

Halamphora izadii sp. nov., a new diatom species from the hottest place on earth, Lut Desert, Iran

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ABSTRACT

In a study on the diatom flora of the Lut desert, the hottest point on Earth, we report a new species *Halamphora izadii* sp. nov. This species is described based on LM and SEM observations and belongs among the many small-sized species distributed across the *Halamphora* lineage. The new species can withstand extreme air temperatures and high salinity concentrations found in waterways of the Lut Desert. *Halamphora izadii* is differentiated by possessing fine striae, hardly resolvable in LM at 26–30 striae in 10 µm, a subcentral raphe, and areolae opening externally by narrow slit-like openings with dilated ends. The species is compared to morphologically similar *Halamphora* species, and its ecology and phylogenetic placement is discussed.

KEYWORDS

amphoroid diatoms, Bacillariophyceae, extremophile, hypersaline, morphology, taxonomy

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INTRODUCTION

The Lut Desert (Dasht-e-Lut), Iran has an area of over 54,000 km² (Alai Taleghani, 2002) with three subregions, northern, central and southern Lut (Mostofi, 1972) and is considered the world's hottest and driest desert. Satellite measurements of the surface air temperatures have been recorded at over 80 °C (Azarderakh *et al.*, 2020). The arid region contains a complex geomorphology of

sand dunes, ergs (shifting sand dunes), mega yardangs (hydro-aeolian landforms, regional in extent, also termed “*kaluts*”), desert pavement, evaporite basins, and playas (Gouldi, 2007; Yazdi *et al.*, 2014). While these studies have described the unusual desert geomorphology, there has been little investigation of other surficial and shallow subsurface processes, particularly relating to surface and subsurface water of the Lut Desert (Lyons *et al.*, 2020).

The importance of subsurface water in this

extreme desert has not yet been determined; however, Stone (2016) writes of a “hidden sea” as a shallow layer of salt-rich groundwater crucial to life in the Lut Desert. Salinity of Lut Desert groundwater is attributed to both evaporative processes and dissolution of previously deposited salts (Lyons *et al.*, 2020). Furthermore, alternate wetting and drying influence the geochemistry of surface and subsurface brines. The brines were found to be in equilibrium with gypsum and supersaturated with respect to carbonate (Lyons *et al.*, 2020). Such brines are often inhospitable to diatoms because of high pH and alkalinity, which may allow dissolution of the silicon cell wall of diatoms. Yet, recent works demonstrate that diatoms may survive and even be well preserved in such chemical conditions (Pellagrino *et al.*, 2023).

There have been few studies on diatom flora of the watercourses and ponds of the central Lut to date (Compère, 1981; Léonard, 1991–1992; Sabouri & Alimohammadian, 2013). These investigations

have contributed to our understanding of the unique adaptations diatoms have developed to survive in such extreme environments.

Recently, a new diatom genus, *Lutophila* Kheiri *et al.* was described from hypersaline waters of the Lut Desert (Kheiri *et al.*, 2024). Like that taxon, the *Halamphora* (Cleve) Levkov species that we investigate here is also small and ecologically adapted to the extreme conditions of the habitat, although environmental tolerances remain to be determined. *Halamphora* has received a great deal of attention recently, as the diversity, taxonomy, ecology, and phylogeny of freshwater, brackish, and marine representatives are clarified (An *et al.*, 2022, 2024; Cantonati *et al.*, 2019; Levkov & Zaova, 2023; López-Fuerte & Siqueiros-Beltrones, 2018; López-Fuerte *et al.*, 2020; Olivares-Rubio *et al.*, 2017; Pane *et al.*, 2024; Stepanek & Kociolek, 2018, 2019; Wu *et al.*, 2020; Yilmaz *et al.*, 2024; Zhang *et al.*, 2019; Zidarova *et al.*, 2025). This work adds to discovery of new taxa in brackish to hypersaline waters

Table 1. Sampling site characteristics at time of collection from Lut Desert, Iran.

Coordinates	Site	Sample Date	Sample Depth	Air temp (°C)	Surface temp (°C)
31° 00' 31"N, 57° 37' 48" E	Kale-Shoor River, south-western Gandom Beryan region (Iran-Lut)	July 2010	30 cm	65	73
31° 00' 21"N, 58° 06' 55" E	Artificial pond in the Gojar Depression, (LutB)	Aug. 2014	3–4 m	63	70

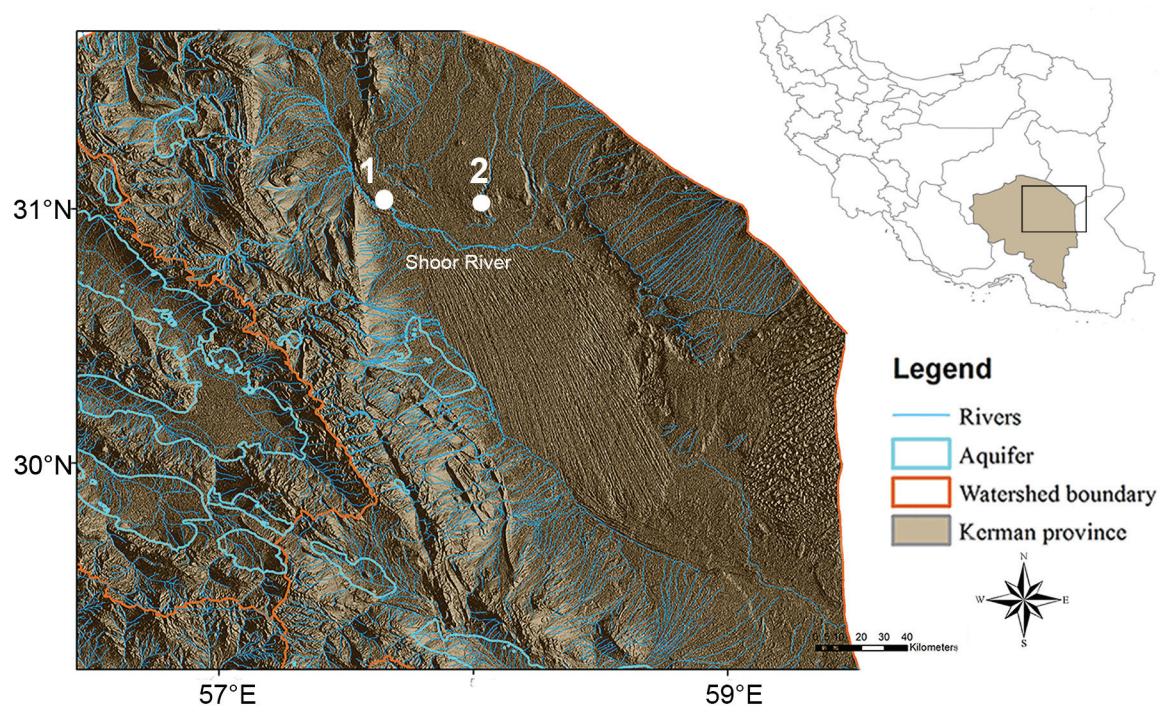


Figure 1. Map of Iran (inset) showing Kerman Province and the location of the Central Lut Desert. 1) marks the sample site on the Kale–Shoor River and 2) is the artificial pond in the Gojar depression, along the Shahdad–Nehbandan Road. (adapted from Kheiri *et al.*, 2024).



Figures 2–4. Sampling sites in the central Lut Desert. (2) Image of the Kale–Shoor River within the Lut Desert. (3) Artificial pond. (4) Detail of the halite/gypsum crystal precipitate from the hypersaline artificial pond. (Image credit: Bahman Izadi).

and in extreme environments.

Morphologically, amphoroid diatoms are strongly dorsiventral raphe diatoms with dorsally broadened copulae that nearly align both valve faces and raphe in a similar plane. They have been the subject of extensive study and revised classification due to ecological, morphological, and molecular differences within the polyphyletic group. This morphological group is recognized by genera including: *Amphora* Ehrenb. ex Kütz., *Seminavis* D.G.Mann, *Halamphora* (Cleve) Levkov, *Eunophora* W.Vyverman, K.Sabbe et D.G.Mann, and *Tetramphora* Mereschkowsky (Levkov, 2009; Mereschkowsky, 1903; Round *et al.*, 1990; Vyverman *et al.*, 1998).

Halamphora is recognized to contain over 160 named species worldwide (Guiry & Guiry, 2025);

however, identifying synapomorphies defining the genus has been challenging (Stepanek & Kociolek, 2019). Morphological features that distinguish the genus *Halamphora* from other amphoroid diatoms include chloroplast type, and areolae with recessed foramina and internal central raphe ends terminating in a rectelevatum or, as earlier described, a fused, central helictoglossa (Ács *et al.*, 2011; Levkov, 2009).

Ecologically, *Halamphora* prefers inland waters of high conductivity, brackish, and marine waters (Levkov, 2009; Sala *et al.*, 2021; Spaulding *et al.*, 2021; Stepanek & Kociolek, 2018, 2019). However, reports have also documented *Halamphora* from freshwater habitats (Van de Vijver *et al.*, 2014; Zhang *et al.*, 2019). In our analysis of collections from extreme habitats in the Lut Desert, we noted several potentially novel *Halamphora* taxa. In this study, we propose and describe a new species from the genus *Halamphora* from hypersaline inland waters in the central Lut Region and discuss its ecology and potential phylogenetic position.

MATERIAL AND METHODS

Study area: The Kale-Shoor River is 300 km in length and is the longest perennial river in the Lut Desert. The river flows from the Khusef Mountains in the southern Khorasan Province to the central Lut depression, where it terminates in a playa. The second site sampled, an artificial pond, was initially excavated in 1997 during construction of a road from Shahdad to Nehbandan within the Gojar depression. The pond was further increased in size as the road was expanded. The long, thin pond filled with hypersaline groundwater following construction and is now estimated to be approximately 144 m long, 3–4 m wide, have a surface area of 700 m², and depth up to 4 m.

Samples: Epipellic diatom communities were collected from sites along the Kale-Shoor River (July 2010, sample Iran-Lut) and from the artificial pond (August 2014, sample LutB) (Figures 1–4, Table 1). Samples for water chemistry were collected in August 2014 from the artificial pond and measured for pH, conductivity, and concentrations of organic carbon, phosphate, total phosphorus, nitrate, sulfate, chloride, silica, potassium, sodium, calcium, total hardness, and chemical oxygen demand (COD). All analyses followed APHA (2017). X-ray diffraction (XRD) analysis to determine constituent ions of salt crystals was completed at the Geological Survey of Iran, Tehran.

Sample material for light microscopy (LM) and scanning electron microscopy (SEM) was prepared by treatment with 10% HCl and 30% H₂O₂ to oxidize organic material (Renberg, 1990). To obtain permanent microscopic slides, cleaned material was mounted in Naphrax or Zrax. LM observations were made at the Science Museum of Minnesota, USA using an Olympus BX51 compound microscope with full immersion differential interference contrast optics capable of 1250X and NA of 1.40. SEM observations were made with a Hitachi SU8010 at Rzeszow University, Poland. Samples and slides were deposited in the Diatom Collection of the Research Institute of Forests and Rangelands in Tehran (TARI), Academy of Natural Sciences (ANSP; Philadelphia, USA), and Science Museum of Minnesota (SMM).

RESULTS

Taxonomy

Phylum Heterokontophyta Moestrup, R.A.Andersen *et* Guiry

Class Bacillariophyceae Haeckel

Family Amphipleuraceae Grunow

Genus *Halamphora* (Cleve) Levkov

Halamphora izadii S.Kheiri, Edlund *et* S.A.Spauld. sp. nov. (Figures 5–10, 17–24)

Description

LM (Figures 5–10): Frustules oval with subrostrate truncate ends. Valves semi-lanceolate to semi-elliptic, dorsiventral with smoothly arched dorsal margin and straight to slightly tumid ventral margin. Apices protracted, capitate to subcapitate to attenuate (rostrate). Apices slightly ventrally bent in some specimens. Valve length 16.0–25.3 μ m; valve width 2.4–3.5 μ m, frustule width 6.0–8.6 μ m. Striae hard to resolve in LM, mostly parallel mid-valve, in some specimens becoming radiate; striae number 26–30 in 10 μ m. Raphe straight or slightly arched, appearing located near median line of the valve or slightly ventral (in valve view), central rectelevatum evident. Chloroplast unknown.

SEM (Figures 11–18): In external valve view, the striae are uniseriate, areolae are elongate with different lengths, some areolae sinuate to denticulate with expanded ends. Dorsal striae comprise three transapically elongate areolae, becoming two and eventually single areolae at the valve ends (Figures 11–14). Ventral striae of a single opening of variable length, shorter in the valve center and ends (Figures 11, 13). The dorsal striae are crossed and areolae separated by some wavy longitudinal external costa as hyaline lines, especially near the dorsal margin and close to the dorsal axial area, which are only evident in SEM. Areolae have narrow slit-like external openings with dilated ends (Figure 13). Externally the raphe is straight with proximal raphe ends dilated or slightly expanded, straight or slightly bent dorsally (Figures 11, 13). Externally, the distal raphe ends are dorsally bent (Figure 14). Raphe ledge is narrow, linear and continuous with a prominent step separating it from a valve face dorsally (Figures 11–13) or the raphe ledge is

bordered with a more irregular line/ridge separating the raphe/axial area from the valve face in some specimens (Figure 14). There are multiple girdle bands each with two longitudinal rows of cross-like to dumbbell-shaped areolae; however, in some bands only a single row is visible (Figure 18). In the internal valve view, the areolae are elongated and occluded by hymens (Figures 15–17). The central area is more easily detectable internally than in external view with its prominent rectelevatum (fused central helictoglossae) at the proximal raphe endings (Figure 17). Internal distal raphe endings are straight with the terminal fissure ending in a tiny helictoglossum (Figures 15–16).

Holotype: ANSP! GC38131, slide (Zrax) and material ANSP! GCM22024 are deposited in the diatom collection at Academy of Natural Sciences (Philadelphia, USA). Holotype specimen illustrated in Figure 7 and circled on slide (Artificial pond site 2, sample LutB)

Isotype 1: SMM! 2561a, slide (Zrax) and material in diatom collection of Mark Edlund, Science Museum of Minnesota, USA. Isotype specimen illustrated in Figure 10 (Artificial pond site 2, sample LutB)

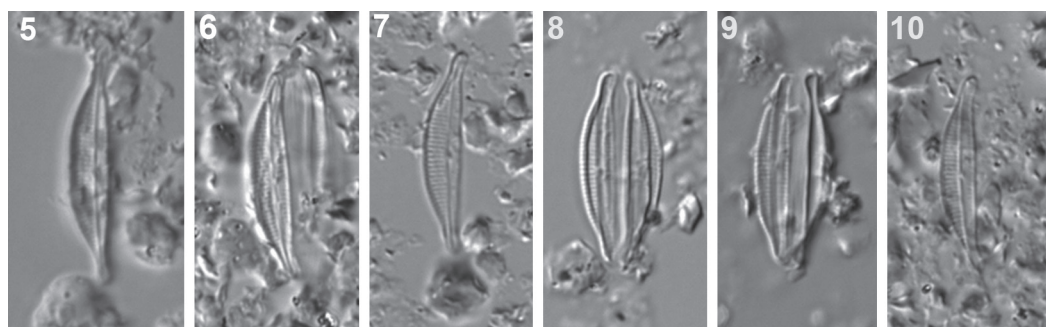
Isotype 2: TARI! DIA31-01 slide (Naphrax) and material number DIA31 are deposited in the diatom collection of the herbarium of the Research Institute of Forests and Rangelands, Tehran, Iran.

Paratype: Lut Desert, Central Lut, Gandom Beryan, the Kale-Shoor River, 31°00'31"N, 57°37'48"E, epipelon, sample Iran-Lut. SMM! MBE2562a slide (Zrax) and material in diatom collection of Mark Edlund, Science Museum of Minnesota, USA, paratype specimen illustrated in Figure 6 and circled on slide. TARI! DIA33-01 slide (Naphrax) and material DIA33 are deposited in the diatom collection of the herbarium of the Research Institute of Forests and Rangelands, Tehran, Iran.

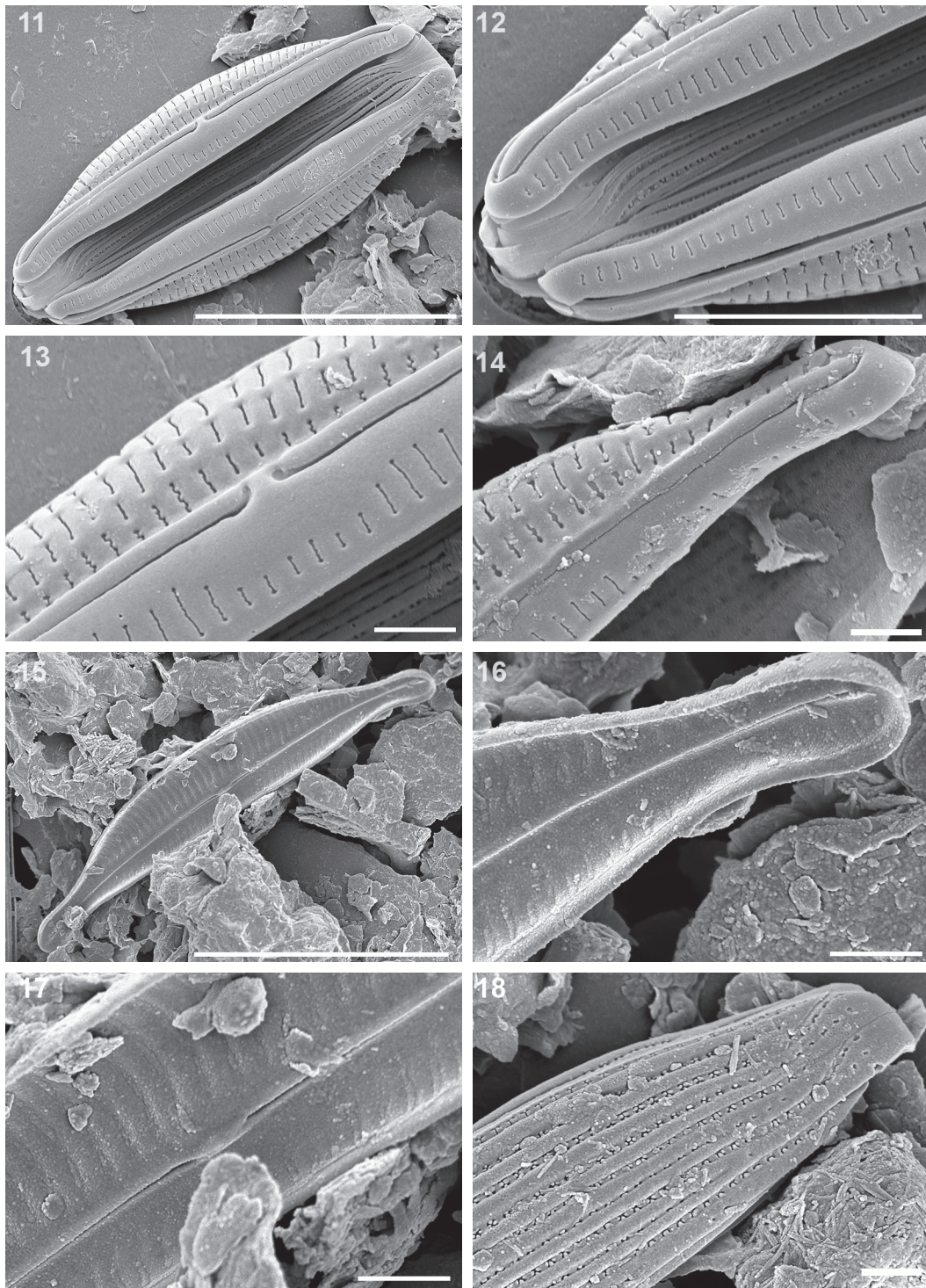
Type Locality: Iran, Lut Desert, central Lut, Gojar depression, Artificial pond, 31°00'21"N, 58°06'56"E, sample 2, LutB collected by Bahman Izadi, August 2014.

Registration: <http://phycobank.org/106701>

Etymology: The species is named in the honor of Bahman Izadi, to acknowledge his enormous work in the Lut Desert as an environmentalist and desert expert.



Figures 5–10. *Halamphora izadii* S.Kheiri, Edlund *et* S.A.Spauld. sp. nov. light micrographs showing size diminution, valve views from holotype and paratype material. (6) Paratype specimen. (7) Holotype specimen. (10) Isotype specimen. Scale bars 10 μ m.



Figures 11–18. *Halamphora izadii* S.Kheiri, Edlund *et* S.A.Spauld. *sp. nov.* SEM images taken from the LutB sample (Artificial pond in Gojar depression, Central Lut, Lut Desert, Iran, ANSP! GCM22024). **(11)** SEM view of a full frustule with girdle bands. **(12)** SEM external details of valve apices of the frustule showing elongate areolae that compose the ventral striae. **(13)** SEM external detail of central valve showing proximal raphe ends closely spaced and dorsally deflected next to dorsal raphe ledge. **(14)** SEM external detail of valve apex showing distal raphe position. Note the raphe ledge irregularly extended. **(15)** SEM internal view of the entire valve showing occluded striae and a fused central helictoglossa (rectelevatum). **(16)** SEM internal detail of the valve apex showing an apical simple helictoglossae and areolae occluded by hymenes. **(17)** SEM internal detail of the valve center with the proximal raphe ends, showing raised internal central rectelevatum. **(18)** SEM detail of external view of multiple girdle bands, each with two longitudinal rows of areolae. Scale bars 5 μ m (11, 15), 3 μ m (18) and 2 μ m (12–14, 16–17)

Habitat and Ecology: This taxon was found benthic and epipellic in the hypersaline Artificial pond and the Shoor River (Table 1). Water quality conditions at the time of type collection (site 2, LutB) included pH of 7.52, conductivity of 323.4 mS·cm⁻¹, organic carbon with the concentration of 390 mg·L⁻¹, COD of 70.78 mg·L⁻¹, silica with the concentration of 349 mg·L⁻¹, anions including nitrate (348.7 mg·L⁻¹), sulfate (1968 mg·L⁻¹), phosphate (1.17 mg·L⁻¹), total phosphorus (2.68 mg·L⁻¹), chloride (75685 mg·L⁻¹), and cations including potassium (35.5 mg·L⁻¹), sodium (1417.8 mg·L⁻¹), calcium (727.27 mg·L⁻¹) and total hardness of 19400 mg·L⁻¹. XRD analysis indicated that the main salt minerals were gypsum and halites.

Distribution: Currently known only from the type and paratype locality.

Remarks: *Halamphora izadii* has areolae that open externally by narrow slit-like openings with dilated ends, a character not seen commonly in other *Halamphora* taxa. *Halamphora izadii* is similar to *H. punctata* J.G. Stepanek *et* Kociolek in shape and placement of the raphe (Table S1). However, it is different from *H. punctata* in the striation pattern, striae number, the visibility of striae and the form of raphe. *Halamphora izadii* resembles *H. stepanekiana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov, *H. wachnickana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov and *H. kociolekiana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov in the overall shape and striation and dorsal striae number as these three species have fine, parallel striation with subcapitate to rostrate apices. However, *H. izadii* differs from the three mentioned species in the placement of raphe. They all have a marginal raphe in contrast to *H. izadii* which has a subcentral raphe. *Halamphora tenerrima* (Aleem *et* Hustedt) Levkov resembles small specimens of *H. izadii* as both have similar shape, striation pattern, and striae number. However, the placement of raphe in *H. tenerrima* is marginal and the ventral margin is straight (Table S1).

DISCUSSION

The genus *Halamphora* is well represented by over 160 named species (Guiry & Guiry, 2025). Importantly, diversity within the genus is being newly appreciated as it has long been overlooked due to its small size and its preference for habitats that have not been well studied by diatomists. As a result, many new taxa are being described from across the globe (e.g. Zidarova *et al.*, 2025).

One factor accounting for the diversity within this group is the broad ecological range that *Halamphora* taxa can inhabit. A recent phylogenetic study of the group treated 77 *Halamphora* clones (Stepanek & Kociolek, 2019), and in addition to resolving many clades within the genus, *Halamphora* was shown to contrast many observations of genera that are either constrained to

marine or freshwaters or exhibit singular transitions from marine to freshwater. Instead, *Halamphora* taxa exhibited multiple transitions from coastal marine to fresh waters as well as probable evidence for a return transition from fresh to marine among the lineages. The resulting modern distribution of the genus encompasses habitats from fresh to hypersaline, a pattern not readily seen in many diatom genera.

Levkov (2009) provided the first modern treatment of diversity in *Halamphora* in a monograph of European taxa describing 16 new taxa and transferring over 60 taxa into the newly recognized genus. However, subgroups within the genus were not readily recognized until broader phylogenetic treatments by Stepanek & Kociolek (2019). Based on four genetic markers, 11 clades within *Halamphora* were recognized. Morphological characters were subsequently mapped on the phylogenies to define both morphological and molecular characteristics of the *Halamphora* clades (Stepanek & Kociolek, 2019).

The newly described *Halamphora* species (*H. izadii*) is comparable to other small-sized *Halamphora* species that include *H. subsalina* Levkov, *H. tenerrima* (Aleem *et* Hustedt) Levkov, *H. borealis* (Kützing) Levkov, and *H. aponina* (Kützing) Levkov as described by Levkov (2009) and to other more recently described small *Halamphora* species including *H. kociolekiana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov, *H. wachnickana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov, *H. stepanekiana* Zidarova, Pottiez, M.de Haan *et* P.Ivanov (Zidarova *et al.*, 2025). The species that are most similar with *H. izadii* in terms of the visibility of dorsal striae include *H. tenerrima*, *H. subsalina*, *H. stepanekiana*, *H. kociolekiana*, *H. wachnickana*. All these species share a similar fine striation pattern with *H. izadii*; however, the areolae of *H. izadii* open externally by narrow slit-like openings with dilated ends. Most species have similar stria density with *H. izadii*, although *H. aponina* has a lower stria density than *H. izadii*. Other common differences between *H. izadii* and the other small taxa include the shape and the placement of raphe. The only species that have similar raphe placement is *H. punctata*, which has coarser striation, a characteristic that differentiates it from *H. izadii*. When considering to which *Halamphora* clade *H. izadii* might belong, we consider morphological characters for the new taxon illustrated above such as loss of dorsal marginal ridge, hymenate areolae occlusions, and areolate dorsal striae that place *H. izadii* within *Halamphora* Clade E based on morphological characters mapped by Stepanek & Kociolek (2019) on their molecular phylogeny. Although members of this clade should also share biseriolate ventral striae, this character appears to not be expressed in *H. izadii*.

The new species represents a growing list of diatom taxa able to tolerate and even thrive under extreme environmental conditions. These diatoms are recognized as extremophiles because of their ability to grow and even thrive in such habitats. This includes

diatoms able to withstand high temperatures of thermal springs (Delgado *et al.*, 2020; Nikulina & Kociolek, 2011), and diatoms at the other extreme, that thrive in sub-freezing temperatures and polar darkness (Thomas & Dieckmann, 2002), and diatoms that tolerate hypersalinity (Davidovich *et al.*, 2024) such as encountered in the Lut Desert. Globally, *Halamphora* species are found in a wide range of habitats, from hypersaline to freshwater (Saber *et al.*, 2025). Stepanek & Kociolek (2019) considered the ecological distribution within the group and noted multiple instances of clades moving from marine to fresh systems (and in reverse). Among the taxa Stepanek & Kociolek (2019) studied were four hypersaline species distributed among several clades including *H. semperpalorum* (Wachnicka *et al.*), *H. tenuicostata* J.G.Stepanek *et al.* in Clade A, *H. intramaritima* J.G.Stepanek *et al.* in Clade D, *H. halophila* J.G.Stepanek *et al.* in Clade K, and *H. izadii* represents another hypersaline member of Clade E capable of living in waters that are a magnitude more concentrated than seawater.

The Lut Desert is aptly named the “hottest place on Earth” and these conditions produce extreme environmental habitats in both its terrestrial and aquatic desert systems (Mildrexler *et al.*, 2006). Among its terrestrial inhabitants, endemic extremophiles include a bird, the Persian ground jay (*Podoces pleskei* Zarudny; (Sehhatisabet, 2007)), several lizards (Misonne’s spider gecko: *Rhinogekko misonnei* De Witte, Akbarpour *et al.* and the toad-headed agama: *Phrynocephalus lutensis* Kamali *et al.* and Anderson (Kamali & Anderson, 2015)), and spiders (the jumping spider: *Proszynskiana izadii* Azarkina *et al.* (2019); *Iranotricha lutensis* Zamani *et al.* (2018); *Oecobius fahimii* Zamani & Marusik, (2018)) adapted to living in the extreme dry and heat of the Lut Desert.

In the Lut’s aquatic habitats, the endemic fairy shrimp *Phallocryptus fahimii* Schwentner, Rodov & Rajaei tolerates lengthy periods of desiccation and heat as it awaits the formation of ephemeral pools following infrequent spring precipitation (Schwentner *et al.*, 2020). Perennial wet areas in the Lut Desert exhibit both temperature and salinity extremes. Recently a new diatom genus, *Lutophila* S.Kheiri, Edlund, S.A.Spauld. *et al.* C.N.Solak, recognized by a single taxon, *L. iranica* S.Kheiri, Edlund, S.A.Spauld. *et al.* C.N.Solak, was described from Lut Desert streams and artificial pools. With air temperatures over 65 °C, the pools were relatively cool and groundwater fed at 20 °C; however, the sites’ conductivity ranged from 120 to 323 mS·cm⁻¹ or hypersaline (Kheiri *et al.*, 2024). The new *Halamphora* species represents a new extremophilic taxon from the Lut Desert’s streams and artificial pools. These observations and finding of new extremophile taxa make exploration and analysis of extreme habitats imperative. In a world where habitat integrity and biodiversity are threatened, it is important to document such habitats and their organisms.

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DISCLOSURE STATEMENT

The authors report there are no competing interests to declare.

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