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To cite this article: Roksana Majewska, Käthe Robert, Bart Van de Vijver & Ronel Nel (2020) A new species of *Lucanicum* (Cyclophorales, Bacillariophyta) associated with loggerhead sea turtles from South Africa, Botany Letters, 167:1, 7-14, DOI: [10.1080/23818107.2019.1691648](https://doi.org/10.1080/23818107.2019.1691648)

To link to this article: <https://doi.org/10.1080/23818107.2019.1691648>



Published online: 13 Nov 2019.



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A new species of *Lucanicum* (Cyclophorales, Bacillariophyta) associated with loggerhead sea turtles from South Africa

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ABSTRACT

A new *Lucanicum* species, *L. ashworthianum* Majewska, K.Robert & Van de Vijver *sp. nov.*, was found in multiple samples of biofilm growing on loggerhead sea turtles *Caretta caretta* and their symbiotic barnacles *Chelonibia testudinaria* collected on the beaches of Kosi Bay, eastern coast of South Africa, during the two nesting seasons (the austral summers of 2017/2018 and 2018/2019). The new species possesses several features typical of the genus *Lucanicum*, including the uniseriate striae composed of one large macroareola, the presence of large apical slit fields and transapically elongated rimoportulae at both poles, and a cingulum composed of numerous open, doubly perforated copulae. It differs from the only other *Lucanicum* species known to date, the coral-associated *L. concatenatum*, in having considerably smaller cells with clearly rostrate or sub-capitate apices and internal rimoportula opening composed of a C-shaped inner lip and an oval, flap-like outer lip – a feature not observed previously in *Lucanicum*. Based on these new observations, an amendment of the genus description is proposed.

ARTICLE HISTORY

Received 6 November 2019

Accepted 6 November 2019

KEYWORDS

Barnacle; biofilm; epibiosis; epizoid diatom; Indian Ocean; loggerhead; marine; South Africa

Introduction

It is a well-agreed fact that even the relatively easily accessible shallow-water marine habitats harbour a difficult to assess, though likely very high, number of yet undescribed organisms. The discovery of novel taxa is, however, inevitably limited by the inconsistent and uneven sampling effort. Recent studies clearly show that rarely explored marine substrata, such as carapaces and skin of sea turtles, may constitute excellent and ecologically unique habitats for a range of macro- and micro-organisms not observed on other types of surfaces (Hollenberg 1971; Monroe and Limpus 1979; Serio et al. 2011; Frankovich et al. 2015, 2016; Majewska et al. 2015, 2017a, 2018, 2019).

Diatom communities constitute an essential element of the sea turtle microflora (Majewska et al. 2017b, 2018), though many of the observed taxa remain unidentified and undescribed. Identifying members of epibiont communities allows us to characterize the epibioses, which can inform on ecology and migration patterns of the host as well as biogeography and evolutionary relationships among epi- and basibionts (Robinson et al. 2016). Epizoid organisms include both the truly epizoid taxa (i.e. species that require the substratum of an animal host) and opportunistic species that live in the surrounding planktonic or benthic environments and are occasionally

transferred to the biofilm. Truly epizoid taxa may be associated with a specific host species, or may thrive on a group of closely related species, and are likely well-adapted to, or dependent on, the microhabitat sculptured by host animal physiology. Opportunistic taxa may show host specificity as well, as different host species and populations exhibit different feeding behaviours and migration patterns bringing them in contact with different surrounding environments. The number of specialized truly epizoid sea turtle-associated taxa may be significantly lower than that of opportunistic taxa that originate from a larger pool of species in a diverse and more variable surrounding environment. The proportion of these two groups is currently unknown on sea turtles, and our knowledge is limited by the largely incomplete characterization of the epizoid flora.

The diatom genus *Lucanicum* Lobban & Ashworth was originally described, and has so far been only observed, on living blue corals (*Heliopora coerulea* Pallas 1766) inhabiting the benthic ecosystems in the vicinity of Guam, western Pacific. The genus is characterised by having linear valves with broadly rounded apices, uniseriate striae composed of one macroareola, well-developed apical slit fields at both poles, the presence of one rimoportula with equal labia at each apex, and numerous copulae showing two rows of slits

(Lobban and Ashworth 2014a). Based on available morphological and molecular data, it was tentatively placed within Cyclophorales (Cyclophoraceae) as the phylogenetic analysis indicated its close relationship to other araphid genera such as *Astrosyne* Ashworth & Lobban, *Cyclophora* Castracane, and *Florella* J.N. Navarro (Lobban and Ashworth 2014a).

The present study describes a second species of *Lucanicum*, *L. ashworthianum* Majewska, K.Robert & Van de Vijver, *sp. nov.*, found in multiple biofilm samples, collected from loggerhead sea turtles (*Caretta caretta* L.) and their commensal barnacles (*Chelonibia testudinaria* L.) (Zardus and Hadfield 2004) during two nesting seasons on the beaches of Kosi Bay, iSimangaliso Wetland Park, eastern coast of South Africa. The new taxon bears a clear resemblance to the only other currently known member of the genus, *L. concatenatum* Lobban & Ashworth, but exhibits a few distinct features that justify its description as a new species (Lobban and Ashworth 2014a). Upon the description of this novel species and additional morphological observations, the original description of the genus *Lucanicum* is emended.

Materials and methods

Sampling site

Biofilm and barnacle samples examined in this study were collected from the carapaces of egg-laying loggerhead sea turtles on the beaches of Kosi Bay (Indian Ocean), South Africa during the two consecutive nesting seasons in December 2017, December 2018, and January 2019. Observed sea turtles were encountered and examined for epibionts during the night monitoring patrols along the beach within a circa 6-km stretch north from the Bhanga Nek field station, a zone with the highest density of the loggerhead nests in South Africa (Nel et al. 2013). Here, on the northern beaches of iSimangaliso Wetland Park, the South African sea turtle monitoring programme is successfully conducted since 1973 (Nel et al. 2013).

Diatom material collection and processing

Epizoid diatom samples were collected from the lateral and posterior parts of the sea turtle carapaces. Each time, approximately 20–25 % of the carapace was vigorously brushed with a single-use toothbrush to remove the carapace-associated diatom biofilm. After collection, the material was placed in separate 50 ml plastic tubes and preserved immediately in 70 % ethanol solution following the sampling protocol proposed by Pinou et al. (2019). When present, barnacles were carefully detached from the carapace using a plastic paint scraper or a blunt knife, placed in separate plastic bags, and frozen (−20°C) after returning to the field

station, i.e. within 1–6h of collection. All materials were taken by, or under close supervision, of highly qualified researchers. The procedures involved in this study respect ethical standards in the Declaration of Helsinki (World Medical Association 2013) and all applicable national laws.

In total, 65 barnacle and 156 (skin and carapace) biofilm samples collected from 78 loggerhead sea turtles were analysed for diatoms. To detach diatoms from the barnacle surface, frozen barnacle samples were placed in separate glass beakers with ca. 25–50 ml of distilled water and sonicated for 30 minutes in a Transsonic T310 (Elma, Singen, Germany) ultrasound bath following the protocol previously used by Majewska et al. (2018). Subsequently, the barnacles were removed from the beakers and the remaining liquid was left under the fume hood for ca. 24h, which allowed a significant reduction of the sample volume. To remove all organic matter from both carapace and barnacle samples, small portions of diatom material were digested with a mixture of boiling concentrated acid (55 % nitric acid and 98 % sulphuric acid added at a 2:1 volume ratio) following a slightly modified method by von Stosch (Hasle and Syvertsen 1997). The boiling time ranged from ca. 3 to 15 min depending on the amount of organic matter present in the sample. Digested material was then rinsed with deionized water and centrifuged several times at 1400 x g (2500 rpm in a rotor with radius[max] 20 cm) to remove the excess acid. For light microscopy (LM) analysis, permanent slides were prepared using Naphrax® and observed under an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and the Olympus UC30 Imaging System. Samples and slides are deposited in the South African Diatom Collection housed by North-West University (South Africa) and the BR-collection housed by Meise Botanic Garden (Belgium). For scanning electron microscopy (SEM), portions of the cleaned diatom material were filtered through a 1.2-µm Isopore™ polycarbonate membrane filter (Merck Millipore) that were then mounted on aluminium stubs with carbon tape. The stubs were sputter-coated with a gold-palladium layer of ca. 20 nm and examined with a JEOL JSM-7001F FEG scanning electron microscope at 3 kV (Centre for High Resolution Electron Microscopy, Nelson Mandela University, Port Elizabeth, South Africa).

Diatom terminology used in the current paper follows Ross et al. (1979), Round et al. (1990), and Lobban and Ashworth (2014a). The morphology of the new taxon has been compared with the ultrastructure of the other known *Lucanicum* species (Lobban and Ashworth 2014a) and several related araphid diatom genera, currently placed within Cyclophorales Round & Crawford, emend. Lobban & Ashworth such as *Cyclophora* Castracane and *Neosynedra* D.M. Williams & Round.

Results

Description

Lucanicum ashworthianum Majewska, K.Robert & Van de Vijver, sp. nov. (Figures 1–17)

LM (Figures 1–6): Frustules isovalvar, lightly silicified and fragile (intact frustules not observed in cleaned material; Figures 1–6). Valves araphid, linear to linear-elliptic with almost parallel to weakly convex margins and broadly rounded rostrate to sub-capitate apices (Figures 1–6). Valve dimensions ($n = 25$): length 20–45 μm , width 4.5–9.5 μm . Axial area very narrow, discernible in LM (Figures 2–6) as a thickened sternum. One transapically elongated rimoportula present at each apex on the opposite sides on the sternum (Figures 3, 4 and 6, arrows). Striae indiscernible, except for those with broken areola occlusions (Figures 2 and 5).

SEM (Figures 7–17): Valve face flat, with shallow mantle, lacking a distinct valve face-mantle junction (Figures 7–10). Axial area very narrow, linear (Figures 7–11). Central area absent (Figure 7). Striae uniseriate, 44–48 in 10 μm , parallel or nearly parallel and equally spaced throughout the entire valve, continuing without interruption onto the shallow mantle, almost reaching the mantle edge, composed of one macroareola, except for the apical areas (Figures 7–11). At the apices, striae composed of up to 9 rounded or transapically elongated areolae (Figures 8–10). Areolae occluded externally by perforated vela (Figures 8–11). Transapically elongated rimoportula adjacent to the axial area at each of the apices, on the opposite sides of the sternum (Figure 7, arrowheads, Figures 8–10). Large oval apical slit field composed of 10–15 slits starting on the valve face and continuing onto the mantle on both apices (Figures 7–10). An irregular row of simple pores on the valve face bordering the apical slit field (Figures 8–10).

Internally, axial area thickened and slightly raised (Figures 12 and 13). Areolae sunken between the slightly thickened virgae, covered externally by vela (Figures 12 and 13). Rimoportulae at the apices with asymmetrical labia forming a C-shaped opening perpendicular to the sternum (Figures 12 and 13).

Cingulum composed of numerous (~12) open copulae, each perforated by two rows of squarish, rectangular (transapically elongated), or irregularly shaped areolae, ca. 60 in 10 μm (Figures 14–17). Areolae on the cingulum occluded externally by vela (Figures 14–17). Last-formed, “immature” (Lobban and Ashworth 2014b) copula with large, transapically elongated areolae opened towards the opposite valve at the ligula (Figure 14, arrow, Figure 15, arrowheads).

Holotype. Permanent slide BR-4572 deposited in the BR-collection, Meise Botanic Garden, Belgium.

Isotype. Permanent slide SANDC-ST010 deposited in the South African National Diatom Collection, North-West University, South Africa.

Type locality. Kosi Bay, iSimangaliso Wetland Park, South Africa (26° 59' 38.9" S, 32° 51' 59.8" E). Collected from the carapace of a nesting loggerhead sea turtle *Caretta caretta* (tag numbers ZA0447D, ZA0427D), by F. De Ridder, 16 January 2018

Etymology. The specific epithet honours Dr Matt P. Ashworth (The University of Texas at Austin, USA), the co-author of the genus, in recognition of his important contribution to marine and epizoic diatom research.

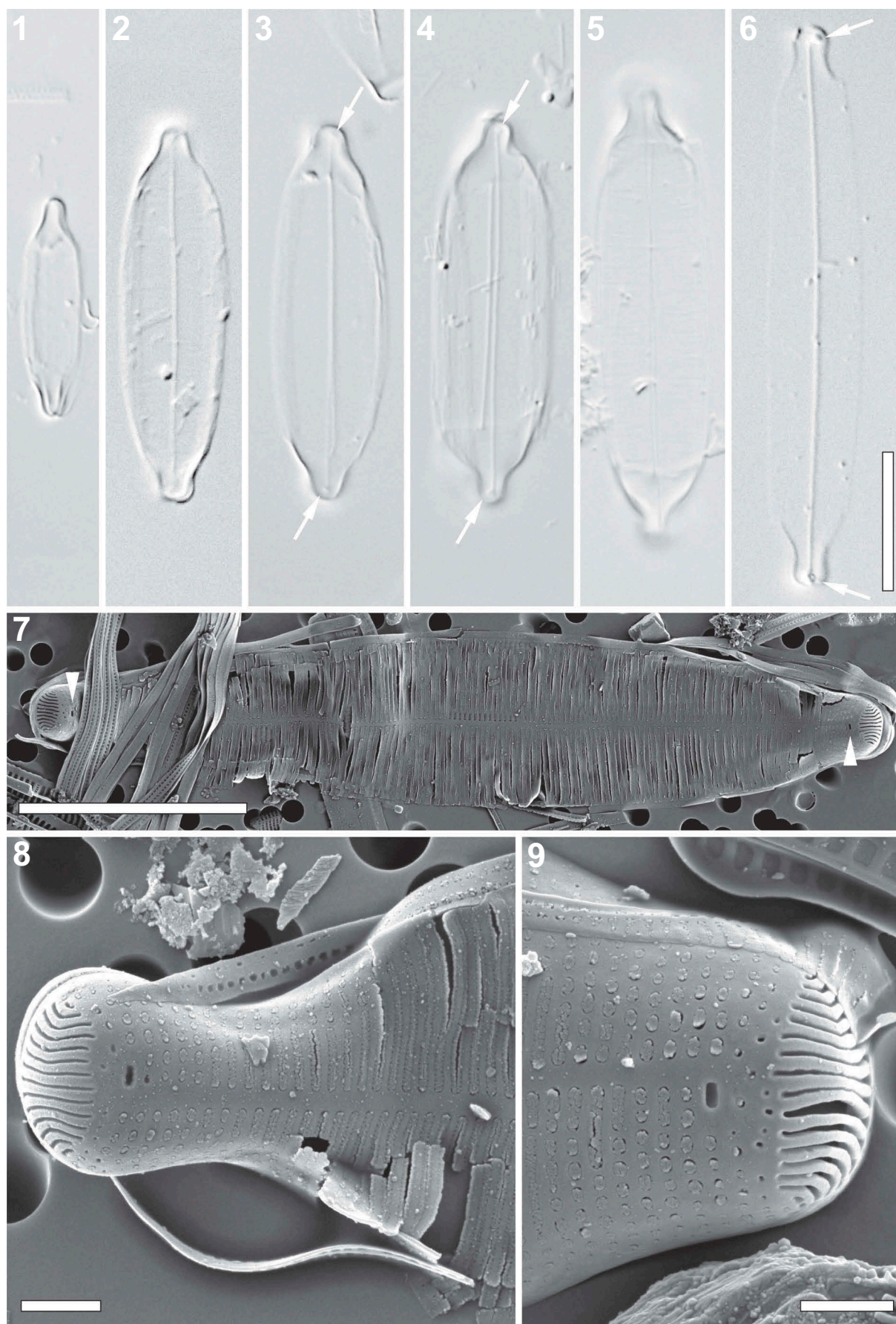
Ecology. *Lucanicum ashworthianum* was found in multiple biofilm samples collected from carapaces of loggerhead sea turtles and their associated barnacles (*Chelonibia testudinaria*) during two nesting seasons in Kosi Bay, eastern coast of South Africa. The taxon contributed up to ca. 5% to the total diatom abundance. All samples containing *L. ashworthianum* were dominated by small-celled taxa, such as the so-called marine “gomphonemoids” (*Poulinea* Majewska, De Stefano & Van de Vijver/*Chelonicola* Majewska, De Stefano & Van de Vijver complex) and *Nitzschia* spp., the former being particularly abundant in the carapace samples. Often, however, several other erect or chain-building araphid taxa, such as *Cyclophora* spp., *Hyalosira* spp., *Licmophora* spp., *Microtabella* sp., and *Striatella unipunctata* (Lyngbye) C.Agardh were also present. *Lucanicum ashworthianum* was found neither in the biofilm (twelve samples collected from twelve sea turtles) nor on barnacles (eight samples collected from eight sea turtles) growing on leatherback *Dermochelys coriacea* Vandelli sea turtles nesting in the same area during the same sampling seasons (Majewska R., unpublished).

Emended description of *Lucanicum*

Based on the new observations, we propose to emend the generic description of *Lucanicum* removing the equal labia in the internal opening of rimoportula as a character specific to the genus.

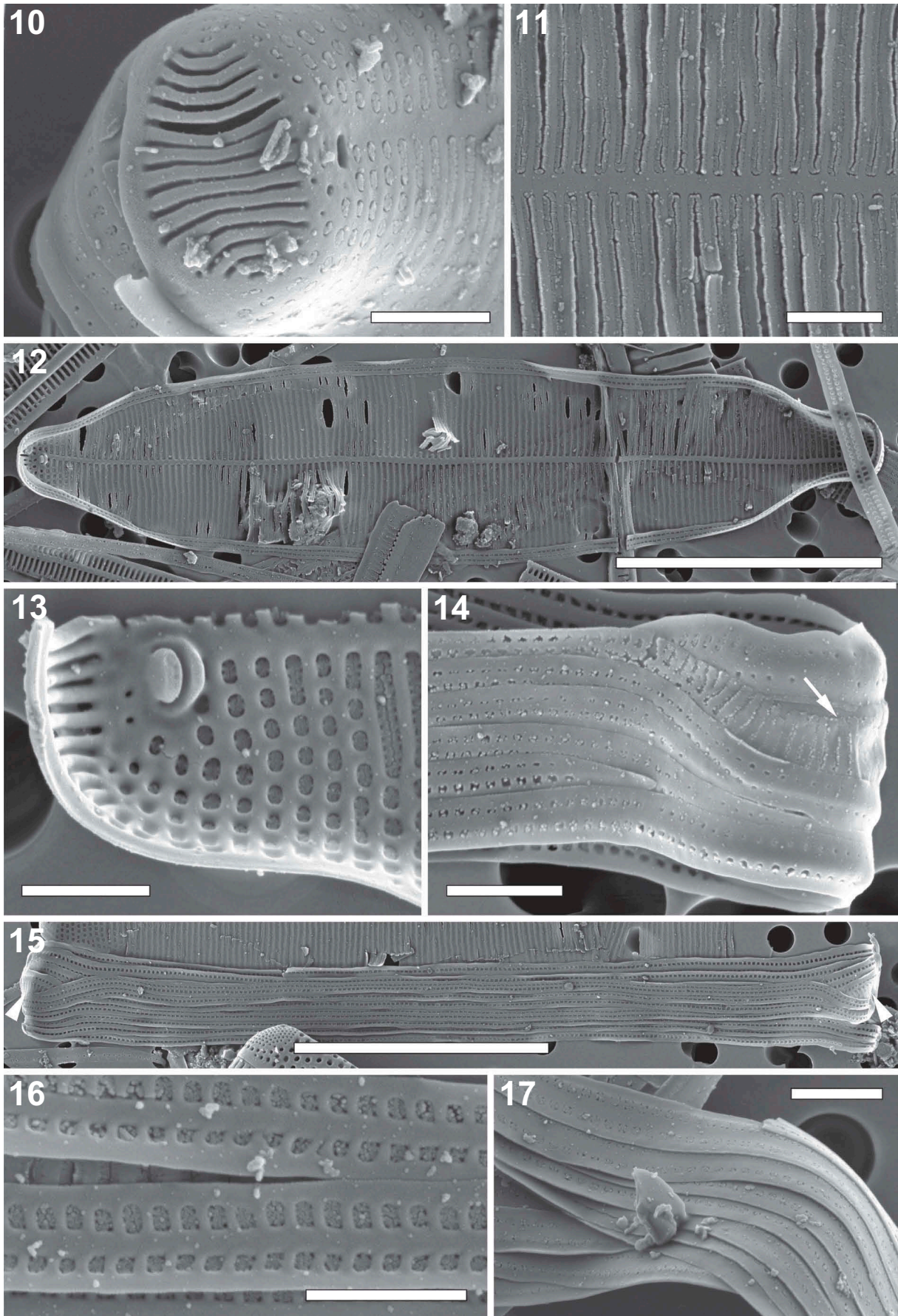
Lucanicum Lobban & Ashworth emend. Majewska, K.Robert & Van de Vijver

Valves araphid with broadly rounded apices, narrow sternum, and apical slit field at each of the poles. Striae uniseriate, nearly parallel throughout the entire valve, consisting of one macroareola, except for the apices. At the apices, striae composed of several smaller areolae. Transapically elongated rimoportula, with



Figures 1–9. *Lucanicum ashworthianum* sp. nov. Figures 1–6. Light micrographs. Specimens in valve view. Arrows indicate the apical rimoportulae. Figures 7–9. Scanning electron micrographs. Figure 7. External valve view. Arrowheads indicate the apical rimoportulae. Figures 8 and 9. Apical part of the frustule (external view). Figure 8. Specimen with sub-capitate apices. Figure 9. Specimen with rostrate apices.

Scale bars: **Figures 1–7** = 10 μ m; **Figures 8 and 9** = 1 μ m.



Figures 10–17. *Lucanicum ashworthianum* sp. nov., scanning electron micrographs. Figure 10. Apical part of the valve showing the oval slit field (external view). Figure 11. Central part of the valve showing striae composed of a single macroareola (external view). Figure 12. Internal valve view. Figure 13. Apical part of the frustule (internal view). Figures 14 and 15. Girdle bands (external view). Arrow and arrowheads indicate the last-formed copula with large, transapically elongated areolae opened towards the opposite valve at the ligula. Figures 16 and 17. Girdle bands. Images showing areolae externally occluded by vela. Figure 16. Internal view. Figure 17. External view.

Scale bars: **Figures 10, 11, 13, 14, 16 and 17** = 1 µm; **Figures 12 and 15** = 10 µm.

either equal or asymmetrical labia, adjacent to the axial area at each of the apices, on the opposite sides of the sternum. Girdle bands open, with two rows of squarish, rectangular (transapically elongated), or irregularly shaped areolae.

Discussion

Since the new taxon exhibits several distinct features, such as parallel striae composed of one macroareola, the open, doubly perforated girdle bands with squarish or rectangular areolae, rimoportula at each apex lying on the opposite sides of the sternum, and distinct apical slit fields at both poles (Lobban and Ashworth 2014a), a careful morphological analysis allowed its rather unambiguous placement within the genus *Lucanicum*. Other genera showing similar features include *Neosynedra* and *Cyclophora*, based on the presence of the apical slit fields and the structure of the multiple, doubly perforated girdle bands. Both genera however possess cribrate, uniseriate striae as opposed to one macroareola per stria in *Lucanicum*. Moreover, *Cyclophora* has pseudosepta on its valves (absent in both *Lucanicum* and *Neosynedra*) excluding the genus as possible host for the new species (Lobban and Ashworth 2014a).

Lobban and Ashworth (2014a) documented the multiple, ribbon-like plastids in *L. concatenatum* that differed clearly from the four plate-like plastids observed in *Neosynedra*, and proposed this feature as a character distinguishing *Lucanicum* from *Neosynedra*. Although the number and shape of plastids in *L. ashworthianum* could not be documented at this time, we believe that, based on the currently available information presented and discussed above, the new taxon is best placed in the genus *Lucanicum*.

The new taxon differs from the only other currently known *Lucanicum* species, *L. concatenatum*, in having considerably smaller cells (110–140 µm vs 20–45 µm, for *L. concatenatum* and *L. ashworthianum*, respectively) with clearly rostrate or even sub-capitate apices (absent in *L. concatenatum*). The distinct apical slit fields are composed of a smaller number of apically elongated slits (~20 in *L. concatenatum* vs 10–15 in *L. ashworthianum*) that show no horizontal breaks (as opposed to the slit pattern observed in *L. concatenatum*). Moreover, except for a few irregular pores adjacent to the apical slit field beyond the apical rimoportula, striae in *L. ashworthianum* are nearly parallel throughout the entire valve, whereas striae in *L. concatenatum* become clearly radiate at the valve apices (Lobban and Ashworth 2014a, figs 2C & 2E). Further dissimilarities include differences in the internal structure of the rimoportula opening, which is composed of two equal labia in *L. concatenatum* but possesses a C-shaped (or crescent-shaped) inner lip and an oval, flap-like outer lip, resembling the

structure present in *Neosynedra* (Williams and Round 1986; Lobban and Ashworth 2014a), in *L. ashworthianum*.

As previously highlighted, further studies, including observations of live material and DNA analyses, exploring a wider variety of marine substrata and geographic regions are required to better assess the phylogenetic relationship between *Lucanicum* and *Neosynedra*, and more satisfactorily resolve the families within Cyclophorales (Lobban and Ashworth 2014a).

In the current study, an ultrasound bath was used to detach diatoms from the hard-surfaced animal tissue. Although it was suggested that such treatment may significantly increase the number of broken and damaged frustules in the cleaned material and the technique should be used with caution (Majewska et al. 2019), similar effects of sonication were not observed during the diatom ultrastructure analysis, as *Lucanicum* specimens extracted from both non-sonicated carapace biofilm samples and sonicated barnacle samples presented a very similar degree of frustule damage.

Lucanicum ashworthianum is yet another taxon described recently from the biofilm covering sea turtles and their macroepibionts. Interestingly, *L. concatenatum* has so far been only observed growing on blue corals (*Heliopora coerulea*) and it cannot be excluded that this genus prefers animal or living substrata. However, considering the extremely large number of biotic and abiotic habitats and geographical areas that have not yet been sampled for diatoms, the level of host specificity in *Lucanicum*, as in many other newly described animal-associated taxa (e.g. Frankovich et al. 2015; Majewska et al. 2017a, 2018, 2019), cannot be reliably assessed at this time, and further studies and observations are necessary to provide the more detailed data on epizoic diatoms worldwide.

Acknowledgments

All sampling activities were carried out under research permits issued by the South African Department of Environmental Affairs (RES2016/67, RES2017/73, RES 2018/68, and RES 2019/05). The authors are grateful to Diane ZM Le Gouvello du Timat, Anthony Evlambiou, and Wynand van Losenoord (Nelson Mandela University, South Africa) for their invaluable help during the material collection. Franco De Ridder (North-West University, South Africa) and Christopher R. Nolte (Nelson Mandela University, South Africa) collected some of the samples containing the new taxon, Danay Stoppel and Carla Swanepoel (North-West University, South Africa) performed some of the laboratory procedures, and William Goosen (Nelson Mandela University, South Africa) assisted during the scanning electron microscopy observations. The authors further thank Prof. Jan Neethling and the team from the Centre for High Resolution Electron Microscopy (Nelson Mandela University, Port Elizabeth, South Africa)

for their generous support of this project and the possibility to use the scanning electron microscope. Luc Ector and one anonymous reviewer are thanked for their useful comments on the previous version of this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was done with partial financial support from The Systematics Association (UK) through the Systematics Research Fund Award granted to R. Majewska (2017).

Notes on contributors

Roksana Majewska is a post-doctoral research fellow at North-West University, South Africa. Her studies focus mainly on the ecology and taxonomy of marine and brackish diatoms. She has collaborated on various multidisciplinary projects in subjects including biotechnology, geology, biophysics, nanostructures, pharmacology and medicine. Nevertheless, her primary interests remain in microbial biology and biodiversity. One of her current research projects deals with the phenomenon of diatom epibiosis and surface associations in marine communities. Author's contribution: original concept and supervision of the sea turtle diatom project in South Africa, material collection and processing, microscopic analyses, writing the manuscript.

Käthe Robert graduated in biology (MSc), with a specialization in biodiversity, conservation and restoration, at the University of Antwerp in Belgium. Her master thesis focusses on the diversity of epibiotic diatom communities associated with loggerhead sea turtles from four geographically different populations. She likes to practice nature photography and scuba diving, especially in a scientific context. As a volunteer, she participated in a coral reef monitoring project in Egypt with the Red Sea Environmental Center, where she obtained a Reef Check Ecodiver certificate. She plans to follow an educational master program while staying involved in the epibiotic diatom research as a volunteer at the Meise Botanic Garden. Author's contribution: material processing, microscopic analyses, editing the manuscript.

Bart Van de Vijver is a full-time researcher at the Meise Botanic Garden, Belgium, and a part-time professor at the University of Antwerp, Belgium. His research focuses mainly on the taxonomy, morphology and biogeography of Antarctic freshwater and terrestrial diatoms. He has been studying diatoms in various parts of the Antarctic region for more than 20 years. His second research topic concentrates epizoic diatoms living on marine vertebrates. He has described almost 400 new taxa and revised an additional 250 taxa. Author's contribution: microscopic analyses, discussing the results, editing the manuscript.

Ronel Nel is an academic and marine ecologist at Nelson Mandela University, South Africa with specializations in sandy beach ecology, coastal conservation and management and sea turtle biology and conservation. She has more than 40 publications that investigate aspects of ecosystems function and match conservation policy with sound science. Author's contribution: providing access to the research

station and equipment, organizing fieldwork, editing the manuscript.

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