# 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 oxic—anoxic interface 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 oxic–anoxic transition zone of recent marine sediments (see Nielsen and Risgaard-Petersen, 2015 for review). 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). One reason could be that effects of such

bacterial processes, leading to oxygenation of the anoxic sediments on the sea floor, are eventually destroyed by subsequent bioturbation (Malkin et al., 2014). We propose here that the usually pyritized marine trace fossil *Trichichnus* Frey, 1970 can be interpreted as a fossil record of complex bioelectrical operations resulting from bacterial activities in the oxygen

5   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 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

10   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;

15   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).

20   *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

25   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*

30   assisted electron transfer between different redox zones of the sediment.

## 2    Material and methods summary

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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 of 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* (Tab. 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 Sawlowicz. 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 shows 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 depends on the type of the host rock. The boundary between the trace fossil and the rock is usually sharp (Fig. 1e).

The SEM studies revealed that majority of the studied *Trichichnus* is filled with framboids and framboidal aggregates (Fig. 1e and f). Framboidal forms are composed of iron sulphides (most probably pyrite), Fe oxy/hydroxides or a mixture of both. The microcrystals building framboids are generally well-developed and their sizes are usually about 1–2 μm, generally dependent on the size of the framboid. Most of the microcrystals in framboids are closely packed. SEM-EDS study shows that the colourful halo around traces does not reveal any chemical differences from the composition of the surrounding rock. It is likely that the amount of iron minerals in the halo is below the detection limit of the EDS method. Apart

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from the iron minerals, subordinate amounts of several other minerals, generally corresponding to the host rock, such as calcite, quartz and gypsum, are observed.

MicroCT scans allowed three dimensional visualization of several *Trichichnus* embedded in a dark mudstone from the Oligocene Menilite Formation in the Western Carpathians, Poland.

5      The density difference between the sediment matrix and the pyritic trace fossil fillings allowed extremely accurate three dimensional visualization (Fig. 2). The results show a very dense fabric composed of *Trichichnus* fillings of variable size and orientation, which are only partly visible on a sample surface. Since the resolution of the 3-D model here presented is 9.97 μm, all the structures larger than 10 μm are visible and renderable. The distribution of

10     diameters of the traces displays two major peaks: 600 μm for the thickest traces and 90 μm for the very thin ones (Fig. 2a; Supplement).

The *Trichichnus* morphology seen in 3-D microCT scanner image (Fig. 2a—c) is similar to structures produced by filamentous bacteria (e.g., Pfeffer et al., 2012) or to large, mat-forming, filamentous sulphur bacteria, e.g., *Thioploca* spp. (Fossing et al., 1995 – Fig. 3a;

15     Schulz et al., 1996 – Fig. 8; Jørgensen and Gallardo, 1999 – Fig. 5) (see also Heutell et al., 1996). The microCT scanner images also reveal different spatial organizations, density, diameters and shapes of the *Trichichnus.* These correspond to different parts of vertical system of the *Thioploca* mat in sediment. Also the density of *Trichichnus* (Fig. 2a), which constitutes 3.1% of the whole scanned sediment volume, is comparable to the *Thioploca* mat

20     in their upper shallow subsurface part. Other 3-D scanner images (Fig. 2b and c) show lowered density of *Trichichnus,* comparable to middle and bottom parts of the *Thioploca* filamentous mat spatial system.

**4      Discussion**

Three-dimensional reconstructions of *Thioploca* spp. (Fossing et al., 1995; Schulz et al., 1996;

25     Jørgensen and Gallardo, 1999) resemble *Trichichnus* in the 3-D scanner images. Moreover, the common pyritization of *Trichichnus* is related to sulphate-reducing bacteria, like δ-proteobacteria *Desulfovibrio* sp., which can co-occur with sulphur-oxidizing bacteria, such as *Beggiatoa* or *Thioploca* (e.g., Jiang et al., 2012).  Therefore, we consider *Thioploca*-like, mat-forming, large, sulphur bacteria and related filamentous sulphide-oxidizing bacteria (see

30     Teske et al., 1995) as a tracemaker of *Trichichnus* tunnels and their spatial organization. The

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*Thioploca*-like mat, usually hosting other bacteria or small protists (e.g., Buck et al., 2014), combined with the post-mortem history of sulphur bacterial mat systems, are referred to the idea of bioelectrochemical systems (BESs), including the microbial fuel cells (MFCs) and biogeobatteries (e.g., Naudet et al., 2003, 2004; Naudet and Revil, 2005; Linde and Revil,

5 2007; Ntarlagiannis et al., 2007; Logan, 2009; Teske et al., 2009; Nielsen and Girguis, 2010; Revil et al., 2010; Borole et al., 2011; Hubbard et al., 2011; Risgaard-Petersen et al., 2014; Nielsen and Risgaard-Petersen, 2015 for review).

In biogeobattery systems, bacteria are interconnected cells to cells or cells to mineral surfaces via electrically conductive appendages – bacterial pili (nanowires) – making a complex

10 electroactive network (biofilm) (Ntarlagiannis et al., 2007; Revil et al., 2010; Borole et al., 2011; Reguera et al., 2005; Gorby et al., 2006; El-Naggar et al., 2010; Nielsen et al., 2010; Risgaard-Petersen et al., 2014; Nielsen and Risgaard-Petersen, 2015). The electron transport in BESs may be realized in various ways, including transfer through long bacterial nanowires or along biofilm matrix (Lovley, 2008). Its magnitude and duration mostly depend on

15 atmospheric oxygen (electron acceptor) availability that generates electrical self-potentials in the sediments between oxidized and anoxic zones (see Ntarlagiannis, 2007; Risgaard-Petersen et al., 2014). Studies reporting extracellular bioelectric current concerned dissimilatory metal-reducing bacteria, such as *Geobacter sulfurreducens*, *Shewanella oneidensis* MR-1 and the thermophilic, fermentative bacterium *Pelotomaculum thermopropionicum* or the oxygenic

20 phototrophic cyanobacterium *Synechocystis* (Borole et al., 2011). Natural conductive minerals (e.g., magnetite, greigite – an intermediate stage for pyrite formation) 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

25 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, have been regarded as geobatteries for many years and used by geophysicists for an exploration. In natural electrochemical processes

30 ore serves as a conductor to transfer the electrons from anoxic to oxic environments (Sato and Mooney, 1960; Naudet et al., 2003). Newer reports show that coupling of geochemical reactions between shallower and deeper layers of the sediment can be also realized by vertical

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centimetre-long filaments of multicellular bacteria of the family Desulfobulbaceae, the so-called cable bacteria (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 at the interface of oxic–anoxic zone of marine sediments (see Nielsen and Risgaard-Petersen, 2015). 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 thousands 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 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 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 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). Empty sheaths were found even at >20 cm depth into the sediment. In contrast, the sheaths were not found shallower than a depth of a few centimetres in the sediments. Therefore, the surface and topmost part of the *Thioploca* mat system is formed by single bacterial filaments only (Schulz et al., 1996). However, brackish/freshwater *T. ingrica* may not form any mats at the sediment surface, showing biomasses peak 4–7 cm below the sediment surface (Høgslund et al., 2010).

The *Thioploca* sheaths – either filled with trichomes or abandoned – may be closely associated with other filamentous sulphate-reducing bacteria like *Desulfonema* sp. (Jørgensen

and Gallardo, 1999; Teske et al., 2009). *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).

5     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 sulphate-reducing bacteria. Schulz et al. (2000) observed that empty sheaths of

10    *Thioploca* from the Bay of Conception during autumn/winter time were stained with iron sulphides. As the most abundant metal sulphide in nature, pyrite $FeS_2$ has a major influence on the biogeochemical cycles of sulphur and iron, and through its oxidation also of oxygen. There have been several important reviews on sedimentary pyrite formation (e.g., Berner, 1970; Schoonen, 2004; Rickard and Luther, 2007, and references therein), and specifically on

15    iron sulphide framboids (e.g., Love and Amstutz, 1966; Raiswell, 1982; Wilkin and Barnes, 1997; Sawłowicz, 2000; Ohfuji and Rickard, 2005, and references therein). It is important to stress that at low temperature pyrite growth is usually preceded by the formation of unstable iron monosulphides, such as mackinawite and greigite. The latter is the ferrimagnetic inverse thiospinel of iron. Pyrite, like other sulphide minerals, is a semiconductor determined to be

20    "semi-metallic" but its conductivity in different admixtures varies widely between 0.02 and 562 $(\Omega cm)^{-1}$ (Rimstidt and Vaughan, 2003, and references therein).
      Pyrite has a great potential in both interaction with microorganisms and electron transfer as its range of morphological, chemical and electric characteristics is quite large. Both iron and sulphur, necessary for pyrite formation, are pivotal for microbes. For instance, more than 50%

25    of reduced sulphate in sediments inhabited by *Thioploca* off the Chilean coast is accumulated in the pyrite pool (Ferdelman et al., 1997). Iron is an important carrier of electrons in microbial ecosystems (Wielenga et al., 2001) and bacteria play important role in different processes of iron oxidation and reduction (Weber et al., 2006). Interestingly, some Firmicutes bacteria species *Desulfitobacterium frappieri* are capable of both reducing $Fe^{3+}$ with $H_2$ as an

30    electron donor and oxidizing $Fe^{2+}$ with nitrate as an electron acceptor (Shelobolina, 2003). In sedimentary environments the major source of sulphur incorporated into iron sulphides is $H_2S$ or $HS^-$ resulting from bacterial sulphate reduction. Sulphate-reducing bacteria (SRB) use

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sulphate as the terminal electron acceptor of their electron transport chain (e.g., Widdel and Hansen, 1992). SRB are usually regarded as strictly anaerobic, but recent investigations showed that SRB are both abundant and active in the oxic zones of mats (see Baumgartner et al., 2006 for review). Iron monosulphides and pyrite, including framboids, are quite common

5　in some microbial mats (e.g., Popa et al., 2004; Huerta-Diaz et al., 2012) but their formation is complicated and difficult to study. 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

10　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).

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## 6　Conclusions and model of *Trichichnus*

*Trichichnus* is a good example of microbiological and mineralogical collaboration, propounded earlier by Naudet et al. (2003, 2004). 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

20　length of *Trichichnus* and its continuation through different redox zones may result in its vertical internal zonation. As suggested earlier, *Trichichnus* may reflects 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

25　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

30　sediment (Pfeffer et al., 2012; Risgaard-Petersen et al., 2014). The filamentous multicellular, aerobic bacteria of the family Desulfobulbaceae (cable bacteria), living together with *Thioploca* in the sheath, conduct electrons through internal insulated wires from cells in the

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sulphide oxidation zone to cells in the oxygen reduction zone Pfeffer et al. (2012). For *Thioploca* itself such behaviour has not been proven yet (see Nielsen and Risgaard-Petersen, 2015 for review). The electric circuit is balanced by charge transport by ions in the surrounding environment (Risgaard-Petersen et al., 2014; Nielsen and Risgaard-Petersen,

5    2015).

(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)

10   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

15   iron sulphides. Formation of pyrite, probably formerly ferromagnetic greigite, depends on availability of soluble Fe(II) from a surrounding sediment and sulphides ($H_2S$ 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

20   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).

25   (3) The process of electron transfer can continue also after termination of microbial consortia. Decomposition of organic matter inside the channel creates the local 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 (stored intra- and

30   extracellularly by chemolithoautotrophic bacteria, e.g., *Thioploca* or by purple and green sulphur bacteria, Oschmann, 2000), either inside sulphur bacteria cells or after their lysing. Spheroidal crystalline aggregates representing early pyrite and subsequently replaced by iron

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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 monosulphide infilling the trace fossil. The oxidation stage can take place both during the 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.

Summarizing, we believe that *Trichichnus* is a good example of a potential ancient place where several bioprocesses related to electron transfer in sediment could proceed. A number of evidences for such processes, both in the field and laboratory investigations, has been growing significantly for last few years. Development of new technologies, e.g., multipurpose electrodes which combine reactive measurements with electrical geophysical measurements (Zhang et al., 2010), opens new frontiers in monitoring microbial processes in sediments. We believe that our idea enhances special attention to *Thioploca* endobionts in respect of their electron exchange along the cell-to-mineral wires. Our interpretation shows how this phenomenon could have been widespread in sedimentary environments and through the 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.

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| Scanner | SkyScan 1173 |
|---|---|
| Camera Pixel Size | 50.0 μm |
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| Source Current | 61 μA |
| Camera binning | 1 x 1 |
| Filter | Al 1mm |
| Exposure | 650 ms |
| Rotation step | 0.15° |
| Frame averaging | 30 |
| 360° Rotation | On |
| Scan Duration | 14h 22m |
| Pixel Size | 9.97646 μm |

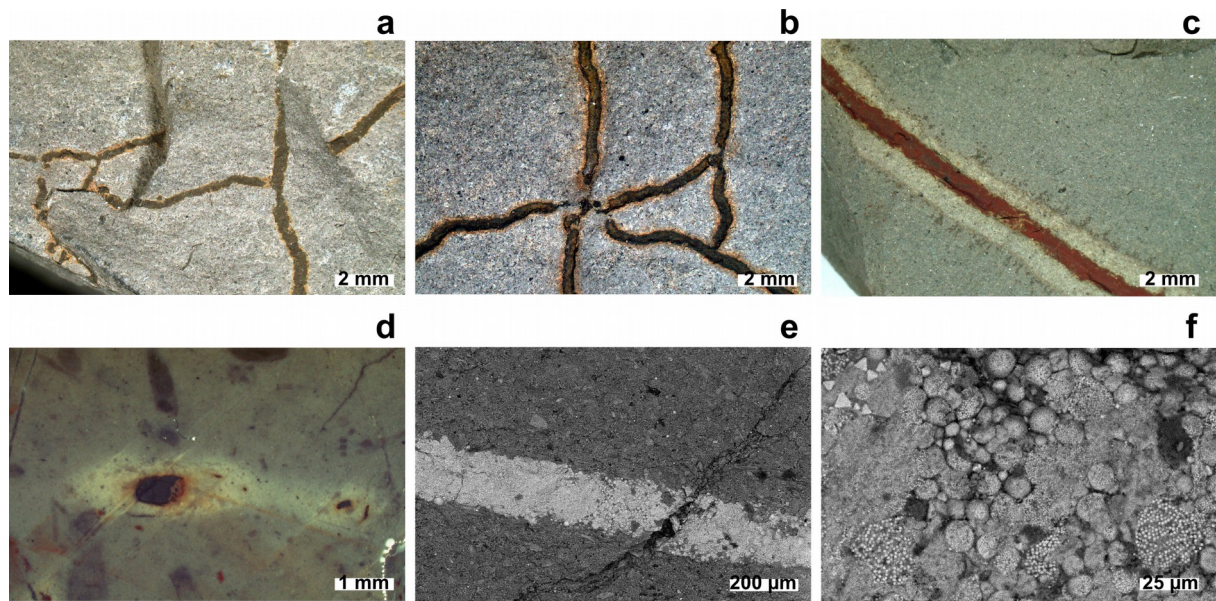Tab. 1. Scanner setting data used for X-ray computed microtomography (microCT).

Fig. 1. **Macro- and microimages of *Trichichnus* in the rock fractures and slabs (a–c -** Albian turbidtic marly mudstones, Kozy, Polish Carpathians; **d** – Valanginian–Hauterivian pelagic marlstones. Dolina Kościeliska valley, Tatra Mountains, Poland, **e, f** – Eocene silty shales, Zbludza, Polish Carpathians). **a, b,** subhorizontal network of *Trichichnus*. **c**, **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, f – INGUJ144P159.
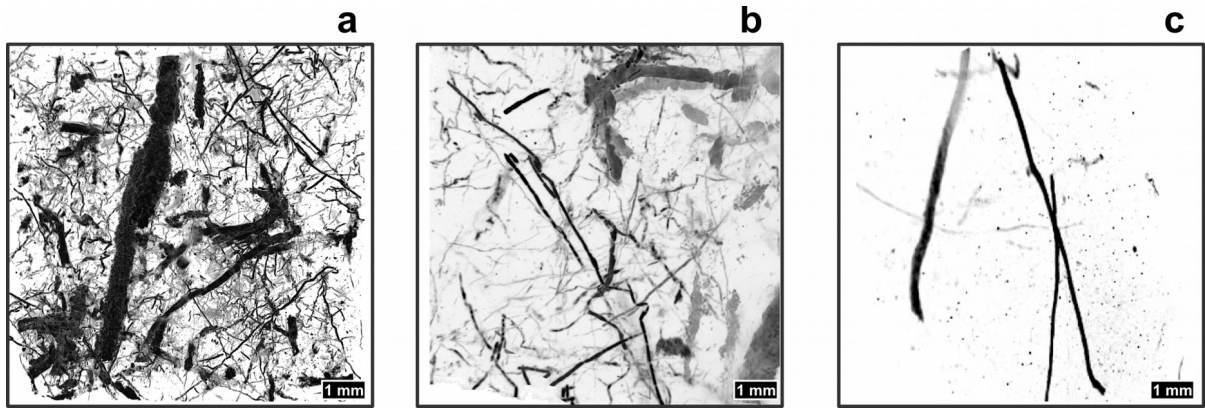
Fig. 2. **X-ray computed microtomography scanner images of different parts of**
***Trichichnus* spatial complex, Oligocene, Skole Nappe Polish Flysch Carpathians**. **a**, dense
*Trichichnus* fabric, similar to the upper part of the *Thioploca* mat system. **b**, *Trichichnus*
fabric comparable with the middle part of the *Thioploca* mat system. **c**, *Trichichnus* fabric
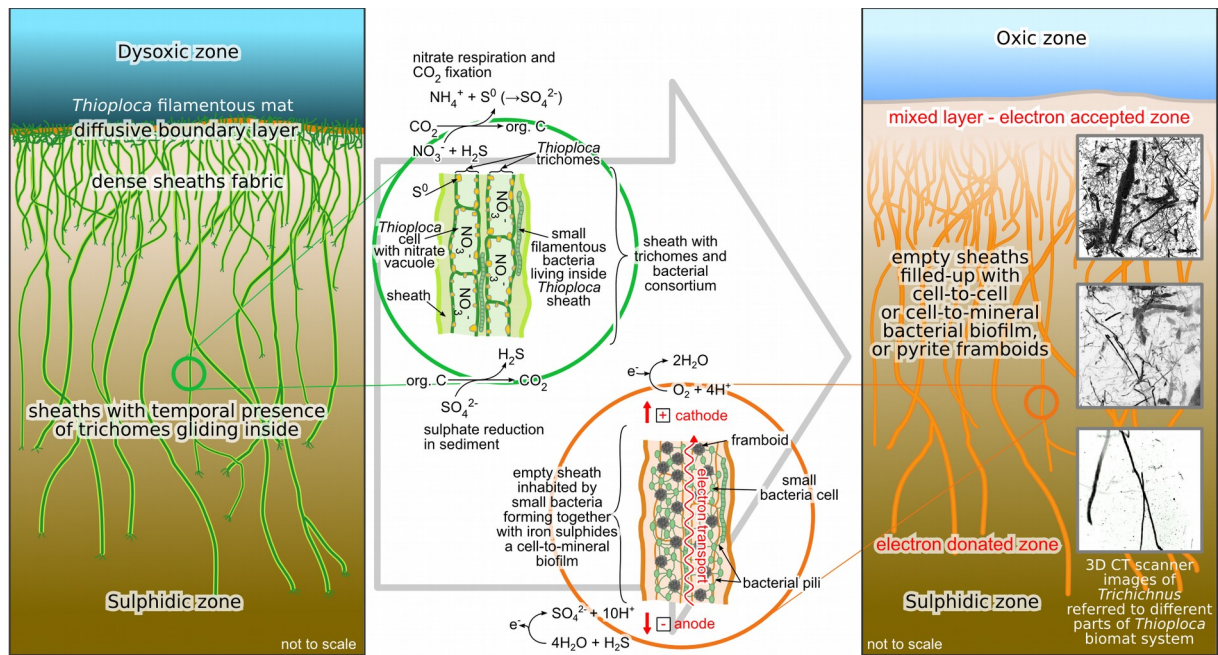depicting the lower part of the *Thioploca* mat system.

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Fig. 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**). *Thioploca* spp. nitrogen, carbon and sulphur metabolism reactions taken from Teske and Nelson (2006); half-reactions on *Trichichnus* adapted from Nielsen and Risgaard-Petersen, 2015.