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Middle and Upper Jurassic sessile polychaetes of Poland

Środkowo- i górnojurajskie wieloszczety osiadłe Polski

Rozprawa doktorska w dziedzinie nauk ścisłych i przyrodniczych,

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Słowiński J., Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924.

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Słowiński, J., Banasik, K., Vinn, O. (2023). Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications. *Lethaia* 56, 1-12.

Słowiński, J., Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. *PeerJ* 12, e17389.

Podziękowania

Lista publikacji

Przedstawiona dysertacja doktorska składa się ze spójnego tematycznie zbioru czterech artykułów opublikowanych w czasopismach naukowych posiadających współczynnik wpływu Impact Factor (IF). Ich sumaryczny IF wynosi 9,548. W skład rozprawy wchodzą następujące publikacje:

1. **Słowiński J.**, Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924. DOI: 10.1371.0242924. **IF(2020)=3,24. MEiN=100 pkt.**

2. **Słowiński, J**., Vinn, O, Jäger, M., Zatoń, M. (2022). Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. *Acta Palaeontologica Polonica* 67, 827-864. DOI: 10.4202/app.01006.2022. **IF(2022)=2,108. MEiN=100 pkt.**

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4. Słowiński, J., Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. *PeerJ* 12, e17389. DOI:10.7717/peerj.17389. **IF(2024)=2,7. MEiN=100 pkt.**

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Streszczenie

Wieloszczety to prawie wyłącznie morskie bezkręgowce należące do typu pierścienic. Zdecydowana większość wieloszczetów reprezentowana jest przez organizmy miękkocielne, dlatego są rzadkie w zapisie kopalnym i ograniczone tylko do osadów o wyjątkowym stopniu zachowania skamieniałości (tzw. Lagerstätte). Zapis kopalny wieloszczetów zdominowany jest przez ich twarde części szkieletowe reprezentowane przez węglanowe rurki mieszkalne oraz rzadziej przez elementy aparatu szczękowego (skolekodonty), czy też wieczka (operculum). Spośród wszystkich grup wieloszczetów, twarde, zmineralizowane węglanem wapnia rurki mieszkalne są wytwarzane jedynie przez przedstawicieli trzech rodzin osiadłych wieloszczetów – Serpulidae, Sabellidae i Cirratulidae, z których tylko serpulidy powszechnie posiadają zmineralizowane, węglanowe rurki. Dotychczasowe badania poświęcone tym organizmom z okresu jurajskiego są bardzo nieliczne i obejmują jedynie kilka publikacji, w tym jedną z obszaru Polski. Celem tego projektu naukowego było wypełnienie tych braków poprzez kompleksowe badania skamieniałości jurajskich serpulidów pochodzących z obszaru Polski.

Skamieniałości rurek jurajskich serpulidów i sabellidów pochodzących z osadów reprezentujących interwały stratygraficzne od górnego bajosu po dolny kimeryd zbadano pod kątem ich taksonomii, paleoekologii oraz mikrostruktury. Badania taksonomiczne miały na celu przyporządkowanie zebranych okazów do konkretnego rodzaju i gatunku. Na podstawie różnorodnych zespołów skamieniałości opisano 24 taksony, w tym rozpoznano dwa nowe gatunki – *Filogranula spongiophila* i *Cementula radwanskae*. 23 taksony reprezentują dwa (Filograninae i Serpulinae) spośród trzech głównych kladów serpulidów, a jeden gatunek (*Glomerula gordialis*) należy do rodziny Sabellidae.

W oparciu o zidentyfikowany skład taksonomiczny zespołów rozpoznano specyficzne dla danego rodzaju środowiska zespoły wieloszczetów sesylnych. Ich liczebność i różnorodność jest ściśle związana z określonym rodzajem substratu, jego charakterem i ogólną morfologią, podczas gdy interwał stratygraficzny odgrywa drugorzędną rolę. Duże znaczenie odgrywają również inne zmienne paleośrodowiskowe takie jak dostępność pokarmu czy hydrodynamika środowiska. Oprócz tego wiele wieloszczetów wykazuje charakterystyczny sposób rozmieszczenia odzwierciedlający ich adaptacje paleoekologiczne jak np. kryptyczny tryb życia czy rywalizacja o przestrzeń.

Analiza materiału paleontologicznego w ujęciu ekologiczno-paleośrodowiskowym dotyczyła również relacji symbiotycznych między serpulidami i innymi organizmami.

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Serpulidy wchodziły w relacje symbiotyczne ze stułbiopławami zachowanymi w obrębie ich szkieletu w procesie bioklaustracji. Choć symbioza między serpulidami i stułbiopławami z gatunku *Protulophila gestroi* ma długą historię ewolucyjną, to zapis kopalny tego zjawiska jest bardzo rozproszony w czasie i w przestrzeni. W obrębie jurajskiego basenu polskiego częstotliwość występowania tej interakcji jest niezwykle niska. W niniejszych badaniach stułbiopławy wykazywały ogromną selektywność w wyborze swojego gospodarza, zasiedlając wyłącznie jeden rodzaj serpulidów (*Propomatoceros*). Ponadto, znacząca większość przypadków tej symbiozy została zarejestrowana wyłącznie w jednej lokalizacji i w bardzo wąskim interwale stratygraficznym. Do wizualizacji wewnętrznej morfologii kolonii symbiotycznych stułbiopławów po raz pierwszy zastosowano mikrotomografię komputerową (micro-CT).

Na podstawie analizy mikrostrukturalnej dwunastu taksonów serpulidów reprezentujących dwa z trzech głównych kladów tej rodziny, rozpoznano trzy rodzaje mikrostruktur – nieregularną pryzmatyczną (IOP), sferulityczną pryzmatyczną (SPHP), oraz prostą pryzmatyczną (SP). Sześć z taksonów posiada ściany szkieletu zbudowane z pojedynczej warstwy, a sześć jest dwuwarstwowych. Rodzaje mikrostruktur są charakterystyczne dla poszczególnych kladów i dostarczają istotnych sygnałów filogenetycznych w ewolucyjnych trendach budowy mikrostrukturalnej serpulidów. W przeciwieństwie do niektórych młodszych geologicznie wieloszczetów osiadłych mikrostruktura jurajskich serpulidów nie nadaje się jednak do rozpoznawania konkretnych rodzajów i gatunków. Rozwój różnorodności mikrostruktur serpulidów i pojawienie się rurek zbudowanych z co najmniej dwóch warstw był prawdopodobnie związany z dużym ewolucyjnym znaczeniem rurek dla całego taksonu, co mogło być również spotęgowane przez zwiększony poziom drapieżnictwa podczas mezozoicznej rewolucji morskiej.

System biomineralizacji serpulidów różni się od tego u sabellidów i jest bardziej złożony. Jurajskie sabellidy tworzą jednowarstwową rurkę, której sekrecja przebiega wzdłuż długich linii wzrostu zorientowanych równolegle do ściany rurki, a kolejne pasma przyrostowe są dodawane do wnętrza rurki. Z tego powodu *Glomerula* nie jest w stanie modyfikować zewnętrznej, prostej morfologii szkieletu, co sprawia, że rurka jest delikatna i podatna na mechaniczne uszkodzenia. Z drugiej strony sabellidy ponoszą stosunkowo niewielkie koszty energetyczne podczas kalcyfikacji, dzięki czemu są w stanie znacząco wydłużać swoją rurkę w relatywnie szybkim tempie. Pozwala to na stosowanie oportunistycznej strategii tzw. „ucieczki" i unikania konkurencji. U serpulidów kolejne pasma przyrostowe są dodawane do

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krawędzi apertury, dzięki czemu mogą aktywnie modyfikować swoją zewnętrzną morfologię. Nie są w stanie tak szybko tworzyć szkieletu, jednak jest on znacznie wytrzymalszy i mniej podatny na uszkodzenia. Oprócz bogatej ornamentacji rurek serpulidy często tworzą różne struktury wzmacniające mechanicznie rurkę jak np. struktury przyczepu do substratu.

Mineralogia szkieletu wielu grup organizmów zmieniała się w zależności od składu chemicznego wody morskiej w całej historii ewolucji. Sabellidy po raz pierwszy tworzyły zmineralizowany szkielet w permie, w okresie, w którym dominowały morza aragonitowe. Szkielet współczesnych sabellidów posiadających węglanowy szkielet, reprezentowany przez jeden endemiczny gatunek – *Glomerula piloseta*, jest aragonitowy. Na podstawie badań przeprowadzonych przy użyciu spektroskopii ramanowskiej skład mineralogiczny szkieletu jurajskich sabellidów został zindetyfikowany jako niskomagnezowy kalcyt, co odpowiada okresowi dominacji mórz kalcytowych. Geneza i późniejsze długoterminowe wahania mineralogii szkieletu sabellidów były najprawdopodobniej zależne w znacznym stopniu od zmieniającego się w ciągu interwałów stratygraficznych stosunku jonowego wody morskiej.

Abstract

Polychaetes (Annelida) are almost exclusively marine invertebrates. As an immense majority of them are represented by soft-bodied organisms, their fossil record is scarce and most often restricted to the Lagerstätte (conservation) deposits. In the fossil record, polychaete fossils are dominated by hard parts of the exoskeleton represented by biomineralized dwelling tubes and less often by jaw elements (scolecodonts), as well as opercula. Among the all polychaete groups only the sessile Serpulidae, Sabellidae, and Cirratulidae are known to produce hard tubes made of calcium carbonate, of which only the family Serpulidae encompasses common calcareous tube builders. Previous research on the Jurassic sessile polychaetes is rather poor in comparison to other invertebrate groups, comprising only a few published articles, and only one concerning the Juassic serpulids from the area of Poland. This scientific project aimed to fill up these deficiencies.

Fossil tubes of Jurassic serpulids and sabellids derived from the upper Bajocian-lower Kimmeridgian deposits of the Polish Basin were subjected to taxonomic, paleoecological, and ultrastructural research. Based on the diverse assemblages of serpulids and sabellids, 24 taxa were reported including two new species – *Filogranula spongiophila* and *Cementula*

radwanskae. 23 taxa represent two of three main serpulid clades and one species (*Glomerula gordialis*) belongs to the family Sabellidae.

Based on the identified taxonomic composition of the communities, distinct groups corresponding to certain paleoenvironments have been recognized. The abundance, diversity, and colonization patterns of the assemblages are strictly dependent on the nature of the colonized substrate and other paleoecological variables (e.g., nutrient availability, environmental energy), whereas the stratigraphic interval plays a secondary role. Other paleoenvironmental factors, such as nutrient availability and environmental hydrodynamics, also play a significant role. In addition, many tube-dwelling polychaetes show a characteristic distribution pattern reflecting their paleoecological adaptations, such as a cryptic lifestyle or spatial competition.

The analysis of paleontological material from an ecological and paleoenvironmental perspective also concerned symbiotic relationships between serpulids and hydroids, which were preserved in the process of bioclaustration. Although this kind of interaction has a very long evolutionary history (Pliensbachian-Recent), the fossil record of this phenomenon is highly dispersed both in time and space. In the Jurassic sea of the Polish Basin, serpulids very rarely hosted symbiotic hydroids referred to as the species *Protulophila gestroi*. In the herein research, hydroids were highly selective in the choice of their host colonizing only one serpulid genus, *Propomatoceros*. Moreover, the vast majority of the infestation cases (17 out of 20) was recorded from a single site and a single stratigraphic zone. In order to visualize the internal morphology of the symbiotic hydroids, micro-computed tomography (micro-CT) has been applied for the first time.

The microstructural analysis of serpulid tubes encompassing 12 taxa revealed a relatively low microstructural diversity comprising three types – irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP) and simple prismatic structure (SP). Six of the taxa have skeletal walls composed of a single layer and six taxa have two-layered tubes. Microstructure types correspond to the specific clades and provide important phylogenetic signals; however, they are neither genus nor species-dependent. Therefore, contrary to some geologically younger serpulids, they are not suitable for ultrastructure-based recognition. Anyhow, the development of ultrastructural diversity in serpulids and the emergence of multi-layered tubes was presumably connected with the evolutionary importance of the tubes for the taxon, which could be enhanced by increased predation levels during the Marine Mesozoic Revolution.

The biomineralization system of serpulids differs from that of sabellids and remains more complex. Jurassic calcareous sabellids built a single-layered tube, the secretion of which proceeds along the long and oriented parallelly to the tube wall growth lines, where the subsequent growth increments are added to the interior of the tube - therefore *Glomerula* is unable to modify its external morphology. It also results in a very uniform set of tube characters and makes the tube fragile and susceptible to mechanical damage. On the other hand, sabellids bear a relatively low energy expenditure during tube secretion, being able to perform an opportunistic, "fugitive" strategy. Serpulids instead, add their subsequent growth increments to the rim of the aperture and are able to actively modify their external morphology. As a result, serpulids are capable of mechanically strengthening the tube being more resistant to any damage.

Throughout evolutionary history, the skeleton mineralogy of numerous groups of organisms has changed in response to oscillations in the chemical composition of seawater. Sabellids first formed a mineralized skeleton in the Middle Permian, a period when aragonite seas dominated. The skeleton of contemporary calcareous sabellids, represented by one endemic species - *Glomerula piloseta*, is aragonitic. Based on the Raman spectroscopy the mineralogy of the tube of the sabellid *Glomerula gordialis* has been identified for the first time as low-Mg calcite, which corresponds to the Middle Jurassic-Eocene calcite seas. The ambient seawater chemistry had a significant impact on the sabellid skeleton mineralogy. The origin and subsequent long-term fluctuations in the mineral composition of the sabellid skeleton were presumably dependent to a large extent on the changes of the ionic ratio of seawater over geological periods.

1. Introduction

Polychaetes are a class of invertebrates that belong to the phylum Annelida (Rouse and Pleijel, 2001). Although the oldest, soft-bodied representatives of this group are known from the Lower Cambrian (Vinther et al., 2011; Han et al., 2019), due to the lack of mineralized exoskeleton they are uncommon in the fossil record, being restricted mainly to the deposits characterized by exceptional fossil preservation (so-called Fossil-Lagerstätte). The abundance of polychaetes in the fossil record is thus strictly dependent on the presence of hard, calcareous external skeleton, secreted by these animals most often in the form of dwelling tubes of diverse shapes and sizes (see e.g., ten Hove and Kupriyanova, 2009; Ippolitov et al., 2014 for a review). Amongst the all known polychaete families, only three of them bear tubes made of calcium carbonate of which only Serpulidae are obligatory carbonate tube builders (Vinn et al., 2008b), while the other two (Cirratullidae, Sabellidae) are represented by single genera (Reish, 1952; Perkins, 1991; Fischer et al., 2000; Vinn et al., 2008a; Kočí et al., 2021; Słowiński et al., 2023; Guido et al., 2024).

Serpulids are sessile, almost exclusively marine (see Bosák et al., 2004; Kupriyanova et al., 2009) invertebrates attaching to hard substrates such as rocks and shells. Representatives of this group appeared for the first time in the fossil record during the Middle Permian (Sanfilippo et al., 2017; 2018); however, they were very uncommon until the end of the Early Triassic (e.g., Ramsdale, 2021) with rare, genuine reports from Middle Triassic, as well (Assmann, 1937; Stiller, 2000; Senowbari-Daryan et al., 2007). The diversity and abundance of serpulid fauna, as well as their paleogeographic distribution, have been growing since the Middle-Late Triassic (Ziegler and Michalík, 1980; Berra and Jadoul, 1996; Cirilli et al., 1999); however, their significant diversification occurred during the Middle Jurassic, with the continuing growth in the Cretaceous (Jäger, 1983; 2005; Ippolitov et al., 2014; Kočí and Jäger, 2015b; Kočí et al., 2017; Słowiński et al., 2022). That increase in diversity and abundance of serpulid fauna during the Middle-Late Jurassic coincided with the general development of various organisms colonizing hard substrates (Taylor and Wilson, 2003; Vinn and Mutvei, 2009; Zatoń et al., 2011a; b; 2012). Similarly, the first unequivocal sabellids appeared during the Middle Permian (Sanfilippo et al., 2017).

Despite being widespread and abundant, the Jurassic tube-dwelling, sessile polychaetes are relatively poorly studied as compared to their Cretaceous representatives (e.g., Brünnich Nielsen, 1931; Jäger, 1983; 2005; 2011; Macellari, 1984; Tapaswi, 1988; Radwańska, 1996;

Koči and Jäger, 2015a; b; Koči et al., 2017). Although considerably more research has been conducted in recent years (e.g., Ippolitov, 2007a; b; Jäger and Schubert, 2008; Vinn and Wilson, 2010; Koči et al., 2019; Breton et al., 2020), still most of the complex elaborations on the Jurassic serpulids are now obsolete (e.g., Parsch, 1956). From the area of Poland, there is only one publication focusing on the taxonomy and paleoecology of Upper Jurassic species from the Kuyavia region (Radwańska, 2004), and one report from the uppermost Jurassic (Tithonian) of Brzostówka and Sławno, central Poland (Radwańska, 2003).

The lack of a comprehensive review on the taxonomy and paleoecology of the Middle and Upper Jurassic serpulids from Poland, combined with numerous, fossiliferous exposures of the Polish Basin sediments was both approachable and necessary due to these meaningful deficiencies. Thus, this scientific project was aimed at filling up all these gaps by a multifaceted examination of ample fossil material derived from 11 sites from southern and south-central Poland representing diverse paleoenvironments and stratigraphic intervals (Fig. 1). The main aims encompassed: 1) taxonomic identification of the serpulid and sabellid tubes; 2) paleoecology of serpulid/sabellid assemblages through time and across paleoenvironments; 3) ultrastructural analysis of serpulid and sabellid tubes.

2. Geological setting
2.1. Paleogeographical background

The Polish Basin was the easternmost region of the Central European Basin System (CEBS), a wider system of epicontinental seas that existed during the Mesozoic era (Ziegler, 1990). During the Middle Jurassic, the Polish Basin was bounded by the Fennoscandian shield from the north, by the Belarusian massif and the Ukrainian shield from the east, and by Meta-Carpathian and Bohemian landmasses from the south, which separated it from the Tethys Ocean (Dadlez, 1989). Thus, the Polish Basin's connection to other Central European basins was quite limited, as it was only connected to the west by the Germanic Basin and to the south-east by the East Carpathian Gate (Dayczak-Calikowska and Moryc, 1988; Dadlez, 1989; Dayczak-Calikowska et al., 1997). The sedimentation was dominated by siliciclastic material, the major source areas of which were the Fennoscandian Shield and Bohemian Massif (Dadlez, 1997; Marynowski et al., 2007). From the onset of the Middle Jurassic, the Polish Basin underwent gradual transgression interrupted by two regressive episodes (lower-upper Bajocian boundary

and in the lower Callovian; see Marynowski et al., 2007), which were generally coincident with the global sea-level fluctuation (Feldman-Olszewska, 1997).

Callovian was a time of further deepening and widening of the marine basin and a decreasing input of terrigenous material (Giżejewska and Wieczorek, 1977; Dembicz and Praszkier, 2007; Wierzbowski et al., 2009; Matyszkiewicz et al., 2015). During the Late Jurassic, the Polish Basin underwent a shift with the onset of carbonate platform deposition on the northern margins of the Tethys Ocean (Kutek, 1994; Matyja and Wierzbowski, 2006; Matyszkiewicz et al., 2016). The extensive development of massive microbial-sponge and microbial reef complexes (e.g., Trammer, 1982; Ostrowski, 2005) was governed by diversified architecture of the Paleozoic basement and synsedimentary tectonics, as well as sea-level and climate fluctuations (e.g., Leinfelder, 1993; Kutek, 1994; Gutowski et al., 2005, Krajewski et al., 2011; 2016; Matyszkiewicz et al., 2012; 2016). During the Kimmeridgian different carbonate facies emerged including shell beds, pelitic limestones, as well as oolitic and oncolitic facies with common hardgrounds (Kaźmierczak and Pszczółkowski, 1968; Gruszczyński, 1986; Kutek, 1994; Machalski, 1998; Krajewski et al., 2017).

2.2. Material and its provenance

The examined fossils consist of 7048 serpulids and sabellids (of which ca 1/3 is well-preserved) and were derived from 11 outcrops from the area of Polish Jura and the Mesozoic Margin of the Holy Cross-Mountains (Fig. 1). The localities represent various stratigraphic intervals spanning the upper Bajocian–lower Kimmeridgian representing different marine paleoenvironments of the Polish Basin. In the ascending stratigraphic order, the localities are as follows:

Mokrsko: Deposits from Mokrsko and from the subsequent seven localities occur as epicontinental sediments in the form of monotonous sequences of dark siliciclastics with calcitic hiatus concretions and siderite nodules belonging to the Częstochowa Ore-bearing Clay Formation (e.g., Majewski, 2000; Matyja and Wierzbowski, 2000; Zatoń et al., 2011a; Leonowicz, 2015b). These deposits are characterized by a monoclinal structure referred to as the Polish Jura and extend in a belt from southeast to northwest in southern and south-central Poland. Apart from Ogrodzieniec and Ogrodzieniec-Świertowiec, this and the remaining five localities (Kawodrza Górna, Gnaszyn Dolny, Bugaj, Krzyworzeka, Żarki) are confined to the northern sedimentary region of the Polish Jura, which is considered to represent deeper parts of

the Polish Basin characterized by fully developed and of great thickness ore-bearing sequences (Różycki, 1953). The deposits of the above-mentioned localities represent slightly different bathymetric regimes of epicontinental paleoenvironments, generally interpreted to have been deposited in located below the storm wave-base, calm conditions with well-oxygenated bottom waters (Marynowski et al., 2007; Szczepanik et al., 2007; Leonowicz, 2012; 2013). It has to be noted, however, that within these deposits some sedimentological fabrics indicate the occurrence of episodic storm events. Such evidences include accumulations of shell detritus, sand inclusions, erosional surfaces (Leonowicz, 2015a), or hiatus concretions (Majewski, 2000; Zatoń et al., 2011a) indicating breaks in sediments supply and seafloor erosion. In Mokrsko, mudstones and siltstones are frequently intercalated with levels of both isolated and horizon-forming carbonate hiatus concretions, which are commonly encrusted by sabellid and serpulid tubes. Although the concretions form a continuous horizon, some of them are dispersed unevenly within clay deposits, that have been glaciotectonically disturbed during the Pleistocene glaciation (Zatoń et al., 2011a). The upper Bajocian age of the deposits was determined based on the presence of *Parkinsonia* ammonites (Parkinsoni Zone). The deposits in Mokrsko represent a paleoenvironment probably located below the storm wave base (Zatoń et al., 2011a). In total, 358 tube-dwelling polychaete fossils have been collected.

Ogrodzieniec-Świertowiec: Serpulids and sabellids from this outcrop heavily encrust oncoids of cyanobacterial genesis (Zatoń et al., 2012). The oncoids have been derived from condensed, sandy, and carbonate layers, being overlain by mudstones of the Ore-bearing Częstochowa Clay Formation. The late Bajocian–early Bathonian age (up to the Macrescens Subzone of the Zigzag Zone) of the oncoid-bearing deposits was based on ammonites *Parkinsonia* spp. and *Parkinsonia* (*Oraniceras*) *gyrumbilica* (Zatoń and Taylor, 2009a; Zatoń et al., 2012), dinoflagellate cysts (*Valansiella ovula* and *Ctenidodinium* cf. *combazii*, Przemysław Gedl, written communication, 2019), and *Paleomilliolina czestochowiensis* foraminifers (Zofia Dubicka, written communication, 2019; see Słowiński, 2019). The locality is confined to the southern sedimentary region of the Polish Jura, representing shallow, marginal parts of the basin (Leonowicz, 2013; Różycki, 1953) and characterized by smaller thicknesses of the deposits with common hiatuses (Różycki, 1953). Due to the origin of oncoids, the paleoenvironment was interpreted as shallow marine, located within the photic zone, and slightly below a fair-weather wave base (Zatoń et al., 2012). In total, 1103 tube-dwelling polychaete fossils have been collected.

Kawodrza Górna: The fossil material from Kawodrza Górna derives from the "Sowa" brick pit. Serpulids and sabellids encrusting oyster shells come from the lower Bathonian (Zigzag Zone) mudstones (Matyja and Wierzbowski, 2000; Zatoń, 2010), which were deposited in deeper, below storm wave-base conditions (Matyja and Wierzbowski, 2000; Gedl et al., 2012). In total, 90 tube-dwelling polychaete fossils have been collected.

Gnaszyn Dolny: Serpulid and sabellid tubes from this locality come from the lower part of the "Gnaszyn" brick pit (Zatoń et al., 2011a). In the majority, they densely encrust belemnite rostra and oyster shells. The fossils derive from the middle Bathonian (Morissi Zone) mudstones originating in the marine environment, below the storm wave base (Gedl and Kaim, 2012; Gedl et al., 2012). In total, 777 tube-dwelling polychaete fossils have been collected.

Bugaj: Tube-dwelling polychaetes from this site were cemented to the middle Bathonian (likely Morissi or Subcontractus Zone; see Zatoń, 2010; Zatoń et al., 2006; 2011a) hiatus concretions. At present, the site is unavailable for any field research due to its transformation into a construction area, which makes the already collected material scientifically valuable. In total, 553 tube-dwelling polychaete fossils have been collected.

Ogrodzieniec: Similarly to Ogrodzieniec-Świertowiec, this locality is confined to the southern sedimentary region of the Polish Jura. Serpulid and sabellid fauna encrusted calcareous hiatus concretions derived from the upper Bathonian sediments (Hodsoni Zone; Zatoń et al., 2006; 2011a; Zatoń and Taylor, 2009b; Zatoń, 2010), ranging even to its topmost Discus Zone (Barski et al., 2004). In total, 337 tube-dwelling polychaete fossils have been collected.

Krzyworzeka: Polychaetes from this site encrust carbonate hiatus concretions. The concretion-bearing sediments from this locality are confined to the upper Bathonian (Poulsen, 1998; Zatoń, 2010). The deposits from Krzyworzeka originated in a calm outer shelf environment (Zatoń et al., 2011a; Sadlok and Zatoń, 2020), located below the storm wave base (Różycki, 1953; Leonowicz, 2013) and belong to the northernmost of the studied sites. In total, 920 tube-dwelling polychaete fossils have been collected.

Żarki: Serpulids and sabellids encrusting hiatus concretions have been derived from the upper Bathonian mudstones. The concretion-bearing sediments are late Bathonian (Hodsoni Zone) in age (Zatoń and Taylor, 2009b; Zatoń, 2010). Deposits within this location originated in a relatively calm but interrupted by episodic storm events (Leonowicz, 2015a), marine paleoenvironment (Marynowski et al., 2007; Leonowicz, 2012; 2013). In total, 58 tube-dwelling polychaete fossils have been collected.

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Bolęcin: The serpulid and sabellid tubes have been found within sandy limestones containing abundant grains of non-skeletal origin, presumably referring to the so-called "Balin Oolite." The polychaete tubes have been found fixed to a variety of fossils including bivalves, gastropods, and ammonites, as well as belemnite rostra. These condensed sediments (see Tarkowski et al., 1994; Mangold et al., 1996) were deposited presumably in an open marine paleoenvironment and are of late Bathonian (Retrocostatum and Discus Zones)–early Callovian (Herveyi, Koenigi, and Calloviense Zones), age as evidenced from ammonite fauna (Mangold et al., 1996). In total, 1011 tube-dwelling polychaete fossils have been collected.

Zalas: The fossil material collected from this locality comes from two sites: 1) an active quarry with sandy limestones forming a hardground of middle-earliest late Callovian age (Giżejewska and Wieczorek, 1977; Dembicz and Praszkier, 2007); here, the serpulids encrust notably large *Ctenostreon proboscideum* (J. Sowerby and G.B. Sowerby, 1820) bivalves, but also a wide variety of other invertebrate fossils such as ammonites, belemnites, and nautiloids. Transgressive Callovian sediments lie discordantly over Lower Permian porphyres and rhyodacites (Giżejewska and Wieczorek, 1977), which form a laccolith (Nawrocki et al., 2005). Hardground deposits originated in a deeper open marine setting corresponding to a shelf environment (Dembicz and Praszkier, 2007; Zatoń et al., 2011b); 2) overlying, lower Oxfordian light limestones hosting sponge bioherms (Trammer, 1982; Matyszkiewicz et al., 2012), to which serpulid tubes were attached. In total, 1174 tube-dwelling polychaete fossils have been collected from the Callovian deposits and 510 from the Oxfordian sponge facies.

Małogoszcz: Serpulid and sabellid fauna has been derived from an active quarry located in close proximity to the town of Małogoszcz. This site is located in the southwestern part of the Mesozoic margin of the Holy Cross Mountains. The tubes are attached to bivalve shells, particularly the oyster *Actinostreon gregareum* (J. Sowerby, 1815). Lower Kimmeridgian fossiliferous deposits are referred to as the Skorków Lumachelle (Kutek, 1994; Machalski, 1998; Zatoń and Machalski, 2013). These shell beds were deposited during episodic storms in a relatively shallow marine paleoenvironment (Machalski, 1998). In total, 157 tube-dwelling polychaete fossils have been collected.

Pliocene
Miocene
Cretaceous
Upper Jurassic
Middle Jurassic
Lower Jurassic
Jurassic undivided
Upper Triassic
Pre-Jurassic deposits

Carpathian overthrust
Faults
Investigated sites

A
B
Warszawa
Kraków
Kielce
HCM
PJ

Częstochowa
Bugaj
Żarki
Zawiercie
Ogrodzieniec &
Ogrodzieniec-Świertowiec
Kłobuck
Olsztyn Dolny
Kawodrza Górna
Wieluń
Krzyworzeka
Mokrsko

Prosna
Warta
Liswarta
Pilica

10 km
5   0   5

N

Figure 1. **A.** Geological sketch-map of Poland without the Cenozoic cover showing three investigated locations. HCM, Holy Cross Mountains; PJ, Polish Jura; 1. Bolęcin; 2. Zalas; 3. Małogoszcz. **B.** Geological map of the Polish Jura area without Quaternary cover, with sampled localities indicated (modified after Zatoń et al., 2006).

3. Methods

Collected fossils were subjected to taxonomic, paleoecological, and microstructural research. The study on the taxonomy of tube-dwelling polychaetes was focused on assigning each morphotype to the lowest taxonomic level possible. All damaged or strongly abraded tubes have been discarded from further inspection, as their potential taxonomic determination would be ambiguous or impossible. Sufficiently preserved research material was carefully cleaned and inspected, paying special attention to the specific characters of the tubes (e.g., sculpture, presence or lack of tabulae and attachment structures, type and direction of coiling, internal tube structures (ITS), type of aggregation and shape, size and expansion rate of a tube diameter; see Ippolitov et al., 2014). The recognition was based on comparative external and internal morphology and morphometric analyses. For this purpose, apart from macroscopic observations, Prolab binocular microscope was used. The selected specimens were coated with ammonium chloride and photographed using the Canon EOS camera.

In order to examine the distribution and relative abundance of serpulids and sabellids in relation to a specific substrate within a given paleoenvironment, statistical tools have been used based on the already obtained systematic account and the total number of specimens. Using the PAST software (Hammer et al., 2001), Q-mode cluster analysis was performed in order to investigate quantitatively the similarities of different paleoenvironments. The Raup-Crick similarity index and the unweighted pair group method with arithmetic mean (UPGMA) algorithm were employed. The Raup-Crick index was applied due to the use of Monte Carlo randomization, which compares the observed number of taxa occurring within two associations with the distribution of their co-occurrences on the basis of 200 random interactions. Assessment of the communities' structure was based on the employment of the popular biodiversity indices: Dominance (D), Simpson's (1-D), Shannon's (H), and evenness (eH/S) using the PAST software (Hammer et al., 2001).

Serpulids were also examined for their symbiosis with hydroids to obtain data on the frequency of this phenomenon in the Polish Basin, and to determine whether there is any preference for hosts. Tubes bearing unique characters in the form of bioclaustrated traces after

hydroid symbionts (Słowiński et al., 2020) were selected for further examination using micro-computed tomography (micro-CT) to provide virtual sections of the hydroid colony appearance within the serpulid tubes. Prior to micro-CT scanning, serpulid tubes infested by hydroids were cleaned using an ultrasonic cleaner. Virtual sections were made using the GE Phoenix v|tome|x micro-CT equipment with scanning voltage ranging 140–180 kV, current intensity 50–90 μA, and scanning time of 25 to 35 min depending on the sample. The investigations were conducted in the X-ray Microtomography Laboratory at the Faculty of Computer Science and Materials Science, University of Silesia in Katowice, Chorzów, Poland. To process the obtained micro-CT scans the Volume Graphics® VGSTUDIO Max software and Volume Graphics® myVGL Viewer App and Fiji were utilized (Schindelin et al., 2015). The collected images were used to produce a volumetric rendering and a movie using Drishti (Limaye, 2012).

Toward microstructural recognition of the fossils, well-preserved tubes of selected taxa were cut longitudinally, polished, and etched with a 1% solution of acetic acid. Such prepared samples were subsequently examined in an uncoated state using a scanning electron microscope SEM Zeiss EVO MA15 using a back-scattered electron detector (BSE) in a low vacuum regime. The beam voltage was 20 kV (Department of Geology, University of Tartu, Estonia). The polished tubes were also studied under the environmental scanning electron microscope (ESEM) Philips XL30, and the Quanta 250 scanning electron microscope (SEM) at the Institute of Earth Sciences in Sosnowiec. The latter SEM, equipped with Thermo-Fisher's EDS UltraDry analyzer, was also used for supplementary investigation of the mineral composition of the sabellid tubes. Selected specimens were tested in high vacuum mode (<1.19 * 10-4 Pa) at 15 KeV accelerating voltages. An analytical EDS detector (Energy Dispersive Spectroscopy) was used to map the elemental distribution and conduct chemical microanalyses at selected areas of the tube wall. This technique enables a quick semi-quantitative identification of the elemental composition of the samples analyzed.

In order to determine the exact mineral composition of the sabellid tubes Confocal Raman Spectroscopy (CRS) was used. A WITec alpha 300R Confocal Raman Microscope (housed at the Institute of Earth Sciences in Sosnowiec) equipped with an air-cooled solid laser 488 nm and a CCD camera operating at –61°C was used to record the raman spectra of the selected samples. The laser radiation was coupled to a microscope through a single-mode optical fiber with a diameter of 3.5 μm. An air Zeiss LD EC Epiplan-Neofluan DIC (100/0.75NA) objective was used. Raman scattered light was focused by a broad band single mode fiber with an effective pinhole size of about 30 μm and a monochromator with a 600 mm–

1 grating. The power of the laser at the sample position was 42 mW. Integration times of 5 sec with the accumulation of 15 scans and a resolution of 3 cm–1 were chosen. The monochromator was calibrated using the Raman scattering line of a silicon plate (520.7 cm–1). Spectra processing, such as baseline correction and smoothing was applied using the SpectraCalc software package GRAMS (Galactic Industries Corporation, NH, USA). Bands fitting was performed using a Gauss-Lorentz cross-product function, with a minimum number of component bands used for the fitting process.

4. The article overview and results

The main body of the herein thesis comprises four articles, a brief description of which is provided below. I am the first and corresponding author of all these publications; my scientific contribution is specified in the "Authorship statements" section.

1. **Słowiński J.**, Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924. DOI: 10.1371.0242924. **IF(2020)=3,24. MEiN=100 pkt.**

The first article was focused on the inspection of the symbiotic relationship between serpulids and hydroids. Serpulid tubes infested by hydroids were derived from the Middle and Upper Jurassic sediments representing different paleoenvironments of the Polish Basin. The hydroids are preserved within the external part of the serpulids' tube as a result of *syn vivo* incorporation due to the worm's skeletal overgrowth. The external appearance is manifested by many tiny opened apertures, surrounded by bulges of different shapes, which are scattered over the tube's surface. The internal morphology was visualized using micro-computed tomography. It shows a network of thin branching stolonal tubes and polyp chambers, which open on the outer surface. Serpulid-hydroid symbiosis was an extremely rare phenomenon in the Jurassic Polish Basin with an infestation rate of 0,6%. The interaction has been recorded in four outcrops spanning upper Bajocian–Callovian. Anyhow, 17 out of 20 cases have been found on a single species (*Propomatoceros lumbricalis*) coming from the middle Bathonian Morissi Zone of Gnaszyn Dolny. Such a pattern of infestation attests to an extremely high selectivity of *Protulophila gestroi* in the choice of its host.

2. **Słowiński, J**., Vinn, O, Jäger, M., Zatoń, M. (2022). Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. *Acta Palaeontologica Polonica* 67, 827-864. DOI: 10.4202/app.01006.2022. **IF(2022)=2,108. MEiN=100 pkt.**

The second article illustrates the systematic account of Jurassic (upper Bajocian to lower Kimmeridgian) serpulids and sabellids inhabiting diverse paleoenvironments of the Polish Basin, their abundance, diversity, and distribution. A total of 24 taxa were reported, comprising two new species (*Filogranula spongiophila* sp. nov. and *Cementula radwanskae* sp. nov.). The most significant factors affecting the structure of the examined assemblages were the kind and character of the colonized substrate, the energy of the paleoenvironment, and the food supply. The highest biodiversity indices are characteristic of the Middle Jurassic communities inhabiting hardgrounds, oncoids, and skeletal remnants on the soft muddy substrates. In turn, the least diverse are tube-dwelling polychaetes from the Middle Jurassic hiatus concretions and Upper Jurassic oyster shell beds. Some species are linked with specific kinds of substrate, whereas stratigraphic interval is less important. Sponge build-ups are characterized by the most distinct taxa of serpulids and sabellids, followed by soft muddy substrates. Apart from sponge facies, in all locations, the basis of the tube-dwelling polychaete communities constitute the ubiquitous sabellid *Glomerula gordialis* and serpulid *Propomatoceros lumbricalis*. The assemblages from the Polish Basin are mostly comparable in their abundance and diversity with other tube-dwelling polychaete assemblages inhabiting various Jurassic paleoenvironments.

3. **Słowiński, J.**, Banasik, K., Vinn, O. (2023). Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications. *Lethaia* 56(3), s. 1-12. DOI: 10.18261/let.56.3.8. **IF(2022)=1,5. MEiN=100 pkt.**

The third article concerns the ultrastructure and mineralogy of the Middle and Upper Jurassic sabellid *Glomerula gordialis* and their evolutionary significance. The tube of *Glomerula* is built of a single layer, composed of an oriented, spherulitic prismatic structure (SPHP), which stays congruent with previous reports on the sabellid tube ultrastructure. To determine the mineral composition of the calcareous sabellid tubes, Raman spectroscopy and supplementary SEM-EDS analyses were used. In all

cases, the mineralogy of the Jurassic sabellid tubes was low-Mg calcite matching chemistry of the Middle Jurassic-Eocene calcitic seas. Biomineralized skeletons of sabellids are first recorded in the Middle Permian, a time of aragonite sea dominance. Similarly to Oligocene cirratulids, calcareous sabellids are envisaged to have independently evolved their calcareous skeleton with the mineral composition corresponding to the seawater chemistry during the time of their origin. The biomineralization system of sabellids is simpler than that of serpulids. Bearing lower energy expenditure in the formation of the skeleton, *Glomerula* is capable of fast spreading over the substrate and avoiding competition, as well as other obstacles.

4. **Słowiński, J.**, Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. *PeerJ* 12, e17389. DOI:10.7717/peerj.17389. **IF(2024)=2,7. MEiN=100 pkt.**

The fourth article describes the ultrastructural diversity of the Jurassic serpulids from the Polish Basin, its phylogenetic constraints and paleoecological implications. On the basis of 12 serpulid species constituting two out of three major serpulid clades, three distinct ultrastructure types have been described – irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP). Half of the investigated species have a single-layered tube wall and half are two-layered. Distinct ultrastructure types are related to particular clades. The representatives of Filograninae possess a single-layered tube wall, which is usually composed of a primitive, irregularly oriented prismatic structure (IOP). Most members of the clade Serpulinae have a two-layered tube wall. While the internal layer is composed of irregularly oriented prismatic structure (IOP) too, the denser, outer layer is built of regularly oriented prismatic structures – spherulitic (SPHP) or simple (SP). Formation of such ultrastructures requires a higher degree of biological control over biomineralization compared to the isotropic, non-oriented prismatic structure of Filograninae. The growth of ultrastructural diversity and the emergence of the dense outer protective layer (DOL) likely arose as a response against predation and environmental vagaries. The biomineralization system of serpulids is more complex as compared to sabellids. Serpulids have a well-developed parabolic layer, which allows them to actively modify external morphology during secretion of subsequent growth

increments at the rim of the worm's aperture. Although bearing higher energy expenditures, serpulids are able to enhance tube durability by the formation of attachment structures and a thicker, robust skeleton.

5. Discussion

5.1. Taxonomy and paleoecological analysis of the Middle and Upper Jurassic tube-dwelling polychaetes from the Polish Basin

5.1.1. Systematic account

Taxonomic research aimed to assign the collected specimens to the lowest taxonomic level possible. Due to the bad state of preservation, a part of the collection was discarded from further taxonomic studies being uninformative. Based on 2314 sufficiently preserved specimens of tube-dwelling polychaetes, 24 taxa have been recognized (Tab. 1), including the two new species – *Filogranula spongiophila* (Fig. 2D) and *Cementula radwanskae* (Fig. 2H). 23 species constitute two of the three main serpulid clades – Filograninae and Serpulinae – the latter being subdivided into two tribes – Serpulini and Ficopomatini. Within the family Serpulidae, only the members of the Spirorbinae clade are absent in the studied material. One species – *Glomerula gordialis* – belongs to the family Sabellidae.

Taxa	Mokrsko	Kawodrza Górna	Gnaszyn Dolny	Bugaj	Ogrodzieniec	Krzyworzeka	Żarki	Ogrodzieniec-Świertowiec	Bolęcin	Zalas (Callovian)	Zalas (Oxfordian)	Małogoszcz	Total number of individuals (per taxon)
Glomerula gordialis	66	13	80	52	60	62	8	174	102	181	36	45	879
Metavermilia cf. *striatissima*					2	33	1	18	24	56			134
Metavermilia? sp.			11										11
Filogranula runcinata	3	3	13	5				5	15	11			55
Filogranula spongiophila sp. nov.											16		16
Cementula spirolinites											122		122
Cementula radwanskae sp. nov.									4	29			33
Cementula cf. *circinnalis*								38					38
"*Serpula cingulata*"											3		3
Propomatoceros lumbricalis	21	31	228	81	33	23	9	156	81	149		28	840
Propomatoceros sp. 1	1		4										5
Propomatoceros sp. 2										1			1
Propomatoceros sp. 3												1	1
Nogrobs aff. *quadrilatera*			36										36
Nogrobs? aff. *tricristata*			8										8
Nogrobs aff. *tetragona*			29										29
Mucroserpula tricarinata										2			2
Mucroserpula? sp.			2										2
Placostegus planorbiformis											7		7
Pseudovermilia sp.										4			4
Serpulidae sp. 1								23	5	43			71
Serpulidae sp. 2			1										1
Serpulidae sp. 3			10										10
Serpulidae sp. 4												6	6
Total number of individuals (per locality)	91	47	422	138	95	118	18	414	231	476	184	80	2314

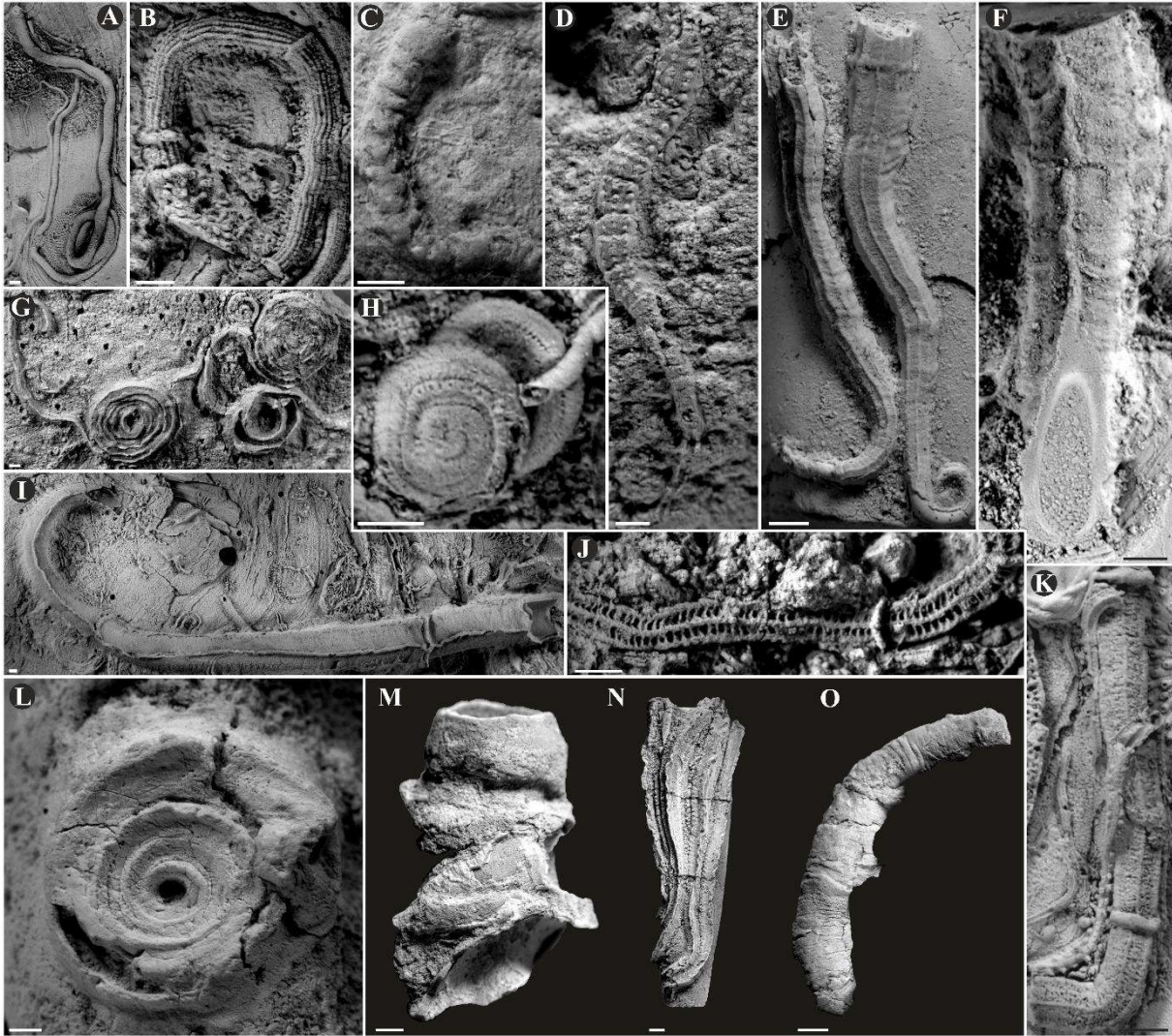**Table 1.** Data on provenance and number of the well-preserved sabellids and serpulids (Słowiński et al., 2022).

Figure 2. Serpulid and sabellid polychaetes from the Jurassic of Poland. A. *Glomerula gordialis* (Schlotheim, 1820) from the Callovian of Zalas (GIUS 8-3589/2). **B.** *Metavermilia* cf. *striatissima* (Fürsich, Palmer and Goodyear, 1994) from the Callovian of Zalas (GIUS 8-3589/3). **C.** "*Serpula cingulata*" (Münster in Goldfuss, 1831) from the Oxfordian of Zalas (GIUS 8-3746/7). **D.** *Filogranula spongiophila* (Słowiński, Vinn, Jäger and Zatoń, 2022) from the Oxfordian of Zalas (GIUS 8-3746/2). **E.** *Nogrobs* aff. *quadrilatera* (Goldfuss, 1831) from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/17). **F.** *Mucroserpula* sp. (Regenhardt, 1961) from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/26). **G.** *Cementula spirolinites* (Münster in Goldfuss, 1831) from the Oxfordian of Zalas (GIUS 8-3746/4). **H.** *Cementula radwanskae* (Słowiński, Vinn, Jäger and Zatoń, 2022) from the Callovian of Zalas (GIUS 8-3589/7). **I.** *Propomatoceros lumbricalis* (Schlotheim, 1820) from the Callovian of Zalas (GIUS 8-3589/11). **J.** *Pseudovermilia* sp. (Bush, 1907) from the Callovian of Zalas (GIUS 8-3589/15). **K.** Serpulidae sp. 1 from the Callovian of Zalas (GIUS 8-3589/16). **L.** *Placostegus planorbiformis* (Münster in Goldfuss, 1831) from the Oxfordian of Zalas (GIUS 8-3746/8). **M.** Serpulidae sp. 2 from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/27). **N.** Serpulidae sp. 3 from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/28). **O.** Serpulidae sp. 4 from the lower Kimmeridgian of Małogoszcz (GIUS 8-3747/3). (Modified after Słowiński et al., 2022). Scale: 1 mm.

5.1.2. Diversity and distribution

The paleoecological study of the already recognized species demonstrates, that serpulids and sabellids are dependent to a significant degree on the inhabited substrate, its nature, and physical properties (Słowiński et al., 2022; see also Ippolitov, 2010). Other factors influencing larval settlement and subsequent colonization of tube-dwelling polychaetes are temperature, light availability, as well as salinity and oxygen levels (Kupriyanova et al., 2019). The stratigraphic interval in which they occur plays a marginal role, which generally stays congruent with a common opinion of highly constrained serpulid biostratigraphy (but see Macellari, 1984; Tapaswi, 1988).

By applying cluster analysis, we were able to group the tube-dwelling polychaetes into several clusters of different substrates sharing similar taxa (Słowiński et al., 2022). The community within the Oxfordian sponge facies of Zalas displays the highest distinctness with the majority of taxa reported nowhere else – the substrate provided by sponges was dominated by compact (e.g., *Placostegus planorbiformis*; Fig. 2L) and fast-growing forms with tiny diameters (e.g., *Cementula spirolinites*; Fig. 2G). The highest degree of similarity is shown between serpulid and sabellid assemblages inhabiting mobile substrates such as hiatus concretions and oncoids, which were susceptible (although to a different degree) to physical disturbances and resulting overturning (e.g., Wilson, 1987; Zatoń et al., 2011a; 2012). As a result, the qualitative composition of the tube-dwelling polychaete assemblages living on such substrates is very similar, where the most opportunistic and scour-resilient species dominate.

Anyhow, hiatus concretions and oncoids differed in the nature of the colonized surface, which strongly influenced the quantitative composition of serpulids and sabellids. The least diverse communities have been recorded on the Middle Jurassic hiatus concretions (Słowiński et al., 2022), which presumably resulted from their repeated overturning leading to abrasion and smothering of the colonizing larvae. Rather rare, episodic storm events (Zatoń et al., 2011a) resulted in a low diversity and predominance of the most opportunistic species, such as *Glomerula gordialis* (Fig. 2A) and *Propomatoceros lumbricalis* (Fig. 2I). Although oncoids served as a mobile substrate too, their stability on the seafloor was higher due to a more flat shape and increasing volume of an oncoid during the continuous formation of its cortex layers, which made them less prone to overturning. Another environmental advantage of oncoids from Ogrodzieniec-Świertowiec over locations with hiatus concretion was a high nutrient availability in the photic zone, which could have facilitated intense colonization and flourishment of

serpulids and sabellids (e.g., Kupriyanova et al., 2001; Gosselin and Sewell, 2013; but see e.g., Kuklinski, 2009).

Based on the values of Shannon index (H), as well as Simpson index of diversity (1-D) and dominance (D) (see Słowiński et al., 2022), the highest biodiversity is noted for Bathonian and Callovian hardgrounds (Bolęcin and Zalas), Bajocian–Bathonian oncoids (Ogrodzieniec-Świertowiec), and the middle Bathonian skeletal remains from soft muddy substrates. Unlike other kinds of substrates, flat oyster shells and belemnite rostra lying on the soft, muddy bottom from Gnaszyn Dolny served as "benthic islands" (e.g., Zuschin et al., 1999; Taylor and Wilson, 2003) and were a stable substrate not only for tube-dwelling polychaetes but also for other epibionts. Moreover, the paleoenvironment is generally interpreted as deposited in relatively calm conditions, below the storm wave-base (Gedl et al., 2012). The low hydrodynamics also contributed to the best state of preservation compared to other sites. The lowest evenness value from this locality attests to both the high number of individuals and species richness (Słowiński et al., 2022). In the case of hardgrounds and oncoids, convenient conditions, but also time-averaging, influenced the final composition of the assemblages. The evenness value of Ogrodzieniec-Świertowiec points to the lower biodiversity, which, however, resulted from comparable proportions between the representatives of different taxa (Słowiński et al., 2022).

Simpson index of diversity (1-D), dominance (D), Shannon index (H), as well as evenness values, point to the moderate level of biodiversity within parautochtonous shell beds from the lower Kimmeridgian of Małogoszcz (Słowiński et al., 2022). Although characterized by a low taxonomic richness, which was an effect of a relatively shallow paleoenvironment with episodically occurring storm events (Machalski, 1998) hampering colonization, the number of individuals within different species was relatively similar.

In addition, many tube-dwelling polychaetes displayed a characteristic distribution over the substrate, which resulted from resolving similar adaptive strategies, such as mechanical strengthening of the skeleton leading to morphological resistance against tube damage, cryptic lifestyle (Kobluk, 1988), or a "fugitive" strategy (Taylor, 2016). The latter two allowed for a withdrawal away from dominating species and either inhabiting empty borings, concavities, and deflections (Palmer and Fürsich, 1974; Wilson, 1998; Taylor and Wilson, 2003; Schlögl et al., 2008) or fast retreating during unfavorable conditions (Słowiński et al., 2022; 2023).

5.1.3. Symbiotic relationship between serpulids and hydroids

Throughout their evolutionary history serpulids formed symbiotic relationships with representatives of different invertebrate groups. The vast majority of such serpulid relationships were formed with hydroids, which could be explained by utilizing different feeding strategies of both partners (see Vinn et al., 2023). Such a specific kind of symbiotic interaction between the serpulid *Propomatoceros* and the hydroid referred to as *Protulophila gestroi* (Rovereto, 1901) was recorded in the Jurassic of the Polish Basin (Fig. 3A-B; Słowiński et al., 2020). The symbionts are preserved in the form of bioclaustrated (embedment) traces (see Palmer and Wilson, 1988; Taylor, 1990; Tapanila and Ekdale, 2007) within the serpulid tube wall, which indicates that the interaction took place *syn vivo*. The process of bioclaustration provides here a unique glimpse of these soft-bodied fossils. Hydroid colonies embedded within the serpulid skeleton are represented by the hollow traces left after their thin stolonal network and polyp chambers, which are bent outwardly and open on the serpulid tube surface. Their external appearance is marked by tiny, circular, or oval openings representing apertures and minute bulges occurring around them (Fig. 3B; see also Scrutton, 1975; Radwańska, 2004; Jäger, 2005; Niebuhr and Wilmsen, 2005; Zágoršek et al., 2009; Kamali Sarvestani et al., 2015; Słowiński et al., 2020). The morphology of fossils is rather uniform across different stratigraphic intervals (Scrutton, 1975; Radwańska, 1996; 2004; Jäger, 2005; Niebuhr and Wilmsen, 2005; Jäger and Schubert, 2008; Zágoršek et al., 2009; Zatoń et al., 2011a; Kamali Sarvestani et al., 2015; Słowiński et al., 2020) and slight differences are presumably an effect of variable physiological (e.g., calcification rate of the host and consequent avoidance of the symbiont of being completely embedded by the overgrowing organism) or paleoecological conditions.

Although the true systematic position and the mode of origin of the hydroid symbionts has been examined and recognized by Scrutton (1975), the phylogenetic position of *Protulophila gestroi*, usually described as selective in the choice of its host (see below), spanning Pliensbachian (Jäger and Schubert, 2008) to recent (Taylor et al., 2015), is at least questionable. However, with recently acquired by micro-CT scanning internal morphology of the embedded hydroid colonies (Fig. 3C; Słowiński et al., 2020), we are able to obtain a better picture of the symbionts' persistence through the geological time by cautious comparisons of the hydroid morphologies derived from different stratigraphic intervals. Such research is currently underway by the author, thanks to the financial support (Preludium grant).

In the Middle–Late Jurassic sea of the Polish Basin, serpulids very rarely played the role of hosts for their symbiotic hydroids. *Protulophila gestroi* was highly selective in choosing their host. The majority of *Protulophila gestroi* colonies, spanning the Lower Jurassic (Jäger and Schubert, 2008) to Pliocene (Scrutton, 1975; Carboni et al., 1982), generally infested very few, or even one serpulid species within a single stratigraphic interval. Similarly, in the Polish Basin in all the cases, they colonized serpulids belonging to only one species – *Propomatoceros lumbricalis*, the vast majority of which (17 out of 20 cases) were recorded in a single location from a single stratigraphic zone (Gnaszyn Dolny, middle Bathonian, Morrisi Zone; Słowiński et al., 2020). The possible explanations of settlement preferences of hydroids are different beneficial conditions, such as a conducive chemical composition enhancing settling and subsequent recruitment, and other physiological and behavioral factors (see Mokady and Brickner, 2001; Savazzi, 2001). Anyhow, the movement capability of hydroid larvae is highly restricted (Mokady and Brickner, 2001). Therefore, it cannot also be ruled out that free-living larvae encountered serpulids randomly and only a small part of the population had a chance to recruit and develop. Combined with the specific kind of substrate provided by large, flat-lying oysters, which acted as "benthic islands" on the otherwise soft, muddy sea bottom, hydroid larvae had the biggest opportunity to settle on closely adjacent serpulids encrusting the same substrate. Such distribution of several hydroid colonies preserved on single oysters is here well exemplified (Słowiński et al., 2020).

Considering the nature of the serpulid-hydroid symbiosis, mutualism, parasitism, and commensalism could be involved, the latter of which seems to be the most plausible explanation. There is no evidence that hydroids provided any advantages for serpulids, whereas hydroids presumably benefited from the serpulid's radiole-propelled nutrient currents, as well as from receiving shelter from being partially overgrown by serpulid skeleton (Fig. 3A). Moreover, commensalism is often characterized by a strong host preference that results in some obligate cohabitation of host and colonizer (Tapanila and Ekdale, 2007), which could account for the host selection of *Protulophila gestroi*. In the case of mutualism, hydroids were presumably insignificant for serpulids. Extreme selectivity in the choice of its host and scarcity of infestation cases rather precludes mutualism as a confident kind of relationship. Furthermore, even if the protective role of hydroid cnidocytes (see Słowiński et al., 2020) is indeed true, it played a minor role. There is also no evidence for any harmful activity of hydroids to take parasitism into consideration.
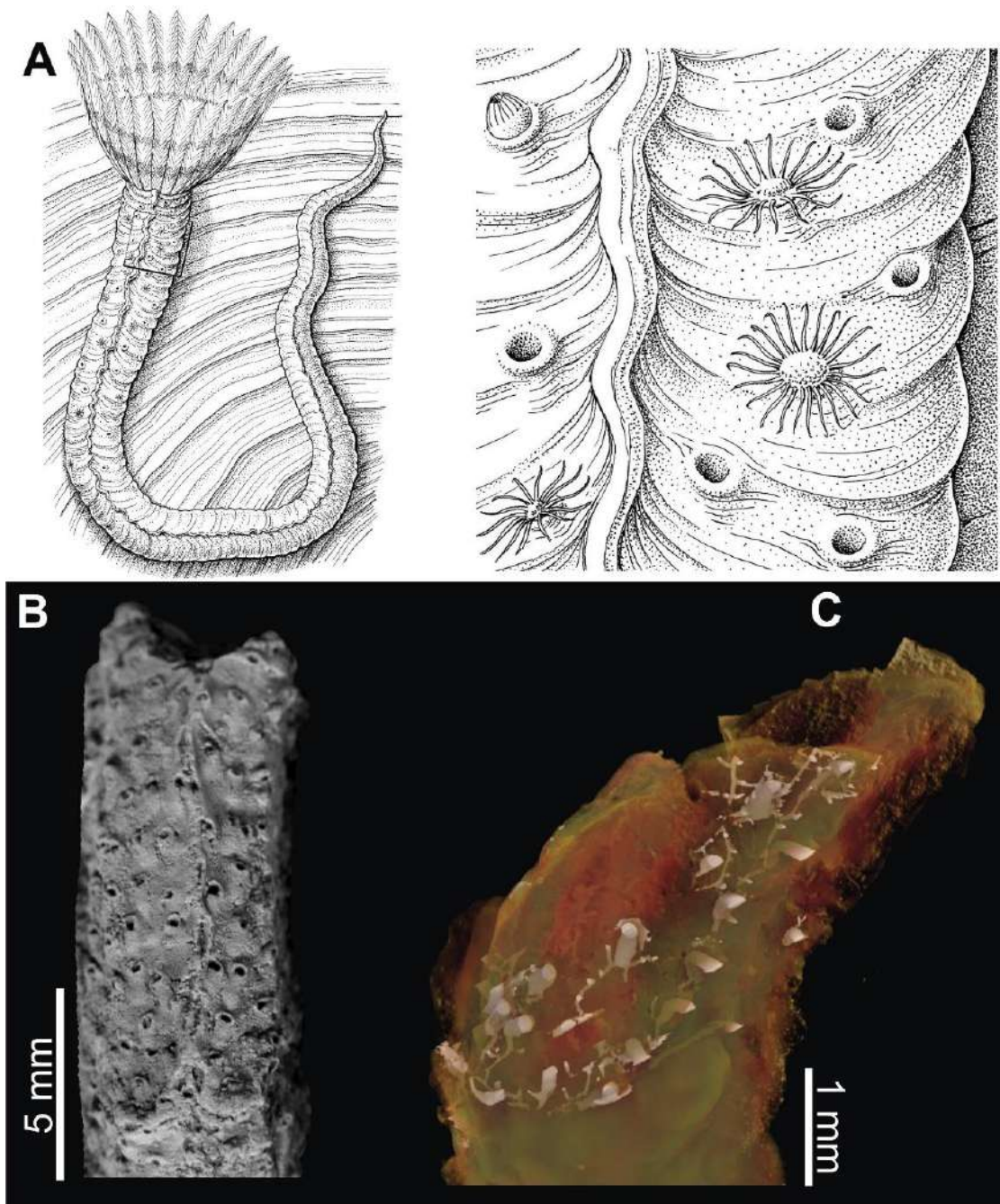
Figure 3. A. Reconstruction of the symbiotic relationship between serpulid *Propomatoceros* **and hydroids** *Protulophila gestroi* (**Rovereto, 1901**); drawings by Bogusław Waksmundzki. **B.** *Protulophila gestroi* bioclaustrated by the serpulid *Propomatoceros* from the upper Bajocian of Mokrsko (GIUS 8-3730/1). **C.** Visualization of the bioclaustrated hydroid colony by the host serpulid from the middle Bathonian of Gnaszyn Dolny showing the internal morphology of the colony and the arrangement of stolonal network and zooids (GIUS 8-3730/8).

5.2. Ultrastructural analysis of the Middle and Upper Jurassic tube-dwelling polychaetes from the Polish Basin

5.2.1. Phylogenetic constraints and ecological implications of the serpulid tube ultrastructure

Serpulids can build calcareous tubes composed of up to four layers exhibiting various ultrastructural characters (Vinn et al., 2008b). Anyhow, the majority of the Jurassic serpulid species was single-layered and the percentage of species secreting multi-layered tubes constituted ca 25% (Vinn and Furrer, 2008). Ultrastructural diversity and the number of serpulid species possessing at least two tube wall layers gradually increased across geological time (Vinn et al., 2008b), which possibly resulted from the importance of the tube for serpulids. Although the most sophisticated ultrastructure types evolved during the Eocene (Vinn, 2008; Buckman, 2020) and the Jurassic was a time of limited ultrastructural diversity comprising ten types (Vinn, 2007); still, relatively complex, oriented prismatic structures evolved at the latest during the Middle Jurassic (Słowiński et al., 2024).

During the examination of 12 serpulid taxa derived from the Middle and Upper Jurassic of the Polish Basin, three distinct ultrastructural types were recognized – irregularly oriented prismatic structure (IOP; Fig. 4E-F), spherulitic prismatic structure (SPHP; Fig. 4A-B), and simple prismatic structure (SP; Fig. 4C-D). Six of these taxa are single-layered and six possess two-layered tube walls (Słowiński et al., 2024). The investigated species represent two of three main serpulid clades – Filograninae and Serpulinae (which is further subdivided into two tribes: Serpulini and Ficopomatini; Kupriyanova et al., 2023). Different types of ultrastructure are characteristic of individual clades; however, in spite of some younger serpulid representatives (e.g., Sanfilippo, 1998; Vinn, 2007; Ippolitov and Rzhavsky, 2008; Kupriyanova and Ippolitov, 2015; Buckman, 2020), the ultrastructure of the Jurassic serpulids is not suitable for recognizing certain species or genera. Regardless, the ultrastructure of the Jurassic serpulid tubes may still be useful for obtaining important phylogenetic signals and serpulid evolutionary trends.

Members of Filograninae are most often characterized by single-layered tube walls composed of irregularly oriented prismatic structure (IOP; Fig. 4F)(Vinn, 2007), which determine optically opaque tubes in the recent serpulids (Vinn et al., 2008b). Compared to more advanced, regularly oriented structures (see below), the formation of IOP appears to be under the animal's lower biological control. This kind of ultrastructure undoubtedly appeared at the latest during the Early Jurassic (Vinn et al., 2008c). Nevertheless, such a primitive way of

skeletal secretion suggests an earlier origin of this ultrastructure type implying its plesiomorphic character (see also Vinn, 2013; Ippolitov and Rzhavsky, 2015a; 2015b), especially that rather unequivocal members of Filograninae were present already in the Permian (Sanfilippo et al., 2017; Ramsdale, 2021). Filograninae is represented in the studied material by *Metavermilia* cf. *striatissima* (Fig. 2B) possessing a single-layered tube wall composed of IOP and by the genus *Filogranula* having a tube wall built of a single layer with simple and spherulitic prismatic structure (*F. spongiophila* and *F. runcinata* respectively; see Słowiński et al., 2024). *Filogranula* remains slightly problematic in the fossil record, as it may be a polyphyletic taxon (see Ippolitov et al., 2014; Kočí and Jäger, 2015a). Although the Recent (Kupriyanova et al., 2023) and Cretaceous (Kočí and Jäger, 2015a) representatives of this genus are considered to belong to Filograninae, the phylogenetic position of the Jurassic *Filogranula* remains uncertain due to its prismatic microstructure, characteristic of Serpulinae. Anyhow, prismatic structures might be insufficient in distinguishing between these two clades (see Ippolitov and Rzhavsky, 2014; 2015a; b).

In contrast to Filograninae, Serpulinae governs a higher biological control over biomineralization, being able to form oriented (Słowiński et al., 2024), or even more complex microstructure types (e.g., Vinn and Furrer, 2008; Vinn and Kupriyanova, 2011). In the Jurassic Polish Basin, Serpulinae were widely represented by the Serpulini genus *Cementula* (Fig. 2G-H) and members of the tribe Ficopomatini including *Propomatoceros* (Fig. 2I), *Mucroserpula* (Fig. 2F), *Nogrobs* (Fig. 2E), and *Placostegus* (Fig. 2L). Most representatives of the clade Serpulinae have two-layered skeletal walls, with the internal thin layer composed of irregularly oriented prismatic structure (IOP) and the denser, external layer built of a regular prismatic microstructure, either simple or spherulitic (Fig. 4D; Słowiński et al., 2024). Prismatic structures are very characteristic of the Jurassic Serpulinae members and are considered to be apomorphic (see Vinn and Kupriyanova, 2011). Recent serpulids with tubes composed of prismatic structures, which show the uniform orientation of crystals, are optically transparent (Zibrowius and ten Hove, 1987; Ippolitov and Rzhavsky, 2008).

Dense outer protective layers (DOLs) occur in a vast majority of tubes of the members of the clade Serpulinae and are present in serpulids living in a wide range of habitats (Vinn and Kupriyanova, 2011), indicating their evolutionary significance regardless of environment. Formation of DOL could have served as a deterrent adaptation against predation, especially intensified during the Marine Mesozoic Revolution (Vermeij, 1977). Additionally, the dense external layer might have been a response to carbonate dissolution, especially in the case of

deep-sea serpulids (Kupriyanova et al., 2011; Kupriyanova and Ippolitov, 2015). Furthermore, the ability to form multi-layered tubes, as well as a general increase in ultrastructural diversity (Vinn et al., 2008b) enhanced the development of diverse morphogenetic programs (e.g., free, vertical growth off the substrate), which increased functional adjusting to paleoenvironmental constraints (see Vinn et al., 2024).
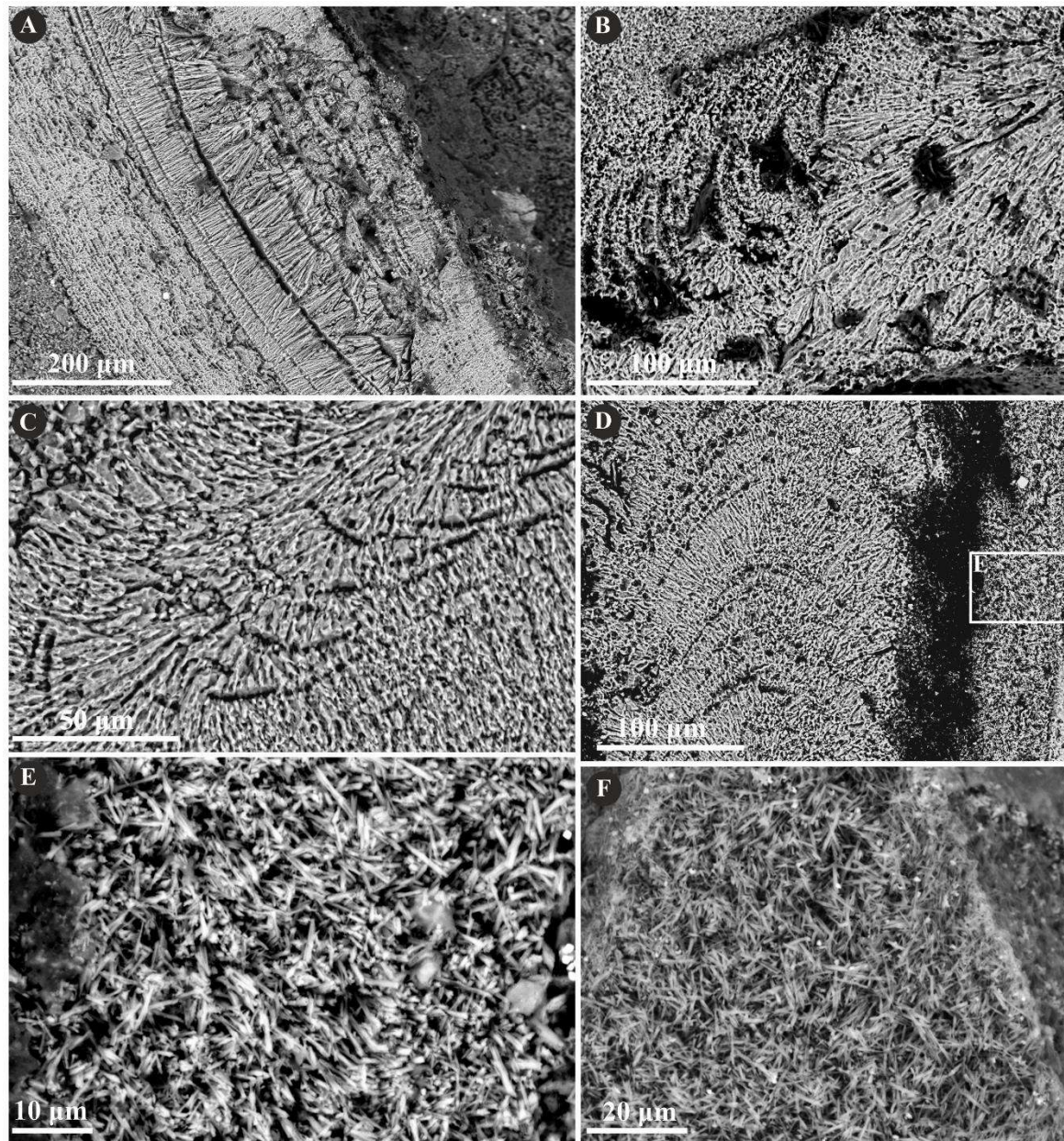

Figure 4. Longitudinal sections of the selected tube-dwelling polychaetes from the Jurassic of Poland showing ultrastructural diversity. **A, B.** Spherulitic prismatic structure (SPHP) of the sabellid *Glomerula gordialis* (**A**; GIUS 8-3751/7) and the serpulid *Filogranula runcinata* (**B;** GIUS 8-3730/10) **C.** Simple prismatic (SP) structure of *Placostegus planorbiformis* from the Oxfordian of Zalas (GIUS 8-3746/8). **D.** *Nogrobs*? aff. *tricristata* from the middle Bathonian of Gnaszyn Dolny exhibiting two distinct layers: the external simple prismatic structure (SP) and internal irregularly oriented prismatic structure (IOP)(GIUS 8-3730/20). **E.** A close-up of

the internal tube layer of *Nogrobs*? aff. *tricristata* showed in D. **F.** Irregularly oriented prismatic (IOP) structure of *Metavermilia* cf. *striatissima* from the upper Bathonian of Krzyworzeka (GIUS 8-3751/3)(Modified after Słowiński et al., 2024).

5.2.2. Comparison of the biomineralization systems of serpulids and sabellids

Serpulids and sabellids employ a biomineralization system that differs in complexity, which is reflected in the paleoecology of both groups. Two kinds of tube layers can be distinguished in terms of their origin and application. Jurassic calcareous sabellids are composed of a single layer of skeleton (Vinn et al., 2008a; Słowiński et al., 2023) referred to as a cylindrical layer (see Jäger, 1983). Secretion of this layer proceeds along the long growth lines oriented parallel to the tube wall with subsequent growth increments added to the interior of the tube (Jäger, 1983); therefore, *Glomerula* is unable to modify its external morphology, which results in a very simple set of tube characters. In contrast, serpulids are capable of forming also a parabolic layer (Jäger, 1983) with successive chevron-shaped growth increments (Weedon, 1994) added to the rim of the worm's aperture, which contributes to a sophisticated architecture of many serpulid tubes and their variety of forms. Such a way of skeleton secretion is a serious limitation for calcareous sabellids because their tubes are fragile and prone to damage. On the other hand, parallel to the tube wall, the much longer secretion zone of *Glomerula*, allows for a faster calcification while incurring comparatively lower physiological costs, which enables a significant tube extension at a relatively fast pace. It facilitates retreating from competition and temporarily inconvenient conditions performing an opportunistic, "fugitive" strategy (see Taylor, 2016; Słowiński et al., 2023). Serpulids are rather not capable of such quick dispersal over the substrate; however, the presence of a parabolic layer enables them to form robust, durable, and strongly ornamented tubes, often equipped with attachment structures enhancing a better anchorage to the substrate (Słowiński et al., 2024).

5.2.3. Ultrastructure and mineralogy of the Jurassic calcareous sabellids and the evolution of sabellid calcification

The tube of the calcareous Jurassic sabellids represented by *Glomerula gordialis* is built of a single layer, composed of oriented, spherulitic prismatic microstructure (Fig. 4A), corroborating previous ultrastructural investigations of calcareous sabellids (e.g., Vinn et al., 2008a).

Based on the Confocal Raman Spectroscopy and supplementary SEM-EDS analyses, the mineralogy of the Middle to Upper Jurassic tube-dwelling sabellids was determined as low-Mg calcite (Słowiński et al., 2023). The mineralogical composition of non-skeletal precipitates oscillated throughout the entire Phanerozoic with periods of calcite precipitation alternating with aragonite precipitation (Sandberg, 1983; 1985). Skeletal mineralogy of many groups of organisms (e.g., Ries, 2004; 2006; 2009; 2010; Stanley et al., 2005; Ries et al., 2006; Stolarski et al., 2007; Taylor et al., 2014) was influenced by the chemical composition of the ambient seawater during changing calcite and aragonite seas (Stanley, 2006), in most cases fitting the seawater chemistry during their origin (see Porter, 2007).

Sabellids first formed biomineralized skeletons during the Middle Permian (Sanfilippo et al., 2017), a period, that coincided with the Late Carboniferous–Early Jurassic episode of aragonitic seas (Stanley, 2006). The skeleton of the Recent calcareous sabellids represented by *Glomerula piloseta* is aragonitic (Vinn et al., 2008a), matching the contemporary seawater chemistry. In turn, during the Middle and Late Jurassic and the period of calcite seas dominance, the skeleton of *Glomerula gordialis* was of low-Mg calcite mineralogy (Słowiński et al., 2023). The origin and following shifts in the mineralogical composition of the sabellid skeleton were possibly strongly reliant upon the fluctuating ionic ratio of the seawater throughout geological time. Similarly, calcareous cirratulids had their origin in the Oligocene (Fischer et al., 1989; 2000) and corresponded to the chemical composition of seawater of that time (Taylor et al., 2010).

Sabellid worms utilize biologically controlled biomineralization (Vinn et al., 2008a) and although ions are acquired from the ambient seawater, the nucleation of biominerals and secretion of the skeleton is controlled by the physiological activity of the animal (see Neff 1971a; b; Vinn, 2021). Nevertheless, the long-term variations in the ratio of magnesium and calcium ions could have had an indirect effect on the skeleton secretion of sabellids through natural selection. Formation of skeletons that are not supported by seawater chemistry is more

difficult for calcifying organisms (e.g., Stanley et al., 2002; Ries, 2004; 2009). Being vulnerable to inconvenient conditions they are not capable of fully controlling their biomineralization, which may lead to a slower precipitation rate (e.g., Ries et al., 2006), or developing a weaker skeleton (Dixon-Anderson, 2021).

6. Conclusions

1) 24 serpulid and sabellid taxa were recognized in 11 outcrops hosting deposits of the Middle and Late Jurassic Polish Basin; two new species were described – *Filogranula spongiophila* and *Cementula radwanskae*. (Article 2)

2) Distribution and abundance of certain species are strongly dependent upon a specific kind of substrate, its nature, morphology, as well as energy of the environment, whereas the stratigraphic interval plays a secondary role. (Article 2)

3) Serpulids formed a symbiotic relationship with hydroids preserved in the process of bioclaustration evidencing *syn vivo* interaction. This phenomenon was very rare and host-selective. The internal morphology of the bioclaustrated hydroid colony was visualized using micro-computed tomography. (Article 1)

4) Investigation of 12 taxa representing two of three major serpulid clades revealed a relatively modest ultrastructural diversity comprising three types – irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP); ultrastructure types are characteristic of certain serpulid clades. (Article 4)

5) The biomineralization system of sabellids is simpler as compared to serpulids, which results in the scarcity of sabellid forms and is reflected in the paleoecology of both groups. (Articles 3 and 4)

6) Based on the Raman spectroscopy, the mineralogical composition of the Jurassic tube-dwelling sabellids was determined as low-magnesium calcite; the origin and further long-term fluctuations in the tube mineralogy of sabellids depended on the ionic ratio of seawater changing over geological time. (Article 3)

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2 (1): 1–68 (1834); 2 (2): 69–140 (1835); 2 (3): 141–224 (1837); 2 (4): i–iii + 225–312 (1840); 3 (1): 1–20 (1841); 3 (2): 21–28 (1844); 3 (3): i–iv + 29–128 (1844). Arnz and Co., Düsseldorf.

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Article 1

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Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin.

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RESEARCH ARTICLE

Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin

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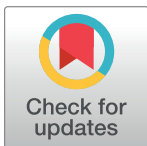
Abstract

The coexistence of sessile, tube-dwelling polychaetes (serpulids) and hydroids, has been investigated. Serpulid tubes bearing traces after hydroids are derived from different stratigraphic intervals spanning the Middle and Upper Jurassic, the rocks of which represent the diverse paleoenvironments of the Polish Basin. Although fossil colonial hydroids classified under the species *Protulophila gestroi* are a commonly occurring symbiont of these polychaetes during the Late Cretaceous and Cenozoic, they seem to be significantly less frequent during the Jurassic and limited to specific paleoenvironments. The hydroids described here are represented by traces after a thin stolonal network with elongated polyp chambers that open to the outer polychaete tube's surface with small, more or less subcircular apertures. Small chimney-like bulges around openings are an effect of the incorporation of the organism by *in vivo* embedment (bioclaustration) within the outer layers of the calcareous tube of the serpulid host. Considering the rich collection of well-preserved serpulid tubes (>3000 specimens), the frequency of bioclaustrated hydroids is very low, with an infestation percentage of only 0.6% (20 cases). It has been noticed that only specimens of the genus *Propomatoceros* from the Upper Bajocian, Lower Bathonian, Middle Bathonian, and Callovian have been found infested. However, the majority of bioclaustrated hydroids (17 cases) have been recorded in the Middle Bathonian serpulid species *Propomatoceros lumbricalis* coming from a single sampled site. Representatives of other genera are not affected, which is congruent with previous reports indicating that *Protulophila gestroi* was strongly selective in the choice of its host. A presumably commensal relationship is compared with the recent symbiosis between the hydroids of the genus *Proboscidactyla* and certain genera of sabellid polychaetes.

Introduction

Organisms colonizing other organisms are usually referred to as epibionts ([1]; see also [2]). Such organisms have been present throughout the entire Phanerozoic, colonizing a variety of available hosts (see [2] for a comprehensive review). In many instances, such epibiont-host

organism associations were symbiotic (e.g., [3–5]) with a fossil record extending as far back as the Cambrian (e.g., [5–7]).

An immense majority of epibionts bear calcareous skeletons that can easily be fossilized, leaving behind many soft-bodied colonizers unpreserved. However, some soft-bodied organisms adhering to the substrate they colonized may have been preserved due to bioimmuration or bioclaustration (see [8–18]), the processes that provide a unique glimpse of the morphology, diversity, and abundance of tiny, soft-bodied epibionts, which otherwise would have not been fossilized.

One such group of soft-bodied organisms, which are the focus of the present paper, are colonial hydroids symbiotically inhabiting serpulid polychaetes. The hydroids grew simultaneously within the outer layers of infested polychaete tubes, embedded within their skeleton due to the process known as bioclaustration ([10]; see also [11, 17, 19, 20]). Although the polychaete–hydroid association has already been noticed by J.D.C. Sowerby [21], Rovereto [22] was the first to describe it. Based on the material from the Pliocene of Italy, Rovereto [22] classified the bioclaustrated hydroids as *Protulophila gestroi*. However, despite the fact that the name was adopted for the fossil, his taxonomic interpretation was incorrect, as he inferred the traces of an organism to be a new genus and species of ctenostomatous bryozoan being adherent to the surface of a tube belonging to the serpulid species *Protula firma*. Further discussions of the affinities of *Protulophila gestroi* did not reveal the true origin of an organism, including interpretations such as the formation of molds on the surface of the tube by a serpulid itself [23] and describing it as a new species of bryozoans [24].

The first full description of the nature of the relationship as well as a detailed description of the fossil itself, which allowed to unequivocally classify the organism taxonomically, was provided by Scrutton [8]. He proved that colonial hydroids infested certain species of tube-dwelling polychaetes and concluded that the first available name for the molds left by the bioclaustrated hydroids is *Protulophila gestroi* Rovereto, 1901. Since then, serpulid–hydroid associations have been reported from sedimentary rocks of different ages, beginning from the Lower Jurassic (Pliensbachian, see [25]), Middle to Upper Jurassic [14, 26], and Cretaceous [15, 27–29]. Interestingly, in all these cases, the hydroid bioclaustrations were invariably classified as a single species–*Protulophila gestroi*. It must also be mentioned that the existence of Recent examples of *Protulophila gestroi* was mentioned for the first time by Jäger in 1993 [30], but no scientific description has been published so far. Recently, Taylor and co-workers announced that investigation of *Protulophila* infesting serpulids from modern seas is under way [31].

To date, any data concerning the serpulid–hydroid relationship come from single stratigraphic units and/or localities, which limit our understanding of the nature of this association. To fill this gap, in the present study, we decided to conduct a thorough assessment of this relationship through an inspection of rich material of serpulid tubes derived from different stratigraphic intervals of the Middle to Upper Jurassic (Bajocian-Kimmeridgian) deposits, representing diverse paleoenvironments within a single paleogeographic entity–the Polish Basin. Such an approach may allow a better picture of the persistence, abundance, and symbiotic relationship of such an association both through time and across paleoenvironments. Additionally, we traced the morphology of the hydroid symbionts and their relationship with the serpulid hosts using scanning electron microscopy and, for the first time for these fossils, micro-computed tomography methods. The phylogenetic affinity of the Jurassic hydroid symbionts was also discussed.

Materials and methods

Materials and their provenance

The fossils discussed herein were derived from eleven outcrops representing different stratigraphic intervals, spanning the Middle to Upper Jurassic, and various marine
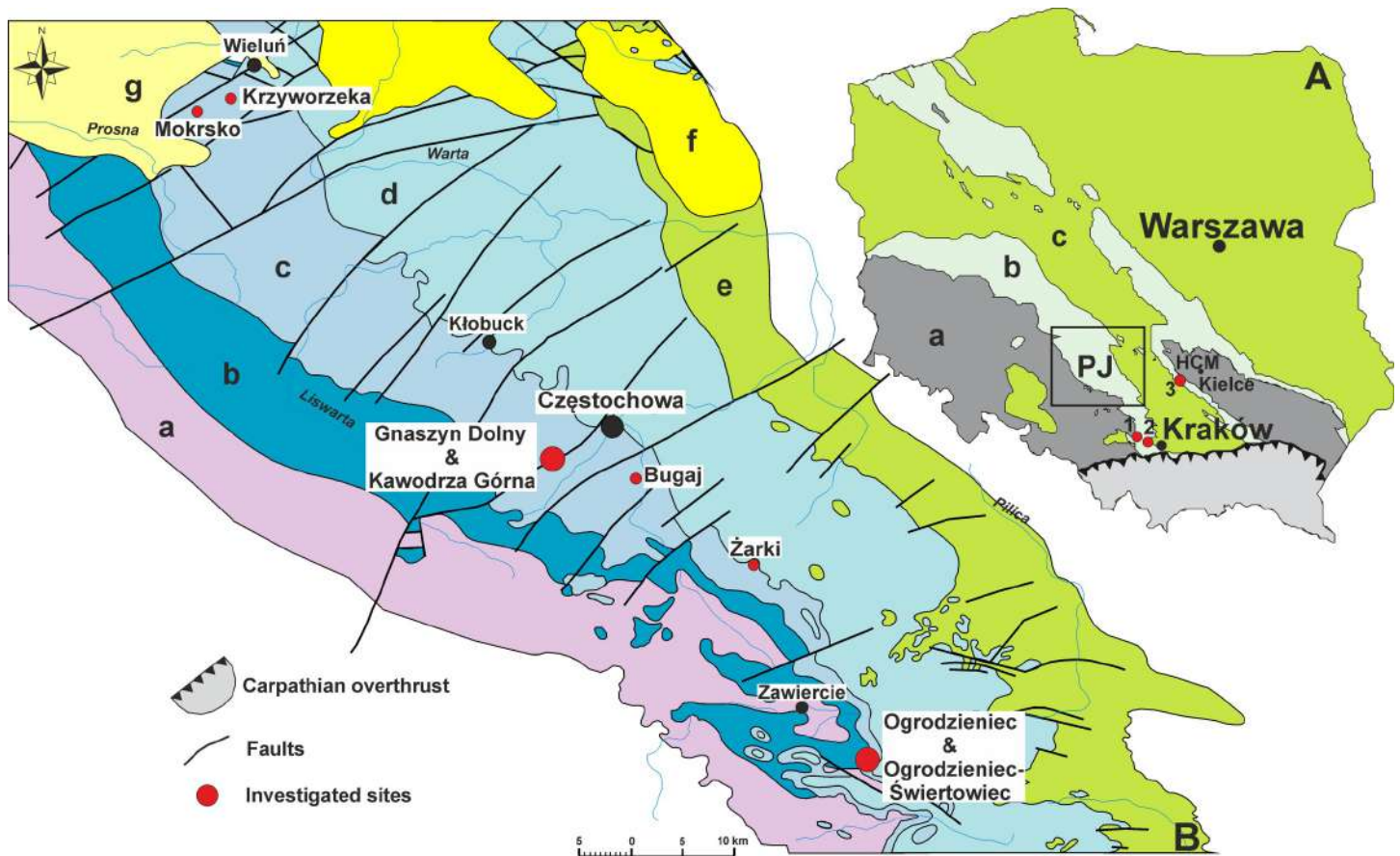
Fig 1. A. Geological sketch-map of Poland without the Cenozoic cover with three sampled localities indicated; **a**–pre-Jurassic, **b**–Jurassic, **c**–Cretaceous, HCM–Holy Cross Mountains; PJ–Polish Jura; 1 –Bolęcin; 2 –Zalas; 3 –Małogoszcz. **B**. Geological map of the Polish Jura area without Quaternary cover, with sampled localities indicated; **a**–Upper Triassic, **b**–Lower Jurassic, **c**–Middle Jurassic, **d**–Upper Jurassic, **e**–Cretaceous, **f**–Miocene, **g**–Pliocene (modified after Zatoń et al. [32]).

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paleoenvironments of the Polish Basin (Fig 1). All of the fossil material collected is stored at the Institute of Earth Sciences in Sosnowiec (abbreviated GIUS 8–3730).

Bolęcin. Bolęcin is located in the area of the Polish Jura about 6 km to the east of the town of Chrzanów (50˚06'25"N, 19˚29'25"E), between Katowice and Kraków (Fig 1). The fossils collected from this locality have been found in highly fossiliferous, sandy limestones containing abundant non-skeletal grains (such as quartz pebbles and ooids), most probably referring to the so-called "Balin Oolite." Fossils are irregularly distributed within the deposits. Polychaete tubes are attached to various fossils such as bivalves, gastropods, ammonites, and belemnites, which act as substrates for these episkeletozoans (*sensu* [33]). Using ammonite fauna [34], the Balin Oolite was dated as Upper Bathonian (Retrocostatum and Discus zones) to Lower Callovian (Herveyi, Koenigi, and Calloviense zones), with a possible base of the Middle Callovian (Jason Zone) also present (see [35]). The stratigraphic ranges of diverse ammonite genera and low thickness (less than 1 m) of reworked deposits indicate that the carbonates are condensed, as previously noted by Tarkowski et al. [36] and Mangold et al. [34]. The presence of diverse fauna, including ammonites (e.g., [34]), may indicate an open marine paleoenvironment. In total, 1,011 polychaete tubes were inspected, of which 589 were well-preserved. From now on, the term "well-preserved" refers to those specimens which have unabraded external tube portion showing any signs of bioclaustrated hydroids.

Zalas.   The material was collected in an active quarry located in the Zalas village near Krzeszowice (50˚05'06.7"N 19˚38'49.5"E) in the southern part of the Polish Jura (Fig 1). Fossils were derived from both Callovian sandy limestones and overlying Oxfordian deposits. Transgressive Middle Jurassic deposits discordantly overlie uneven Lower Permian porphyres and rhyodacites [37], forming a laccolith [38], which are the major subjects of quarry exploitation. Within the Callovian deposits, sclerozoan hosts occur within a hardground (Middle Callovian and the lower part of Upper Callovian; see [37, 39]), which originated in an open-sea, deep shelf environment [39, 40]. Diverse organisms bearing hard exoskeletons play a role as substrates for diverse and abundant sclerobionts (see [40]). A substantial majority of serpulids have been found fixed to large bivalves *Ctenostreon proboscideum* (J.D.C. Sowerby); however, some of them have also been found encrusting belemnites, ammonites (*Macrocephalites*), and nautiloids. Lower Oxfordian serpulids have been found attached only to sponges that form sponge bioherms (e.g., [41]). In total, 1,684 specimens (976 well-preserved) from both Callovian and Oxfordian were inspected.

Małogoszcz.   Fossils from Małogoszcz are derived from an active quarry located about 1 km to the north of Małogoszcz town center (50˚49'21.6"N 20˚15'39.2"E) and about 30 km to the west of the city of Kielce (Fig 1). It is situated in the southwestern part of the Mesozoic Border of the Holy Cross Mountains [42–44]. In this locality, all the collected polychaete tubes encrust bivalve shells, the majority of which belong to the genus *Actinostreon*. The fossil-rich, Lower Kimmeridgian (Hypselocyclum and Divisum zones, see [43–45]) deposits are referred to as the Skorków Lumachelle [43]. The shell-bearing deposits are an effect of storm episodes in a relatively shallow marine environment [43]. In total, 157 serpulid polychaetes (104 well-preserved) encrusting oyster bivalves were examined.

Ogrodzieniec.   Sediments from Ogrodzieniec, together with the following localities, occur as epicontinental deposits forming monotonous sequences of dark mudstones and siltstones [46–50]. These deposits are referred to as the Ore-bearing Częstochowa Clay Formation (see [46, 51, 52]). These siliciclastics are intercalated with numerous levels of isolated and horizon-forming, carbonate, and fossil-rich concretions (e.g., [51, 53]). This and the following locality are confined to the southern sedimentary region of the Polish Jura, which is considered to represent the shallow, marginal part of the Polish Basin [49, 54]. The deposits originating in the southern sedimentary region are more variable with respect to facies, are thinner, and bear common hiatuses [54], which are also evidenced by widespread exhumed carbonate concretions (hiatus concretions) marking distinct breaks in sediment supply and/or sea-floor erosion (see [26]). In Ogrodzieniec, the fossils were cemented to the hiatus concretions collected in a small clay-pit (50˚27'31.1"N 19˚30'13.1"E) with an exposure of siltstones of ca. 8 m thick. The concretion-bearing deposits represent the Upper Bathonian, ranging up to its topmost Discus Zone, as evidenced from dinocysts [55]. In total, 337 serpulid fossils (122 well-preserved) were inspected.

Ogrodzieniec-Świertowiec.   The specimens collected were derived from a small outcrop located approximately 1 km south of the town center of Ogrodzieniec (50˚26'23.8"N 19˚31'13.0"E). Condensed, sandy, and carbonate sediments underlying the dark mudstones of the ore-bearing Częstochowa Clay Formation are exposed (e.g., [48, 56]). Polychaete tubes form dense aggregations on the surface of large oncoids. Due to the occurrence of dinoflagellate cysts (*Valansiella ovula* and *Ctenidodinium* cf. *combazii*, Przemysław Gedl, written communication, March 2019), foraminifers *Paleomilliolina czestochowiensis* (Zofia Dubicka, written communication, March 2019) found within the oncoid cortices [57], and previously noted ammonites *Parkinsonia* spp. and *Parkinsonia* (*Oraniceras*) *gyrumbilica* (see [48]), the condensed oncoid-bearing interval is confined to the Upper Bajocian–Lower Bathonian (up to the Macrescens Subzone of the Zigzag Zone). Considering the cyanobacterial genesis of the

oncoids [56, 57], serpulid polychaete worms inhabited photic conditions, slightly beneath the fair weather wave base. In total, 1,103 specimens (621 well-preserved) were examined.

Żarki.   Deposits in Żarki, together with all the following localities, are confined to the northern sedimentary region of the Polish Jura, which is characterized by thicker and more complete sequences of ore-bearing clays [54]. Sediments within these localities are interpreted to have been deposited in calm, epicontinental paleoenvironments with generally well-oxygenated bottom waters (e.g., [49, 58–60]). However, some ichnofabrics, accumulations of shell detritus, and erosional surfaces indicate episodic storm events [61]. All of the fossils investigated herein are attached to carbonate hiatus concretions. In this locality (an active brick-pit, 50˚37'09.0"N 19˚22'02.7"E), concretions were partly collected *in situ* from the bottom part of a 15 m thick section [62]. The age of the concretion-bearing horizon is Upper Bathonian (Hodsoni Zone, see [47]). In total, 58 polychaete tubes have been investigated, of which 23 are well-preserved.

Bugaj.   In this locality, serpulid polychaetes inhabited Middle Bathonian (likely Morrisi Zone) carbonate hiatus concretions (see [26]). Currently, the excavation in Bugaj (50˚45'51.5"N 19˚10'05.9"E) is abandoned, and the clay-pit filled by dumped waste material is unavailable for field research. Therefore, the collection of fossils from Bugaj is scientifically valuable. In total, 553 fossils (170 well-preserved) were collected and inspected from this locality.

Gnaszyn Dolny.   The fossils are derived from the Middle Bathonian (Morrisi Zone) mudstones exposed in the lower part of the "Gnaszyn" brick-pit [26] (50˚48'12.6"N 19˚02'26.8"E). The serpulid tubes are preserved on bivalve shells (mainly oysters), where they form densely packed aggregations. Clay sediments containing encrusted shells were deposited in a deeper marine paleoenvironment, below the storm wave base (e.g., [26, 63, 64]. In this locality, 777 polychaete tubes have been found, of which 374 are well-preserved.

Kawodrza Górna.   The specimens collected in Kawodrza Górna ("Sowa" brick-pit, 50˚ 47'05.1"N 19˚02'35.4"E) are from the Lower Bathonian deposits (Zigzag Zone, e.g., [46, 53]), which represent similar siliciclastic facies and paleoenvironment as those present in neighboring Gnaszyn Dolny (e.g., [46, 64]). All of the fossils found encrust oyster shells. In total, 90 polychaete tubes were collected (57 well-preserved).

Mokrsko.   Polychaete tubes from this locality commonly encrust carbonate hiatus concretions occurring in the "Mokrsko" brick-pit (see [26], 51˚10'00.4"N 18˚26'05.7"E). The concretions form a continuous horizon; however, some of them are irregularly distributed within glaciotectonically deformed clay sediments [26]. Due to the presence of the ammonites *Parkinsonia* [32], the age of sediments is Upper Bajocian (Parkinsoni Zone). The deposits in Mokrsko, as in the case of the above-mentioned deposits, represent a paleoenvironment probably located below the storm wave base [26]. In total, 358 specimens (111 well-preserved) were inspected.

Krzyworzeka.   At this locality (51˚10'06.9"N 18˚31'07.1"E), all the collected polychaete fossils encrust hiatus concretions; however, the majority of them are strongly abraded. Krzyworzeka is the northernmost locality in the area investigated and the sediments thought to have been deposited in a calm environment related to an outer shelf (e.g., [26, 65]), located below the storm wave base. However, due to the overturning of the concretions, episodic storms are not excluded (see [26]). Dinoflagellate cyst dating indicates that deposits from Krzyworzeka range up to the Upper Bathonian Discus Zone [66]. In total, 920 specimens (199 well-preserved) were inspected.

Methods

All the specimens derived from the localities listed above were carefully inspected under a binocular microscope, paying special attention to the potential occurrence of bioclaustrations

after hydroids. Although all serpulid tubes in each locality were counted, we separately counted unabraded, externally well-preserved tubes, and poorly-preserved specimens, having abraded or strongly exfoliated tubes showing no signs of bioclaustration. Those tubes bearing hydroid symbionts were determined to at least the generic level.

Polychaete tubes bearing hydroid traces were cleaned using an ultrasonic cleaner, and selected specimens were examined under an environmental scanning electron microscope (ESEM) Philips XL30 at the Institute of Earth Sciences in Sosnowiec. The fossils were scanned in an uncoated state in back-scattered electron (BSE) imaging mode.

Four serpulid tubes (two from Gnaszyn Dolny, one from Kawodrza Górna, and one from Mokrsko) with the best-preserved and visible bioclaustration traces were selected for further examination using computed microtomography (micro-CT). Virtual sections were made in the X-ray Microtomography Laboratory at the Faculty of Computer Science and Materials Science, University of Silesia in Katowice, Chorzów, Poland, using the GE Phoenix v|tome|x micro-CT equipment with scanning voltage ranging 140–180 kV, current intensity 50–90 μA, and scanning time of 25 to 35 min depending on the sample. The collected images were processed using Volume Graphics® VGSTUDIO Max software and Volume Graphics® myVGL Viewer App and Fiji [67]. Based on the micro-CT scans, a volumetric rendering and movie were produced using Drishti [68].

Results

Morphology of the bioclaustrated hydroids

The bioclaustrated traces after hydroids referred to as *Protulophila gestroi* are represented by systems of stolons and polyp chambers (reflecting casts of zooids) preserved by the skeletal overgrowth of the host serpulid polychaetes. Thus, the structures preserved within the serpulids investigated here are in agreement with other hydroid bioclaustrations reported so far.

The external appearance of the hydroids dwelling within the serpulid's tube is shown by the presence of small, more or less subcircular apertures superficially resembling borings (see [10]), and chimney-like bosses scattered both regularly and irregularly over the serpulid tube's exterior (Fig 2A–2E). With a few exceptions, the apertures are declivous toward the anterior of the tube with a proximal lip slightly flattened, and distal lip curved and uplifted, often forming a small hood, or a bigger, irregular lump (Fig 2). In some cases, the apertures are gently bent in different directions, which might reflect the adjustment of zooids to the ontogenic skeletal growth of the tube as well as to its bulges and curvatures (Fig 2B and 2D). Due to the increasing stolonal network depth of burial and the rugosity of a tube, bosses become bigger, more robust and solid, and occasionally overhang orifices (Fig 2B and 2F). A large majority of these small polyp openings, exhibiting the external appearance of the particular zooids, is located in the anterior part of the dwelling tube (Fig 2A–2D). None of the specimens of *Protulophila gestroi* have been found bioclaustrated in the tube's posterior (however, one specimen is represented by a fragmented tube with indistinct characters providing recognition of the part of the tube). Some hydroid colonies encircle nearly a whole serpulid tube, occupying the surface from the keel on the top to the same base (Fig 2B and 2C). Both the shape and size of the apertures are variable, even within the same specimen. The orifice size ranges from 0.15 to 0.25 mm in diameter (Fig 3E and 3F), with bosses up to even 1 mm across.

Based on the micro-CT scans and resulting visualization (Fig 4), an internal appearance of this association shows a network of branching stolonal tubes embedded in the tube wall, joining together in the hydroid's chambers (Fig 4B, 4C, 4E and 4F). These elongated, cylinder-shaped internal cavities after particular polyps, well-visible in the visualization (Fig 4), are buried concurrently to the surface of a tube and are bent outward, which is revealed on the
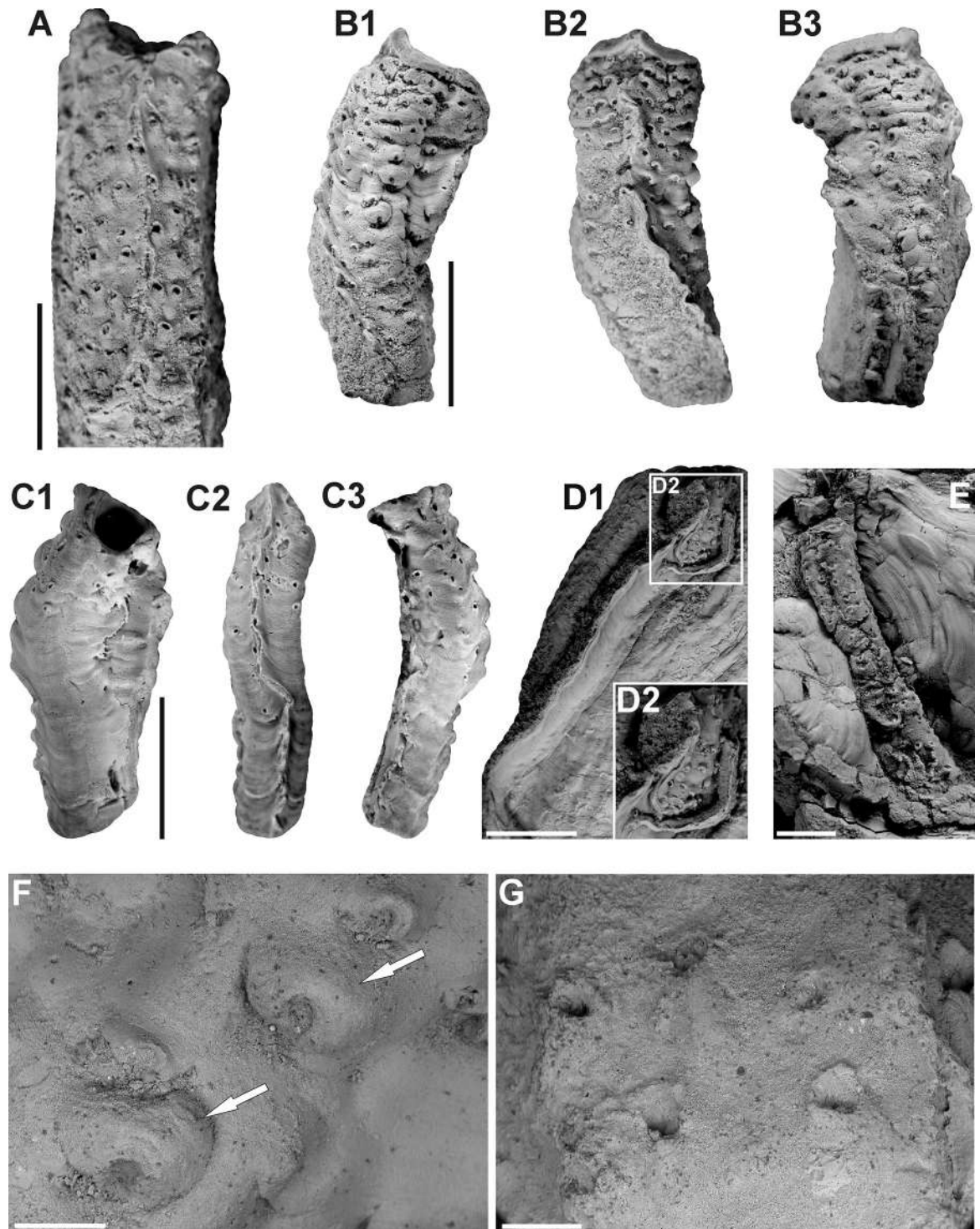
Fig 2. *Protulophila gestroi* Rovereto bioclaustrated by two species of the serpulid *Propomatoceros* from the Polish Jura. A. A strongly infested *Propomatoceros* sp. from the Upper Bajocian of Mokrsko, exhibiting a regular arrangement of the colony. External appearance shows apertures slightly bent toward the anterior of the tube; elongation of polyp chambers to the serpulid's growth direction is visible, GIUS 8-3730/1. **B.** Strongly infested *Propomatoceros lumbricalis* (von Schlotheim) from the Middle Bathonian of Gnaszyn Dolny. Dense arrangement of the hydroid colony shows different apertural morphologies within one specimen. Three views (two lateral and one dorsal) show hydroid colony embedment around nearly entire tube, GIUS 8-3730/2. **C.** Infested *Propomatoceros lumbricalis* from the Lower Bathonian of Kawodrza Górna, showing an irregular colony pattern with small polyp openings scattered over the tube. Aperture lips are slightly flattened, forming only indistinct hoods. A hydroid colony encircled the whole tube from the base to the keel

(as shown in three views of the tube), GIUS 8-3730/3. **D.** A hydroid colony located in the anterior part of the tube of *Propomatoceros lumbricalis* from the Middle Bathonian of Gnaszyn Dolny. Single apertures are bent backward, GIUS 8-3730/4. **E.** Moderately infested tube from the Middle Bathonian of Gnaszyn Dolny with a relatively regular colony pattern, GIUS 8-3730/5. **F-G.** ESEM back-scattered images presenting detailed morphology of hydroid apertures. In **F**, two robust bosses overhanging the apertures (indicated by white arrows) and a few smaller hoods are shown, GIUS 8-3730/2. **G** indicates delicate lumps, GIUS 8-3730/1. Scale bars: 5 mm **(A-E)**, 0.5 mm **(F-G)**.

external part of the tubes by small orifices (Fig 4). Polyp chambers are elongated in the direction of the skeletal growth of the worm (Fig 2A, 2E and 2G). The mean chamber size is 0.84 mm long and 0.31 mm wide, while stolons have a diameter of 50 μm (Fig 3A–3D). Depending on the depth of embedment, the stolonal network is visible in some specimens, being embedded relatively shallowly in the external part of a tube (Figs 2C and 3A). The irregular arrangement of the colony in some cases might be a result of the tube's external morphology or inconstant skeletal growth. However, despite the differences in particular hydroid's stolonal network depth within the serpulid tube, it tends to be incorporated at an approximately constant depth in the tube's interior within the same specimen of the host serpulid. The depth of hydroid network embedment varies from 0.19 to 0.63 mm, depending on the specimen (Fig 3A).

Frequency and occurrence of bioclaustrated hydroids

Following an examination of 7,048 specimens of tube-dwelling polychaetes, of which 3,346 are well-preserved, biocluastration traces after the hydroids *Protulophila gestroi* have been noted in only 20 specimens of serpulid tubes (Table 1). Thus, in the present case, the overall percentage of hydroid infestation was notably low, with a rate of only 0.28% among all the specimens of polychaete tubes collected. Although the percentage of infestation among the well-preserved fossils is more than twice as high, at 0.6%, this value is very low. However, due to the significant abrasion of the tubes acting as a substrate for *Protulophila gestroi*, potentially embedded hydroids, if they ever existed, would not have been preserved in the fossil record. Thus, it is possible that the real percentage of hydroid infestation might have been higher than presented herein.

Serpulid tubes played the role of a substrate for colonial hydroids, potentially providing both insight into the paleoecological issues and information about the relationship. Of all the polychaete tube fossils examined, only specimens assigned to the genus *Propomatoceros* Ware have been found to be infested by *Protulophila gestroi*, the data on which is presented in Table 2. The tubes of *Propomatoceros* investigated here possibly represent two species: 1) slender, gracile forms with distinctive longitudinal keels on the top of the Lower Bathonian of Kawodrza Górna and Middle Bathonian of Gnaszyn Dolny, referred to as the species *Propomatoceros lumbricalis* (von Schlotheim) on the basis of similarity to the Middle Jurassic species described by Ippolitov [69], and 2) larger, robust tubes from the Upper Bajocian of Mokrsko and Callovian of Zalas, referred to as the species *Propomatoceros* sp. The tubes may be slightly curved, increasing in diameter toward the anterior part (faster in *Propomatoceros lumbricalis*), with a subtriangular cross-section (more distinct in *Propomatoceros lumbricalis*). The external surface is relatively smooth and sometimes uneven with very small bulges. Attachment structures are usually well-developed and visible. The arrangement of the hydroid colonies seems to be more regular within the species *Propomatoceros* sp.

The other serpulid taxa present on the Upper Bajocian through Kimmeridgian substrates investigated here (see [26, 56, 70, 71]), such as *Nogrobs*, *Cementula*, *Filogranula*, *Spiraserpula*, *Metavermillia*, *Mucroserpula*, *Placostegus*, and the most abundant species *Glomerula gordialis*, lack any traces after bioclaustrated hydroids. Moreover, 17 out of 20 specimens of *Protulophila*

Fig 3. Internal appearance of serpulid-hydroid association shown on micro-CT scans (**A-D**) and ESEM back-scattered images (**E-F**). **A.** Scan of the serpulid tube from the Lower Bathonian of Kawodrza Górna (the lateral view of the tube); black arrows show two polyp chambers with the depth of embedment visible, GIUS 8-3730/3. **B.** Scan of the tube from the Middle Bathonian of Gnaszyn Dolny; black arrow indicates the longitudinal section of the stolonal tube, GIUS 8-3730/2. **C-D.** Cross-section scans of the infested serpulid tube from the Lower Bathonian of Kawodrza Górna, GIUS 8-3730/3. In **C,** the arrows show the stolonal tubes in cross-section (black arrows), and longitudinal (slightly inclined) section (white arrow). In **D,** cross-sections of polyp chambers are visible, as well as the branching stolonal tubes connected to them. **E-F.** Single hydroid apertures. **E.** Specimen from the Lower Bathonian of Kawodrza Górna, GIUS 8-3730/3. **F.** Specimen from the Upper Bajocian of Mokrsko, GIUS 8-3730/1. Scale bars: 0.25 mm (**A-C**), 0.35 mm (**D**), 0.2 mm (**E**), 0.1 mm (**F**).

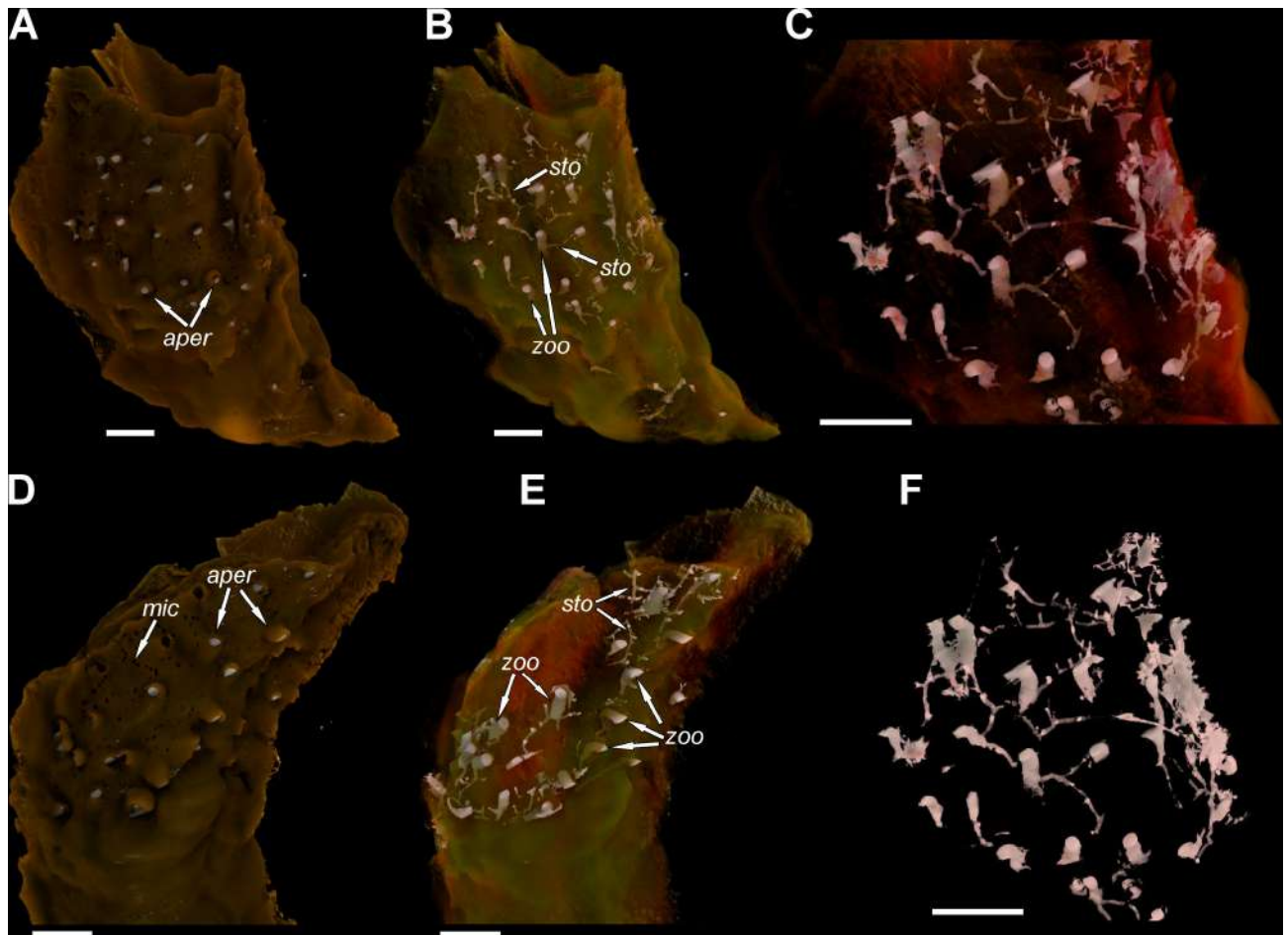https://doi.org/10.1371/journal.pone.0242924.g003

Fig 4. Visualization of the bioclaustrated hydroid colony *Protulophila gestroi* by the host serpulid *Propomatoceros lumbricalis* from the Middle Bathonian of Gnaszyn Dolny, GIUS 8-3730/8. A. External left side of the tube showing bioclaustrated apertures after hydroids (*aper*). **B-C**. The same side showing the morphology and internal arrangement of hydroid zooids (*zoo*) and stolons (*sto*), magnified in **C**. **D**. Right side of the tube showing bioclaustrated apertures after hydroids (*aper*) and numerous microborings (*mic*). **E**. The same side showing the morphology and internal arrangement of hydroid zooids (*zoo*) and stolons (*sto*). **F**. Isolated system of stolons and hydroid zooids embedded within the tube showed in **C**. Serpulid aperture is on the top. Scale bars: 1 mm (**A-F**).

gestroi have been found only on the tubes coming from a single locality and stratigraphic interval (Gnaszyn Dolny, Middle Bathonian, Morrisi Zone, Table 2).

Discussion

Morphology and phylogenetic affinity of *Protulophila gestroi*

The overall pattern of the colonial hydroids clearly indicates that stolonal network and polyp chambers were incorporated *in vivo* within the external parts of the host's tube during its skeletal growth and, as previously recognized by Scrutton [8], cannot be considered as a boring activity. Deflected apertural lips (marked by the differential rate of skeletal secretion of the host) and the fact that none of the polyp orifices is fully overgrown by the serpulid (which might have happened after the death of the hydroid) indicate that both the colonizer and the host must have been alive during interaction. The general arrangement of stoloniferous hydroids is more or less convergent with all the reported cases from different stratigraphic intervals (e.g., [8, 14, 15, 18, 25–29]). Slight differences in morphological details may only

Table 1. Data on stratigraphy, provenance, encrusted substrate type, number of all and well-preserved serpulid tubes, and number of tubes infested by hydroids.

Stratigraphic interval →	Upper Bajocian	Lower Bathonian	Middle Bathonian	Middle Bathonian	Upper Bathonian	Upper Bathonian	Upper Bathonian	Bajocian-Bathonian	Upper Bathonian-Lower Callovian	Callovian	Oxfordian	Lower Kimeridgian	
Kind of substrate / Locality →	Mokrsko	Kawodrza Górna	Gnaszyn Dolny	Bugaj	Ogrodzieniec	Krzyworzeka	Żarki	Ogrodzieniec-Świertowiec	Bolęcin	Zalas	Zalas	Małogoszcz	
Bivalves		57 / 33	220 / 262						283 / 255	667 / 413		104 / 53	
Belemnites			154 / 141						22 / 9	15 / 11			
Hiatus concretions	111 / 247			170 / 383	122 / 215	199 / 721	23 / 35						
Oncoids								621 / 482					
Sponges											249 / 261		
Ammonites									33 / 16	8 / 12			
Nautiloids										37 / 11			
Gastropods									251 / 142				
No. specimens	358	90	777	553	337	920	58	1,103	1,011	1,174	510	157	**7,048**
Well-preserved specimens	111	57	374	170	122	199	23	621	589	727	249	104	**3,346**
No. hydroids	1	1	17	0	0	0	0	0	0	1	0	0	**20**

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Table 2. Data on the occurrence of bioclaustrated hydroids on the background of the investigated *Propomatoceros* tubes.

	Mokrsko	Kawodrza Górna	Gnaszyn Dolny	Zalas
	(Upper Bajocian)	(Lower Bathonian)	(Middle Bathonian)	(Callovian)
Well-preserved specimens	9	16	187	52
Poorly preserved specimens	15	5	74	36
No. hydroids	**1**	**1**	**17**	**1**
% infestation of well-preserved specimens	11,11%	6,25%	9,09%	1,92%

imply different physiological and/or paleoecological conditions as well as supposedly interspecific variations (see below).

Although the mode of origin of the fossils has already been well recognized by Scrutton [8], with the corroboration of all subsequent reports, the close phylogenetic relationships of *Protulophila gestroi* are still uncertain. In attempts to link *Protulophila gestroi* with contemporary species of hydroids, it is generally affiliated with the living genus *Proboscidactyla* Brandt [72]; however, apart from Scrutton [8], who provided a detailed description of its possible affinity, little attention has been paid to this problem. *Proboscidactyla* is an obligatory inhabitant of sabellid polychaetes (e.g., [73, 74]). This modern hydroid captures nutrients from polychaete-propelled feeding currents and directly from a worm's radiole [73, 75]. Although this symbiotic relationship is well recognized and has been described several times (e.g., [73, 74, 76]), more attention has been paid to the life cycle and ecology of the medusa form of *Proboscidactyla* (e.g., [77–80]) than to the symbiotic association itself. The comparison of Scrutton [8] seems to be appropriate in terms of lifestyle; however, the overall arrangement of the colony differs strikingly from the colonial pattern of *Protulophila gestroi*. It might be putatively explained as evolutionary changes, from a simple, relatively regular pattern of *Protulophila* to more complex, anastomosing stolons and polyps of *Proboscidactyla*. Moreover, due to taphonomic processes, the morphology of the stolonal network and tentacles of the living organism cannot be directly compared to the fossil preserved solely as an embedded cast. Scrutton [8] also mentioned *Tubularia* as an example of hydroids with a colony growth pattern similar to that observed in *Protulophila gestroi*. However, except this feature, the ecology of *Tubularia* [81] in no way resembles that of *Protulophila gestroi*.

Reports on the arrangement of *Protulophila gestroi* colonies, with the majority of them located in the anterior parts of polychaetes' tubes (e.g., [8, 15, 27]; the present study) is convergent with the manner of *Proboscidactyla* colony [73, 75], suggesting a similar lifestyle. Only Zágoršek et al. [29] reported Cretaceous *Protulophila gestroi* as being located in the middle part of the serpulid's tube, which was interpreted as a growth ceasement before the serpulid's death [29]. Located close to the tube's rim, hydroids could have captured food particles from the feeding currents generated by the worm or directly from the brachial crown. The direction of hydranths' growth (hence the resulting hoods and apertural shape as evidenced in the fossils described here, see Fig 2A–2C and 2F) toward the proximal parts of the tube may also express an attempt to be located closer to the "feathery" radiole of the polychaete and its propelled feeding currents bearing nutrients (Fig 5). However, single apertures have also been found to be bent backward–some hydranths' growth direction might have been influenced by external currents as well. The second important advantage gained by these hydroids was the protection provided by a hard, mineralized tube of serpulid, which probably became the only profit during astogeny, as the older hydranths gradually receded from the polychaete's radiole and thus were excluded from the benefits of the host's feeding currents. Such older hydranths could
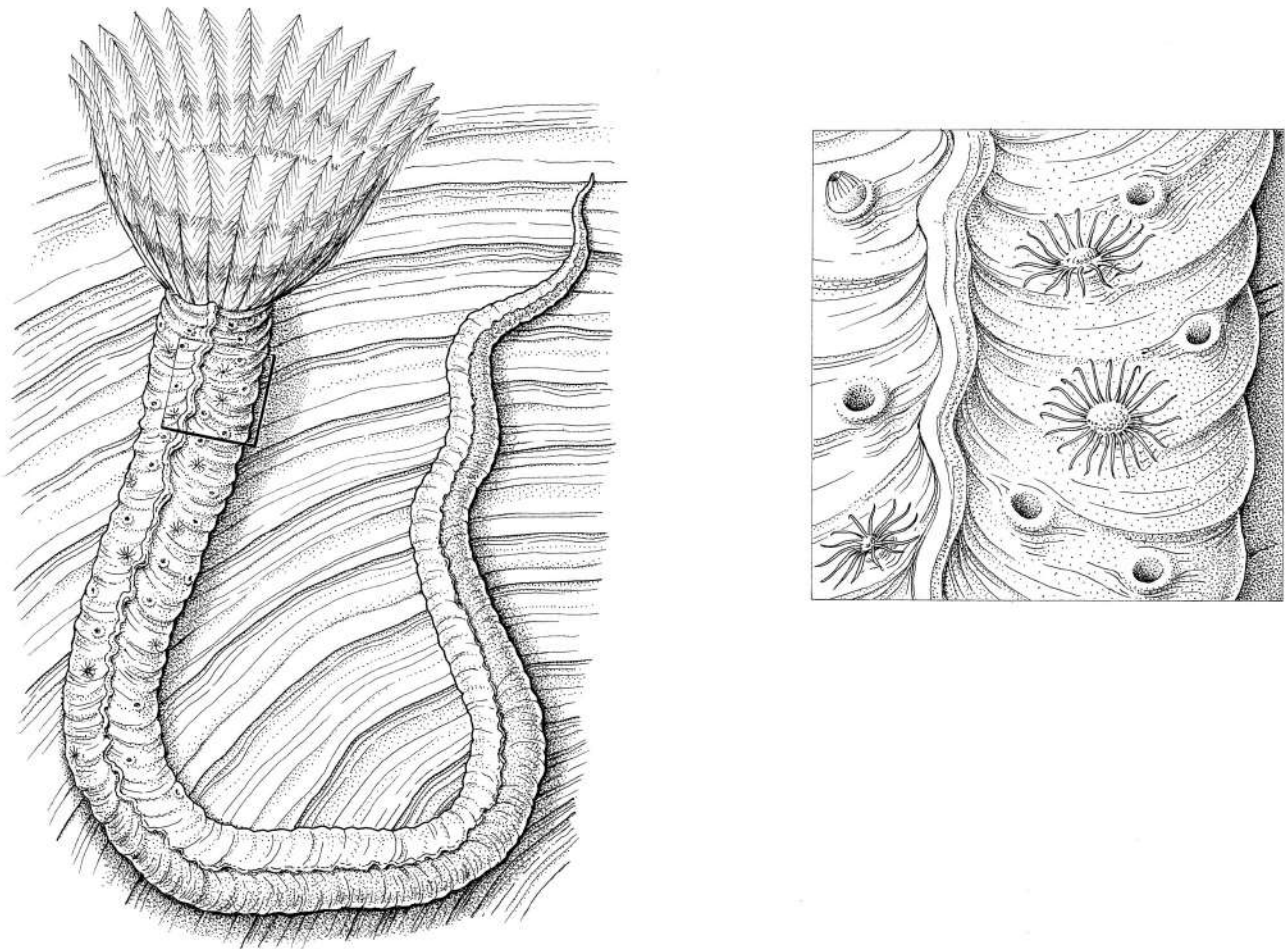
Fig 5. Artistic reconstruction of a Middle Jurassic serpulid *Propomatoceros lumbricalis syn vivo* infested by hydroids *Protulophila gestroi*. It is hypothesized that the everted polyps in older part of the serpulid tube may have relied on the food particles delivered by external currents. An inset shows some everted polyps from the host serpulid's tube (drawn by Bogusław Waksmundzki).

have been active, anyway, gathering the food delivering by external currents (Fig 5), which is evidenced in the apertures bent backward, a feature which was mentioned above.

Although we cannot phylogenetically link exclusively modern *Proboscidactyla* with the fossil hydroid with full confidence, all of the data collected hitherto on both symbionts seem to be sufficient to provide a reliable comparison, at least in the means of their lifestyles. The possible affinity is strengthened by the bilateral symmetry of apertures of Jurassic hydroids, as suggested by Baliński et al. [82]. However, the phylogenetic affinity of modern *Protulophila* is still under study [31] and, therefore, nothing more can be added here at the moment.

Morphological disparities between specimens of both the external and internal appearance of colonial hydroids are also presumably a reflection of different ecological issues, such as the host's calcification rate, which directly reflects the external appearance of a hydroid colony. Individual zooids might have adjusted to the skeletal growth of the tube, varying on the calcification activity of the serpulid (see Scrutton's experiment [8]). Polyps most likely changed their growth orientation to avoid a complete embedment due to calcium carbonate tube

precipitation (for the serpulid skeletal formation, see e.g., [83, 84]). Changes in skeletal activity may also be reflected in the depth of burial of the stolonal network (see [8]) and density of the colony. Some morphological modifications potentially may also correspond to the functional specialization of single zooids. According to modern *Proboscidactyla* [73], ancient hydroids might have also possessed different kinds of individuals playing various roles in a colony, such as gastrozooids, gonozooids, and dactylozooids.

The overall appearance of the fossils studied is relatively similar to all previous reports. Disparities are slight: from elongated orifices with broad sinuses and flattened lips (rare in the present study, see [8], Pl. 39, Figs 1–8; [27, 29]), through some intermediate forms exhibiting delicate hoods (Fig 2A, 2C, 2E and 2G; see also e.g., [8], Pl. 39, Fig 11, Pl. 41, Fig 9), to circular, with robust, chimney-like bosses occasionally overhanging apertures (Fig 2B and 2F; see also e.g., [8], Pl. 39, Figs 13–14; [15], Fig 4A–4D). The size of the polyp opening and density of the colony is variable, as well as the total number of apertures and different tube area infested– either encircling the tube from the keel to its flanges or being scattered more irregularly. The presence of morphological disparities within all the stratigraphic intervals suggests that morphology itself is not particularly useful in taxonomic classification, as it presumably represents differences in the calcifying activity of polychaetes and other ecological factors. As not all *Protulophila gestroi* bioclaustrations reported so far are as well-preserved as those present in some exfoliated serpulid tubes illustrated by Zágoršek et al. [29], the best solution for proper comparison of different colonies, is a micro-CT scanning of various specimens. Further visualization, as made for the present paper, may be helpful in better recognition of key features which then could be used for taxonomic differentiation of particular colonies.

Selection of the host by hydroids

Proboscidactyla is distinctly selective in the choice of the host, often restricted to one or very few species of polychaetes [73, 75]. This may at least partially explain why hydroids (all assigned to *Protulophila gestroi*) spanning from the Pliensbachian [25] to the Pliocene [8, 85], with possible modern representatives [31], have often been described to be selective in their choice of the host, predominantly infesting very few, or even one serpulid species within a given stratigraphic unit and geographic area. Scrutton [8] conducted a comprehensive review of the previously reported Jurassic, Cretaceous, and Cenozoic serpulids from Europe and the Middle East acting as hosts for symbiotic hydroids. All the Jurassic (Bajocian-Oxfordian) hydroids infested different species of his genus *Serpula*, some of which may belong to the genus *Propomatoceros*. Radwańska [14] found only one tube of *Ditrupula* from the Oxfordian of central Poland bearing the hydroids *Protulophila gestroi*. Cretaceous hydroids infested *Rotularia*, *Parsimonia*, *Glomerula* (the only ancient sabellid worm found to be infested), while Cenozoic hydroids were restricted to *Sclerostyla* and *Protula*. Jäger [86] found over 50% of Cretaceous (Coniacian to Upper Maastrichtian) *Martina turbinella* (*Laqueoserpula*?) tubes from northern Germany infested by *Protulophila gestroi*, while other species were clearly more rarely infested. In Poland, Radwańska [27] described hydroids associated with three polychaete species from the Campanian (*Proliserpula ampullacea*, *Pentaditrupa subtorquata*, *Sclerostyla macropus*) and only one from Maastrichtian (*Ditrupula quadrisulcata*). Niebuhr and Wilmsen [15] reported hydroid-bearing serpulids exclusively represented by the genus *Rotulispira* from the Middle Cenomanian of northern Germany. Kamali Sarvestani et al. [18] also reported infested *Rotulispira* serpulids from the Lower-Middle Cenomanian of Iran. All the current data from the Middle and Upper Jurassic of Poland presented here clearly show that each encountered *Protulophila gestroi* colony is associated with a single genus *Propomatoceros*, of which most often infested (18 cases) is the species *Propomatoceros lumbricalis*. Interestingly,

Ippolitov [69] also mentioned that the latter serpulid species was most often colonized by *Protulophila gestroi* in the Middle Jurassic (Callovian) of Russia.

It seems less likely that a single (as stated here) species of hydroid, generally described as a selective in its choice of the host, had colonized many diverse species of polychaete worms through such a long geologic time (ca. 190 Ma) in different locations around the world. Comparing this with *Proboscidactyla*, where a variety of species are found fixed to different sabellids [73], it seems to be even more hesitant. The general pattern of *Protulophila gestroi* shows only slight morphological disparities (as described above) among all, very extensive fossil records, and none specific characteristics of fossils seem to correspond with any specific stratigraphic interval. Here appears a dilemma: despite the high probability of the existence of more than one species within all specimens assigned to *Protulophila gestroi*, we are not able to distinguish potentially separate species for taphonomic reasons and the resulting scarce, insufficient data of indistinct modifications of these fossils, regardless of the geological time. Thus, the putative interspecific variation of *Protulophila gestroi* is very difficult, or even impossible, to assess objectively based on the external morphology alone.

The settlement preferences of hydroids throughout the Mesozoic and Cenozoic surely indicate some favorable conditions for the settler. A possible factor strongly influencing larval recruitment and subsequent bioclaustration is a conducive chemical composition. The settling of a juvenile form and its subsequent development may have also been enhanced by physiological and behavioral factors (see [87, 88]), some of which may be unobtainable from the fossil record. Allegedly, the selectivity of hydroid could even concern particular specimens, for example, due to a particular characteristic of the potential host providing a stable substrate to anchor. Some hydroid larvae settled on small, slender tubes representing juvenile forms of serpulids, which indicate that bioclaustration took place in the early ontogenetic stages of the worm. Another putative explanation is a random acquisition of the host, which might have resulted in the recruitment of only those larvae where "the good" choices have been made, whereas most of them, in all likelihood, never develop. The substantiation of such a mechanism is that the capability of free-living larvae to control their movement is very limited (see [88]). Recent bioclaustrated symbionts also show host preferences ([20, 89, 90]; however, see [91]), and some of them are completely dependent on the host [92].

Possible interpretations of hydroid-serpulid symbiosis involve mutualism, commensalism, and parasitism. Due to the large host's selectivity of *Protulophila gestroi* as well as a lack of evidence for serpulid deriving benefits from this interaction (except the supposed protection provided by the hydroids' nematocysts), commensalism appears to be the most plausible kind of relationship. Furthermore, this type of interaction demonstrates a strong host preference leading to some obligate host-colonizer cohabitants [20], which might at least partially explain the selectivity of the hydroids.

Both mutualism and parasitism between *Protulophila gestroi* and *Propomatoceros* seem to be unlikely. In the first case, as already mentioned above, we don't have any evidence that *Protulophila* possessed nematocysts which could have protected the serpulid host. Additionally, the percentage of infestation is too low to consider mutualism as a confident type of interaction–hydroids probably have not been notably advantageous for serpulids. In the second case, although the assumption that the incorporation of hydroids bears energy expenditure for serpulids may be reasonable, nothing indicates that the bioclaustrated hydroids might have been parasites. In both cases, there are no disparities between the infested and non-infested serpulids of the genus *Propomatoceros* (and other genera), resulting either in the exhibition of particular patterns by serpulids, which might have provided any successful ecological solutions (mutualism), or in malformations of the polychaetes' tubes and conceivably smaller size and/ or slower skeletal growth of the host due to the harmful activity of the hydroids. Moreover,

symbiotic relations can range (shifting during ontogeny) from mutualistic to parasitic and *vice versa* (e.g., [93]), which makes this assessment even more difficult. Even if the explanation of hydroid cnidocytes' protective contribution (whichever way possible) is true, in all likelihood, it did not play any significant role. A fully confident determination of the relationship between mutualistic, commensal, and parasitic is not easy in the fossil record. In the present case, however, a commensal relationship, even though it is still difficult to prove in the fossil record (see [94]), is the most plausible and acceptable on the grounds of the available evidence presented above.

How common was the serpulid-hydroid symbiosis in the marine Jurassic Polish Basin?

Generally, the presence of *Protulophila gestroi* in the fossil record coincided with the growing diversification of serpulids that started during the Late Triassic-Lower Jurassic and continued during the entire Mesozoic [95]. Thus, this symbiotic relationship may have originated somewhere during the Triassic–Jurassic transition, as the oldest example comes from the Pliensbachian [25]. An increase in the abundance of *Protulophila gestroi* over time appears to be related to two factors: 1) higher taxonomic diversity and abundance of serpulid fauna in the Cretaceous [96], whose skeletons provided a suitable substrate for colonization and 2) generally better taxonomic recognition of Upper Cretaceous serpulid worms compared to the Jurassic ones, a factor which increases a chance for detection of hydroid symbionts in a larger collection of host serpulids.

The percentage of infestation cases in the present study (0.6% among all 3,346 well-preserved fossils, see Table 1) was much lower than in most settings previously investigated, where the rates may even reach 45% [15] or 50% [86]. However, despite several reports of *Protulophila gestroi*, its paleoecology and the rate of infestation have rarely been studied, as the main scope of the research was polychaete fossils and not hydroids (e.g., [14, 25, 27]), or the study was based on a single specimen only [29]. The infestation rate seems to be commonly higher in younger, Cretaceous deposits [15, 18, 86]. Except for very few reports of this association from the Jurassic [8, 14, 26], no complex research has been conducted to better understand the abundance and paleoecology of this relationship. Reports on this association from the Cenozoic are also rarer than those from the Cretaceous. Despite the growing diversity in Palaeogene, serpulid fauna has been relatively poorly studied from this stratigraphic interval (see [95]), which also possibly reflects very few reports on the serpulid-hydroid relationship from this time interval [8, 22, 85]. The lack of comprehensive reviews of the hydroid-serpulid coexistence in the Jurassic may result from a significantly lower percentage of infestation, which may, in turn, be a consequence of unfavorable conditions for *Protulophila gestroi* to settle.

It has to be highlighted that most of the collected specimens of bioclaustrated hydroids (17 cases per 187 well-preserved serpulids) were derived from a single stratigraphic interval (Gnaszyn Dolny, Middle Bathonian, Morrisi Zone, Table 2) representing deeper (transgressive cycle T5 of [50]), calm paleoenvironment characterized by a muddy bottom on which a hard substrate suitable for serpulid colonization was very patchy or completely absent. There, 17 hydroid infestation cases have been noted in *Propomatoceros lumbricalis*, which constitute 9% of the all 187 well-preserved serpulids collected (Table 2). However, the infestation percentage could even be higher here, if the rest of 74 *Propomatoceros* tubes weren't worn. The single cases of infestation of *Propomatoceros* tubes noted in the remaining assemblages (Table 2), certainly result from a much lower number of perspective specimens. In Gnaszyn Dolny, hydroids have been found to infest serpulid tubes located on the same, very small substrate
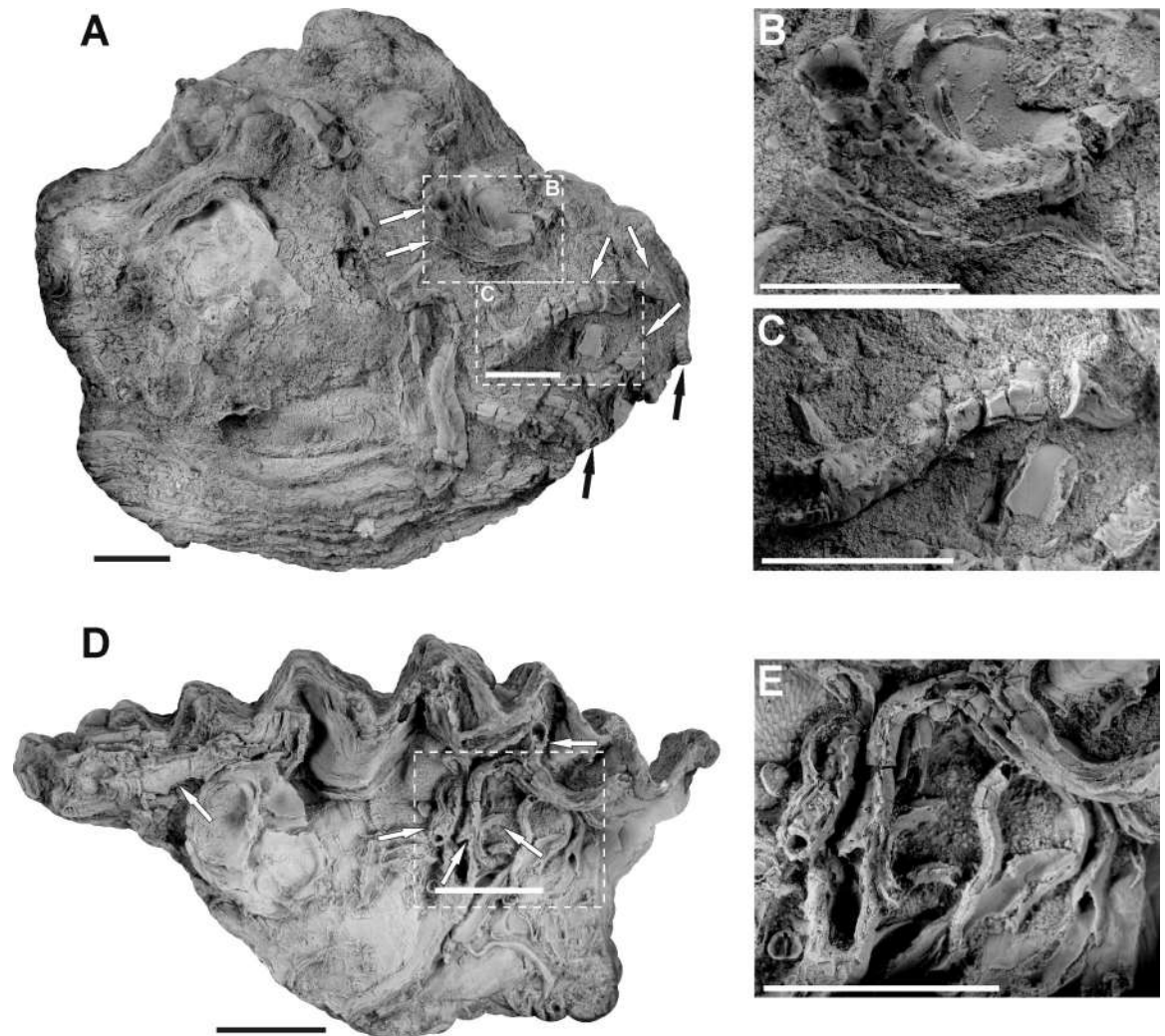
Fig 6. Aggregation of several serpulid tubes on two single oyster valves from the Middle Bathonian of Gnaszyn Dolny, Polish Jura, a number of which (arrowed) possess traces after bioclaustrated hydroids. A. An aggregation of six (arrowed) serpulids with *Protulophila gestroi*, GIUS 8-3730/6. **B-C.** Magnified shell areas showing bioclaustrated serpulid tubes, GIUS 8-3730/6a and GIUS 8-3730/6b, respectively. **D.** Aggregation of five (arrowed) serpulid specimens with *Protulophila gestroi*, GIUS 8-3730/7. **E.** Magnified part showing very dense aggregation of tubes on a small substrate surface bearing indistinct bioclaustrated traces (GIUS 8-3730/7a). Scale bars equal 1 cm.

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surfaces provided by oyster shells (Fig 6). This may favor the explanation that due to the very limited mobility of hydroid larvae, most of them presumably have not been able to recruit, unless settled on a convenient substrate (serpulid tube) providing bioclaustration (protection of colonies) and possibly also nutrient supply. In the case of the successful settlement of hydroid larvae on a given serpulid, their further spread was strongly limited by the available hard substrate with other potential hosts. Thus, the hydroid larvae had the greatest chance to colonize the neighboring serpulids on the same substrate, as exemplified by those present on the single oyster shells (Fig 6). The colonization of other hosts, growing on separate substrates, might have been exceedingly difficult or impossible for the larvae. The lack of any hydroid symbionts noted in abundant serpulids, including *Propomatoceros*, colonizing the Middle and Upper Bathonian hiatus concretions from Bugaj, Ogrodzieniec, and Krzyworzeka [26], or large oncoids from Ogrodzieniec [56] is striking. However, in these cases, the

paleoenvironmental conditions might have, at least to some extent, played a role. The hiatus concretions and oncoids were repeatedly overturned on the seabed due to hydrodynamical processes and/or animal activities (e.g., [26, 48, 56]); thus, they might not have provided a sufficiently stable habitat for the host serpulids and thus for the colonizing hydroids, as well. Even though some larvae may have been recruited on some serpulid hosts, they could not have developed when substrate with the hosts were overturned. Additionally, stronger currents in such settings might have prevented the hydroid larvae from settling on the hosts.

The lack of any bioclaustrated hydroids within the polychaete tubes from the Oxfordian sponge buildups of Zalas may be caused by a lack of suitable specific species of the host. In the present study, the polychaete tubes are represented by dominating *Glomerula*, followed by *Propomatoceros* and *Tetraserpula* (*Nogrobs*), constituting 75%, 24.8%, and 0.2% of the polychaete assemblage, respectively (as calculated from Kuziomko-Szewczuk [71]). There, either 1) the hydroids have not been present or 2) did not develop following settlement on the host, or 3) these polychaete species were not suitable hosts for the symbionts. Interestingly, in the Oxfordian of central Poland, Radwańska [14] noted only one example of *Protulophila gestroi* preserved within the tube of *Ditrupula*, a genus not found in the Oxfordian assemblage of Zalas. A similar situation might have been responsible for the lack of any *Protulophila gestroi* specimen preserved within the polychaete tubes from the Kimmeridgian of Małogoszcz, which are represented by similar forms as in the Oxfordian of Zalas (see [70]). In summary, the fossil record of serpulid-hydroid symbiosis within the Polish Basin during the Middle and Late Jurassic was a rare phenomenon with a very patchy distribution, mostly limited to a single setting characterized by a calm paleoenvironment with a slow (or even halted) sedimentation rate, allowing for the establishment and persistence of a suitable hard substrate for hydroid hosts.

Conclusions

The overall appearance of a hydroid colony is shown by external, subcircular apertures with bosses of different shapes and sizes and an internal network of branching stolons and polyp chambers. The morphology of the bioclaustrated traces left by hydroids shows a very independent arrangement of the colony, both within a given stratigraphic interval and through time. The differences in morphological details occur regardless of the geological interval, as it presumably reflects physiological and paleoecological conditions rather than interspecific variability. Although there is a faint probability that all the hydroid remnants described hitherto spanning through ca. 190 Ma belong to the single species *Protulophila gestroi*, we are not able to provide any reliable lower taxonomic classification based exclusively on the bioclaustrated traces as morphological disparities occur within all stratigraphic intervals. In order to make better comparisons of different colonies for any future taxonomic classification, a micro-CT scanning and volumetric rendering providing a number of features not visible externally, would be a good solution.

The studied hydroids show a significant bias toward certain serpulid genera. It possibly reflects some favorable conditions for *Protulophila gestroi* recruitment, comprising chemical composition, sufficient protection, and nutrient supply. The dependence on certain paleoecological conditions is striking, as current findings are almost restricted to only one stratigraphic zone, representing a specific paleoenvironment. The mobility of larvae might have been poor, which is also reflected in accumulated hydroid occurrences on a very small substrate. If convenient recruitment conditions existed, hydroids colonized close neighboring tubes and might not be able to colonize more distant, separated substrates. Based on all the available data, the most probable type of hydroid-serpulid symbiosis is commensalism.

The frequency of bioclaustrated hydroids is scarce in the material studied with a percentage of infestation of 0.6% among the well-preserved polychaete fossils. Such a pattern of occurrence of serpulid-hydroid symbiosis during the Middle and Late Jurassic within the Polish Basin seems to have resulted from an interplay of biological (host specificity, mobility of symbiont larvae and their survival) and paleoenvironmental (hydrodynamism and sedimentation rate) factors. The presence of hydroid symbionts only within the tubes of a single genus *Propomatoceros* indicates that host specificity plays an important role in the hydroid larvae. Taphonomy (preservation of tubes) probably played a minor role, as well-preserved tubes in a given assemblage analyzed here constituted a fairly large sample size.

The present case study shows that serpulid polychaete-hydroid symbiosis over a long-time interval within a single basin may show a very patchy distribution, concentrated only in single intervals where appropriate conditions for its development occurred. The morphological stasis of the preserved structures after hydroid *Protulophila gestroi* combined with its rarity in many stratigraphic intervals precludes any firm analyses concerning the co-evolution of both symbionts in both time and space of the same paleogeographic entity.

Supporting information

S1 Movie. CT longitudinal sectioning of specimen GIUS 8-3730/3 showing internal appearance of serpulid-hydroid association where polyp chambers and connected with them branching stolonal tubes are visible.
(AVI)

S2 Movie. Visualization of the individual tube of the serpulid *Propomatoceros lumbricalis* infested by hydroids *Protulophila gestroi*.
(AVI)

Acknowledgments

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Article 2

Słowiński, J., Vinn, O, Jäger, M., Zatoń, M.

Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages.

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Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages

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This study describes diverse assemblages of serpulid and sabellid polychaetes from various Middle and Upper Jurassic (upper Bajocian to lower Kimmeridgian) deposits of the Polish Basin. Twenty four taxa are reported in total, including two new species (*Cementula radwanskae* sp. nov. and *Filogranula spongiophila* sp. nov.). Abundance, distribution, and colonization patterns of serpulids and sabellids significantly depended on many palaeoenvironmental variables including the nature of the colonized substrate and its overall shape, food supply, and hydrodynamism. The most diverse assemblages have been noted on the Middle Jurassic shells inhabiting soft muddy substrates, on hardgrounds and oncoids, whereas the lowest biodiversity levels have been found on the Middle Jurassic hiatus concretions and Kimmeridgian oyster shell beds. Some species are clearly associated with certain substrate types, whereas stratigraphic interval is not that important. Middle Jurassic mobile rockgrounds (hiatus concretions and oncoids) and hardgrounds are characterized by the most similar species associations, while Middle Jurassic shelly substrates from soft-bottom environments and Upper Jurassic shell beds and sponge build-ups are most dissimilar with respect to the colonizing tube dwelling polychaete taxa. Among the diverse assemblages of the encrusting faunas, serpulid and sabellid tubeworms are the most abundant constituents in the majority of settings, what is explained by their opportunism and ability to effectively outcompete other contenders. In the majority of locations, the most abundant tube-dwelling polychaete is the ubiquitous sabellid *Glomerula gordialis*, followed by the serpulid species *Propomatoceros lumbricalis*. The dominance of these species is congruent with many other serpulid and sabellid communities inhabiting various Jurassic palaeoenvironments.

Key words: Sabellidae, Serpulidae, exrusters, taxonomy, tubeworms, Mesozoic, Poland.

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Introduction

Among the all tube-dwelling polychaete families, only Serpulidae dwell exclusively in calcareous tubes, while in the Sabellidae and Cirratulidae, calcareous species are restricted to single genera in each family, *Glomerula* and *Dodecaceria*, respectively (Perkins 1991; Fischer et al. 1989, 2000; Vinn et al. 2008a). Moreover, another extinct cirratulid genus—*Diplochaetetes*—dwelled in partly calcareous tubes (Kočí et al. 2021). During the Jurassic, calcareous cirratulids were absent (Fischer et al. 2000), and thus the only representatives bearing hard, mineralized skeletons were sabellids and, obviously, the most abundant serpulids.

Tube-dwelling polychaetes are sessile, almost exclusively marine (but see Bosák et al. 2004; Kupriyanova et al. 2009) invertebrates predominantly attaching to hard substrates, such as rocks and shells. The oldest known serpulids are middle Permian in age (Sanfilippo et al. 2017, 2018). However, there are only very few reports of true tube-dwelling polychaetes of the late Permian (e.g., Ramsdale 2021) to Early Triassic age. In the Middle Triassic (Assmann 1937; Flügel et al. 1984; Stiller 2000; Senowbari-Daryan et al. 2007), the abundance and diversity of serpulids, as well as their palaeogeographic distribution, started to increase, which continued further during the Late Triassic (Ziegler and Michalík 1980; Berra and Jadoul 1996; Cirilli et al.

1999). Tube-dwelling polychaetes have been widespread since the Early Jurassic, and their major diversification took place during the Middle and Late Jurassic, and continued during the Cretaceous (for review see Ippolitov et al. 2014). Such an increase in both diversity and abundance of sessile polychaete fauna during the Middle and Late Jurassic coincided with an overall evolutionary radiation of various organisms colonizing hard substrates (e.g., Palmer and Fürsch 1974; Wilson and Palmer 1990; Feldman and Brett 1998; Taylor and Wilson 2003; Wilson et al. 2008; Zatoń and Taylor 2009b; Zatoń et al. 2011a, b; Breton et al. 2020). This sclerobiont (sensu Taylor and Wilson 2002) "bloom" during the Jurassic resulted from an increase of carbonate, lithified substrates and hard, calcareous skeletons of diverse sessile organisms (see e.g., Taylor and Wilson 2003 for a comprehensive review). The last factor might have also been a response to increasing levels of predation during the so-called Mesozoic Marine Revolution (Vermeij 1977).

In spite of their large number and wide distribution, tube-dwelling polychaetes are a group which seems to have been omitted quite often in palaeontological research, possibly due to their morphological simplicity and a common opinion that they are an unimportant group for biostratigraphy. Among the best studied serpulid and sabellid taxa are those from the Upper Cretaceous (e.g., Brünnich Nielsen 1931; Jäger 1983, 2005, 2011; Macellari 1984; Tapaswi 1988; Radwańska 1996; Kočí and Jäger 2015a, b; Kočí et al. 2017), whereas other stratigraphic intervals are characterized by scattered reports. Although in recent years much more effort has been made towards a better recognition of Jurassic serpulids and sabellids (e.g., Ippolitov 2007a, b; Jäger and Schubert 2008; Vinn and Wilson 2010; Kočí et al. 2019), the more complex treatments of Jurassic representatives are now clearly outdated (e.g., Parsch 1956). Despite extensive Middle and Upper Jurassic outcrops in Poland, with deposits bearing a vast abundance of tube-dwelling polychaetes, there is only one publication focusing only on the taxonomy and palaeoecology of the Oxfordian (now Kimmeridgian, see Loba and Radwańska 2022) species from the Kuyavia region in central Poland (Radwańska 2004). Some other, single reports either treated a single species (*Filograna socialis* from the Tithonian (Upper Jurassic) of Sławno, see Radwańska 2003) or only mentioned serpulids and sabellids on the palaeoecological background and were not the main scope of the research (e.g., Kaim 2011; Zatoń et al. 2011a, b, 2012).

The lack of a comprehensive study of Middle and Upper Jurassic tube-dwelling polychaetes from Poland hampers our understanding of evolution and ecology of encrusting faunas of the Jurassic Polish Basin and Jurassic serpulids and sabellids in general. This serious gap in knowledge is here filled by our systematic and palaeoecological study of serpulids and sabellids derived from numerous outcrops of Middle and Upper Jurassic deposits, representing various palaeoenvironments in the Polish Basin.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:1F0C99C5-769A-4C82-80C8-1A92584BF19D

Institutional abbreviations.—GIUS, Institute of Earth Sciences, University of Silesia in Katowice, Poland.

Other abbreviations.—CEBS, Central European Basin System; ITS, Internal Tube Structures; UPGMA, unweighted pair group method with arithmetic mean algorithm.

Geological setting

Palaeogeographical background.—During the Mesozoic, the epicontinental Polish Basin constituted the easternmost part of the larger system of epicontinental seas called the Central European Basin System (CEBS). During the Middle Jurassic, the Polish Basin was restricted from the north, east and south by Fennoscandian, Ukrainian, Meta-Carpathian and Bohemian landmasses, respectively (Fig. 1A), so its connection with other Central European basins was quite limited and only existed to the west via the Germanic Basin and to the south-east via the East Carpathian Gate which linked the Polish Basin with the Tethys Ocean (Dayczak-Calikowska and Moryc 1988; Dayczak-Calikowska et al. 1997). From the Aalenian, the basin progressively widened during gradual transgression, punctuated by some regressive events, and in the late Bathonian the entire area of the Polish Lowlands was submerged (Matyja and Wierzbowski 1998). During this time, sedimentation was dominated by clastics derived from the surrounding land masses (especially from the largest Fennoscandian land, Marynowski et al. 2007), the depositional systems of which followed transgressive-regressive cycles (Feldman-Olszewska 1997; Leonowicz 2015a). During the Callovian (Middle Jurassic), the Polish Basin witnessed further progressive deepening with a peak transgression noted in the late Callovian (Wierzbowski et al. 2009). The Late Jurassic was a time of reorganization of the Polish Basin and the onset of carbonate platform deposition. After this time, the Polish Basin became part of the northern shelf of the Tethys Ocean (Kutek 1994; Matyja and Wierzbowski 2006), where the development of the carbonate platform was controlled by sea-level and climate changes, as well as the architecture of the Paleozoic basement and synsedimentary tectonics (Kutek 1994; Gutowski et al. 2005; Krajewski et al. 2011, 2016, 2017; Matyszkiewicz et al. 2012, 2016). Characteristic bioherms formed by siliceous sponges and microbial consortia were extensively developed during the Oxfordian (Late Jurassic; e.g., Trammer 1982; Ostrowski 2005; Matyja 2006; Matyszkiewicz et al. 2012) and various carbonate facies commenced during the Kimmeridgian (Late Jurassic), including oolites and oncolites with hardgrounds, and shell-beds in a variety of marine
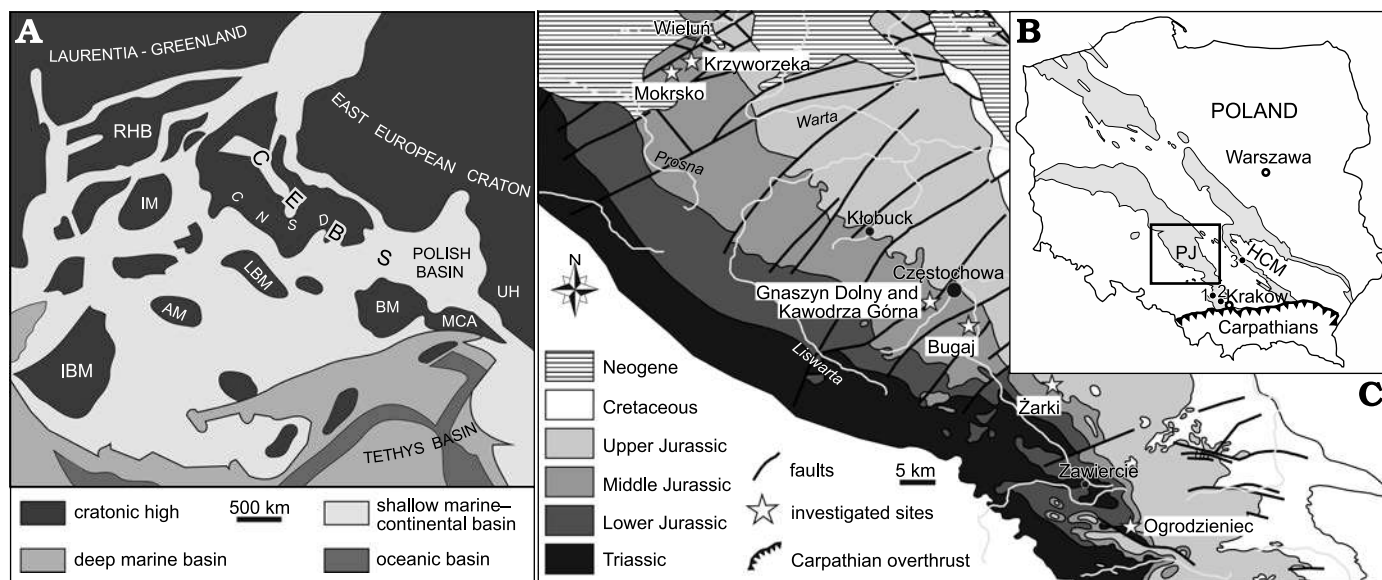
Fig. 1. Palaeogeography and geology of the investigated area. **A**. Paleogeographical sketch-map of Europe during the Middle Jurassic (from Leonowicz 2016, modified after Ziegler 1990). AM, Armorican Massif; BM, Bohemian Massif; CEBS, Central European Basin System; CNSD, Central North Sea Dome; IBM, Iberian Meseta,; IM, Irish Massif; LBM, London-Brabant Massif; MCA, Meta-Carpathian Arc; RHB, Rockall-Hatton Bank; UH, Ukrainian High. **B**. Geological sketch-map of Poland without the Cenozoic cover with three sampled localities indicated. HCM, Holy Cross Mountains; PJ, Polish Jura; 1, Bolęcin; 2, Zalas; 3, Małogoszcz. **C**. Geological map of the Polish Jura area without Quaternary cover, with sampled localities indicated (after Zatoń and Taylor 2009b).

environments (Kutek 1994; Machalski 1998; Matyja et al. 2006; Krajewski et al. 2017).

Investigated outcrops.—In total, 11 localities exposing Middle to Upper Jurassic deposits in the Polish Jura area and the Mesozoic margin of the Holy Cross Mountains have been sampled (Fig. 1B, C; Table 1). As the details of the sampled sites have already been presented by Słowiński et al. (2020), here we provide only those stratigraphic and palaeoenvironmental data which are most important for the present paper. In ascending stratigraphic order, these are as follows:

Ogrodzieniec-Świertowiec: The outcrop is located 1 km south of the town of Ogrodzieniec, Polish Jura. The serpulid and sabellid fauna has been found encrusting large oncoids encased within condensed, sandy and carbonate deposits underlain by the dark mudstone of the Częstochowa Ore-bearing Clay Formation. Dinoflagellate cysts and foraminifers found in the oncoid cortices (Słowiński 2019), as well as ammonites found within the host rocks, indicate that the oncoid-bearing deposits are confined to the upper Bajocian–lower Bathonian (up to the *Morphoceras macrescens* Subzone of the *Zigzagiceras zigzag* Zone, see Zatoń and Taylor 2009a; Zatoń et al. 2012). The palaeoenvironment was interpreted as a shallow-water marine habitat within the photic zone and slightly below fair-weather wave base (Zatoń et al. 2012).

Ogrodzieniec, Żarki, Bugaj, Kawodrza Górna, Gnaszyn Dolny, Mokrsko, and Krzyworzeka: These seven sites are located in the Polish Jura (Fig. 1B, C) area and contain Middle Jurassic (upper Bajocian–Bathonian) siliciclastic deposits in the form of dark mudstone and siltstone beds with siderite nodules and calcite hiatus concretions belonging to the Częstochowa Ore-bearing Clay Formation (e.g., Majewski 2000; Matyja and Wierzbowski 2000; Zatoń et al. 2011a; Leonowicz 2015b). The tube-dwelling polychaetes have been found encrusting bivalve shells and belemnite rostra collected in Kawodrza Górna (lower Bathonian) and Gnaszyn Dolny (middle Bathonian), as well as the hiatus concretions from Mokrsko (upper Bajocian), Bugaj (middle Bathonian), Ogrodzieniec, Żarki, and Krzyworzeka (upper Bathonian). Mudstone beds of the Częstochowa Ore-bearing Clays were deposited in various bathymetric regimes, ranging from lower offshore to offshore transition, e.g., below, and above storm wave-base (Gedl et al. 2012; Leonowicz 2015a). The horizons with tubeworm-bearing hiatus concretions mark distinct decreases (or even pauses) in sedimentation rate and erosion of the seafloor (Zatoń et al. 2011a; Leonowicz 2015b).

Bolęcin: This site is about 6 km to the east of the town of Chrzanów, between Katowice and Kraków, Polish Jura (Fig. 1B). The trench dug in a nearby wood exposed highly fossiliferous, condensed sandy limestone with abundant quartz pebbles and ooids, which most probably correspond to the so-called "Balin Oolite" of upper Bathonian–lower Callovian (Middle Jurassic), with possible base of middle Callovian present (Tarkowski et al. 1994; Mangold et al. 1996; Taylor 2008). The presence of a diverse macrofauna, including ammonites (Mangold et al. 1996), may indicate an open marine palaeoenvironment. Tube-dwelling polychaetes were found encrusting various shells and skeletal remains of different mollusks.

Zalas: The active quarry is located in the Zalas village near Krzeszowice, southern part of the Polish Jura (Fig. 1B).

Table 1. Data on provenance and number of all sabellid and serpulid specimens.

Taxa	Mokrsko	Kawodrza Górna	Gnaszyn Dolny	Bugaj	Ogrodzieniec	Krzyworzeka	Żarki	Ogrodzieniec-Świertowiec	Bolęcin	Zalas (Callovian)	Zalas (Oxfordian)	Małogoszcz	Total number of individuals (per taxon)
Glomerula gordialis	66	13	80	52	60	62	8	174	102	181	36	45	879
Metavermilia cf. *striatissima*					2	33	1	18	24	56			134
Metavermilia? sp.			11										11
Filogranula runcinata	3	3	13	5				5	15	11			55
Filogranula spongiophila sp. nov.											16		16
Cementula spirolinites											122		122
Cementula radwanskae sp. nov.									4	29			33
Cementula cf. *circinnalis*								38					38
"*Serpula cingulata*"											3		3
Propomatoceros lumbricalis	21	31	228	81	33	23	9	156	81	149		28	840
Propomatoceros sp. 1	1		4										5
Propomatoceros sp. 2										1			1
Propomatoceros sp. 3											1		1
Nogrobs aff. *quadrilatera*			36										36
Nogrobs? aff. *tricristata*			8										8
Nogrobs aff. *tetragona*			29										29
Mucroserpula tricarinata										2			2
Mucroserpula? sp.			2										2
Placostegus planorbiformis											7		7
Pseudovermilia sp.										4			4
Serpulidae sp. 1								23	5	43			71
Serpulidae sp. 2			1										1
Serpulidae sp. 3			10										10
Serpulidae sp. 4												6	6
Total number of individuals (per locality)	91	47	422	138	95	118	18	414	231	476	184	80	2314

The serpulid and sabellid fauna has been derived from two different lithologies and stratigraphic units. Stratigraphically older specimens have been found encrusting various macrofossils (especially the large bivalve *Ctenostreon proboscideum* (Sowerby and Sowerby, 1820) encased within a hardground of middle Callovian–earliest late Callovian age (Middle Jurassic; Giżejewska and Wieczorek 1977; Dembicz and Praszkier 2007), and originating in an open-sea, offshore environment (Dembicz and Praszkier 2007; Zatoń et al. 2011b). Stratigraphically younger specimens were found on lower Oxfordian (Upper Jurassic) sponge-forming bioherms (Matyja 2006; Matyszkiewicz et al. 2012).

Małogoszcz: Serpulid and sabellid fauna has been collected in an active quarry situated in the southwestern part of the Mesozoic margin of the Holy Cross Mountains, ca. 1 km north of Małogoszcz town centre (Fig. 1B). The specimens encrusted bivalve shells, especially specimens of *Actinostreon gregareum* (Sowerby, 1815), derived from the lower Kimmeridgian (Upper Jurassic) shell-beds referred to as the Skorków Lumachelle (Kutek 1994; Machalski 1998; Matyja et al. 2006; Zatoń and Machalski 2013), which resulted from storm-induced deposition in a relatively shallow marine environment (Machalski 1998).

Material and methods

The investigated material encompasses in total 2314 specimens of fossil serpulids and sabellids (Table 1), most of which are relatively well-preserved, allowing for proper taxonomic assignment. All strongly abraded tubes, whose determination was ambiguous, were eliminated from further examination.

Sufficiently well-preserved specimens have been cleaned and carefully studied under a binocular microscope paying special attention to all the diagnostic characters of the tubes, which allowed for a reliable identification to the lowest possible taxonomic level. Following their taxonomic identification, the total number of specimens, their relative abundance and distribution in relation to and within the specific substrate have been assessed, employing biodiversity indices such as Dominance (D), Simpson's (1-D), Shannon's (H) and evenness (e^H/S) using the PAST software (Hammer et al. 2001).

In order to analyse the relationship of particular tube-dwelling polychaete assemblages inhabiting different substrates and palaeoenvironments, cluster analysis using the PAST software (Hammer et al. 2001) was performed. In order to quantitatively examine the similarities of the

communities between particular substrates/palaeoenvironments, Q-mode cluster analysis was used. The analysis was performed using the Raup-Crick similarity index and the unweighted pair group method with arithmetic mean (UPGMA) algorithm. The Raup-Crick index was applied as it uses Monte Carlo randomization, which compares the observed number of taxa occurring within two associations with the distribution of their co-occurrences on the basis of 200 random interactions.

The specimens were coated with ammonium chloride prior to photography. All the material investigated is housed at the Institute of Earth Sciences in Sosnowiec, under collection numbers GIUS 8-3589 (Callovian of Zalas), GIUS 8-3730 (Gnaszyn Dolny and Kawodrza Górna), GIUS 8-3745 (Bolęcin), GIUS 8-3746 (Oxfordian of Zalas), GIUS 8-3747 (Małogoszcz), GIUS 8-3750 (Ogrodzieniec-Świertowiec), GIUS 8-3751 (Mokrsko, Bugaj, Ogrodzieniec, Krzyworzeka, and Żarki).

Systematic palaeontology

Phylum Annelida Lamarck, 1802

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818

Infraclass Canalipalpata Rouse and Fauchald, 1997

Order Sabellida Levinsen, 1883

Family Sabellidae Latreille, 1825

Subfamily Sabellinae Chamberlin, 1919

Genus *Glomerula* Brünnich Nielsen, 1931

Type species: *Serpulites gordialis* (Schlotheim, 1820); Schlotheim (1820) lists seven specimens from the Alps and Jurassic limestone, from different localities; Switzerland; no precise location mentioned; Heidenheim, South Germany, Upper Jurassic; Ermreuth, South Germany, Jurassic (possibly Middle or Upper Jurassic); more precise stratigraphy unknown.

Glomerula gordialis (Schlotheim, 1820)

Figs. 2A–H, 3A, B, E, F, 5D, 10A, 12A.

1820 *Serpulites gordialis* sp. nov.; Schlotheim 1820: 96.
1831 *Serpula gordialis* Schloth.; Goldfuss 1831: 234, pl. 69: 8a–c.
1956 *Serpula* (*Cycloserpula*) *gordialis* Schlotheim, 1820; Parsch 1956: 214, pl. 20: 15, 16.
pars 1983 *Glomerula gordialis* (Schlotheim, 1820); Jäger 1983: 26, pl. 2: 1, non pl. 2: 2–18 (with a large synonymy including Cretaceous and Palaeogene specimens which Jäger [2005: 127–131, pl. 1: 1–10] later considered as belonging to two separate species).
2004 *Glomerula gordialis* (Schlotheim, 1820); Radwańska 2004: 38, pl. 1: 1–10.
2010 *Glomerula gordialis* (Schlotheim, 1820); Vinn and Wilson 2010: 36: 6.7, 6.8.

Material.—879 variably preserved specimens encrusting hiatus concretions (66 from Mokrsko, 52 from Bugaj, 60 from Ogrodzieniec, 62 from Krzyworzeka, and 8 from Żarki), oncoids (174 from Ogrodzieniec-Świertowiec), bi-valve, cephalopod, and gastropod shells (and moulds to a lesser extent) (13 from Kawodrza Górna, 80 from Gnaszyn Dolny, 102 from Bolęcin, and 181 from the Callovian of Zalas), and sponges (36 from the Oxfordian of Zalas from the Middle–Upper Jurassic of the Polish Jura and 45 from Upper Jurassic of Małogoszcz) (see Table 1); GIUS 8-3589, GIUS 8-3730, GIUS 8-3745, GIUS 8-3746, GIUS 8-3747, GIUS 8-3750, GIUS 8-3751.

Description.—Tubes small to large, up to 100–150 mm long, forming numerous, usually irregularly curved loops and dense, coiled aggregations; some specimens are also represented by straight or slightly meandering, only occasionally complex and coiled tubes. Tube diameter nearly constant along the whole length, and cross-section always circular to subcircular. Relative to the diameter of the tube (up to 2 mm, most often 1 mm or less), the wall is relatively thick. Tubes do not possess any flanges or attachment structures, and the base is not distinctly flattened. Surface entirely smooth, lacking ornamentation and peristomes. Interior smooth without any internal tube structures.

Remarks.—The specimens studied are assigned to *Glomerula gordialis* because of their irregularly curved loops and dense aggregations, which are characteristic of the species. Specimens also lack any internal tube structures, which—if present—cause a trilobate shape of the lumen. Some specimens with coiled tube parts alternating with straight to curved parts somewhat resemble *Glomerula flaccida* (Goldfuss, 1831); however, presumably all such specimens (especially those lacking characteristic knee-like bends) belong in fact to *G. gordialis*, which is abundant on substrates with unlimited surface. Some specimens of *G. gordialis* (both in this collection and elsewhere) are superficially similar to *Glomerula serpentina* (Goldfuss, 1831) in having their tubes coiled in a characteristic, meandering fashion. However, the primary character distinguishing *G. gordialis* from *G. serpentina* is the potential ability of *G. serpentina* to form trilobate constrictions of the tube's lumen (see e.g., Jäger 1983: 191, pl. 2: 14B, 17). Such constrictions have been relatively common only since the Late Cretaceous, during the Early Cretaceous they occur rarely, but are totally absent in the Jurassic (Jäger 2005). Thus, similarly to *Glomerula gordialis* tubes resembling *G. flaccida*, those resembling *G. serpentina* are presumably also a result of ecophenotypic variation resulting in a specific shape of *G. gordialis*. Therefore, a specific shape of the *Glomerula* tube alone cannot be considered as a good taxonomic indicator.

Stratigraphic and geographic range.—In the material studied the species occurs in the Bajocian–lower Oxfordian (Middle–Upper Jurassic) of the Polish Jura and in the lower Kimmeridgian (Upper Jurassic) of the Mesozoic margin of the Holy Cross Mountains (Małogoszcz). Previously, tubes identified as *G. gordialis* were reported from Jurassic (Pugaczewska 1970; Radwańska 2004; Zatoń et al. 2011a), Cretaceous (Radwańska 1996), and Paleocene localities (Pugaczewska 1967) in Poland. The species is widespread
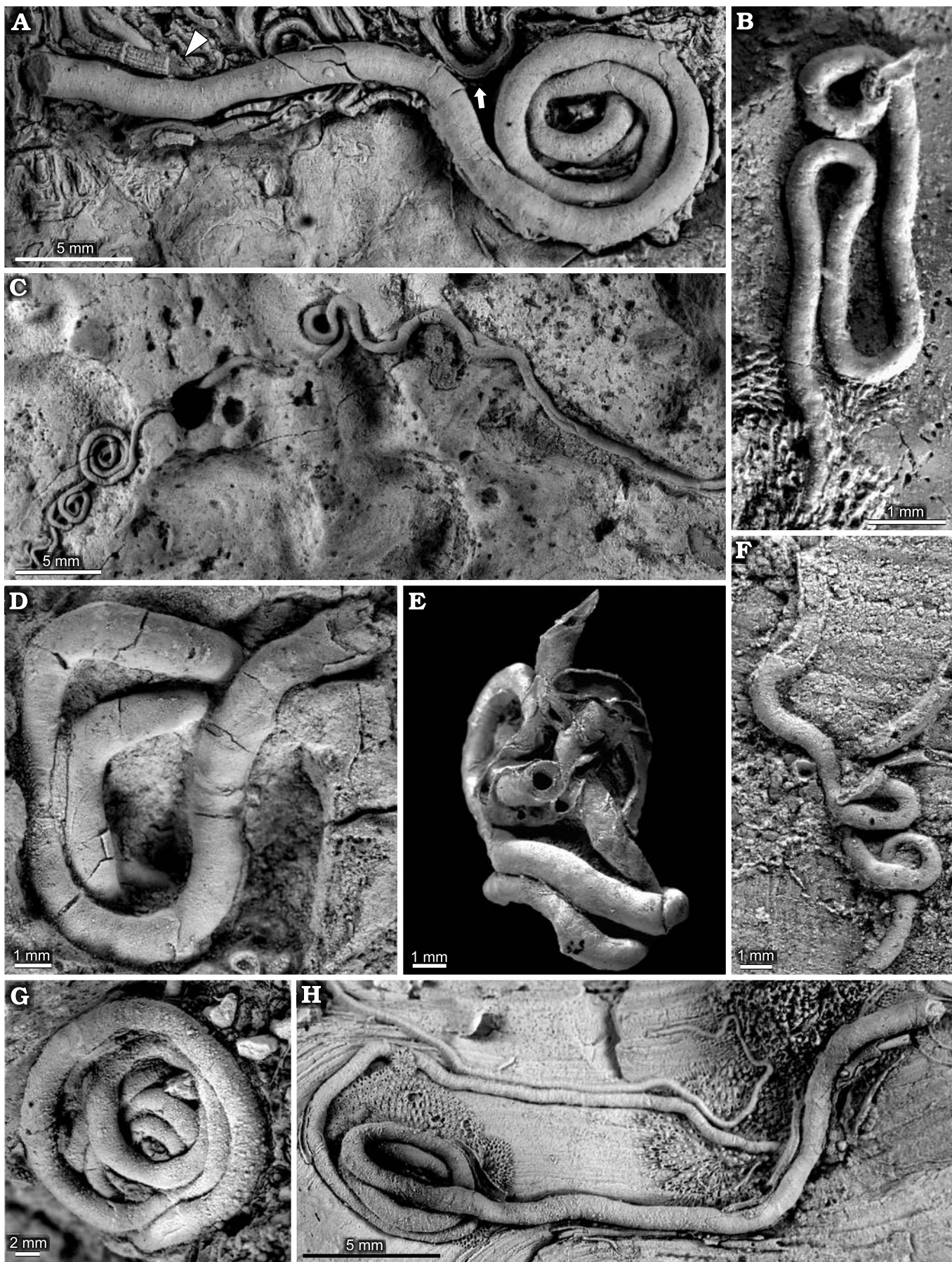
in the Jurassic of England (Sowerby 1844), Germany (Parsch 1956), Czech Republic (Kočí et al. 2019), and France (Breton et al. 2020). It has also been described from the Jurassic of Israel (Wilson et al. 2008; Vinn and Wilson 2010). *Glomerula* tubes cited as *G. gordialis* are also widespread in the Cretaceous of Europe (e.g., in Germany, Jäger 1983) and India (Chiplonkar and Tapaswi 1973).

Family Serpulidae Rafinesque, 1815
Genus *Metavermilia* Bush, 1905

Type species: *Vermilia multicristata* (Philippi, 1844); Recent, Mediterranean Sea.

Metavermilia cf. *striatissima* (Fürsich, Palmer, and Goodyear, 1994)

Figs. 2A, 3C–F, 5D, 7B.

Material.—134 well-preserved specimens encrusting hiatus concretions (2 from Ogrodzieniec, 33 from Krzyworzeka, and 1 from Żarki), bivalve shells (and moulds to a lesser extent) (24 from Bolęcin and 56 from the Callovian of Zalas), and oncoids (18 from Ogrodzieniec-Świertowiec) from the Bajocian–Callovian (Middle Jurassic) of the Polish Jura (see Table 1); GIUS 8-3589, GIUS 8-3745, GIUS 8-3759, GIUS 8-3751.

Description.—Tubes irregularly and strongly curved, but not coiled. Solitary tubes relatively small, however, some specimens may be up to 30–40 mm long. Tube diameter nearly constant throughout the entire length, rarely exceeding 1 mm. Cross-section subcircular or more frequently angular due to a multi-keeled tube. In some specimens, the cross-section may be more subtriangular due to a widened tube base. Tubes usually lack specific attachment structures and are attached to the substrate by a flattened and occasionally widened base, without a free apertural tube part. Tubes usually covered by six longitudinal keels, evenly spaced from the top of the tube to its flanges. Ampullacea-type peristomes (proles ampullacea) usually thick, prominent and irregularly distributed. Apart from longitudinal ornamentation and peristomes, the tube's external surface is variable, being smooth or ornamented by corrugations and wrinkles. Some tubes bear a characteristic combination of transverse and longitudinal ornamentation, resulting in a strongly developed but very irregular reticulate "honeycomb" structure.

Remarks.—The type specimens of *Metavermilia striatissima* from the Tithonian (Upper Jurassic) of southern England (Fürsich et al. 1994) are somewhat smaller than our specimens. Except for the specimens from the type area, five or six-keeled specimens like the one described here have been relatively rarely reported from the Jurassic of western and central Europe. *Metavermilia* cf. *striatissima* may locally be a common species in the Jurassic of Poland. This species encompasses two kinds of populations slightly differing in details. The general tube aspect of both groups is very similar, characterized by such features as: presence of six (rarely five) distinct keels consistent in outline; subcircular to subangular cross-section; presence of irregularly scattered ampullacea-type peristomes, and the mode of curvature. The slight differences are in the ornamentation. The populations from Zalas and Bolęcin (hardgrounds) have smooth outer surfaces (between keels and peristomes) and bear better developed flanges (Fig. 3D–F), whereas the other group (primarily from Krzyworzeka) bears some additional transverse elements resulting in a delicate "honeycomb" structure (Fig. 3C; see also Kupriyanova 1993: 155, for comparison), and less developed attachment structures, although basal margins are widened in some specimens as well. These slight differences presumably resulted from ecophenotypic variations.

Metavermilia? sp.

Fig. 4A.

Material.—Eleven specimens attached to belemnite rostra from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—Tubes medium-sized (ca. 15 mm long), gently curved to straight without peristomes, very slowly increasing in diameter (up to 1 mm in total diameter). Tubes attached to the substrate along their entire length and have well-developed, widened flanges. The tubes have three prominent keels which are continuous and rather unmodified along the whole length of the tube and are separated by well-developed furrows. Keels are directed outwards forming a centrifugal pattern. Tubes covered with usually weak perpendicular growth lines. Cross-section subcircular, slightly angular.

Remarks.—The specimens studied are tentatively assigned to an unidentified species of *Metavermilia* because of similarity in ornamentation to other species of this genus which usually bear 3 to 7 keels. Alternatively, the fossils might belong to *Mucroserpula*. In spite of the fact that tubes assigned to the latter genus commonly tend to form curved loops and may considerably increase in diameter, the studied specimens have been found only on straight belemnite rostra, where they might have not been able to form curves and loops. Moreover, Ippolitov (2007b) suggested that during

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Fig. 2. Sabellid and serpulid polychaetes from the Jurassic of Poland. **A**. Sabellid polychaete *Glomerula gordialis* (Schlotheim, 1820), tiny serpulid polychaete *Metavermilia* cf. *striatissima* (Fürsich, Palmer, and Goodyear, 1994) (arrowhead), and tiny, juvenile serpulid polychaete *Propomatoceros lumbricalis* (Schlotheim, 1820) (arrow) encrusting oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec (GIUS 8-3750/1). **B**–**H**. *Glomerula gordialis*, specimen encrusting: oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec (**B**, GIUS 8-3750/2); hiatus concretions from the upper Bathonian of Ogrodzieniec (**C**, GIUS 8-3751/1; **D**, GIUS 8-3751/2); shell fragments from the upper Bathonian–lower Callovian of Bolęcin (**F**, GIUS 8-3745/1) and Callovian of Zalas (**G**, GIUS 8-3589/1; **H**, GIUS 8-3589/2); specimen partially detached from a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (**E**, GIUS 8-3730/8).
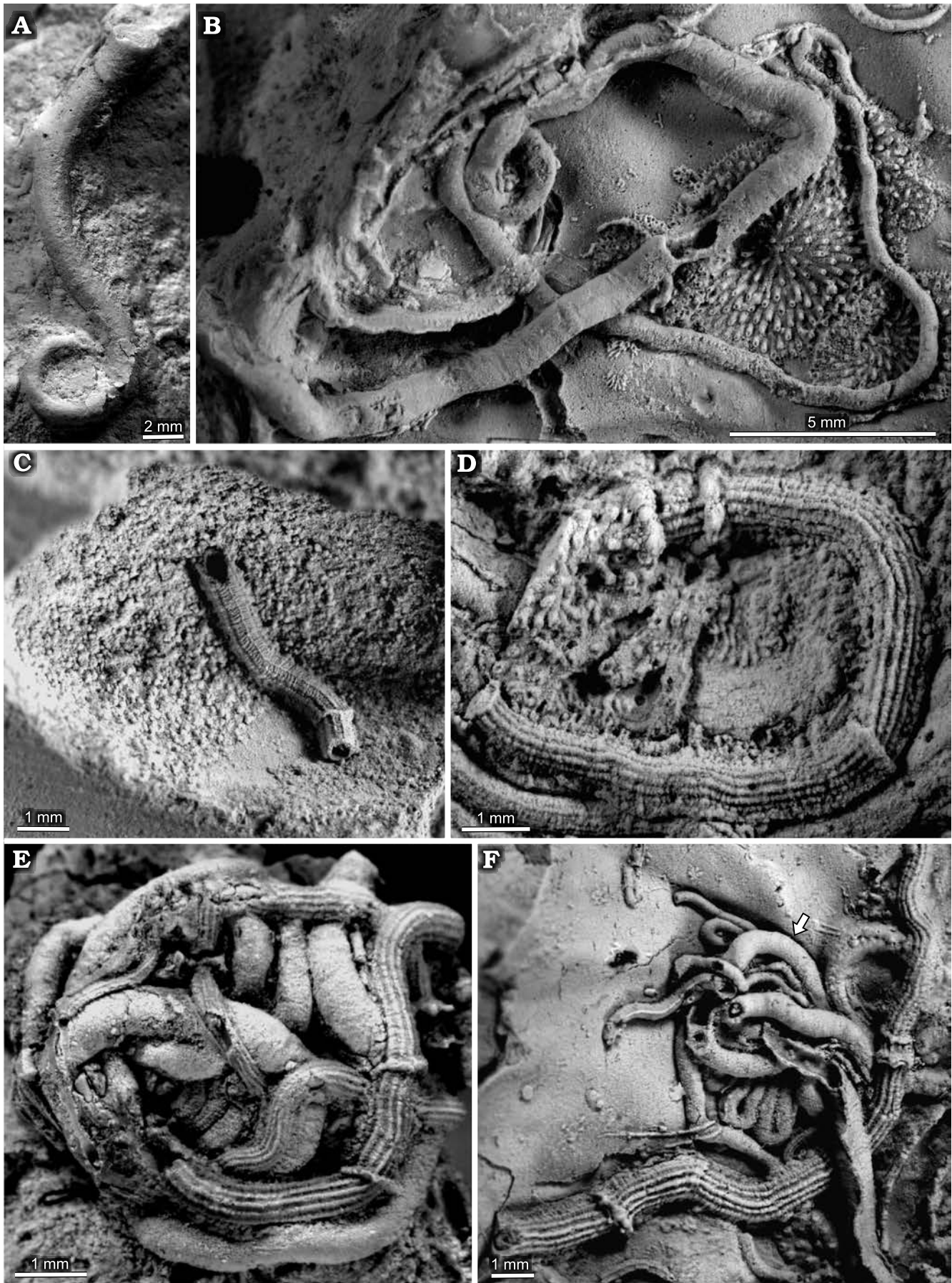
the Bathonian–Callovian (Middle Jurassic), some straight, three-keeled *Mucroserpula* representatives might have co-existed with those of *Propomatoceros*, which indicates both genera diverged earlier. The arrangement of the three keels of *Metavermilia*? sp. described here remains somewhat similar to "*Tetraserpula quinquangularis* (Goldfuss, 1831)" sensu Parsch 1956: 224, pl. 21: 25), however, "*Tetraserpula quinquangularis*" sensu Parsch (1956) presumably should be synonymized with *Mucroserpula tricarinata* (Sowerby, 1829). The specific name "*quinquangularis*" is doubtful; in any case, the overall appearance of the tubes does not fully resemble species of *Mucroserpula* sensu stricto, and more likely is a member of the genus *Metavermilia*. It differs from *Mucroserpula tricarinata* in the much wider arrangement of the lateral keels, the keels being less prominent and only slightly undulating.

Genus *Filogranula* Langerhans, 1884

Type species: *Filogranula gracilis* (Langerhans, 1884); Recent, Atlantic.

Filogranula runcinata (Sowerby, 1829)

Figs. 4B–E, 12B.

1829 *Serpula runcinata* sp. nov.; Sowerby 1829: 227, pl. 608: 6.
1955 *Serpula tricarinata* Sowerby, 1829; Gerasimov 1955: 29, pl. 9: 1–14.
2007 *Filogranula runcinata* (Sowerby, 1829); Ippolitov 2007a: 263, pl. 7: 7–12.
2020 "*Filogranula*" *runcinata* (J. de C. Sow.); Kosenko and Ippolitov 2020: 117, pl. 1: 2, pl. 2: 2a.

Material.—55 mostly well-preserved specimens encrusting bivalves, belemnites, nautiloids, ammonites (3 from Kawodrza Górna, 13 from Gnaszyn Dolny, 15 from Bolęcin, and 11 from The Callovian of Zalas), hiatus concretions (3 from Mokrsko and 5 from Bugaj), and oncoids (5 from Ogrodzieniec-Świertowiec) from the Middle Jurassic of the Polish Jura (see Table 1); GIUS 8-3589, GIUS 8-3730, GIUS 8-3745, GIUS 8-3750, GIUS 8-3751.

Description.—Tubes small, most often slightly undulating, but curved specimens also occur, though these are not loop-forming. The tubes are attached to the substrate along their entire length and grow to rather small diameter (usually up to 1 mm). Except for the lower lateral tube parts, which remain almost smooth, the tubes are distinctly ornamented by three parallel and longitudinal keels (of which the middle one is usually more elevated) separated by grooves. Each keel is either topped or replaced by a row of distinctive denticles, usually distributed evenly throughout the entire length of the keels; however, the appearance of the keels is sometimes inconsistent, varying in shape and size, depending on locality. Denticles are directed forward, sometimes forming a centrifugal pattern. Peristomes absent. Cross-section subtriangular, slightly flattened, relatively narrow at the top, widens downward, and sometimes widens even more at the base.

Remarks.—The specimens are assigned to *Filogranula runcinata* due to their distinctive three keels, which are most often topped or replaced by pronounced denticles. The species most similar to *F. runcinata* is *Metavermilia goldfussi* (Ippolitov, 2007a), which co-occurs at some European localities (Ippolitov 2007a). These two species bear similarly well-developed external ornamentation. However, *M. goldfussi* differs from *F. runcinata* mainly by the lack of such specific features as stronger developed/more denticulate keels or lack of free anterior tube portion. Although *M. goldfussi* usually bears better developed basal margins and attachment structures, which are present in a part of the specimens studied here, this feature seems to be insufficient for an unequivocal designation. Within *Filogranula runcinata*, a few populations consisting of very similar tubes (sometimes represented by only several specimens in each locality) can be distinguished in different localities. The tubes, however, only slightly differ in details, presumably depending on (i) different palaeoenvironments recorded in particular localities, and/or (ii) evolutionary change. Nevertheless, despite minor differences, these few forms are included into single species due to the presence of distinct features such as: (i) three strongly denticulate, rather consistent keels present throughout entire ontogeny; (ii) most often slightly widened tube base; (iii) lateral walls being smooth in their lowermost part and strongly ornamented closer to the upper part; (iv) tube attached to the substrate along its entire length; (v) universal lack of peristomes. It must be also noticed that due to the differences in wall microstructures between *F. runcinata* and other species of *Filogranula*, the former was also referred to as "*Filogranula*" *runcinata* by Ippolitov et al. (2014), suggesting its uncertain affiliation to this genus, and even to different clade than geologically younger species of *Filogranula* (see also Koči and Jäger 2015a).

Stratigraphic and geographic range.—The specimens of *Filogranula runcinata* studied herein come from the Bajocian–Callovian (Middle Jurassic) of the Polish Jura. This species was reported also from the Middle and Upper Jurassic of Russia (Gerasimov 1955; Ippolitov 2007a; Kosenko and Ippolitov 2020) and UK (Sowerby 1829).

← Fig. 3. Sabellid and serpulid polychaetes from the Jurassic of Poland. **A**. Sabellid polychaete *Glomerula gordialis* (Schlotheim, 1820) encrusting a sponge fragment from the Oxfordian of Zalas (GIUS 8-3746/1). **B**. *Glomerula gordialis* and cyclostome bryozoan colony encrusting an oyster fragment from the lower Kimmeridgian of Małogoszcz (GIUS 8-3747/1). **C**. Serpulid polychaete *Metavermilia* cf. *striatissima* (Fürsich, Palmer, and Goodyear, 1994) encrusting the interior of the boring *Gastrochaenolites* from the upper Bathonian of Krzyworzeka (GIUS 8-3751/3); note the additional, delicate transverse elements. **D**–**F**. *Metavermilia* cf. *striatissima* encrusting shell fragments from the Callovian of Zalas (**D**, GIUS 8-3589/3; **E**, GIUS 8-3589/4; **F**, GIUS 8-3589/5), note specimen in E is intertwined with *Glomerula gordialis* tube, specimen in F is encrusted by a juvenile *Propomatoceros lumbricalis*; *Glomerula gordialis* indicated by an arrow.

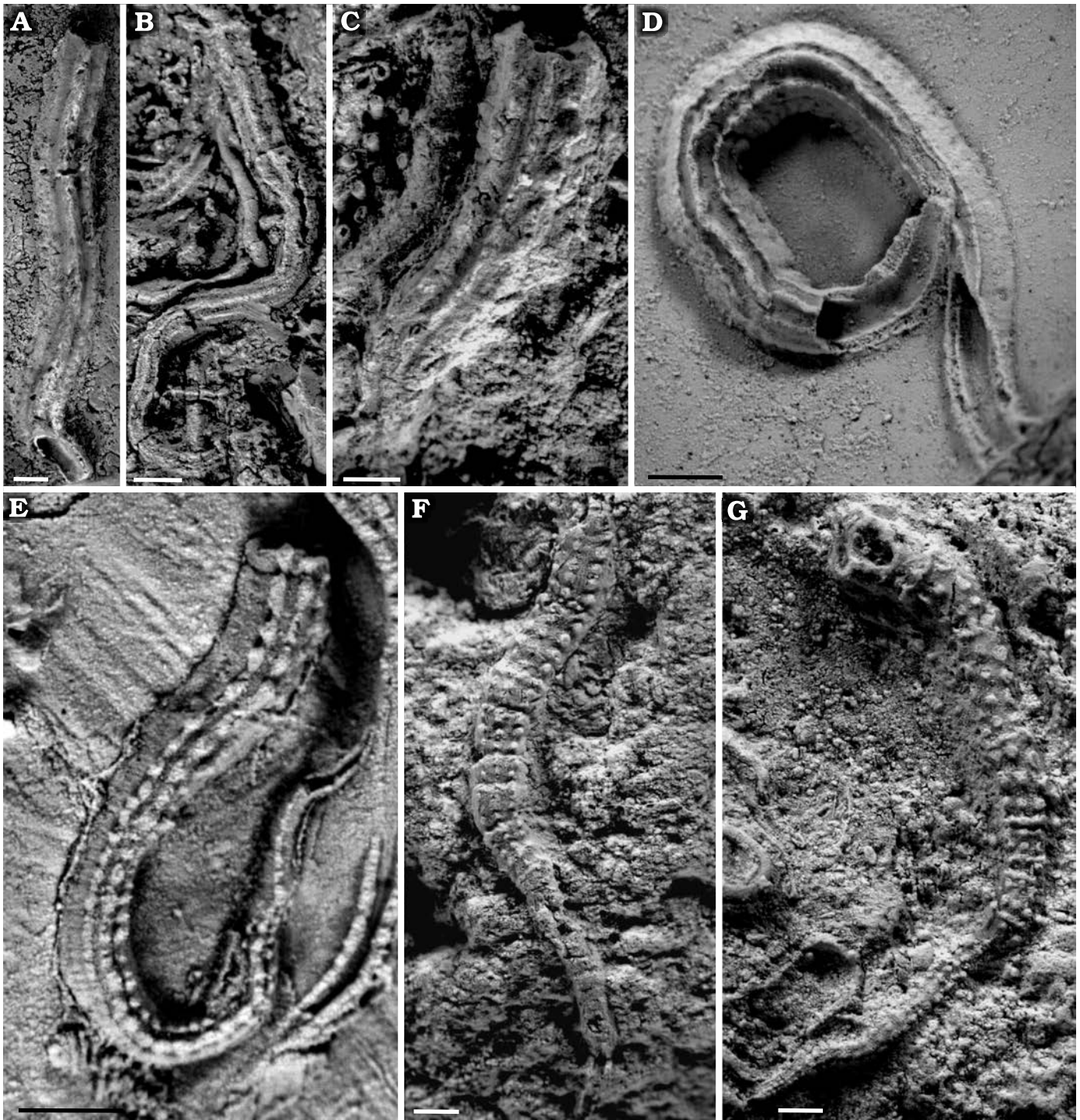Fig. 4. Serpulid polychaetes from the Jurassic of Poland. **A**. *Metavermilia*? sp. encrusting a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/9). **B–E**. *Filogranula runcinata* (Sowerby, 1829), specimens encrusting: an oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec (**B**, GIUS 8-3750/3); a hiatus concretion from the upper Bajocian of Mokrsko (**C**, GIUS 8-3751/4); shell fragments from the middle Bathonian of Gnaszyn Dolny (**D**, GIUS 8-3730/10), the Callovian of Zalas (**E**, GIUS 8-3589/6). **F**, **G**. *Filogranula spongiophila* sp. nov. encrusting sponge fragments from the Oxfordian of Zalas (**F**, holotype, GIUS 8-3746/2; **G**, paratype, GIUS 8-3746/3). Scale bars 1 mm.

Filogranula spongiophila sp. nov.

Fig. 4F, G.

Zoobank LSID: urn:lsid:zoobank.org:act:D9C5AD2A-271B-4D41-B6
C9-0D02C21E584D

Etymology: After the substrate (sponges), the sole substrate this species encrusts.

Type material: Holotype: GIUS 8-3746/2 (almost completely preserved tube attached to a sponge substrate). Paratype: GIUS 8-3746/3 (almost completely preserved tube attached to a sponge substrate) from the type locality and horizon.

Type locality: Zalas near Krzeszowice, southern Poland.

Type horizon: Lower Oxfordian, Upper Jurassic.

Material.—16 specimens encrusting sponges from the type locality and horizon (see Table 1); GIUS 8-3746.

Diagnosis.—A species of the genus *Filogranula* which lacks continuous keels; instead, it has three longitudinal rows of large granules. Moreover, occasionally a free apertural part and peristomes occurring like thickenings on the tube may be present.

Description.—Tubes small to medium-sized (5–20 mm long; tube diameter 0.5–1.5 mm), usually straight or only slightly undulating, and attached to the substrate by most of their length; however, in some specimens the anterior part is detached by angular folding and erected upwards. Lateral tube walls are almost parallel, only slightly rounded. Tube base is not widened and lacks any flanges or attachment structures. Longitudinal ornamentation is strongly developed and becomes most distinctive in the anterior part of the tube. Keels are lacking; instead, each tube bears three longitudinal rows of large granules which are present along the entire tube length. They may project over the aperture. The median line of granules may be slightly weaker in some specimens. Transverse elements are occasionally represented by irregularly distributed, thick, somewhat nodular (due to the granules), very slightly flaring peristomes occurring rather like thickenings on the tube. However, peristomes are not always present. Tube cross-section rounded pentagonal or petaloid.

Remarks.—*Filogranula spongiophila* sp. nov. differs from *F. runcinata* by having rows of granules instead of continuous keels. Moreover, it differs from *Filogranula tricristata* (Goldfuss, 1831) by its thicker peristomes and the presence of occasionally a free-apertural part. *Filogranula spongiophila* sp. nov. differs from other species investigated in the present study in the presence of petaloid aperture sometimes raised above the substrate, and keels substituted by rows of granules. However, these regularly ornamented, denticulated forms occur solely within the lower Oxfordian sponge facies of Zalas and are clearly different from *Filogranula runcinata* from the upper Bajocian–Callovian of other localities mentioned above. To the best of our knowledge, these and similar fossils have not been found in any other locality and currently are known only encrusting sponges from Zalas. Thus, their assignment to a new species is justified.

Stratigraphic and geographic range.—Lower Oxfordian (Upper Jurassic), Zalas, Poland.

Genus *Cementula* Regenhardt, 1961

Type species: *Cementula sphaerica* (Brünnich Nielsen, 1931); Maastrichtian (Upper Cretaceous), Nørre Uttrup, Denmark.

Cementula spirolinites (Münster in Goldfuss, 1831)

Fig. 5A–C.

1831 *Serpula spirolinites* sp. nov.; Münster in Goldfuss 1931: 229, pl. 68: 5a–c.

1956 *Serpula* (*Dorsoserpula*) *spirolinites* Münster, 1831; Parsch 1956: 221, pl. 21: 29.

2004 *Cementula spirolinites* (Münster in Goldfuss, 1831); Radwańska 2004: 39, pl. 2: 6–8.

2019 *Cementula spirolinites* (Münster in Goldfuss, 1831); Kočí et al. 2019: 317: 4D.

Material.—122 specimens attached to sponges from the lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura (see Table 1); GIUS 8-3746.

Description.—Tubes up to 100 mm long. Predominantly straight or slightly undulating tube portions alternate with planispiral coils. Tube diameter small (not exceeding 2 mm), almost constant throughout the length of the tube and apparently small also if compared to the diameter of the spiral. Within most spirals, the tube not overgrowing its previous whorls, so that all whorls most often remain visible. About five whorls usually tightly contiguous; however, in some loops the whorls without tight contact and more or less irregularly coiled, and most often with a small open umbilicus in the center of the spiral. Usually, the tubes attached to the substrate by indistinctive basal flanges. A single well-developed median keel present along the entire length of the tube. Transverse elements represented by rare, irregularly occurring alae-type peristomes, strongly developed on top of the tube and less strongly and less often developed in the upper-lateral position where the peristome may resemble a pair of "ears". However, they stay rather faint outside these positions and close to the basal margins. Apart from the median keel and peristomes, the tube's external surface smooth and without any additional ornamentation. The cross-section usually rounded-triangular.

Remarks.—Our specimens described above resemble tubes of *Spiraserpula oligospiralis* Ippolitov, 2007b, in several features: consistent median keel throughout entire length of the tube, alternation of straight portions with contiguous coiled spirals leaving an open umbilicus, and absence of ITS (Internal Tube Structures). However, they differ by the spirals growing larger in diameter and amounting to a considerably higher percentage of the total tube length, as well as by the keel being conspicuous already in the posterior tube portion. The genera *Spiraserpula* Regenhardt, 1961, and *Cementula* are hardly distinguishable due to similarities in external appearance, in spite of the fact that *Spiraserpula* tends to grow to a larger size forming a more complex tube system consisting of alternating straight tube portions and several spirals. A reliable distinction between the genera *Spiraserpula* and *Cementula*, as previously mentioned by Pillai (1993) and Pillai and Hove (1994), is based only on the presence of ITS, which are present in *Spiraserpula*, while in *Cementula* they are absent. Thus, the principal character allowing distinction between these two genera is the potential ability to form ITS in *Spiraserpula*. To prevent ambiguous determinations where ITS would be an exclusive feature determining this taxon, Ippolitov (2007b) proposed to consider *Cementula* as a subgenus of *Spiraserpula*. Although an ability to form ITS cannot be taken as the only taxonomic feature simply
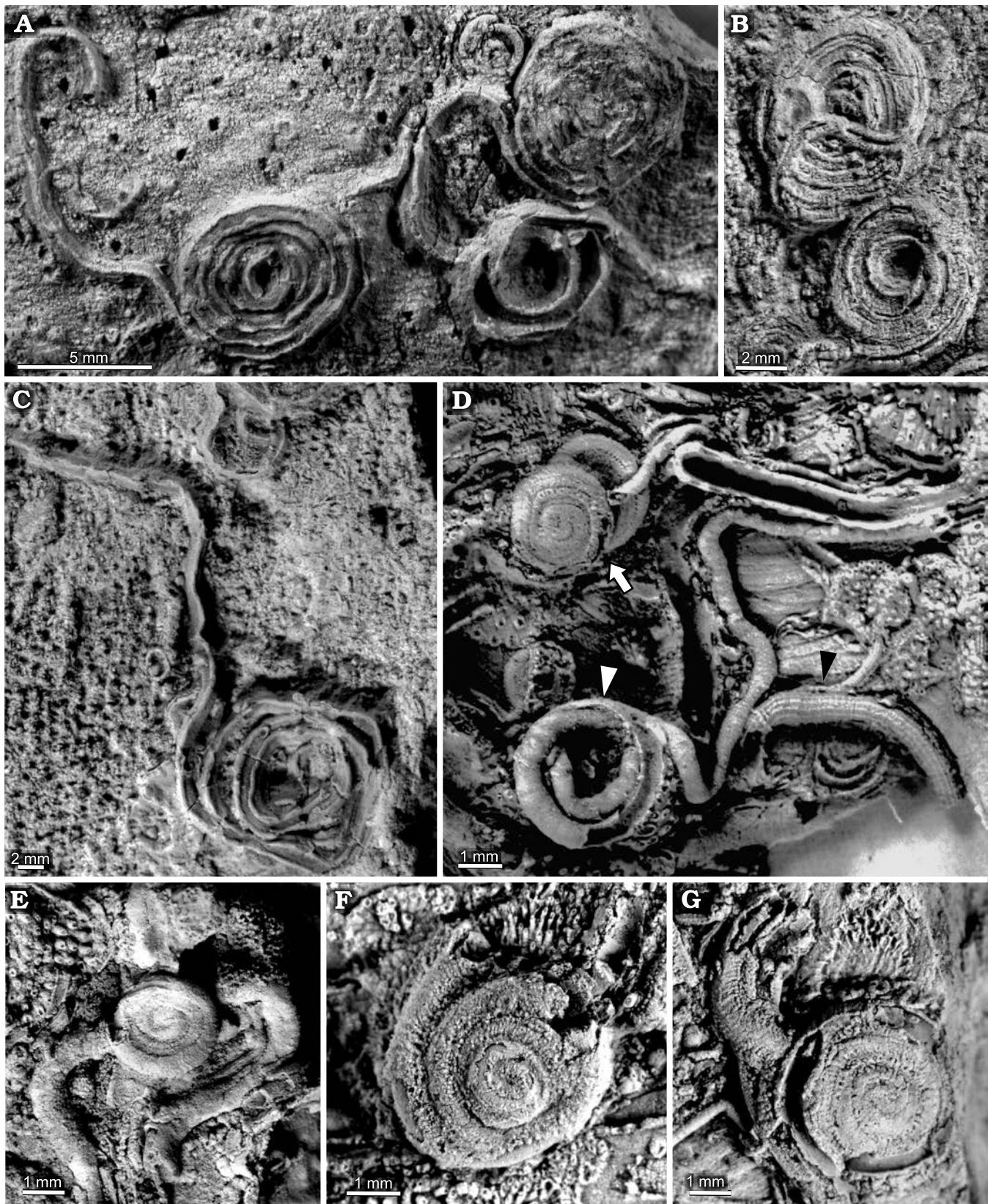
Fig. 5. Serpulid polychaetes from the Jurassic of Poland. **A–C**. *Cementula spirolinites* (Münster in Goldfuss, 1831), specimen encrusting: sponge fragment from the Oxfordian of Zalas (**A**, GIUS 8-3746/4; **B**, GIUS 8-3746/5; **C**, GIUS 8-3746/6). **D**. *Cementula radwanskae* sp. nov., holotype (GIUS 8-3589/7, arrow) encrusting a shell fragment from the Callovian of Zalas; partially encrusting another *C. radwanskae*, sabellid *Glomerula gordialis* (Schlotheim, 1820) (white arrowhead), and serpulid *Metavermilia* cf. *striatissima* (Fürsich, Palmer, and Goodyear, 1994) (black arrowhead). **E–G**. *Cementula radwanskae* sp. nov. encrusting shell fragments from the Callovian of Zalas (**E**, paratype, GIUS 8-3589/8; **F**, paratype, GIUS 8-3589/9; **G**, GIUS 8-3589/10).

due to taphonomic reasons, possibly except for well-recognizable species within certain stratigraphic intervals (e.g., *Cementula spirolinites*), in principle this problem seems to refer to younger species than those described here. To the best of our knowledge, until now not a single ITS in tubes of any *Spiraserpula* species older than Campanian has been found (see Pillai 1993; Pillai and Hove 1994; Jäger 2005).

Stratigraphic and geographic range.—The material studied herein come from lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura. This species was also reported from the Oxfordian (Upper Jurassic) of central Poland (Wapienno Quarry) by Radwańska (2004), Germany (Goldfuss 1831; Parsch 1956), and Czech Republic (Kočí et al. 2019).

Cementula radwanskae sp. nov.

Fig. 5D–G.

Zoobank LSID: urn:lsid:zoobank.org:act:67B0722D-4F88-4DDD-A 813-C090E89B4E54

Etymology: In honor of Urszula Radwańska in recognition of her studies on tube-dwelling polychaetes.

Type material: Holotype: GIUS 8-3589/7 (almost complete coiled tube attached to a bivalve shell fragment, partially encrusting another *Cementula radwanskae* sp. nov.). Paratypes: GIUS 8-3589/8, GIUS 8-3589/9 (two slightly eroded coiled tubes attached to a bivalve shell fragment). All from type locality and type horizon, see below.

Type locality: Zalas near Krzeszowice, southern Poland.

Type horizon: Middle–upper Callovian (Middle Jurassic).

Material.—33 well-preserved specimens encrusting mainly bivalves from the Middle Jurassic of the Polish Jura (4 from Bolęcin and 29 from the Callovian of Zalas) (see Table 1); GIUS 8-3589, GIUS 8-3745.

Diagnosis.—The tubes forming rather small spirals which are coiled in a compact tight mode. Keels and peristomes lacking. The entire surface covered by delicate wrinkles and corrugations and lines of tiny granules.

Description.—Tubes very small, planispirally coiled. Spirals reaching only up to 3 mm in diameter, usually consisting of up to five whorls. Predominately sinistrally coiled, but both directions of coiling may occur. Rarely, small anterior tube portions uncoiled. All the whorls are tightly adherent to each other. The umbilicus in the center of the spiral is tiny or absent. Tubes are attached to the substrate by their entire length and do not overgrow each other. Tube diameter (less than 0.5 mm) increasing only very slowly or constant in the anterior part. The tubes lacking any strongly developed ornamentation such as keels or peristomes, but usually the entire surface densely covered by somewhat irregular delicate corrugations, wrinkles and lines of tiny granules protruding slightly at the tube's median line. Cross-section circular or subcircular.

Remarks.—The specimens studied are similar to *Cementula* cf. *circinnalis* (Münster in Goldfuss, 1831) occurring in Bajocian–Bathonian (Middle Jurassic) deposits of Ogrodzieniec-Świertowiec, but differ from this species in granulate ornamentation present on a vast majority of *Cementula rad-*

wanskae sp. nov. specimens and more tightly coiled whorls. *Cementula radwanskae* sp. nov. bears features somewhat similar to the species *Cementula* sp. 2 from the Bajocian of Normandy, France, described by Breton et al. (2020), whose spirals, however, may reach more than twice the diameter of the spirals of *C. radwanskae* sp. nov. *Cementula radwanskae* sp. nov. differs from *C. spirolinites* by its much smaller size, compact coiling mode, and universal lack of keels and peristomes. In contrast to *C. circinnalis*, *C. radwanskae* sp. nov. possesses delicate wrinkles and corrugations on the entire surface and has more tightly coiled whorls. In contrast to *Cementula complanata* (Goldfuss, 1831) (see Jäger and Schubert 2008), *C. radwanskae* sp. nov. possesses occasionally straightened anteriormost tube portion and has delicate ornamentation.

Stratigraphic and geographic range.—The material studied herein comes from upper Bathonian–lower Callovian (Middle Jurassic) of Bolęcin, and Callovian (Middle Jurassic) of Zalas, Polish Jura. Possibly, the species may also occur in the Bajocian of Normandy, France (Breton et al. 2020).

Cementula cf. *circinnalis* (Münster in Goldfuss, 1831)

Fig. 6A, C.

Material.—38 well-preserved specimens exclusively encrusting oncoids from the upper Bajocian–lower Bathonian (Middle Jurassic) of Ogrodzieniec-Świertowiec, Polish Jura (see Table 1); GIUS 8-3750.

Description.—Tubes very small, planispirally coiled, usually consisting of three to five whorls. Sinistral and dextral spirals occur. The maximum diameter of entire spiral reaching only 3 mm, while the tube diameter does not exceed 0.5 mm. Most of the whorls very tightly coiled; however, in some specimens they are not completely adpressed, and show small chinks left between subsequent whorls. A minute umbilicus occasionally present in the center of the spiral. In some cases, anteriormost tube portions straight and not adhering to the previous whorl. The attachment area sometimes widened at the basal margins. The tube diameter increasing moderately fast in the early ontogenetic stages, but rather constant in the adult tube portions. The external surface of the tubes completely smooth. Cross-section circular to subcircular.

Remarks.—In overall shape, these tubes are similar to those assigned to *Cementula radwanskae* sp. nov.; however, in all cases they differ in having an entirely smooth surface lacking any ornamentation, whereas *C. radwanskae* sp. nov. possesses granulate ornamentation. Coiling mode is also slightly different in the vast majority of spirals, the tubes are less tightly coiled than in *C. radwanskae* sp. nov. and straight tube portions in the anterior occur more frequently. Therefore, we consider them separate species. The type of *Cementula circinnalis* comes from the lower Aalenian (Middle Jurassic; Goldfuss 1831). Another possible affiliation is *Cementula filaria* (Goldfuss, 1831), but due to the unification of species from two presumably different genera under this name by Goldfuss (1831), the species name "*filaria*" seems to be not

Fig. 6. Serpulid polychaetes from the Jurassic of Poland. **A**. *Cementula* cf. *circinnalis* (Münster in Goldfuss, 1831) encrusting an oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec (GIUS 8-3750/4). **B**. "*Serpula cingulata* Münster in Goldfuss, 1831" encrusting a sponge fragment from the the Oxfordian of Zalas (GIUS 8-3746/7). **C**. *Propomatoceros lumbricalis* (Schlotheim, 1820) (arrowhead) and *Cementula* cf. *circinnalis* (arrow) encrusting an oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec (GIUS 8-3750/5). **D–F**. *Propomatoceros lumbricalis*, specimen encrusting: a piece of a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (**D**, GIUS 8-3730/11); an oyster shell from the middle Bathonian of Gnaszyn Dolny (**E**, GIUS 8-3730/12); a shell fragment from the Callovian of Zalas (**F**, GIUS 8-3589/11).

a good choice for these Middle Jurassic forms. Specimens presumably of the same species as those discussed here were described from the Bajocian of Normandy under the name *Cementula* sp. 1 by Breton et al. (2020).

Genus *Serpula* Linnaeus, 1758

Type species: *Serpula vermicularis* (Linnaeus, 1767); Recent, western European seas.

"*Serpula cingulata* Münster in Goldfuss, 1831"

Fig. 6B.

Material.—Three specimens attached to sponges from the lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura (see Table 1); GIUS 8-3746.

Description.—Tubes relatively short (ca. 10 mm long), attached to the substrate along their entire length. Tube diameter increases slowly, up to 1 mm. Tubes slightly undulate forming delicate curves. Attachment structures absent, although basal parts of the tubes are slightly widened. Ornamentation consisting of thick, densely and regularly spaced, ring-like peristomes present along the whole length of the tube. Longitudinal elements are absent. Cross-section not well-visible; likely subcircular due to the overall shape of the tube.

Remarks.—The name "*Serpula cingulata*" is derived from Münster in Goldfuss (1831), although the true generic affiliation of the present species to the genus *Serpula* is unclear.

Stratigraphic and geographic range.—The material studied herein comes from the lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura; present also in the Upper Jurassic sponge facies of Germany (Parsch 1956: 215).

Genus *Propomatoceros* Ware, 1975

Type species: *Propomatoceros sulcicarinata* (Ware, 1975); Aptian (Lower Cretaceous), Faringdon, UK.

Propomatoceros lumbricalis (Schlotheim, 1820)

Figs. 2A, 3F, 6C–F, 7A–D.

1820 *Serpulites lumbricalis* sp. nov.; Schlotheim 1820: 96.
1952 *Serpula* cf. *lumbricalis* Schlotheim; Makowski 1952: 4, pl. 2: 2, 3.
1956 *Serpula* (*Dorsoserpula*) *lumbricalis* (Schlotheim) 1820; Parsch 1956: 219, pl. 20: 18, 20.
2007 *Propomatoceros lumbricalis* (Schlotheim, 1820); Ippolitov 2007b: 432, pl. 12: 1c, 3, 6–8, 9c, 9d.

Material.—840 variably preserved specimens, mainly encrusting oysters and belemnites (31 from Kawodrza Górna, 228 from Gnaszyn Dolny, 81 from Bolęcin, and 149 from the Callovian of Zalas), but also hiatus concretions (21 from Mokrsko, 81 from Bugaj, 33 from Ogrodzieniec, 23 from Krzyworzeka, and 9 from Żarki) and oncoids (156 from Ogrodzieniec-Świertowiec) from the Middle Jurassic of the Polish Jura and Upper Jurassic of Małogoszcz (28) (see Table 1); GIUS 8-3589, GIUS 8-3730, GIUS 8-3745, GIUS 8-3747, GIUS 8-3750, GIUS 8-3751.

Description.—Tubes of different, sometimes large sizes (up to 80 mm long), straight to strongly curved, very rarely forming loops; large and robust tubes dominate in the majority of localities. Tubes grow in diameter (up to 6 mm) at a moderately fast rate. Attachment structures well developed, forming characteristic tubulae, sometimes resulting in a widened tube base; however, in some specimens flanges are less developed. Tubulae are most often divided into chambers which are visible in the abraded tube parts where the irregularly distributed transverse elements occur; hollow tubulae are rare. A prominent median keel on the top of the tube running along its entire length. In the middle and anterior parts, the keel sometimes tends to undulate. Curved alae-type peristomes, most often well developed, occur occasionally at irregular intervals. Growth lines most prominently near the median keel, seldom visible along the whole length of the tube. The tube surface usually smooth, only occasionally covered irregularly by tiny granules. Cross-section depending on the ontogenetic stage, most often being triangular, and subtriangular at early ontogenetic stages, and becoming more subcircular at later stages, with the lateral walls becoming more convex, and the longitudinal keel on top only delicately marked.

Remarks.—Among fossil serpulids, *Propomatoceros* is one of the most common, geographically widespread and geologically long-ranging genera. Its occurrence in Jurassic and Cretaceous deposits combined with conservative morphology, which varies intraspecifically and depending on palaeoenvironment and ontogeny, makes reliable species determinations within this genus remarkably difficult. The species name *Serpulites lumbricalis* is historically the oldest available species name which can be included into *Propomatoceros*. It was introduced by Schlotheim (1820) for Middle and Late Jurassic species, but unfortunately without providing any figure or type specimen. Nevertheless, as this is the oldest available name, we decided to use it, including also some informal names such as e.g., forma "*limax*", which Goldfuss (1831) had introduced as a species name for Bajocian (Middle Jurassic) serpulids from Southern Germany. In contrast to Schlotheim (1820), Goldfuss (1831) provided figures and more detailed information on several species which now can be included into *Propomatoceros*. Parsch (1956) and Ippolitov (2007b) validated the species status of *Promopatoceros lumbricalis*, and they considered forma "*limax*" of Goldfuss (1831) as its subjective synonym.

Considering the difficulties in proposing a morphologically well-defined species concept for this genus with a well-defined stratigraphic range, here, we consider all specimens having a similar suite of features as belonging to a single species *Propomatoceros lumbricalis*. Although the specimens are slightly variable within certain populations, they display rather congruent morphology as all the easily-distinguishable features of species of *Propomatoceros*, such as e.g., distinctive keel which may vary inter- and intraspecifically, and ontogenically. Thus, we regard such small-scale morphological differences which might have led to the introduction of separate species as a result of intraspecific, palaeoenvironmentally controlled changes within a given population. However,
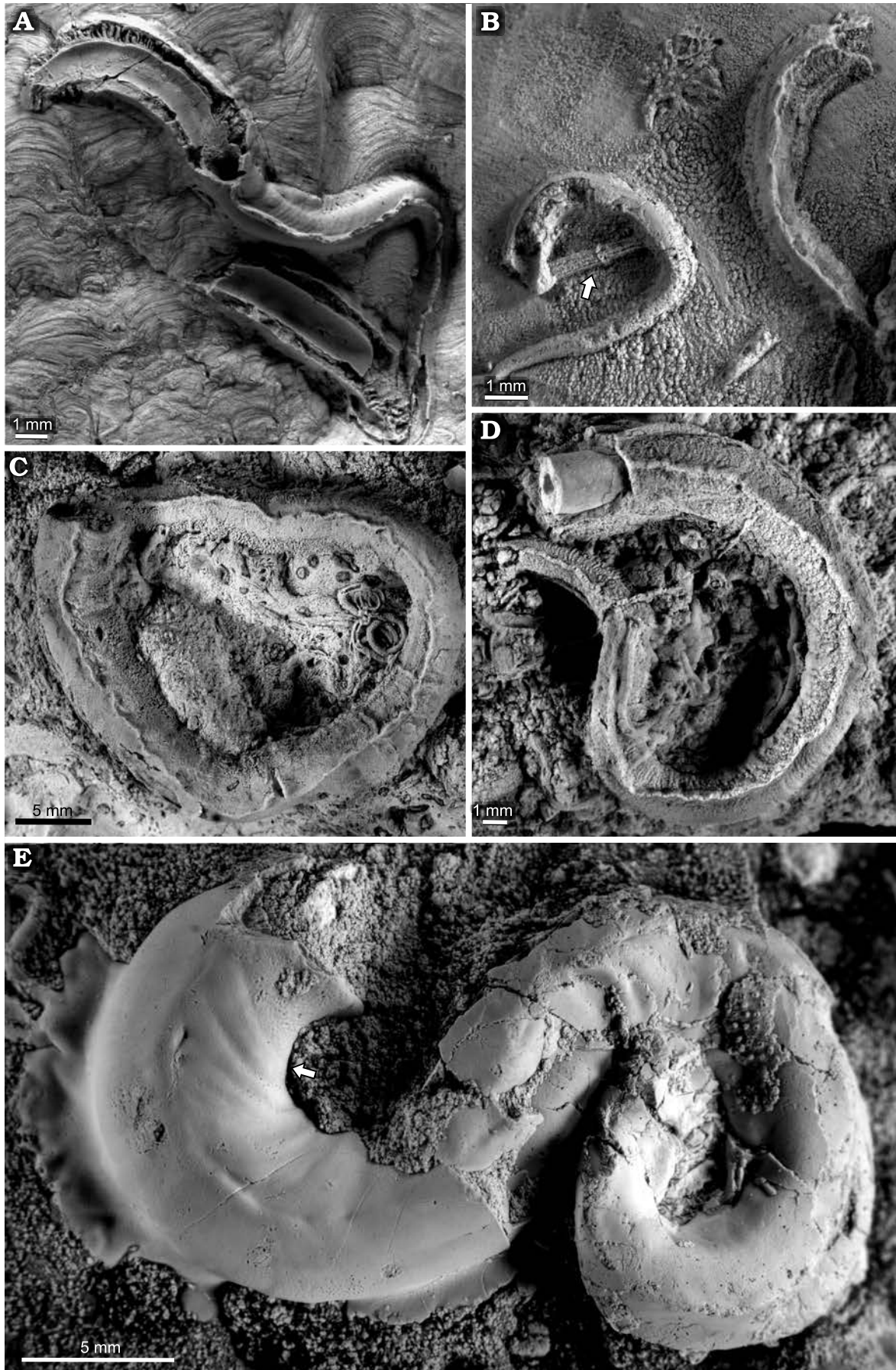
for the sake of coherence, we use such taxonomic names as forma "*limax*" and forma "*conformis*" (both of Goldfuss 1831) only as names of particular morphotypes. In fact, a part of the studied specimens of *Propomatoceros lumbricalis* might have been represented by the genuine representatives of *Propomatoceros limax* (Goldfuss, 1831) and *Propomatoceros conformis* (Goldfuss, 1831).

Propomatoceros lumbricalis sensu stricto differs from the forma "*limax*" by its more prominent keel, better developed but less common peristomes, and smooth surface, as well as less convex lateral walls due to a usually faster growth. It differs from forma "*conformis*" in the more prominent and rather more undulating median keel and in the more rounded cross-section. Our specimens also exhibit a striking morphological resemblance to this species as described and figured by Ippolitov (2007b; see also Słowiński et al. 2020).

Further detailed studies are needed concerning the affinity and the true systematic position of the genus *Propomatoceros* within the "*Spirobranchus* group", as well as a reliable intrageneric division of the genus. Detailed morphological studies engaging statistical methods within and between certain groups of *Propomatoceros* serpulids inhabiting different palaeoenvironments, both different-aged and coeval, together with microstructural data of different morphotypes will possibly help to solve this problem. Perhaps, it will allow to draw a proper universal concept of Jurassic species of *Propomatoceros*. All in all, at the moment it is not possible to provide unambiguous determination of species, proper differentiation between them, and exact stratigraphic ranges of all *Propomatoceros* fossils studied herein.

Stratigraphic and geographic range.—The material studied herein comes from the middle Bathonian–Callovian (Middle Jurassic) of the Polish Jura, and lower Kimmeridgian (Upper Jurassic) of the Mesozoic margin of the Holy Cross Mountains (Małogoszcz). This species was also reported from the Middle and Upper Jurassic of Germany (Schlotheim 1820; Parsch 1956) and the Middle Jurassic of Central Russia (Ippolitov 2007b).

Propomatoceros sp. 1

Figs. 7E, 8A, B.

Material.—Five variously preserved specimens, four of which encrust oyster shells and one encrusting a hiatus concretion from the upper Bajocian (Middle Jurassic) of Mokrsko and the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730, GIUS 8-3751.

Description.—Tubes large (up to 60 mm long) and robust, strongly curved or serpentine, rarely forming loops, but also with straight portions. Tube diameter growing moderately slowly and reaching up to 4 mm. Uneroded tube parts with an indistinct median keel presumably present along the entire tube length and forming only a slightly marked denticle above the aperture. Tubes with densely and regularly spaced, chevron-shaped transverse growth lines; interspaces between the growth lines only slightly wider than the width of growth lines. Common but indistinct alae-type peristomes occur at irregular intervals. The shape of growth lines and peristomes is identical, but peristomes are about twice as prominent as growth lines. Cross-section subtriangular to subcircular due to strongly convex walls in later ontogenetic stages. The tube wall is thick and often breaks along the boundary between its two layers.

Remarks.—The specimens studied superficially resemble *Propomatoceros semicostatus* (Regenhardt, 1961) sensu Luci et al. (2013) in their large size, strong, characteristic ornamentation, and typical coiling. However, the type specimen figured by Regenhardt (1961) is smaller than *Propomatoceros* sp. 1 studied herein and more straight. In addition, the type specimen of *Propomatoceros semicostatus* as well as the tubes described by Luci et al. (2013) were found in Lower Cretaceous deposits; therefore, it is rather unlikely that our specimens belong to *P. semicostatus*. Our tubes may represent a new species; however, due to the highly limited number of specimens, we refrain from designation of the new species.
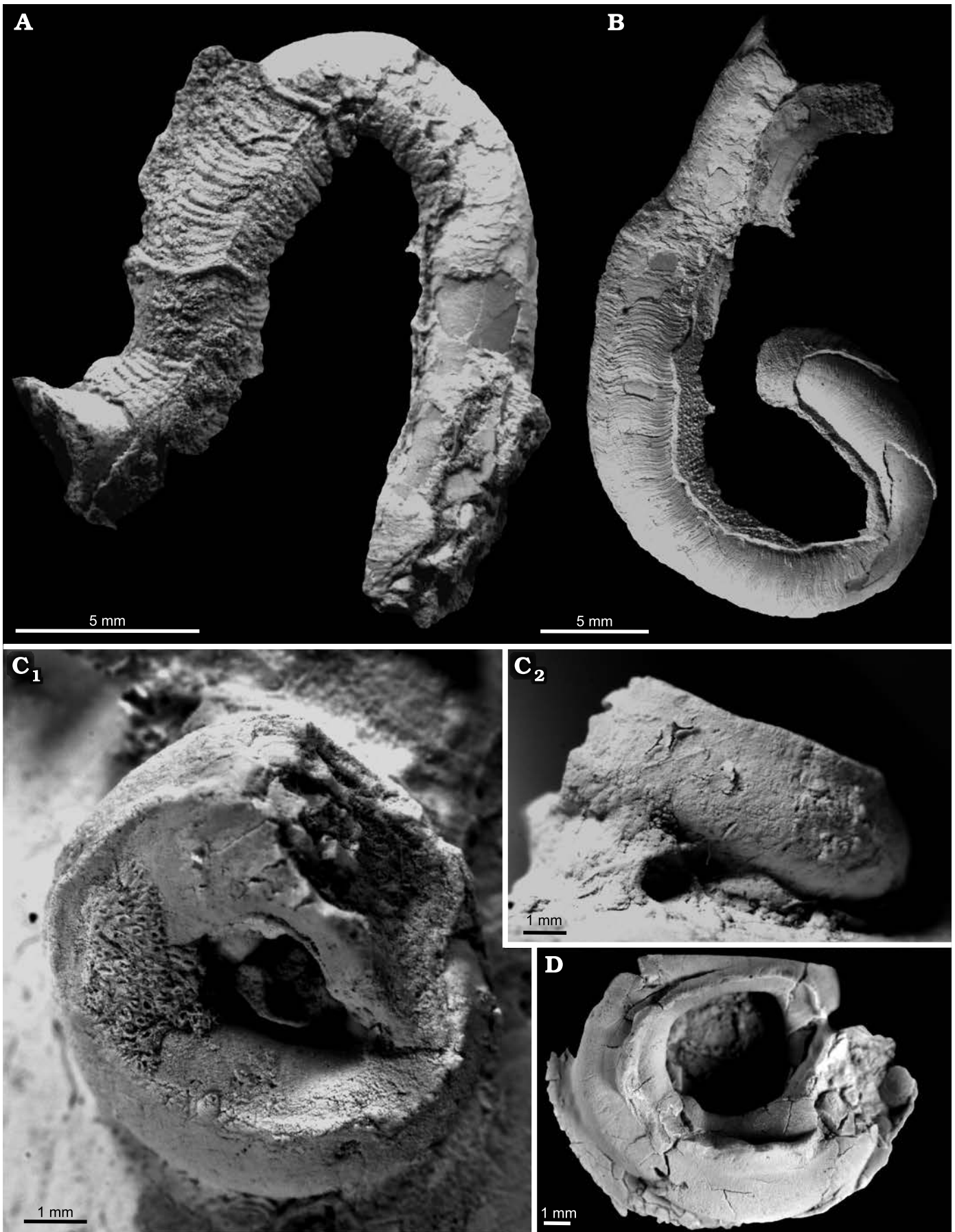
Propomatoceros sp. 2

Fig. 8C.

Material.—One specimen encrusting a small shell fragment of *Ctenostreon proboscideum* (Sowerby and Sowerby, 1820) from the Callovian (Middle Jurassic) of Zalas, Polish Jura (see Table 1); GIUS 8-3589.

Description.—The tube diameter reaching 2.5 mm, but the diameter of the entire tightly coiled specimen not exceeding 10 mm. Posterior tube parts planispirally coiled and attached to the substrate along their entire length, the anterior part of the tube overgrows older portions, forming a loop with an open but narrow umbilicus, and rising above the substrate. The tube robust and possessing a not very high but consistent, only slightly undulating median keel. Otherwise the surface smooth. The base not distinctly widened; however, attachment structures visible due to expansion of the lowermost tube parts. Lateral walls distinctly convex and the tube is delicately flattened, resulting in a subtriangular or even almost circular cross-section and slightly lowered lateral sides below the median keel.

← Fig. 7. Representatives of the serpulid polychaete *Propomatoceros* spp. from the Jurassic of Poland. **A**. Partially eroded *Propomatoceros lumbricalis* (Schlotheim, 1820) encrusting an oyster shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/13); eroded tube fragments show well-developed tubules, which are divided into chambers by densely spaced septa. **B**. Two specimens of *Propomatoceros lumbricalis* forma "*conformis*" and partially preserved, straight, tiny serpulid *Metavermilia* cf. *striatissima* (Fürsich, Palmer, and Goodyear, 1994) (arrow) inside an unclosed loop of *P. lumbricalis* encrusting a shell fragment from the upper Bathonian–lower Callovian of Bolęcin (GIUS 8-3745/2). **C**, **D**. *Propomatoceros lumbricalis* forma "*limax*" encrusting shell fragments from the Callovian of Zalas (**C**, GIUS 8-3589/12; **D**, GIUS 8-3589/13). **E**. Robust *Propomatoceros* sp. 1 encrusting a hiatus concretion from the upper Bajocian of Mokrsko (GIUS 8-3751/5); the arrow points to the delicate growth lines.

Remarks.—The single tube is assigned to the *Propomatoceros* due to its low but distinctive keel and relatively large size. The specimen is characterized by a kind of tight coiling, which, although not common, is not so rare in *Propomatoceros.*

Propomatoceros sp. 3

Fig. 8D.

Material.—One specimen attached to a bivalve shell from the lower Kimmeridgian (Upper Jurassic) of Małogoszcz, the Mesozoic margin of the Holy Cross Mountains, Poland (see Table 1); GIUS 8-3747.

Description.—The tube large, robust, and significantly increasing in diameter (up to 4 mm). The entire specimen coiled and forms a loop. A very prominent, slightly undulating keel on the top of the tube, which results in its subtriangular cross-section. Otherwise, the surface completely smooth, lacking any ornamentation. Flanges are very well-developed.

Remarks.—The specimen is assigned to the genus *Propomatoceros* because of the large size, the very distinctive keel and very well-developed flanges. Nevertheless, it seems to differ from other species of *Propomatoceros* by its completely smooth surface lacking any growth lines or ornamentation except for the keel.

Genus *Nogrobs* Montfort, 1808

Type species: *Nogrobs vermicularis* Montfort, 1808, Middle Jurassic (presumably Stephanoceras humphriesanum Zone of the Bajocian), Muttenz, Switzerland.

Nogrobs aff. *quadrilatera* (Goldfuss, 1831)

Fig. 9A–C.

Material.—36 specimens, the majority of which are well-preserved, encrusting belemnite rostra from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—Tubes medium-sized (up to 25 mm long), straight to slightly curved, adjusting to the available solid substrates to which they are attached: small to medium-sized, but relatively long belemnite rostra. Tubes growing relatively fast in diameter in the early ontogenetic stages where some of the specimens forming either a loose or a tight spiral, whereas in the adult anterior tube portions increase in diameter (up to 1.5 mm) slowly or very slowly. The tube base sometimes delicately widened and rarely possesses hollow flanges, which are visible in a few cases where the tubes are partly worn out. Tubes distinctly flattened on top and have three median longitudinal crests, of which the two marginal ones more con-

spicuous than the central one, which is faint or barely present. The vast majority of specimens attached to the substrate along their entire length; only in a few tubes the anterior portions raised above a substrate. Transverse ornamentation represented by well-visible, regular growth lines which are especially well-developed between the keels. Weakly developed nodular peristomes occasionally occur. Lateral walls nearly parallel, resulting in a subquadrangular to subcircular cross-section, in some specimens slightly convex in profile. The tube wall composed of two layers.

Remarks.—The tubes are assigned to *Nogrobs* aff. *quadrilatera* (Goldfuss, 1831) because their cross-section, shape and ornamentation are characteristic for this species. Similarly to our specimens, *N. quadrilatera* sensu stricto has a flattened upper side, three small median keels and a subquadrangular cross-section. However, unlike in species of *Nogrobs* from many other localities (e.g., Germany, England), the broken-off, free tube portions which originally rose above the substrate are relatively rare in our materials. Our tubes somewhat resemble *Nogrobs tricarinata* (Goldfuss, 1831) (see Parsch 1956: 224, pl. 21: 21). Moreover, *Serpula tricarinata* (Goldfuss, 1831), is a junior homonym of *Serpula tricarinata* Sowerby, 1829, the latter correctly affiliated to *Mucroserpula* by Ippolitov (2007b). To replace Goldfuss' (1831) invalid junior homonym, Ippolitov (2007a) proposed a new combination *Metavermilia goldfussi*. *Nogrobs* aff. *quadricarinata* reported by Vinn et al. (2014: fig. 4G, H) bears similar growth lines to those present in our specimens; however, these are less visible.

Nogrobs? aff. *tricristata* (Goldfuss, 1831)

Fig. 9D, E.

Material.—Eight, mostly well-preserved specimens encrusting belemnite rostra from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—Tubes medium-sized (up to 20 mm long), straight or only slightly undulating; however, in two cases they form a loose loop in the early ontogenetic stages. The upper surface flattened and bears three consistent longitudinal keels. The central keel rather weakly developed, the lateral two are more distinct. All three keels well-visible and present in all specimens along the entire tube length. The lateral walls nearly parallel. The tubes with many irregularly distributed, flaring peristomes which in some specimens slightly protrude at the keels to form short and blunt spines. In some specimens, after forming a sharp, angular folding, the anterior tube part projecting upwards and rising above the substrate. In the anteriormost tube part, walls slightly concave. Prominent and regular growth lines

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← Fig. 8. Representatives of the serpulid polychaete *Propomatoceros* spp. from the Jurassic of Poland. **A**, **B**. *Propomatoceros* sp. 1 detached from fragmented shell from the middle Bathonian of Gnaszyn Dolny (**A**, GIUS 8-3730/14, **B**, GIUS 8-3730/15). **C**. *Propomatoceros* sp. 2 encrusting a shell fragment of *Ctenostreon proboscideum* (Sowerby and Sowerby, 1820) from the Callovian of Zalas (GIUS 8-3745/3); top (C_1) and lateral (C_2) views. Note the anterior tube part overgrowing older portion of the tube and rising above the substrate (C_2). **D**. *Propomatoceros* sp. 3 encrusting a small piece of a shell from the Kimmeridgian of Małogoszcz (GIUS 8-3747/2).
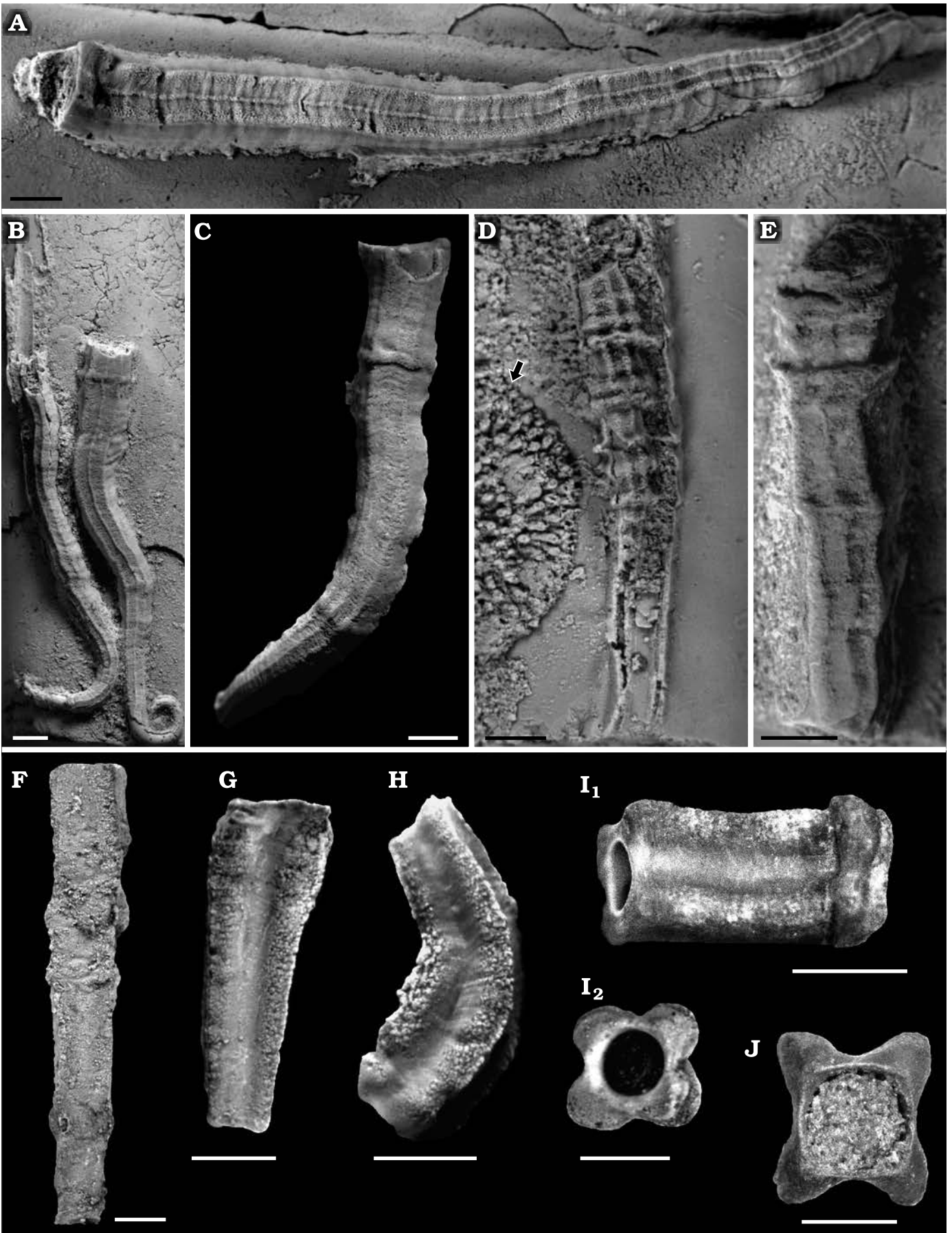
covering the flattened upper surface between the lateral keels. Perpendicular growth lines well-visible also on the lateral tube sides. The tubes gently curved, quadrangular in cross-section, and slowly growing in diameter up to 1 mm. The tube wall composed of two layers.

Remarks.—The specimens studied are tentatively assigned to *Nogrobs* because of their overall shape, quadrangular cross-section and perpendicular growth lines. However, these specimens may also be referred to *Filogranula* due to a characteristic rising above substrate in the anterior part, often slightly flaring and weakly spiny peristomes, and three consistent keels running along the entire tube, although the keels are not denticulate. Specimens discussed here are also similar in general shape to *Nogrobs* aff. *quadrilatera* described above and might also be a variation of that species from the same locality; however, differences comprise flaring and more frequent peristomes, three better developed keels, and parallel or delicately concave lateral walls (see Parsch 1956: 225, pl. 19: 17). *Filogranula tricristata* (Goldfuss, 1831) described from Toarcian–Aalenian (Lower–Middle Jurassic) deposits of Germany has occasionally widened base of the tubes resulting in the trapezoidal cross-section (MJ own observations), which clearly differs from the tubes described here. Moreover, *Filogranula tricristata* is attached to the substrate along its entire length, while the specimens discussed herein have their anterior portions occasionally raised up. This supports the distinction between the studied specimens from Poland and the typical *Filogranula tricristata* from the Toarcian and Aalenian from Germany.

Nogrobs aff. *tetragona* (Sowerby, 1829)

Fig. 9F–J.

Material.—29 specimens from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730; three of the specimens encrust two belemnite rostra and the rest are free-lying/detached.

Description.—Tubes small (up to 10 mm long), almost straight or only slightly curved. Nearly all free-lying; only three partially attached to the substrate. Only the attached posterior tube portion bearing a small median keel on the tube's upper side, whereas the free anterior portion with no median keel. No growth lines visible except those on the lateral walls. Peristomes occasionally occurring; they consist of four thick nodes situated at the edges of the square. The tube diameter expanding very slowly, except for the anterior end where it (up to 1 mm) increases more abruptly. The most distinctive character of the tube, especially of its free anterior portion, is the quadrangular cross-section, with all the walls markedly concave between the edges.

Remarks.—*Nogrobs tetragona* was described from claystone of late Oxfordian–early Kimmeridgian age in England, and is characterized by masses of densely entangled clusters of tubes (Sowerby 1829), which are not attached to the substrate, lack any attachment scars and never tend to form a compact spiral in the posterior tube part (MJ own observations). However, *N. tetragona* has been used in the literature in a wider sense (e.g., Sowerby 1829; Gerasimov 1955; Ippolitov 2007a) for predominantly free tube portions, which lack or possess only inconspicuous, rare peristomes with a quadrangular cross-section, found in many localities from the Middle and Upper Jurassic of England (Sowerby 1829) and Germany (Parsch 1956). The tubes described here match *N. tetragona* well, if it is understood in that wider sense. The specimens described show a very close resemblance to "*Serpula* (*Tetraserpula*) *tetragona*" (see Parsch 1956: 223, pl. 21: 14), "*Tetraserpula tetragona*" (see Ippolitov 2007a), and to a lesser extent to "*Serpula* (*Tetraserpula*) *quadrisulcata*" (see Parsch 1956: 227, pl. 21: 15), which bears more prominent and sharp margins.

Genus *Mucroserpula* Regenhardt, 1961

Type species: *Mucroserpula mucroserpula* (Regenhardt, 1961); Hauterivian (Lower Cretaceous), Schandelah, north Germany.

Mucroserpula tricarinata (Sowerby, 1829)

Fig. 10A.

1829 *Serpula tricarinata* sp. nov.; Sowerby 1829: 226, pl. 608: 3, 4.
1956 *Serpula* (*Tetraserpula*) *quinquangularis* Goldfuss 1831; Parsch 1956: 224, pl. 19: 9, pl. 20: 13, pl. 21: 25.
2007 *Mucroserpula tricarinata* (J. de C. Sowerby, 1829); Ippolitov 2007b: 429, pl. 12: 1a, 1b, 2.

Material.—Two partially preserved specimens attached to bivalve shells from the Callovian (Middle Jurassic) of Zalas, Polish Jura (see Table 1); GIUS 8-3589.

Description.—Tubes medium-sized (less than 20 mm long), curved in a loose loop, moderately increasing in diameter (ca. 1 mm). The tubes possessing a consistent, slightly undulating median keel and two weaker lateral keels. Delicate, perpendicular growth lines visible along most of the tubes' length. Specimens are attached to the substrate along their entire length, and the tube base is widened, resulting in a triangular to subtriangular cross-section; however, the anteriormost parts are pentagonal due to the three keels and the edges of the base.

Remarks.—The specimens described are assigned to the genus *Mucroserpula* due to their characteristic three keels and the mode of coiling. In spite of the fact that the tubes are not very well-preserved, the features indicative of *Mucroserpula*

← Fig. 9. Representatives of the serpulid polychaete *Nogrobs* spp. from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Poland. **A**–**C**. *Nogrobs* aff. *quadrilatera* (Goldfuss, 1831) encrusting belemnite rostra (**A**, GIUS 8-3730/16; **B**, GIUS 8-3730/17; **C**, GIUS 8-3730/18); the specimen in C has been partially detached from its substrate. **D**, **E**. *Nogrobs*? aff. *tricristata* (Goldfuss, 1831) encrusting belemnite rostra (**D**, GIUS 8-3730/19; **E**, GIUS 8-3730/20); ctenostome bryozoan colony indicated by arrow in D. **F**–**J**. Free-lying tubes of *Nogrobs* aff. *tetragona* (Sowerby, 1829) (GIUS 8-3730/21–25, respectively); lateral (I_1) and cross-section (I_2) view; I_2 shows characteristic quadrangular cross-section with distinctly concave walls between the edges. Notice characteristic quadrangular cross-section with distinctly concave walls between the edges visible in J. Scale bars 1 mm.
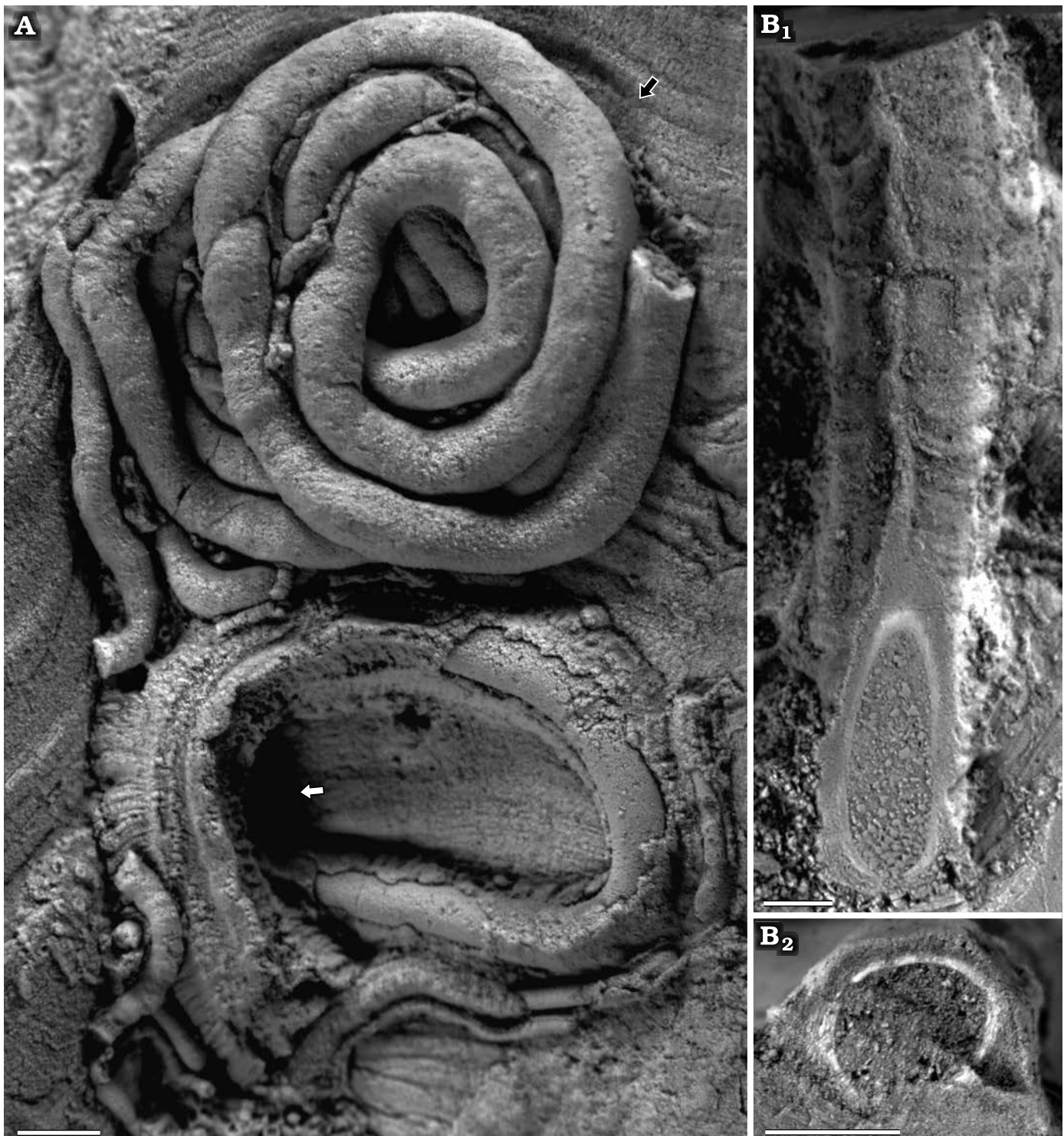
Fig. 10. Serpulid and sabellid polychaetes from the Jurassic of Poland. **A**. *Mucroserpula tricarinata* (Sowerby, 1829) (white arrow) and sabellid *Glomerula gordialis* (black arrow) encrusting a fragment of a shell from the Callovian of Zalas (GIUS 8-3589/14). **B**. *Mucroserpula*? sp. encrusting a fragment of a shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/26); top (B$_1$) and cross-section view (B$_2$). Notice the characteristic pentagonal cross-section (B$_2$) due to the presence of three keels. Scale bars 1 mm.

are sufficiently visible. Our specimens are small compared to other specimens of *Mucroserpula tricarinata*, presumably representing juveniles. *Mucroserpula jaegeri* Radwańska, 2004, from the lower Kimmeridgian (Upper Jurassic; see Wierzbowski et al. 2016) of central Poland differs from *M.* *tricarinata* by its very regular spiral coiling: the posterior tube portion forms a tightly coiled spiral, whereas the anterior, which is still attached all along its length, forms a wide open spiral curve. Moreover, *M. jaegeri* has weaker developed lateral keels and a more distinctly flattened tube.

Stratigraphic and geographic range.—The material studied here come from Callovian (Middle Jurassic) of Zalas, Polish Jura. *Mucroserpula tricarinata* was also reported from the Middle and Upper Jurassic of England (Sowerby 1829), Germany (Parsch 1956), and Russia (Ippolitov 2007b).

Mucroserpula? sp.

Fig. 10B.

Material.—Two specimens attached to an oyster shell and a belemnite from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—Tubes relatively small, up to 15 mm long, increase slowly in diameter (up to ca. 1 mm), straight and attached to the substrate along their entire length. Tubes with three slightly developed keels, of which the median one may be slightly undulating and with very delicate alae-type peristomes forming a short denticle above the aperture. The tube surface slightly rough and its base only gently widened. Cross-section pentagonal.

Remarks.—The specimens investigated are tentatively assigned to *Mucroserpula* due to their median and supralateral keels and resulting pentagonal cross-section. However, due to their slightly undulating median keel and relatively small size, the tubes may also belong to the genus *Filogranula*. Apart from the distinctive pentagonal cross-section and a short denticle marked above the aperture, both typical for the species of *Mucroserpula*, these tubes also resemble those of species of *Propomatoceros* from the same locality. The somewhat artificial classification of strictly single-keeled *Propomatoceros* and three-keeled *Mucroserpula* is not completely satisfactory, and it is highly subjective where to put a boundary between these genera. Cross-section and appearance of the keels may vary during ontogeny, making clear designations difficult. Additionally, diagenetic compression may also change the curvature and general outline. Although species of *Mucroserpula* are usually described as forming loop-like tubes (e.g., Ippolitov 2007b), coiling mode cannot be a primary indicative feature as the coiling may be facultative and strongly dependent on the kind of substrate and restriction of space for winding and coiling. Finally, the number of specimens described here is limited, hampering proper and unambiguous determination.

Genus *Placostegus* Philippi, 1844

Type species: *Serpula tridentata* (Fabricius, 1779); Recent, Greenlandic part of the Arctic Ocean.

Placostegus planorbiformis (Münster in Goldfuss, 1831)

Fig. 11A.

1831 *Serpula planorbiformis* sp. nov.; Münster in Goldfuss 1831: 231, pl. 68: 12a, b.
1956 *Serpula* (*Tetraserpula*) *planorbiformis* Münster 1831; Parsch 1956: 225, pl. 19: 10, pl. 20: 1, 2.

Material.—Seven relatively well-preserved specimens encrusting sponges from the lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura; GIUS 8-3746.

Description.—Tubes medium-sized, planispirally (sinistrally) and tightly coiled; diameter of the tube up to 2.5 mm, while the diameter of the entire spiral is ca. 10 mm. Spiral leaves only a narrow but deep central umbilicus open; however, coiling is evolute, leaving parts of the inner whorls well visible and countable. The tubes consist of four whorls increasing moderately rapidly in diameter. Tubes attached to the substrate along most of their length, except for the anterior part which may be attached predominantly to the previous whorl. The tube base widened. Cross-section subtriangular due to the presence of an explicit keel running uniformly along the entire tube length and forms a spine above the aperture. The anteriormost part projecting upwards; possibly it grew vertically (see Radwańska 2004); however, this is not evident in the material studied. The tube wall thick.

Remarks.—The studied specimens are very similar to those described by Radwańska (2004) as *Placostegus conchophilus* (Radwańska, 2004). However, *P. conchophilus* possesses a rather convex outer wall, whereas in *P. planorbiformis* the cross-section is roof-shaped, topped by a low, consistent keel.

Stratigraphic and geographic range.—The material studied herein comes from lower Oxfordian (Upper Jurassic) of Zalas, Polish Jura. *P. planorbiformis* is also common in the Oxfordian (Upper Jurassic) of South Germany (e.g., Parsch 1956; MJ own observation).

Genus *Pseudovermilia* Bush, 1907

Type species: *Spirobranchus occidentalis* (McIntosh, 1885); Recent, The Bermuda Archipelago.

Pseudovermilia sp.

Fig. 11B.

Material.—Four tubes attached to rock fragments from the Callovian (Middle Jurassic) of Zalas, Polish Jura (see Table 1); GIUS 8-3589.

Description.—Tubes long (up to 50 mm), rather flat, irregularly curved, having nearly constant diameter (ca. 1 mm). Ornamentation composed of closely and regularly spaced transverse elements subdivided in the middle by a slightly thicker longitudinal crest running through the entire tube length, and two similar longitudinal crests situated at the lateral margins of the flat upper side. The combination of transverse and longitudinal ornamentation results in a regular, reticular pattern which is disturbed only by larger, slightly nodular peristomes. Some of the transverse elements are slightly curved forward near the longitudinal crests, but this curvature is not always well-developed. Structures resembling tubulae usually present within basal flanges occur uniformly throughout the entire tube.
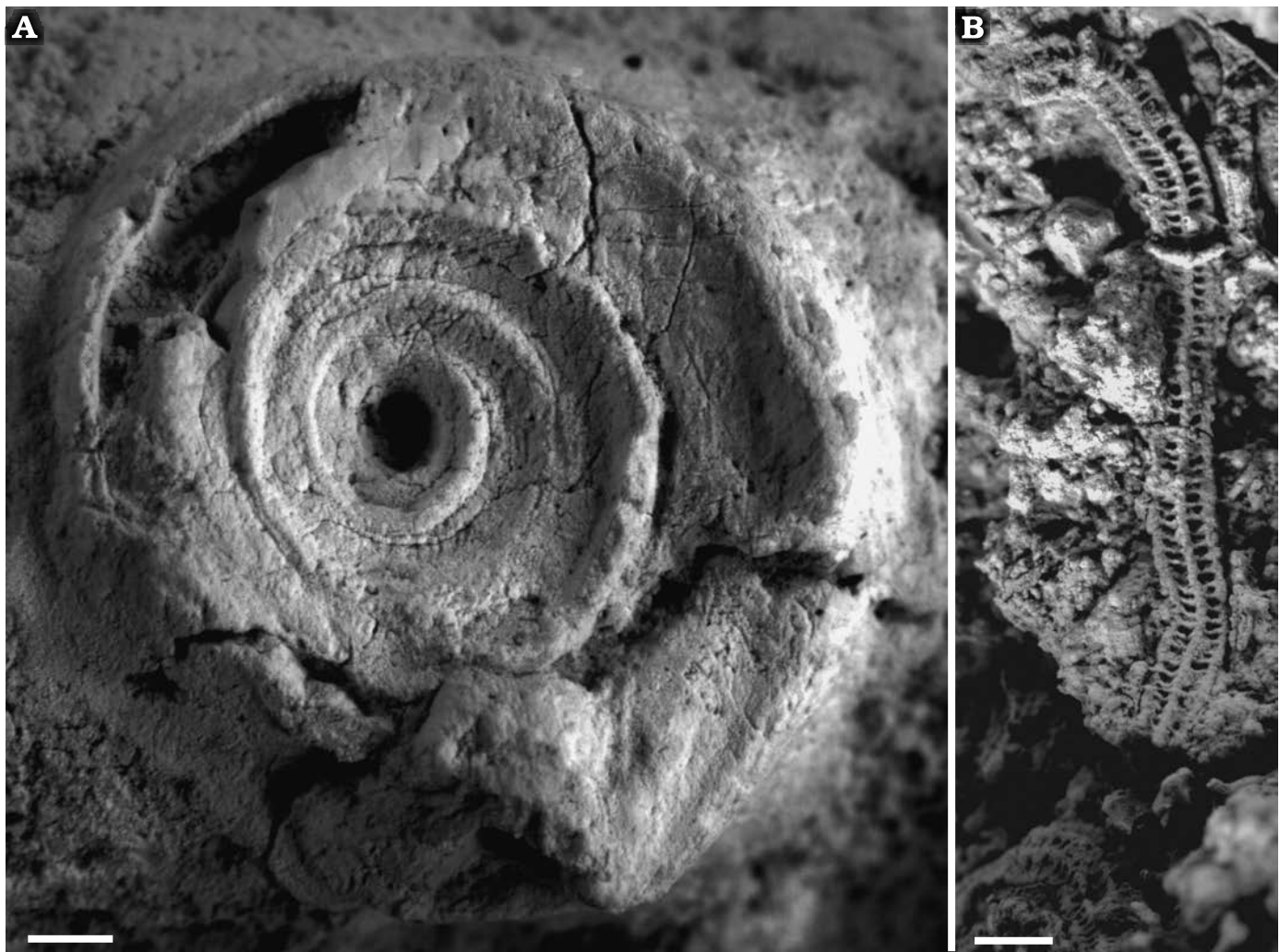
Fig. 11. Serpulid polychaetes from the Jurassic of Poland. **A**. *Placostegus planorbiformis* (Münster in Goldfuss, 1831) encrusting a sponge fragment from the Oxfordian of Zalas (GIUS 8-3746/8). **B**. *Pseudovermilia* sp. encrusting a rock fragment from the Callovian of Zalas (GIUS 8-3589/15). Scale bars 1 mm.

Remarks.—The four specimens studied are assigned to the genus *Pseudovermilia* due to their very distinctive, reticulate tube morphology (see Hove 1975; Jäger and Lang 2017). In the Mesozoic, *Pseudovermilia* occurs very rarely. The genus was previously reported by Jäger and Lang (2017) from the Kimmeridgian (Upper Jurassic), based on a single specimen only. Because of a very limited material, scarce reports, and scarce occurrences, we are unable to provide a reliable specific name. It is possible that our specimens represent a new species. To the best of our knowledge this is the first report of this genus from Poland.

Serpulidae sp. 1

Fig. 12A, B.

Material.—71 specimens attached to bivalve shells (and moulds to a lesser extent), and oncoids from the upper Bajocian–lower Bathonian (Middle Jurassic) of Ogrodzieniec-Świertowiec (23), upper Bathonian–lower Callovian (Middle Jurassic) of Bolęcin (5), and Callovian (Middle Jurassic) of Zalas (43), Polish Jura (see Table 1); GIUS 8-3589, GIUS 8-3745, GIUS 8-3750.

Description.—Tubes small to medium-sized (up to 100 mm long). Tubes are morphologically diverse, ranging from almost straight, gently curved to more strongly coiled. Tube diameter (slightly exceeding 1 mm) almost constant in the adult part. Depending on the specimen, tubes may be either smooth without any ornamentation, except for well-developed, irregularly scattered ampullacea-type to slightly nodular peristomes, or bear some corrugations and/or striae on the tube's outer surface. On the upper side of some of the tubes a faint, crest-like keel present, as well as two longitudinal, lateral edges on the marginal parts of the tube. The tube attached to the substrate by its entire length with minor flanges. The tube base seems to be even narrowed below the lateral margins which are directed outwards. All the specimens are distinctly flattened which results in the rounded-rectangular, or at least angular, to subcircular cross-section.

Remarks.—The general shape of the tubes (irregularly curved, of nearly constant diameter and substantial length, bearing ampullacea-type to slightly nodular peristomes and longitudinal ornamentation) is similar to the *Pseudovermilia*
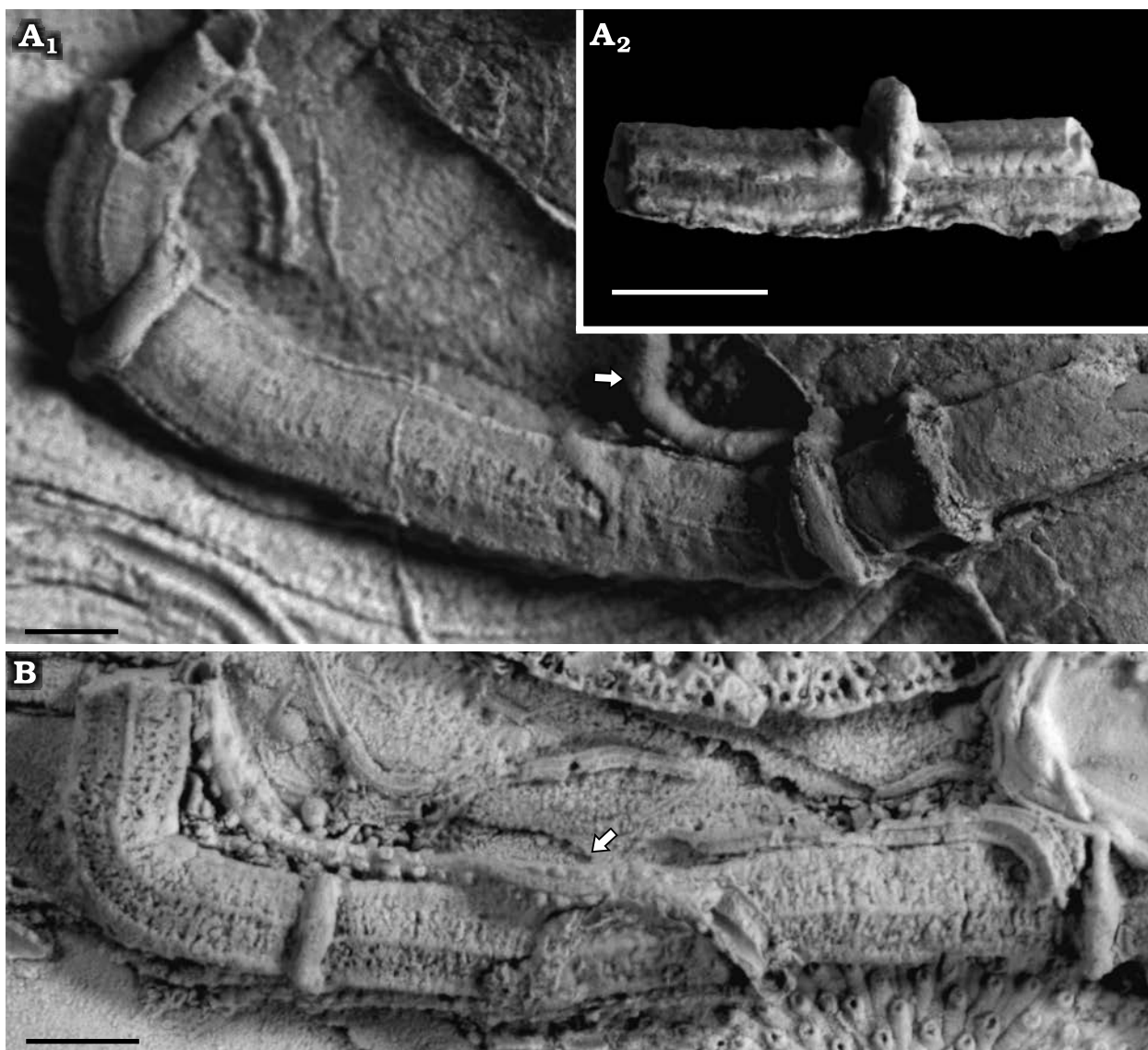
Fig. 12. Serpulidae sp. 1 from the Jurassic of Poland. **A**. Serpulidae sp. 1 and a tiny *Glomerula gordialis* (Schlotheim, 1820) (arrowed) encrusting a shell fragment from the upper Bathonian–lower Callovian of Bolęcin (GIUS 8-3745/4); top (A_1) and lateral (A_2) view; A_2 shows a flattened shape of the tube. **B**. Serpulidae sp. 1 and a tiny, presumably juvenile *Filogranula runcinata* (Sowerby, 1829) (above, arrowed) encrusting a shell fragment from the Callovian of Zalas (GIUS 8-3589/16). Scale bars 1 mm.

sp. described above. The difference is the intensity of the reticulate ornamentation, which is very prominent in *Pseudovermilia* sp., whereas in the Serpulidae sp. 1 it is less pronounced, or even occasionally lacking in some parts of the tubes. The reticulate ornamentation of Recent tubes of *Pseudovermilia* may be very variable, but remains strong (Hove 1975), which rather excludes our specimens from this genus. Alternatively, at least a part of the tubes may represent a species of either *Filogranula* or *Nogrobs* with relatively well-developed transverse ornamentation.

Serpulidae sp. 2

Fig. 13A.

Material.—One unattached and partially eroded specimen from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—The tube is thick and robust, 7 mm in diameter, less than 16 mm long, consisting of a small attached and a short free tube portion. bearing irregular but prominent ampullacea-type peristomes. The specimen bearing some well-visible, perpendicular growth lines. Cross-section circular, wall composed of two layers.

Remarks.—The specimen shows some superficial resemblance to *Neovermilia ampullacea* (Sowerby, 1829) (Jäger 1983: 41, pl. 5: 3, as "*Proliserpula ampullacea*") due to distinctive, thick, bulge-like ampullacea-type peristomes and circular cross-section.

Serpulidae sp. 3

Fig. 13B.

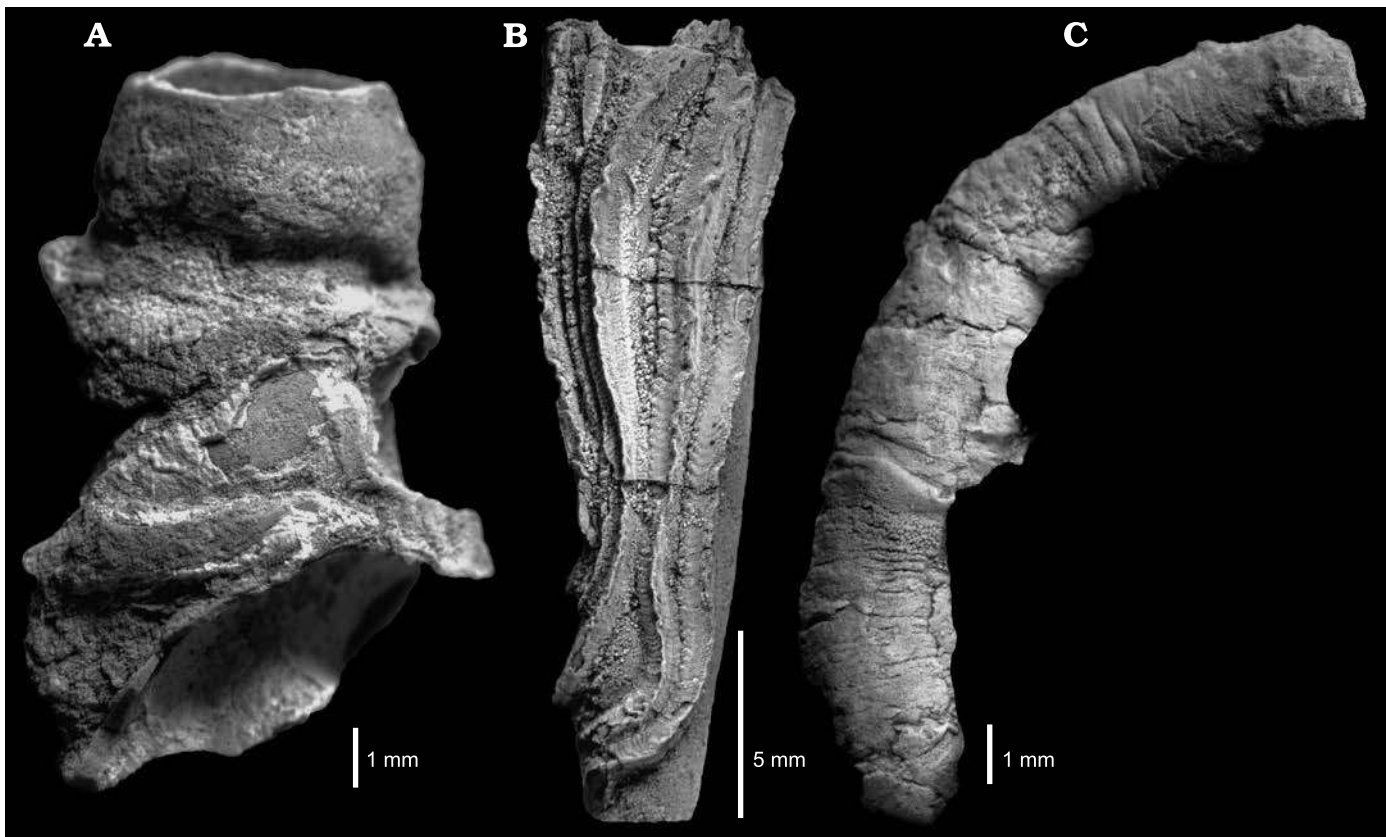*Material*.—Ten specimens attached to belemnite rostra from

Fig. 13. Serpulid polychaetes from the Jurassic of Poland. **A**. Unattached Serpulidae sp. 2 from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/27). **B**. Dense aggregation of closely spaced Serpulidae sp. 3 encrusting a fragment of a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/28). **C**. Serpulidae sp. 4 from the lower Kimmeridgian of Małogoszcz (GIUS 8-3747/3).

the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny, Polish Jura (see Table 1); GIUS 8-3730.

Description.—Tubes medium-sized (ca. 20 mm long), straight to slightly curved or slightly serpentine, nearly constant in diameter (up to 1 mm). The tubes with three very widely spaced keels; the two relatively weakly developed lateral keels located very close to the tube base. The prominent and thick median keel is occasionally slightly undulating. Small transverse ribs are most often well-visible, especially in the anterior tube part; they are densely and regularly spaced and curved forward, towards the three keels. Tubes most often attached to the substrate for their entire length with rare exceptions, where a part of the tube rises slightly above the substrate. The characteristic distribution of keels resulting in wide furrows in between them and thus triangular, subtriangular or otherwise angular cross-section.

Remarks.—Most of the tubes have been found on a single belemnite rostrum; they form a dense aggregation of closely spaced tubes. The specimens somewhat resemble species of several genera, but do not fully match any of those, so that we decided not to assign them to a definite genus. They resemble species of *Propomatoceros* and *Placostegus* in their triangular cross-section with a prominent median keel, and of *Placostegus* in the small and only slowly increasing tube diameter and small transverse ribs. However, they

differ from these genera by possessing two lateral keels. Moreover, they slightly resemble *Metavermilia*? sp. described above; however, their longitudinal ornamentation is less pronounced; the median keel forms a simple upper edge to the tube ("Kante" sensu Jäger 1983: 14, fig. 4a), and the lateral crests are only very delicate, placed at the very bottom lateral parts of the tubes.

Serpulidae sp. 4

Fig. 13C.

Material.—Six specimens (four partially preserved, attached to oyster shells and two specimens detached) from the lower Kimmeridgian (Upper Jurassic) of Małogoszcz, Mesozoic margin of the Holy Cross Mountains, Poland (see Table 1); GIUS 8-3747.

Description.—Tubes large (up to 30 mm long, however, none of the specimens fully preserved), externally covered with prominent growth lines running perpendicularly to the tube long axis but showing no other ornamentation. Some thick, slightly curved tubes are attached to the substrate, but most specimens represent broken off anterior tube fragments. The cross-section is circular with the diameter up to 2 mm.

Remarks.—The specimens are superficially similar in general outline to *Glomerula gordialis* (Schlotheim, 1820) apart from the perpendicular growth lines and much thicker tubes.

Discussion

Serpulid and sabellid diversity and distribution across palaeoenvironments.—The use of cluster analysis allowed us to group the investigated fossils into several clusters (Fig. 14). The study shows that serpulids and sabellids are highly dependent on the habitat, especially the substrate they are cemented to, whereas the geological age or the stratigraphical distance between compared localities plays a minor role. This is in agreement with studies of other ancient serpulid and sabellid tubeworms. Although some morphotypes might have not been confined to certain substrates (e.g., Kočí et al. 2019), the nature and resultant physical properties of the substrate appear to have been among the most crucial factors inducing serpulid and sabellid colonization (see Ippolitov 2010). However, tube-dwelling polychaetes in general are also reliant upon factors other than substrate. Temperature, oxygen and salinity levels, as well as light availability might also influence larval settlement (Kupriyanova et al. 2019).

The tube-dwelling polychaetes are preserved attached to a variety of available hard substrates (see Fig. 15). The highest similarity in serpulid and sabellid communities between certain localities is displayed between hiatus concretions and oncoids (Fig. 14), both of which served as mobile substrates prone to physical disturbances (e.g., Wilson 1987; Zatoń et al. 2011a, 2012), differing, however, in the nature of encrusted surface, which had a quantitative and (to a lesser extent) qualitative impact on the communities. Relatively similar to them are hardgrounds sensu stricto, where all taxa present on mobile rockgrounds occur as well. Hardgrounds, hiatus concretions and oncoids evidently witnessed, albeit to a different degree, time-averaging, so that factor could have potentially played a role in composition of tubeworm assemblages. The serpulid and sabellid faunas at the hardground localities are among the most diverse.

Tubeworm faunas encrusting oyster shell beds and those encrusting bivalve shells derived from soft muddy substrates exhibit moderate similarity levels (Fig. 14). Although the substrate available for tube dwelling polychaete colonization was similar, the prevailing conditions were quite different. Low taxonomic variability of serpulid and sabellid worm tubes encrusting parautochthonous oyster shells from the lower Kimmeridgian of Małogoszcz possibly was a result of impeded colonization in a relatively shallow marine environment affected by storm episodes (Machalski 1998).
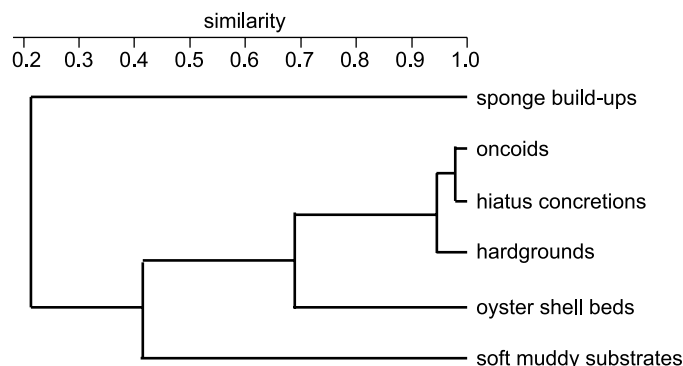

Fig. 14. Dendrogram showing clustering of substrates sharing similar taxa of tube-dwelling polychaetes from the Polish Basin.

On the other hand, oyster shells and their aggregations, together with belemnite rostra, provided isolated benthic islands (e.g., Zuschin et al. 1999; Taylor and Wilson 2003) on otherwise muddy seafloor in relatively calm (below storm wave-base) palaeoenvironments (Gedl et al. 2012). On a soft-bottom, they offered a sufficiently stable substrate for colonization and further establishment of populations. Such conditions led to the highest taxonomic variability among the all palaeoenvironments.

The community from the lower Oxfordian (Upper Jurassic) sponge bioherms of Zalas shows the highest taxonomic distinctness (Fig. 14). Biotic substrate provided by sponges led to domination by usually compact (e.g., *Placostegus planorbiformis*) and fast-growing forms with minute diameters (e.g., *Cementula spirolinites*) and possibly hampered colonization of larger, slowly growing serpulids.

For the majority of localities and settings, moderate Simpson Index of Diversity (1-D) and Dominance (D) values indicate intermediate polychaete variability, with no species highly dominating (see Table 2). Such diversity and dominance values are confined to locations with intermediate levels of hydrodynamic and physical disturbances (e.g., Wilson 1987). Highest biodiversity has been noted on upper Bathonian–lower Callovian and Callovian hardgrounds (Bolęcin and Zalas, respectively) and upper Bajocian–lower Bathonian oncoids (Ogrodzieniec-Świertowiec) (see Table 2); it may attest to time-averaging of deposits with lowered sedimentation rates (hardgrounds) and particularly favourable conditions (oncoids). Slightly lower, but still among the highest diversity levels of Simpson and Dominance indices, are serpulid and sabellid communities derived from

Table 2. Biodiversity indices calculated for the investigated polychaete assemblages.

| Index	Mokrsko	Kawodrza Górna	Gnaszyn Dolny	Bugaj	Ogrodzieniec	Krzyworzeka	Żarki	Ogrodzieniec Świertowiec	Bolęcin	Zalas (Callovian)	Zalas (Oxfordian)	Małogoszcz
Dominance (D)	0.5805	0.481	0.335	0.4692	0.52	0.3795	0.4506	0.2991	0.3219	0.2642	0.4762	0.4403
Simpson (1-D)	0.4195	0.519	0.665	0.5308	0.48	0.6205	0.5494	0.7009	0.6781	0.7358	0.5238	0.5597
Shannon (H)	0.7334	0.8746	1.503	0.8491	0.7388	1.021	0.8676	1.4	1.334	1.546	1.005	0.9683
Evenness e^H/S	0.5205	0.7993	0.4087	0.7792	0.6978	0.9252	0.7937	0.6762	0.6325	0.5213	0.5463	0.6584
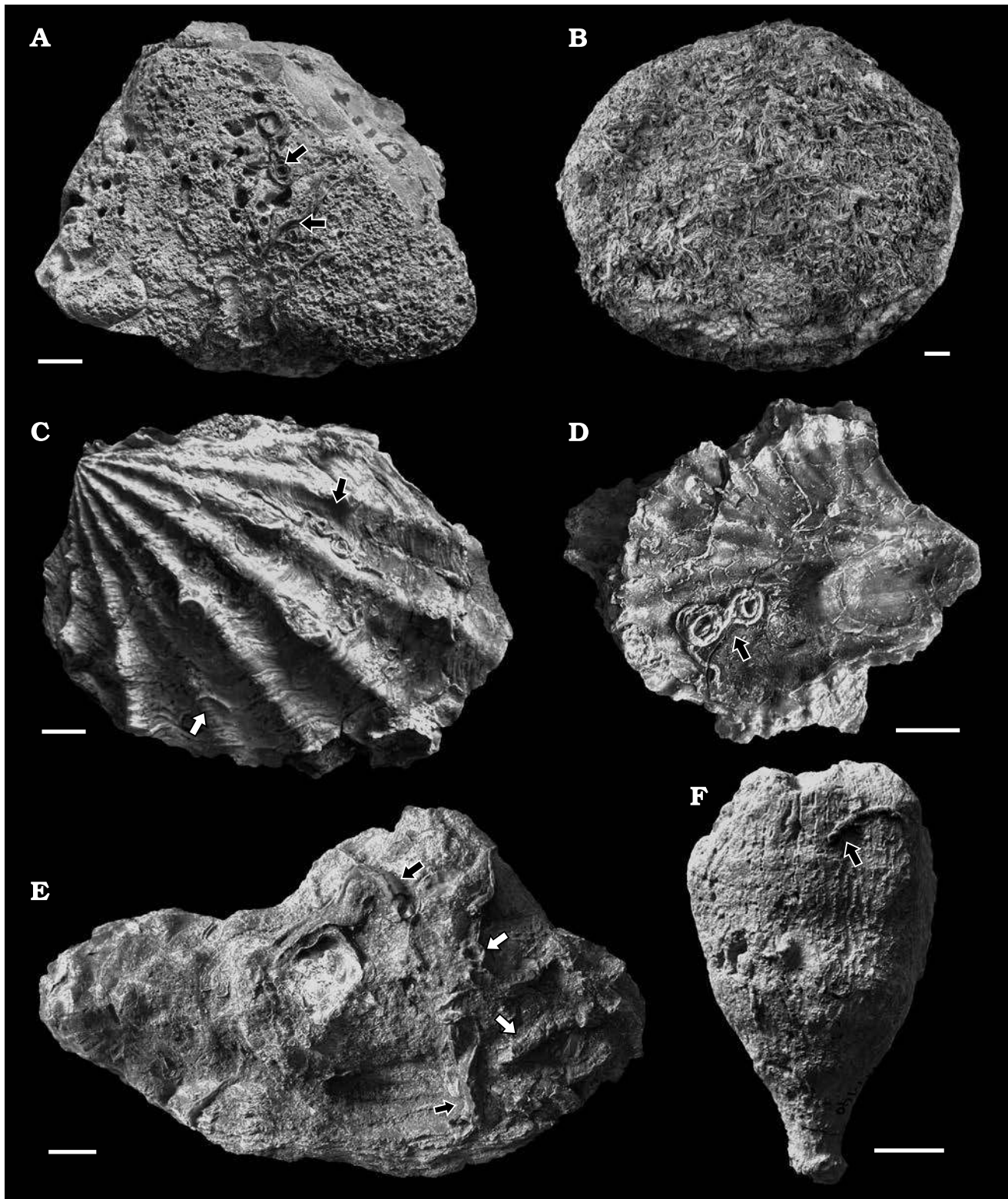
Fig. 15. Representative hard substrates colonized by the Middle and Upper Jurassic tube-dwelling polychaetes from the Polish Basin. **A**. Upper Bathonian hiatus concretion from Ogrodzieniec; sabellid *Glomerula gordialis* (Schlotheim, 1820) (GIUS 8-3751), indicated by arrows. **B**. Bajocian–Bathonian oncoid from Ogrodzieniec-Świertowiec; the entire oncoid is intensively encrusted by serpulids and sabellids (GIUS 8-3750). **C**. Callovian bivalve *Ctenostreon proboscideum* (Sowerby, 1820) from hardground of Zalas; black arrow indicates sabellid *Glomerula gordialis*, white arrow indicates juvenile serpulid *Propomatoceros lumbricalis* (GIUS 8-3589). **D**. Lower Kimmeridgian oyster from oyster shell beds of Małogoszcz; an arrow indicates sabellid *Glomerula gordialis* (Schlotheim, 1820) (GIUS 8-3747). **E**. Middle Bathonian oyster from soft muddy substrates of Gnaszyn Dolny; serpulid *Propomatoceros lumbricalis* (Schlotheim, 1820) is exemplified by arrows (black and white). White arrows point the specimens infested by the hydroid *Protulophila gestroi* (Rovereto, 1901) (GIUS 8-3730). **F**. Oxfordian sponge from Zalas; an arrow indicates serpulid *Filogranula spongiophila* sp. nov. (GIUS 8-3746). Scale bars 10 mm.

middle Bathonian skeletal remains from Gnaszyn Dolny, serving as benthic islands on the soft sediment (see Table 2). Such quiet water conditions may have fitted best with the feeding strategy of most tube-dwelling polychaete species. Based on the values of Shannon index (H), polychaetes from these substrates, together with hardgrounds, are also among the most diverse, followed by oncoids (see Table 2). Evenness values point to moderate (in the case of oncoids from Ogrodzieniec-Świertowiec and lower Kimmeridgian oyster shell beds from Małogoszcz, as well as a part of hiatus concretion localities, e.g., Ogrodzieniec, upper Bathonian), or even low biodiversity (in the case of a part of hiatus concretion localities, e.g., Krzyworzeka, upper Bathonian, and the Callovian hardground of Zalas) (see Table 2), which is an effect of similar proportions of different species' representatives within these assemblages. The lowest evenness level in the case of the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny (see Table 2) testifies to the highest species richness and abundance of both species and individuals at this locality, indicating highly advantageous palaeoenvironmental conditions (see Table 1).

Mobile rockgrounds.—Both fossil (e.g., Wilson 1985; Lee et al. 1997; Zatoń et al. 2011a) and Recent (e.g., Osman 1977; Sousa 1979; Maughan and Barnes 2000; Kuklinski 2009) encrusting biotas inhabiting mobile lithic substrates are strongly affected and restrained by physical disruptions within marine environments, which strongly influences the ecology of substrate-dwellers. Generally, an increase in physical energy in the environment leading to frequent overturning of loose lithic substrates such as hiatus concretions and oncoids causes an increase in diversity of the fauna and hampers single species prevalence (Wilson 1987; Barnes and Kuklinski 2005). On the other hand, too high levels of physical disturbance, where the cobble and pebble overturning is continuous and frequent, may be destructive, leading to a lethal outcome even for the most opportunistic, robust, and scour-resilient serpulids, highly impeding any ecological succession.

Sediments from which the concretions were derived are interpreted to have been deposited in calm conditions, usually located below storm wave-base (e.g., Leonowicz 2013). Hiatus concretions (Majewski 2000; Zatoń et al. 2006, 2011a) and such sedimentological fabrics, as e.g., trace fossil associations, alternating laminated and bioturbated intervals, or biodeformational structures (Leonowicz 2015a) within the Middle Jurassic siliciclastic sediments of the Polish Jura indicate episodic storm events causing distinct sedimentation breaks and seafloor erosion. Rather rare episodic overturning of the mobile substrates resulted in relatively low diversity (in total five species, Table 1) leading to a predominance of robust, thick-walled species of *Propomatoceros* and ubiquitous *Glomerula gordialis*.

The shape and regularity of the concretions' surfaces is another important factor strongly influencing the quantity and distribution of serpulids and sabellids (Wilson 1987). Larger and more rounded hiatus concretions (as well as on-coids; see below) were less resilient to hydrodynamic events and overturning on the sea bottom, compared to wider and more flattened ones. While resting on the seafloor, only the upper sides of these substrates were available for serpulid and sabellid colonization, while lower surfaces facing the sediment were inaccessible. It is possible that even such relatively stable concretions did not offer full stability against overturning. Minor differences in the encrustation pattern between certain localities seem to reflect slight disparities in the general concretions' outlook which in turn presumably resulted from the frequency of episodic hydrodynamic activities, depth of concretions' burial or biological activity of animals inhabiting firmgrounds (Zatoń et al. 2011a). The differences in concretions' bioerosional patterns between the localities, likewise, reflect the position of the certain setting (proximal/distal) and thus the intensity and the frequency of palaeoenvironmental currents (Sadlok and Zatoń 2020). Organisms burrowing in the ambient sediment might have also loosened it enhancing exhumation of the concretions (Hesselbo and Palmer 1992).

The most important serpulid and sabellid adaptive strategies for persistence on mobile lithic grounds (Wilson 1987) were: (i) the morphological resistance to abrasion which was possible by hard and solid tubes; (ii) cavity dwelling; hazardous impact of repeated substrate overturning in highly energetic environments might have entailed attempts of withdrawal, whenever an opportunity had arisen. Tube-dwelling polychaetes often resolve to cryptic lifestyle (Kobluk 1988) hiding in places such as empty borings and concavities (e.g., Palmer and Fürsich 1974; Wilson and Palmer 1990; Palmer and Wilson 1990; Wilson 1998; Taylor and Wilson 2003; Mallela 2007; Schlögl et al. 2008). Such a solution facilitates also retreating from competition with dominating species. Anyhow, in spite of the presence of borings, some of the tubes encrust the surface of the concretions. A possible explanation is that such cavities have already been occupied by boring bivalves, which made the unavailable for nestling by tubeworms, thus of necessity colonizing the outer surface (see also Zatoń et al. 2011a).

Concretions from Mokrsko, Bugaj, Ogrodzieniec, Krzyworzeka, and Żarki experienced high taphonomic loss as the vast majority of encrusters inhabiting the surface of the concretions were prone to abrasion/corrasion, what is evidenced by many poorly preserved fossils, presumably representing various ecological successions.

Although serpulids and sabellids inhabiting large oncoids are only slightly more taxonomically diverse than that from hiatus concretions, attaining one species more (in total six species, Table 1), their abundance is much higher. Tube-dwelling polychaetes thrived inhabiting these coated grains in spite of the fact, that cryptic places were highly limited by the lack of borings, which were common on the hiatus concretions. Intense colonization and further flourishment of serpulids and sabellids must have been enhanced by the photic conditions, where cyanobacterial mats covering oncoids could develop (Zatoń et al. 2012; Słowiński 2019). A high

availability of food supply, especially composed of mixed algae species, significantly induced larval development and subsequent growth (Leone 1970; Kupriyanova et al. 2001; Gosselin and Sewell 2013). Although algal mats covering substrates may hamper epibionts' development (McKinney 1996; Kuklinski 2009; Zatoń et al. 2011b), they may also facilitate it (Wieczorek and Todd 1998; Kupriyanova et al. 2019). Additionally, in contrast to the tubeworms encrusting hiatus concretions, tubeworms colonizing oncoids were able to settle on the not yet lithified substrate during the formation of possibly still mucous biofilm forming on the oncoids (Taylor and Wilson 2003). Another advantage of oncoids over hiatus concretions (serving as a substrate for colonization) is that their stability might have been enhanced during growth. The formation of subsequent cortex layers increased the volume and thus reduced the susceptibility to overturning on the sea bottom.

Hardgrounds.—Serpulids and sabellids from hardgrounds are derived from two localities (Zalas and Bolęcin) of slightly different in palaeoecological conditions. Limited supply of sediment and resulting time-averaging (Giżejewska and Wieczorek 1977; Tarkowski et al. 1994; Mangold et al. 1996; Taylor 2008; Zatoń et al. 2011b) strongly influenced encrustation patterns of both communities. The species richness of tube-dwelling polychaetes in these localities could have resulted from favorable palaeoenvironmental conditions and long-term exposure of the hard substrates; however, some time-averaging responsible for the final assemblage preserved is not excluded (Taylor 2008; Zatoń et al. 2011b).

The Zalas deposits are characterized by a much more abundant and more taxonomically diverse sessile polychaete fauna (in total nine species, see Table 1) as compared to Bolęcin (in total six species, see Table 1). Such differences presumably resulted from more favourable conditions for the settlers, such as a relatively steady salinity level, a calm, sublittoral environment located within a dysphotic zone (Zatoń et al. 2011b), and a slow sedimentation rate at Zalas (Giżejewska and Wieczorek 1977). The total number of tube-dwelling polychaetes from Bolęcin, the deposits of which may be an equivalent of the uppermost Bathonian–lowermost Callovian Balin Oolite (e.g., Tarkowski et al. 1994; Mangold et al. 1996; Taylor 2008), is not among the lowest. However, the investigated number of substrate-serving fossils was ample. Therefore, the percentage of inhabiting sessile polychaetes is low, possibly due to higher abrasion levels and Quaternary periglacial events, which may have reworked the sediments (Mangold et al. 1996), affecting the preservation of the fossils.

Any reciprocal interactions (see Taylor 2016) were very rare, or even absent in Bolęcin; therefore, most of them might have simply resulted from random settling of worms in close proximity and are not an evidence of spatial competition (Zatoń et al. 2011b; Taylor 2016). Most often, tube-dwelling polychaetes are overgrown by bryozoans and other polychaetes, both of the same and different genera, sup-

porting an explanation of random and post-mortem overgrowth on a small surface of substrate (Taylor and Wilson 2003). Anyhow, a scarce number of mutual (reciprocal) overgrowths and intraspecific stand-offs ("when growth of both interacting individuals is halted at their junction"; see Taylor 2016) may suggest that at least some sclerobionts, notably serpulids, were actively competing for available substrate. Some individuals tended to grow towards the deflections between *Ctenostreon proboscideum* (Sowerby and Sowerby, 1820) shell ribs or on the underside of lower valves indicating the preferences of inhabiting cryptic niches.

Oyster shell beds.—In the shell beds with *Actinostreon gregareum* (Sowerby, 1815) within lower Kimmeridgian (Upper Jurassic) deposits of Małogoszcz quarry, many oyster shells which served as substrate for serpulids and sabellids are disarticulated. The oysters set up parautochtonous accumulations, resulting from storm events in a relatively shallow-marine environment (Seilacher et al. 1985; Machalski 1998; Zatoń and Machalski 2013). In spite of the high substrate availability for these polychaetes, their colonization was there impeded by mode of life of the oysters. These bivalves displayed different kinds of ecophenotypic adjustments, such as mud-sticker mode of life populating the sediment in a vertical position, sometimes cementing to other individuals; and recliners, which lay flat on the sediment and might have cemented to various hard objects, as e.g., fragmented rocks, shells or oncoids (Machalski 1998). While the flat-lying shells provided convenient settling conditions and relatively much space, in the vertically arranged ones, it was highly limited, especially when only an anteriormost part of the shell protruded from the sediment.

Possibly, a part of the shells forming small clusters of cemented valves, which displayed a three-dimensional shape might have been occasionally overturned. Such a situation occurred in slightly younger shell beds with *Nanogyra nana* (Sowerby, 1822) from the lower Kimmeridgian (Upper Jurassic) of Małogoszcz, which contributed to the formation of ostreoliths (Zatoń and Machalski 2013). Such large, spherical objects were prone to overturning due to hydrodynamic and biological agents (Zatoń and Machalski 2013). However, even isolated shells or shell clusters exhibiting rather flat morphology presumably might have been occasionally overturned due to their smaller sizes and a relatively shallow marine palaeoenvironment with episodic storm events (Machalski 1998; Radwańska and Radwański 2003).

The diversity of serpulid and sabellid fauna from these deposits is among the lowest of all the sites investigated (in total four species, Table 1). On the ostreoliths mentioned above, Zatoń and Machalski (2013) noted only two sessile polychaete species. Interestingly, similarly low sessile polychaete diversity was noted on lower Kimmeridgian carbonate cobbles from nearby Sobków locality by Krajewski et al. (2017). Presumably, such low diversity might have been

governed by salinity fluctuations in shallow water settings, as evidenced by stable isotopes (Krajewski et al. 2017).

Nonetheless, oysters provided a range of places to be colonized, offering many cryptic and upward-facing habitats, what may reveal encrusters' polarization. Although the slight majority of tube-dwelling polychaetes inhabited the exterior surfaces of the valves (Szewczuk 2010), many of them settled on the interiors, evidencing that encrustation of the oyster shells also took place post-mortem (e.g., McKinney 1995; Fagerstrom et al. 2000). Clustered oyster valves also could have acted as a good cryptic habitat due to an increased accessibility of fissures and crevices (e.g., Kidwell 1986; Zuschin et al. 1999; Coen and Grizzle 2007; Zatoń and Machalski 2013).

Soft muddy substrates.—Serpulids and sabellids derived from the middle Bathonian (Middle Jurassic) of Gnaszyn Dolny and lower Bathonian (Middle Jurassic) of Kawodrza Górna inhabited mainly oyster shells and belemnite rostra, as well as wood-falls (see Kaim 2011), scattered over the soft muddy seafloor. Thus, biogenic substrates suitable for sclerobiont colonization were very patchy. Tube-dwelling polychaetes on such benthic islands frequently occur crowded, forming dense aggregations, and exhibit the highest diversity among the all studied sites (in total eleven species, see Table 1).

In contrast to other kinds of substrates, oyster shells provided here a sufficiently stable habitat for the encrusters. The sediments are interpreted to have been deposited in a relatively deep, calm, oxygenated environment below the storm-wave base (Marynowski et al. 2007; Zatoń et al. 2009; Gedl and Kaim 2012; Gedl et al. 2012). However, colonization might have been intermittent as presumably a bulk of larvae did not even have a chance to settle on a convenient hard substrate. In the case of successful colonization, subsequent larvae possibly had a greater chance to be recruited in the direct vicinity because of available adjacent space. Even though serpulid larvae exhibit either lecithotrophic or planktotrophic larval development strategies (Kupriyanova et al. 2001; Rouse and Pleijel 2001), many serpulids settle non-randomly (Kupriyanova et al. 2019), which may result in a relatively distant dispersal (Andrews and Anderson 1962; Dirnberger 1993; Kupriyanova et al. 2001). The larvae may develop into dense monospecific assemblages with regard to attached individuals of their own species (Scheltema et al. 1981). To encourage gregarious settling, chemical signals associated with living adults may be used (Pawlik 1992; Toonen and Pawlik 1996; Bryan et al. 1997). On the other hand, the absence of a mature source population in close proximity to an accessible hard substrate will highly reduce the chance of recruitment (see Taylor and Wilson 2003).

Restriction of the surface may have resulted in occasional competitive interactions. Despite difficulties in a clear designation between syn vivo and post-mortem interactions (see Fagerstrom et al. 2000), possibly at least a part of overgrowths between epibionts did not result from overgrowing dead skeletons. Although clear reciprocal overgrowths are absent, a part of intraspecific interactions resulted in stand-offs (see Taylor 2016). Such an outcome may support the interpretation that encounters of the same species acted syn vivo (Taylor 2016). It is evident that some sclerobionts colonized the interiors of bivalve valves, being a proof of post-mortem colonization (e.g., McKinney 1995; Fagerstrom et al. 2000). Some tubes of *Propomatoceros lumbricalis* also acted as hosts for in vivo bioclaustrating hydroids; however, such interactions were extremely rare (Słowiński et al. 2020).

Large, flat-lying oyster valves were highly resilient against physical agents, especially in calm settings as in the present case, offering a stable substrate, where irregularly, slowly growing, large *Propomatoceros lumbricalis* constituted the basis of the community. Smaller, compact and faster-growing tube-dwellers were outcompeted. Nonetheless, because sclerobionts were substrate-restricted in settlement and colonization, they were forced to settle together with more opportunistic and thus dominating polychaetes, sometimes displaying cryptic behavior, encrusting e.g., the deflections between the oyster shell ribs. A different situation occurred on the substrate provided by belemnite rostra. Regardless of the calm palaeoenvironment, they were less stable on the seabed, being much more susceptible to any disturbances. Despite scarce exceptions, robust, slowly growing species were unable to successfully colonize the rostra, whereas smaller species like species of *Nogrobs* showed higher plasticity enabling them to adjust to such small, conical/cylindrical substrates. Yet another ecological adjustment was performed by flat, free-living *Nogrobs* aff. *tetragona*, which was favored by a slow sedimentation rate. Possibly, juvenile representative first encrusted a small surface of any hard substrate available, subsequently detaching, and terminating as a free-lying on the soft sediment (Sanfilippo 2009). Rare, curved tube portions may have resulted from shifting due to a response to a temporary instability within a sediment, showing an attempt to avoid ecologically unpleasant conditions (Fig. 9H; see also Sanfilippo 2009: fig. 6A, C, L). Alternatively, they may have lived embedded within the sediment with only their apertures protruding and lying upon the sea floor, as do the Recent soft bottom-inhabiting species *Ditrupa arietina* (Hove and Smith 1990; Vinn et al. 2008b).

Due to a stable palaeoenvironment with low hydrodynamics (Gedl et al. 2012), most encrusters were not intensively abraded, which attests that negative taphonomic processes affecting the fossil assemblages were insignificant.

Sponge build-ups.—The substrate for the tube-dwelling polychaetes from the Oxfordian (Upper Jurassic) of Zalas was provided by lithistid sponges (Trammer 1982), that formed biohermal structures (Trammer 1982, 1985; Ostrowski 2005; Matyszkiewicz et al. 2012). Such sponge mounds provided "live" substratum for sclerozoans. With respect to taxonomic composition (in total five species, Table 1), sessile polychaetes are here completely different

from the all other sites, as the species composition was presumably strongly influenced by substrate-specific preferences (see Kupriyanova et al. 2001, 2019; Ippolitov 2010).

Relatively calm environment, quite low sedimentation rates, and high nutrient availability (Matyszkiewicz et al. 2012) probably escalated spatial and resource competition (Palmer and Fürsich 1981). Faster calcification rates seem to have been favored in the environment of the reefal substrate, which promoted polychaetes, which were easily adaptable to the prevailing conditions by a higher ecophenotypic plasticity. It may explain the absence of any species of *Propomatoceros* within sponge build-ups of Zalas. Conspicuous in this population is also the relative scarcity of *Glomerula gordialis*. Being rather easy-adjustable to different conditions (e.g., Parsch 1956; Ippolitov 2010; Vinn and Wilson 2010; Breton et al. 2020), this sabellid is here dominated by much more abundant and possibly more opportunistic *Cementula spirolinites*, which tended to occur in the advantageous conspecific aggregations (e.g., Palmer and Palmer 1977; Palmer and Fürsich 1981; Schlögl et al. 2008).

Tube-dwelling polychaetes from Zalas were attached to both sides of the sponges, being slightly more numerous on the exterior (33% compared to 22% on the interior, as calculated from Kuziomko-Szewczuk 2010). Such a polarization of space occupation could have arisen from relatively equal preferences towards certain sides. Anyway, it appears that more serpulids and sabellids inhabited the external sides of sponges. With their often irregular shapes, these principal frame-builders provided a variety of microhabitats where tubeworms might have led a cryptic mode of life (Riding 2002). Outwardly projected growth of sponges, laterally widening to the top possibly provided shaded, cryptic niches on the undersides of the mushroom-shaped sponge skeleton (Palmer and Fürsich 1981; Wilson et al. 2008).

Many sponges are fragmented, limiting an insight into actual shape of the entire organism. Such fragments possibly constituted a biohermal talus. Nevertheless, the differences in the level of tube-dwelling polychaete encrustation on both sides seem to be small. Presumably, they were able to settle on any available hard substrate provided by sponges surrounded by soft sediment (see Trammer 1982, 1989).

Remarks on serpulid and sabellid evolution during the Middle and Late Jurassic.—Following the radiation that commenced in the aftermath of the Triassic/Jurassic mass extinction, significant diversification of tube-dwelling polychaetes occurred during the Early and Middle Jurassic, when the total number of known morphotypes increased greatly. However, the Middle Jurassic was also a time of a relative stagnation within the already established clades, such as e.g., the sabellid *Glomerula* and serpulids *Filograna*, three-keeled *Metavermilia*, or *Propomatoceros* (see Ippolitov et al. 2014, for a review). Among the new evolutionary clades that appeared is *Metavermilia striatissima* (Fürsich et al. 1994), regarded as a possibly separate minor lineage within the genus *Metavermilia*, and

Genicularia (Quenstedt 1856: 589), a genus which has not been reported in the Polish Basin.

Biostratigraphy of serpulids is highly constrained (but see Macellari 1984; Tapaswi 1988) and specific morphotypes most often do not correspond to certain stratigraphic intervals. It is further complicated by slow intrageneric radiation during the Middle Jurassic and an increase in tube disparity within particular species, which possibly may be an outcome of the evolution of the group, but also a result of some local, ecophenotypic adjustments. These make taxonomic attribution of many Jurassic serpulids and sabellids problematic, and there is still no widely acknowledged current scheme of species and morphological or stratigraphical borders between species in most of these clades.

The serpulid fauna became more diversified with the emergence of sponge and microbial facies. The advent of some new forms occurred during Oxfordian (Late Jurassic), when such build-ups became widespread in Europe (e.g., Goldfuss 1831; Parsch 1956; Trammer 1982; Pisera 1991; Radwańska 2004; Matyszkiewicz et al. 2012), and locally being present even in the Bathonian (Middle Jurassic; Palmer and Fürsich 1981). Such new forms include here "*Serpula cingulata*", *Cementula spirolinites*, *Placostegus planorbiformis*, and *Filogranula spongiophila* sp. nov. However, tube-dwelling polychaete faunas during the Oxfordian and Kimmeridgian beyond these reefal deposits still remained rather "old-fashioned" (e.g., Wignall 1990; this study). Such distribution supports an explanation for high substrate-dependent serpulid and sabellid settlement (Ippolitov 2010).

Apart from the serpulid genera of clade BII represented by monophyletic Spirorbinae, members of all the informally established clades (see Kupriyanova et al. 2009) are present in our material. Some of them, like e.g., *Filogranula*, which possibly is a polyphyletic taxon (see Ippolitov et al. 2014; Kočí and Jäger 2015a) need further investigation. However, such considerations, although essential, are beyond the scope of the present study.

Comparisons with other Middle and Upper Jurassic tube-dwelling polychaete assemblages.—The great majority of all known Middle and Late Jurassic tube-dwelling polychaete communities are described from Europe, including the European part of Russia (among more recent publications e.g., Pugaczewska 1970; Jäger et al. 2001; Radwańska 2004; Ippolitov 2007a, b; Kočí et al. 2019; Breton et al. 2020). Except of some clearly outdated studies (e.g., Parsch 1956), the majority of these reports dealt with assemblages coming from single stratigraphic intervals (e.g. Ippolitov 2007a, b), or with assemblages which were not the main objective of the investigation (e.g., Zatoń et al. 2011a). Thus, this research dealing with fossil material spanning the upper Bajocian to lower Kimmeridgian, representing a variety of palaeoenvironments, may serve as a potential reference point for future investigations.

Relatively little data is available on Jurassic serpulids and sabellids settling on mobile rockgrounds. Investigations by

Kaźmierczak (1974), Chudzikiewicz and Wieczorek (1985), Fürsich et al. (1992), Zatoń et al. (2011a), and Krajewski et al. (2014, 2017) did not deal with tube-dwelling polychaete assemblages as the major scope. The total number of the taxa reported in above mentioned studies was rather low, comprising two, or three species compared to five noted during the present study. Despite different stratigraphic intervals, the taxonomic composition of the assemblages indicated above was very similar to the hiatus concretions described here, dominated by the genera *Glomerula* and *Propomatoceros*. The quantitative data also seem to be comparable, with polychaetes being at least not abundant.

In comparison to hiatus concretions, oncoids are significantly more heavily encrusted. Tube-dwelling polychaetes preserved on this kind of substrate have been mentioned from, e.g., the Bajocian (Middle Jurassic) of England (Gatrall et al. 1972; Palmer and Wilson 1990) and France (Palmer and Wilson 1990), Bathonian (Middle Jurassic) of Poland (Zatoń and Taylor 2009a; Zatoń et al. 2012), or Oxfordian (Upper Jurassic) of Switzerland (Védrine et al. 2007). The record of serpulid and sabellid taxa present on the oncoids in the current study (six taxa) is comparable to those in the studies listed above, reaching seven (Palmer and Wilson 1990) to nine species (Zatoń et al. 2012). These assemblages are dominated by species of *Glomerula*, followed by those of *Propomatoceros*. It has to be noted that Zatoń et al. (2011a) and Zatoń et al. (2012) used most of the same research material as in the current study revealing eight and nine tubeworm species, respectively. However, presumably due to overinterpretations of certain morphotypes, which rather represented ecophenotypic variations of the same species, the number of serpulid and sabellid species is lower, comparable to the present study. Although the species richness is not significantly higher as compared to hiatus concretions, the overall number of polychaete tubes is substantially larger. In spite of the fact that at least a part of the investigations listed above (e.g., Gatrall et al. 1972; Védrine et al. 2007) might have not been sufficiently focused on serpulids and sabellids, their abundance has usually been noted.

In comparison to various mobile rockgrounds, more is known about tube-dwelling polychaetes from metazoan build-ups and a variety of hardgrounds. Serpulids and sabellids preserved on Jurassic reefal structures extending across Europe have been mentioned many times (e.g., Goldfuss 1831; Parsch 1956; Flügel and Steiger 1981; Palmer and Fürsich 1981; Pisera 1991; Radwańska 2004; Matyszkiewicz et al. 2012; Pleş et al. 2013). However, more recent investigations focusing on sessile polychaetes in more detail have been performed only by Radwańska (2004) and to a lesser extent by Palmer and Fürsich (1981). Compared to only five species from the Oxfordian (Upper Jurassic) of Zalas, Radwańska (2004) reported 14 polychaete taxa occurring in Kimmeridgian sponge buildups of Wapienno/Bielawy in Kuyavia region (see also Loba and Radwańska 2022). In spite of striking differences in species numbers, the serpulid and sabellid fauna from Zalas appears to be more abundant

than that of Kuyavia (Radwańska 2004). The Wapienno/Bielawy quarries (Radwańska 2004) contain the majority of the taxa found in Zalas, including *Glomerula gordialis*, *Cementula spirolinites*, and the genera *Placostegus* and *Filogranula*. They are also present in the Oxfordian (Upper Jurassic) sponge facies of southern Germany (Parsch 1956). Upper Bathonian (Middle Jurassic) tube-dwelling polychaetes described by Palmer and Fürsich (1981) consist of seven species. However, "*Spirorbula* sp.", which has been described as the most abundant tubeworm within the upper Bathonian sclerobiont assemblage (Palmer and Fürsich 1981), has been proven to actually represent a microconchid (Vinn and Taylor 2007). Other species may also require systematic reinvestigation, although the genera *Glomerula*, *Propomatoceros* and *Cementula* are likely to be represented.

Serpulid and sabellid communities inhabiting lithic substrates (e.g., hardgrounds) and carbonate skeletal remains of various organisms seem to be more diverse due to a wider range of substrate types and prevailing conditions (up to eleven taxa in the present study). Breton et al. (2020) described tube-dwelling polychaetes among other sclerobionts from the Bajocian (Middle Jurassic) ferruginous oolithic facies of France. They are mostly preserved on mollusk shells, with diversity reaching nine species, where *Glomerula gordialis* and *Propomatoceros lumbricalis* dominate. Krajewski et al. (2017) mentioned only one serpulid species, *Tetraserpula* sp. (possibly representing *Nogrobs*); and two sabellid species represented by *Cycloserpula* sp. and *Glomerula gordialis* (presumably representing a single species) from the Kimmeridgian (Upper Jurassic) carbonate cobbles from the Mesozoic margin of the Holy Cross Mountains.

Serpulid and sabellid assemblages preserved on marl nodules and invertebrate skeletons from the Callovian (Middle Jurassic) of Russia described by Ippolitov (2007a, b) are represented by eight species. Interestingly, in contrast to the majority of reports, sabellids (e.g., *Glomerula*) are a minor component there, with a predominance of *Propomatoceros lumbricalis* constituting hundreds of specimens.

Outside of Europe, Middle Jurassic serpulid and sabellid fauna has also been described from the Matmor Formation in Israel, being the closest to the equator assemblage during the Middle Jurassic (Vinn and Wilson 2010). It differs in the high dominance of the species of sabellid genus *Glomerula* and the presence of the genus *Vermiliopsis*, which seems to be uniformly absent in the Jurassic of Europe. Such differences might have resulted from a domination of the species of opportunistic *Glomerula*; however, *Vermiliopsis* might have originated in the warm equatorial, shallow seas before its further dispersal towards higher latitudes (Vinn and Wilson 2010).

Kočí et al. (2019) described nine serpulid and sabellid species from the Oxfordian (Upper Jurassic) of the Czech Republic, mainly encrusting brachiopod shells and sponge remains. However, all the taxa are represented by only a few individuals limiting an insight into the community. Even though the species composition differs from site to site, di-

versity remains relatively similar, often displaying a pattern of biodiversity increase through time (see Ippolitov 2010). Moreover, tube-dwelling polychaete assemblages are frequently dominated by a single, possibly most opportunistic species. Finally and crucially, true sabellid and serpulid diversity was likely higher in all studied Jurassic sites. This is because the taxonomy of fossil tube-dwelling polychaetes is based exclusively on the morphology of their tubes, while many different modern serpulid species produce similar or identical tubes (Hove and Kupriyanova 2009).

Conclusions

The first comprehensive investigation dealing with the Middle and Late Jurassic tube-dwelling polychaetes (sabellids and serpulids) from the Polish Basin reveals the presence of 24 species, of which *Filogranula spongiophila* sp. nov. and *Cementula radwanskae* sp. nov. are considered new. Certain species (e.g., *Cementula spirolinites*, *Placostegus planorbiformis*, *Filogranula spongiophila* sp. nov.) are clearly associated with specific kinds of substrate, while stratigraphic interval plays a secondary role in determining patterns of distribution. At the majority of locations and substrates, however, the stratigraphically and geographically widespread sabellid species *Glomerula gordialis* dominates over the serpulids and very often seems to be the most opportunistic tubeworm species. The second most abundant species is *Propomatoceros lumbricalis*, although it is uniformly absent within the sponge build-ups of the Polish Jura.

Taking the distribution patterns and abundance of serpulids and sabellids into account, it is evident that prevailing conditions had a significant impact on the composition of assemblages. Aside from substrate type, food availability, hydrodynamism of the palaeoenvironment and sedimentation rate were among the most important factors influencing colonization and subsequent development of serpulids and sabellids. Biodiversity indices show, that the most diverse tube-dwelling polychaete faunas are those inhabiting skeletal remains derived from soft muddy bottoms, as well as those inhabiting hardgrounds and large oncoids, which resulted from highly suitable conditions at these sites. The lowest biodiversity occurs in communities colonizing hiatus concretions, which possibly was an effect of their repeated overturning due to external agents, such as bottom-currents and/or animal activity. Many of the tube-dwelling polychaetes display similar distributional patterns featuring e.g., a cryptic lifestyle, or competition for space with both other polychaetes and other epibionts.

Acknowledgements

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Słowiński, J., Banasik, K., Vinn, O.

Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications.

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Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications

JAKUB SŁOWIŃSKI, KAMILA BANASIK AND OLEV VINN

LETHAIA

The mineral composition and tube ultrastructure of the Middle and Upper Jurassic calcareous sabellid *Glomerula gordialis* (Schlotheim, 1820) from the Polish Basin have been assessed. In all cases, the Jurassic sabellid tubes studied were found to consist of low-Mg calcite, as revealed by Raman spectroscopy and supplementary SEM-EDS analyses. The tube of *Glomerula gordialis* is single-layered and its ultrastructure has been identified as a spherulitic prismatic structure (oriented prismatic structure), supporting earlier ultrastructural observations of calcareous sabellids. The ambient seawater chemistry largely influenced the formation and evolution of sabellid skeletal mineralogy, and their mineral composition at the times of their first appearance presumably corresponded to the Permian aragonitic seas. The earliest skeletons of each calcareous polychaete group are considered to have autonomously evolved according to the chemistry of the seawater at the time of their origin. The relatively simple biomineralization system of sabellids is similar to that of calcareous cirratulids and remains less complex compared to serpulids. Physiologically less expensive formation of the calcareous tube in sabellids implies their palaeoecological avoidance strategy, allowing for a faster dispersal over the substrate during potentially unfavourable conditions. □ *Sabellidae, Glomerula, tubeworms, biomineralization, seawater chemistry, Raman spectroscopy.*

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Almost all calcareous tube-dwelling polychaetes belong to the family Serpulidae (Weedon 1994, Vinn *et al.* 2008b). Having appeared at least during the Middle Permian (Sanfilippo *et al.* 2017, 2018), serpulids became a common constituent of hard substrate benthos since the Jurassic. Hard skeleton, composed of calcium carbonate, also occurs in the two genera of the family Cirratulidae – *Dodecaceria* and *Diplochaetetes* (Reish 1952, Fischer *et al.* 1989, 2000, Taylor *et al.* 2010, Kočí *et al.* 2021), as well as in one genus of the family Sabellidae – *Glomerula* (Perkins 1991, Jäger 2005, Vinn *et al.* 2008a). The oldest unambiguous known fossil cirratulids are Oligocene in age (Fischer *et al.* 1989, 2000). It is noteworthy, however, that *Diplochaetetes* was also mistakenly referred to Eocene anthozoans (Weissermel 1913, 1926), and subsequently, Oligocene and Miocene poriferan (Wilson 1986), due to internal tabulation of the skeleton. Therefore, it is possible that cirratulids existed since the Eocene. The first unequivocal sabellids appeared in the Middle Permian (Sanfilippo *et al.* 2017). Moreover, Hoare *et al.* (2002) reported tiny worm tubes encrusting rostroconchs derived

from the Late Carboniferous sediments. It cannot be ruled out that these minute epibionts represent the first sabellids due to their at least superficial resemblance to this polychaete group. However, the oldest record of sabellids as confirmed by a tube microstructure study is from the Middle Jurassic (Vinn *et al.* 2008a).

The skeletal microstructure of the tube-forming polychaetes has received much interest in recent years allowing a wide microstructural variability in both modern and fossil polychaetes to be revealed (e.g. Bubel *et al.* 1983; Nishi 1993; Weedon 1994; Sanfilippo 1998; Fischer *et al.* 2000; Vinn 2005, 2020, 2021; Vinn *et al.* 2008a, b; Buckman 2020). Although not flawless (see Ippolitov *et al.* 2014), such research has enabled analysis of the phylogeny of some taxa and to assess a model of biomineralization, as well as its evolutionary and palaeoecological implications (e.g., Bornhold & Milliman 1973; Vinn *et al.* 2008a; Vinn & Kupriyanova 2011; Kupriyanova & Ippolitov 2012; Vinn 2013; Buckman 2020; Buckman & Harries 2020). However, for obvious reasons, only the tube ultrastructure of serpulids has been studied

thoroughly. Research conducted on tube microstructure, including formation and mineral composition, of cirratulids (Fischer *et al.* 1989, 2000; Taylor *et al.* 2010) and sabellids (Vinn *et al.* 2008a) is far more limited.

Serpulids may be composed of calcite, aragonite, or a combination of both (Bornhold & Milliman 1973, Vinn *et al.* 2008b). Tube-dwelling cirratulids have been confirmed to be of purely aragonitic mineralogy (Taylor *et al.* 2010). Calcareous sabellids were maintained to be composed of aragonite in the case of both fossil and recent representatives (Vinn *et al.* 2008a). Although the recent *Glomerula piloseta* (the only recent sabellid possessing a calcareous skeletal tube instead of an organic one) has been proven to be aragonitic based on the high content of strontium obtained during SEM-EDS studies (Vinn *et al.* 2008a), the mineral composition of the tube wall of fossil sabellid representatives has not yet been thoroughly investigated.

The chemistry of abiotic carbonate precipitates fluctuated over the Phanerozoic period (Sandberg 1983, 1985, Dickson 2002) due to changing Mg/Ca ratios of the seawater, which promoted either calcitic or aragonitic precipitation (Sandberg 1983, Ries 2010). Aragonite precipitation was favoured in the Early Cambrian, Late Carboniferous to Early Jurassic, and Oligocene to Recent seas. There were also two intervals of calcite seas in the Middle Cambrian to Early Carboniferous, and in the Middle Jurassic to Eocene (Stanley 2006). Seawater chemistry had a significant impact on the biomineralization of various invertebrates (see Ries 2006; Ries *et al.* 2006; Porter 2007; Stolarski *et al.* 2007; Taylor 2008; Zhuravlev & Wood 2008; Taylor *et al.* 2014; Wood 2018); this, however, has not been investigated in sabellids. The sabellids very likely appeared during times of aragonitic seas of the Permian, or at the latest in the Early Jurassic (Jäger 2005, Sanfilippo *et al.* 2017), and there could have been some correlation between the aragonite-calcite seas and the skeletal mineralogy of sabellid polychaetes (see Vinn & Mutvei 2009). Before embarking on such conjecture, sabellid mineralogy and its evolution require more study.

As a step towards filling this gap, here we provide a detailed microscopic and spectroscopic investigation of Middle and Upper Jurassic sabellid tubes in order to decipher their ultrastructure and, most importantly, to identify their mineral composition. Such an approach may further help us to provide a better understanding of the evolution of sabellid biomineralization and its potential relationship to palaeoenvironmental conditions, particularly the oscillations in seawater chemistry across geological time.

Material and methods

Geological setting and material provenance

The investigated materials encompass eight tubes of the sabellid species *Glomerula gordialis*. Two specimens from both Gnaszyn Dolny and Ogrodzieniec and one from each of the other locations were selected from a rich fossil material (see Słowiński *et al.* 2020, 2022) based on their well-preserved microstructure deciphered using scanning electron microscopy (SEM). In total, six localities with deposits representing different marine palaeoenvironments and various stratigraphical intervals, spanning the upper Bajocian-lower Kimmeridgian, have been sampled. The investigated outcrops expose deposits of the Polish Jura and the Mesozoic margin of the Holy Cross Mountains (Fig. 1). These are listed in ascending stratigraphical order. All the collected fossils are housed at the Institute of Earth Sciences in Sosnowiec, abbreviated GIUS 8–3589 (Zalas), GIUS 8–3730 (Gnaszyn Dolny), GIUS 8–3747 (Małogoszcz), GIUS 8–3750 (Ogrodzieniec-Świertowiec), GIUS 8–3751 (Mokrsko and Ogrodzieniec) (Fig. 2).

Mokrsko.—This outcrop, together with the subsequent localities (except Małogoszcz), is located within the area of the Polish Jura (Fig. 1). The deposits occur in the form of dark siliciclastics belonging to the Częstochowa Ore-bearing Clay Formation (e.g., Majewski 2000; Matyja & Wierzbowski 2000; Zatoń *et al.* 2011a; Leonowicz 2015). In Mokrsko, these sediments are upper Bajocian in age. Sabellid tubes from this site encrust carbonate hiatus concretions, which occur either isolated or more often form a continuous horizon within the surrounding dark mudstones and siltstones. Hiatus concretions indicate a much lower sedimentation rate or even pauses in the accumulation and mark seafloor erosion (Zatoń *et al.* 2011a, Leonowicz 2015). The deposits represent a palaeoenvironment that presumably corresponds to below the storm wave-base conditions (Zatoń *et al.* 2011a).

Ogrodzieniec-Świertowiec.—This site is situated approximately 1 km south of Ogrodzieniec, Polish Jura (Fig. 1). Sabellids from this locality densely encrust large oncoids, which were found within condensed, sandy, and carbonate deposits. These are overlain by dark siliciclastics belonging to Częstochowa Ore-bearing Clay Formation. Ammonites (Zatoń & Taylor 2009, Zatoń *et al.* 2012), as well as dinoflagellate cysts, and foraminifers (Słowiński 2019), indicate upper Bajocian–lower Bathonian age of the oncoid-bearing deposits. Based on the cyanobacterial genesis of
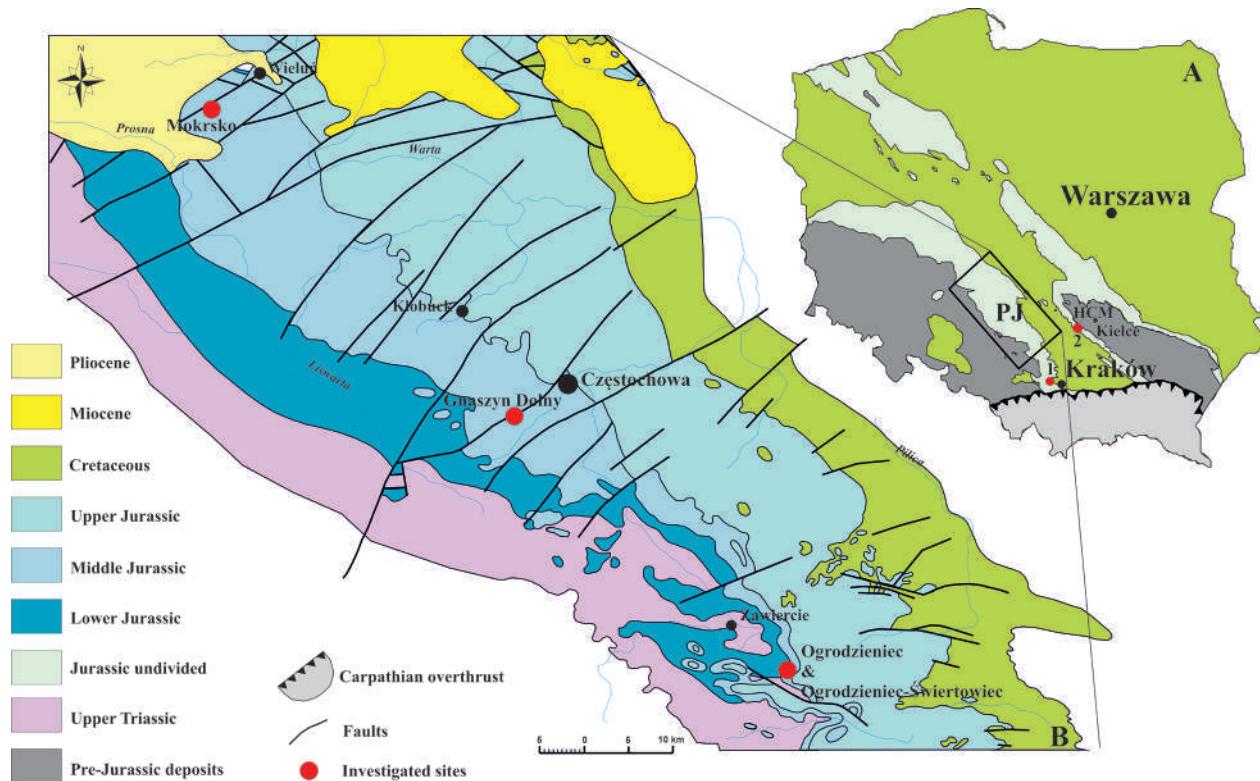
Fig. 1. Geology of the studied area A, geological sketch-map of Poland without the Cenozoic cover showing two sampled localities; HCM–Holy Cross Mountains; PJ–Polish Jura; 1–Zalas; 2–Małogoszcz. B, geological map of the Polish Jura area without Quaternary cover, with sampled localities indicated; (modified after Zatoń *et al.* 2006).

the oncoids, the habitat was situated within the photic zone, characterized as a shallow marine palaeoenvironment located slightly below a fair-weather wave base (Zatoń *et al.* 2012).

Gnaszyn Dolny.—*Glomerula* tubes from this locality have been found fixed mainly to belemnite rostra and bivalve shells. The fossils were derived from clay sediments of the middle Bathonian age. These mudstones were deposited deeper, below the storm wave base marine conditions (Gedl & Kaim 2012, Gedl *et al.* 2012).

Ogrodzieniec.—Sabellids from this site encrust hiatus concretions. Concretion-bearing sediments from this locality are confined to the upper Bathonian (Barski *et al.* 2004). The deposits from Ogrodzieniec belong to the southern sedimentary region of the Polish representing the marginal part of the Polish Basin (Fig. 1), characterized by the shallow marine conditions (Różycki 1953, Leonowicz 2013).

Zalas.—An active quarry is located in the Zalas village in close proximity to Krzeszowice. The locality belongs to the southern part of the Polish Jura (Fig. 1).

The investigated sabellid tubes were cemented mainly to big bivalves *Ctenostreon proboscideum* (Sowerby & Sowerby 1820). These fossils were derived from middle-earliest late Callovian sandy limestones forming a hardground (Giżejewska & Wieczorek 1977, Dembicz & Praszkier 2007), which formed in an open sea, deep shelf environment (Dembicz & Praszkier 2007, Zatoń *et al.* 2011b).

Małogoszcz.—Sabellids have been collected in an active quarry near the town centre of Małogoszcz. It is located in the southwestern part of the Mesozoic margin of the Holy Cross Mountains (Fig. 1). *Glomerula* tubes have been found fixed to bivalve shells, especially *Actinostreon gregareum* (Sowerby, 1815). The fossil-bearing deposits are lower Kimmeridgian and are referred to as the Skorków Lumachelle (Kutek 1994, Machalski 1998, Zatoń & Machalski 2013). The shell beds originated in a relatively shallow marine environment due to storm episodes (Machalski 1998).

Methods

The specimens were coated with ammonium chloride and photographed prior to the preparation of the
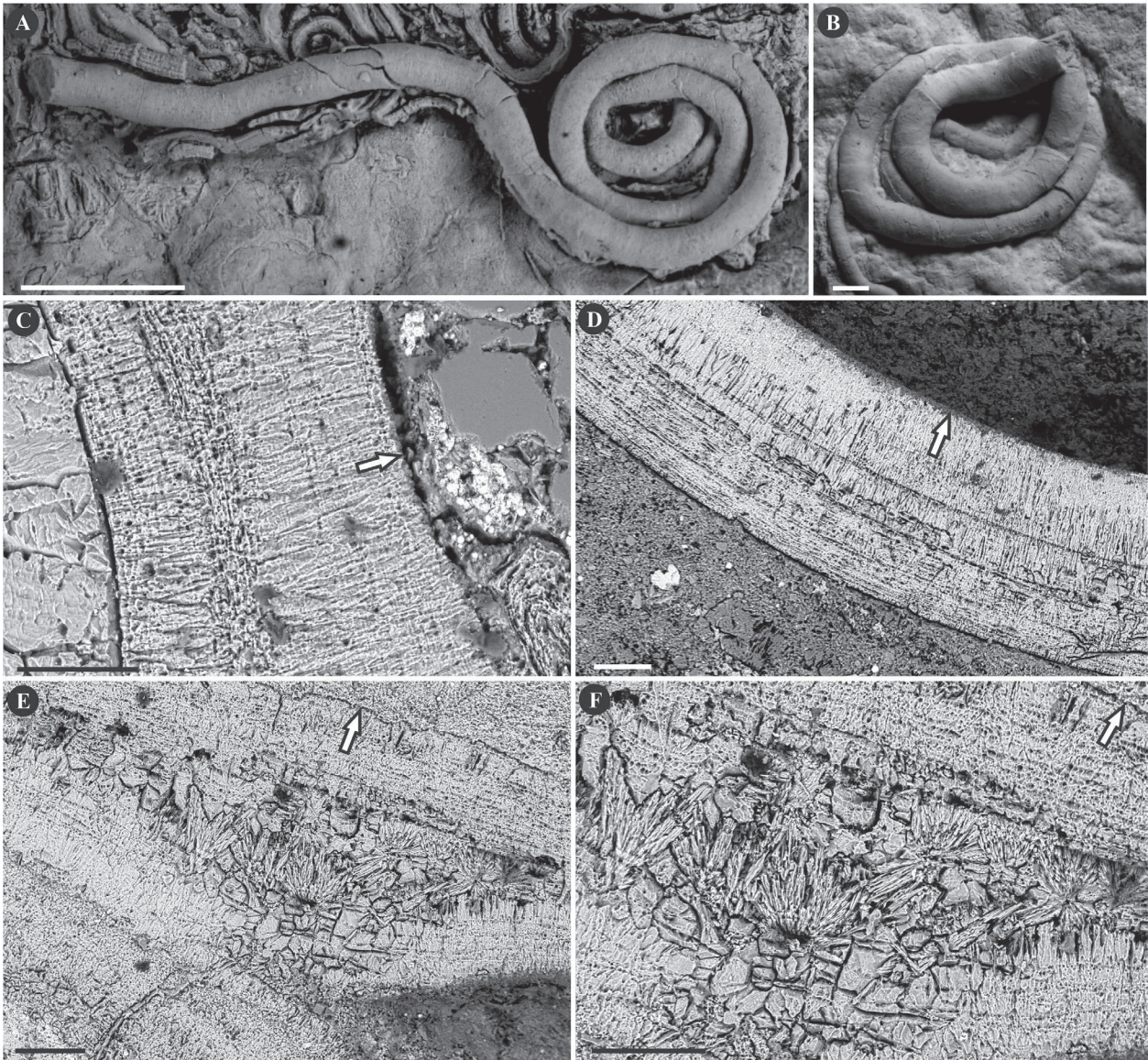
Fig. 2. Selected specimens of *Glomerula gordialis* (Schlotheim, 1820) from the Jurassic of Poland. A, *Glomerula gordialis* encrusting an oncoid from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec, Polish Jura; GIUS 8-3750/1. B, *Glomerula gordialis* encrusting a hiatus concretion from the upper Bathonian of Ogrodzieniec, Polish Jura; GIUS 8-3751/7. C–F, longitudinally ground, polished, and etched sections of the tubes, show the ultrastructure spherulitic prismatic structure of *Glomerula gordialis*; the ultrastructure in C, D exhibits densely patched, elongated prismatic crystals of slightly spherulitic arrangement; the growth increments are visible. C, section of *Glomerula gordialis* tube from the upper Bajocian of Mokrsko, Polish Jura; GIUS 8-3751/6. D–F, section of *Glomerula gordialis* tube from the upper Bathonian of Ogrodzieniec, Polish Jura; GIUS 8-3751/7. Arrows point to the exterior of the tube; the tips of arrows touch the limit of an external surface. Note the spherulites are composed of a bunch of acicular crystals oriented outwardly in E, F. Scale bars: 5 mm (A), 1 mm (B), 100 μm (C-F).

fossils for scanning electron microscopy. Subsequently, the samples were ground longitudinally, polished, and etched with a 1% solution of acetic acid for five minutes. Subsequently, the tube microstructure of the tubes has been examined under a SEM Zeiss EVO MA15 using a back-scattered electron detector (BSE) in a low vacuum regime. The beam voltage was 20 kV (Department of Geology, University of Tartu, Estonia). The samples were also studied using the environmental scanning electron microscope (ESEM)

Philips XL30, and a Quanta 250 scanning electron microscope (both at the Institute of Earth Sciences in Sosnowiec). The fossils were scanned in an uncoated state using a BSE imaging.

The mineral composition of the tubes was examined using a Quanta 250 scanning microscope with Thermo-Fisher's EDS UltraDry analyser (Institute of Earth Sciences in Sosnowiec). Samples were tested in high vacuum mode (<1.19 * 10-4 Pa) at 15 KeV accelerating voltages. Chemical microanalyses and

mapping of the elemental distribution were performed at selected areas of the tube wall using the analytical detector EDS (Energy Dispersive Spectroscopy), which allows for quick semi-quantitative determination of the elemental composition of the tested materials.

The Raman spectra were recorded using a WITec alpha 300R Confocal Raman Microscope (Institute of Earth Sciences in Sosnowiec), equipped with an air-cooled solid laser 488 nm and a CCD camera operating at –61°C. The laser radiation was coupled to a microscope through a single-mode optical fibre with a diameter of 3.5 μm. An air Zeiss LD EC Epiplan-Neofluan DIC – 100/0.75NA objective was used. Raman scattered light was focused by a broadband single mode fibre with an effective pinhole size of about 30 μm and a monochromator with a 600 mm⁻¹ grating. The power of the laser at the sample position was 42 mW. Integration times of 5 sec with the accumulation of 15 scans and a resolution of 3 cm⁻¹ were chosen. The monochromator was calibrated using the Raman scattering line of a silicon plate (520.7 cm⁻¹). Spectra processing, such as baseline correction and smoothing was performed using the SpectraCalc software package GRAMS (Galactic Industries Corporation, NH, USA). Bands fitting was performed using a Gauss-Lorentz cross-product function, with a minimum number of component bands used for the fitting process.

Results

Skeletal microstructure of sabellids

In line with previous research conducted by Vinn *et al.* (2008a), the Jurassic *Glomerula gordialis* (as opposed to the Recent sabellids, which have a two-layered tube wall; see Vinn *et al.* 2008a), possesses a tube wall consisting of a single layer composed of calcium carbonate (Fig. 2C, D). The single-layered tube consists of a spherulitic prismatic structure (SPHP), which is an oriented prismatic structure (see Vinn *et al.* 2008b, Vinn 2020). The elongated, prismatic, densely packed crystals constituting the microstructure, have an approximately perpendicular orientation to the tube wall. Distinct growth lamellae are oriented parallel or subparallel to the tube wall and pass through the prisms (Fig. 2C, D). Occasionally, distinct spherulites occur between the growth lines. They are composed of a bunch of acicular crystals oriented outwardly (Fig. 2E, F).

Mineral composition of sabellid tubes

Confocal Raman Spectroscopy (CRS).—Raman spectra of low-Mg calcite in all the examined samples showed

vibrations in the same range of spectral values, typical for this mineral (Fig. 3). In most of the Raman spectra obtained, along with the calcite ones, the broad bands related to vibrations in the D and G regions of organic matter were observed (Fig. 3C, D). The dispersed organic matter showed slight differentiation depending on the analysed location. In the Raman spectrum of calcite, the following bands are distinguished: 156 cm⁻¹, 282 cm⁻¹, 714 cm⁻¹, 1087 cm⁻¹, 1437 cm⁻¹, and 1749 cm⁻¹. Characteristic Raman bands related to the CO_3 group are as follows: $\nu1$ (symmetric stretching) and $\nu4$ (symmetric bending) modes are 1087⁻¹ and 714 cm⁻¹, respectively (Buzgar & Apopei 2009). Asymmetric stretching vibration ($\nu3$) is attributed to a line at 1438 cm⁻¹. The asymmetric bending ($\nu2$) vibration mode of the CO_3 group does not appear in the Raman spectrum. A weak band observed at 1749 cm⁻¹ may be regarded as the combination of bands of
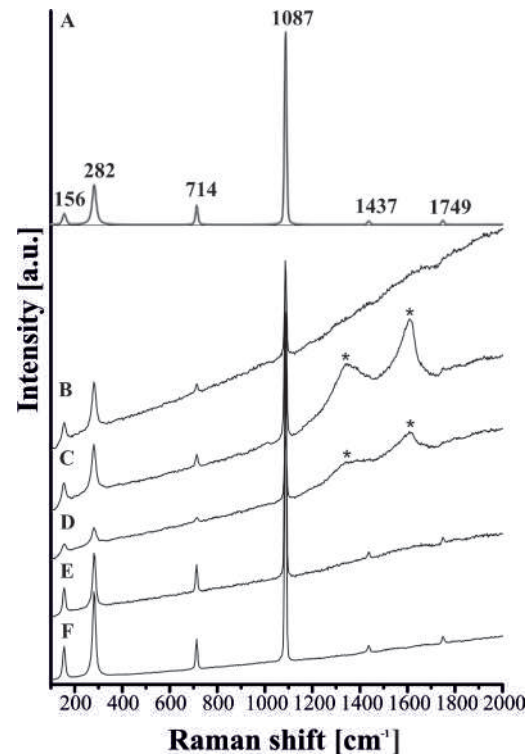

Fig. 3. Compiled Raman spectra of calcite structures, obtained from the *Glomerula gordialis* (Schlotheim, 1820) tubes. A, Raman spectrum after deconvolution showing the low-Mg content in the calcite structure of *Glomerula gordialis* tube from the upper Bajocian–lower Bathonian of Ogrodzieniec-Świertowiec, Polish Jura; GIUS 8-3750/1. B-F, stacked, not converted Raman spectra from the B, Upper Bathonian of Ogrodzieniec, Polish Jura; GIUS 8-3751/7. C, Middle Bathonian of Gnaszyn Dolny, Polish Jura; GIUS 8-3730/29. D, Upper Bajocian of Mokrsko, Polish Jura; GIUS 8-3751/6. E, Lower Kimmeridgian of Małogoszcz, Mesozoic margin of the Holy Cross Mountains; GIUS 8-3747/4. F, Callovian of Zalas, Polish Jura; GIUS 8-3589/17. The symbols * indicate an admixture of organic matter.

v1+ v4 modes or explained as the 2 × v2 (O-C-O out-of-plane bend) mode (Gunasekaran *et al.* 2006, Bell 2016). The lower wave numbers of calcite (156 cm^{-1}, 282 cm^{-1}) arise from the external vibrations of the CO_3 groups involving translatory and rotatory oscillations of these groups (relative translations between the cation and anionic groups, see Gunasekaran *et al.* 2006, Buzgar & Apopei 2009).

Scanning Electron Microscopy (SEM).—SEM analyses determined the chemical composition of the tubes of *Glomerula gordialis* as calcium carbonate. The surface distribution of elements confirms the predominance of calcium crystalline phases (Fig. 4). Magnesium and iron cations have a negligible share in the calcite structure (see Fig. 4F, I). In the association of the *Glomerula gordialis* calcitic skeleton, aluminum-silicate phases and sulphide minerals (mainly iron sulphides) are visible, which in most of the cases matches with the claystone-type lithology of the studied area, constituting the Formation of the Częstochowa Ore-bearing Clays. The scarce occurrence of strontium (Fig. 4H) is presumably associated with the mineralization of the sediment, rather than with the primary microstructure of *Glomerula gordialis* tubes themselves.

The supplementary SEM-EDS analyses (Fig. 5) showed variable Mg content in the tube walls of *Glomerula gordialis*. Sr was barely discernible, and even when it was detected, it displayed microlocal dispersion, and presumably was not connected with the primary microstructure of the polychaete tubes themselves. The EDS analyses varied between ca 0.3 weight% and 2.54 weight% of Mg (usually between 1 weight% and 1.5 weight% of Mg). Such analyses remain consistent with the low-Mg calcitic mineralogy of the sabellid tubes determined using CRS since the presence of Mg is employed as a proxy for calcite detection.
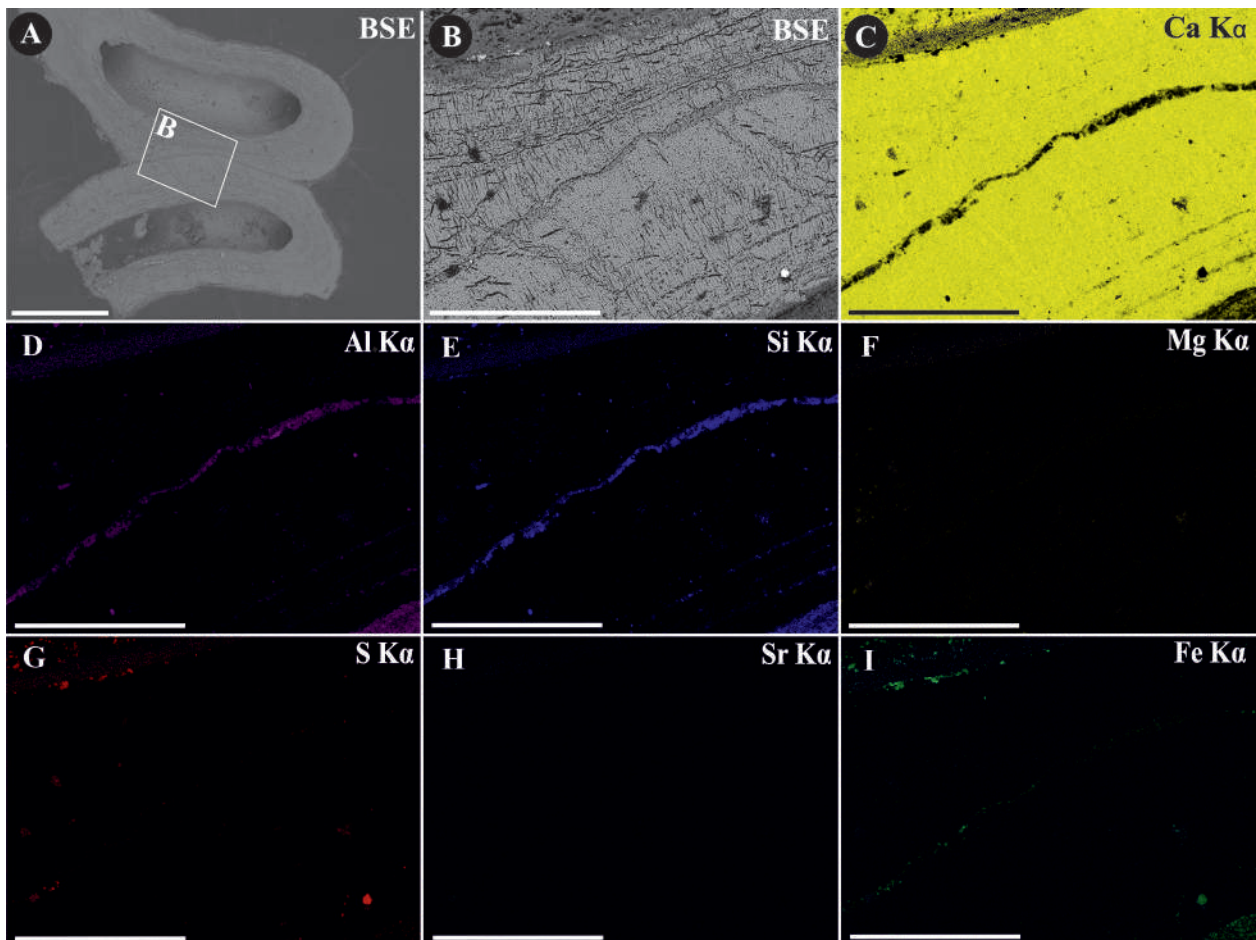
Fig. 4. A, SEM BSE image of two *Glomerula gordialis* tubes from the middle Bathonian of Gnaszyn Dolny, Polish Jura (GIUS 8-3730/29), magnified in B. C–I, Surface distribution of selected elements in characteristic X-rays of the image fragment showed in B. Scale bars: 1 mm (A), 200 μm (B-I).
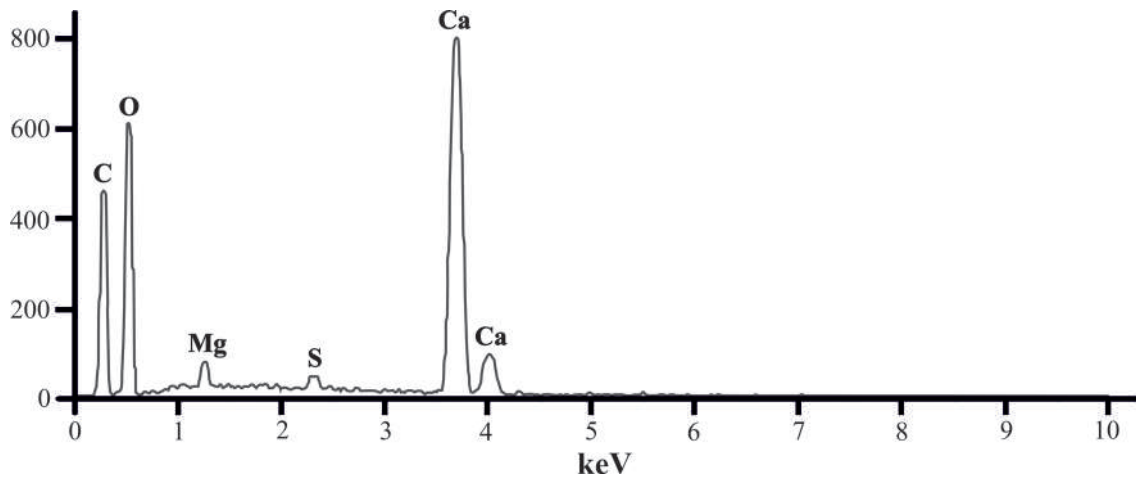
Fig. 5. Representative SEM-EDS spectrum obtained from the tube of *Glomerula gordialis* from the middle Bathonian of Gnaszyn Dolny, Polish Jura; GIUS 8-3730/29. The spectrum exhibits the presence of magnesium suggesting a calcitic mineralogy of the skeleton, corroborating evidence from Raman spectroscopy.

Discussion

Evolution of sabellid calcification and its influence on their abundance

The acquisition of a given mineralogical skeleton composition has changed according to the seawater chemistry throughout the evolutionary history of many groups of organisms, such as for example, bryozoans (Taylor *et al*. 2014), corals (Ries *et al*. 2006, Stolarski *et al*. 2007), echinoids and crustaceans (Ries 2004), calcareous algae (Ries, 2006, 2009), or coccolithophores (Stanley *et al*. 2005). Mineralogical switchovers of the sabellid skeleton during the evolution of these tube-dwelling polychaetes possibly also occurred several times, implying a biological reliance on the ionic ratio of seawater.

Although the first representatives of the family Sabellidae, as confirmed by tube microstructural investigation, have existed since the Middle Jurassic (Vinn *et al*. 2008a), unequivocal sabellids have already been present in the Middle Permian (Sanfilippo *et al*. 2017), if not even earlier in the Carboniferous (Hoare *et al*. 2002). Regardless, their first appearance coincided with the Late Carboniferous – Early Jurassic episode of aragonitic seas (Stanley 2006). It suggests that the skeleton of sabellids acquired aragonitic mineralogy during their origin, which presumably was regulated by the prevailing seawater conditions (e.g., Porter 2007). The tube of the Recent *Glomerula piloseta*, the only extant tube-dwelling sabellid (Perkins 1991), is composed of aragonite as well (Vinn *et al*. 2008a). In turn, our research provides evidence that Middle and Late Jurassic *Glomerula gordialis* had low-Mg calcitic mineralogy. It is noteworthy that in the siliciclastic deposits belonging to the Formation of the Częstochowa Ore-bearing Clays from which the majority of the investigated specimens are derived, primary aragonitic skeletons of gastropods (Kaim 2012) and ammonites (Wierzbowski & Joachimski 2007, Wierzbowski *et al*. 2012) are preserved. Hence, apart from the evidence of well-preserved microstructure mentioned here, the calcitic mineralogy of our sabellid tubes is primary and did not form from the post-burial diagenetic alteration of aragonite. Thus, sabellids may have altered their mineralogy in response to changes in seawater chemistry from aragonitic to calcitic in the Middle Jurassic, and from calcitic to aragonitic during the Eocene-Oligocene transition. Interestingly, the SPHP ultrastructure of the sabellids' tube remained unchanged at least since the Middle Jurassic (Vinn *et al*. 2008a).

It has to be noted, however, that the secretion of the calcareous tube by the sabellid (and similarly by serpulid) worms is not fully environmentally driven, as these animals engage biologically-controlled biomineralization (Vinn *et al*. 2008a). Although tube-dwelling polychaetes form their skeleton by an ion uptake from the seawater, the nucleation, and subsequent biomineral growth are controlled by cellular activities of an animal (see Neff 1971a, b), mediated also by the organic matrix and secreted together with calcium cations by an epithelium (Vinn *et al*. 2008a, Vinn 2021). Contrary to biologically-induced or biologically-influenced biomineralization (Weiner & Dove 2003, Dupraz *et al*. 2009), the nucleation of a biomineral is rather isolated from the ambient environment and controlled by intrinsic

factors, thus the biomineralization processes are biologically-controlled.

Anyhow, the long-term fluctuations of Mg/Ca ratio of the seawater presumably had an indirect effect on the skeletal production of sabellids governing their radiation and decline through natural selection. Calcareous sabellids' scarcity during their times of origin could have been connected with disadvantageous conditions to secrete calcite as a potentially favoured biomineral. In such cases, sabellids were vulnerable to ambient seawater chemistry which imposed aragonitic mineralogy and thereby incurred higher energy expenditure to precipitate aragonite during unfavourable ionic ratios. Such an assumption can be also supported by experimental studies of organisms, which adjusted the secreted biomineral negatively affected by artificial conditions (e.g., Stanley *et al*. 2002, Ries 2004, 2009). It is more challenging for calcifying organisms to secrete skeletons not encouraged by the chemistry of seawater. As a result, their growth rates remain slower (e.g., Ries *et al*. 2006), or they are unable to fully regulate their biomineralization, which may lead to the precipitation of a less robust skeleton (Dixon-Anderson 2021).

On the other hand, calcareous sabellids could have simply favoured the easiest biomineral to obtain (which was aragonite during aragonite-facilitating conditions) to produce a skeleton during the times of their emergence. Similarly, many other groups of organisms secreted skeletons matching the seawater chemistry during the times of their first appearance (Porter 2007). Their very low richness and abundance during the times of aragonitic seas were then not only related to the ionic ratio of the seawater but also to other palaeoecological and biotic factors (such as e.g., oxygen and salinity level, availability of substrate to colonization and its kind, nutrient availability) which could have negatively affected their occurrence. Such an explanation for the scarcity of sabellids (and serpulids) during the times of their origin may be the ecological pressure by microconchids (and also other encrusters), which during Late Paleozoic (e.g., Toomey & Cys 1977, Wilson *et al*. 2011) and early Mesozoic (e.g., Ball 1980, Vinn 2010, Zatoń *et al*. 2013) were still a relatively important component encrusting biogenic substrates, gradually vanishing, and disappearing in the upper Bathonian (Vinn & Taylor 2007, Zatoń & Vinn 2011).

Bloom of calcareous sabellids began with the onset of calcite sea interval in the Middle Jurassic when they became a common constituent of many hard substrates, which coincided with the sclerobiont (*sensu* Taylor & Wilson 2002) bloom in general (see Taylor & Wilson 2003). In contrast to the calcite seas of the Jurassic (Palmer & Fürsich 1974, Wilson & Palmer 1990, Feldman & Brett 1998, Taylor & Wilson 2003, Zatoń *et al*. 2011b, Krajewski *et al*. 2017), carbonate hardgrounds were sparse, if present at all, during the Permian (Taylor & Wilson 2003, Christ *et al*. 2015). Thus, although of a big probability sabellids' mineralogical transition into calcite during the Jurassic was correlated with the high abundance and availability of Ca ions in the seawater, their further speciation and abundance probably were facilitated by a much higher availability of carbonate hard substrates suitable for colonization (e.g., Palmer & Fürsich 1974, Palmer 1982, Wilson & Palmer 1990, Taylor & Wilson 2003, Zatoń *et al*. 2011b, Krajewski *et al*. 2017).

Cenozoic calcareous sabellids underwent a gradual decline since the Eocene/Oligocene transition (see Ippolitov *et al*. 2014 for a review) and are represented nowadays by one endemic species *Glomerula piloseta* (Perkins 1991). This big decline may be connected with the transition into aragonitic seas, supporting an explanation of aragonite as an unfavourable biomineral for sabellids and higher energy expenditures. However, the decrease of importance of sabellids during the Cenozoic may be simply linked with the rise of serpulid biodiversity (see Ippolitov *et al*. 2014).

The biodiversity of calcareous sabellids has possibly been also affected by the significant ecological changes driven by mass extinctions (see Kiessling *et al*. 2008), which led to biotic turnovers, and which also indirectly influenced changes in the ionic ratio of seawater. The restoration of deserted ecosystems after extinction could have exerted a strong control over the evolution of the mineralogical composition of the sabellid skeleton. Although the fluctuations of different variables such as temperature (e.g. Morse *et al*. 1997), salinity (e.g. Borremans *et al*. 2009), or acidification (e.g. Morse *et al*. 2006) also influenced the ocean chemistry, the scope of such changes seems to have been rather regional (see Ries 2010 for a review). The evolution of the skeletal mineralogy of sabellids must have been governed by the protracted changes in the chemistry of global oceans, adjusting to facilitating Mg/Ca ratio conditions and driving their biodiversity dynamics.

In line with all previous assumptions and investigations (e.g. Taylor *et al*. 2010) we envisage that the families Serpulidae and Cirratulidae, as well as the discussed sabellids, evolved their skeletons independently and presumably, their mineralogy corresponded to that of the ambient seawater during their origin. Serpulids undoubtedly originated before the second calcitic sea interval, which lasted from the Middle Jurassic to Eocene. Although they may be composed of calcite,

aragonite, or the combination of these two phases (e.g., Bornhold & Milliman 1973, Vinn *et al.* 2008b), the majority of them build a calcitic skeleton, at least since their radiation in the Middle Jurassic. However, the first, Middle Permian serpulids (Sanfilippo *et al.* 2017, 2018) possibly formed their tubes utilizing aragonite during Late Carboniferous – Early Jurassic aragonitic sea episode. Similarly, aragonitic Cirratulids (see Taylor *et al.* 2010), which originated in the Oligocene (Fischer *et al.* 1989, 2000), fit in the Eocene-recent aragonitic sea interval. The lack of impoverishment within the family Serpulidae during the Eocene-Oligocene transition may be explained by their broad ecological tolerance and often mixed mineralogy of their tubes (Bornhold & Milliman 1973, Vinn *et al.* 2008b). This would mean, that they are not so strongly reliant upon a certain mineralogy and perform higher plasticity in the secretion of a particular phase of $CaCO_3$.

Palaeoecological implications of biomineralization system in sabellids

The biomineralization system of sabellids differs from other calcareous polychaetes. Serpulid tubes may consist of up to four layers and manifest different ultrastructures according to the arrangement and orientation of calcium carbonate crystals (e.g., Vinn *et al.* 2008b). Sabellids, similarly cirratulids (Taylor *et al.* 2010), have a single-layered spherulitic prismatic structure (Vinn *et al.* 2008a). A relatively simple system of biomineralization could have impeded the diversity of sabellids' tube morphology resulting in their very uniform set of tube characters, such as smooth surface, universal lack of longitudinal and transverse ornamentation, and the lack of attachment structures. The main morphological differences within the genus *Glomerula* (e.g. the shape of a tube) resulted from the ecophenotypic adjustments dictated by the palaeoenvironment allowing either to spread over the substrate in a meandering or straight fashion or coiling when there was a restriction of space.

On the other hand, lower incurred physiological costs in the production of the skeleton could have been a convenient evolutionary adjustment allowing for a faster calcification and thereby, faster tube dispersal due to potential palaeoenvironmental vagaries. Instead of competing for space with a mechanical strengthening of a tube and/or firmly attaching to a substrate like the majority of serpulids do, sabellids may perform a fugitive strategy being capable of a 'quick escape'. Such an opportunistic adaptation is used among colonial organisms, such as e.g., bryozoans, which avoid active competition for space (see

Taylor 2016). When encountering hazards, narrowly arranged rows of zooids allow for a relatively fast spreading over a substrate, enabling the survival of at least a part of a colony. Sabellids fit well in such a strategy.

In comparison to other calcareous tube-dwelling polychaetes, the only calcareous sabellid, *Glomerula*, achieves a very considerable tube length, especially taking into consideration the tube diameter. Such length directly follows the biomineralization abilities of these worms. Having a relatively brittle and thin tube wall, *Glomerula* avoids direct competition for space through the fast formation of the elongated tube. As the worm animal is located in its anterior-most portion, this strategy fulfills well its protective function.

Conclusions

The mineralogy and ultrastructure of Middle and Upper Jurassic sabellid tubes were studied. Although the aspects of biomineralization in calcareous polychaetes, including sabellids, were the subject of interest of several studies, the mineralogy of Jurassic *Glomerula* (the only calcareous tube-dwelling sabellid) has been investigated in detail for the first time using confocal Raman spectroscopy and supplementary SEM-EDS studies. The data obtained indicate a low-Mg calcitic mineralogy of the single-layered sabellid tubes composed of an oriented spherulitic prismatic structure (SPHP). While the kind of ultrastructure stays congruent with earlier observations, the mineralogy of the tubes is inconsistent with previous studies. The calcitic composition of Jurassic sabellids is also different from the Recent *Glomerula piloseta* and most probably from their Permian ancestors. The origin and further long-term fluctuations in the skeletal mineralogy of sabellids and other calcareous polychaete groups (serpulids and cirratulids) were dependent to a significant extent upon the changes of the ionic ratio of the ambient seawater across long stratigraphical intervals. Sabellids produced mineralized skeletons for the first time in the Permian, an interval when aragonitic seas prevailed. Calcareous serpulids and cirratulids originated in the Permian and Oligocene, respectively. In both cases, they matched the seawater chemistry of that time. Biomineralization in sabellids and cirratulids remains simple, whereas serpulids employ a more sophisticated biomineralization system. This results in a paucity of forms within sabellids producing calcareous habitation tubes. However, faster skeletal secretion of sabellids bearing lower energy expenditures (compared to

their counterparts in the family Serpulidae) possibly served as a mean of avoiding direct competition. Instead, they were able to spread fast over the substrate during deteriorating conditions.

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Article 4

Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications.

Ultrastructure of the Jurassic serpulid tubes–phylogenetic and paleoecological implications

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ABSTRACT

The ultrastructural diversity of the Middle and Late Jurassic serpulid tubes from the Polish Basin has been investigated. The inspection of 12 taxa representing the two major serpulid clades allowed for the identification of three ultrastructure types— irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP). Six of the studied species are single-layered and six species possess two distinct layers. Ultrastructural diversity corresponds to certain serpulid clades. The members of Filograninae have single-layered tube walls composed of possibly plesiomorphic, irregularly oriented prismatic structure (IOP). Two-layered tubes occur solely within the clade Serpulinae, where the external, denser layer is built of either the ordered spherulitic (SPHP) or simple prismatic microstructure (SP), and the internal layer is composed of irregularly oriented prismatic structure (IOP). Apart from phylogenetic signals provided by the tube ultrastructure, it can be used in analyzing paleoecological aspects of tube-dwelling polychaetes. Compared to the more primitive, irregularly oriented microstructures of Filograninae, the regularly oriented microstructures of Serpulinae need a higher level of biological control over biomineralization. The advent of the dense outer protective layer (DOL) in serpulids, as well as the general increase in ultrastructure diversity, was likely a result of the evolutionary importance of the tubes for serpulids. Such diversity of the tube ultrastructural fabrics allowed for maximizing functionality by utilizing a variety of morphogenetic programs. The biomineralization system of serpulids remains more complex compared to other tube-dwelling polychaetes. Physiologically more expensive tube formation allows for mechanical strengthening of the tube by building robust, strongly ornamented tubes and firm attachment to the substrate. Contrary to sabellids, which perform a fugitive strategy, an increased tube durability allows serpulids a competitive advantage over other encrusters.

INTRODUCTION

Numerous polychaete families produce habitation tubes (*Rouse & Pleijel, 2001*). Tubicolous polychaetes may either agglutinate exogenous material, such as sand particles and shell fragments, using a proteinaceous cement to form a tube (*e.g.*, *Stewart et al., 2004*; *Zhao*

et al., 2005; *Fournier, Etienne & Le Cam, 2010*; *Vinn & Luque, 2013*) or produce secretions by themselves utilizing a variety of glands (*e.g.*, *Hausen, 2005*; *Tanur et al., 2010*). Secreted tubes may be composed of organic substances, such as proteins and polysaccharides (*e.g.*, *Barnes, 1965*; *Chamoy et al., 2001*; *Nishi & Rouse, 2013*), and mineral substances such as calcium carbonate (*Weedon, 1994*; *Fischer, Pernet & Reitner, 2000*; *Vinn et al., 2008*). Amongst tube-dwelling polychaetes producing hard, mineralized exoskeletons are the families Sabellidae, Cirratulidae, and Serpulidae. Whereas calcareous sabellids (*Perkins, 1991*; *Vinn, ten Hove & Mutvei, 2008*; *Słowiński, Banasik & Vinn, 2023*) and cirratulids (*Reish, 1952*; *Fischer, Oliver & Reitner, 1989*; *Fischer, Pernet & Reitner, 2000*; *Taylor et al., 2010*; *Kočí et al., 2021*; *Guido et al., 2024*) are restricted to one (*Glomerula*) and two genera (*Dodecaceria*, *Diplochaetetes*) in each family respectively, only serpulids dwell exclusively in tubes composed of calcium carbonate (*Vinn et al., 2008*).

Thus, having a hard, mineralized exoskeleton, serpulids are the most abundant polychaetes in the fossil record, appearing as far back as the Middle Permian (*Sanfilippo et al., 2017*; *Sanfilippo et al., 2018*). However, their hard parts are not strictly related to the organism's soft body and form only a habitation tube serving, among others, for protection against predators (*e.g.*, *Morton & Harper, 2009*; *Klompmaker, 2012*). Although tubes' taxonomic usefulness is not without validity, as many genera possess easily recognizable tubes, which are diagnostic displaying different longitudinal and transverse elements (see *e.g.*, *Ippolitov et al., 2014*), homeomorphy is still a common feature in serpulid tube morphology (*e.g.*, *Kupriyanova & Ippolitov, 2015*) due to convergence and high ecophenotypic plasticity. This leads to certain discrepancies between paleontological and biological classification, the latter of which is based solely on the molecular data, soft parts, and their reciprocal relationships (*Kupriyanova, Macdonald & Rouse, 2006*; *ten Hove & Kupriyanova, 2009*). Moreover, it makes the linkage of contemporary species with their ancestors difficult due to the lack of fully reliable taxonomic tools.

Serpulid tubes can be composed of up to four layers; however, most of them are single-layered (*Vinn et al., 2008*). They exhibit different ultrastructural fabrics, depending on how calcium carbonate crystals are arranged and oriented (see *Vinn et al., 2008*). During the progressing expansion of the tube, an animal secretes consecutive growth lamellae, which correspond to a single growth episode. Such growth lines may be either straight, perpendicular to the direction of growth (*e.g.*, *Bałuk & Radwański, 1997*) or much more frequently chevron-shaped (see *Weedon, 1994*). Serpulid ultrastructures may provide phylogenetic signals in the case of Jurassic taxa but also serve as a record of the physiological changes of the worm during its entire lifespan, providing important ecological signatures that may be successfully implemented in paleoecological analyses. Moreover, serpulid tubes may exhibit additional skeletal structures such as tubulae, alveolar structures, or internal tube structures, helping in unraveling their true systematics (*e.g.*, *Thomas, 1940*; *Pillai, 1993*; *Pillai & ten Hove, 1994*; *Jäger, 2005*).

Recent studies have proven a tube microstructure to be a useful tool in deciphering the true affinity of fossil serpulid (*e.g.*, *Bornhold & Milliman, 1973*; *Vinn, ten Hove & Mutvei, 2008*; *Vinn & Kupriyanova, 2011*; *Kupriyanova & Ippolitov, 2012*; *Vinn, 2013*; *Buckman, 2020*; *Buckman & Harries, 2020*), and other calcareous tube-dwelling polychaete species

(*Vinn, ten Hove & Mutvei, 2008*; *Taylor et al., 2010*; *Słowiński, Banasik & Vinn, 2023*). However, the majority of them were conducted based on single species, and/or single specimens.

In the present study, we performed a microstructural investigation of the Jurassic serpulid tubes based on the representatives of the two main serpulid clades according to the newest systematics (*Kupriyanova, ten Hove & Rouse, 2023*). We provide paleoecological implications of different microstructures and consequently biomineralization system and highlight some phylogenetic signals and evolutionary patterns of distinct microstructures.

MATERIAL AND METHODS

The examined fossils consist of 47 specimens of serpulids representing 12 taxa (Table 1). The studied material has been selected from an ample collection (see *Słowiński et al., 2020*; *Słowiński et al., 2022*) concerning the well-preserved specimens, which allowed for a reliable ultrastructural investigation. All diagenetically altered tubes have been discarded from further studies. Almost all specimens encrust a variety of invertebrate fossils, oncoids, and hiatus concretions, and have been derived from various localities with Middle and Upper Jurassic (upper Bajocian–lower Kimmeridgian) deposits (Fig. 1) representing an array of paleoenvironments. The investigated material is stored at the Institute of Earth Sciences in Sosnowiec, abbreviated GIUS 8-3589 (Callovian of Zalas), GIUS 8-3730 (middle Bathonian of Gnaszyn Dolny), GIUS 8-3745 (upper Bathonian-lower Callovian of Bolęcin), GIUS 8-3746 (Oxfordian of Zalas), GIUS 8-3747 (lower Kimmeridgian of Małogoszcz), GIUS 8-3750 (Bajocian-Bathonian of Ogrodzieniec-Świertowiec), GIUS 8-3751 (upper Bathonian of Krzyworzeka and upper Bathonian of Żarki). Their paleogeographic and geological background is beyond the scope of the present research and has already been discussed in detail by *Słowiński et al. (2020)* and *Słowiński et al. (2022)*.

Before the preparation of specimens for the SEM examination, they were coated with ammonium chloride and photographed using the Canon EOS 350D digital camera. All previously selected samples were cut longitudinally, polished, and etched with a 5% solution of acetic acid for one minute prior to the SEM study. Part of these tube portions were oriented and mounted in epoxy resin before polishing. Subsequently, the serpulid tube microstructure investigations were performed on a SEM Zeiss EVO MA15 under a back-scattered electron detector (BSE) in a low vacuum regime (Department of Geology, University of Tartu, Estonia). The sections were also inspected under an environmental scanning electron microscope (ESEM) Philips XL30, and a Quanta 250 scanning electron microscope using BSE imaging (both at the Institute of Earth Sciences in Sosnowiec). The beam voltage was operated at 20 kV.

RESULTS

During the examination of 12 taxa within eight genera representing two major clades, three types of ultrastructure were distinguished: irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP) (Table 1).

Table 1 Ultrastructural diversity of the Jurassic serpulid tubes from Poland.

Taxon	Ultrastructure			Age	Locality	Number of individuals investigated
	IOP	SPHP	SP			
Metavermilia cf. *striatissima* ∗	1			upper Bathonian	Krzyworzeka	3
Filogranula runcinata *	[2]	1		middle Bathonian, Callovian	Gnaszyn Dolny, Zalas	5
Filogranula spongiophila *			1	Oxfordian	Zalas	3
Cementula spirolinites ●			1	Oxfordian	Zalas	9
Cementula radwanskae ●			[1]	Callovian	Zalas	4
Propomatoceros lumbricalis ×	2	1, [3]		Bajocian-Bathonian, middle Bathonian, upper Bathonian, Bathonian-Callovian, Callovian, lower Kimmeridgian	Ogrodzieniec-Świertowiec, Gnaszyn Dolny, Żarki, Bolęcin, Zalas, Małogoszcz	8
Nogrobs aff. *quadrilatera* ×	2		1	middle Bathonian	Gnaszyn Dolny	3
Nogrobs? aff. *tricristata* ×	2		1	middle Bathonian	Gnaszyn Dolny	1
Nogrobs aff. *tetragona* ×	2		1	middle Bathonian	Gnaszyn Dolny	2
Mucroserpula sp. ×	2	1		middle Bathonian	Gnaszyn Dolny	3
Placostegus planorbiformis ×			1	Oxfordian	Zalas	3
Serpulidae sp. ×	2		1	middle Bathonian	Gnaszyn Dolny	3
Total						47

Notes.

IOP, irregularly oriented prismatic structure; SPHP, spherulitic prismatic structure; SP, simple prismatic structure.

Numbers (1, 2, 3) indicate the position of the layer within the tube counted from the exterior. Square brackets denote partially preserved or equivocal microstructure precluding a fully reliable recognition. Asterisk, circle, and ×mark correspond to Filograninae, Serpulini, and Ficopomatini respectively. All the taxa have been described taxonomically in *Słowiński et al. (2022)*.

Filograninae (BI)

Members of the clade Filograninae, formerly referred to as BI (see *Kupriyanova, Macdonald & Rouse, 2006*; *Kupriyanova et al., 2009*), are represented in the herein material by two genera: *Metavermilia* and *Filogranula*, the latter one consisting of two species: *F. runcinata* (*Sowerby, 1829*) and *F. spongiophila* (*Słowiński et al., 2022*).

The tube wall of *Metavermilia* cf. *striatissima* (*Fürsich, Palmer & Goodyear, 1994*) is single-layered, and composed of an irregularly oriented prismatic structure (IOP) (Fig. 2). Minute (maximally a few μm), needle-like crystals are deployed more or less evenly within the entire tube wall. The longitudinal axes of crystals lack a uniform orientation.

The tube of *Filogranula runcinata* is presumably single-layered and is composed of a spherulitic, regularly oriented prismatic microstructure (SPHP) (Fig. 3). It is formed by crystals of prismatic shape exhibiting a slightly spherulitic arrangement. Some internal parts of the tube are built of irregularly oriented, tiny, elongated crystals indicating an irregularly oriented prismatic structure (IOP). However, the boundary between the two putative layers is transitional and the latter microstructure occurs rather like inclusions in certain areas of the tube wall. Growth lines are apparent across almost the entire tube. Some minor, external parts of the section may appear like fine homogeneous granular microstructure; however, more likely it corresponds to the differences in preservation
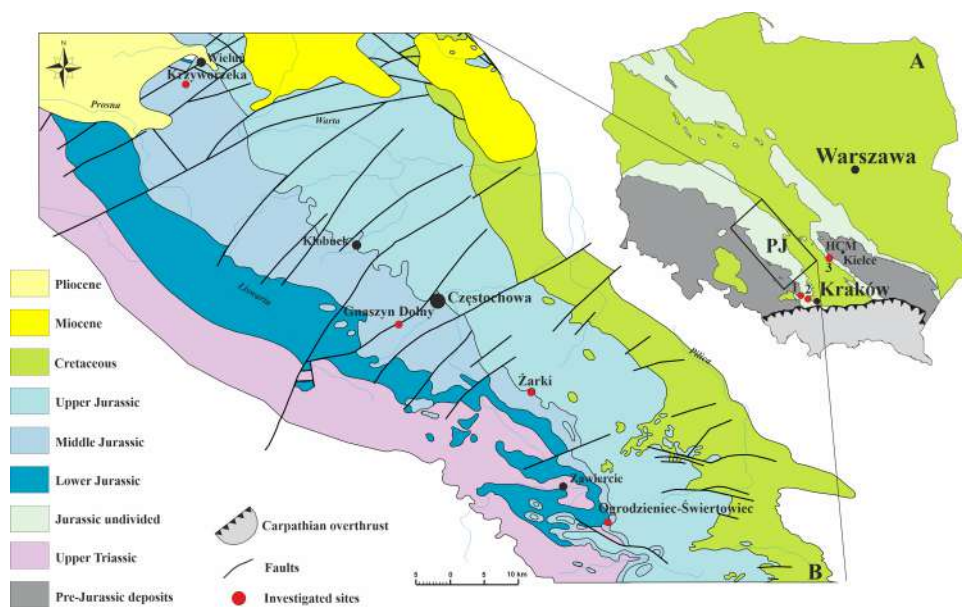
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between the external and internal parts of the tube due to the diagenetic alteration of irregularly oriented prismatic microstructure.

The tube of *Filogranula spongiophila* consists of a single layer that is composed of a simple, regularly oriented prismatic structure (SP) (Fig. 4). Growth increments are visible across almost the whole tube (Figs. 4C–4E).

Serpulinae, tribe Serpulini (AI)

This tribe is represented in the investigated material by one genus comprising two species: *Cementula spirolinites* (Münster in *Goldfuss, 1831*) and *Cementula radwanskae* (*Słowiński et al., 2022*).

The tube wall of *C. spirolinites* is single-layered and consists of a simple prismatic structure (SP) (Fig. 5). This microstructure is formed by parallel prismatic crystals oriented perpendicularly to each growth line showing incremental zonation. The crystals are arranged perpendicularly or obliquely to the tube wall.

The tube microstructure of the investigated specimens of *C. radwanskae* is altered in most places. However, some places exhibiting faint growth increments indicate possibly a simple (SP) or spherulitic prismatic structure (SPHP) constituting a single layer (Fig. 6). Certain areas with tiny, elongated irregularly oriented crystals presumably are an effect of a diagenetic distortion of the tube wall.

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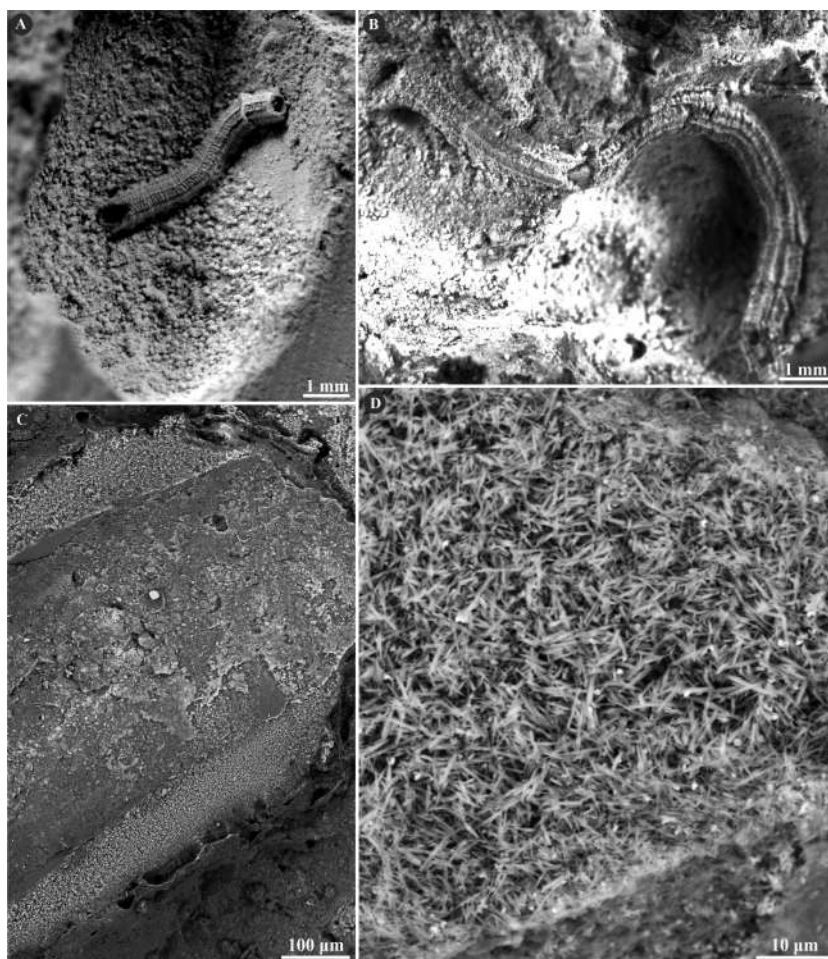
Figure 2 Selected specimens of *Metavermilia*. cf. *striatissima* (*Fürsich, Palmer & Goodyear, 1994*) from the Jurassic of Poland. (A, B) *Metavermilia* cf. *striatissima* encrusting the interior of the boring *Gastrochaenolites* from the upper Bathonian of Krzyworzeka, Polish Jura ((A) GIUS 8-3751/3; (B) GIUS 8-3751/8). (C, D) Longitudinal sections of the tubes from the upper Bathonian of Krzyworzeka with visible irregularly oriented prismatic structure (IOP). (C) General look of the ground, polished and etched tube with visible thin, single-layered walls (GIUS 8-3751/3). (D) Close-up of the tube wall section showing densely packed, tiny, elongated prismatic crystals of irregular arrangement (GIUS 8-3751/3).

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Serpulinae, tribe Ficopomatini (AII)

The tribe Ficopomatini, formerly referred to as AII (see *Kupriyanova, Macdonald & Rouse, 2006*; *Kupriyanova et al., 2009*), includes here five genera with seven species. *Propomatoceros lumbricalis* (*von Schlotheim, 1820*) possesses a tube wall consisting of two or three layers (Fig. 7). The majority of the examined specimens have two-layered tubes. The external part is formed by a spherulitic prismatic structure (SPHP), which consists of parallel crystals of a slightly spherulitic arrangement. The inner part has an irregularly oriented prismatic microstructure (IOP) comprising elongated, but relatively short, tiny crystals with inconsistent orientation axes. In some areas of the tubes' wall, the IOP structure is diagenetically altered superficially resembling a fine homogeneous granular structure. The

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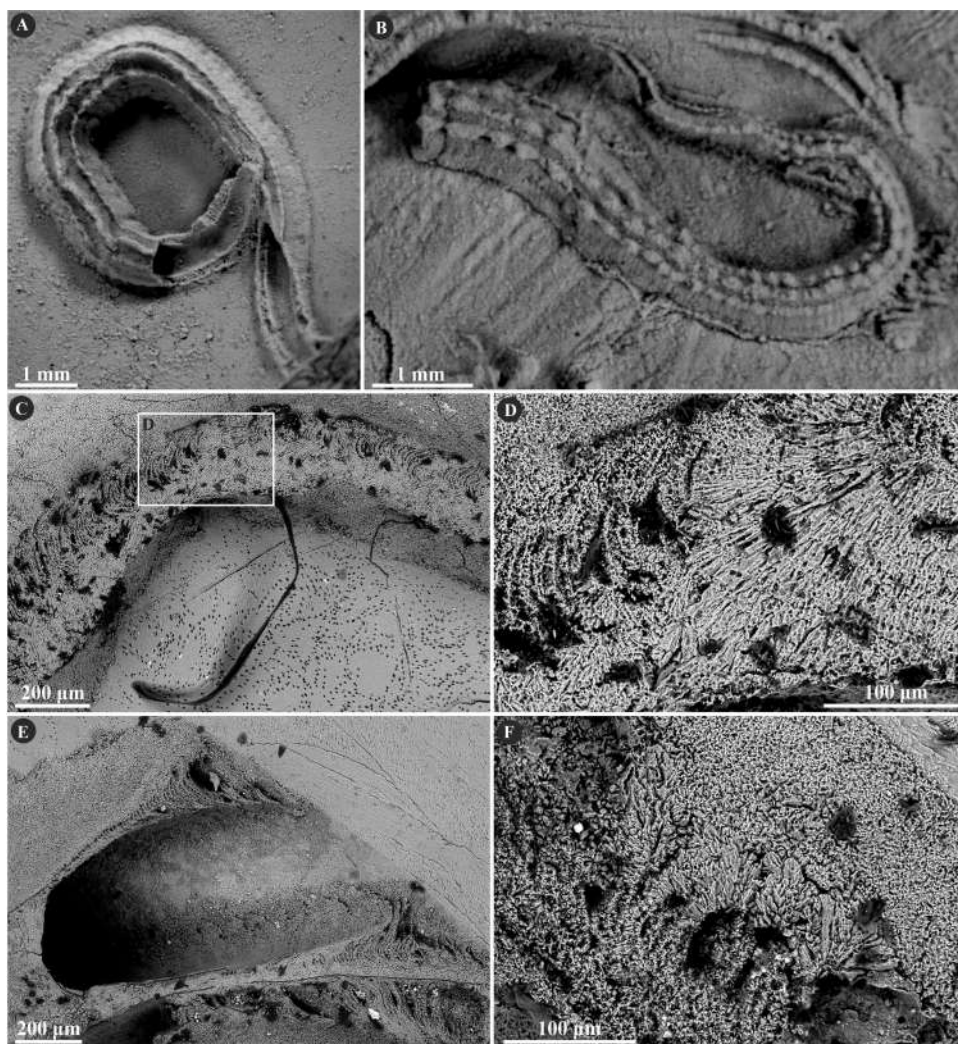
Figure 3 Selected specimens of *Filogranula runcinata* (*Sowerby, 1829*) from the Jurassic of Poland. (A, B) *Filogranula runcinata* from the middle Bathonian of Gnaszyn Dolny (A. GIUS 8-3730/10) and the Callovian of Zalas (B. GIUS 8-3589/6) encrusting shell fragments. (C–F) Longitudinal sections of the tubes showing a single-layered tube wall built of spherulitic prismatic structure (SPHP) with well-visible growth increments (GIUS 8-3730/10).

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putative three-layered tube wall (Fig. 7D) is built of the external and internal (uncertain) parts composed of a spherulitic prismatic structure (SPHP). The middle part shows a fine homogeneous granular microstructure, which may be either a primary microstructure or similarly to other specimens, an obliterated IOP structure. In contrast to two-layered *P. lumbricalis* tubes, no areas exhibiting irregularly oriented prismatic structures have been found. As such, it is not evident, whether these microstructures are primary or have undergone diagenetic alteration. The external parts exhibit incremental zonation with prominent chevron-shaped growth lines. The crystals are continuously and regularly positioned through successive growth increments.

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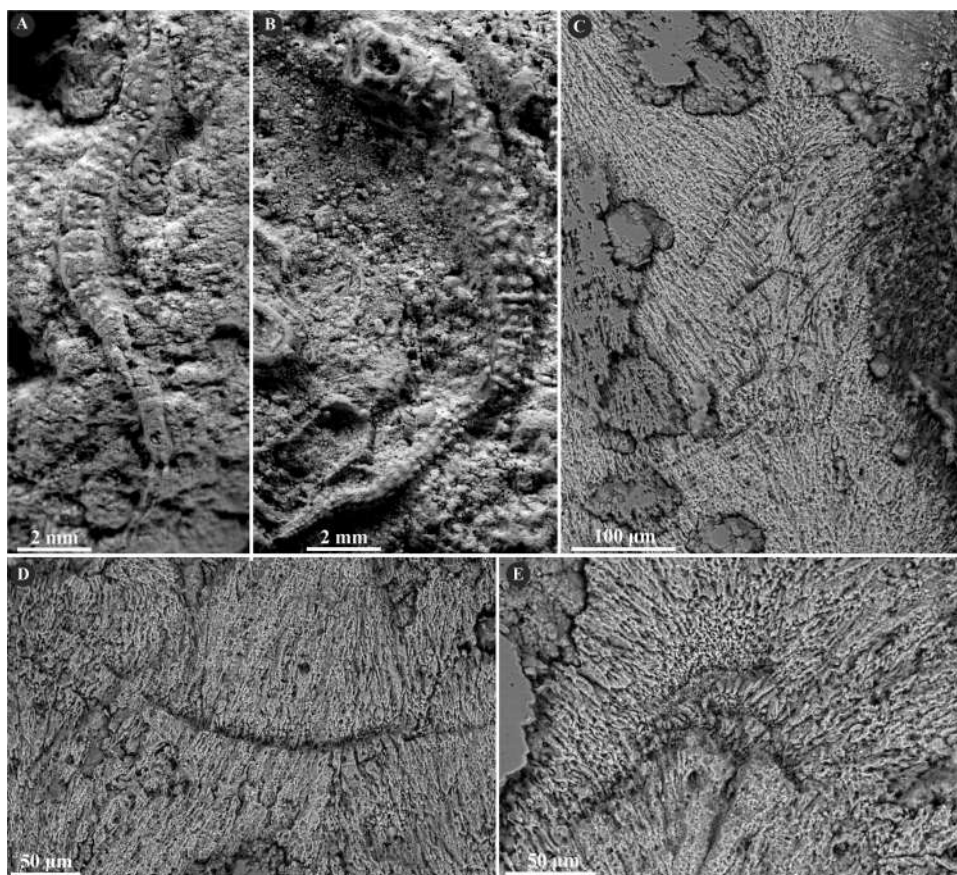
Figure 4 Selected specimens of *Filogranula spongiophila* (*Słowiński et al., 2022*) from the Jurassic of Poland. (A, B) *Filogranula spongiophila* from the Oxfordian of Zalas ((A) GIUS 8-3746/2; (B) GIUS 8-3746/3) encrusting sponge fragments. (C–E) Longitudinal sections of the tubes showing the simple prismatic structure (SP) with well-visible growth increments (GIUS 8-3746/9).

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Herein, *Nogrobs* is represented by three species: *N.* aff. *quadrilatera* (*Goldfuss, 1831*), *N.* aff. *tetragona* (*Sowerby, 1829*), and *N*? aff. *tricristata* (*Goldfuss, 1831*), which, however, share all the major microstructural characters. The tube walls of all the species have two layers, which are separated from each other with a sharp boundary. The external layer is composed of a simple prismatic structure (SP), whereas the internal layer is composed of very thin, short, needle-like crystals, which make up an irregularly oriented prismatic structure (IOP) (Fig. 8).

Mucroserpula sp. (*Regenhardt, 1961*) possesses a two-layered tube wall (Fig. 9). The internal layer is composed of an irregularly oriented prismatic structure (IOP) consisting of bunches of densely packed, short but elongated crystals lacking uniform orientation axes. The external layer is composed of a regular spherulitic prismatic structure (SPHP), which constitutes the major part of the tube wall. Within this layer, crystals are oriented perpendicularly with respect to each incremental zone and have a somewhat prismatic arrangement. The chevron-shaped growth lines are very well-visible alongside almost the whole tube length. The border between the two layers is somewhat transitional.

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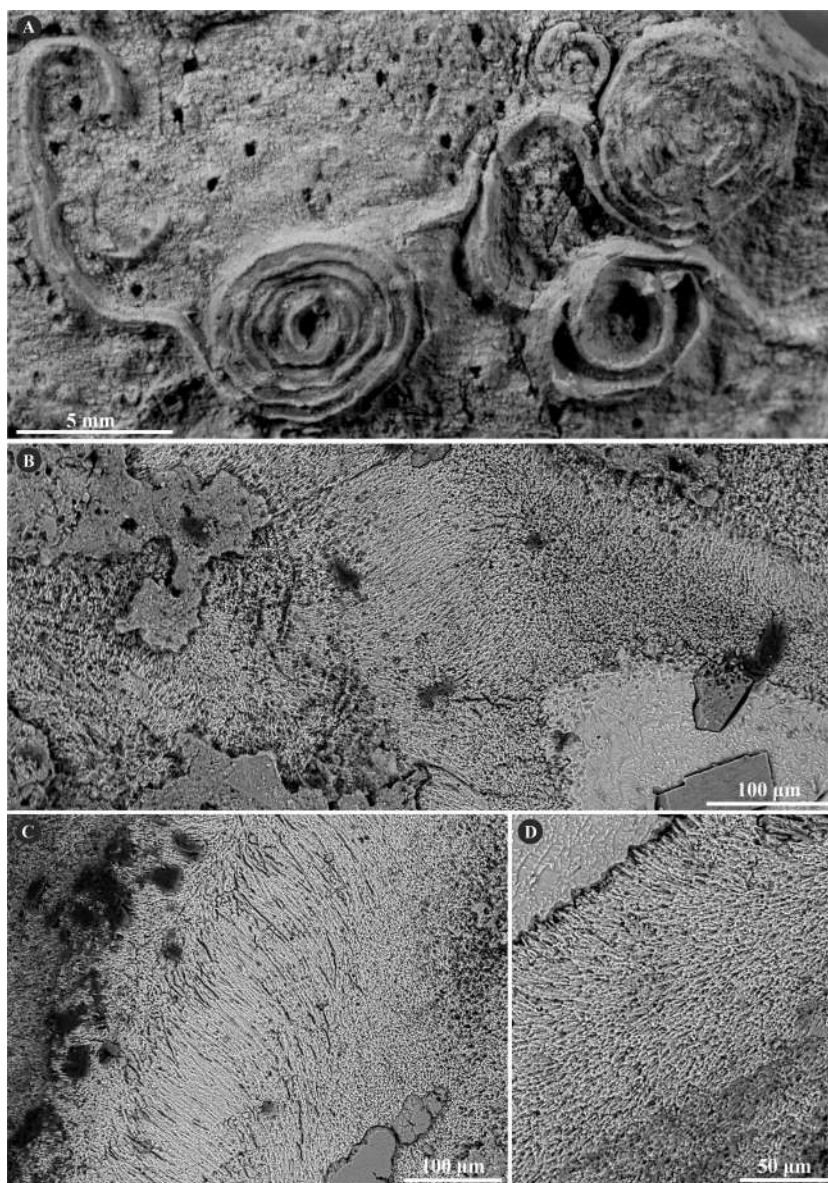
Figure 5 **Selected specimens of *Cementula spirolinites* (Münster in *Goldfuss, 1831*) from the Jurassic of Poland.** (A) *Cementula spirolinites* from the Oxfordian of Zalas encrusting a sponge fragment (GIUS 8-3746/4). (B–D) Longitudinal sections of the tubes showing the simple prismatic structure (SP). (B) GIUS 8-3746/10; (C, D) GIUS 8-3746/11.

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The tube wall of *Placostegus planorbiformis* (Münster in *Goldfuss, 1831*) is single-layered, and composed of a simple prismatic structure (SP) (Fig. 10). All crystals are more or less parallel within each incremental zone. Within the outermost part of the tube, the crystals are oriented perpendicularly to the tube wall.

The specimens of undetermined serpulid, Serpulidae sp. possess a two-layered tube wall (Fig. 11). The external part features a regularly oriented simple prismatic structure (SP). The internal, thinner part, separated from the external with a sharp boundary is formed

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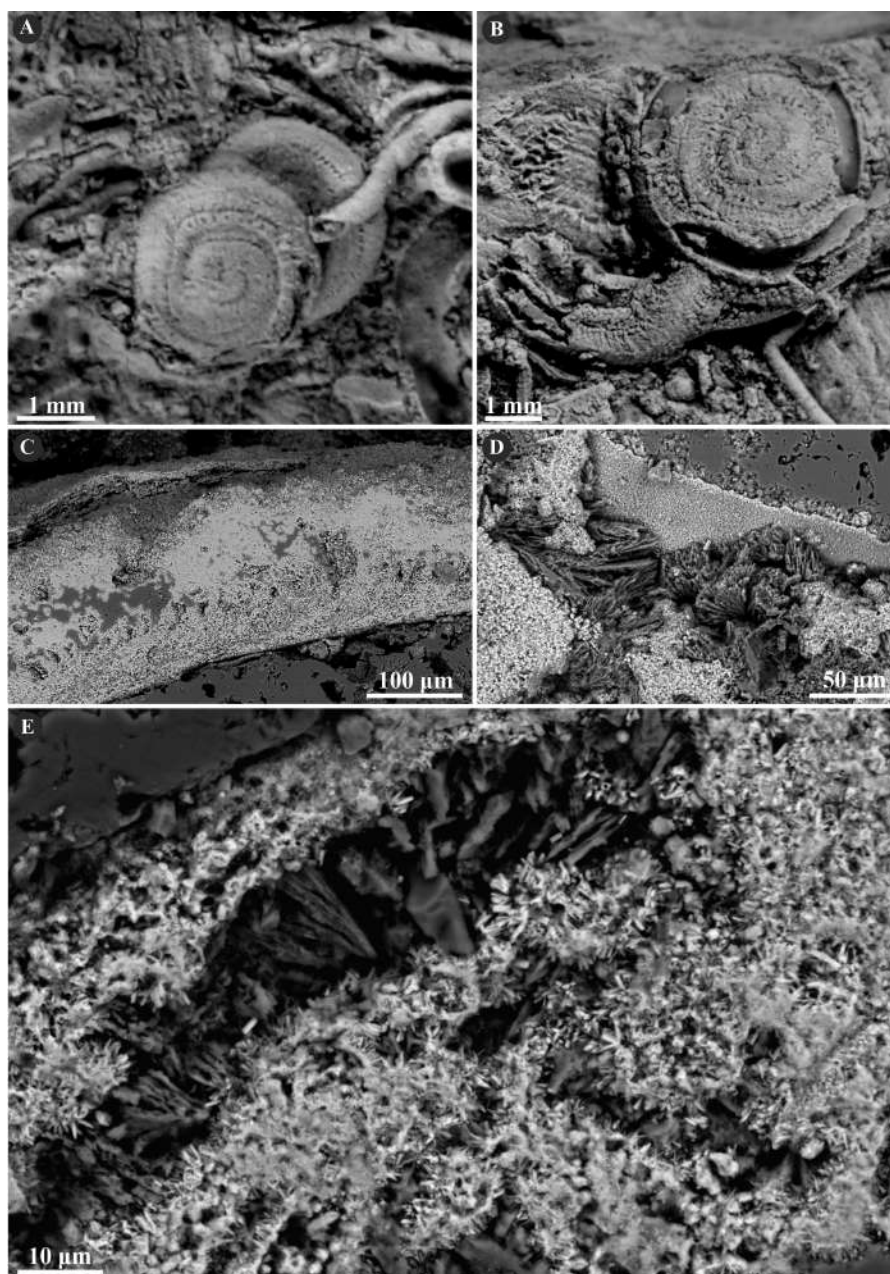
Figure 6 **Selected specimens of *Cementula radwanskae* (*Słowiński et al., 2022*) from the Jurassic of Poland.** (A, B) *Cementula radwanskae* from the Callovian of Zalas encrusting shell fragments (A) 8-3589/7; (B) GIUS 8-3589/10). (C–E) Longitudinal sections of the tubes showing mostly altered, presumably simple prismatic microstructure (SP); GIUS 8-3589/18. Note the weak growth increments in C.

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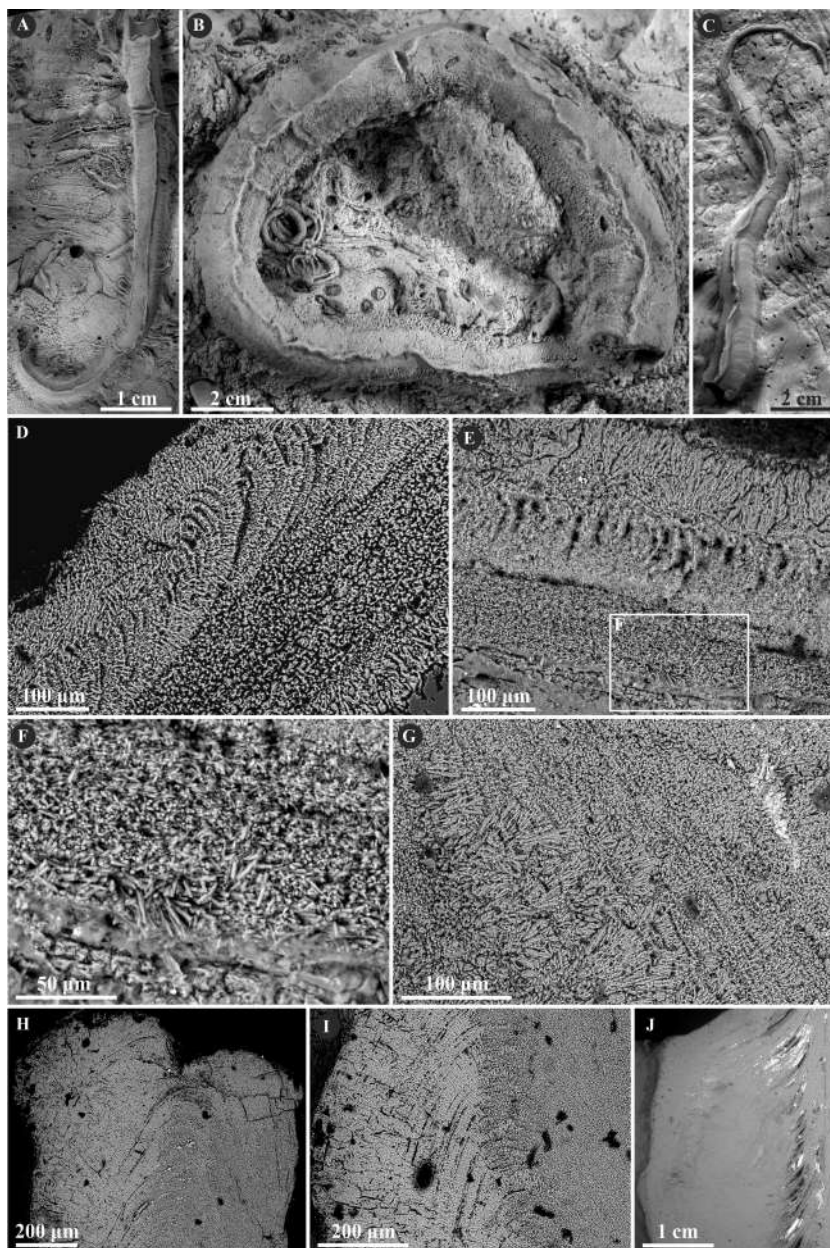
Figure 7 **Selected specimens of *Propomatoceros lumbricalis* (Schlotheim, 1820) from the Jurassic of Poland.** (A, B) *Propomatoceros lumbricalis* encrusting a shell fragment from the Callovian of Zalas (A) GIUS 8-3589/11; (B) GIUS 8-3589/12. (C) *Propomatoceros lumbricalis* encrusting an oyster shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/12). (D–J) Sections of the tubes showing the ultrastructural details. (continued on next page…)

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Figure 7 (…continued)
(D) The longitudinal section of the *P. lumbricalis* tube from the upper Bathonian–lower Callovian of Bolęcin showing the putative three-layered tube (GIUS 8-3745/5). The external layer shows spherulitic prismatic structure (SPHP) with growth increments; the middle part exhibits presumably altered irregularly oriented prismatic structure (IOP) superficially resembling homogeneous structure; the internal layer shows uncertain spherulitic prismatic structure. (E) The longitudinal section of the two-layered *P. lumbricalis* tube from the middle Bathonian of Gnaszyn Dolny showing the external spherulitic prismatic structure (SPHP) with growth increments and the internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/30). (F) A close-up showing the internal layer built of irregularly oriented prismatic structure (IOP) with short, needle-like crystals of different length and orientation (GIUS 8-3730/30). (G) The longitudinal section of the *P. lumbricalis* tube from the lower Kimmeridgian of Małogoszcz (GIUS 8-3747/5) showing the spherulitic arrangement of crystals within the external tube layer. (H, I) Longitudinal sections of the two *P. lumbricalis* tubes from the middle Bathonian of Gnaszyn Dolny showing the external spherulitic prismatic structure (SPHP) with well-visible growth increments and the internal, partially recrystallized irregularly oriented prismatic structure (IOP) (H. GIUS 8-3730/31; I. GIUS 8-3730/32). (J) The lateral section of the *P. lumbricalis* tube from the middle Bathonian of Gnaszyn Dolny showing tubulae subdivided densely by septae (GIUS 8-3730/33).

by an irregularly oriented prismatic structure (IOP) composed of densely packed, minute, elongated crystals.

DISCUSSION

Tube ultrastructure evolution and its phylogenetic constraints

Three distinct types of ultrastructure have been identified within 12 taxa corresponding to the two of three main clades of serpulids—Filograninae and Serpulinae (*Kupriyanova, ten Hove & Rouse, 2023*). These microstructures comprise irregularly oriented prismatic structure (IOP), spherulitic prismatic structure (SPHP), and simple prismatic structure (SP) (see Table 1), which are among the most prevalent microstructure type in fossil serpulids (*Vinn et al., 2008*; *Vinn, 2020*). Six of these taxa have single-layered tubes and six are two-layered, of which one taxon perhaps may possess either two or three ultrastructural layers (see discussion). The majority of both Cenozoic and contemporary serpulids are single-layered, only about one-third of serpulid species have at least two or up to four distinct ultrastructural layers (*Vinn et al., 2008*). During the Jurassic, the percentage of multi-layered serpulid species was lower, constituting approximately 25% (*Vinn & Furrer, 2008*). It may have resulted from the evolutionary pattern where more complex tube walls with at least two layers were more common from the beginning of the Cenozoic onward—the growing complexity of microstructures combined with relatively fast biomineralization likely enhanced the strengthening abilities of the tubes. It can also be explained by the vagaries of the fossil record resulting in incomplete preservation of the outermost layers, which might be similar to the case of calcareous sabellids (*Vinn, ten Hove & Mutvei, 2008*; *Słowiński, Banasik & Vinn, 2023*).

Sanfilippo (1998) presented a concept to utilize the ultrastructural diversity of serpulids to assess their generic determination. Further studies revealed that microstructure characters may be species-dependent (*Vinn, 2007*; *Vinn et al., 2008*; *Kupriyanova & Ippolitov, 2015*), which limits the application of tube microstructures in deciphering the generic affiliation of serpulids. Regardless, ultrastructural fabrics of tubes may still be used to approach the
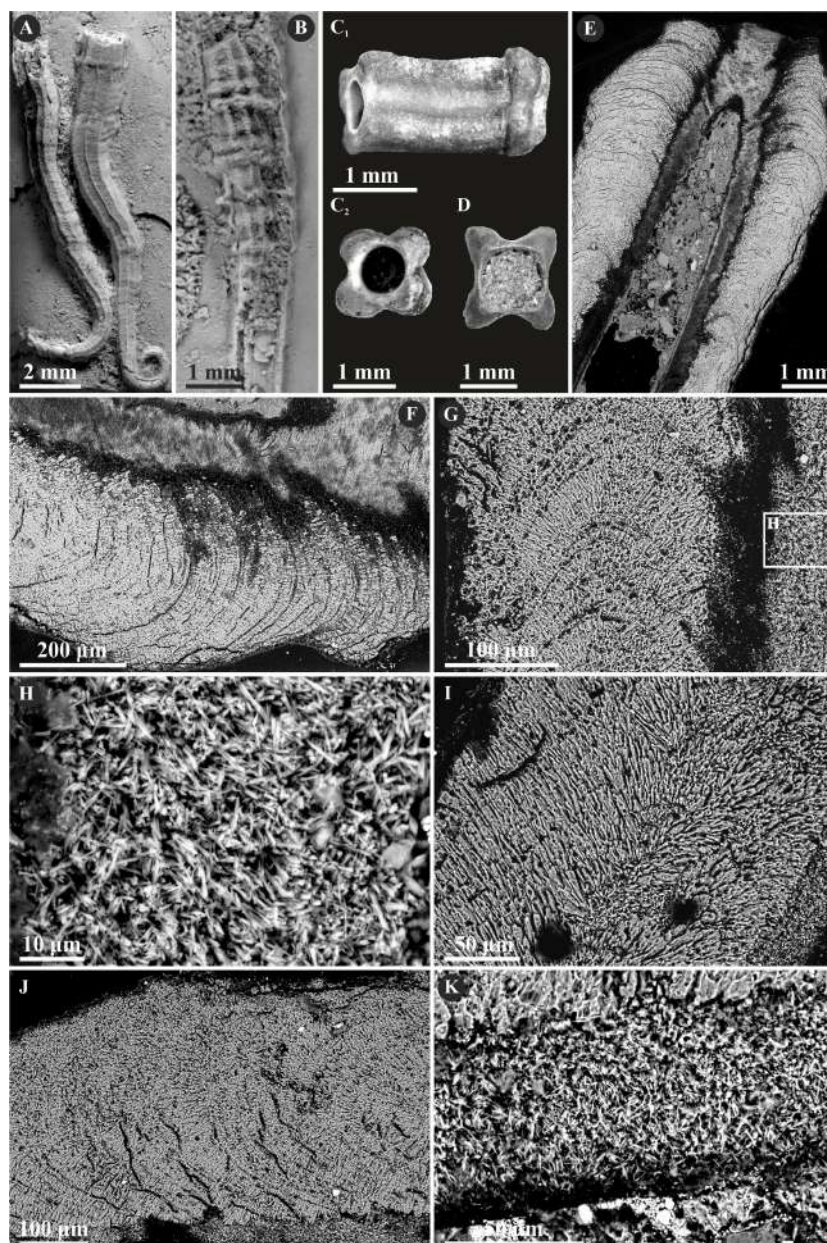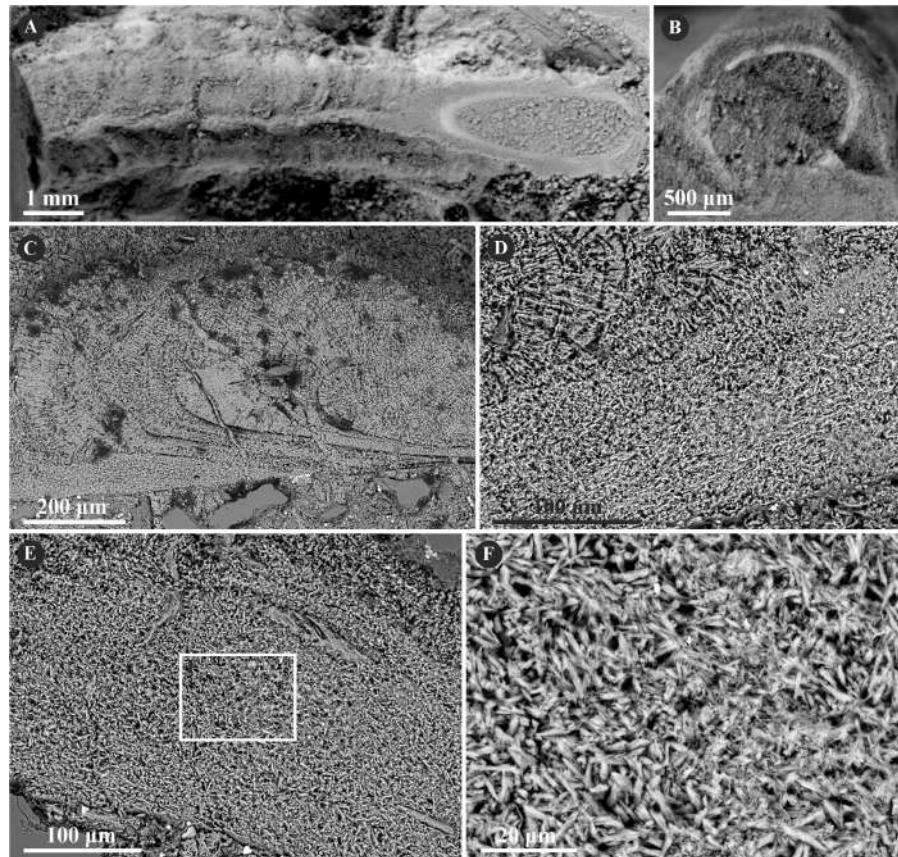
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Figure 8 Selected specimens of *Nogrobs* from the Jurassic of Poland. (A) Two specimens of *Nogrobs* aff. *quadrilatera* (*Goldfuss, 1831*) encrusting a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/17). (B) *Nogrobs*? aff. *tricristata* (*Goldfuss, 1831*) encrusting a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/19). (C, D) Free-lying tubes of *Nogrobs* aff. *tetragona* (*Sowerby, 1829*) (C. GIUS 8-3730/24; D. GIUS 8-3730/25); lateral (C_1) and cross-section (C_2, D) view. (continued on next page...)

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Figure 9 Selected specimens of *Mucroserpula* (*Regenhardt, 1961*) from the Jurassic of Poland. (A, B) *Mucroserpula* sp. encrusting a fragment of a shell from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/26); top (A) and cross-section view (B). (C–E) Longitudinal sections of the *Mucroserpula* sp. tube from the middle Bathonian of Gnaszyn Dolny showing two distinct layers: the external spherulitic prismatic structure (SPHP) with distinct, chevron-shaped growth lines (C) and internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/26). (F) A close-up of the longitudinal section of the internal tube layer showing irregularly oriented prismatic structure (IOP) with short, needle-like crystals of different length and orientation (GIUS 8-3730/26).

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relationships between distinct types of structures throughout the evolution of the main serpulid clades (*e.g.*, *Vinn et al., 2008*; *Vinn & Kupriyanova, 2011*; *Vinn, 2013*; *Ippolitov & Rzhavsky, 2014*; *Ippolitov & Rzhavsky, 2015a*; *Ippolitov & Rzhavsky, 2015b*).

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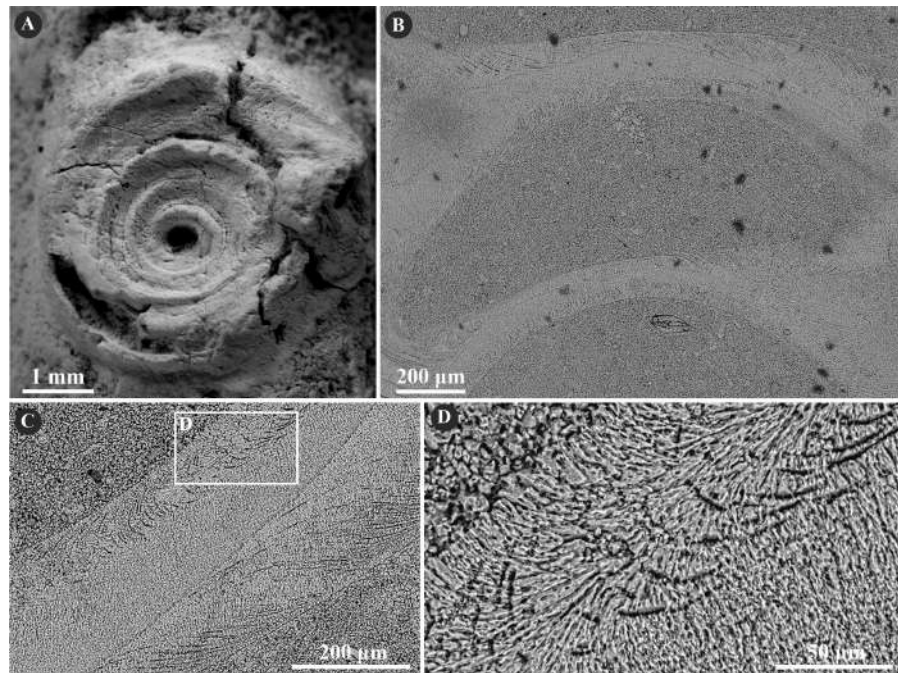
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Figure 10 **Selected specimens of *Placostegus planorbiformis* (Münster in *Goldfuss, 1831*) from the Jurassic of Poland.** (A) *P. planorbiformis* encrusting a sponge fragment from the Oxfordian of Zalas (GIUS 8-3746/8). (B–D) Longitudinal sections of the tubes showing the simple prismatic structure (SP) with well-visible growth increments (GIUS 8-3746/8).

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The most recent phylogenetic analyses indicate that serpulids are split into three major clades—Filograninae, Spirorbinae, and Serpulinae, the last of which is further subdivided into two tribes: Serpulini and Ficopomatini (*Kupriyanova, ten Hove & Rouse, 2023*). The family Serpulidae until recently was maintained to comprise two major clades referred to as B and A, separated into BI, BII, AI, and AII (*Kupriyanova, Macdonald & Rouse, 2006*; *Kupriyanova et al., 2009*; *Kupriyanova & Nishi, 2010*). Formerly recognized clades BI and BII generally may be related to Filograninae and Spirorbinae, whereas AI and AII, both settled within Serpulinae, correspond to the tribes Serpulini and Ficopomatini, respectively (*Kupriyanova, Macdonald & Rouse, 2006*; *Kupriyanova et al., 2009*; *Kupriyanova, ten Hove & Rouse, 2023*). Apart from Spirorbinae (former BII), members of all clades are present in the material studied.

Clade Filograninae is possibly rooted even in the Permian with primitive tubes such as *Filograna* (*Sanfilippo et al., 2017*; *Ramsdale, 2021*), and abundantly represented in the fossil record during the Mesozoic by many strongly ornamented tubes with several keels, *e.g.*, *Vermiliopsis*, *Metavermilia*, and *Filogranula*, the latter two of which are present in the material investigated. *Metavemilia* cf. *striatissima* is single-layered and possesses irregularly oriented prismatic microstructure (IOP), which has been also found in the recent *Metavermilia multicristata* (*Vinn et al., 2008*). It is characteristic of this clade and is also the most common microstructure in the recent serpulids encompassing ca 60% of
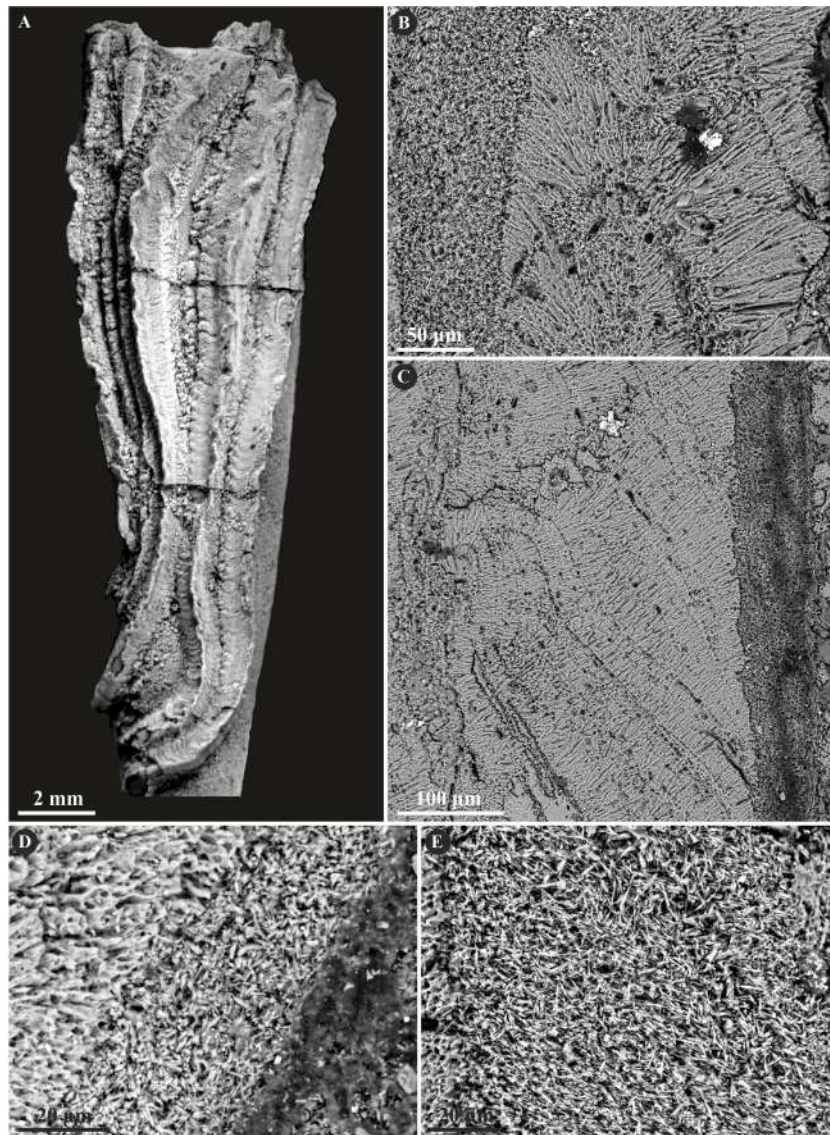
Figure 11 **Selected specimens of Serpulidae sp. from the Jurassic of Poland.** (A) Dense aggregation of closely spaced Serpulidae sp. 3 (see *Słowiński et al., 2022*) encrusting a fragment of a belemnite rostrum from the middle Bathonian of Gnaszyn Dolny (GIUS 8-3730/28). (B–E) Longitudinal sections of the Serpulidae sp. tube from the middle Bathonian of Gnaszyn Dolny showing two distinct layers: the external simple prismatic structure (SP) and internal irregularly oriented prismatic structure (IOP) (GIUS 8-3730/28).

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species (*Vinn, 2007*). IOP microstructure most often builds the wall of single-layered tubes, or alternatively the inner part of multi-layered tubes (see *Vinn & Furrer, 2008*).

The representatives of Filograninae are generally characterized in the fossil record by more or less uniform fabrics of tube microstructures forming irregularly oriented structures, notably irregularly oriented prismatic structure (IOP). Secretion of such microstructures seems to be governed by the lower biological control of an animal, compared to more

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advanced microstructures. The first confirmed appearance of such ultrastructure dates back to the Early Jurassic, possibly being present already in the Triassic (*Vinn, Jäger & Kirsimäe, 2008*). Such a simpler way of tube formation may indicate its plesiomorphic character and earlier origin (see also *Vinn, 2013*; *Ippolitov & Rzhavsky, 2015a*; *Ippolitov & Rzhavsky, 2015b*).

Another representative of this clade in the investigated material is the genus *Filogranula* comprising the recently discovered new species *F. spongiophila* (*Słowiński et al., 2022*), which has been studied with respect to ultrastructure for the first time, and by *F. runcinata*. The tube wall of *F. spongiophila* is single-layered and has a simple prismatic structure (SP), whereas *F. runcinata* possesses one well-preserved layer composed of spherulitic prismatic structure (SPHP) and a dubious IOP layer consisting of somewhat distorted, occasionally occurring areas of tiny, irregularly oriented crystals. As a result, the tube wall is interpreted as single-layered, composed of SPHP structure. Such microstructure occurs commonly in the clade Serpulinae comprising both formerly established "A" clades. The systematic position of the fossil *Filogranula* seems to be complicated, as the recent *Filogranula* is considered to be settled within Filograninae, relatively closely related to *Vermiliopsis* and *Metavermilia* (*Kupriyanova, ten Hove & Rouse, 2023*). While the Cretaceous *Filogranula cincta* (*Goldfuss, 1831*) is classified as belonging to Filograninae too, the Jurassic *Filogranula runcinata* was considered to be placed in Serpulinae, within the tribe Ficopomatini (see *Ippolitov et al., 2014*; *Kočí & Jäger, 2015*), due to its prismatic microstructure, characteristic of the serpulid tubes appearing transparent in the recent species, such as *e.g.*, *Placostegus*. On the other hand, prismatic structures are not a fully satisfactory character in differentiating between former A and B clades. *Ippolitov & Rzhavsky (2014)*, *Ippolitov & Rzhavsky (2015a)* and *Ippolitov & Rzhavsky (2015b)* found out that some spirorbins may also have their tubes composed of regularly oriented prismatic microstructures, in spite of the fact, that Spirorbinae is phylogenetically closely related to Filograninae, which commonly form irregularly oriented structures.

Serpulinae constitutes two well-supported tribes–Serpulini and Ficopomatini (*Kupriyanova, ten Hove & Rouse, 2023*). The first unequivocal members of Serpulinae very likely existed since the Triassic (*Assmann, 1937*; see *Ippolitov et al., 2014*) if not even since the Permian (*Sanfilippo et al., 2017*; *Sanfilippo et al., 2018*). In contrast to Filograninae, which have mostly non-oriented structures, serpulids within this lineage have a more advanced biomineralization system and are capable of forming complex microstructures, such as *e.g.*, oriented, lamello-fibrillar, or oriented-fibrillar (see *Vinn & Furrer, 2008*; *Vinn & Kupriyanova, 2011*). During the Jurassic, serpulid microstructure diversity was relatively modest (ten types; see *Schlögl et al., 2018*; *Vinn, 2020*) compared to an array of contemporary and Cenozoic ones (*Vinn, 2007*; *Kočí, Milàn & Jäger, 2023*). The most sophisticated microstructures in serpulids evolved in the Eocene (*e.g.*, (*Vinn, 2008*; *Buckman, 2020*; *Kočí, Goedert & Buckeridge, 2022*). Although such complex microstructures as lamello-fibrillar or regularly ridged prismatic appeared quite late in the evolution of serpulids, the oriented prismatic structures evolved at the latest during the Middle Jurassic. Simple and spherulitic prismatic microstructures are very common and characteristic of the Jurassic Serpulinae and are considered to be apomorphic.

Oriented prismatic structures are unknown from any genus of Filograninae; however, they were found to persist in the clade Spirorbinae (*Ippolitov & Rzhavsky, 2015a*; *Ippolitov & Rzhavsky, 2015b*), which appeared in the Cretaceous. It may mean, that either it is plesiomorphic, or the prismatic structures have evolved at least twice.

The tribe Serpulini is represented in the Jurassic by characteristically coiled *Spiraserpula* and related *Cementula*, which is present in the herein material. *C. spirolinites* and *C. radwanskae* are both single-layered and possess their tube walls built of simple prismatic microstructure (SP), though in the latter it is somewhat obliterated. Simple and spherulitic prismatic microstructures exhibit the predominantly uniform orientation of calcium carbonate crystals which determines the optical transparency of the tubes (*Ippolitov & Rzhavsky, 2008*; *Zibrowius & ten Hove, 1987*), supported also by the dense arrangement of crystals and their large size (*Vinn & Kupriyanova, 2011*). In contrast, the recent tubes with IOP microstructure most often are optically opaque (*Vinn et al., 2008*).

All the main members of the Jurassic representatives of Ficopomatini are present in the investigated material. They contain genera with various morphotypes comprising a robust, single-keeled *Propomatoceros*, a three-keeled *Mucroserpula*, quadrangular tubes attributed most often to *Nogrobs*, and a well-defined, planispirally coiled *Placostegus*. Serpulids in this tribe commonly possess two layers of tube walls having the outer dense layer built of ordered prismatic structures (simple or spherulitic), and the internal layer composed of irregularly oriented prismatic structure. Two-layered tubes appeared in the Jurassic (*Vinn & Furrer, 2008*) and have their external layer denser than the internal, which is composed of thinner mineral microstructure. Dense outer protective layers (DOL) have been found in tube walls of serpulids inhabiting diverse environments (see *Vinn & Kupriyanova, 2011*). Consequently, rather than being dependent on the environment, the advent of DOLs during the Jurassic appears to be a significant evolutionary adaptation of serpulids. Except for some members of Spirorbinae (*Ippolitov & Rzhavsky, 2014*; *Ippolitov & Rzhavsky, 2015a*; *Ippolitov & Rzhavsky, 2015b*) and one species in the clade Filograninae, dense, outer layers exist exclusively in the clade Serpulinae (*Vinn & Kupriyanova, 2011*).

Propomatoceros lumbricalis and *Mucroserpula* possess here two well-distinguishable layers: internal IOP and external SPHP. A single *Propomatoceros* specimen may have three layers, which, however, is ambiguous, as its internal layer may be diagenetically obliterated, and therefore all the specimens are considered two-layered. As discussed previously (*Ippolitov et al., 2014*; *Słowiński et al., 2022*), it cannot be ruled out, that *Mucroserpula* and *Propomatoceros* may represent the same genus. The diagnostic characters of both genera are highly transitional, subjective, and dependent to a large extent on different variables, such as *e.g.*, ontogenetic stage (see *Słowiński et al., 2022*). Nonetheless, the microstructural fabrics of the two genera in our investigation are essentially the same and typical of Ficopomatini.

Nogrobs consists here of three species: *N.* aff. *quadrilatera*, *N?* aff. *tricristata*, and *N.* aff. *tetragona*. All of them are two-layered composed of internal IOP and external SP microstructure. Apart from *Nogrobs*, Jurassic quadrangular fossils of serpulids that share morphological similarities with this genus were attributed by various authors to different genera, partially of questionable validity—*Tetraserpula* (*Parsch, 1956*), *Tetraditrupa* (*Regenhardt, 1961*), *Glandifera* (*Regenhardt, 1961*), *Tubulostium* (*Stoliczka, 1868*),

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Tectorotularia (*Regenhardt, 1961*), and *Ditrupula* (*Brünnich Nielsen, 1931*). *Kupriyanova & Ippolitov (2015)* examined and reviewed a number of microstructures of extant and fossil taxa having tusk-shaped, tetragonal in cross-section tubes, concluding, that these morphologically similar forms belong to several different genera, most likely being an effect of convergence. Not surprisingly, these recent taxa cannot be synonymized with the fossil *Nogrobs*. Nevertheless, the authors claim that at least the majority of fossil *Nogrobs* species may be members of a single clade, as opposed to morphologically-related recent species. According to its external tube layer composed of simple prismatic microstructure (responding to a transparent tube), the three investigated species fit well Ficopomatini, confirming previous ultrastructural studies (*Kupriyanova & Ippolitov, 2015*). It has to be noted, however, that the recent *Nogrobs grimaldii* (*Fauvel, 1909*) has been found to possess an opaque tube (*Kupriyanova & Nishi, 2011*).

The only exception not having a two-layered tube wall within this tribe is *Placostegus*, represented here by *P. planorbiformis*, which has a single layer made entirely of a simple prismatic structure (SP). Similarly, contemporary *P. tridentatus* (*Fabricius, 1779*) possesses a tube wall composed of a simple prismatic microstructure resulting in a completely transparent tube (*ten Hove & Kupriyanova, 2009*: 8, fig. 1F; *Vinn & Kupriyanova, 2011*).

The undetermined serpulid taxon Serpulidae sp., described recently by *Słowiński et al. (2022)* has been studied here with respect to its microstructure. Although the investigated specimens externally resemble a few genera, such as *Propomatoceros*, *Placostegus*, and *Metavermilia*, they do not exactly fit any of those taxa (see *Słowiński et al., 2022*). The specimens possess a tube wall composed of two layers—external simple prismatic (SP), and internal irregularly oriented prismatic microstructure (IOP), which is of a very close resemblance to other members of Ficopomatini, notably *Nogrobs*.

Ecological implications and comparisons with sabellids

Serpulids perform biologically controlled biomineralization where their cellular activity regulates the nucleation and extracellular growth of the calcium carbonate crystals by the ion uptake from the surrounding water (see *Neff, 1971a*; *Neff, 1971b*) using a secretory epithelium, mediated and controlled by the organic matrix (*Vinn, Kirsimäe & ten Hove, 2009*; *Vinn, 2021a*). As a result, serpulids accomplish a specified crystal orientation within the tube wall, which is reflected by their variety of ultrastructural fabrics—the growth direction of crystals may be anisotropic, semi-oriented, or oriented (*Weedon, 1994*; *Vinn et al., 2008*). Apart from a matrix-mediated crystallization (*Vinn, 2021a*), an alternative explanation has been proposed recently to define the crystal orientation mechanism, which is based on a variable application of the serpulid's collar rotational force between the formation of ordered and unordered microstructures (*Buckman & Harries, 2020*). Considering the fact that the same growth increments may occur across zones with diverse ultrastructures makes (*Vinn, 2021a*; *Vinn, 2021b*) this model strongly disputable.

The serpulid biomineralization system differs from that of other tube-dwelling polychaetes. By the formation of the cylindrical and parabolic layers (see *Jäger, 1983*) serpulids are capable of forming multi-layered tubes arranged in distinct microstructures (see *Vinn et al., 2008*). Importantly, the parabolic layer is formed by adding secretory

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increments to the rim of the worm's aperture allowing it to actively modify the external morphology according to the tube's sculpture, but also depending on the temporary ecological requirements. Such a solution results in a wide array of serpulid tube characters including attachment structures and base widenings of the tube, which combined with the ability to form several layers greatly improves the durability of the tube. Fossil cirratulids (*Vinn, 2009*; *Taylor et al., 2010*) and sabellids (*Vinn, ten Hove & Mutvei, 2008*; *Słowiński, Banasik & Vinn, 2023*) possess single-layered tube wall composed of a spherulitic prismatic structure. The presence of only cylindrical layer in sabellids strongly impairs their biomineralization abilities. Unlike serpulids having mostly chevron-shaped growth lines (see *Weedon, 1994*), they form their tubes by secreting calcareous material along distinct growth lamellae oriented parallel to the tube wall (*Vinn, ten Hove & Mutvei, 2008*; *Słowiński, Banasik & Vinn, 2023*). Subsequent increments are added to the internal surface of the tube, and therefore *Glomerula* is unable to modify its simple tube architecture. A much longer secretion zone in sabellids compared to serpulids enables them for a fast calcification incurring comparably lower physiological costs, which allows them to considerably prolong their tubes. On the other hand, such fast dispersal may be required by the diminishing inside of the tube, insufficient for the growing worm. Interestingly, cirratulids perform a double-phased, combined controlled, and influenced biomineralization. The products of an influenced biomineralization such as agglutinated xenolithic granules within a calcareous matrix, as well as the anisotropic orientation of different-sized crystals, indicate, that cirratulids govern even a weaker than sabellids control over biomineralization (*Guido et al., 2024*).

A much more advanced biomineralization system of serpulids and the resulting variety of microstructures are an important evolutionary adaptation for this taxon, which is an obligatory tube-dweller. The emergence of multi-layered tubes with dense, outer protective layers during the Jurassic could have been triggered by the intensified predation during the Mesozoic Marine Revolution (*Vermeij, 1977*). Interestingly, the development of dense, outer protective layers in spirorbins was shown to have a relationship with the type of paleoenvironment, its energy, and substrate kind (see *Ippolitov & Rzhavsky, 2015a*; *Ippolitov & Rzhavsky, 2015b*). With the skeleton development, serpulids could perform competitive strategies against other organisms instead of avoiding competition or temporary paleoenvironmental vagaries. Gradual increase in abundance of serpulids during the Mesozoic and Cenozoic (see *Ippolitov et al., 2014* for a review), and their advantage over other organisms allowed for higher plasticity and divergence of different morphotypes (*Vinn et al., 2024*). Different morphogenetic programs in turn enhanced their functional utilization not only by mechanical strengthening of the tubes but also by optimizing their space by planispiral coiling, providing a higher feeding tier, avoiding being overgrown or coated by sediment thanks to upward growth. Free-living serpulids with tusk-shaped tubes were presumably adapted to live in or on the surface of soft sediment during episodes of increased sedimentation rates (see *Vinn et al., 2024* for a review). Sabellid biomineralization system allowed them to quickly elongate their tubes but these polychaetes did not exhibit such diverse morphotypes. Instead, they could grow irregularly away from the initial point of encrustation and perform an opportunistic, fugitive strategy (see *Taylor, 2016*; *Słowiński,*

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Banasik & Vinn, 2023). Additionally, it could be the outcome of biomineralization's lack of significance in this group as calcareous sabellids were restricted to a single genus in the family.

CONCLUSIONS

The first thorough assessment of the ultrastructural diversity of Middle and Late Jurassic serpulid tubes has been conducted. The obtained data reveal a characteristic of the Jurassic serpulids, a relatively low diversity of ultrastructural fabrics, which generally correspond to certain clades recognized among extant taxa. Amongst 12 taxa representing two (Filograninae and Serpulinae) of the three main serpulid clades, six of them possess tube walls composed of a single layer, and six are two-layered. There are certain evolutionary trends in tube ultrastructures. The representatives of the clade Filograninae are single-layered and have their tube walls built of a primitive, irregularly oriented prismatic microstructure (IOP). The majority of members of possibly apomorphic clade Serpulinae possess two-layered tube walls, where the denser, external layer is composed of oriented, prismatic microstructures (either spherulitic (SPHP) or simple (SP)), and the internal is irregularly oriented prismatic (IOP). The exceptions are *Placostegus planorbiformis* and the genus *Cementula*, which are single-layered, and built of simple prismatic structure (SP).

Serpulid tube ultrastructures reflect their biomineralization abilities providing important paleoecological signatures. Formation of the regularly oriented microstructures of Serpulinae requires a higher biological control over biomineralization compared to the more primitive, anisotropic microstructures of Filograninae. The development of serpulid ultrastructure diversity was likely triggered by the evolutionary importance of the tubes for this group. A variety of microstructure types and the ability to form multi-layered tubes allowed serpulids to employ different morphogenetic programs, which had an impact on their functional utilization.

The differences in the biomineralization system between serpulids and other tube-dwelling polychaetes resulted from the importance of tubes for the former taxon. The complex biomineralization system of serpulids resulted in a multiplicity of forms and an ability to form robust, strongly ornamented tubes, which mechanically strengthened their durability. Although higher energy expenditure of skeletal secretion decreased the rate of tube formation, the solid attachment and skeleton robustness allowed for a competitive advantage over other encrusters. Conversely, sabellid primitive biomineralization abilities presumably were elicited by the unimportance of skeleton for this taxon resulting in a simplicity of forms. On the other hand, it enabled a fast spreading over the substrate, shunning competition and disadvantageous conditions by utilizing an opportunistic strategy of quick tube elongation.

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Sosnowiec, 03.06.2024

miejscowość, data

Jakub Słowiński

OŚWIADCZENIE OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Oświadczam, że w pracy:

- Słowiński J., Surmik D., Duda P., Zatoń M. (2020). **Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, PLOS ONE 15, e0242924. DOI: 10.1371.0242924.**

Mój udział polegał na konceptualizacji badań, przygotowaniu materiału paleontologicznego do badań i jego późniejszej dokumentacji, przeglądzie stosownej literatury, makro- i mikroskopowej analizie materiału badawczego, głównie pod kątem paleoekologicznym, jak również jego późniejszej interpretacji, napisaniu pierwszej wersji manuskryptu (z wyłączeniem charakterystyki geologicznej badanych odsłonięć) i jego późniejszej edycji, przygotowaniu figur.

- Słowiński, J., Vinn, O, Jäger, M., Zatoń, M. (2022). **Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. Acta Palaeontologica Polonica 67, 827-864. DOI: 10.4202/app.01006.2022.**

Mój udział polegał na konceptualizacji badań, przygotowaniu materiału paleontologicznego do badań i jego późniejszej dokumentacji, przeglądzie stosownej literatury, makro- i mikroskopowej analizie materiału badawczego pod kątem taksonomicznym i paleoekologicznym, jak również jego późniejszej interpretacji,

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analizie statystycznej zebranych danych, napisaniu pierwszej wersji manuskryptu i jego późniejszej edycji, przygotowaniu wszystkich figur.

- **Słowiński, J., Banasik, K., Vinn, O. (2023). Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications. Lethaia 56, 1-12. DOI: 10.18261/let.56.3.8.**

Mój udział polegał na konceptualizacji badań, częściowym przygotowaniu materiału paleontologicznego do badań i jego późniejszej dokumentacji, przeglądzie stosownej literatury, analizie mikrostruktury jurajskich sabellidów przy użyciu środowiskowego mikroskopu elektronowego (ESEM) Philips XL30, jak również częściowej analizie przy użyciu mikroskopu elektronowego SEM Zeiss EVO MA15, jego późniejszej interpretacji, napisaniu pierwszej wersji manuskryptu i jego późniejszej edycji, przygotowaniu wszystkich figur.

- **Słowiński, J., Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. PeerJ 12, e17389. DOI:10.7717/peerj.17389.**

Mój udział polegał na konceptualizacji badań, częściowym przygotowaniu materiału paleontologicznego do badań i jego późniejszej dokumentacji, przeglądzie stosownej literatury, częściowej analizie materiału paleontologicznego przy użyciu środowiskowego mikroskopu elektronowego (ESEM) Philips XL30, oraz przy użyciu mikroskopu elektronowego SEM Zeiss EVO MA15, jego późniejszej interpretacji, napisaniu pierwszej wersji manuskryptu i jego późniejszej edycji, przygotowaniu wszystkich figur.

....
podpis

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Sosnowiec, 16.05.2024

Michał Zatoń
Imię i nazwisko współautora publikacji

Instytut Nauk o Ziemi UŚ
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

- Słowiński J., Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924. DOI: 10.1371.0242924.

Mój udział polegał na dostarczeniu części materiału paleontologicznego, charakterystyki geologicznej badanych odsłonięć i udzieleniu pomocy przy redagowaniu całego manuskryptu.

Oświadczam, że w pracy:

- Słowiński, J., Vinn, O, Jäger, M., Zatoń, M. (2022). Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. *Acta Palaeontologica Polonica* 67, 827-864. DOI: 10.4202/app.01006.2022.

Mój udział polegał na dostarczeniu części materiału paleontologicznego, nadzorze nad częścią paleoekologiczną i udzieleniu pomocy przy redagowaniu całego manuskryptu.

158:8819335878

Oświadczam, że w pracy:

- Słowiński, J., Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. PeerJ 12, e17389. DOI:10.7717/peerj.17389.

Mój udział polegał na obrazowaniu i dokumentacji rurek wieloszczetów przy użyciu środowiskowego mikroskopu elektronowego (ESEM) Philips XL30 i udzieleniu pomocy przy redagowaniu całego manuskryptu.

....

Podpis współautora publikacji

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Location: Tartu., date 24.05.2024

OLEV VINN
....
First and last name of co-author of the publication

UNIVERSITY OF TARTU
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STATEMENT

I declare that for the following works:

- Słowiński, J., Vinn, O, Jäger, M., Zatoń, M. (2022). Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. *Acta Palaeontologica Polonica* 67, 827-864. DOI: 10.4202/app.01006.2022.

My participation consisted of the discussion on the taxonomy of the fossil serpulids and sabellids, particularly on the problematic species, and co-editing the manuscript.

- Słowiński, J., Banasik, K., Vinn, O. (2023). Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications. *Lethaia* 56(3), s. 1-12. DOI: 10.18261/let.56.3.8.

My participation consisted of assistance in the preparation of the samples prior to the SEM study and in documentation using scanning electron microscope SEM Zeiss EVO MA15, and co-editing the manuscript.

- Słowiński, J., Vinn, O., Zatoń, M. (2024). Ultrastructure of the Jurassic serpulid tubes – phylogenetic and paleoecological implications. *PeerJ* 12, e17389. DOI:10.7717/peerj.17389.

My participation consisted of assistance in the preparation of the samples prior to the SEM study and in documentation using scanning electron microscope SEM Zeiss EVO MA15, discussions with the main author on some problematic microstructures, as well as co-editing the manuscript.
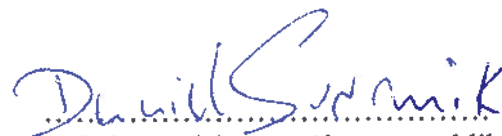
Olev Vinn   Signature of the co-author of the publication

* applies to co-authors

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Sosnowiec, dnia 23.05.24
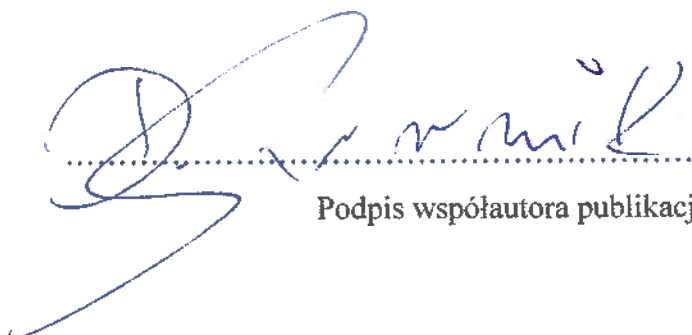
Imię i nazwisko współautora publikacji

WNP IINoZ

Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

- Słowiński J., Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924. DOI: 10.1371.0242924.

Mój udział polegał na pomocy przy obróbce danych uzyskanych z mikrotomografii komputerowej, opisie metodyki skanowania skamieniałości przy użyciu mikrotomografii komputerowej, oraz przy edytowaniu manuskryptu.

Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce ...*Sosnowiec*............., dnia *27.05.2024*

Piotr Jan Duda
Imię i nazwisko współautora publikacji

Uniwersytet Śląski. Wydział Nauk Ścisłych i Technicznych Instytut Inżynierii Biomedycznej
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

- Słowiński J., Surmik D., Duda P., Zatoń M. (2020). Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin, *PLOS ONE* 15, e0242924. DOI: 10.1371.0242924.

Mój udział polegał na wykonaniu skanów wybranych skamieniałości przy użyciu mikrotomografii komputerowej, obróbce uzyskanych danych, oraz pomocy przy edycji manuskryptu.

.........................*Duda Piotr*.........................
Podpis współautora publikacji

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Location   Rosenfeld, Germany,   date 22.05.2024

Dr. rer. nat. Manfred Jäger.
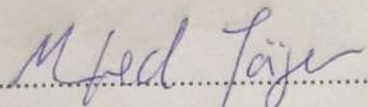First and last name of co-author of the publication

Affiliation
retired

STATEMENT

I declare that for the following work:

Słowiński, J., Vinn, O, Jäger, M., Zatoń, M. (2022). Middle and Late Jurassic tube-dwelling polychaetes from the Polish Basin: diversity, palaeoecology and comparisons with other assemblages. *Acta Palaeontologica Polonica* 67, 827-864. DOI: 10.4202/app.01006.2022.

My participation consisted of the discussion on the systematic account of the fossil tube-dwelling polychaetes, especially on the controversial issues, and providing assistance in editing the manuscript.

....
Signature of the co-author of the publication

*applies to co-authors

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Sosnowiec, 17.05.2024

Kamila Banasik

INoZ WNP UŚ

OŚWIADCZENIE

Oświadczam, że w pracy:

- Słowiński, J., Banasik, K., Vinn, O. (2023). Insights into mineral composition and ultrastructure of Jurassic sabellid tubes (Annelida, Polychaeta): the evolution of sabellid calcification and its palaeoecological implications. *Lethaia* 56(3), s. 1-12. DOI: 10.18261/let.56.3.8.

Mój udział polegał na przeprowadzeniu: analiz mineralogii skamieniałości jurajskich sabellidów przy użyciu spektroskopii ramanowskiej, charakterystki metodyki badań mineralogicznych, oraz udzieleniu pomocy przy redagowaniu manuskryptu.

opisać szczegółowo swój własny – (a nie osoby ubiegającej się*) – udział w powstaniu pracy, (np. mój udział w powstanie tej publikacji polegał na wykonaniu doświadczeń techniką ....., analizie statystycznej wyników eksperymentów zilustrowanych na ryc. ...., przygotowaniu tekstu manuskryptu zamieszczonego w rozdziale......, kierowaniu projektem naukowym obejmującym badania opisane w tej pracy, itp.).

...........Kamila Banasik...........

Podpis współautora publikacji