Bioerosion in the Late Devonian placoderm remains from the Holy Cross Mountains, Poland

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Dworczak, P.G., Szrek, P., and Wilk, O. 2025. Bioerosion in the Late Devonian placoderm remains from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 70 (4): 629–639.

We report the first occurrence of trace fossils in placoderm bones from the Upper Devonian of the Holy Cross Mountains. A taxonomic analysis of three ichnogenera revealed the earliest evidence of *Sulculites* (ie., *Sulculites bellus*), characterised by curved grooves known from the tortoise shells, the potential *Osteocallis*? isp. consists of irregular and shallow grooves, which were first described on dinosaur bones from continental deposits, while *Karethraichnus*? isp. being a deep and cylindrical boring, recognized for the first time in turtle shells. They show the evidence of post mortem erosional activity by organisms (e.g., worms) that penetrated the decaying carcasses to search for nutritional particles, graze microbial mats and colonize the osteic substrate. The massive dermal bones of placoderms seem to be appealing to scavengers, albeit rather as an opportunistic behaviour. Nevertheless, this uncommon finding may be caused by the relatively limited attention that has been paid to this phenomenon. The described traces also represent the oldest evidence of macrobioerosion in osteic substrate, as well as the oldest documented occurrence of these forms that have been known so far.

Key words: Placodermi, trace fossils, *Sulculites*, Famennian, Devonian, Holy Cross Mountains, Poland.

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Received 29 October 2024, accepted 12 August 2025, published online 30 October 2025 .

Introduction

Bioerosion structures, representing the results of chemical and/or mechanical processing (e.g., Neumann 1966; Bromley 1992; Taylor and Wilson 2003; Pirrone et al. 2014), have the significant importance in the analysis of taphonomy and are essential to understanding the relationships among ancient organisms and the structure of hard ground communities (Knaust and Bromley 2012; Vinn et al. 2015; Vinn and Toom 2016; Höpner and Bertling 2017; Wisshak et al. 2019). Trace fossils in osteic substrates are rare in the fossil record, however, a recent study by Jaminson-Todd et al. (2023) has significantly expanded the documented occurrences of invertebrate bioerosion in the Mesozoic vertebrate remains. This phenomenon has been observed in both marine (e.g., Bystrov 1956; Tapanila et al. 2004; Muñiz et al. 2010; Belaústegui et al. 2012; Karl et al. 2012; Collareta et al. 2022; Jamison-Todd et al. 2024) and terrestrial environnements (e.g., Paik 2000; Roberts et al. 2007; Britt et al. 2008; Paes Neto et al. 2016; Cunha et al. 2024). The bioerosional activity of invertebrates is responsible for the formation of various trace fossils on osteic substrates, including etchings, grooves, lesions, and pits (e.g., Kaiser 2000; Paik 2000; Britt et al. 2008; Roberts et al. 2007; Zonneveld et al. 2022a). The organisms bored into a structurally varied substrate composed of alternating layers of compact and spongy hydroxyapatite (Zonneveld et al. 2016, 2022a). The primary functions of this behaviour are the extraction of nutrients both from the soft body and the hydroxyapatite, grazing on microbial mats or algae developed on the osteic substrate, the founding of combined protection from predators, and also the colonisation of hard substrate on the seafloor (e.g., Wisshak et al. 2019; Jaminson-Todd et al. 2023, 2024). Since trace makers rarely reach the endoskeletons of living vertebrates, such a form of bioerosion occurring on osteic substrates is typically interpreted as a part of the post mortem degradation process (Kaiser 2000; Roberts et al. 2007; Sato and Jenkins 2020).

Herein, we provide the first report of the bioerosion traces in the Late Devonian placoderm bones from the Holy Cross Mountains, Poland. Among the hundreds of collected Devonian vertebrate macrofossils in the Holy Cross Mountains, placoderm remains are most common and they provide a wealth of data on their morphology, distribution and taphonomy (e.g., Gorizdro-Kulczycka 1934; Kulczycki 1957; Ivanov and Ginter 1997; Szrek 2009, 2020; Dworczak and Szrek 2016; Grygorczyk et al. 2024). Placoderms (armoured fish) were the most common and diverse group of the Devonian fishes, which are known from freshwater, brackish, and marine environments (e.g., Dupret 2008; Young 2010). They had robust dermal bones that formed the armour at the anterior part of the body. Additionally, the group Antiarcha possessed the armour that also covered the pectoral fins (e.g., Young 2010; Béchard et al. 2013). Despite the massive plate bones and the frequent occurrence of placoderms in the Devonian rocks from the Holy Cross Mountains, the trace fossils in their remains escaped attention of the researchers so far. Owing to the fact that borings in placoderm remains are considered a rare phenomenon, the evaluation of significance, origin, and frequency of trace fossils in placoderm skeletons is still pending.

The aim of this study is to describe a suite of bioerosional traces on the placoderm bones collected from the Upper Devonian deposits of the Holy Cross Mountains, Poland. Additionally, an attempt has been made to distinguish if borings were produced during the host's lifetime (syn vivo) or after its death (post mortem). The presented material significantly expands the known stratigraphic range and diversity of the hard ground communities.

Institutional abbreviations.—Muz. PGI-NRI, Geological Museum of the Polish Geological Institute-National Research Institute in Warsaw, Poland; MWG UW, Faculty of Geology, University of Warsaw, Poland.

Geological setting

In the Late Devonian, the southern region of the Holy Cross Mountains, the Kielce region, was situated in a subtropical zone at the southern margin of Laurussia. The region constituted a wide shallow carbonate platform (Szulczewski 1995). During Frasnian, the platform was divided into blocks and stepwisely drowned (Szulczewski 1989, 1995). The submersion of the carbonate platform ended during the Visean (Mississippian) and caused the development of a deep-sea pelagic environment (Szulczewski 1989, 1995; Szulczewski et al. 1996). The deepening of the region was a result of synsedimentary block tectonics (Szulczewski 1995; Narkiewicz et al. 2006).

The Wietrznia quarry in the city of Kielce, is located in the western part of the Holy Cross Mountains (about 190 km south of Warsaw), in a chain of hills known as the Kadzielnia Range (Fig. 1). The range is built up of Upper

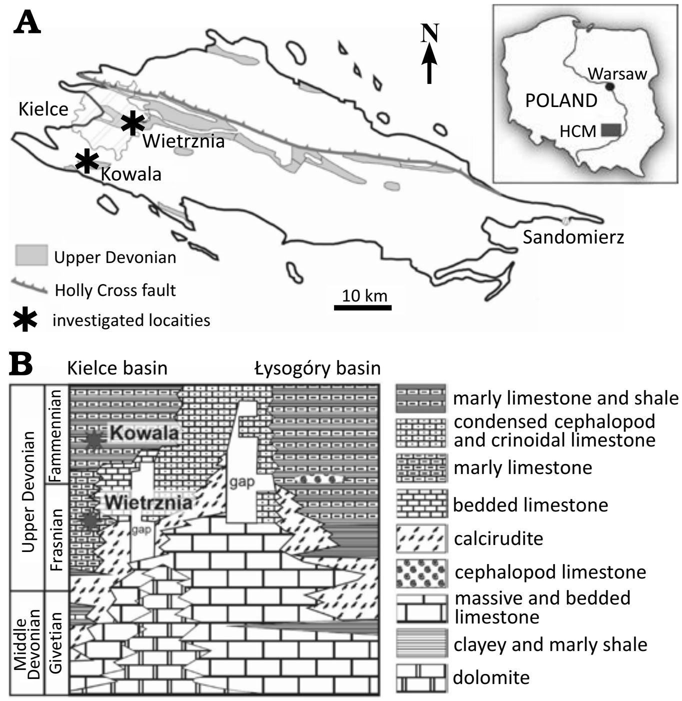


Fig. 1. Location of the investigated outcrop in the Holy Cross Mountains. **A**. Location map of the Holy Cross Mountains (HCM), central Poland (modified from Kowalczewski 1971 and Szrek 2020). **B**. Schematic cross-section through the Holy Cross Mountains from the Givetian to the top of the Upper Devonian (after Szulczewski 1995, modified) with the probable position of the localities investigated.

Devonian rocks and belongs structurally to the western part of the Kielce-Łagów Synclinorium. The details of the Late Devonian facies evolution of the present-day Kadzielnia Range area remain under discussion. Synsedimentary block tectonics resulted in a wide variety of marine environments in this small area, mainly during the Frasnian Stage (Szulczewski 1971, 1973, 1995; Racki 1993; Racki and Bultynck 1993; Racki and Narkiewicz 2000; Pisarzowska et al. 2006). The succession shows progressing stepwise drowning of the carbonate platform, expressed by an increasingly finer sediment fraction with nektonic fauna. However, the horizons of carbonate sediments of coarse-grained sediments appear with brachiopods, fragments of stromatoporoids and rugose corals, and crinoid segments. The age of the studied placoderm bones was determined based on brachiopods (Gorizdro-Kulczycka 1934). Their age in standard conodont zonation may be ranged from the *Palmatolepis falsiovalis* Zone to the early *Palmatolepis triangularis* Zone according to Szulczewski (1971) and Ivanov and Ginter (1997). The specimens described herein have been found in such a kind of high-energy event horizon. Among other fauna arthrodires, coelacanths, dipnoans, porolepiforms, ptyctodonts, and sharks were identified from Wietrznia and constitute one of the better preserved and diverse assemblages of the Late Devonian vertebrates from Poland (Gorizdro-Kulczycka 1934, 1950; Kulczycki 1957; Liszkowski and Racki 1993, Ginter 1994, 2004; Ivanov and Ginter 1997; Szrek 2007, 2020).

The Kowala quarry is a large, active open-pit limestone and marl quarry located in the eastern part of a syncline (Fig. 1). The quarry exposes a profile of sediments including Givetian–lower Carboniferous, developed in typical hemipelagic non reef phases. A detailed description of the profile exposed both in the quarry itself and in the adjacent railroad cutting has been the subject of many works, including i.e., Czermiński (1960), Szulczewski (1971), Racki (1993) and Racki et al. (2002), Marynowski and Filipiak (2007), Kaźmierczak et al. (2012), Malec (2014) and Zatoń et al. (2014). The profile exposed in the quarry reflects in its fundamental features the tectonic evolution of the entire region. It records the gradual development of increasingly deeper-water facies, but in a more continuous and complete manner than in the Kielce area. The manifestations of seismic activity in the form of synsedimentary folds, have been documented elsewhere (Szulczewski 1971). No significant sedimentation breaks were found in this profile, which made it possible to study the global events that took place in the Late Devonian, and which were documented at this site, i.e., the Kellwasser (Racki et al. 2002), the Annulata (Racka et al. 2010), the Dasberg (Marynowski et al. 2010; Pisarzowska et al. 2024) and the Hangenberg (Marynowski et al. 2012; Myrow et al. 2014) events. This applies in particular to the most prominent of these, the so-called “Great Extinction” at the Frasnian/Famennian boundary, the geochemical aspects of which have been studied in detail at Kowala (Bond et al. 2004; Racki et al. 2002). In recent years, the site has become again intensively studied, and in particular the Devonian/Carboniferous boundary well-exposed in the northern part of the quarry (see Filipiak and Racki 2005; Racki 2006; Rakociński et al. 2021).

Material and methods

Among over 200 of investigated placoderm bone specimens, 17 displayed borings on their surfaces, which were sporadically filled with sediment. Most of these bones are poorly preserved, but four have features that are valuable for further research and have been studied in detail. The best-preserved traces were found on the external surfaces of unidentified plate fragments of arthrodiran placoderms from the Kowala quarry (MWG UW ZI/43/0070 and Muz. PGI-NRI 1809.II.30) and the Wietrznia quarry (Muz. PGI-NRI 1809.II.31 and 36). The MWG UW ZI/43/0070 and Muz. PGI-NRI 1809.II.36 (Fig. 2) display deep, cylindrical borings with rounded, hemispherical termini. Additionally, Muz. PGI-NRI 1809.II.36 was cut perpendicularly to the boring with a diamond blade, grinding and polishing by the using aluminium oxide in the lab at the Friedrich-Alexander University (FAU) in Erlangen, Germany. Muz. PGI-NRI 1809.II.30 (Fig. 3) shows elongated and shallow grooves, which cross each other, whereas Muz. PGI-NRI 1809.II.31 (Fig. 4) displays numerous elongated, narrow and straight to curved structures. All studied specimens were photographed using an Axiocam digital camera attached to a ZEISS AXIO Zoom-V16 microscope with ZEISS ZEN-2-core software at the Friedrich-Alexander University (FAU) in Erlangen, Germany. The specimens are housed in the Geological Museum of the Polish Geological Institute in Warsaw and at the Faculty of Geology, University of Warsaw.

Systematic palaeoichnology

Ichnogenus *Karethraichnus* Zonneveld et al., 2016

Type ichnospecies: *Karethraichus lakkos* Zonneveld et al., 2016, the Green River Basin, Wyoming (USA), Eocene.

Emended diagnosis.—Circular to subcircular non-penetrative and penetrative holes bored into osteic substrates. The boring that terminates within the substrate, forms a shallow, bowl-shaped pit. If the holes are deeper, they display a deeper shaft with a rounded to flattened terminus. Penetrative holes usually have straight or convex vertical edges.

Remarks.—*Karethraichnus* displays similar morphology and dimensions to the ichnogenus *Sedilichnus* Müller, 1977. However, *Karethraichnus* shows a higher morphological variability in the circularity of the external burrow opening, the symmetry of their cross-sectional profile (Zonneveld et al. 2016). Additionally, the two ichnogenera also vary in a specific type of substrate. *Sedilichnus* occurs within carbonate substrates (usually invertebrate shells), whereas *Karethraichnus* is known within phosphatic substrates such as carapace of armadillos and turtles (Zonneveld et al. 2016; Moura et al. 2021).

Stratigraphic and geographic range.—*Karethraichnus* was previously described from the Upper Cretaceous of Japan (Sato and Jenkins 2020) and Egypt (El Hedeny et al. 2023), the middle and upper Eocene of the USA (Zonneveld et al. 2016; Adrian et al. 2021; Zonneveld and Bartels 2023), the Miocene of Peru and Egypt (Collareta et al. 2022; Zonneveld et al. 2022a), the upper Pliocene of Italy (Collareta et al. 2023), the Upper Pleistocene of Brasil (Moura et al. 2021), and the Recent (Zonneveld et al. 2022b). This documentation may extend the stratigraphic range of the ichnotaxon into the Upper Devonian, representing the first known occurrence from Poland.

Karethraichnus? isp.

Fig. 2.

Material.—Two specimens from the Upper Devonian of Poland: MWG UW ZI/43/0070, the Kowala quarry, *Palmatolepis crepida*–*Palmatolepis postera* zones, Famennian, and Muz. PGI-NRI 1809.II.36, the Wietrznia quarry, Frasnian.

Description.—Rounded borings 2–10 mm in diameter and 3–5 mm in depth, located on the dermal bone from the Kowala quarry (MWG UW ZI/43/0070, Fig. 2A) and on the dermal bone from the Wietrznia quarry (Muz. PGI-NRI 1809.II.36, Fig. 2B). The precise measurements of the depths of the origi-

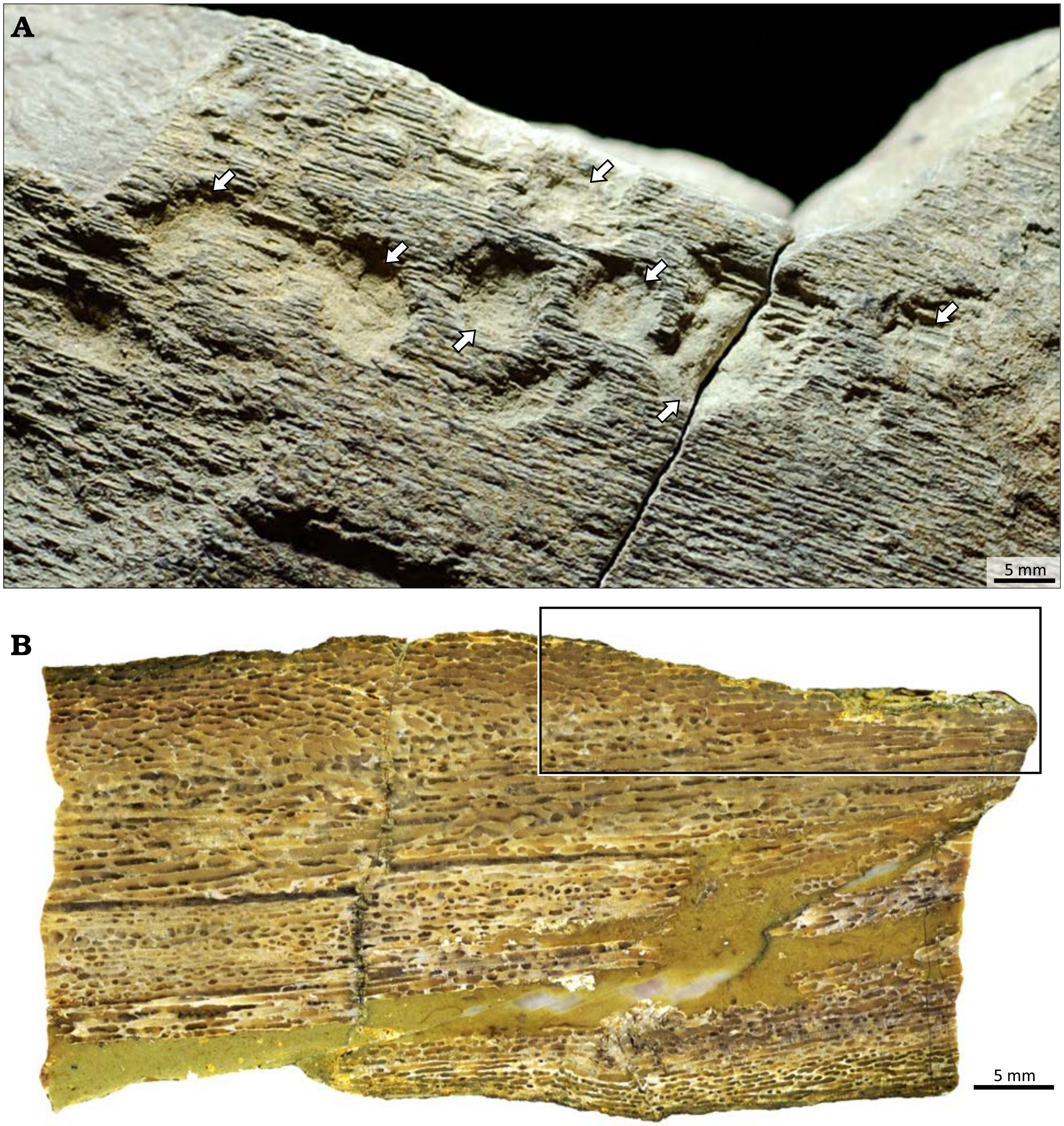


Fig. 2. Dermal bones of placoderm with *Karethraichnus*? isp. from the Upper Devonian of the Holy Cross Mountains, Poland. **A**. MWG UW ZI/43/0070, external side of unidentified plate fragment of anarthrodiran placoderm indicates rounded borings (arrows), Famennian, Kowala quarry. **B**. Muz. PGI-NRI 1809.II.36, polished slab displays cross section through the boring, Frasnian, Wietrznia quarry. The rectangle indicates the location of the boring within the bone.

nal borings of both specimens are difficult to ascertain due to the presence of sediment at their bottoms, as well as from the erosional surface of the bone. They terminate in the bone and have rounded, flattened termini. The traces are hemispherical cavities with a circular transversal section and smooth walls. In longitudinal section, they are almost cylindrical-shape and their axis approximately perpendicular to the substrate surface. They appear only on the one side on both specimens, and are irregularly arranged on the surface, spaced from each other in distances of 5–10 mm increment.

Remarks.—The studied borings in the Late Devonian placoderm bones are interpreted as a species of *Karethraichnus*? Zonneveld et al., 2016. The oldest known occurrence of this genus was described from fossil turtle remains of the Late Cretaceous (Sato and Jenkins 2020). *Karethraichnus* are considerably variable in size and circularity. *Karethraichnus kulindros* Zonneveld et al., 2016, displays deep, cylindrical, non-penetrative wholes with smooth margins and rounded to flattened, hemispherical terminus. Other non-penetrative ichnospecies, *Karethraichnus lakkos* Zonneveld et al., 2016, displays shallow hemispherical pits with rounded termini; *Karethraichnus minimum* Moura et al., 2021, shows cone-shaped profiles with circular to semicircular outline and *Karethraichnus zaraton* Sato & Jenkins, 2020, shows clavate-shaped holes with a smooth surface. Only *Karethraichnus fiale* Zonneveld et al., 2016 (deep, cylindrical holes with smooth margins) passes through the bony substrates (Sato and Jenkins 2020; Zonneveld and Bartles 2023).

Ichnogenus *Osteocallis* Roberts et al., 2007

Type ichnospecies: *Osteocallis mandibulus* Roberts et al., 2007, Maevarano Formation, Madagascar, Maastrichtian (Upper Cretaceous).

Emended diagnosis.—Shallow, curved or straight grooves bored into external bone surfaces. They may occur in pairs or as meandering trails. The latter may form a network of randomly overlapping trails.

Remarks.—*Osteocallis* has been observed in bones from both continental and marine settings. *Osteocallis* differs from etchings in shells and rocks, such as *Gnathichnus* Bromley, 1975 (radially arranged scratches) and *Radulichnus* Voigt, 1977 (linear traces forming small meandering clusters), which are also known from osteic substrates, by having accurate, often paired scratches (e.g., Jagt 2003; Mudler et al. 2005; Janssen et al. 2013). Although *Osteocallis* can resemble the ichnogenera *Paleoscolytus* Walker, 1938, described as branched channels in fossil wood, it lacks the shallow grooves or scratches that are diagnostic of *Osteocallis* (Collareta et al. 2023).

Stratigraphic and geographic range.—Ichnogenus *Osteocalis* was previously documented from the Upper Triassic of Brazil (Paes Neto et al. 2016; Cunha et al. 2024), the Upper Jurassic of USA (McHugh et al. 2020), the Upper Cretaceous of Madagascar, USA (Roberts et al. 2007) and

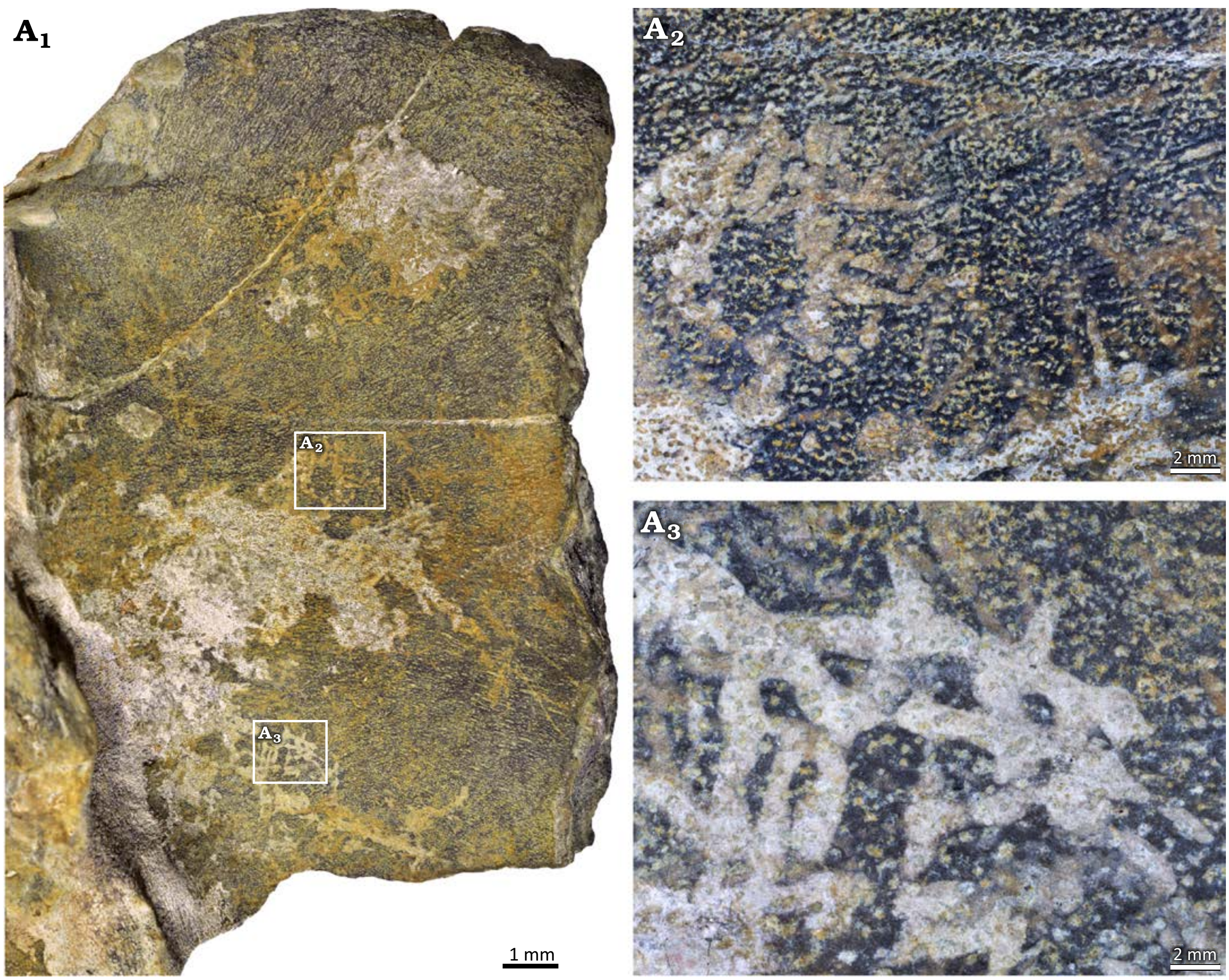


Fig. 3. The external surface of bioeroded unidentified arthrodiran placoderm bone fragment demonstrating *Osteocallis*? isp. (Muz. PGI-NRI 1809.II.30) from Famennian, Upper Devonian, Kowala quarry, Holy Cross Mountains, Poland (A_1); cluster of shallow borings filled with sediment (A_2); cluster of trace fossils overlapping each other (A_3).

Egypt (El Hedeny et al. 2023), and the lower Pliocene of Italy (Collareta et al. 2023). This determination may extend the stratigraphic range of *Osteocalis* up into the Late Devonian, providing the first occurrence from Poland.

?*Osteocallis* isp.

Fig. 3.

Material.—Muz. PGI-NRI 1809.II.30, the Kowala quarry, *Palmatolepis crepida–Palmatolepis postera* Zones, Famennian, Upper Devonian.

Description.—On the surface of the placoderm dermal bone (Muz. PGI-NRI 1809.II.30, Fig. 3) traces have been preserved as abundant, although irregular grooves, which are shallow in depth (0.5–1 mm). Their diameter varies from 0.4 to 1 mm and the length ranges from 1 to 3 mm. The grooves occur in dense cluster. They often overlap perpendicular or parallel other grooves. The ridges between them are partially invisible.

Remarks.—This specimen was interpreted by Szrek (2009, 2020) as a supposed bryozoan etching traces, but its morphology, especially regarding no multiple ramifications and a smaller diameter of single traces render this identification rather unlikely. These bioerosional marks closely correspond to *Osteocallis* Roberts et al., 2007, already known from vertebrate fossils. *Osteocallis mandibulus* shows a network of shallow randomly overlapping trails or paired grooves, creating long paths (Roberts et al. 2007: fig. 4) and *Osteocallis infestans* meandering trails of generally straight overlapping grooves which were excavated into the bone surfaces. Both ichnospecies are randomly oriented and cross each other which are either perpendicular or parallel to one another (Peas Neto et al. 2016: fig. 6), whereas *Osteocallis leonardii* has a characteristic arrangement in pairs "side-by-side" (Collareta et al. 2023: fig. 3).

Ichnogenus *Sulculites* Vialov & Nessov, 1974

Type ichnospecies: *Sulculites bellus* Vialov & Nessov, 1974, the south-eastern Fergana, Uzbekistan, Albian (Lower Cretaceous).

Emended diagnosis.—Shallow, straight to curved grooves. They occur as a single furrow or create chains of parallel traces. Their bottom is flat and has 0.18–0.5 mm in diameter (usually 0.3–0.4 mm). The ends of the furrows either gradually narrow or abruptly break off. The long, continuous and parallel grooves may occur close to each other and be oriented in various directions. The short furrows are usually curved and may intertwine the longer traces (after Vialov and Nessov 1974).

Remarks.—*Sulculites* has been recognized in osteic substrates—the Cretaceous turtle carapaces (Vialov and Nessov 1974; El Hedeny et al. 2023). It is morphologically similar to *Cubiculum* Roberts et al., 2007, which occurs also as isolated grooves and forms dense, sometimes overlapping groups of grooves. However, *Cubiculum* is typically much larger (7–20 mm in length and 2–6 mm in diameter; Roberts et al. 2007). The ichnogenus *Gunnellichnus* Zonneveld et al., 2022b, is considerably wider than *Sulculites* and creates branching structures that are not observed in *Sulculites.*

Stratigraphic and geographic range.—As for the monotypic type species.

Sulculites bellus Vialov & Nessov, 1974

Fig. 4.

Material.—Muz. PGI-NRI 1809.II.31 (Fig. 4), the Wietrznia quarry, *Palmatolepis falsiovalis*–lower *Palmatolepis hassi* zones, Frasnian, Upper Devonian.

Description.—The external side of a placoderm bone (Muz. PGI-NRI 1809.II.31, Fig. 4) exhibits elongated, narrow and shallow grooves (Fig. 4). Their diameters are 0.2–0.4 mm and their lengths 0.5–3 mm. The furrows are straight to curved and do not branch. They occur as either single furrows or form clusters of intersected grooves and pairs of long, parallel, closely spaced traces (Fig. 4A_2). The groove ends gently taper or abruptly sever (Fig. 4A_4, A_5). The furrows cross each other in a different angle (Fig. 4A_3, A_5), creating complicated intertwines. The presence of thin, curved wrinkles is observed on the bottom of furrows (Fig. 4A_5).

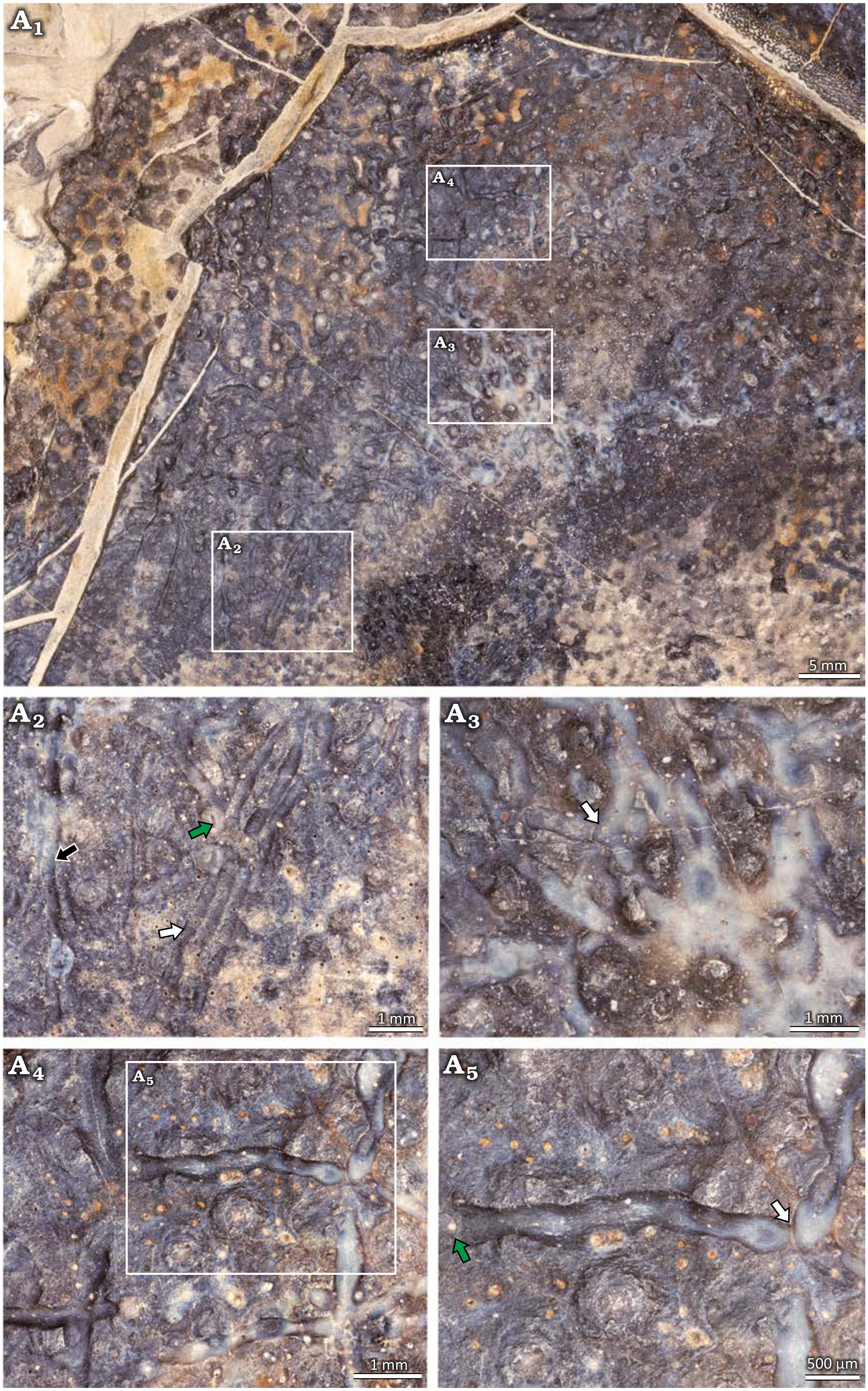
Remarks.—The trace fossils occur on the well-preserved surface of the placoderm bone. They were interpreted as *Sulculites bellus* Vialov & Nessov, 1974. The traces exhibit both straight and curved furrows, which appear solitarily or in pairs and chains. They cross each other, creating complicated intertwines and have thin, curved wrinkles on the bottom, similar to the traces described by Vialov and Nessov (1974) and El Hedeny et al. (2023).

Stratigraphic and geographic range.—Sulculites bellus was previously reported from the Lower Cretaceous (Albian) of Uzbekistan (Vialov and Nessov 1974), and the Upper Cretaceous (Campanian) of Egypt (El Hedeny et al. 2023). This study expands the stratigraphic range of the ichnotaxon up into the Upper Devonian, thereby providing the first documented examples from Poland.

Discussion

The bioerosion traces reported from the dermal bone of placoderms from the Upper Devonian of Poland represent the earliest known record of the macrobioerosion in the

Fig. 4. Traces of *Sulculites bellus* Vialov & Nessov, 1974, on the external surface of a placoderm bone; Frasnian, Upper Devonian, Wietrznia quarry, Holy Cross Mountains, Poland. Muz. PGI-NRI 1809.II.31. A_1, general view of the fragment showing long traces; A_2, traces occur as single furrows (black arrow) or form clusters of intersected grooves (green arrow) and pairs of long, parallel, closely spaced traces (white arrow); A_3, the elongated borings cross each other in different angle (white arrow); A_4, A_5 show furrows with thin, curved wrinkles on the bottom, green arrow shows where the groove ends abruptly, white arrow indicates the ends where the grooves gently taper. →


A1
A4
A3
A2
5 mm
A2
1 mm
A3
1 mm
A4
A5
1 mm
A5
500 µm

osteic substrates. Hitherto, one case of microbioerosion (*Mycelites ossifragus*) in placoderm remains has only been reported by Bystrov (1956). Furthermore, two examples of epibionts on placoderm remains have been reported until present, one from the Middle Devonian of Australia (White 1978; BMNH P.50313) with the tabulate coral *Aulopora* sp., and one from the Holy Cross Mountains as possible bryozoans (Szrek 2009, 2020: fig. 6A, B). Consequently, these finds provide the oldest evidence for *Sulculites bellus,* as well as the earliest potential records of the ichnogenera *Karethraichnus*? and *Osteocallis*?. Judging by the numbers of bones studied here, it can be inferred that this low number of finds likely results from the limited attention that has been paid to this phenomenon. Contrary to previous suggestions, traces of bioerosion may be present on a considerable number of specimens. During the Middle Paleozoic, the diversity of bioerosion increased but has hardly been recorded from vertebrate remains (e.g., Taylor and Wilson 2003; Wilson 2007). Our research shows that bioerosional activity on phosphate substrates, such as placoderm bones, was much more common in the Late Devonian than previously reported.

So far, the oldest evidence of *Karethraichnus* was found in sea turtles remains of the Late Cretaceous age (Sato and Jenkins 2020). The bioerosion is known from both marine (Sato and Jenkins 2020; Collareta et al. 2022; Zonneveld et al. 2022b; this paper) and nonmarine environments (e.g., Moura et al. 2021; Zonneveld et al. 2022a; Zonneveld and Bartles 2023; El Hadeny et al. 2023). The ichnotaxon has been produced by arthropods such as dipterans and ixodid arachnids in terrestrial environment, and by leeches in freshwater settings (e.g., Zonneveld et al. 2016, 2022a; Zonneveld and Bartles 2022, 2023). In marine environments, *Karethraichnus* can be produced by bivalves and barnacles (see Sato and Jenkins 2020; Zonneveld et al. 2022b). The organisms mechanically bore into the substrates, thereby producing dwelling structures. Although barnacles commonly settle on mobile substrates, such as sea turtles and crabs (e.g., Seilacher 2005), they are also capable of boring into vertebrate remains, suggesting that their involvement in the traces on the placoderm remains cannot be entirely excluded. Additionally, the investigated borings occur on only one surface of the bones, which excluded predation.

The ichnogenus *Osteocallis* is known both from marine and especially nonmarine environments (e.g., Roberts et al. 2007; Peas Neto et al. 2016; Collareta et al. 2023). The oldest confirmed occurrence of this ichnogenus was found in the Upper Triassic rhynchosaur carcass (Cunha et al. 2024). *Osteocallis* is a grazing trace typically produced by osteophagous silphid and histerid beetles (e.g., Cunha et al. 2024), or alternatively by polyplacophoran trace makers (Collareta et al. 2023). In the marine environment, chitons are considered to be the producers of *Osteocallis.* Chitons possess a hard radula with teeth arranged in two elongated rows (Voigt 1977; Collareta et al. 2023). The radula abrades the substrate to enable feeding on embedded algae or microbial mats. The process results in the formation of grazing traces on the bones. The large placoderm plate could indicate the development and distribution of algae and microbial mats on the bone forming a secondary hard substrate on the muddy seafloor. Furthermore, the traces are similar to borings *Gibbula* isp. illustrated by Thompson et al. (1997) and Gibert et al. (2007), which create groups of shallow, short and curve scratches. Additionally, we observe two sizes of these traces, indicating that two different organisms could graze on the placoderm bone.

Previously, *Sulculites bellus* was known from the Cretaceous turtle carapaces from Eastern Uzbekistan (Vialov and Nessov 1974) and Egypt (El Hedeny et al. 2023). The bioerosion has been exclusively observed in osteic substrates, and it has been produced by invertebrates, most likely vermiform organism or larvae of marine organisms, such as arthropods (Vialov and Nessov 1974; El Hedeny et al. 2023; Zonneveld and Bartles 2023). These traces are rare and none of them appears to have caused the death of the host organisms (e.g., El Hedeny et al. 2023). The previous studies (Vialov and Nessov 1974; El Hedeny et al. 2023) suggest post mortem colonization of placoderm bones by scavengers, which bored into the bones to search for nutrients.

The study of bioerosional activity in vertebrate remains offers insights into the relationship between organisms, the taphonomic history of carcasses, as well as the development of hard ground communities (e.g., Kelley and Hansen 2006; Roberts et al. 2007). Bioerosion in osteic material is typically described as predation, parasitism, or scavenging, and may be part of the post mortem degradation process (Kaiser 2000; Roberts et al. 2007; Sato and Jenkins 2020). Our studies show that all of the investigated dermal bones have been affected post mortem. In case of *Karethraichnus*, many authors have indicated that fossilized turtle and armadillo bones display evidences of healing of the borings, which suggest a parasitic relationship (e.g., Zonneveld et al. 2022a, b). In the Muz. PGI-NRI 1809.II.36 (Fig. 2B), no malformations of bone were observed that would indicate a syn vivo interaction between the placoderm and the trace maker. Therefore, the studied bioerosion most likely resulted from opportunistic behaviour of the trace makers. It is unclear whether the placoderm bones were chosen selectively by trace makers as desirable phosphatic clasts or just have represented the only available hard substrate on the seafloor (e.g., Tapanila et al. 2004; Jaminson-Todd et al. 2023). Additionally, the findings suggest a temporally low energy depositional environment of the placoderm remains with low sedimentation rates. The organism which produced *Sulculites bellus* which has apparently mined for the nutrients contained in the bone and the remains of the soft tissue, had to settle on the bone immediately after their deposition. However, the presence of *Osteocalis* isp., whose trace maker fed on algae or microbial mats, indicates a temporal window during which microbes were capable of producing bio-mats on the bone surfaces after their deposition on the seafloor.

Conclusions

The trace fossils described herein represent the first documented example of bioerosion in placoderm bones from the Upper Devonian of the Holy Cross Mountains, Poland. Our results reveal the earliest occurrence of the ichnospecies *Sulculites bellus* and the potential ichnogenera *Karethraichnus*? and *Osteocallis*? in placoderm remains, significantly extending their stratigraphic range into the Late Devonian. The traces constitute the earliest appearance of macrobioerosion in placoderm bones, as well as in osteic substrates. All studied bioerosion show the post mortem erosional activity of the organisms that bored into the bones either to search for nutritional particles, to colonize the osteic substrate for shelter, or to graze on microbial mats that had developed on the bone surfaces.

Acknowledgements

We are very grateful to Alfred Uchman (Jagiellonian University, Cracow, Poland) for constructive discussion and comments, and to Birgit Leipner-Mata (Friedrich-Alexander University, Erlangen, Germany) for assist with laboratory work. We thank Michał Poros (Geonatura, Kielce, Poland) and Błażej Dziewięcki (Kielce, Poland) for providing specimens (Muz. PGI-NRI 1809.II.36 and Muz. PGI-NRI 1809.II.31 respectively) used in our studies. The manuscript was improved by the constructive reviews of Michał Zatoń (University of Silesia, Sosnowiec, Poland) and two anonymous reviewers. The authors express their sincere gratitude for these insightful contributions.

Editor: Andrzej Kaim

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