Miocene siliceous microfossils from the open cast coal mine Graćanica (Bugojno paleolake, Bosnia and Herzegovina) and their significance: a preliminary report

Andrzej Pisera 1 · Peter A. Siver 2 · Oleg Mandic 3

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Abstract
The Langhian (middle Miocene) marls of lacustrine succession cropping out in the open cast coal mine Graćanica (Bugojno basin, central Bosnia and Herzegovina) yielded a rich siliceous microfauna. The most common are sponge spicules (megascleres), less common are diatoms and chrysophyte cysts. Cell wall remains of a green alga Botryococcus sp. were often observed in one sample. The most common spicules are spinose oxees that strongly resemble the extant species Ochridaspongia rotunda Arndt, 1937 (family Malawispongiidae Manconi and Pronzato, 2002) that is endemic to Lake Ohrid, and we believe that the fossil material belongs to the same genus. Other, much less common spicules, birotules and thick smooth strongyles were attributed to the genus Ephydatia Lamouroux, 1816 (family Spongillidae Gray, 1867) and most probably Potamolepidae Brien, 1967 respectively. All together, they belong to 5–6 different taxa.

The diatoms are represented by 11 species, the most common being Staurosirella leptostauron (Ehrenberg) D.M.Williams and Round 1988, Epithemia sp., Ellerbeckia sp. and Encyonema sp. Much less common are Staurosirella pinnata (Ehrenberg) D.M.Williams and Round 1988 and two undetermined species of Fragilaria as well as Eunotia. Eleven chrysophyte cyst morphotypes were uncovered. Alkaline and oligotrophic conditions in the paleolake are suggested by the presence of the representative of the genus Ochridaspongia Arndt, 1937 that thrives in such environments. The most common diatom species further suggest that the water of this paleolake was shallow, high in mineral content, alkaline, with a high pH and moderately to highly productive. Common occurrence of Botryococcus sp. suggests rather oligotrophic condition, indicating that conditions and nutrient levels were variable. The first fossil occurrence of the sponge genus Ochridaspongia indicates that this genus originated not in the Lake Ohrid, but much earlier during the early middle Miocene in the Dinarides Lake System.

Keywords Bugojno paleolake · Spongillida · Sponge spicules · Diatoms · Chrysophyte cysts · Botryococcus · Environmental and evolutionary significance

Introduction
During field trip to the Miocene Bugojno basin (central Bosnia and Herzegovina—Fig. 1), organised in 2016 by the Regional Committee on Mediterranean Neogene Stratigraphy Interim Colloquium “Lake-Basin-Evolution”, 20 samples were collected from a 40-m-thick lacustrine succession of the open cast coal mine Graćanica (Mandic et al. 2016). In the search for siliceous sponge remains (Porifera), different lithologies have been sampled mostly from loose blocks of the mining debris. Two of these samples (encoded GR4 and GR9), originated
from grey laminated marls, yielded a rich siliceous microfauna consisting of sponge spicules, diatoms and chrysophyte cysts. Here, we present a preliminary report on these findings and discuss their significance for palaeoenvironmental reconstruction.

Geological setting

The lacustrine deposits of the Bugojno basin (Fig. 1) in the central Bosnia and Herzegovina are settled in one of the larger intra-mountain depression of the Dinarides with a total surface of 125 km². They build an ~900-m-thick continental succession, composed of three lacustrine to terrestrial depositional cycles. Lower and middle cycles comprise Miocene, the upper cycle Pliocene deposits (Mandic et al. 2016 and references therein). The studied sediments of the open coal mine Gračanica are settled in the southeastern part of the Bugojno basin (43° 59’ 44.88” N; 17° 31’ 17.49” E). The ~40-m-thick succession shows in its lower part an alternation of lignite and marl, representing proximal to distal swamp facies. Upwards, the succession grades to massive and laminated littoral and profundal lacustrine marl. The section is dated bio-magnetostratigraphically to ~15 Ma (Langhian, middle Miocene; Mandic et al., in prep., this issue). The sample lithology marked by grey laminated marls attributes the studied samples to the upper part of the section (Mandic et al. 2016). For a detailed geological

Fig. 1 Location of the Bugojno paleolake basin, Lake Ohrid and the Gračanica open cast lignite mine (modified after Mandic et al. 2012, 2016, base maps from ArcGIS by ESRI Inc.)
setting and lithofacies description, see Mandic et al. (in prep., this issue).

**Material and methods**

Small, about 0.5 cm large samples of the sediment were treated with hydrogen peroxide during 24 h in a glass tube. After removal of the reagent, the samples were washed several times in distilled water and finally with pure propanol. Obtained suspensions were used to prepare two standard microscope preparations (slides) from each sample that were later examined in a light microscope (LM). Samples that contained siliceous microfossils were selected and further studied under scanning electron microscopy (SEM). They were dried onto a microscope cover glass, attached with carbon glue to a SEM stub, sputter coated with platinum and examined with a Phillips XL20 SEM at magnifications from ×100 to ×10,000, at the Institute of Paleobiology, Warsaw.

The studied material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa under the collection number ZPAL V.64.

**Results**

The most common siliceous microfossils in the studied samples are sponge spicules and diatoms. Apart from them, chrysophyte cysts and remains a green alga *Botryococcus* sp. have been found. The diversity of siliceous microfossils is clearly much higher in sample GR4 compared to sample GR9.

**Sponge spicules**

The most common megasclere spicules in both samples GR4 and GR9 (hundreds of specimens in each preparation) are spinose oxeas (Figs. 2a–s and 4a–p) that are from straight (rare) to curved to different degree. Degree of spinosity also

![Fig. 2 Megascleres of *Ochridaspongia* sp. Sample GR4 (ZPAL V.64); note that spicules differ in degree of spinosity and some having central swelling (d)](image-url)
differs, and larger spicules have smaller and less numerous spines, while those that are smaller have more and larger triangular spines. Rare centrotylote spicules were also observed (Fig. 2d). The spicules measure 123–282 (341) μm in length and are 5–14 μm thick. Morphological comparison with Spongillida (with spiny oxeas as megascleres) presently living on the Balkan Peninsula, e.g. genera Ohridospongilla (Lake Ohrid shallow water), Ochridaspongia (O. rotunda; O. interlithonis) and Spongilla (Spongilla stankovici from Lake Ohrid shallow water) led us to conclude that these spicules most closely resemble spicules occurring in the extant species of Ochridaspongia rotunda Arndt (1937) from the Lake Ohrid (Fig. 1) (see Pronzato and Manconi 2001; Albrecht and Wilke 2008) but differ slightly in character of spines, displaying similar shape and size variability (see figures 7 and 8 in Arndt 1937). According to Manconi and Pronzato (2002), the species O. rotunda has “Megascleres oxeas (175–367/5–23 μm), ranging from slender to stout, from straight to slightly curved, from smooth to spined mainly towards the ends; acerate tips. Spherical swellings occur in some oxeas”. These characters fit very well with the studied material except that the fossil spicules are slightly smaller on average than those reported in O. rotunda. Due to these differences, and the fact that we have only loose spicules, the specific attribution of fossil material to the extant species from Lake Ohrid is precarious, but we have no doubts that the fossil spicules represent genus Ochridaspongia. Such attribution is further supported by the fact that only megascleres have been found in our material, and no microscleres or gemmuloscleres were observed, as the genus Ochridaspongia is characterised by the presence of megascleres only. The genus is considered as endemic and evolved in the Lake Ohrid or that is a relict of Neogene (Albrecht and Wilke 2008).

Another category of spicules (rather uncommon) that occur in both studied samples (GR4 and GR9) are thick and smooth, usually curved, sometimes contorted strongyles (Figs. 3a–d, 4r–s) that represent gemmuloscleres, such spicules are known in the family Potamolepidae Brien, 1967 (Demospongiae, Spongillida). Similar spicules are known also from other genera of extant freshwater sponges but they are usually accompanied by other types of spicules (Manconi and Pronzato 2002) that were not observed in the studied samples; thus, we consider them as belonging to the Potamolepidae. Very similar spicules attributed to fossil species of Potamophloioes were recently described in an Eocene lake from Northern Canada (Pisera et al. 2013).

The genus Ephydatia Lamouroux, 1816 (Fig. 3h–k) was recognised in the studied Gračanica material (sample GR4), based on the presence (very rare) of gemmular birotules (one aberrant). Large smooth and curved oxeas, co-occurring in the same sample, have also been attributed to this genus. Fossil Ephydatia is known since the Eocene (Pisera et al. 2016; Pronzato et al. 2017). From the Miocene of Europe, the species E. sarmatica Traxler, 1894 was described (Pronzato et al. 2017), but our material is too scarce to allow for specific attribution.

Finally, three spicules of strange morphology (Fig. 3e–g, e–f, most probably gemmuloscleres) and unknown affinity were found in the sample GR4.

Diatoms

Eleven diatom species dominated sample GR4, while only one species was recovered in the sample GR9. The most abundant diatom taxa in sample GR4 were Staurosirella leptostauron (Ehrenberg) D.M. Williams and Round 1988

Fig. 3 Sponge spicules, sample GR4 (ZPAL V.64). a–d Spicules (probably gemmuloscleres) of Potamolepidae sponges. e–f spicules (gemmuloscleres) of unknown affinity. g Undetermined megasclere (style). h–l Ephydatia sp. gemmuloscleres (birotules) h–i and megasclere oxeas j–l
Valves of *S. leptostauron* were strongly cruciate with rounded apices, a broad central region, and wide striae consisting of lineolae. Striae were equal to, or slightly smaller than, the diameter of the costae. One or sometimes two spines were situated on each costa near the valve margin and specimens lacked rimoportulae. Characters of the *S. leptostauron* specimens matched those discussed in detail by Morales (2006) and Morales and Manoylov (2011), and this was the only diatom taxon uncovered in sample GR9. Some characteristics of the *Epithemia* sp. specimens match those for the genus (Patrick and Reimer 1966; Round et al. 1990). Valves were lunate-shaped, strongly asymmetric about the apical axis, symmetrical about the transapical axis and with rounded apices (Fig. 5l–o). Striae were slightly radiate and with internally thickened costae spanning the valve margins. The raphe is eccentrically placed on the valve face with the central area reaching close to the dorsal margin. The girdle was slightly wider along the dorsal margin, and the girdle bands possessed thickened projections that merge internally near the centre of the cell. However, this taxon also has features typically found on its close relative, *Rhopalodia* O. Müller, 1895, including the structure of the areolae, making identification difficult. Further work is necessary to confirm the relationship of this species within both *Epithemia* F.T. Kützing, 1844 and *Rhopalodia*. Characteristics of the *Ellerbeckia* sp. specimens fit those discussed by Crawford (1988) and Schmid and Crawford (2001). *Ellerbeckia* sp. (Fig. 5s–v) was the only centric diatom observed in the Gračanica samples. The majority of valves had a marginal ring of parallel thickened ridges on the valve face, or a corresponding ring of depressions on the adjoining valve. The central region of the valve face was hyaline and lacked areolae. The spacing between the ridges within the ring was variable between specimens. The mantle contains numerous rows of small pores characteristic of the genus.

The remaining diatom species uncovered in sample GR4 were less common. Three of the araphid species, including *Staurosirella pinnata* (Ehrenberg) D.M. Williams and Round 1988 (Fig. 5h) and two species of *Fragilaria* Lyngbye 1819, belong in the order Fragilariales (Fig. 5j–k). All three of these species possessed marginal spines presumably used to link frustules together into filaments or chains. Multiple specimens of a species of *Encyonema* F.T. Kützing, 1833 (Fig. 5p–r) and a single specimen belonging to *Eunotia* Ehrenberg, 1837 (Fig. 5h) were also uncovered in sample GR4. Lastly, a species belonging to the raphe-bearing genus and specimens of
Fig. 5 Diatoms a–d Staurosirella leptostauron. a Sample GR9. b–d Sample GR4. e–f Unknown pennate species. g Undetermined, sample GR4. h Eunotia sp. i Staurosirella pinnata. j Fragilaria sp. 1. k Fragilaria sp. 2. l–o Epithemia sp., sample GR4. p–r Encyonema. s–v Ellerbeckia sp. sample GR4 (ZPAL V.64)
two unknown pennate species (Fig. 5e–f) were also uncovered in sample GR4.

Chrysophyte cysts

Cysts in sample GR4, eight different morphotypes, represent a wide diversity with respect to size, wall ornamentation and collar structure (Fig. 6a–h). Cyst morphotype 1 was spherical with a smooth wall, a sunken concave pore and ranged in diameter from 10 to 15 μm (Fig. 6c). Cyst morphotype 2 was small with a mean diameter of 6 μm, and with widely spaced, short, baculate spines (Fig. 6e). Cyst morphotype 3 was similar to cyst morphotype 1 in size and wall structure, but possessed a distinctive wide (4.5 μm), conical collar (Fig. 6d). Cyst morphotype 4 was one of the larger cyst types, with a mean diameter of 22 μm, and large, widely spaced verrucae (Fig. 6h). Cyst morphotype 5 was similar to types 1 and 3 in size and with a smooth wall, but possessed a wide, short and cylindrical collar (Fig. 6a). The collar structure of cyst morphotype 6 differed from all others in having a shallow, double collar form (Fig. 6b). Cyst morphotype 7 was a common form, large (22–23 μm), with closely spaced verrucae and a wide (11–12 μm), thick and cylindrical collar (Fig. 6g). Morphotype 8 was the largest cyst uncovered with a diameter of 35 μm, spherical and with small, unevenly spaced verrucae (Fig. 6f). This is one of the largest known chrysophyte cysts (Siver 2019).

The three cyst morphotypes uncovered in sample GR9 were all relatively large, with smooth and unornamented walls (Fig. 6i–k) that are different than those recovered from the

![Fig. 6 Chrysophyte cysts a–k. a Morphotype 5. b Morphotype 6. c Morphotype 1. d Morphotype 3. e Morphotype 2. f Morphotype 8. g Morphotype 7. h Morphotype 4. i Morphotype 9. j Morphotype 11. k Morphotype 10. l Botryococcus. a–h Sample GR4. i–l Sample GR9 (ZPAL V.64)](image-url)
from Gra
cien 2016; Pronzato et al. 2017), our find further supports the idea
unquestionable African endemics) suggesting that the family is poly-
orally to
Ephydatia
(2007) had found that
Ochridaspongia
phylogeny of the genus
Arndt (1937), Por (1963) and especially Gilbert and Hadzišce
inhabits waters 25–70 m deep (Gilbert and Hadzišce 1977).

Discussion

Seven morphotypes of sponge spicules were found in the
sample GR4 that were interpreted as representing 6 different
spicule taxa, while sample GR9 yielded only two different
morphotypes representing two different taxa, but the same
occurring also in the sample GR4.

In both samples, one type of spicule belonging to a species
of
Ochridaspongia
dominates the assemblage. This species
most closely matches the description of
O. rotunda,
Ephydatia
species, the
of
Ochridaspongia
is not known from the fossil record. Such
taxonomic attribution of the fossil spicules has important con-
sequences for understanding the extant sponge fauna of Lake
Ohríd (Albrecht and Wilke 2008): at present, the dominant
opinion is that the sponge fauna evolved in the lake between
1.9 and 1.3 Ma ago and remains endemic to the waterbody
(Wagner et al. 2017). Given our findings, the case for the
genius
Ochridaspongia
fits the “reservoir hypothesis”, be-
cause it clearly evolved much earlier in the Miocene (or ear-
lier) in other lakes of the Dinarides Lake Systems (see Mandic
et al. 2016), and
Ochridaspongia
from the Lake Ohríd is the
relict of those ancient lake systems, as already speculated by
Amatl (1937), Por (1963) and especially Gilbert and Hadzišce
(1975, 1977, 1984). Our findings give definitive support for
this hypothesis. This does not refute the idea that for other
species, the “cradle function” fits.

Our results shed also an interesting light on the question of
phylogeny of the genus
Ochridaspongia.
Meixner et al.
(2007) had found that
Ochridaspongia
may be more closely related to
Ephydatia
than to other Malawispongiidae (consid-
ered as African endemics) suggesting that the family is poly-
phylectic. Because undisputed
Ephydatia
occurs in our material
from Gračanica, and it is known since the Eocene (Pisera et al.
2016; Pronzato et al. 2017), our find further supports the idea
of Meixner et al. (2007) that Malawispongiidae are polyphy-
lectic, and that sponges endemic to isolated freshwater ecosys-
tems originated independently from a few cosmopolitan taxa
such as
Ephydatia.

Today, waters of the Lake Ohríd, where
Ochridaspongia
occurs, are slightly alkaline and oligotrophic, and
O. rotunda
inhabits waters 25–70 m deep (Gilbert and Hadzišce 1977).

The presence of potamolepid sponge spicules extends its foss-
il occurrence to new areas, suggesting that it is present and
very restricted distribution (is relict in character, similar to the
case with
Ochridaspongia.

The sample GR4, with its higher diversity of sponge spic-
ules, indicates the presence of probably 5–6 different sponge
species, i.e.
Ochridaspongia
sp.,
Ephydatia
sp., potamolepid
spoon and 2–3 other not identified taxa. The sample GR9 has
only two types of sponge spicules attributed here to
Ochridaspongia
sp. and a species of potamolepid sponge.

Based on the diatom flora uncovered in sample GR4, es-
specially the three most abundant species, the waterbody
was shallow, high in mineral content, alkaline and with a
high pH. It was also moderately to highly productive.

Staurosirella leptostauron is a benthic form commonly
reported from alkaline sites with a pH near 8 (Stoerner et al.
1988; Štefková 2008; Johnson et al. 2009), and
known in the fossil record since the Oligocene
(Ognjanova-Rumenova and Pipík 2015). This taxon is of-
ften found in association with other alkaliphilous species
(Štefková 2008), and has been classified as halophobous
(Lowe 1974; Ognjanova-Rumenova and Pipík 2015).

Taxa belonging to
Epithemia
are attached forms, largely
occurring as epiphytes or epipelic on sediments in shallow
environments (Round et al. 1990). As a genus, many
Epithemia
species are alkalibiontic, often found above
pH 8.5 (Whitmore 1989) and common in base-rich
waterbodies (Round et al. 1990), including karstic lakes
(Jasprica and Hafner 2005). Although a freshwater genus,
some species of
Epithemia
can withstand high dissolved
salts concentrations and even brackish water (Pienitz et al.
2006; Staszak-Piekarska and Rzodkiewicz 2015).

Ellerbeckia,
commonly reported from Miocene localities and often found in association with
Actinocyclus
and spe-
cies belonging to order Fragilariales, is primarily a fresh-
water, benthic genus found in shallow environments
(Ramrath et al. 1999; Kociolek and Spaulding 2002).

Ellerbeckia
can also withstand highly fluctuating water
levels, has been found associated with mosses on tufa
limestone deposits (Schmid and Crawford 2001) and is
often a dominant taxon in karstic lakes (Jasprica and Hafner 2005).
In summary, characteristics of the most
abundant diatoms found in sample GR4 indicate a shallow
water environment that was high in base minerals, highly
alkaline and with a high pH.

Other members of the order Fragilariales uncovered in
sample GR4, including
Staurosirella pinnata
and species be-
longing to
Fragilaria,
also represent attached forms commonly
found in shallow environments at higher pH values
(Jasprica and Hafner 2005; Siver et al. 2005; Pienitz et al.
2006). The single specimen of
Eunotia
uncovered in sample
GR4 does not necessarily match conditions inferred from oth-
er diatom taxa. Although some
Eunotia
species can be found
in alkaline waters, the genus as a whole encompasses numerous species largely restricted to acidic conditions low in dissolved salts (Siver and Hamilton 2011).

Although the chrysophyte cysts cannot be linked to specific species, the collection of morphotypes uncovered in sample GR4 indicates a relatively high diversity, especially for such an alkaline site. Although there are certainly chrysophytes that grow in alkaline habitats, the majority favour less alkaline, more acidic habitats (Duff et al. 1995; Siver 2015), probably related to their lack of carbon-concentrating mechanisms (Wolfe and Siver 2013).

Compared to sample GR4, the diversity of microfossil remains in sample GR9 was very low. As noted above, the single diatom taxon uncovered in sample GR9, *S. leptostauron*, likely indicates that this habitat was also shallow and highly alkaline.

The few chrysophyte cysts are also indicative of low diversity, as are sponge spicules. In contrast, sample GR9 was dominated with a species belonging to the green alga *Botryococcus* sp. The fossils of this organism were well preserved and indicate that it thrived. The genus *Botryococcus* is known in the fossil record since the Precambrian and has remained virtually unchanged throughout the Phanerzoic (Guy-Ohlson 1992). This planktonic alga, known from tropical to subarctic regions, has been characterised as an indicator of oligotrophic conditions that competes best in shallow and calm conditions, often in areas of low rainfall (Guy-Ohlson 1992; Smittenberg et al. 2005). The capability of *Botryococcus* to survive long time periods resides in its ability to store excess carbohydrate, a resistance cell wall, and asexual modes of reproduction. These characters may indicate that sample GR9 had low diversity of other microorganisms due to low nutrient levels.

**Conclusions**

Grey marls of the lower lake cycle of the middle Miocene Bugojno paleolake (Bosnia-Herzegovina) cropping out in the open cast coal mine Graćanica revealed a diversified assemblage of siliceous microfossils, i.e. 5–6 sponge species, 11 diatom species, 11 morphotypes of chrysophyte cysts, as well as remains of *Botryococcus* sp. Taxonomic composition of the diatom flora suggests shallow water alkaline environment, which is supported by the presence of *Ochridaspongia*, found today in alkaline and oligotrophic waters. The two samples examined differ strongly in diversity, possibly associated with different nutrient levels, with more oligotrophic conditions being indicated by the very common occurrence of *Botryococcus*. This is the first fossil occurrence of the sponge genus *Ochridaspongia*, indicating that this genus did not originate in Lake Ohrid, and is much older than previously thought dating to at least the middle Miocene.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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