Majewskaea gen. nov. (Bacillariophyta), a new marine benthic diatom genus from the Adriatic Sea

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Abstract: During a survey of the diatom flora attached to carapaces of loggerhead sea turtles (Caretta caretta) from the Adriatic Sea, a large population of an unknown marine achnanthoid species was observed that could not be assigned to any of the currently described monoraphid diatom genera. Detailed morphological analysis based on scanning electron microscopy observations and comparison with a large number of monoraphid genera such as Madinithidium, Scalariella, Kolbesia and Karayevia, resulted in the description of the new benthic marine genus Majewskaea gen. nov. with the newly described Majewskaea istriaca sp. nov. as generitype. The new genus is characterized by a sternum valve showing a clear recurving ridge surrounding the entire valve margin, the presence of macroareolae closed internally by perforated hymenes, separated by a longitudinal hyaline area, a well–developed sternum and vestigial raphe slits. The raphe valve has a simple straight raphe with bent terminal fissures, a very fine striation pattern composed of macroareolae cut in two by a longitudinal hyaline zone, and a very shallow mantle. The new genus is illustrated using both LM and SEM observations and compared with other resembling marine and brackish Planothidium monoraphid species.

Key words: Adriatic Sea, marine diatoms, Majewskaea, sea turtles, new genus

INTRODUCTION

The past five years, the taxonomy of turtle–associated diatom taxa gained an increased interest that resulted in the description of several new species and even several new genera. In 2015, two new genera, Chelonicola Majewska et al. and Poulinea Majewska et al. were described from the carapace of olive ridley sea turtles (MAJEWSKA et al. 2015) followed by a third genus, Medlinella Frankovich et al., which was found on the skin of loggerhead sea turtles (FRANKOVICH et al. 2016) in Florida. Apart from these new strictly epizoic diatom genera, several other new epizooic species were described in established genera living on sea turtles, such as Achnanthes elongata Majewska et Van De Vijver and A. squamiformis Majewska et Van De Vijver, observed on the carapace of olive ridley sea turtles (MAJEWSKA et al. 2017a), Labellulica lecohuiana Majewska et Van de Vijver, observed on the carapace of olive ridley sea turtles (MAJEWSKA et al. 2017b), Olifantiella seblae Kaleli et al., found on loggerhead sea turtles (KALELI et al. 2018) in the Mediterranean Sea and several Prosckinia species (MAJEWSKA et al. 2019).

Recently, during a survey of the epizoic diatom flora living on loggerhead sea turtles from the Adriatic Sea, a new Catenua, C. exigua Robert et al. and a Planothidium species P. kaetherobertianum Van de Vijver et al. were described from the turtle carapace (ROBERT et al. 2019; VAN DE VIJVER & BOSAK 2019). On the same turtle, a relatively large population of a small monoraphid taxon was observed showing some resemblance to several established achnanthoid genera but also presenting important morphological differences placing the unknown species in one of these genera less probable. When the catch–all genus Achnanthes Bory sensu lato proved to be too heterogenous, it was gradually split up starting in 1990 by Round et al. with the re–erection of Eucocconeis Cleve ex Meister and Achnanthidium Kützing. The latter, grouping the majority of freshwater achnanthoid species, was further subdivided several years later when a handful of new genera was described such as Psammothidium Bukhtiyarova et Round, Rossithidium Round et Bukhtiyarova, Karayevia Round et Bukhtiyarova, Kolbesia Round et Bukhtiyarova, Lemnicola Round et Basson and Planothidium Lange–Bertalot (BUKHTIYAROVA & ROUND 1996; ROUND & BUKHTIYAROVA 1996; ROUND...
& Basson 1997). The past few years, new achnanthoid genera have continuously been described, usually based on former freshwater Achnanthes or Achnanthidium species, such as Platessa Lange–Bertalot, Trifonovia Kulikovskiy et al., Gliwiczia Kulikovskiy et al. and Skabitschewskia Kuliskovskiy et Lange–Bertalot (Kramer & Lange–Bertalot 2004; Kulikovskiy et al. 2012, 2013, 2015).

Most of these genera mainly group freshwater and limnoterrestrial species with only Achnanthes and Planothyridium having some marine representatives (Witkowski et al. 2000). In the marine realm however, monoraphid diatoms also play a major role (e.g. Riaux–Gobin & Compère 2008; Lobban et al. 2012; Riaux–Gobin et al. 2010; Desrosiers et al. 2014) with several genera being described in the past 20 years: Astartiella Witkowski et al., Pauliella Round et Basson, Pogoneis Round et Basson, Scalariella Riaux–Gobin et al. and Madinitidium Desrosiers et al. (Round & Basson 1997; Moser et al. 1998; Riaux–Gobin et al. 2012; Desrosiers et al. 2014). Two monoraphid genera proved to be epizoic and associated with marine mammals: Bennettella Holmes and Epipellis Holmes but both show more affinities to cocconeoid than achnanthoid genera (Holmes 1985).

In our sample scraped from a sea turtle carapace biofilm, after a detailed analysis with SEM the unknown achnanthoid taxon could not be placed in any of the established genera based on all currently available literature.

Therefore, a new genus, Majewskaea gen. nov. is described to accommodate the new species. The new species Majewskaea istriaca sp. nov. is described using light (LM) and scanning electron (SEM) microscopy from the carapace of a loggerhead sea turtle and is the generic type. The morphological features of the new genus are compared with all other morphologically similar achnanthoid genera.

**Material and Methods**

On 30. May 2016 the carapace of a juvenile loggerhead turtle named Žanja–Mara (CCL = 44 cm, weight 11 kg) was sampled by Karin Gobić Medica in the Marine Turtle Rescue Centre in Aquarium Pula (eastern Adriatic Sea, Croatia) after having spent more than 6 months in a rehabilitation tank with circulating seawater. Epibiotic non–invasive samples were collected under the necessary permits by randomly scraping ca. 20 cm² of the carapace with a curette. The carapace fragments were preserved in 50 ml Falcon tubes in seawater with circulating seawater. Epibiotic non–invasive samples were preserved in 50 ml Falcon tubes in seawater with circulating seawater after a detailed analysis with SEM the unknown achnanthoid taxon could not be placed in any of the established genera based on all currently available literature. 

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Majewskaea istriaca gen. nov. is formally described. Based on its morphological features and after comparison with similar genera such as Karayevia and Madinitidium, belonging to the same family Achnanthidioceae D.G.Mann in Round et al. (1990), the new genus is likewise placed in this family (Desrosiers et al. 2014).

**Majewskaea gen. nov.**

**Description**

Heterovalvate, monoraphid frustules composed of a raphe–bearing valve and a rapheless valve. Frustules relatively small. Raphe valve (RV): valve face relatively flat, rarely curved. Mantle very shallow. Raphe branches straight. Central raphe endings closely positioned to each other, shortly hooked, weakly expanded. Terminal raphe fissures bent, continuing onto the valve mantle. Striae composed of one macroareola, only near the valve apices continuous from axial area to valve margin. Most of the striae interrupted by large hyaline plate dividing the macroareolae in two parts. Areolae covered externally by porous hymenes. Virgae internally thickened, clearly raised. Raphe sternum clearly raised with developed central nodule. Central raphe endings straight to weakly deflected into opposite directions. Terminal raphe endings terminating onto small helictoglossae. Sternum valve (SV): Valves weakly convex with clearly developed, thickened, linear sternum. Mantle shallow. Striae composed of macroareolae, clearly interrupted by a large hyaline plate forming one rounded areola near the axial area and one transapically elongated areola at valve margin, both covered by porous external hymenes. Distinct, raised ridge surrounding the valve face, folded inwards over the valve margin. Internally, hyaline plate dividing the macroareolae obvious. Small vestige––like raphe slits present. Raphe sternum sunken. Girdle composed of at least two open, narrow, unperforated bands.

**Typus generis:** Majewskaea istriaca sp. nov.
**Etymology:** the new genus is named after our dear friend and colleague, Dr Roksana Majewska (Southwest University, Potchefstroom, South Africa) in honor of her impressive scientific contributions to the study of diatom taxa associated with sea turtles.

*Majewskaea istriaca* sp. nov. (Figs 1–51)

**LM (Figs 1–39):** Frustules heterovalvate. Valves linear, linear–lanceolate to lanceolate with straight to convex margins and weakly protracted, rostrate, broadly rounded apices. Smaller valves becoming almost elliptical. Valve dimensions (n=50): length 6–15 µm, width 3–4 µm. SV: Sternum raised above valve plain, often discernible in LM (Figs 8, 10, 12, 16). Striae parallel throughout almost the entire valve, becoming slight radiate towards the apices, 30–32 in 10 µm. RV: raphe sternum clearly developed, linear running distinctly from apex to apex. Raphe branches not or very weakly (Figs 22, 25, 29): discernible in LM. Axial area very narrow. Central area often rather distinctly but irregularly thickened. Striae nor areolae visible in LM.

**SEM (Figs 40–51):** Girdle not well studied due to lack of observations, even of untreated material. Girdle bands open, narrow, thin, unperforated (Figs 40, 41). Fig. 44 showing open nature of girdle bands. SV (Figs 40–47): Mantle very shallow. Internally sternum depressed, linear (Figs 41, 42). Very short, vestige–like raphe slits visible near apices (Figs 41, 42, 44, arrow). Striae interrupted by continuous hyaline plate subdividing the areolae usually in two parts (Figs 41, 42). Axial sternum bordered by continuous series of large rounded, areolae, part of larger macroareolae (Fig. 42). Near valve edge transapically elongated parts of macroareolae present. Occasionally, third areola visible near valve margin (Fig. 42). Externally, well–developed ridge surrounding the entire valve, larger near valve center. Ridge clearly folded inwards, partly covering the marginal areolae of the striae (Figs 43, 46, 47). Sternum thick, raised, linear to lanceolate (Figs 40, 43). Virgae extending from the sternum towards the valve margins (Figs 40, 43, 47). Striae depressed between virgae (Figs 43, 45). Areolae clearly covered by perforated hymenes (Fig. 45, arrows). Vestigial raphe slits often visible at apices (Fig. 46, arrow). RV (Figs 48–52): Raphe branches straight with shortly, unilaterally hooked central endings bearing only weakly expanded pores (Figs 48, 50). Terminal raphe fissures bent, continuing onto the mantle (Fig. 48). Striae composed of macroareolae, subdivided by large hyaline plate, ca. 50 in 10 µm. Axial area bordered by series of transapically elongated, short areolae whereas larger part of macroareolae visible near valve margin (Fig. 48). At apices, macroareolae never subdivided, composed of one continuous stria (Fig. 48). Internally, raphe sternum well developed, clearly raised. Central nodule thickened, expanding irregularly towards the valve margins, however, never reaching the margins (Fig. 49). Virgae distinctly thickened with striae sunken between them. Raphe branches terminating onto small helictoglossae at the apices (Figs 49, 51). Centrally, raphe endings occasionally deflected in opposite directions (Fig. 49), usually straight (Fig. 52). Areola coverings visible as perforated, external hymenes (Fig. 52).

**Holotype:** BR–4583 (Meise Botanic Garden, Belgium)

**Isotype:** PLP–373 (University of Antwerp, Belgium), HRNDC–00437 (Croatian National Diatom Collection)

**Type locality:** Loggerhead turtle, Pula, Croatia, Adriatic Sea, sample 13 Žanja–Mara carapax, (leg. K. Gobić Medica, 30/05/2016)

**Etymology:** The specific epithet ‘istriaca’ refers to the Istrian peninsula where the loggerhead turtle was found.

**Ecology:** *Majewskaea istriaca* was so far only found on the carapace of a loggerhead turtle. The associated diatom flora was very diverse and species–rich and composed of *Catena exguia* Robert et al., an unknown *Bifibulatia* Takano species and several *Nitzschia* Hassall, *Fallacia* A.J.Stickle et D.G.Mann, *Parlibellus* E.J.Cox and *Amphora* Ehrenberg ex Kützing species.

**DISCUSSION**

The genus *Majewskaea* possesses a unique combination of morphological features that has never been observed in any other monoraphid genus. The frustules are clearly heterovalvate and thus only a few genera come into question as host genus for the unknown species in this paper. The structure of the striae, composed of one large macroareola subdivided by a hyaline plate, is entirely different from the striae in genera such as *Achnanthes*, *Achnanthidium*, *Psammothidium*, *Rossithidium*, *Lemmnicola*, *Platessa*, *Planothidium*, *Gliwiczia* and *Skabitschewkia* (Round et al. 1990; Round & Bukhtiyarova 1996; Round & Basson 1997; Kulikovskiy et al. 2013, 2015) that are composed of uni– to multisieriate series of small, rounded areolae. A similar stria structure composed of macroareolae, on the other hand, is observed in the genera *Scalariella*, *Madininitidium*, *Kolbesia* and *Karayevia* (Bukhtiyarova 1999; Riaux–Gobin et al. 2012; Desrosiers et al. 2014).

Therefore, the new genus *Majewskaea* is compared in detail with these four genera.

Two of the similar genera, *Karayevia* and *Kolbesia*, however, have a rather complicated taxonomic history.

Both genera were described and separated in 1996 by Round & Bukhtiyarova based, however, on unclear morphological characters. Both genera were declared invalid as a formal indication of the generitypes was missing. This was rectified in 1998 by Round who unfortunately made the mistake to indicate twice the name *A. clevei* for both *Karayevia* (correct) and *Kolbesia* (incorrect).

The latter was considered later a lapsus for *A. kolbei* and the genus was considered valid. *Bukhtiyarova* (1999) transferred a year later the generitype of *Kolbesia, K. kolbei* (Hustedt) Round et Bukhtiyarova together with
Figs 1–42. Majewskaea istryaca sp. nov. LM and SEM pictures taken from the holotype population (loggerhead “Žanja–Mara” carapace sample), Adriatic Sea, Croatia: (1–39) Light microscopy observations showing size diminution series and the variability of the sternum valve outline (1–20) and raphe valve outline (21–39); (40) SEM external view of an entire sternum valve showing the typical recurved marginal crest, the split macroareolae and several girdle bands; (41) SEM internal view of an entire sternum valve showing the split macroareolae, the depressed sternum and several girdle bands; (42) SEM internal view of an entire sternum valve showing the split macroareolae, the depressed sternum and the vestigial raphe slits. Scale bar 10 µm (1–39, 42), 1 µm (40, 41).

several other taxa into the genus Karayevia indicating that way the superfluous character of the genus Kolbesia. In 2006, the genus description of Karayevia was emended including the macroareola structure in the genus description. An extra term, postmacroareola, was likewise introduced for striae composed of several macroareolae (Riaux–Gobin et al. 2012). Riaux–Gobin et al. (2012) reported that the genus Karayevia is highly heterogeneous based on several features such as the presence/absence of areolae on the SV mantle and the highly variable stria structure within the emended genus. Witkowski et al. (2016) contested subsequently the inclusion of Kolbesia in Karayevia when they described a new Kolbesia species, K. sinica Krzywda et al. based on morphological and molecular data. According to them, the genus Karayevia consists of species having striae composed of small, rounded areolae such as K. clevei, whereas Kolbesia possesses striae composed of (post)macroareolae covered externally. This subtle difference had been included in the original genus descriptions (Karayevia: ‘areolae circular’ vs. Kolbesia: ‘areolae elongate and separated, few in each stria’, see Round & Bukhtiarova 1996, pp. 353–354). Molecular research including species with different stria/areola types will be necessary to clarify this issue. In the present paper, only these Karayevia/Kolbesia species with (post)macroareolae are used for the morphological comparison. The new genus differs from Karayevia/Kolbesia by the presence of the large external ridge folding over part of the valve face (absent in Karayevia/Kolbesia), the
distinct presence of vestigial raphe slits in SV, the presence of the large hyaline plate, subdividing the striae in two postmacroareolae (absent in Karayevia/Kolbesia), the longitudinal ridges forming the raphe sternum in the valve interior (never observed in any Karayevia/Kolbesia species) and the perforated hymenes closing the areolae halfway in the areolar canal (contrary to the internal closings in Karayevia/Kolbesia). Several Karayevia/Kolbesia taxa such as Karayevia laterostrata or K. nitidiformis possess striae composed of two large areolae with the
Figs 48–52. *Majewskaea istriaca* sp. nov. SEM pictures taken from the holotype population (loggerhead “Žanja–Mara” carapace sample), Adriatic Sea, Croatia: (48) SEM external view of an entire raphe valve showing the course of the raphe, the bent terminal raphe fissures, the split macroareolae and the slightly enlarged central raphe endings; (49) SEM internal view of an entire raphe valve showing the raphe branches, the weakly enlarged central nodule, the very small helictoglossae and the raised virgae; (50) SEM external detail of the central raphe endings and the asymmetrical central area; (51) SEM internal detail of the valve apex with the helictoglossa; (52) SEM internal detail of closed macroareolae. Scale bar 10 µm (48, 49), 1 µm (50–52).
areolae bordering the axial area always being the largest and a second, much smaller areola at the valve margin. The presence of vestigial raphe slits on the SV valve has been reported in the genus *Psammothidium* where species such as *P. incognitum* or *P. confusum* present similar slits (Le Cohu & Maillard 1983). However, later analysis showed that these slits were covered on the inside by perforated hymenes structurally similar to the hymenes covering the areole (Van de Vijver, pers. obs.), contrary to the slits in *Majewskaea* where the slits were never covered internally nor externally by perforated hymenes. The recently described *Kolbesia sinica* shows some resemblance to the genus *Majewskaea*. However, this *Kolbesia* species never possesses the typical hyaline plate subdividing the striae, the areolae seem to be closed internally by hymenes (and not halfway the areolar canal), the typical marginal crest folding over the valve face is absent and the terminal raphe fissures are hooked on the valve face and do not seem to continue onto the mantle. Vestigial raphe slits were never observed. Conspecificity between *K. sinica* and *Majewskaea* has to be excluded therefore.

Two other genera show the typical macroareolae: *Madinithidium* and *Scalariella*. The genus *Scalariella*, described from the sub–Antarctic Kerguelen Islands (Riaux–Gobin et al. 2012) shows one macroareola on the SV whereas the RV is characterized by two postmacroareolae, separated by a hyaline, lunate–shaped plate. A subdivision of the macroareola on the SV, as is the case in *Majewskaea* was never observed in any of the *Scalariella* species (Riaux–Gobin et al. 2012, figs 1, 2, 5). The areolae are closed by non–perforated hymenes (Riaux–Gobin et al. 2012, p.15: “areolae occluded by thin, uniform hymen without visible slits”) contrary to the genus *Majewskaea* where the hymenes are clearly perforated. The internal structure of the striae, forming one large open groove bordered by well–developed virgae as is seen in *Majewskaea* was never observed in *Scalariella* where the hyaline plate subdividing the striae is clearly raised separating both postmacroareolae (see for instance Riaux–Gobin et al. 2012, figs 15–16). The external raphe branches in *Scalariella* are clearly curved (despite the text stating that the raphe is “filiform and straight” (Riaux–Gobin et al. 2012, p. 15), terminating in hooked terminal raphe fissures. It is however unclear from the illustrations in Riaux–Gobin et al. (2012, figs 12, 14, 17) whether the raphe fissures continue onto the mantle or terminate at the valve margin. In *Majewskaea*, the terminal raphe fissures continue onto the valve mantle (see Fig. 48). Riaux–Gobin et al. (2012) also mention the presence of “two lateral sunken recesses in the hymenes of the marginal areolae”, a feature never observed in *Majewskaea*. On the other hand, the typical marginal ridge bordering the entire SV in *Majewskaea*, was never observed in *Scalariella*. Therefore, given these morphological differences, placing the new monoraphid taxon within the genus *Scalariella* is not the most ideal situation.

Finally, the genus *Madinithidium* was recently described by Desrosiers et al. (2014) based on a small monoraphid diatom found in Martinique. *Madinithidium* is characterized by the presence of wide, distinctly depressed macroareolae on both SV and RV occluded internally by perforated hymenes, a clearly raised raphe sternum, both externally and internally, terminal raphe fissures that are doubly hooked, the absence of vestigial raphe slits on the SV and open, non–perforated girdle bands. The typical postmacroareolae found in *Majewskaea* with the large hyaline plate on both SV and RV have never been found in *Madinithidium*. At present, six taxa are placed in the genus, mainly small–celled monoraphid taxa found in tropical coral sands but also taxa originating from Vietnam and Turkey (Riaux–Gobin et al. 2010; Desrosiers et al. 2014; Kulikovskiy et al. 2019). None of these six taxa shows any of the typical features that are found in the new genus *Majewskaea*. The marginal ridge on the SV is absent on all six known *Madinithidium* taxa, the structure of the raised sternum on the SV, the presence of the vestigial raphe slits on the SV, the subdivision of the striae on the RV and the weakly developed stauros on the RV, are all features that at present were observed in *Majewskaea* but absent in *Madinithidium*. Therefore, the separation between *Majewskaea* and *Madinithidium* based on morphological features is justified.

Whether *Majewskaea* is a characteristic component of epizoic diatom community needs to be proven. At present, only one turtle hosted a large population on its carapace. The turtle was brought in the Pula Rescue Center (Croatia) and remained several months in a closed tank with seawater inflowing from the nearby sea for recovery. Unfortunately, no sampling was performed when the turtle arrived in the rescue center and the investigated samples were only taken after several months. Analyses of the diatom flora on the carapace of other Adriatic turtles revealed a different epibiont diatom community (unpublished data). The flora on Žanja–Mara proved to be composed of other unique taxa such as *Catenula exigua*, *Planolithidium kaetheroberitianum* and an unknown *Bifibulata* species, all taxa never observed on other Adriatic turtles (Robert et al. 2019; Van de Vijver & Bosak 2019). However, the diatom survey of the Adriatic turtle flora only recently started and only a limited number of turtle samples has been analysed so far making undersampling and underreporting likely causes for the lack of distribution data of *Majewskaea*. Surveys of the benthic diatom flora in the Mediterranean Sea of the Black Sea such as Álvarez–Blanco & Blanco (2014) or Kaleli et al. (2017) did not mention nor illustrate valves that could be attributed to *Majewskaea*. Further research on the Adriatic turtle diatom flora in combination with an analysis of the benthic flora in the Adriatic Sea will be necessary to determine the correct distribution of *Majewskaea*.

At present it is unclear if other, previously described species should be transferred to the new genus. Hendey (1977) described *Navicula incongruens* Hendey
from the coast of Cornwall, UK. Only one valve bearing a raphe is illustrated (Hendey 1977, fig. 10). The drawing shows an elliptic–lanceolate valve with a clear hyaline interruption in the striae, consistent with what was observed in Majewskaea. Conspecificity has to be excluded based on the much higher stria density in M. istiaca (50 vs 14 in 10 μm). Unfortunately, Hendey (1977) never showed a second valve so we have no idea whether the species should actually be regarded as a monoraphid species rather than a biraphid naviculoid. Analysis of the type material will be necessary to clarify this problem.

Other taxa that might be placed within the genus Majewskaea include several unidentified achnahnoid that were currently successfully collected from Florida. Their molecular phylogeny shows a relation with the clades of Schizostauron, Astarttiella and Madinihidium (Witkowski, pers. comm.). Finally several unpublished valves from the Mozambique Channel coral sand could also belong to Majewskaea (Witkowski, unpubl. res.). Further research will be necessary however to determine their exact taxonomic position.

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