make assumptions about their distributional range. The comparatively smaller number of studies on marine benthic diatoms, the still small knowledge of marine benthic *Halamphora* taxa and the lack of recently developed regional diatom floras hinders taxa identification. This poses a risk of incorrect species assignments and distributional records. Perhaps the best example is *H. coffeiformis*, but many other small *Halamphora* taxa can be easily misidentified in the lack of comprehensive regional guides, or due to technical insufficiencies of the studies. For the species of the genus *Halamphora*, the use of adequate techniques for their study, such as combining light and scanning electron microscopy (e.g. Levkov 2009, Stepanek and Kociolek 2018, Zidarova et al. 2025, Pottiez et al. 2025), and whenever possible adding molecular data

(Stepanek and Kociolek 2018), is crucial for their correct identification, and for understanding their distribution and dispersal.

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Author contribution statement

M.P. – LM and SEM analyses, writing, review, R.Z. – funding, sample collection, LM analyses, writing, review, P.I. – sample collection, editing, review, L.K. – sample collection, editing, review, S.B. – funding, sample collection, editing, review.

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