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Halamphora minima (Catenulaceae, Bacillariophyta), new brackish diatom species from the mudflat in Hampyeong Bay, Korea

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Abstract

The diversity of benthic diatoms living in the tidal flats is thought to be very high but has been somewhat marginalized from our main concern. We propose a new species, *Halamphora minima sp. nov.* isolated as monoclonal cultures from a tidal mudflat based on light and scanning electron microscopy and molecular analysis. This species is the smallest known species of the genus *Halamphora* to date. Other main characteristics that distinguish this species are the biseriate separated by strongly developed costa for the majority of the valve face, and density of dorsal striae. Phylogenetic analysis of the chloroplast ribulose bisphosphate carboxylase large chain gene showed that *H. minima* seems to be related to *H. foramina*, *H. sydowii* and *H. tumida*, but the phylogenetic location of *H. minima* was not clear due to the low bootstrap.

Keywords: *Halamphora*, New species, Benthic diatom, Tidal flat, *rbc*L gene

Introduction

The genus *Halamphora* (Cleve) Levkov (2009: 165) was originally reported as one of nine subgenera within the genus *Amphora* Ehrenberg ex Kützing (1844: 107) (Cleve 1895). However, Levkov (2009) elevated *Halamphora* as a genus by transferring 59 species of the genus *Amphora.* Stepanek & Kociolek (2014 and 2019) reported 16 new species of the genus *Halamphora*, and a taxonomic review has been ongoing since then. This genus is morphologically very similar to the genus *Amphora* but can be distinguished by several morphological features. The raphe ledge exists only on the dorsal side in the genus *Halamphora*, but it is present on both the dorsal and ventral sides in the genus *Amphora*. The areolae in the genus *Amphora* are with simple structure, but the genus *Halamphora* has round, elliptical to transversely elongated areolae occluded by hymens or vela (Levkov 2009). In addition, the genus *Halamphora* has a fused helictoglossa at the internal proximal raphe ends. Despite these morphological differences it is very difficult to distinguish the two genera under a light microscope. Molecular techniques were found to be useful in classifying them because molecular studies have considered the genus *Halamphora* to be a monophyletic group, strongly supporting the morphology-based separation of the genus *Halamphora* from the genus *Amphora* (Stepanek & Kociolek 2014 and 2019).

Halamphora is widely distributed worldwide and is known to be mainly present in marine or brackish environments (Sala *et al.* 2007, Levkov 2009, Spaulding 2022), but new species have been reported in freshwater environments in recent studies (Stepanek and Kociolek, 2015, Zhang *et al.* 2019). According to Guiry and Guiry (2022), there are currently 154 accepted species names and eight varieties in the genus *Halamphora*, because the genus has been proposed relatively recently. Moreover, the discovery of new species, mainly from isolated strains, is continuous in this genus (Jiang *et al.* 2015, Olivares-Rubio *et al.* 2017, López-Fuerte and Siqueiros-Beltrones 2018, Zhang *et al.* 2019, López-Fuerte *et al.* 2020).

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In Korea, 15 *Halamphora* taxa have been reported (NIBR 2020, MABIK 2021), and the reports of unrecorded or new species are rare. In this study, one *Halamphora* species collected in the tidal flat of the West Sea coast of Korea and isolated as monoculture is proposal as new species based on the morphological characteristics observed using optical and scanning electron microscopy (SEM) and molecular characteristics of the *rbc*L gene.

Materials and methods

Sample collection and culture

Samples were obtained from an intertidal mudflat in Hampyeong Bay on the west coast of South Korea on July 19, 2018 (Fig. 1). Single cells were isolated under an Eclipse Ti-U inverted microscope (Nikon, Tokyo, Japan) by the capillary method and transferred to a cell culture flask (SPL Life Sciences, Pocheon, Korea) with F/2 medium (with silicate, Sigma Aldrich Co., St. Louis, MO, USA) and an antibiotic mixture (penicillin-streptomycin-neomycin) (Sigma Aldrich Co.). The strains were transferred to fresh medium at four-week intervals and incubated at 27 ℃ with a 14:10 h light/dark cycle under an irradiance of 100 μmol photons $m^{-2}s^{-1}$.

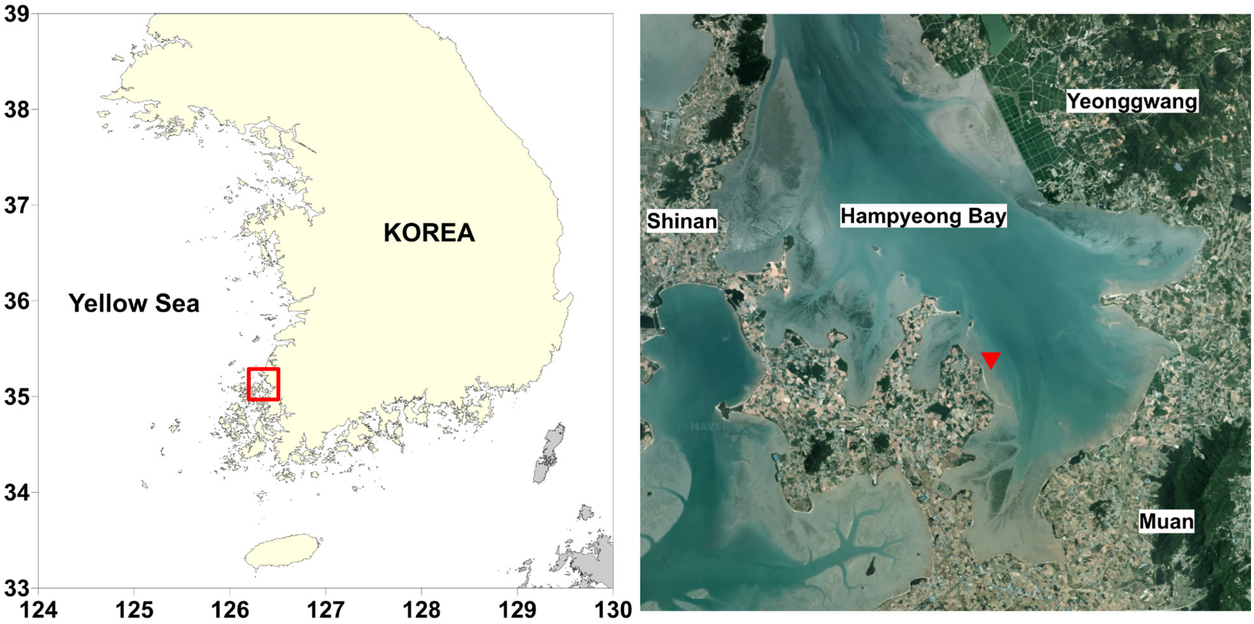


FIGURE 1. Map of sampling localities in Hampyeong Bay, the west coast of Korea. Type locality of *Halamphora minima* (35º03’41.94” N, 126º24’40.06” E).

Observations

For light microscopy, the cultured strains were treated with acids (sulfuric acid and hydrochloric acid) to clean the frustules (modified Hendey 1974) and permanently mounted on slides using Pleurax (Wako Pure Chemical Industries, Osaka, Japan). The slides were observed using Eclipse Ni light microscopy (LM) under a ×100 oil immersion Plan Apo objective lens (Nikon, Tokyo, Japan). For scanning electron microscopy, the cultured strain fixed with 5% Lugol’s solution was filtered through a polycarbonate membrane (25 mm; pore size 2 μm) and then washed with distilled water. The membrane was dehydrated in a graded ethanol series (10~100%) and finally dried using tetramethylsilane (Sigma Aldrich Co.). It was mounted on a stub and sputter-coated with gold using MC1000 ion sputter (Hitachi, Tokyo, Japan). Observations were conducted using a Sigma 500-VP high-resolution field emission (FE)-SEM (Zeiss, Göttingen, Germany). The taxonomic classification system was followed the Algaebase taxonomy (Guiry and Guiry 2022).

Phylogenetic analysis

Cells attached to the wall of the cell culture flask was collected by scraping it off using a sterile cell scraper. The culture medium containing the cells was transferred into a conical tube and centrifuged at 4,000 rpm. The supernatant was removed from the pellet and 1 mL of sterilized Sodium Chloride-Tris-EDTA (STE) buffer solution was added to the pellet and mixed slightly. Genomic DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen Inc., Hilden, Germany) following the manufacturer’s protocol. In this study, the *rbc*L gene was used as a molecular marker, and polymerase chain reaction (PCR) amplification was performed using DPrbcL1 and DPrbcL7 primers (Daugbjerg and Andersen 1997).

Amplification was performed following the protocol described by An *et al.* (2017). The PCR product was cleaned using ExoSAP-IT Express PCR Product Cleanup Reagent (Thermo Fisher Scientific, MA, USA) and sequenced by Macrogen Inc. (Seoul, South Korea). The sequence was trimmed, assembled, and aligned using Geneious R7 v.7.1.2 (Biomatters Ltd., Auckland, New Zealand). A *rbc*L sequence data set was constructed, including the sequences of 70 *Amphora* and *Halamphora* species represented in the GenBank. Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI) using Randomized Axelerated Maximum Likelihood (RAxML) v.8.2.10 (Stamatakis 2014) and MrBayes version 3.2.7 (Ronquist and Huelsenbeck 2003). *Tetramphora chilensis* (Hustedt) Stepanek & Kociolek (2016: 131) (KU665639) was used as an outgroup. The ML analysis with bootstrap 1,000 was performed using the default settings. BI was performed following the methods described by López-Fuerte *et al.* (2020).

Results

Class Bacillariophyceae Haeckel
Order Thalassiophysales D.G.Mann
Family Catenulaceae Mereschkowsky
Genus *Halamphora* (Cleve) Levkov

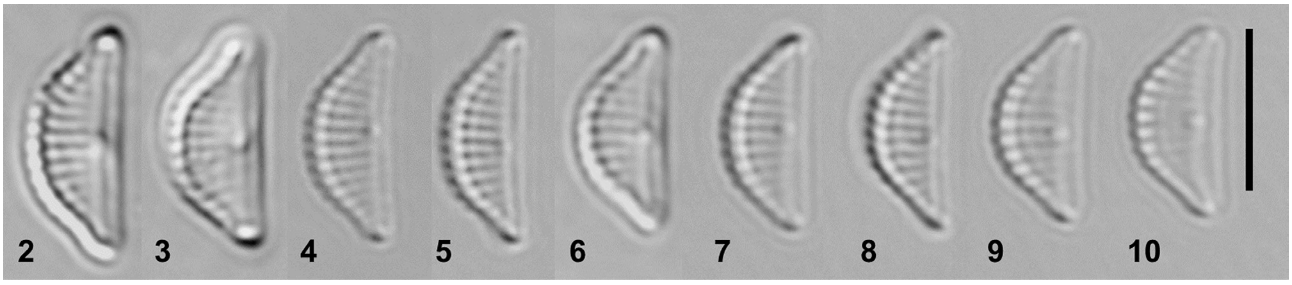
Halamphora minima sp. nov. **S.M. An, J.H. Kim, N.S. Kang, K. Cho, J.A. Lee & E.S. Kim**

Description: The valves are semi-lanceolate with a convex dorsal margin and nearly straight ventral margin (Figs 2–10). The valve length is 5.6–7.4 µm and the breadth is 2.3–3.3 µm (n = 36, Table 1). The central area is expanded on the ventral side only and closed with striae near the valve margin (Fig. 11, 17; asterisk). The raphe is straight with straight distal raphe ending and lie along the ventral margin (Fig. 11). The raphe ledge is fairly well-developed to the dorsal side of the valve (Figs 11, 13, 17; arrow). An axial longitudinal line is not present on the dorsal side. Striae slightly radiate on the dorsal side, but ventral striae parallel to the center and slightly radiated towards the apices. The dorsal striae (27–29 in 10 µm) are biseriate throughout the valve (Table 1), composed of small round or ovoid areolae (Figs 11–15, 17), and are separated by strongly developed costa. The ventral striae are almost invisible under a LM. In SEM, the ventral striae (43–45 in 10 µm, n = 13, Table 1) are uniseriate and interrupted by a central nodule area (Figs 11, 17; asterisk). Internally, a single row of dorsal areolae close to the raphe is delimited by an internal longitudinal rib (Fig. 14; arrow). The dorsal striae and areolae are arranged in one row between the internal longitudinal rib and the raphe (Fig. 14). The areolae are occluded by hymens (Fig. 15; arrows). The fused helictoglossae of the internal proximal raphe endings are small and tongue-shaped (Fig. 14). The internal distal raphe endings terminate with poorly developed helictoglossae (Fig. 14; arrowhead). The girdle bands are numerous, and round or ovoid poroids are arranged in two rows of 44 – 47 in 10 µm on the dorsal side (Fig. 16).

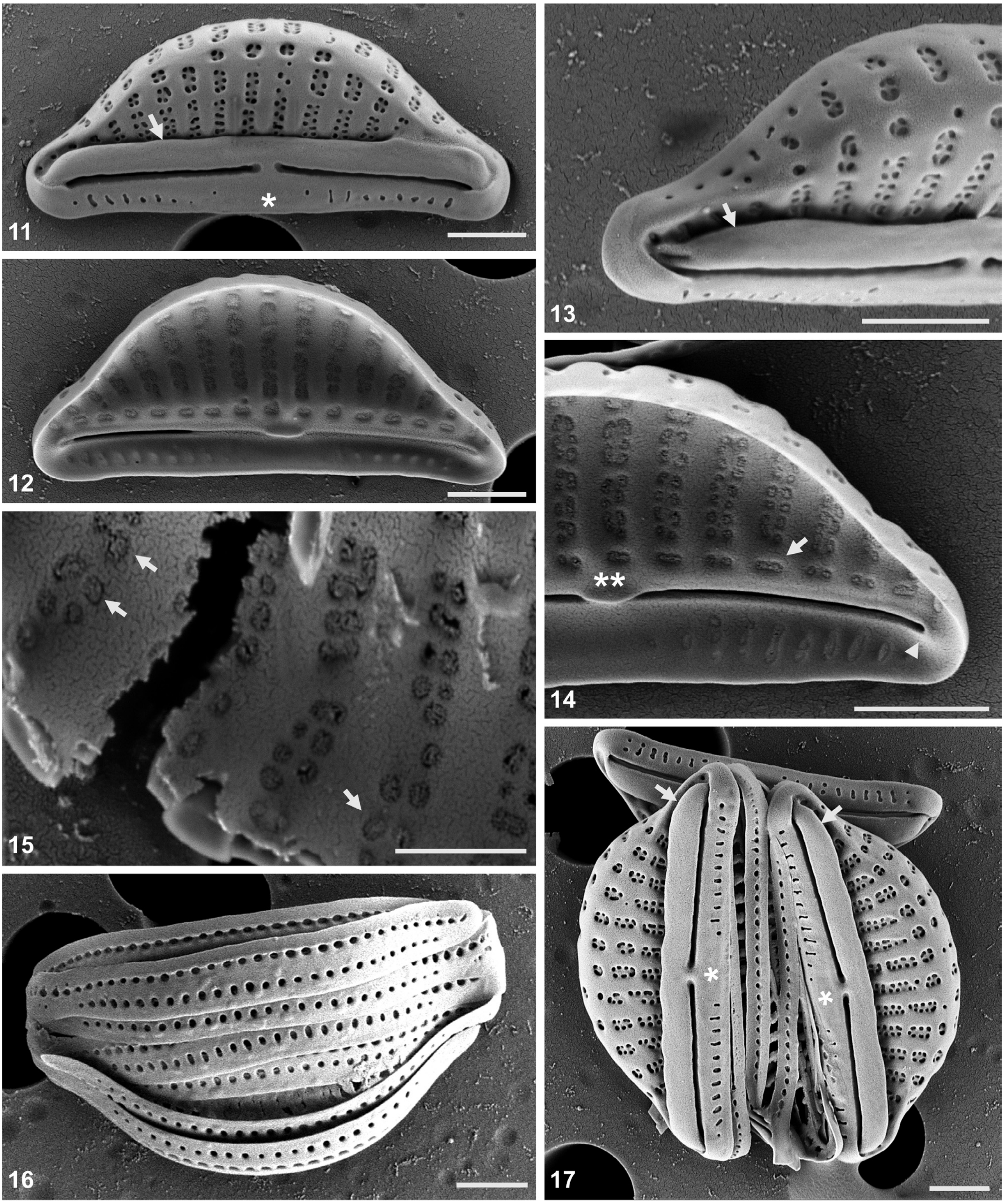
Type material: Intertidal mudflat in Hampyeong Bay (35º03’41.94” N, 126º24’40.06” E), Muan-gun, Jeollanam-do, Republic of Korea (site: HP2-2). Jul 19, 2018.

Holotype: SEM stub no. MABIK DI00043438 (represented by the valve in Fig. 3A) was deposited at the National Marine Biodiversity Institute of Korea (MABIK), Seocheon-gun, Chungcheongnam-do, Republic of Korea.

Isotype: Slide no. MABIK DI00043439 and cleaned material MABIK DI00043440 (preserved in 100% ethanol).



FIGURES 2–10. Light microscopy (LM) micrographs of *Halamphora minima sp. nov.* Scale bars = 5 µm.



FIGURES 11–17. SEM micrographs of *Halamphora minima sp. nov.* Fig. 11. External whole valve view, with central area (asterisk), and dorsal raphe ledge (arrow). Fig. 12. Internal whole valve view. Fig. 13. Detail of external valve apex,with dorsal raphe ledge (arrow) Fig. 14. Detail of internal valve apex showing tongue-like proximal helictoglossae (double asterisk), poorly developed distal helictoglossae (arrowhead), and internal longitudinal rib (arrow). Fig. 15. Detail of internal dorsal areolae occluded by hymens (arrows). Fig. 16. Dorsal girdle bands with two rows of poroids. Fig. 17. frustules showing the ventral girdle bands with dorsal raphe ledge (arrow). Scale bars: Figs 11—14, 16, 17 = 1 µm, Fig. 15 = 0.5 µm.

Etymology: The specific name, minima (Latin = very small, smallest), relates to the small size of this species.
Distribution: Currently known only in type locality.

TABLE 1. Morphometric comparation of *Halamphora minima* with related species. F: freshwater, B: brackish water, M: marine.

Taxa	Valve length (μm)	Valve width (μm)	Dorsal striae (in 10 μm)	Ventral striae (in 10 μm)	marginal ridge	Internal longitudinal rib	Habitat	References
Halamphora minima	**5.6–7.4**	**2.4–3.3**	**27–29 biseriate**	**43–45**	**Absent**	**Present**	**B**	**This study**
H. costata	(17) 45–80	(6) 9–10	8–9 uniseriate	10–11	Absent	ND	B, M	Levkov (2009), Wang *et al.* (2014)
H. veneta var. *somalica*	15–20	4–4.5	22–26 uniseriate	ND	Absent	ND	F	Levkov (2009)
H. pratensis	13–35	4.5–6.0	23–27 uniseriate	ND	Absent	Absent	F	Stepanek and Kociolek (2018)
*H. tumida**	19–33	4–7	16–18 biseriate	22–28	Absent	Present	B	Levkov (2009)
*H. americana**	23–30	4–5	19 bi- and uniseriate	28–31	Absent	Absent	F, B	Stepanek and Kociolek (2018)
*H. foramina**	43–65	7.5–10.5	15–16 biseriate	24–25	Absent	Present	B, M	Stepanek and Kociolek (2018)
*H. sydowii**	25–42	4.5–7	16–22 bi- and uniseriate	28–30	Absent	Present	B, M	Levkov (2009), Stepanek and Kociolek (2018)

* Similar species with *H. minima* according to phylogenetic analysis.
ND = not documented.

Phylogenetic analysis

The lengths of the trimmed and assembled *rbc*L gene sequences for *Halamphora minima* was 1,424 bp. The sequences determined in this study were deposited in the GenBank (ON137727). The BLASTn search showed 97.6% identity of *H. minima* (query cover of 100% and E valve of 0) with *H. montana* (Krasske) Levkov (2009: 207) (KC736590). Phylogenetic analysis conducted to establish the relationship between *H. minima* with 73 species in the genera *Amphora* and *Halamphora* obtained from GenBank using ML and BI methods showed similar topologies of phylogenetic trees. *H. minima* is a sister of *H. foramina* J.G. Stepanek & Kociolek (2018: 75) and *H. sydowii* (Cholnoky) Levkov (2009: 232), but ML bootstrap value and posterior probability for this clade were low at 39 and 73%, respectively (Fig. 18).

Discussion

Halamphora minima has the morphological characteristics of the genus. Nevertheless, is smaller than other species small in the genus *Halamphora,* which includes *H. auricularia* Levkov & Ács (2009: 173) (8–33 μm), *H. oceanica* Olivares-Rubio, L.I.Cabrera, Godínez-Ortega, Salazar-Coria & Vega-López (2017: 191) (9–17 μm), *H. subsalina* Levkov (2009: 230) (12–17 μm), and *H. parathumensis* Levkov, Pavlov & Jovanovska (2009: 214) (9–12 μm). If the size difference is not considered, this species is morphologically similar to *H. costata* (W. Smith) Levkov (2009: 181) and *H. pratensis* J.G. Stepanek & Kociolek (2015: 28) in its valve outline and raphe ledge morphology (Table 1). However, there is a difference in the striae density and row of striae, which are denser and biseriate in *H. minima*. Small-sized *H. veneta* var. *somalica* (Frenguelli) Levkov (2009: 243) is also externally similar to this species. Nevertheless, this species has valve ends that are curved ventrally and the striae are denser (Table 1) (Levkov 2009).

According to the *rbc*L gene phylogenetic tree developed, amphoroid diatoms were split into two monophyletic clades (Fig. 18), and showed that this taxon is new species belonging to the genus *Halamphora*. However, the phylogenetic position of the *H. minima* seems to be unclear (Fig. 18). This species clustered as a sister species of *Halamphora* Clade K, which includes species such as *H. foramina*, *H. sydowii*, *H. tumida* (W. Gregory) Levkov (2009: 239) and *H. americana* Kociolek (2014: 51) presented by Stepanek and Kociolek (2019), but bootstrap value and posterior probability were low. In most species belonging to this clade, the striae are biseriate throughout the valve, longitudinal silica bands or dorsal marginal ridges are absent, and the areolae are occluded internally by the hymen (Stepanek and Kociolek 2019). Although *H. minima* was not supported by high bootstrap values in the *rbc*L gene phylogeny, it shares the aforementioned morphological features with *Halamphora* Clade K. Nevertheless, the striae of most species included in *Halamphora* Clade K are biseriate only near the raphe ledge or uniseriate. Only *H. foramina* and *H. tumida* have biseriate striae throughout the dorsal valve in *Halamphora* Clade K, but it can be distinguished from *H. foramina* by silt-like external foramina and lower striae density (12–16 in 10 µm) (Stepanek & Kociolek 2018), and from *H. tumida* by fine punctate striae, dorsally deflected proximal raphe ends and lower striae density (16–18 in 10 µm) (Levkov 2009). *H. minima* also shares the characteristic that the striae are biseriate for the majority of the valve face with *H. banzuensis* J.G. Stepanek, S. Mayama & Kociolek (2018: 73) belonging to *Halamphora* Clade J. However, *H. banzuensis* has protracted subcapitate valve ends and an axial silica band on the dorsal valve (Stepanek & Kociolek 2018).

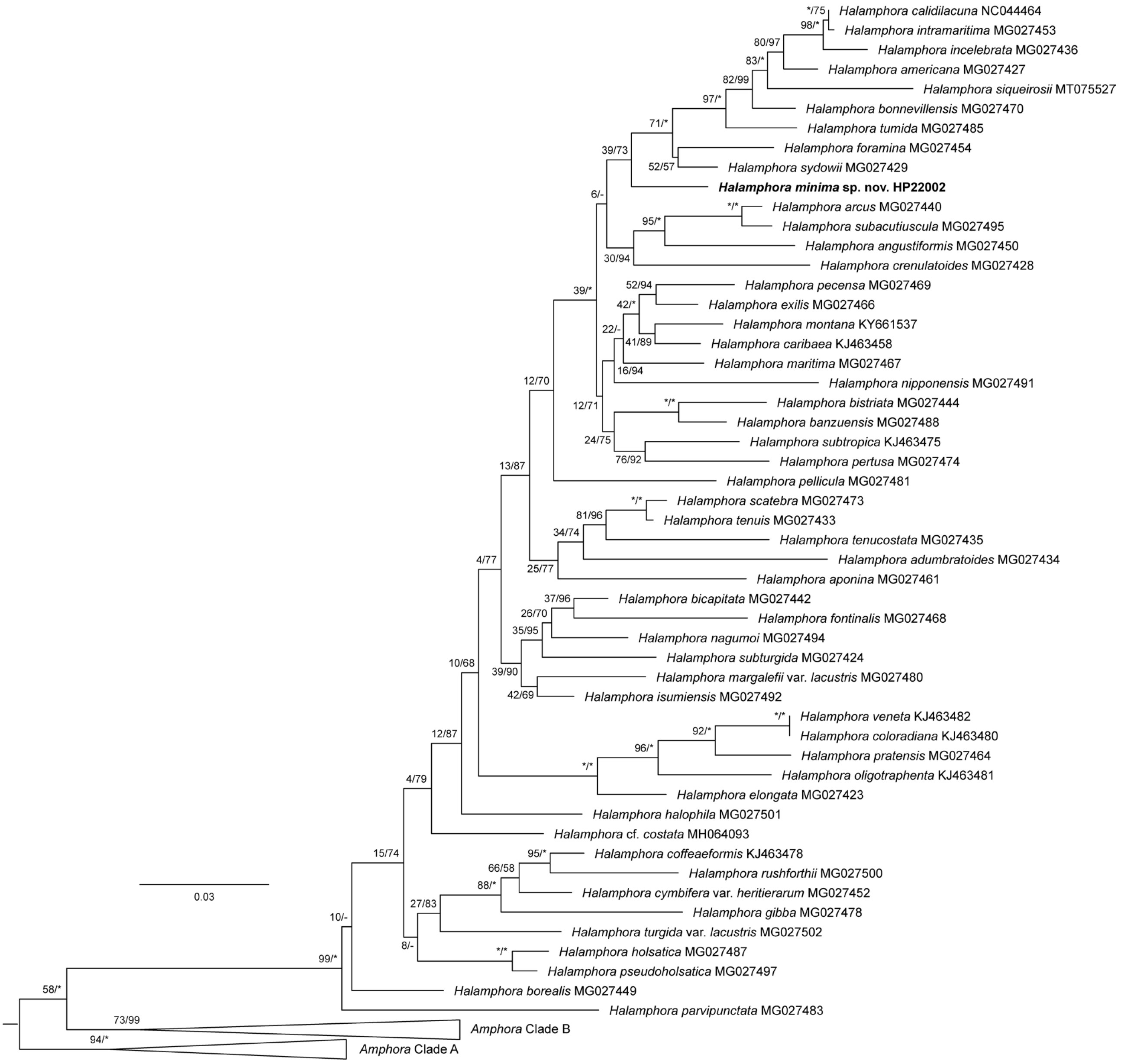


FIGURE 18. Molecular phylogenetic tree obtained from ML and BI analysis based on *rbc*L gene showing the phylogenetic positions of *Halamphora minima*. The values on each node indicate ML bootstrap and Bayesian posterior probabilities (%), respectively. The asterisk indicates 100, and – indicates the topological incongruence between ML and BI trees.

Although benthic diatoms dominate the benthic ecosystems of tidal flats and are known to have high diversity (Underwood and Barnett 2006, Mann and Vanormelingen 2013), they remain largely unknown. Based on the aforementioned, we propose one new species of *Halamphora* found in the tidal flats through this study. Likewise, it is expected that new species will continue to be found, described and reported through additional research in the future.

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