

**Fossilized bioelectric wire – the trace fossil
*Trichichnus***

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Fossilized bioelectric wire – the trace fossil *Trichichnus*

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Abstract

The trace fossil *Trichichnus* is proposed as an indicator of fossil bioelectric bacterial activity at the interface oxic – anoxic zone of marine sediments. This fulfils the idea that such processes, commonly found in the modern realm, should be also present in the geological past. *Trichichnus* is an exceptional trace fossil due to its very thin diameter (mostly less than 1 mm) and common pyritic filling. It is ubiquitous in some fine-grained sediments, where it has been interpreted as a burrow formed deeper than any other trace fossils, below the redox boundary. *Trichichnus* formerly referred to as deeply burrowed invertebrates, has been found as remnant of a fossilized intrasediment bacterial mat that is pyritized. As visualized in 3-D by means of X-ray computed microtomography scanner, *Trichichnus* forms dense filamentous fabric, which reflects that produced by modern large, mat-forming, sulphide-oxidizing bacteria, belonging mostly to *Thioploca*-related taxa, which are able to house a complex bacterial consortium. Several stages of *Trichichnus* formation, including filamentous, bacterial mat and its pyritization, are proposed to explain an electron exchange between oxic and suboxic/anoxic layers in the sediment. Therefore, *Trichichnus* can be considered a fossilized “electric wire”.

1 Introduction

Bioelectric bacterial processes are omnipresent phenomena in the recent oxic–anoxic transition zones of marine sediments (Nielsen and Risgaard-Petersen, 2014). It is intriguing that they have not so far been recognized from the geological past as it was suggested by Risgaard-Petersen et al. (2012). We propose here that the usually pyritized marine trace fossil *Trichichnus* (Frey, 1970) can be interpreted as a fossil record of a bioelectrical micro-cable resulting from bacterial activities in the oxygen depleted part of marine sediments. *Trichichnus* is a branched or unbranched, straight to winding, hair-like, cylindrical structure, mostly 0.1–0.7 mm in diameter, commonly

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pyritized, oriented at various angles (mostly vertical) with respect to the bedding. The common pyritization is a particular feature of *Trichichnus*, which is generally absent in other trace fossils. *Trichichnus* is reported from both shallow- and deep-sea, mostly fine-grained sediments (Frey, 1970; Wetzel, 1983). It ranges from the Cambrian (Stachacz, 2012) to the Holocene (Wetzel, 1983). There are distinguished *Trichichnus appendicus* displaying thin appendages; and *T. linearis* or *T. simplex* probably differ only in the presence of a lining, which likely is diagenetic in origin (see Uchman, 1999, for review). *Trichichnus* is common in sediments in which pore waters were poorly oxygenated (McBride and Picard, 1991; Uchman, 1995) and is considered to be one of the first trace fossils recording colonization of the sea floor after improvement of oxygenation, penetrating sediments below the redox boundary, and having a connection to oxygenated waters on the sea floor (Uchman, 1995). It belongs to the ethological category chemichnia distinguished for trace fossils produced by organisms feeding by means of chemosymbiosis (Uchman, 1999).

Trichichnus was previously interpreted as a deep-tier burrow produced by unknown opportunistic invertebrates in poorly oxygenated sediments (McBride and Picard, 1991; Uchman, 1995). It has also been compared to an open burrow in modern deep-sea sediments more than 2 m long and no more than 0.5 mm thick (Thomson and Wilson, 1980; Weaver and Schultheiss, 1983). The sipunculid worm *Golfingia* has been considered as a possible modern example of tracemakers of very narrow and long tubes similar to *Trichichnus* (Romero-Wetzel, 1987). However, 3-D microCT scanner images of *Trichichnus* presented in this paper reflect fabric produced by modern, large, sulphur bacteria. Therefore, a new interpretation of *Trichichnus* is possible by its comparison to modern sulphur bacteria such as *Thioploca* spp. and their post-mortem history. Moreover, we propose a biogeochemical model of *Trichichnus* assisted electron transfer between different redox zones of the sediment.

2 Material and methods summary

The morphology and chemistry of *Trichichnus* from several samples, represented by Albian turbiditic marly mudstones (Silesian Nappe, Polish Carpathians); Valanginian–Hauterivian pelagic marlstones (Kościeliska Marl Formation, the Tatra Mts.) and Eocene silty shales (Magura Nappe, Polish Carpathians), were studied using a scanning electron microscope with field emission (FE-SEM, Hitachi S4700), equipped with EDS (Noran Vantage) which allows to determine chemical compounds of the examined objects. The studies on morphology and infilling of *Trichichnus* were also supported using the polarising light microscope Nikon Eclipse Pol E-600. All of the above were carried out at the Institute of Geological Sciences of the Jagiellonian University in Kraków. Moreover, the X-ray computed microtomography (microCT) scanner (SkyScan 1173) available at the Institute of Palaeontology, University of Vienna, was used to carry out the main research on the spatial organization of the *Trichichnus* (Table 1).

All samples of trace fossil *Trichichnus* presented in the paper are housed at the Institute of Geological Sciences, Jagiellonian University, Kraków, Poland, collection of Alfred Uchman and Zbigniew Sawłowicz. No permits were required for the described study, which complied with all relevant regulations.

3 Results

With the naked eye or under light microscope *Trichichnus* is easily distinguished in all rocks samples mainly by its different colour (Fig. 1a–d). Macroscopically *Trichichnus* is similar in all samples, and show a light halo around the trace, except in burrows without iron mineral infillings (Fig. 1c and d). Neither the length nor width of the trace depend on the type of the host rock. The boundary between the trace fossil and the rock is usually sharp (Fig. 1e).

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and anoxic zones (see Ntarlagiannis, 2007; Risgaard-Petersen et al., 2014). Studies reporting extracellular bioelectric currents concerned dissimilatory metal-reducing bacteria, such as *Geobacter sulfurreducens*, *Shewanella oneidensis* MR-1 and the thermophilic, fermentative bacterium *Pelotomaculum thermopropionicum* or the oxygenic phototrophic cyanobacterium *Synechocystis* (Borole et al., 2011). Natural conductive minerals (e.g., magnetite, greigite) can facilitate electron transfer between different species of microbes. Presumably microbes should preferentially use mineral particles, discharging electrons to and accepting them from mineral surfaces, in particular for long-distance electron transfer (Kato et al., 2012). The interaction between minerals and bacteria can be quite complex as Kato et al. (2013) showed that e.g., *G. sulfurreducens* constructed two distinct types of extracellular electron transfer (EET) paths, in the presence and absence of iron-oxide minerals. It is worth noting that large scale sulphide ores, where pyrite is commonly a main component, are regarded as geobatteries and used by geophysicists for their exploration. In natural electrochemical processes ore serves as a conductor to transfer the electrons from anoxic to oxic environments (Sato and Mooney, 1960). Newer reports show that coupling of geochemical reactions between shallower and deeper layers of the sediment can be realized by vertical centimetre-long bacterial filaments (Pfeffer et al., 2012; Risgaard-Petersen et al., 2014; Schauer et al., 2014). Nevertheless, only the giant sulphur bacteria, so-called a “macro-bacteria” are able to produce mat spatial system in the scale of *Trichichnus*. Macro-bacteria of Beggiatoacea family are considered to be the most direct competitors to cable bacteria representing Desulfobulbaceae family at the interface of oxic–anoxic zone of marine sediments (see Nielsen and Risgaard-Petersen, 2014). We propose *Thioploca* spp., one of the genus of Beggiatoacea family (see Salman et al., 2011), as a tracemaker of *Trichichnus*.

Large communities of the sulphur bacteria *Thioploca* spp. produce the filaments consisting of thousand of cells that can penetrate 5–15 cm down into the sediment. These filaments (trichomes), bundled in common slime sheaths, make a dense bacterial mat, where the density decreases with depth leaving single sheaths in the

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5 deepest part of the spatial system of the mat. The *Thioploca* sheaths, rarely branched, extend in different directions, mostly vertically. One sheath can accommodate up to 100 filaments of 15–40 µm in diameter each, giving about 4 mm for the maximum diameter of the sheath (Fossing et al., 1995; Schulz et al., 1996). *Thioploca* trichomes gliding
10 within sheaths can migrate through several redox horizons, coupling the reduction of nitrate in the overlying waters and the oxidation of dissolved sulphide in the sulphate reduction zone (Fossing et al., 1995; Heutell et al., 1996). Therefore, the sheaths are used as communication tubes and enable the sulphur bacteria to switch vertically between nitrate and sulphide (electron acceptor and donor, respectively). This sulphide
15 oxidization mechanism leads to accumulation of elemental sulphur globules in the bacterial cells. Moreover, *Thioploca* trichomes may leave their sheaths and move into other sheaths, thus, one sheath can be occupied by different species (Jørgensen and Gallardo, 1999).

The *Thioploca* sheaths – either filled with trichomes or abandoned – may be closely
20 associated with other filamentous sulphate-reducing bacteria like *Desulfonema* sp. (Jørgensen and Gallardo, 1999; Teske et al., 2009). Empty sheaths were found even at > 20 cm depth into the sediment. In contrast, sheaths were not found shallower than a depth of a few centimetres in the sediments. Therefore, the surface and topmost
25 part of the *Thioploca* mat system is formed by single bacterial filaments only (Schulz et al., 1996). *Thioploca* spp. are known from both marine and lake environments. Nevertheless, their mass occurrences are related to high organic production and oxygen depletion, e.g., the Chile and Peru offshore upwelling system (Jørgensen and Gallardo, 1999).

Pyritized organic remains are common in the sedimentary record and various
mechanisms of fossil pyritization have been described (e.g. Canfield and Raiswell, 1991; Briggs et al., 1996). Apart from the similarity between the *Trichichnus* fabric and spatial organization of the *Thioploca* mat system, the common pyritization of
Trichichnus also indicates its close relation to the sulphur bacteria. As the most abundant metal sulphide in nature, pyrite FeS₂ has a major influence on the

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Nevertheless, sulphur content and sulphur speciation may not correlate to microbial metabolic processes (Engel et al., 2007).

Oxidation of iron sulphides is one of the most common processes in marine sediments. For example, Passier et al. (1999) reported that in the Mediterranean sapropels the percentage of initially formed iron sulphides that were re-oxidized varied from 34 to 80 %. Oxidation of iron sulphide framboids to iron (hydro)oxides is often observed in fossils (e.g., Luther et al., 1982; Sawłowicz, 2000). There is a significant difference between oxidation of pyrite and its precursors. For example, FeS, but not pyrite, can be oxidized microbially with NO_3^- as an electron acceptor (Schippers and Jørgensen, 2002).

5 Conclusions and model of *Trichichnus*

Trichichnus is a good example of microbiological and mineralogical collaboration. Its role in electron transfer is still enigmatic, but several stages can be proposed (Fig. 3). It should also be noted that the relatively large length of *Trichichnus* and its continuation through different redox zones may result in its vertical internal zonation. As suggested earlier, *Trichichnus* may reflect former slime sheaths, where large sulphur bacterial trichomes, like *Thioploca* community, move up and down. There is growing evidence (e.g., Teske et al., 2009; Prokopenko et al., 2013; Buck et al., 2014 and references therein), that *Thioploca* sheaths house a complex bacterial consortium. In our opinion it is a matter of time before additional microbes will be found associated with *Thioploca* or their post-mortem sheaths.

1. The earliest stage of the *Trichichnus* formation is related to a sulphuric microbial mat in the dysoxic zone, connecting the anoxic-sulphidic substrate. Long, filamentous bacteria structured like electric cables facilitate electron transport over centimetre distances in marine sediment (Pfeffer et al., 2012; Risgaard-Petersen et al., 2014). The filamentous multicellular, aerobic bacteria of the family *Desulfobulbaceae*, living together with *Thioploca* in the sheath, conduct electrons

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through internal insulated wires from cells in the sulphide oxidation zone to cells in the oxygen reduction zone (Pfeffer et al., 2012). For *Thioploca* itself such behaviour has not been proved yet (see Nielsen and Risgaard-Petersen, 2014 for review). The electric circuit is balanced by charge transport by ions in the surrounding environment (Risgaard-Petersen et al., 2012).

2. The next stage is related to the iron sulphidization process. Microorganisms can influence both the precipitation of sulphides and their morphology. Bacterial components, e.g., cell walls, facilitate mineralization by sequestration of metallic ions from solution and provide local sites for nucleation and growth (Beveridge and Fyfe, 1985). Iron sulphides (framboids) can form within a matrix of bacteria and biopolymers both during the life of bacterial consortium (see MacLean et al., 2008) and after their death. It should be noted that the process of sheath infilling varies within the system. For example, larger sheaths may be abandoned by trichomes of *Thioploca* faster, compared to smaller ones (Schulz et al., 1996). The biofilm in a proto-*Trichichnus* capsule seems to be an ideal place for the formation of iron sulphides. Formation of pyrite, probably formerly ferromagnetic greigite, depends on availability of soluble Fe(II) from a surrounding sediment and sulphides (H₂S or polysulphides). Crystals in framboids are generally closely packed, and framboids themselves often too, but when it is not the case, the bacterial pili are believed to connect dispersed conductive minerals (Revil et al., 2010). Cell-to-mineral wires support the thesis that the metallic conductor-like pyrite occurring in sediment might be responsible for the electron flow (see also Nielsen et al., 2010). Growth of a biofilm – developed in the mucus of the large sulphur bacteria sheath – on pyrite can enhance conductivity supporting the biogeobattery idea. The oldest microbial communities colonising sedimentary pyrite grains were found in a ~ 3.4 billion-year-old sandstone from Australia (Wacey et al., 2011).

3. The process of electron transfer can continue also after death of microbial consortia. Decomposition of organic matter inside the channel creates the local

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reducing microenvironment, which promotes pyrite formation (e.g., Berner, 1980; Raiswell, 1982), even when the surrounding sediment is not fully anoxic. It is tempting to propose that perhaps some iron sulphide forms resulted from a replacement of sulphur globules, either inside sulphur bacteria cells or after their lysing. Pyrite might form the sulphur globules stored intra- and extracellularly by chemolithoautotrophic bacteria (e.g., *Thioploca*) or by purple and green sulphur bacteria (Oschmann, 2000). Spheroidal crystalline aggregates representing early pyrite and subsequently replaced by iron hydroxides were found in Silurian cyanobacterial filaments (Tomescu et al., 2006). Formation of pyrite framboids via replacement of sulphur grains was also shown experimentally by Křibek (1975).

A halo observed around *Trichichnus* (Fig. 1c and d) results from oxidation of pyrite or former iron monoxide infilling the trace fossil. The oxidation stage can take place both during earliest and later stages of diagenesis (the latter is out of the scope of this paper). Re-oxidation processes of pyrite framboids are common in tropical upwelling area, caused by bioturbation and possible contributions from sulphide-oxidizing bacteria (Diaz et al., 2012 and references therein). It would additionally expand, but also complicate, the process of electron transfer in sediments. *Trichichnus* is a good example of fossilized bacterial bioelectrical wire. Such interpretation greatly improves our knowledge about how this phenomenon has been widespread in sedimentary environments and through geological time.

Supplementary information

Video captured from an X-ray CT microscanner provides dimensional visualization of the dense *Trichichnus* fabric comparable with the upper part of the bacterial filamentous *Thioploca*-like mat system.

The Supplement related to this article is available online at
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Author contributions. M. Kędzierski conceived the study and contributed to the bacterial part of paper. A. Uchman delivered the samples of *Trichichnus* and contributed to the trace fossil part of paper. Z. Sawłowicz contributed to the geochemical part of paper. A. Briguglio delivered the X-ray computed microtomography scanner data. M. Kędzierski, A. Uchman and Z. Sawłowicz contributed to the model of *Trichichnus*.

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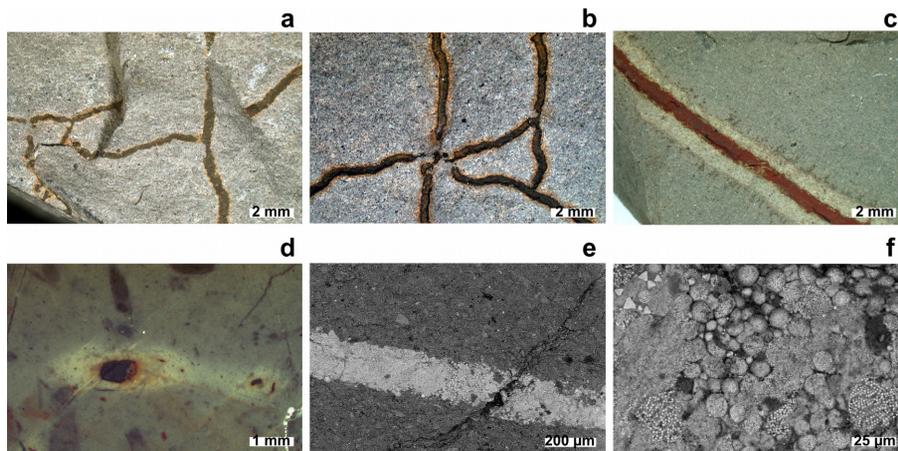


Figure 1. Macro- and microimages of *Trichichnus* in the rock fractures and slabs **(a–c)** Albian turbiditic marly mudstones, Kozy, Polish Carpathians; **(d)** Valanginian–Hauterivian pelagic marlstones. Dolina Kościeliska valley, Tatra Mountains, Poland, **(e and f)** Eocene silty shales (Zbludza, Polish Carpathians). **(a and b)** subhorizontal network of *Trichichnus*. **(c and d)** halo (diffusion zone of Fe (oxy)hydroxides) around horizontal **(c)** and vertical **(d)** *Trichichnus*. **(e)** Infilling of a fragment of *Trichichnus* with abundant pyrite framboids and Fe (oxy)hydroxides (SEM BSE). **(f)** Magnification of image **(e)**. Specimen numbers: **(a)** INGUJ147P70, **(b)** INGUJ147P71, **(c)** INGUJ147P72, **(d)** INGUJ155P20, **(e and f)** INGUJ144P159.

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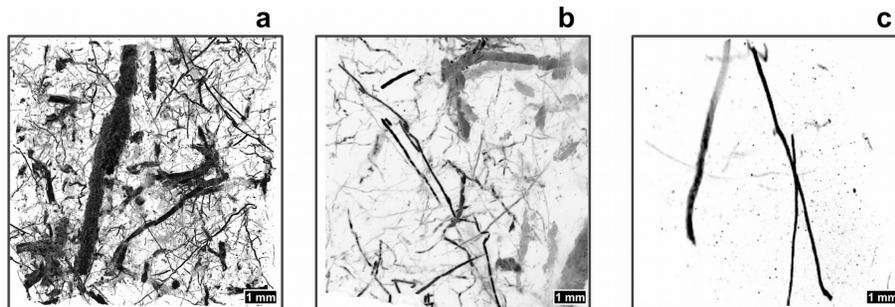


Figure 2. X-ray computed microtomography scanner images of different parts of *Trichichnus* spatial complex, Oligocene, Skole Nappe Polish Flysch Carpathians. **(a)** Dense *Trichichnus* fabric, similar to the upper part of the *Thioploca* mat system. **(b)** *Trichichnus* fabric comparable with the middle part of the *Thioploca* mat system. **(c)** *Trichichnus* fabric depicting the lower part of the *Thioploca* mat system.

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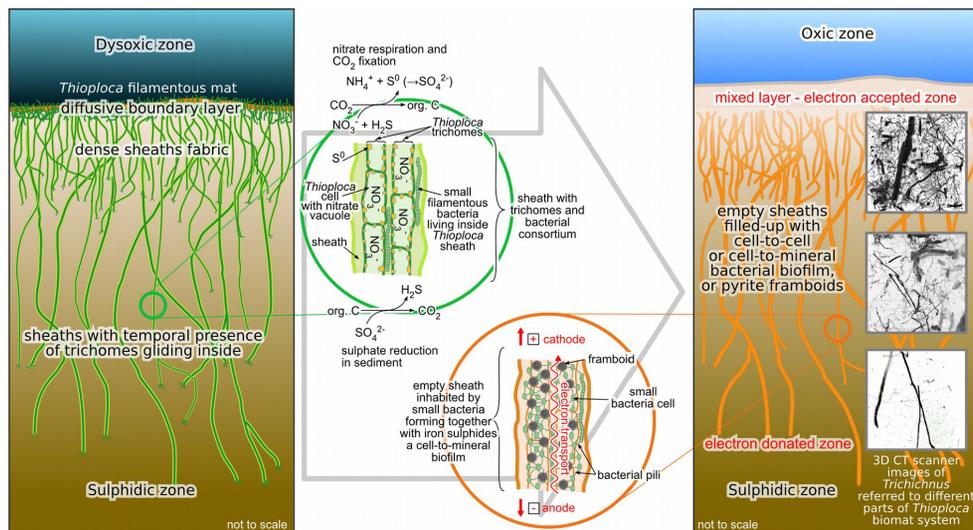


Figure 3. Model of the origin of *Trichichnus*. The ecology of *Thioploca* mat system and their sulphide oxidation chemistry (left). The *Thioploca* sheaths system below the diffusive boundary layer forms a construction which may be inhabited by small bacteria making the conductive nanowire-pyrite framboids biofilm. This triggers the electric self-potential between the sulphidic zone and mixed layer, thus, the electron flow (right). The different part of the *Trichichnus* compared with the different part of the former *Thioploca* mat system are shown for the comparison (right).

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