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Roksana Majewska

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Nagumoea hydrophicola sp. nov. (Bacillariophyta), the first diatom species described from sea snakes

ROKSANA MAJEWSKA ^{1,2*}

¹Unit for Environmental Sciences and Management, School of Biological Sciences, North-West University, Potchefstroom, South Africa;

²South African Institute for Aquatic Biodiversity (SALAB), Grahamstown, South Africa

Although diatoms colonize a vast diversity of immersed hard-surfaced objects and organisms, many diatom species, and sometimes entire genera, show a clear preference towards a particular type of substratum. Studies of animal-associated diatoms indicate that some epizoic forms may require this specific habitat to thrive, and new diatom taxa are expected to be found on as yet unexplored animal hosts. The current study is the first to investigate the diatom flora of sea snakes. Three museum specimens of yellow-bellied sea snakes (*Hydrophis platurus*) collected over a period of 23 years from the south-eastern coast of South Africa were examined for their diatom flora. Diatoms were abundant on the sea snakes, but communities were composed of only a few species. A previously undescribed species of *Nagumoea* contributed over 99% of the total diatom assemblage on both the sea snake skin and sea-snake-associated barnacles (*Octolasmis* sp.). This diatom dominant is described here as *Nagumoea hydrophicola* sp. nov., based on detailed observations of its frustule ultrastructure using light and scanning electron microscopy. The species is most similar to *N. serrata*, sharing a similar valvocopula morphology with two rows of pores. However, it can be distinguished from all currently known congeners by its lanceolate central area, short distal raphe endings not reaching the valve mantle, and doubly perforated abvalvar girdle bands. Environmental preferences of the new species are discussed in the context of its host's biology.

Keywords: marine diatom, epizoic, yellow-bellied sea snake, *Hydrophis platurus*, museum specimen, new species, barnacle, *Octolasmis*, taxonomy

Introduction

Diatoms are particularly efficient colonizers of any hard surface within the photic zone of the global ocean (e.g., Wahl 1989, Cooksey & Wigglesworth-Cooksey 1995, Railkin 2004). Substrata appropriate for diatom attachment and development include both biotic and abiotic objects, although there is growing evidence that the former, in particular, are not accessible to all benthic diatoms, which may lack necessary adaptations to thrive on living, physiologically active, and sometimes mobile surfaces. Numerous reports suggest that marine vertebrates, including cetaceans, manatees and sea turtles, are hosts to unique diatom communities (e.g., Nemoto 1956, Holmes et al. 1993, Denys 1997, Majewska et al. 2015, 2017a, 2019, Frankovich et al. 2016, 2018, Riaux-Gobin et al. 2017, 2020, Azari et al. 2020, Majewska & Goosen 2020, Van de Vijver et al. 2020), which have probably evolved effective adaptations to compete successfully for the resource of sun-lit hard surfaces that are generally scarce in the oceanic environment. As various epizoic diatoms appear

to be consistently associated with a specific group of animals (if not species), implying either geographical or ecophysiological isolation, it is probable that new diatom species will be discovered on as yet unexplored host species.

Sea snakes occupy tropical open-water habitats across the Indo-Pacific Ocean (Rasmussen 2001). Although more than 60 species of sea snakes have been described, with the great majority being entirely marine, the yellow-bellied sea snake (*Hydrophis platurus* L.) is the only pelagic species, and its distribution is wider than that of any other snake, extending from the waters adjacent to eastern Africa to the tropical eastern Pacific (Heatwole 1999, Lillywhite et al. 2010). Yellow-bellied sea snakes are viviparous, giving birth at sea, and do not intentionally leave the marine environment throughout their life (Rasmussen 2001, Lillywhite et al. 2010). Many aspects of the biology of yellow-bellied sea snakes are very poorly understood. For example, it is not clear whether they require fresh drinking water for physiological water balance or how they

*Corresponding author. E-mail: roksana.majewska@nwu.ac.za

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locate their feeding and mating grounds (Lillywhite et al. 2010). Very little is known about their epibionts (Key et al. 1995, Pfaller et al. 2012), and knowledge of sea snake epi-microbiota is virtually non-existent (Zann et al. 1975).

During a survey exploring epizotic diatoms associated with South African populations of yellow-bellied sea snakes, one diatom was found to be dominant on two of the three sea snake specimens analysed, as well as on the associated sea snake barnacles, *Octolasmis* sp. This diatom clearly resembled the five currently known members of the genus *Nagumoea* Witkowski et Kociolek but could not be satisfactorily assigned to any of those species. It is, therefore, described here as a new species *Nagumoea hydrophicola* Majewska sp. nov. The genus *Nagumoea* was erected relatively recently to accommodate two morphologically distinct diatom species previously included in *Denticula* Kützting (Witkowski et al. 2011), with three further species being subsequently included (Van de Vijver & Kociolek 2018, Majewska & Van de Vijver 2020). The genus is characterized by having isopolar, linear to linear-lanceolate valves with rounded apices and a raphe canal supported by robust anastomosing fibulae, but lacking a keel. Apart from *N. livingstonensis* Van de Vijver et Kociolek, which was described from a coastal pool in the maritime Antarctic region and whose ecological preferences are uncertain (Van De Vijver & Kociolek 2018), *Nagumoea* species are epibiotic, growing on seagrasses (Sullivan 2010, Majewska & Van de Vijver 2020), seaweeds (Sullivan 2010, Mayombo et al. 2019), and seabird feathers (Holmes & Croll 1984, Witkowski et al. 2011). The new species is described based on detailed morphological observations of its frustules using light (LM) and scanning electron microscopy (SEM) and comparisons with all known *Nagumoea* species.

Materials and methods

Samples were collected from three yellow-bellied sea snake specimens housed in the Port Elizabeth Museum Herpetology Collection, Port Elizabeth, South Africa, that were stranded and captured alive from three different beaches on the south-eastern coast of South Africa between 1969 and 1992 (Table 1). No cleaning procedures were applied to the euthanised sea snakes prior to preservation. To obtain diatom samples, the sea snake specimens stored in either 50% isopropanol or 10% formalin were placed on a tray and brushed with a plastic toothbrush.

Specimen PEM R25340 (alternative catalogue number ELM 238) showed significant skin sloughing, and brushing removed parts of the flaking external layer of the skin. Of the remaining sea snake specimens (PEM R25341, PEM R25342), brushing did not affect the skin appearance. Collected diatom samples were rinsed with distilled water and centrifuged. The pellets were placed in glass flat-bottomed flasks and digested for ca. 5 min in a mixture of boiling concentrated nitric (64%) and sulphuric (97%) acids following the method described by von Stosch (Hasle & Syvertsen 1997). When the liquid became colourless and transparent, the mixture was cooled, diluted with distilled water, and centrifuged for 10 min at 1400 g. The supernatant was decanted, and the diatom material was resuspended in distilled water and centrifuged. This cycle was repeated until the pH of the supernatant was near-neutral. Cleaned diatom frustules were mounted on glass slides using Pleurax (von Stosch 1974) and were examined using a Nikon 80i light microscope with Differential Interference Contrast (DIC) and a Nikon DS-Fi1 5MP digital camera (Nikon Instruments Inc., Melville, NY). On each slide, more than one thousand diatom valves were counted across arbitrarily chosen transects using LM to assess relative diatom abundances. For scanning electron microscopy (SEM), diatom material was filtered through 1-µm Isopore™ (Merck Millipore, Darmstadt, Germany) polycarbonate membrane filters that were subsequently mounted on aluminium stubs using carbon tape and left overnight under a ventilating hood to air-dry. Dried SEM specimens were sputter-coated with iridium using an Emitech K575X (Emitech Ltd., Ashford, Kent, UK) sputter-coater and analysed with a JEOL JSM-7001F (JEOL, Tokyo, Japan) scanning electron microscopes at 5 kV.

Four individuals of an unidentified species of a stalked barnacle, *Octolasmis* sp. (Fig. 1), were found attached to the neck and tail of sea snake specimen PEM R25340. They were carefully detached from the snake skin, and their morphology was documented using a Nikon AZ100M stereomicroscope (Nikon Instruments Europe, Amstelveen, Netherlands). The barnacles were then dehydrated by 1-h immersion in each of a succession of ethanol solutions (30%, 50%, 70%, 80%, 90%, 96%, 99.9%) and 7-min immersion in hexamethyldisilazane (HMDS; 30%, 50%, 100%). Specimens in HMDS were left in a fume hood to air-dry at room temperature. Dried barnacles were mounted on aluminium SEM stubs using carbon tape and sputter-coated with gold-palladium alloy using

Table 1. List of Port Elizabeth Museum (PEM) specimens of *Hydrophis platurus* collected from the Eastern Cape Province, South Africa, used in this study.

PEM catalog no.	Diatom sample no.	Collection site	Georeference	Collection date	Preservative
PEM R25340	SS001	Gonubie, East London	ca. – 32.9333, 28.0333	13th October 1969	50% isopropanol
PEM R25341	SS002	Gulu, East London	ca. – 33.1197, 27.7298	21st October 1988	50% isopropanol
PEM R25342	SS003	Hougham Park, Port Elizabeth	ca. – 33.7822, 25.7162	22nd September 1992	10% formalin

an SPI-Module Sputter Coater (SPI Supplies, Westchester, PA, USA). SEM images of diatoms still attached to the barnacle surface were produced using a Phenom Pro Desktop SEM (Phenom-World BV, Eindhoven, Netherlands).

Unmounted diatom material, stubs and slides are stored at the South African National Diatom Collection (North-West University, Potchefstroom, South Africa). The terminology used in the species description follows Round et al. (1990) and Witkowski et al. (2011). The new species has been described based on comparisons with all currently known *Nagumoea* species (Sullivan 2010, Witkowski et al. 2011, Van de Vijver & Kociolek 2018, Majewska & Van de Vijver 2020).

Results

Two of the three specimens of *Hydrophis platurus* analysed were dominated by an unknown species of *Nagumoea* (Table 1), which contributed more than 99.9% of the total diatom valves in both samples. Several valves of *Seminavis* sp. (sample SS001) and *Psammodictyon* sp. (sample SS003) were also observed when scanning the slides. Diatom communities on four specimens of the sea snake-associated barnacle, *Octolasmis* sp. (Figs 1–8), were compositionally the same as on the skin of the sea snake specimens hosting the barnacles (sample SS001). Sample SS002 contained only a few broken valves of an unidentifiable diatom species (most likely an *Achnanthes*). After comparison with all known members of *Nagumoea*, the dominant diatom could not be satisfactorily assigned to any of these and is thus described as a new *Nagumoea* species.

Nagumoea hydrophicola Majewska, sp. nov. (Figs 2–34)

Diagnosis

Central area lanceolate; external terminal raphe fissures short, not reaching the valve mantle; girdle bands doubly perforated.

Description

Cells solitary (chains or tubes not observed), motile or attached to substratum via a mucilaginous pad at one end of the valve (Figs 2–8).

Light microscopy (Figs 9–15)

Frustules in girdle view rectangular (Figs 9, arrow, 12). Valves apically and transapically symmetrical, or transapically slightly asymmetrical due to the unequal length of the raphe branches (see Figs 29, 31), linear to linear-lanceolate, with broadly (in smaller cells) to sub-acutely rounded apices (Figs 9, 11, 13–15). Margins straight, parallel to the valve face surface (Figs 9, 10, 12). Valve dimensions ($n = 45$): length 4–11.5 μm , width 1.0–1.5 μm , length/width ratio 3.7–8.1. Central nodule thickened (Figs 11, 13, 14, arrows). Raphe straight, centrally positioned,

barely discernible (Figs 11, 13, 14). Thickened fibulae visible in both valve and girdle view (Figs 9–15), 8–11 in 10 μm (max. 10 per valve).

Scanning electron microscopy (Figs 16–25)

External view. Valve face flat (Figs 16, 18) to very slightly convex (Fig. 17). Mantle deep, with a wide pore-free zone at the mantle edge (Figs 16–18). Valve face-mantle junction marked by greater separation between the valve face and mantle areolae (Figs 16–19). Striae composed of three to six irregular, roundish areolae (Figs 16–19). Stria density 44–48 in 10 μm . Valve face striae composed of a single areola (Figs 19–21). Occasionally additional smaller areolae present close to the raphe sternum (Figs 22–24, arrows). Mantle striae usually formed of two to three (sometimes four, very rarely five; Fig. 17, arrow) areolae (Figs 16–18). Central area small, lanceolate, slightly asymmetrical (Figs 19, 20, 22, 23). Raphe branches very slightly undulate (Figs 19, 22). Central raphe endings close to one another, coaxial, simple or very slightly expanded (Figs 19, 20, 22, 23). Terminal raphe fissures sharply deflected unilaterally, short, not reaching the valve mantle (Figs 19, 21, 22, 24).

Internal view. Central raphe endings simple, terminating on a thickened, apically elongated central nodule (Figs 25, 26, 28, 29, 31–33). Helictoglossae at the terminal raphe endings (Figs 27–33). Areolae covered with hymenes (Fig. 26, arrows). Anastomosing fibulae composed of connected arches extending transapically from the entire depth of the mantle, being the widest at the mantle edge and the valve-face-mantle junction (Figs 25–33). Openings between the fibulae of variable size and shape (Figs 25–33). Ridge connecting the lower arches along the valve face-mantle junction absent (Figs 25–33).

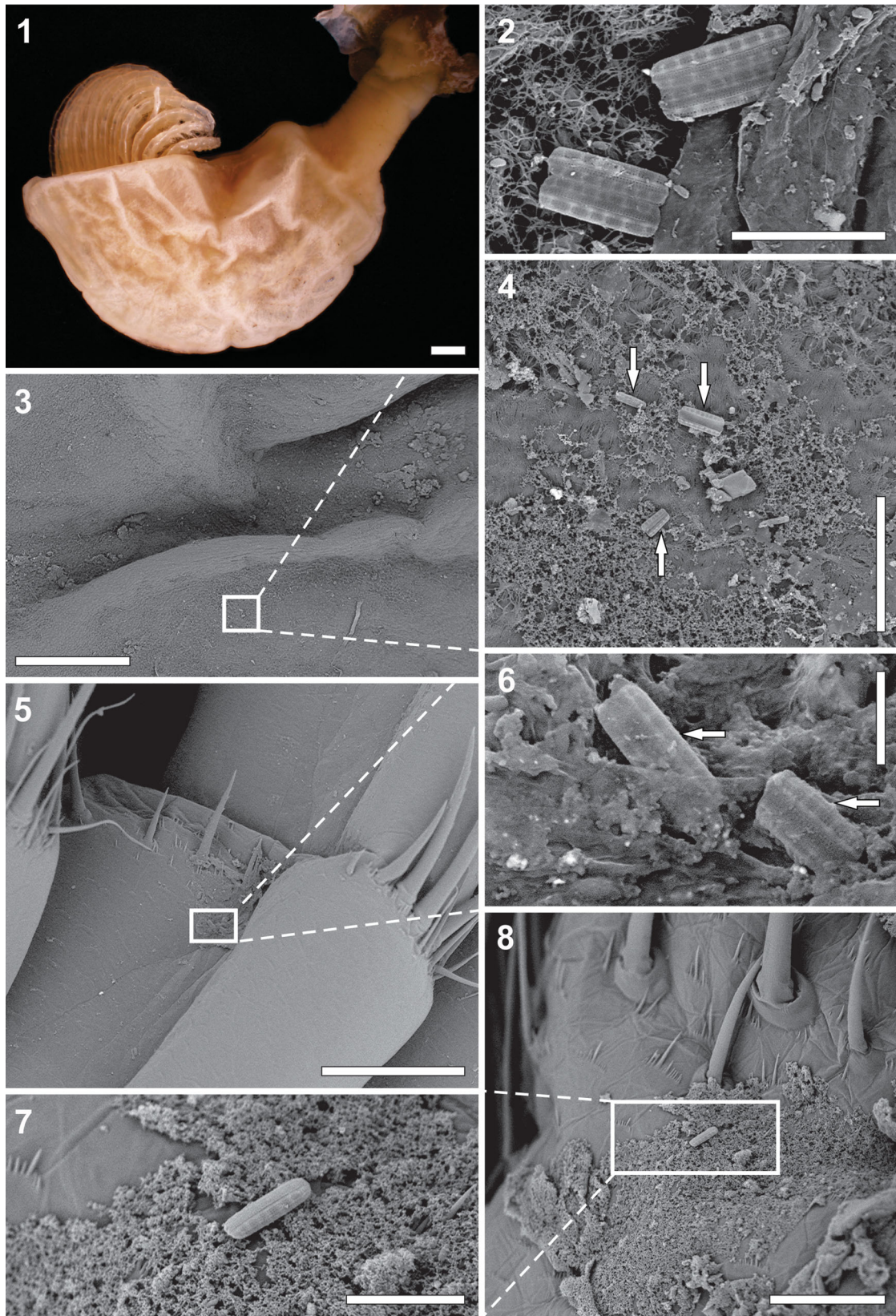
Cingulum composed of several open copulae (up to 4 observed; with additional delicate pleurae) perforated by 2 rows of rounded areolae, 45–50 in 10 μm (Figs 16, 34). Valvocopula with undulate pars interior (Fig. 34).

Holotype: Permanent slide SANDC-SS001 (prepared from sample SS001) deposited in the South African Diatom Collection at North-West University, Potchefstroom, South Africa.

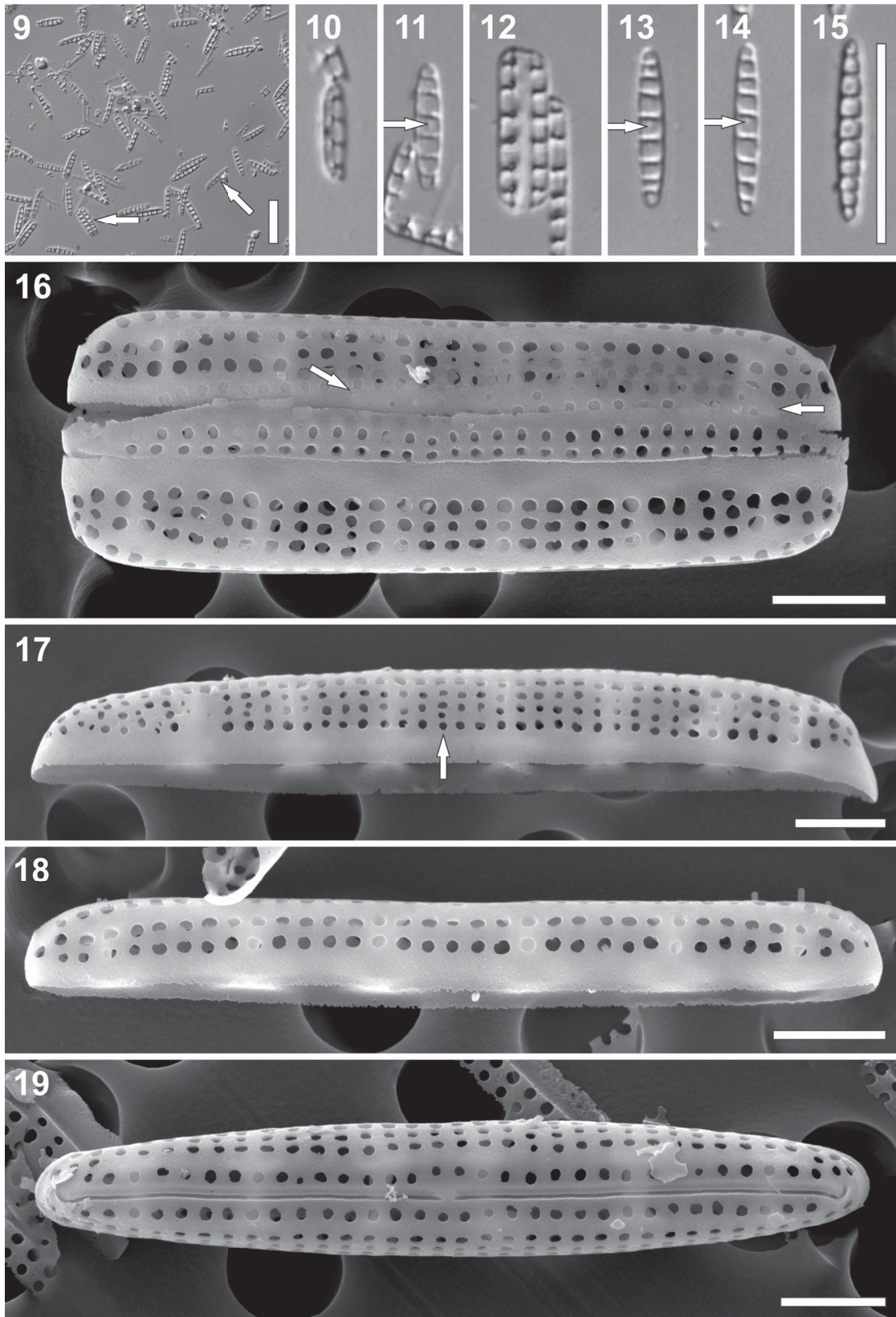
Isotype: Unmounted material SS001 deposited in the South African Diatom Collection at North-West University, Potchefstroom, South Africa.

Type locality: Sandy beach in Gonubie, East London, Eastern Cape, South Africa (no verbatim coordinates available; georeferenced to ca. –32.9333, 28.0333), collected from the skin of a stranded yellow-bellied sea snake *Hydrophis platurus* (leg. East London Aquarium), coll. date 13/10/1969.

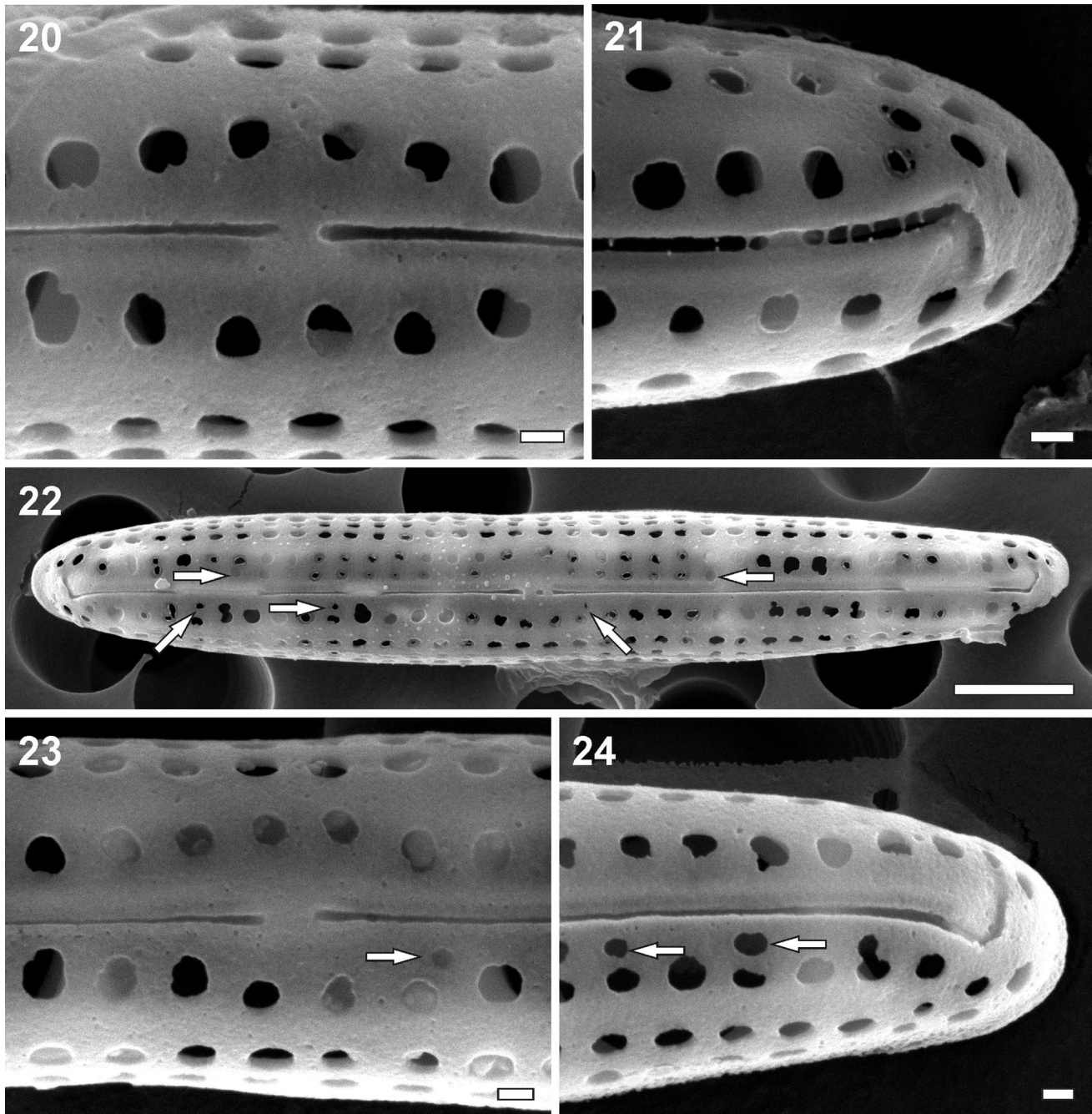
Etymology: The specific epithet is based on the generic name of the host *Hydrophis* and the Latin *-cola* ('inhabitant'). Its literal meaning is 'inhabitant of *Hydrophis*'.



Figs 1–8. Sea snake barnacle, *Octolasmis* sp. and epizoic *Nagumoea hydrophicola*. Fig. 1. Ethanol-preserved specimen of *Octolasmis* sp. (light microscopy). Figs 2–8. Scanning electron micrographs of *N. hydrophicola* on the barnacle surface. Fig. 2. Two pairs of recently divided cells (girdle view). Fig. 3. Barnacle surface (external side of the capitular cavity). Fig. 4. *N. hydrophicola* (arrows) on the external side of the capitular cavity of the barnacle. Figs 5, 8. Detail of the barnacle cirri. Figs 6, 7. *N. hydrophicola* (arrows) on the barnacle cirri. Scale bars: 1 mm = Fig. 1; 300 μ m = Fig. 3; 100 μ m = Fig. 5; 30 μ m = Figs 4, 8; 10 μ m = Figs 2, 7; 5 μ m = Fig. 6.



Figs 9–19. *Nagumoea hydrophicola* (type population). Figs 9–15. Light microscopy images. Fig. 9. Original community. Arrows indicate frustules and valves in girdle view. Fig. 10. Detached valve in girdle view. Figs 11, 13–15. Valve view. Arrows indicate the thickened central nodule. Fig. 12. Frustule in girdle view. Figs 16–19. Scanning electron microscopy images. Figs 16–18. Girdle view. Fig. 16. Frustule with partially detached girdle bands. Arrows indicate the doubly perforated abvalvar girdle band. Figs 17, 18. Detached valve. Arrow indicates an unusual mantle stria composed of five areolae. Fig. 19. External valve view. Scale bars: 10 μm = Figs 9–15; 1 μm = Figs 16–19.

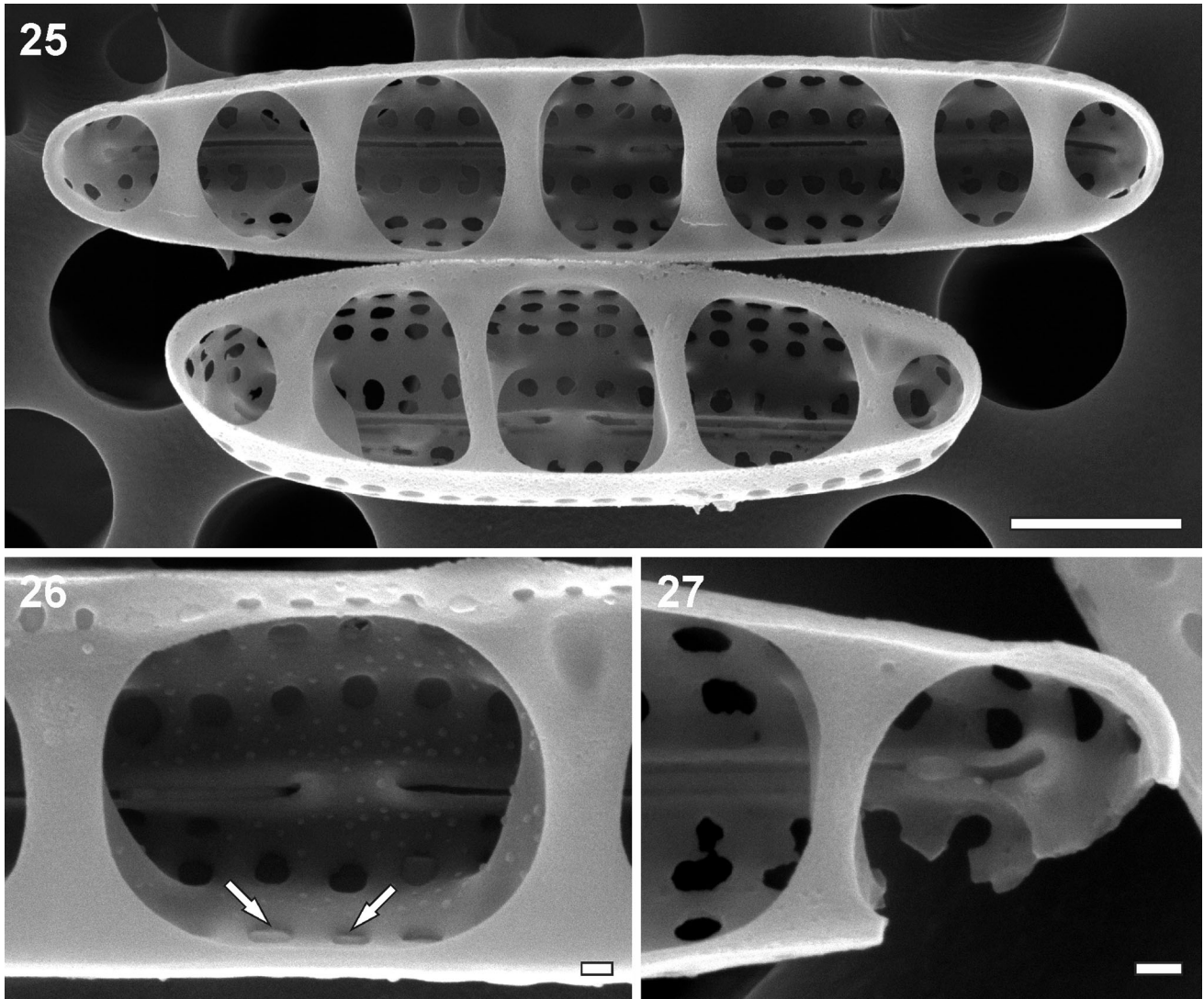


Figs 20–24. Scanning electron microscopy images of *Nagumoea hydrophicola* (type population). Fig. 20. Detail of the central area (external view). Fig. 21. Detail of the apex (external view). Fig. 22. External valve view of a specimen showing additional smaller areolae on the valve face (arrows). Fig. 23. Detail of the central area (external view). Arrow indicates an additional smaller areola. Fig. 24. Detail of the apex (external view). Arrows indicate additional smaller areolae. Scale bars: 1 μm = Fig. 22; 100 nm = Figs 20, 21, 23, 24.

Ecology: Only observed on the skin of two yellow-bellied sea snakes (*Hydrophis platurus*) stranded on South African beaches and sea snake-associated barnacles *Octolasmis* sp., but numerous, reaching almost 100% relative diatom abundance.

Discussion

The new species resembles its congeners in having relatively small rectangular frustules and linear to linear-lanceolate valves with rounded apices and distinct anastomosing fibulae, typical of the genus (Witkowski

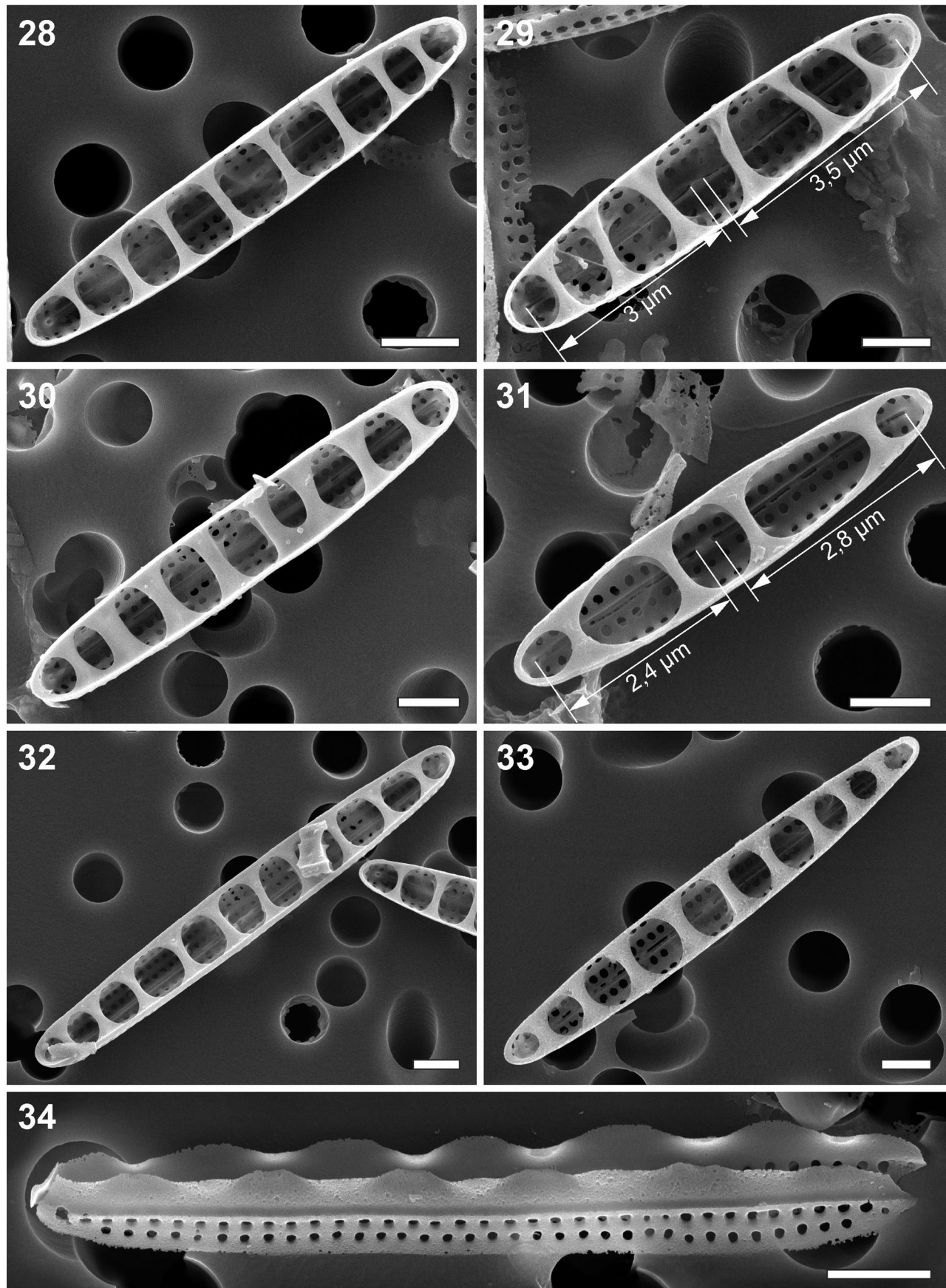


Figs 25–27. *Nagumoea hydrophicola* (type population). Fig. 25. Two valves in valve view (internal view). Fig. 26. Detail of the central area (internal view). Arrows indicate the undamaged hymenes. Fig. 27. Detail of the apex (internal view).

et al. 2011). It also possesses the scalariform valvocopula, flat valve face, deep mantle, and rounded hymenate areolae (Sullivan 2010, Witkowski et al. 2011, Van de Vijver & Kociolek 2018, Majewska & Van de Vijver 2020), and thus its placement within the genus is well justified. However, the new taxon shows features not previously reported for *Nagumoea*, including a lanceolate central area, short external terminal raphe fissures that do not extend onto the valve mantle, and two rows of pores in both the valvocopula and second copula. Apart from *N. hydrophicola*, the only known *Nagumoea* species with doubly perforated girdle bands is *N. serrata* Majewska et al. Van de Vijver. In the latter species, only the valvocopula has two complete rows of areolae, whereas the other copulae possess a single row of perforations with additional smaller pores in the apical parts of the bands (Majewska & Van de Vijver 2020). Moreover, the valvocopulae of *N. serrata* have well-developed digitate fimbriae rather than an undulating

advalvar edge as in *N. hydrophicola*, while the last-formed copula has a clearly serrated edge (hence the specific epithet), which was never observed in *N. hydrophicola*. It is worth mentioning that both the breadth of the fibulae and the size and shape of the openings between them are highly variable in *N. hydrophicola*. Therefore, although those features are listed as taxonomically important characters distinguishing *N. livingstonensis* from congeners (Van de Vijver & Kociolek 2018), their discriminative power may be limited, and, whenever possible, a larger number of valves should be analysed to accurately describe the intraspecific morphological variation within *Nagumoea* species and populations.

Although only three sea snake samples could be analysed at this time, with only two yielding identifiable diatoms, it is particularly interesting that *N. hydrophicola* contributed nearly 100% of the total diatom abundance in these two samples collected at different sampling sites 23



Figs 28–34. *Nagumoea hydrophicola* (type population). Figs 28–33. Internal valve views showing the variable breadth of the fibulae and the size and shape of the openings between them. Fig. 34. Valvocopula with undulate pars interior. Scale bars: 1 µm.

years apart. Both samples contained a very large number of *N. hydrophicola* valves, with no apparent morphological differences between the two populations. This suggests that *N. hydrophicola* may outcompete other diatom species encountered by its host that could potentially colonize sea snake skin. Scales of squamate reptiles (including sea snakes) possess micro- and nano-ornamentations (dermatoglyphics; Maderson 1966, Lillywhite & Maderson 1982) on their outermost, fully cornified layer (stratum corneum) that may provide an excellent attachment surface for diatoms. However, unlike the hydrophobic scales of sea kraits (Lillywhite et al. 2009, Lillywhite 2014, Spinner et al. 2014), the skin of *H. platurus* is hydrophilic (Lillywhite & Menon 2019), which may negatively affect the development of many surface-associated bacterial and diatom communities (Fletcher & Loeb 1979, Railkin 2004). Yellow-bellied sea snakes also undergo ecdysis, i.e., a complete periodical renewal of their epidermis (Lillywhite & Menon 2019), and thus the abundance of biofouling organisms on their skin will depend on the stage of the skin shedding cycle in which the biofilm sample was collected. This may explain the very low number of diatom remnants present in sample SS002, whereas the presence of adult barnacles *Octolasmis* sp. indicates that the epidermis of specimen PEM R25340 (sample SS001) had not been recently shed but exposed to biofouling for a longer period.

It would be premature to make unequivocal statements about the nature of the relationship between the epizoic *N. hydrophicola* and sea snakes in general or *H. platurus* specifically. Nevertheless, the current results contribute to discussions of diatom epizoism. It has been argued that animals with a fully oceanic lifestyle, such as leatherback sea turtles or many cetaceans, would host a lower number of diatom species due to, (1) a low frequency of physical contacts with benthic diatom biofilms that occur almost exclusively in shallow-water coastal regions, (2) lower and fluctuating levels of nutrients (including silica) available to diatoms in the open-ocean waters, and (3) high ecophysiological specificity and the uniqueness of the microniches provided by the body surfaces of marine vertebrates (Wahl 1989, Holmes et al. 1993, Majewska et al. 2017b, Majewska 2020). In open-water environments where, apart from the deep-sea bottom, hard surfaces are extremely rare, energetically and temporally adaptation to an epizoic lifestyle, which often comes at the price of poor competitiveness, may be advantageous. Thus, oceanic animals that rarely visit shallow-water coastal zones may be more likely to host exclusively epizoic species of epibionts, including diatoms.

The yellow-bellied sea snake is the only pelagic sea snake species (Solórzano 2004) and its contact with any benthic substrata that would harbour diverse diatom communities is probably extremely limited. This raises the question of how an epizoic diatom flora composed of surface-associated, non-planktonic forms could be

recruited. Various species of the barnacle genus *Octolasmis* Gray have been observed on several sea snake species, including *Hydrophis platurus*, and it is believed that some members of this genus are obligate epibionts on sea snakes (Jeffries & Voris 1979). It was previously proposed that cirriped larvae present in the plankton may serve as vectors for epizoic diatoms, facilitating diatom colonization of different substrata and hosts (Majewska et al. 2019). However, in the case of the host-specific barnacles, those transfers would only occur intra-specifically and would not increase the overall diversity of epizoic diatoms present on a given host species. The current study may support this hypothesis, as the diatom communities on both sea snake skin and its epizoic barnacles were composed of the same species, the absolute dominant *N. hydrophicola* and the rare *Seminavis* sp. Yellow-bellied sea snakes give birth to their young at sea, and it is possible that epizoic diatoms are transferred directly from the mother's skin to the new-born, as has been proposed for both manatees (Frankovich et al. 2018, Majewska & Goosen 2020) and cetaceans (Holmes et al. 1993). Although the physical contact between adult and young sea snakes may be much briefer than in mammals (e.g., cetaceans, manatees), whose infants require prolonged and frequent contact with their mothers to feed and receive other vital support from the adult individuals, *H. platurus* is believed to drift passively close to the ocean surface (Dunson & Ehlert 1971). Most likely due to this behaviour and lifestyle, yellow-bellied sea snakes are often associated with so-called oceanic slicks, i.e., drift lines where foam, organic particles (including living plankton), and flotsam (including floating plants and seaweeds) accumulate. Sea snakes may use oceanic slicks as a source of fish prey that are attracted to the floating debris for shelter or food (Kropach 1975, Heatwole 1999). Slicks would also expose the sea snake skin to a higher concentration of potential biofoulers, including hard surface-associated diatoms. Several *Nagumoea* species are known from biotic substrata (Holmes & Croll 1984, Sullivan 2010, Witkowski et al. 2011, Mayombo et al. 2019, Majewska & Van de Vijver 2020), and in the absence of survey data it cannot be excluded that *N. hydrophicola* thrives on seaweeds or seabird feathers that are encountered by sea snakes in these ecologically important convergence zones. However, the very high abundances of this diatom species on the sea snake skin suggest that the epizoic habitat is the preferred environment of the new taxon. Concentrations of sea snakes around oceanic slicks would improve not only their opportunity for mating (Kropach 1975) but also the probability of exchanging epizoic diatoms between individuals.

This study is the first to explore diatom community composition on sea snakes. Undoubtedly, the continuing exploration of various marine biotic substrata will reveal the true diversity of diatom forms and offer intriguing new avenues in diatom and microbiome research. The current study takes advantage of historical zoological collections

of marine vertebrates, once more proving that specimens collected decades ago may still constitute an excellent source of well-preserved epizoic diatom frustules that otherwise might be difficult to obtain from the living wild animals (Majewska et al. 2018, 2019).

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Disclosure statement

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ORCID

ROKSANA MAJEWSKA  <http://orcid.org/0000-0003-2681-4304>

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