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New locality for *Leptothrix ochracea* in Poland

Abstract

The iron-oxidising bacterium *Leptothrix ochracea* (Roth) Kützing plays an important role in the biogeochemical cycling of iron through the oxidation of dissolved ferrous iron and the formation of iron-rich deposits. *L. ochracea* exhibits considerable metabolic flexibility and can thrive as a mixotrophic iron oxidiser, utilising iron oxidation as an energy source and both inorganic and organic carbon for biomass and sheath production. This study reports a previously undocumented natural locality of *L. ochracea* in the Western Carpathians, within the Beskid Niski Mountains (Małopolska Region, southern Poland). The bacterium was recorded at Dione Spring, a neutral, iron- and manganese-rich freshwater habitat associated with groundwater seepage. Its presence was confirmed based on characteristic morphological features, including filamentous cells enclosed in sheaths encrusted with iron oxyhydroxides. Dense microbial aggregates dominated by *L. ochracea*, with a minor contribution from *Gallionella ferruginea* Ehrenberg, were observed within biofilms and ferruginous precipitates. This newly documented locality expands our knowledge of the distribution of iron-oxidising bacteria in the Polish Carpathians.

Key words: *Leptothrix* genus, iron-oxidising bacteria, ferruginous waters, Western Carpathians
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Introduction

Iron-oxidising bacteria include unicellular and stalk-forming (e.g. genera *Gallionella* and *Mariprofundus*) and sheathed forms represented by *Leptothrix*, *Sphaerotilus* and *Crenothrix* (Keppler et al., 2016). *Leptothrix ochracea* (Roth) Kützing (syn. *Conferva ochracea* Roth) is a neutrophilic, aerobic Fe(II)-oxidising bacterium that thrives in microoxic niches and oxidises ferrous iron [Fe(II)] to ferric iron [Fe(III)] (Canfield et al., 2005). As the oxidation of

ferrous iron [Fe(II)] to ferric iron [Fe(III)] involves the transfer of only one electron, this process provides relatively little energy. Nevertheless, it enables the bacterium to obtain energy through aerobic respiration and to produce characteristic structures encrusted with iron oxyhydroxides. Moreover, *L. ochracea* is most active at the margins of iron-rich microbial mats, where it contributes to the formation and growth of new mat material. The species occurs in slowly flowing, iron-rich waters, including springs, streams, brooks, and rivers (Emerson, Weiss, 2004; Fleming et al., 2011).

Previous records of this taxon in Poland have been reported by several authors, mainly in floristic and hydrobiological surveys (Siemińska, 1990). Among the earliest reports, Namysłowski (1914) recorded *L. ochracea* in acidic waters of the Małopolska region and subsequently reported its occurrence in iron-rich springs at Mraźnica, Ukraine (Namysłowski, 1922, 1925). Turowska (1930) described the environmental conditions of its habitats. Starmach (1936, 1938) reported the species from mountain streams, including Malinka, Czarna Wisełka, and Suszanka, as well as from the seston of the Wisła and Biała Przemsza rivers. He subsequently documented its occurrence in a pond at Mydlniki (Starmach, 1939) and in a spring flowing from a cliff at Chłapowo (Starmach, 1969). Other records from the Brynica River were provided by Siemińska (1956).

The phylogenetic position of *L. ochracea* has remained unresolved for more than 120 years. According to Fleming et al. (2011), this bacterium has been difficult to cultivate, and until recently, its identification was based primarily on morphological characteristics (Häusler, 1982). However, analysis of a conventional SSU rRNA gene clone library revealed that 42% of the sequences were related to the *Leptothrix/Sphaerotilus* group. PCR, fluorescence *in situ* hybridisation (FISH), and SSU rRNA gene analyses demonstrated that *L. ochracea* is closely related to *L. cholodnii* Mulder & van Veen, forming a morphologically similar group of filamentous, sheathed microorganisms. Phylogenetic analyses showed that *L. ochracea* forms a distinct cluster within the *Leptothrix/Sphaerotilus* group (Nedkov et al., 2016). However, alternative phylogenetic tree reconstruction methods suggest that it is approximately equidistant from the currently recognised *Leptothrix* species. Fleming et al. (2011) hypothesised that *L. ochracea* may be more closely related to members of the family Gallionellaceae Henrici & Johnson, which comprises chemolithotrophic iron-oxidising bacteria (FeOB).

It has long been recognised that bacterial cell surfaces provide sites for the sorption of metal cations. As efficient scavengers of dilute metal ions, bacteria can concentrate metals from their surrounding aqueous environment (Ghiorse, 1984; Schultze-Lam et al., 1996). Owing to their ubiquitous occurrence in natural environments, bacteria may therefore play a

significant role in the formation of fine-grained minerals in soils and sediments. According to Schultze-Lam et al. (1996), their capacity for metal immobilisation may also be exploited to mitigate the harmful effects of acid mine drainage. Ghiorse and Chapnick (1983) suggested that the deposition of large amounts of iron and manganese (oxyhydr)oxides may contribute to the formation of bog iron ore.

The ability of bacteria to bind and immobilise metals (Schultze-Lam et al., 1996) motivated us to investigate iron-oxidising bacteria in natural freshwater environments and to assess their occurrence in streams receiving contaminated post-mining waters enriched with compounds of iron and manganese, among other substances. Therefore, we initiated a search for natural sites inhabited by these bacteria, which led to the discovery of a previously unreported locality in the Beskid Niski Mountains. The aim of this study was to document a new locality of *L. ochracea* and its characterisation.

Material and methods

New locality

The study was conducted in the spring located on the southern slope of the Magura Małastowska Massif (Beskid Niski Mountains, Western Carpathians, southern Poland), an area underlain by Carpathian flysch (N 49° 34′ 18.9″ E 21° 10′ 13.1″) (500-meter horizontal slice map of the region presented in Fig. 1A). Among the numerous springs surveyed, one located in the valley of Przysłupianka was selected for detailed investigation: the small Dione Spring (Fig. 1B), containing iron- and manganese-rich freshwater with a pH of 7.73, containing 250 µg L^{-1} Fe, 70 µg L^{-1} Mn, and 209.5 mg L^{-1} $CaCO_3$. A conspicuous bacterial mats of *Leptothrix ochracea* and very small addition *Gallionella ferruginea* Ehrenberg were observed there. In the Dione source (Fig. 1) they form a characteristic rusty sediment, as well as an oily, iridescent film on the water's surface. However in the autumn activity of *L. ochracea* is partially inhibited, rusty sediments are not produced. Valley of Przysłupianka was earlier investigated by Szajnocha (1886) who found sphaerosiderites inside thick slates. These structures consist of iron and admixtures of manganese. This area belongs to Rača Subunit which is widespread from west to east border of Beskid Niski. We find deep sea sediments such as Belese layers that are 34–56 mln years old. We find many ichnotaxons (Chlebicki, 2020) and minerals such as glauconite, pyrite, variegated slate and rocks – Magura sandstones.

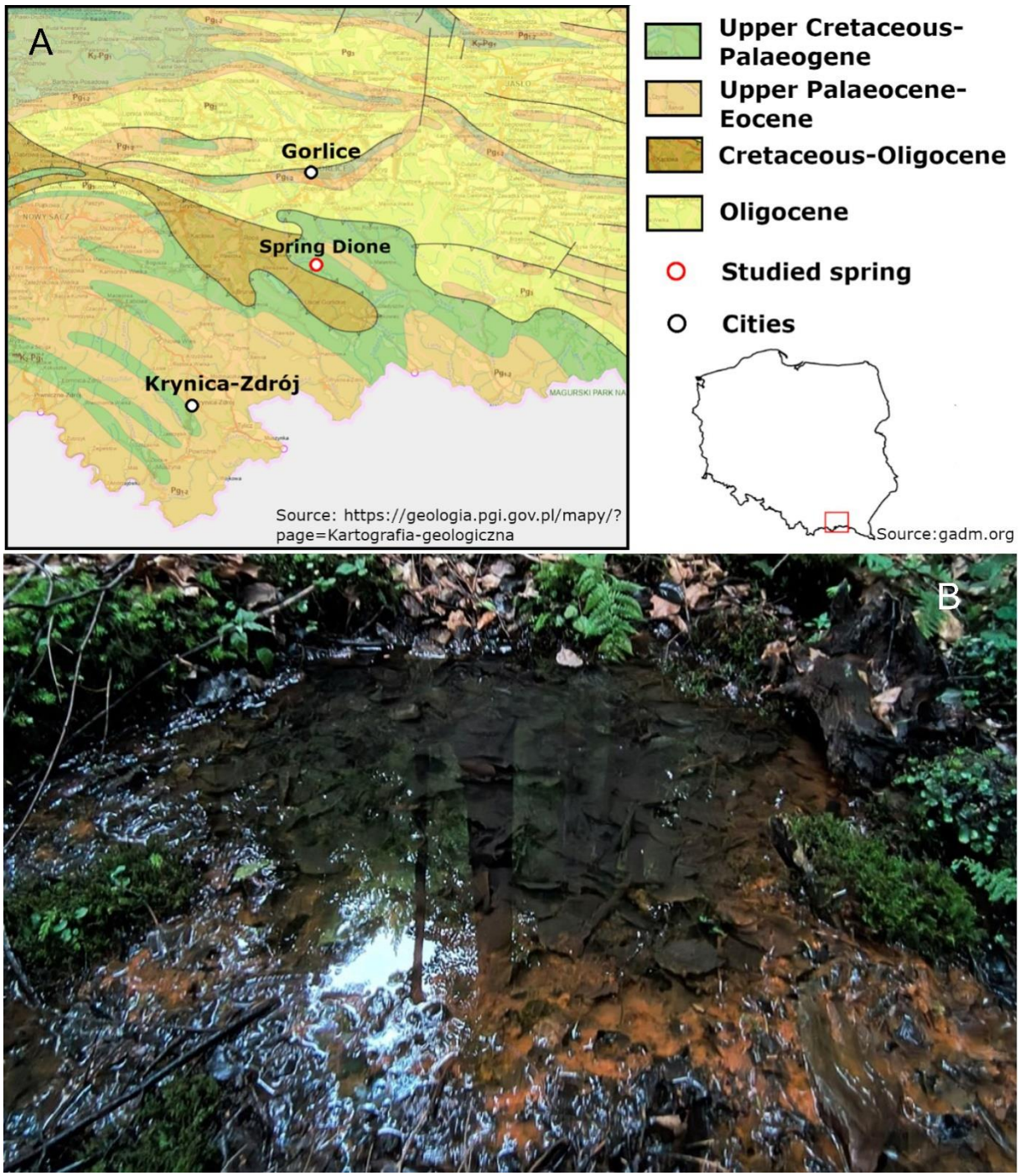


Fig. 1. New locality of *Leptothrix ochracea* (Roth) Kützing: geological horizontal-slice map at 500 m below sea level (A) (Source: Kotański, 1997); Dione Spring: visible leaves of *Fagus sylvatica* L. covered by rusty mats of *L. ochracea* (B) (Photo: Izabela Osadnik)

Sampling

Samples were collected by A. Chlebicki from Dione Spring on 2 July 2026. Water and sediment samples were transferred to sterile 100 mL plastic containers, while bacterial mats, together with associated decaying leaves, were aseptically placed in sterile Petri dishes. The samples were immediately transported to the laboratory of the KRAM-A algal collection at the W. Szafer Institute of Botany, Polish Academy of Sciences (PAS), where they were stored

at room temperature (19–21°C) under a 12:12 h light–dark cycle until analysis by K. Wołowski. Additional water samples from Dione Spring were collected in 1.5 L polyethylene bottles for physicochemical analyses. Same day water analysis was performed by the Laboratory of MPGK in Gorlice (Poland). The following parameters were determined: turbidity, colour, pH, manganese, iron, ammonium, nitrates, nitrites, conductivity, total and bicarbonate hardness.

Microscopic observations

Microscopic observations were carried out with fresh, none-preserved material using Nikon Eclipse 600 and Nikon Eclipse 801 microscopes equipped with Nomarski differential interference contrast (DIC) optics, as well as a Nikon SMZ 1500 stereomicroscope. Photographic documentation was obtained using a Leica M205 A stereomicroscope equipped with a Leica DMC5400 20 MP digital camera. Detailed microstructural analysis for samples was conducted using a Hitachi S-3400N Scanning Electron Microscope SEM (Hitachi High-Technologies Corporation, Tokyo, Japan) with an Energy Dispersive X-ray Spectroscopy EDS (Thermo Noran System Six) chemical composition analyser in microregions. Observations were performed in backscattered electron (BSE) mode at an accelerating voltage of 10 kV to examine surface morphology. The experiments were carried out under low-vacuum conditions at pressure 70 Pa, allowing the specimen to be observed without surface conductive coating.

Results and discussion

Leptothrix ochracea is a chemoorganotrophic bacterium that precipitates iron oxyhydroxides. It consists of rod-shaped cells arranged in chains within sheaths, although free-swimming single cells may also occur. A characteristic feature of this species is the production of numerous empty sheaths. Young filaments are enclosed in delicate, slimy, smooth, and initially colourless sheaths, which gradually acquire a yellow to brown colour as iron and manganese (oxyhydr)oxides accumulate on their surfaces (Fleming et al., 2011). The sheaths maintain a relatively constant width along the entire length of the filament but are brittle and easily broken. Individual cells measure approximately 2.0–3.0 μm in length and 0.8–1.0 μm in width.

As the sheaths age, cells emerge from them at a rate of approximately 1 μm/min and subsequently form new sheaths (Häusler, 1982). It is a cosmopolitan organism occurring mainly in relatively cool, iron- or manganese-rich freshwater environments, particularly in standing or slowly flowing waters. It is often described as a planktonic bacterium.

Description of the taxon and new locality

Microscopic examination of samples collected from Dione Spring, near the Przysłupianka River, revealed the presence of the iron-oxidising bacterium *Leptothrix ochracea* (Fig. 2), representing the first record of this species in the Magura Małastowska Massif. Cells of *Gallionella ferruginea* were also observed, although less frequently.

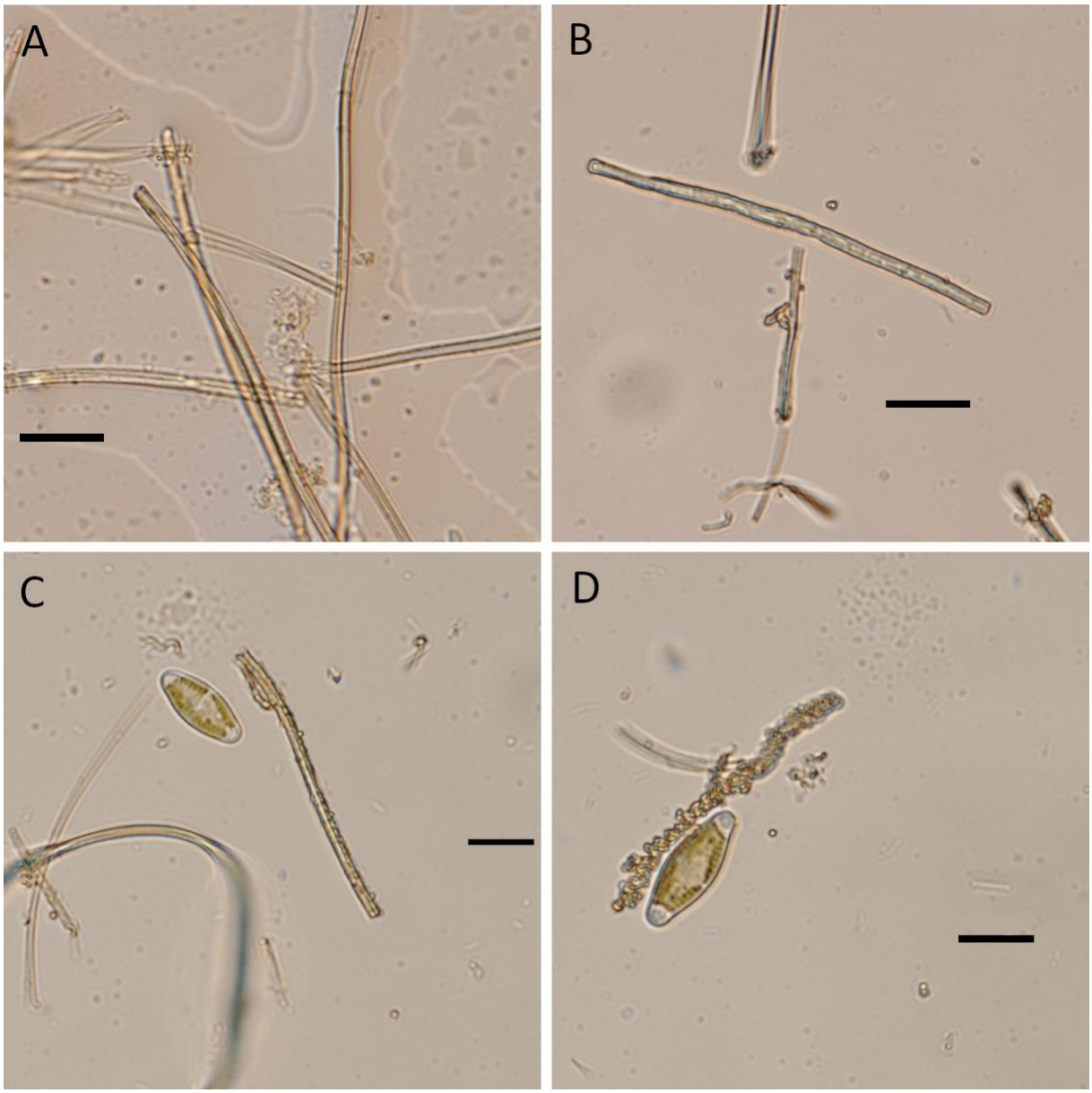


Fig. 2. *Leptothrix ochracea* (Roth) Kützing recognise in Dione Spring: empty sheaths and sheaths with cells (A, B); sheaths with diatom *Planothidium* conf. *lanceoltum* (Bréb. ex Kütz.) Lange-Bertalot and a *Leptothrix* sheath covered with precipitated iron oxides (C, D); scale bar – 10 µm (Photo: K. Wołowski – A, D; A. Chlebicki – B, C)

L. ochracea was found in a shallow, widened section of the spring, growing among decaying leaves of *Fagus sylvatica* L. (Fig. 3). Previous records of this bacterium in Poland have frequently been associated with mountain springs. Such habitats are of considerable ecological importance, as they may provide favourable conditions for the occurrence of rare microorganisms. Dione Spring is situated in a region characterised by numerous mineral springs, including Polykso Spring with calcareous tufa, Fajo Spring with very small production of rusty mats of *L. ochracea* connected with grass roots and Sulphide-rich springs occurring in the vicinity of Poprad Landscape Park and Magura National Park, reflecting the distinctive geological setting of the area. (Rajchel, Rajchel 1999; Rajchel, 2013).

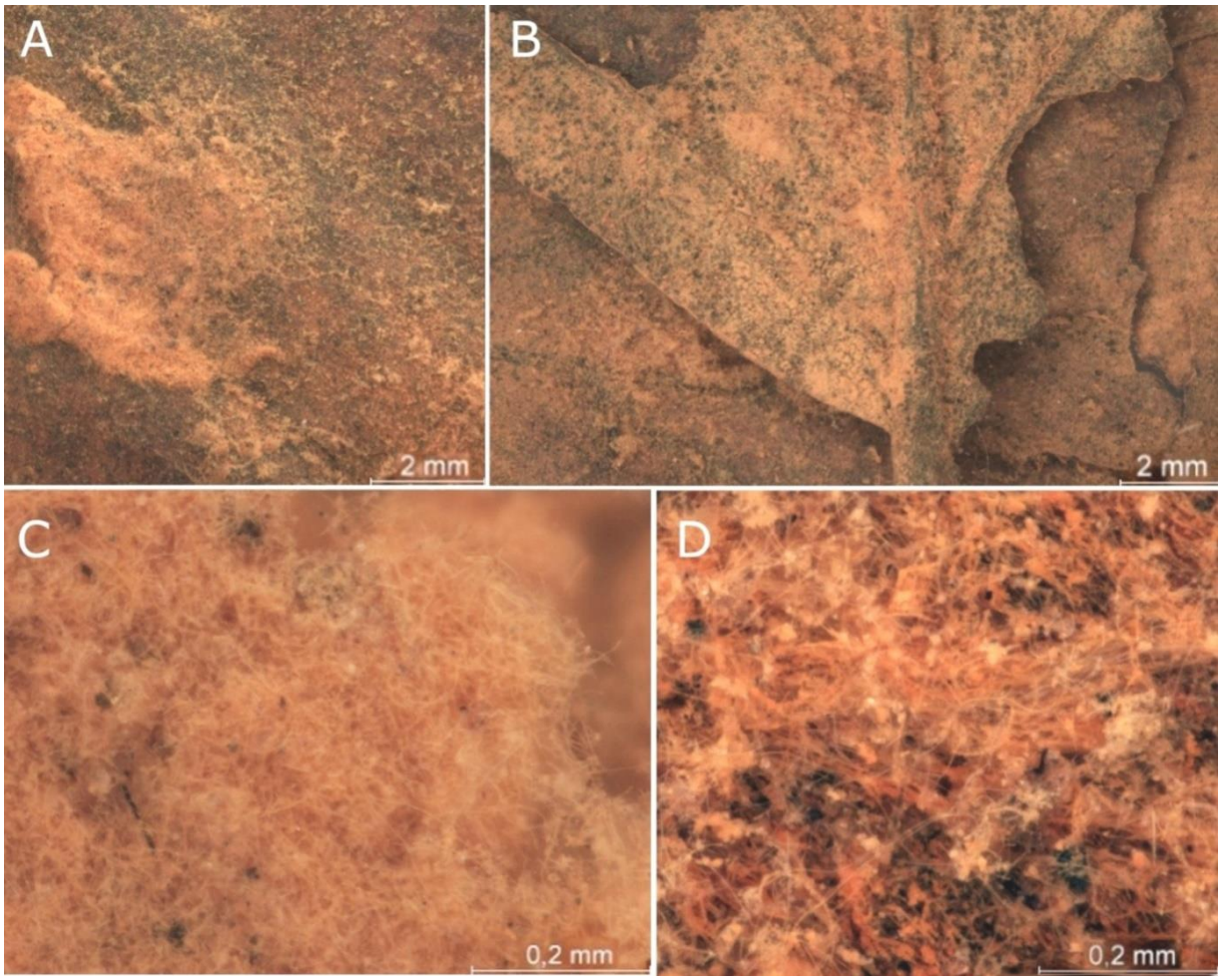


Fig. 3. Material from Dione Spring: pieces of decayed leaves covered with delicate mat (A, B); filamentous structure of the *Leptothrix ochracea* (Roth) Kützing mat (C); filaments of *L. ochracea* building the mat (D) (Photo: K. Stachowicz)

The physicochemical characteristics of Dione Spring waters are presented in table (1). The measured iron and manganese concentrations were considerably lower than those reported for other springs investigated by L. Rajchel and J. Rajchel (1999) and L. Rajchel (2013).

Tab. 1. Selected physicochemical parameters of Dione Spring water analysed at the MPGK Laboratory in Gorlice (Poland)

Tested indicator	Unit	Results for Dione Spring
Turbidity	NTU	2.37
Colour	mg Pt/dm^3	14.00
pH value	pH	7.73
Manganese	µg/dm^3	70.00
Iron	µg/dm^3	250.00
Ammonium ion	mg/dm^3	< 0.26
Nitrates	mg/dm^3	< 0.44
Nitrites	mg/dm^3	< 0.01
Total hardness	°n	11.73
Bicarbonate hardness	mg/dm^3	209.50

Our observations indicate that, in the studied habitat of the Przysłupianka Valley, *Leptothrix* communities develop most abundantly on decaying leaves of *F. sylvatica*, forming a delicate, rusty-brown filamentous coating on their surfaces (Fig. 3–4).

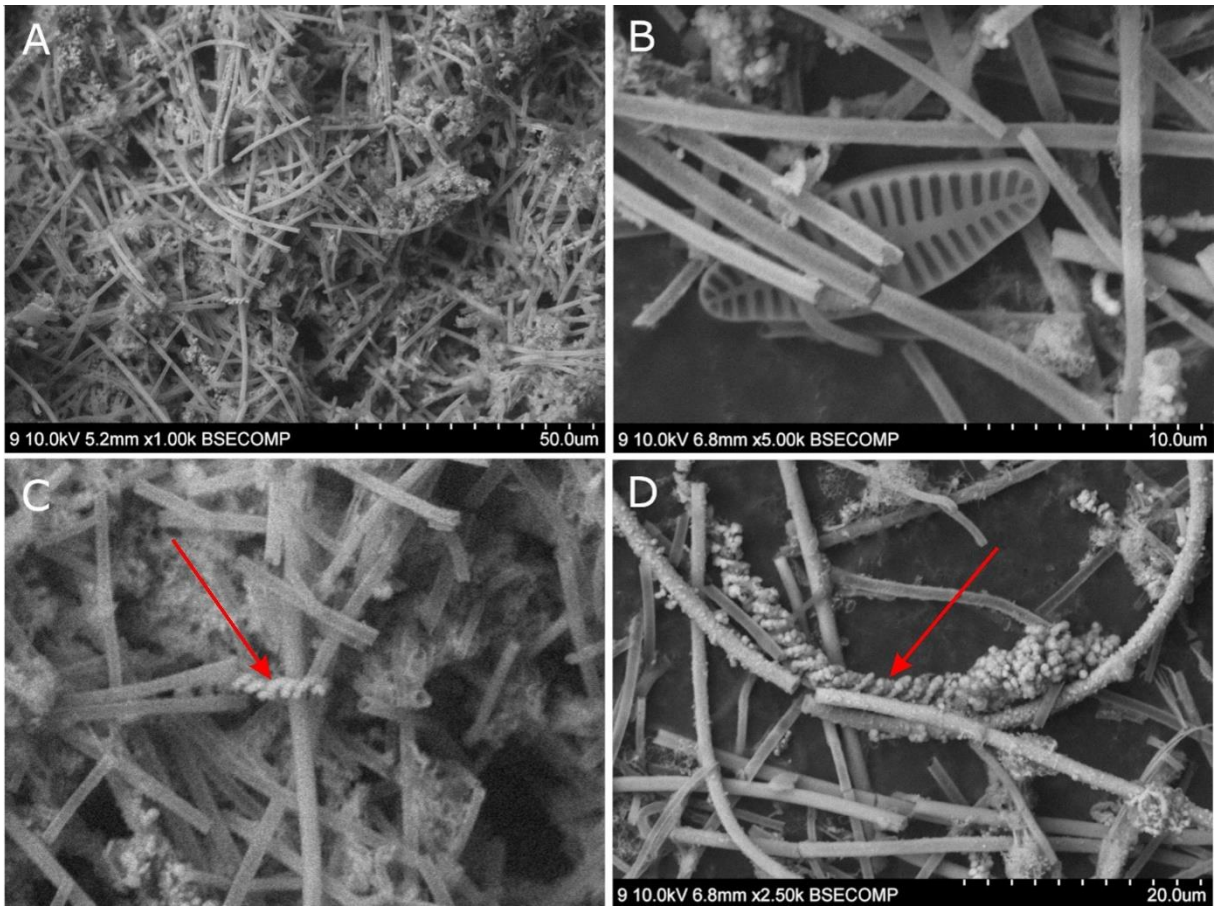


Fig. 4. Filaments of *Leptothrix ochracea* (Roth) Kützing: its sheaths on the surface of a decaying leaf (A); *L. ochracea* and frustule of *Planothidium* conf. *lanceoltum* (Brébisson ex Kützing) Lange-Bertalot (B); cells of *L. ochracea* and *Gallionella ferruginea* Ehrenberg – red arrow (4x magnification of photo A) (C); cells of *G. ferruginea* (red arrow) (D) (Photo: P. Pałka)

Such deposits indicate the presence of living *L. ochracea* populations. The rust-coloured material consists primarily of precipitated iron compounds occurring as fine particles, together with individual, small iron-oxidising bacterial cells measuring up to 3 μm in length.

The distribution of *L. ochracea* appears to be closely related to the availability of organic carbon in the aquatic environment. According to Tothero et al. (2024), *L. ochracea* oxidises ferrous iron (Fe(II)) but also requires dissolved organic carbon to support its metabolism. Our observations suggest that decaying *F. sylvatica* leaves may represent an important local source of organic carbon for these bacteria. The availability of organic matter may therefore contribute to the development of *L. ochracea* populations, while simultaneously influencing the distribution of other iron-oxidising microorganisms, including *Gallionella ferruginea*.

A clear seasonal pattern was observed in the studied bacterial communities. Populations of *L. ochracea* increased from spring to summer but declined in autumn. In contrast, *Gallionella*-like stalks were more abundant during the winter months. This pattern is consistent with the observations of Fleming et al. (2014), who reported that *Gallionella* preferentially develops under conditions of relatively low organic carbon availability. The decline in *L. ochracea* mats observed in autumn in our study further supports the seasonal trends described by these authors.

Recent genomic analyses by Tothero et al. (2024) provide further insight into the ecological preferences and metabolic capabilities of *L. ochracea*. The authors demonstrated that this bacterium occupies a distinct ecological niche, characterised by higher dissolved organic carbon requirements than those of Gallionellaceae, but lower requirements than those of other members of the *Leptothrix–Sphaerotilus* group. Thus, *L. ochracea* appears to be particularly well adapted to iron-rich environments containing moderate amounts of organic carbon, such as wetlands and spring habitats. Its metabolism combines iron oxidation with the utilisation of organic compounds, indicating a mixotrophic lifestyle.

Conclusions

The discovery of a new locality of *Leptothrix ochracea* in the Beskid Niski Mountains provides a valuable addition to the existing knowledge of the distribution of iron-oxidising bacteria in natural freshwater environments in Poland. The presence of representatives of both *Leptothrix* and *Gallionella* at this site further contributes to our understanding of the occurrence of these microorganisms in natural iron-rich springs.

Acknowledgements

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Conflict of interest

The authors declare no conflict of interest related to this article.

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Streszczenie

Bakteria utleniająca żelazo – *Leptothrix ochracea* (Roth) Kützing – odgrywa istotną rolę w biogeochemicznym obiegu żelaza poprzez utlenianie rozpuszczonego żelaza dwuwartościowego oraz tworzenie osadów bogatych w żelazo. *L. ochracea* wykazuje znaczną elastyczność metaboliczną i może rozwijać się jako miksotroficzna bakteria utleniająca żelazo, wykorzystując proces utleniania żelaza jako źródło energii, a zarówno węgiel nieorganiczny, jak i organiczny do produkcji biomasy oraz budowy pochewek. W niniejszej pracy przedstawiono dotychczas nieopisane w literaturze naturalne stanowisko *L. ochracea* w Karpatach Zachodnich, na terenie Beskidu Niskiego (Małopolska, południowa Polska). Bakterię odnotowano w Źródle Dione, neutralnym pod względem pH siedlisku słodkowodnym, bogatym w żelazo i mangan, związanym z wypływem wód podziemnych. Jej obecność potwierdzono na podstawie charakterystycznych cech morfologicznych, obejmujących nitkowate komórki otoczone pochewkami pokrytymi osadami oksywodorotlenków żelaza. W obrębie biofilmów i osadów żelazistych zaobserwowano zwarte agregaty mikroorganizmów, zdominowane przez *L. ochracea*, z niewielkim udziałem *Gallionella ferruginea* Ehrenberg. Nowo udokumentowane stanowisko poszerza wiedzę na temat rozmieszczenia bakterii utleniających żelazo w polskiej części Karpat.

Słowa kluczowe: rodzaj *Leptothrix*, bakterie utleniające żelazo, wody żelaziste, Karpaty Zachodnie

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His research to date has focused on fungi found on Arctic-Alpine plants. In addition, in recent years he has dealt with extremophiles found on rocks, mainly black yeast, and the influence of the electromagnetic field on the development of fungal colonies.

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His research interests focus on the taxonomy, ecology, and biogeography of freshwater algae, particularly phytoflagellates, including members of the Euglenozoa (Euglenaceae). He is also interested in applied phycology and bioremediation—including algal interactions and adaptation to extreme habitats—as well as algal cultivation, herbarium collections, biology education, and astrobiology.

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