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Taphonomy and possible tracemakers of *Psammichnites* from the lower Cambrian of the Holy Cross Mountains, Poland

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The sandstones of the upper part of the Ociesęki Formation (Cambrian Stage 4) contain numerous *Psammichnites gigas arcuatus* specimens that dominate lithologies characteristic of the high-energy *Skolithos* ichnofacies. The burrows are represented by four morphotypes being in fact taphonomic variants. These include horizontal sections displaying meniscate backfill composed of a series of arcuate ridges ("*Arcuatichnus wimani*" Kowalski, 1978), concave furrows with a U-shaped pattern ("*Plagiogmus arcuatus*" Roedel 1929), resembling *Climactichnites* isp., positive hypichnial reliefs visible as bilobate ridges with a median furrow and, occasionally, a V-shaped pattern ("*Cruziana* sp." of Orłowski, 1975b), and complex structures that are combinations of these variants. The differences observed result from stratinomic effects and substrate grain size and consistency. Observations of striae on *P. gigas arcuatus* suggest that these may have been produced by halkieriids or other animals with hard skeletal elements. In the literature, similar ichnofossils were interpreted as traces of "worms", gastropods or other molluscs, and rarely halkieriids and arthropods including trilobites. The different morphology of the examples of *P. gigas arcuatus* studied compared to other common Cambrian specimens may represent evolutionary change, as it reflects a relatively late occurrence of this trace fossil in the Cambrian of the Holy Cross Mountains.

Key words: trace fossils, burrowing, siliciclastic sedimentation, shoreface, *Skolithos* ichnofacies.

INTRODUCTION

Glaessner (1969) was the first to recognize *Plagiogmus arcuatus* (Roedel, 1929) as the floor of a complex backfilled burrow. Subsequently, this trace fossil was regarded by many authors as a synonym of *Psammichnites gigas* (Torell, 1868) (e.g., Hofmann and Patel, 1989; Seilacher, 2007 and references therein; MacNaughton et al., 2021). Following the views of Mángano et al. (2022), it should be considered a ichnosubspecies of *Psammichnites gigas* or, more precisely, a behavioural variant termed *P. gigas arcuatus*. Runnegar et al. (2024) pointed out that this reclassification is justified, but has an unfortunate consequence, namely the replacement of the convenient ichnogeneric name "*Plagiogmus*" with the trinomial ichnosubspecific name *Psammichnites gigas arcuatus*. This may generate confusion when describing these trace fossils at the ichnogenus and ichnospecies levels rather than at the ichnosubspecies level.

A characteristic feature of *Psammichnites gigas arcuatus* is the presence of transverse, ladder-like ridges (Jaeger and Martinsson, 1980; McIlroy and Heys, 1997; Mángano et al., 2022). In addition, this ichnosubspecies commonly forms extensive loops and scribbles, similar to *P. gigas circularis*, in contrast to the typical ichnosubspecies *P. gigas gigas* (Mángano et al., 2022; Runnegar et al., 2024). However, *Psammichnites gigas arcuatus*, as well as other ichnosubspecies and ichnospecies within this ichnogenus, shows significant morphological variation and a high diversity of taphonomic variants (Kowalski, 1978; Pickerill and Peel, 1990; Seilacher-Drexler and Seilacher, 1999; Mángano et al., 2002, 2022; Gámez Vintaned et al., 2006; Seilacher, 2007 and references therein). There are ongoing debates concerning the taxonomy of *Psammichnites* at the ichnogeneric level. Chamberlain (1971) synonymized the Carboniferous *Olivellites* Fenton and Fenton, 1937 under *Psammichnites*, as did Mángano et al. (2002, 2022) and El-Refaiy et al. (2026). However, Seilacher and Hagadorn (2010) were careful to describe Cambrian and Carboniferous "psammichnitids" separately, because they show morphological

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differences attributable to differences in anatomy and behaviour. According to Pazos and Gutiérrez (2023), all post-Cambrian trace fossils previously assigned to *Psammichnites* represent *Olivellites*, and these two ichnogenera probably also had different tracemaker clades. Ethologically, *Psammichnites* is interpreted as a feeding structure (Seilacher, 1997, 2008; Mángano et al., 2002), typical of relatively high-energy, shallow-marine environments with high oxygenation (Hofmann and Patel, 1989).

Psammichnites gigas arcuatus occurs widely from the Fortunian to Cambrian Stage 4 in many regions of the world (Mángano et al., 2022), and Miaolingian examples have also been reported. The occurrence of this ichnosubspecies has been recorded in the Fortunian and Cambrian Stage 2 of eastern Russia (Nagovitsin et al., 2015), Cambrian Stage 2 of eastern and central Australia (Glaessner, 1969; McIlroy and Heys, 1997), Cambrian Stages 2–3 of northeastern Greenland (Pickerill and Peel, 1990), Cambrian Stage 3 of northern Norway (McIlroy and Brasier, 2017), Cambrian Stages 3–4 of Sweden (Jaeger and Martinsson, 1980), and Cambrian Stage 4 (Kowalski, 1978) and the Miaolingian (Orłowski and Żylińska, 1996) of Poland. Younger occurrences of *Psammichnites gigas arcuatus* are also known from the Miaolingian of the Indian Tethyan Himalaya (Verma et al., 2023), where it postdates *P. gigas circularis* and *P. gigas gigas* in this area. According to Verma et al. (2023), each of these ichnosubspecies has local biostratigraphic significance. Runnegar et al. (2024) suggested that *Psammichnites gigas arcuatus* occurs in the lowermost Cambrian (Fortunian) of the western USA, and that its first appearance could serve as a local biostratigraphic indicator of the base of the Cambrian, instead of the historically used FAD of *Treptichnus pedum*.

Specimens of *Psammichnites gigas arcuatus* from the Cambrian Ociesęki Formation were previously studied by Orłowski (1975b, 1992b) and Kowalski (1978). Orłowski (1975b, 1992b) partly attributed them to *Cruziana* isp. and interpreted them as a burrow produced by the trilobite *Kingaspidoides santacrucensis*. Kowalski (1978) described similar trace fossils from this area as *Arcuatichnus wimani*. New material of *Psammichnites gigas arcuatus* from Cambrian Stage 4 of this formation allows a reassessment of the taphonomy and mode of formation of this ichnotaxon, together with an evaluation of its tracemakers. The upper part of the unit studied contains numerous trilobites of low diversity (Ellipsocephalidae) and trace fossils typical of the *Skolithos* and, more rarely, *Cruziana* ichnofacies (Stachacz, 2016; Kozłowska et al., 2024). In this paper, we describe well-preserved *Psammichnites gigas arcuatus* from the upper part of the Ociesęki Formation, their taphonomy, and their potential producer. These trace fossils differ in morphology and preservation from typical specimens of this ichnosubspecies, making them unique.

GEOLOGY

GENERAL SETTING

The study area of the Cambrian Series 2 Ociesęki Formation is located in the Holy Cross Mountains within the tectonic unit known as the Kielce Region, one of the two blocks constituting the Paleozoic massif of this range (Fig. 1). The formation studied consists of various quartz arenites and wackes, with interbeds of siltstone, and is largely coeval with the shales of the Czarna and Kamieniec formations (Fig. 2). Compared with the neighbouring Łysogóry Region to the north, the Kielce Region is characterized by somewhat different lithologies and a distinct geological history, particularly during the Cambrian (e.g., Czarnocki, 1957).

The lower Cambrian of the Kielce Region was deposited in a shallow sea within the Małopolska Block, which at that time was located near the Baltica palaeocontinent (Cocks and Torsvik, 2005). Nevertheless, the presence of ellipsocephalids suggests migration from western Gondwana and Avalonia (Żylińska, 2013).

Cambrian Series 2 strata of the formation studied in the Kielce Block are exposed within the extensive Chęciny–Klimontów Anticlinorium, primarily in its axial part in the Ociesęki and Orłowiny ranges, as well as in its western part within the Dyminy Anticline. The Chęciny–Klimontów Anticlinorium is bordered to the north by the Kielce–Łagów Synclinorium, which is largely infilled with Devonian strata. To the west and southwest, it is bordered by Mesozoic units at the margin of the Holy Cross Mountains, whereas to the south and east it is overlain by Miocene deposits of the Carpathian Foredeep. Within the Chęciny–Klimontów Anticlinorium, several synclines are infilled with rocks younger than the Cambrian. This part of the Holy Cross Mountains was initially deformed during the early Caledonian orogeny; consequently, transgressive Ordovician and younger strata overlie strongly folded Cambrian deposits (e.g., Gągała, 2005). The Cambrian of the Holy Cross Mountains is represented by a relatively monotonous succession of sandstones and siltstones, locally exceeding 2500 m in thickness (e.g., Orłowski, 1975a). In the southern part of this area, the lower Cambrian (Cambrian Series 2 according to Cohen et al., 2025) predominates and is mainly represented by sandstones of the Ociesęki Formation. This formation is notable for its numerous occurrences of trilobites (e.g., Samsonowicz, 1959; Orłowski, 1974, 1985; Żylińska, 2013) and very diverse trace fossils (e.g., Orłowski, 1989, 1992b; Orłowski and Żylińska, 2002; Stachacz, 2016; Kozłowska et al., 2024).

BIOSTRATIGRAPHY

The thick Ociesęki Formation is bipartite and comprises three trilobite zones that represent somewhat different sedimentary environments (Fig. 2). The lower part of the formation corresponds to the *Schmidtiellus*–*Holmia* Superzone (Orłowski, 1974, 1985). The age of this interval is constrained by the presence of the holmiid trilobites *Holmia marginata* Orłowski, 1974, *H. glabra* Orłowski, 1974, *Kjerulfia orcina* Orłowski, 1974, *K. orienta* Orłowski, 1974, *Schmidtiellus panovi* (Samsonowicz, 1959) and *S. nodosus* Orłowski, 1985, as well as the ellipsocephalid trilobites *Strenuella polonica* Czarnocki, 1927, *S. sandomirensis* Orłowski, 1985 and *S. zbelutkae* Orłowski, 1985. This part of the formation contains numerous and diverse trace fossils characteristic of the *Cruziana* ichnofacies, including rare vertical burrows (Orłowski, 1989; Stachacz, 2016). *Rusophycus dispar* (Linnarsson, 1871) is a trilobite trace fossil typical of this interval.

The upper part of the formation is mainly assigned to the *Protolenus*–*Issafeniella* Zone, as indicated by the trilobites *Kingaspidoides santacrusensis* (Samsonowicz, 1959) and *Issafeniella orlowinensis* (Samsonowicz, 1959) (Orłowski, 1985; Mizerski et al., 1986; Geyer, 1990; Żylińska and Masiak, 2007; Żylińska, 2013). The trace fossil typical of this biozone is *Rusophycus magnus* (Orłowski, 1992b) (Orłowski and Mizerski, 1996). However, the uppermost part of the formation is assigned to the *Acadoparadoxides samsonowiczii*–*Acadoparadoxides kozlowskii* Zone of the Miaolingian, based on the occurrence of the trilobites *Ornamentapsis guerichi* (Orłowski, 1959), *O. opatowi* (Orłowski, 1985), *O. puschi* (Orłowski, 1985)

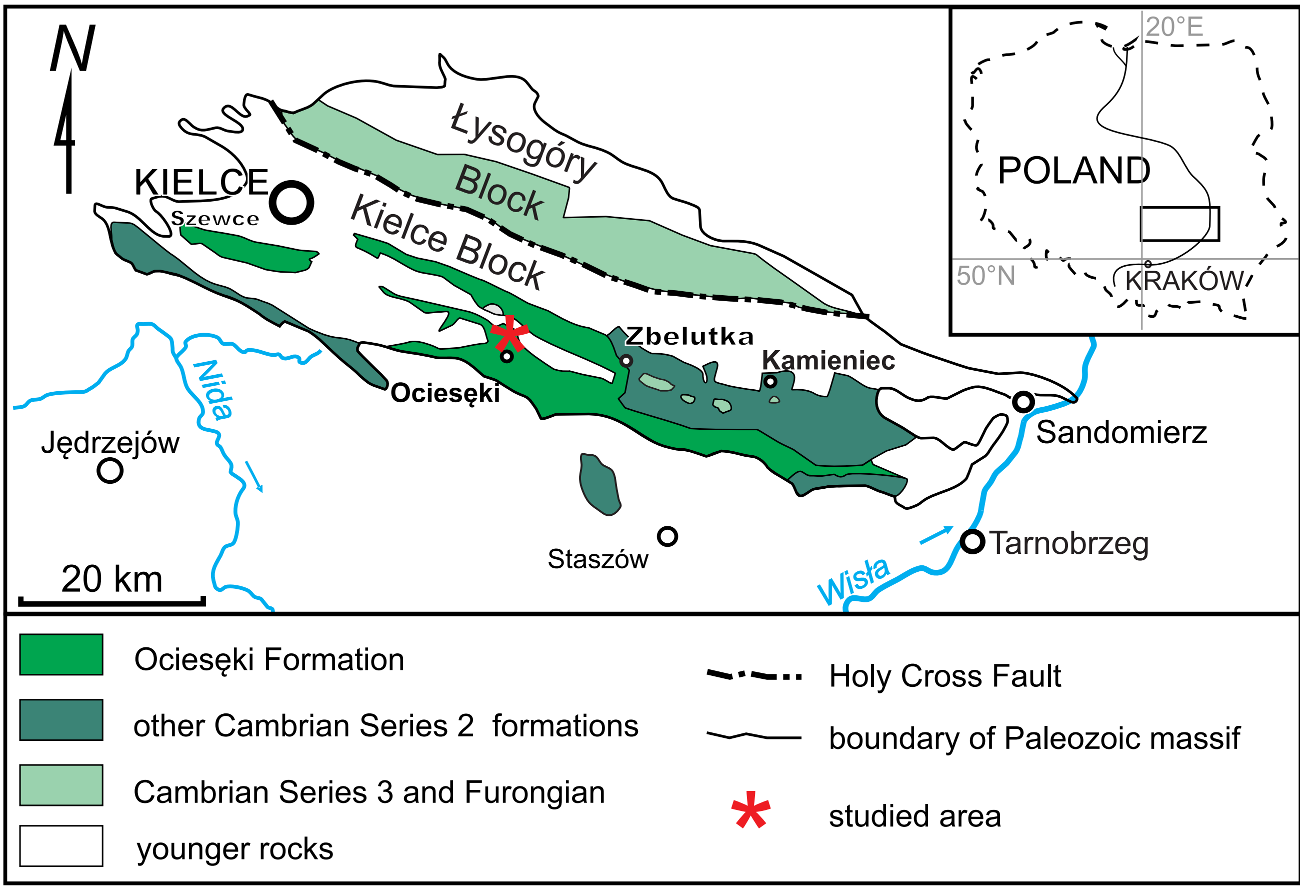

Fig. 1. Locality of the study area (asterisk) and range of the Ocieseki Formation and other Cambrian formations of the Holy Cross Mountains (according to Orłowski, 1975a; Mizerski et al., 1991)

and *Orodes usarzowi* (Orłowski, 1985) (Nowicki and Żylińska, 2021; Kozłowska et al., 2024). The Ocieseki Formation underlies the Słowiec Formation, which also belongs to the *Acadoparadoxides samsonowiczii–Acadoparadoxides kozlowskii* Zone of the Miaolingian (Nowicki and Żylińska, 2021; Kozłowska et al., 2024). The oldest strata (the *Schmidtiellus–Holmia* Zone) of the Ocieseki Formation in the Ocieseki area are exposed in the southern part of the region, on the southern slopes of the Sterczyna and Igrzyczna foothills of the Ocieseki Range, whereas the youngest strata (the *Acadoparadoxides samsonowiczii–Acadoparadoxides kozlowskii* Zone) occur in the northern part of the area within the Zamczysko Range (Mizerski et al., 1986; Nowicki and Żylińska, 2021; Kozłowska et al., 2024).

PALAEOENVIRONMENT

Studencki (1988) suggested that the lower Cambrian clastic strata, including the sandstones of the Ocieseki Formation and siltstones of associated formations, were deposited in an offshore, shallow-marine setting, at the transition between the littoral sand and shelf mud depositional zones, under conditions of low clastic influx (see also Kowalczewski et al., 1987). The sandstones of the Ocieseki Formation were deposited within uplifted zones (e.g., Łydka and Orłowski, 1978; Pożaryski et al., 1981; Lendzion et al., 1982; Kowalski, 1983; Kowalczewski et al., 1987, 2006; Studencki, 1988). Stachacz (2016) interpreted the lower part of this formation as having been deposited on the lower shoreface, just above the fair-weather wave base, based on alternations of arenite-wacke-siltstone beds with the typical ichnoassemblage of the *Cruziana* ichnofacies. In contrast, the upper part of the formation was deposited on the middle shoreface *sensu* Pemberton et al. (2001), within the *Skolithos ichnofacies*, which is indicated by the presence of medium- to thick-bedded, commonly amalgamated quartz arenites with hummocky cross-stratification and numerous vertical burrows, including *Arenicolites, Monocraterion, Diplocraterion* and *Skolithos*. Deposition occurred above the fair-weather wave base under conditions of high wave energy (Reinson, 1984; Pemberton et al., 2001). On the middle shoreface, storms were the primary factor controlling both the rate of deposition and the erosion of previously deposited sediments. In the stratotype area, at the boundary between the lower and upper parts of the Ocieseki Formation, a transition from the *Cruziana* to the *Skolithos* ichnofacies is observed (Stachacz, 2016), and these facies likely interfinger in this part of the profile. In general, the Cambrian succession of the Ocieseki Formation shows an upwards increase in grain size, indicating progressive shallowing of the basin (Mizerski et al., 1986; Studencki, 1988; Kozłowska et al., 2024). However, while the basin shallowed in the west, it simultaneously deepened in the east, resulting in a transition from sandy sedimentation (Ocieseki Formation) to mudstone sedimentation (Kamieniec Formation). Such variability was most likely controlled by tectonic movements during the early Cambrian (Gągała, 2005).

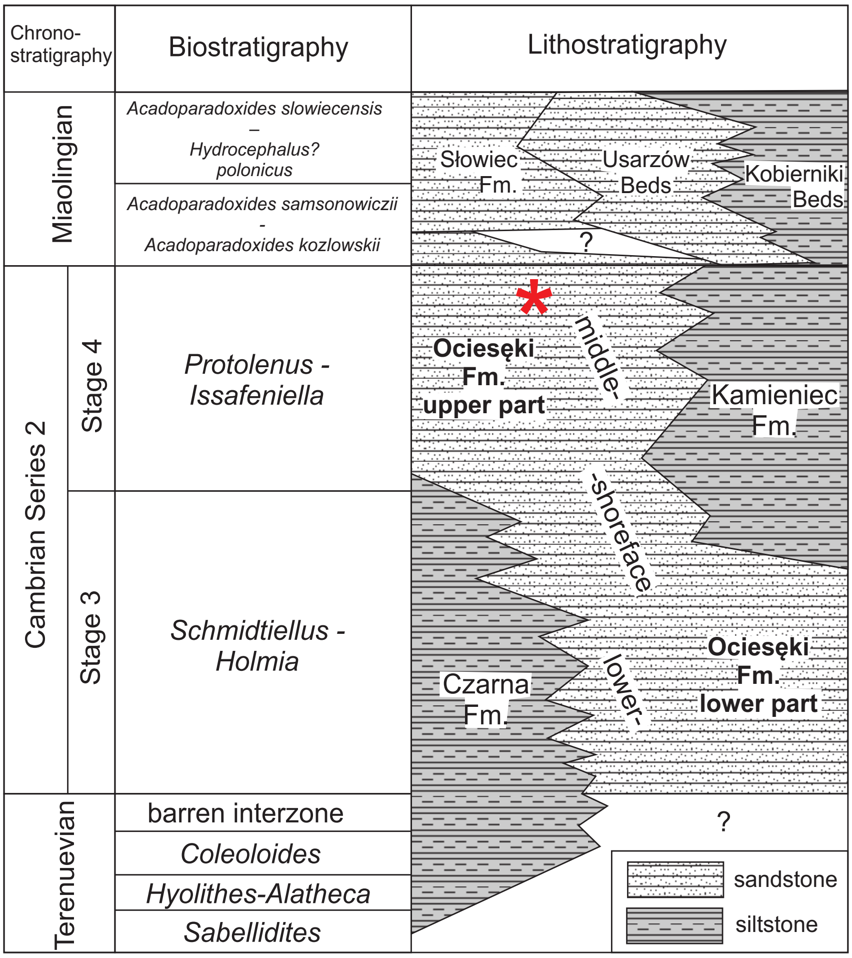

Fig. 2. Stratigraphy and correlation of the part of the Ocieseki Formation studied (asterisk) and other Cambrian formations of the Holy Cross Mountains (lithostratigraphy after: Orłowski, 1975a; Kowalczewski, 1990, 1995; Szczepanik et al., 2004; Kowalczewski et al., 2006; biostratigraphy after: Orłowski, 1992a; Orłowski and Żylińska, 2002; Żylińska and Szczepanik, 2009; Nowicki and Żylińska, 2021; Kozłowska et al., 2024)

MATERIAL

The collected loose samples come from the crest of a ridge north of Zamczysko Hill, near the hamlets of Zagórze and Łapigrosz, in an area with a radius of ~200 metres (GPS coordinates of the centre: N 50°45'52.0", E 20°57'10.6"; Fig. 1). The rocks of the upper part of the Ocieseki Formation in this area are poorly exposed. Sandstone beds weather characteristically into cuboidal pieces, which makes it difficult to observe large bedding surfaces. The samples were taken from rocks piled at the edge of a cultivated field, originally derived from old trenches, rocky ridges, and loose blocks. The loose samples collected come from the hilltop area and certainly originated as bedrock not far below the ground surface.

The local lithology consists of thin- to medium-bedded quartz arenite, fine-grained, yellowish, light grey, dark grey, or brown. The upper part of the profile contains beds of medium- and coarse-grained sandstones, and in some places granule conglomerate composed of siltstone clasts within a sandy matrix. Most of the beds show no lamination, whereas a few exhibit horizontal and small-scale cross-lamination, mainly in the form of ripplemarks. In some places, numerous remains of the trilobite *Kingaspidoides santacrucensis* are present, mostly cranidia, with thoracic and pygidial elements being rare, and complete skeletons. Some beds contain densely crowded trace fossils, *Arenicolites* isp. and *Diplocraterion parallelum*. Several horizons of fine-grained quartz arenites contain numerous *Psammichnites gigas arcuatus*. Notably, the horizons densely bioturbated with *Psammichnites* contain few other trace fossils, even though other intervals of the unit studied contain a wide variety of trace fossils (Orłowski, 1989; Stachacz, 2016; Kozłowska et al., 2024).

The trace fossils described by Orłowski (1975b, 1992b) and Kowalski (1978) come from the same area; however, the authors did not specify their exact locations.

Psammichnites gigas arcuatus (Roedel, 1929) from the outcrops studied

M a t e r i a l. – One hundred and forty collected fossiliferous rock slabs containing even more trace fossils are housed in the Institute of Geological Sciences of the Jagiellonian University in Kraków and labelled INGUJ214P/Wi. In addition, several tens of specimens were observed in the field.

Description. – The trace fossils analysed are preserved in the several following taphonomic variants, that clearly differ in morphology and internal structure (Figs. 3–6).

Morphotype 1 – similar to "*Arcuatichnus wimani*" Kowalski, 1978.

Most specimens are sections of burrows in the horizontal plane, showing meniscate backfill composed of a series of arcuate ridges described as *Arcuatichnus wimani* by Kowalski (1978) (Figs. 3A–C, 4A and 5C). Such specimens are visible on weathered, horizontal intrabed surfaces; they are gently curved or almost straight, although some have sharp bends. The arcs forming the backfill range in width from 16 to 44 mm (Fig. 7) and in thickness from 1 to 15 mm (usually 3–6 mm). However, they are regular, within a single burrow maintaining uniform width and thickness.

Morphotype 2 – similar to "*Plagiogmus arcuatus*" Roedel, 1929.

Another preservational form of this trace fossil is an epichnial groove, consisting of a series of arcuate, U- or V-shaped, and rarely nearly straight, segmented grooves or ridges typical of "*Plagiogmus*" and also resembling the trail or burrow *Climactichnites* Logan, 1860 (Figs. 3D–G, 5A and 6A). Such specimens represent negatives of the typically backfilled burrows described above; in several cases, this was confirmed by splitting the bed along its surface. The grooves are similar in width to the specimens preserved as backfill, but in some cases are slightly wider. The depth of the grooves and individual segmented depressions usually ranges between 1 and 6 mm. The length of individual depressions (segments) within a longitudinal groove ranges from 2 to 15 mm, and tends to be consistent within a single groove, rarely varying within any single specimen (cf. Fig. 3D–G). Some specimens display one or several narrow central grooves or ridges, symmetrically arranged with respect to the width of the burrow (Figs. 3E–G and 5A). In some cases, the specimens show a U- or V-shaped pattern; others are covered only with irregular wrinkles (both perpendicular and longitudinal to the axis) or are almost completely smooth. The patterns of these structures vary depending on the depth within the sandstone bed in which they occur. Shallowly impressed traces generally show gentle U-shaped arcuate ridges and even simple ladder-like bars (Fig. 6A), whereas the deepest traces have a V-shaped pattern (Fig. 3E, F).

A single fragment of a bed, found as a loose block, reveals the presence of large burrows preserved in concave epirelief, accompanied by *Kingaspidoides santacrucensis* fragments (Fig. 6). One of the trilobite cephala, ~30 mm wide, is situated in the middle of the burrow, whereas a large thoracic fragment of similar width is located adjacent to it (Fig. 6A). A smaller cephalon occurs between the burrows. Additionally, other cephala have been collected within the interval bioturbated by *Psammichnites* (Fig. 6B).

Morphotype 3 – bilobate, *Cruziana*-like ridge.

Specimens preserved in full relief display bilobed ridges (in epichnial view), with a central straight or winding groove or ridge (Fig. 3H, I). Other specimens are preserved as positive hyporeliefs, occasionally with a discrete V-shaped pattern (Fig. 5D) ("*Cruziana* sp." of Orłowski, 1975b, 1992b) or as negative bilobate, wrinkled epireliefs (Figs. 4B–G and 5E). A set of narrow, parallel ridges on the bottom of the burrow has also been observed (Fig. 5D). One slab reveals a specimen visible as trilobed concave epireliefs with a lateral ridge (Fig. 4B, D–F), as well as a set of short, parallel grooves (Fig. 4C) resembling those of *Cruziana*. Three slabs show distinct *Cruziana*-like wrinkles in the lower part of the burrow (Figs. 4C, G and 5E). Other specimens lack longitudinal grooves, but display fine striae on the upper surface (Fig. 5C; see also the three-dimensional scan in the Supplementary Material). The specimen showing a smooth, epichnial, bilobed ridge with a central winding groove (Fig. 3H, I) reveals an intrastratal groove composed of arcuate ridges typical of "*Arcuatichnus*", as well as a series of arcuate ridges, typical of "*Plagiogmus*" on the sole of the bed (see three-dimensional scan in the Supplementary Material).

Morphotype 4 – complex structure.

Several specimens exhibit a complex structure, with an impressed lower surface composed of transverse arcuate ridges and grooves, occasionally accompanied by longitudinal grooves, and overlain by backfill (Fig. 5A–C, E). On the upper surface of such beds, an epichnial, bilobed convex form is occasionally present. However, in such cases, it is not possible to observe all clearly developed elements, i.e. arcuate lower surface, meniscate backfill, and bilobed ridge with a central groove within an individual burrow. Vertical cross-sections of beds reveal that *Psammichnites* is mostly filled with massive infill, usually indistinguishable from the surrounding bioturbated sandstone, forming indistinct ichnofabrics. In longitudinal cross-section, the backfill is only poorly distinguishable from the bioturbated deposit. *Psammichnites* is less commonly found in poorly bioturbated beds with visible horizontal lamination or cross-laminated ripplemarks; in such cases, the fill is also massive.

Remarks. – All morphotypes described here appear to represent parts of a complex structure, i.e., *Psammichnites gigas arcuatus*. This interpretation is supported by specimens displaying both the lower surface along which the animal moved and the burrow backfill (Fig. 5). These observations are consistent with the interpretation of Seilacher-Drexler and Seilacher (1999) and Seilacher (2007), who illustrated the presence of an arcuate furrow ("*Plagiogmus* preservation"), an arcuate backfill, and an epichnial, bilobate ridge within a complex burrow system. The upper surface of the burrow (i.e., the epichnial bilobate ridge) is less commonly observed in specimens from the Ocieseki Formation, and in such cases it is difficult to observe both the burrow fill and its lower surface due to collapse. However, the presence of an epichnial full relief on the top of a bed, with the *Plagiogmus* morphotype visible within the bed and numerous *Arcuatichnus* on the sole (Fig. 3H, see also the three-dimensional scan in the Supplementary Material), indicates that these features represent elements of the same structure. Specimens split along the bedding plane, revealing matching concave segmented furrows and arcuate ridges, contradict the concept proposed by Kowalski (1978) that *Arcuatichnus* lacks a distinct locomotion surface of the tracemaker.

According to Kowalski (1978) and Mángano et al. (2022), *Arcuatichnus wimani* consists of thicker transverse, arcuate elements than *Plagiogmus* (= *Psammichnites gigas arcuatus*), extending to the margin of the burrow preserved in full relief. In our view, however, this is not a diagnostic feature, but rather a record of the animal's locomotion or feeding rate. We therefore regard *Arcuatichnus wimani* Kowalski, 1978 as a synonym of *Psammichnites gigas*, as proposed by Pacześna and Żylińska (2008). Unfortunately, it is impractical to observe the internal structure in unweathered specimens due to the lack of contrast in the fresh rock. For this reason, the trace fossils analysed here display various features resulting from their state of preservation. It is difficult to observe all the characteristics typical of *Psammichnites gigas arcuatus* within a single specimen.

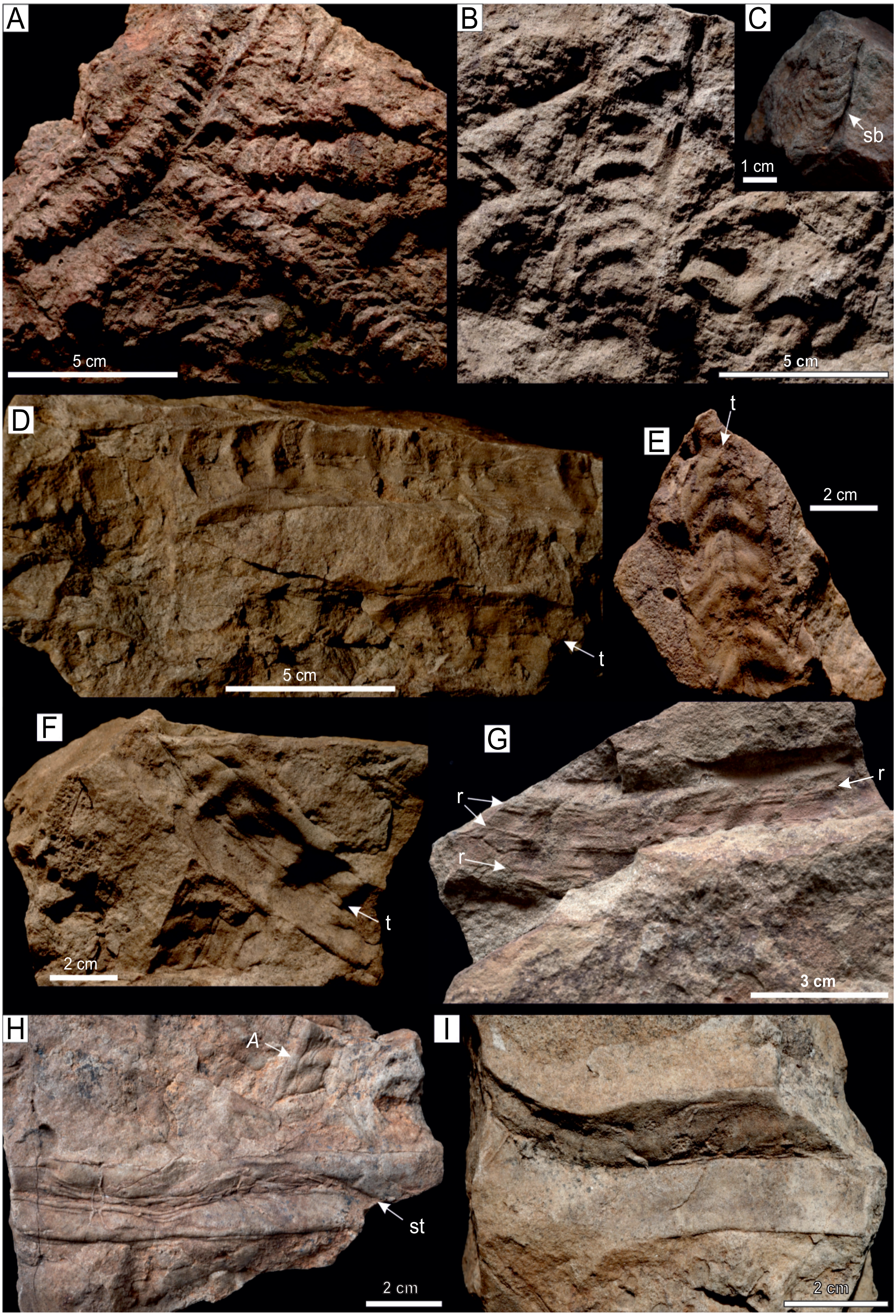

Fig. 3. Various types of preservation of *Psammichnites gigas* from the Cambrian of the Ocieseki Formation from the Widełki area

A–C – Morphotype 1 (INGUJ214P/Wi1, 3, 4), hypichnial views; sb = sharp bend; **D–G** – Morphotype 2 (INGUJ214P/Wi6–9), epichnial views. Some specimens show small median trail (t) or multiple ridges (r); **H, I** – Morphotype 3, upper part of a burrow with a wandering "snorkel trail" (st); the lower, "*Arcuatichnus*"-like part of another burrow is also visible (A); H – epichnial view, INGUJ214P/Wi11; I – hypichnial view, INGUJ214P/Wi77

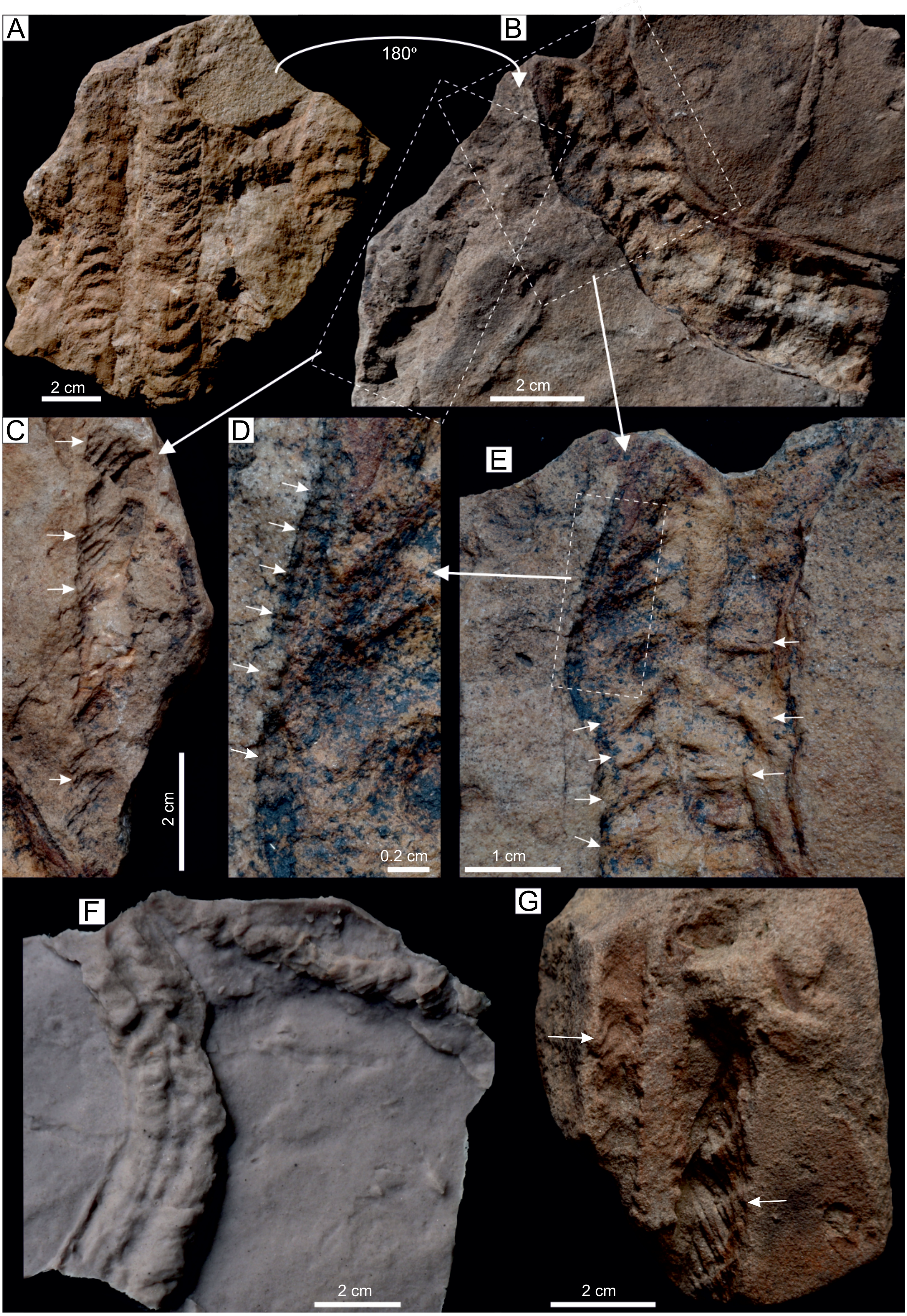

Fig. 4. Details of *Psammichnites gigas* from the Cambrian of the Ociesęki Formation from the Widełki area

A – Morphotype 1; **B–E** – Morphotype 3 concave epichnial semirelief of *Cruziana*-like negative with median ridge and sets of ridges or sclerite moulds (arrowed); (see also three-dimensional scan 1 in the Supplementary Material); **F** – rubber cast of the surface from B–E; A–F: one specimen, INGUJ214P/Wi2; **G** – lower part of the burrow with wrinkles (arrowed); INGUJ214P/Wi25

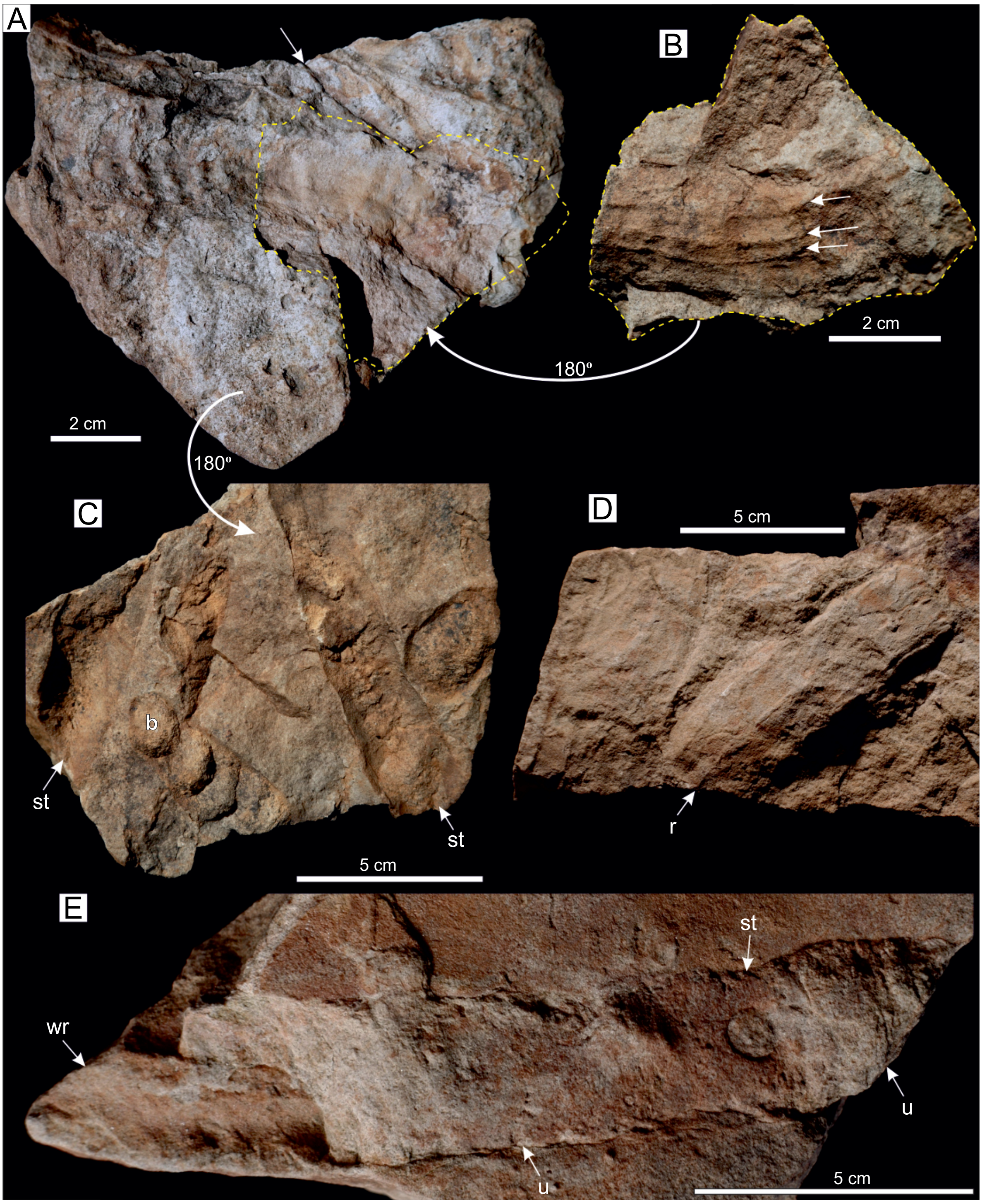

Fig. 5. Details of Morphotype 4: complex structures of *Psammichnites gigas arcuatus* from the Cambrian of the Ocieseki Formation from the Widełki area

A – imprint of the lower part of the burrow composed of imprints of meniscate arcs, top view; **B** – lower part of the burrow with several ridges (arrowed), separated from the "*Arcuatichnus*"-like structure; hypichnial view; **C** – hypichnial view of the burrow with backfill (b) and imprints of the upper parts of discrete striated burrows (st); A–C – one specimen, INGUJ214P/Wi5; **D** – burrow with thin median ridge (r), overcrossing two other burrows, epichnial view, INGUJ214P/Wi10; **E** – deep burrow with meniscate, arcuate infill (u), fine striae (st), and wrinkled lower surface (wr), NGUJ214P/Wi26

Some of the specimens illustrated here differ from the three-dimensional reconstruction of *Psammichnites gigas* proposed by Seilacher-Drexler and Seilacher (1999) and Seilacher (2007) in the presence of longitudinal ridges on the lower surface, while the uppermost part of the burrow, with a meandering groove, is not preserved. Some beds, however, contain the lower surfaces of the burrows, the backfill, and epichnial, bilobed convex forms that clearly demonstrate various taphonomic variants of *Psammichnites gigas arcuatus*, depending on the stratinomy. Such observations indicate that

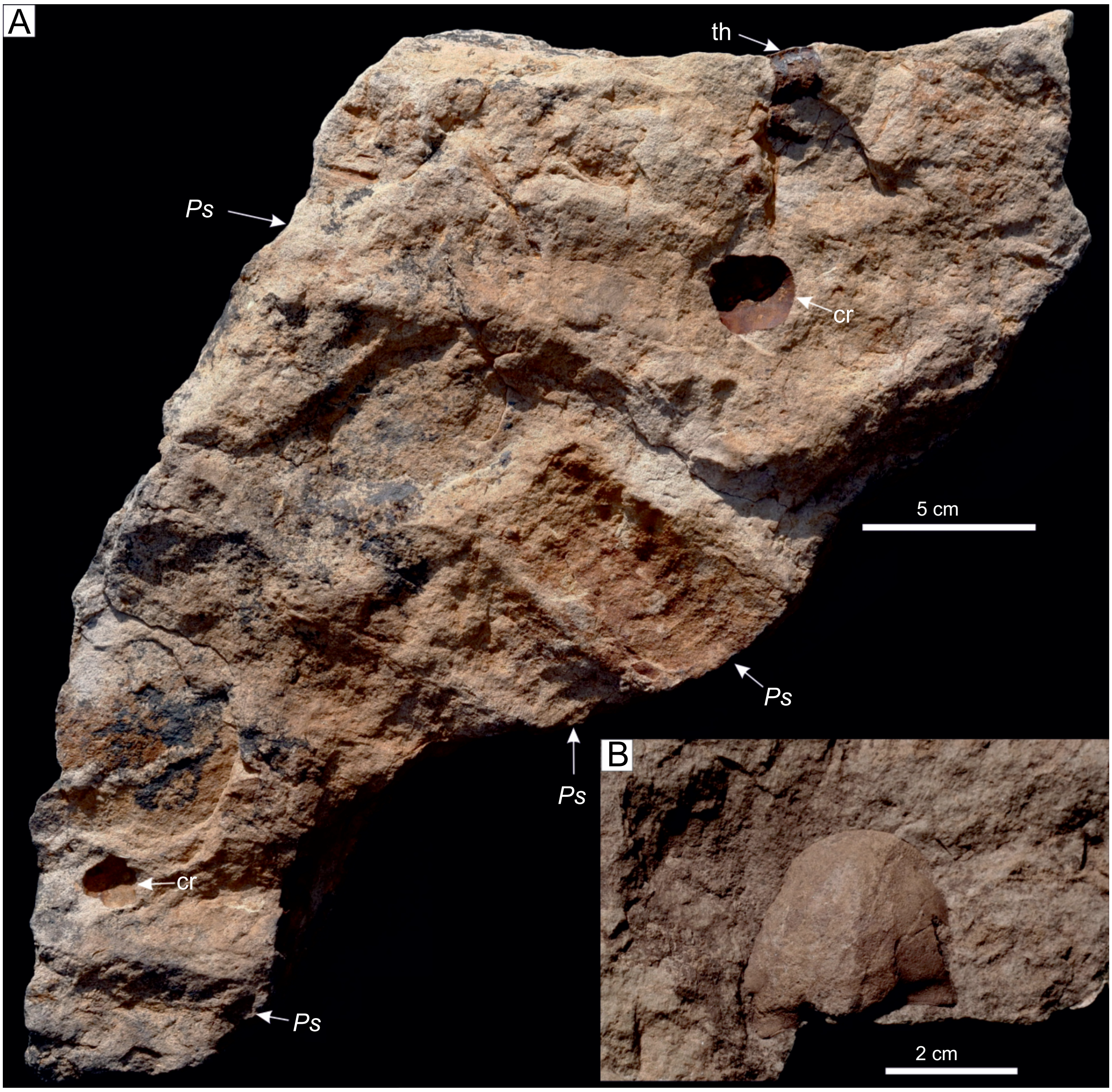

Fig. 6. *Psammichnites gigas arcuatus*, Morphotype 2 associated with trilobite remains, Cambrian of the Ocieseki Formation from the Widełki area

A – trilobite *Kingaspidoides santacrucensis* cranidium (cr) in the burrow (Ps); large fragment of thorax (th) and another cranidium are visible near the burrows; INGUJ214P/Wi40; **B** – *Kingaspidoides santacrucensis* cranidium from the bed bioturbated by *Psammichnites*, INGUJ214P/Wi41; epichnial views

the lower parts of the burrows are preserved at various depths within the sandy beds, whereas the upper parts are preserved only on the top surface of the bed as convex hypichnia, commonly of collapsed burrows.

Moreover, differences between individual specimens result from the type of sediment and its consistency. It appears that more details, especially on the lower and upper surfaces of the burrows, are preserved in beds of very fine-grained sandstone with a high silt content (wacke), or on the surfaces of silty laminae. In contrast, in beds of pure quartz arenite, details such as striae or imprints of small elements (e.g., sclerites) are poorly preserved or absent. This is related both to grain size and to sediment cohesiveness, which is greater in very fine-grained deposits, particularly in silty sandstone. It also appears that the deeply impressed specimens were formed in soft, i.e., water-saturated, sediment, whereas the shallowest, relatively flat forms developed on the surface of a firmer substrate (cf. McIlroy and Heys, 1997). Some relatively shallow specimens, presumably formed above a compact sediment layer, display longitudinal grooves or ridges, interpreted as scratch traces on their underside (Figs. 3G and 5A, B). The morphology of the lower part of the burrows, namely, arcuate impressions in specimens from the Ocieseki Formation, differs from the transverse bars forming a ladder-like pattern in the specimens described by McIlroy and Heys (1997). This difference may have both taphonomic and evolutionary causes. *Psammichnites gigas arcuatus* from the Ocieseki Formation is slightly younger (Cambrian Age 4) than the "*Plagiogmus*" specimens from the Arumbrera Formation illustrated by McIlroy and Heys (1997), whereas the exact age of the specimens from Sweden described by Jaeger and Martinsson (1980) is not specified, although they are considered to represent Cambrian Age 3 or 4. McIlroy and Heys (1997) interpreted the transverse bars as having been formed by a suction disc at the rear of the animal

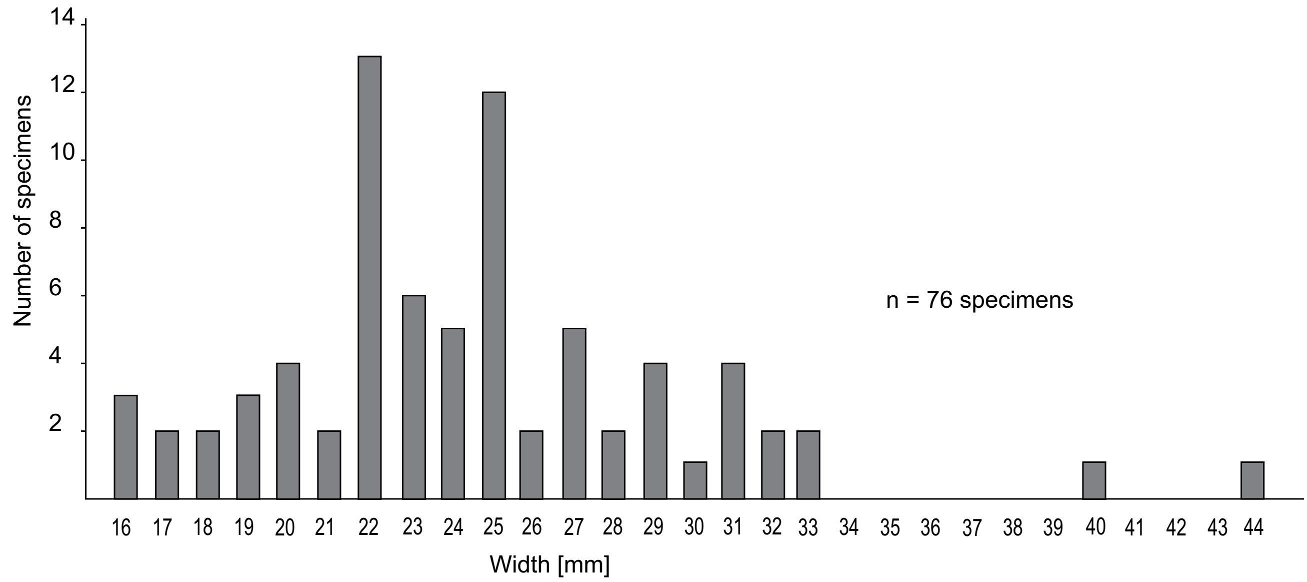

Fig. 7. Plot of width measurements of the specimens studied of *Psammichnites gigas arcuatus*

during locomotion across a relatively firm substrate. Among the specimens from the Ociesęki Formation analysed here, forms with transverse bars (Fig. 6A) are also present, but they are much rarer than structures with an arcuate surface, and appear to occur only in specimens preserved in pure, medium-grained quartz arenite, whereas the arcuate forms are found in very fine-grained arenite and occasionally wacke. This observation supports McIlroy and Heys' (1997) concept regarding substrate consistency.

A specimen from the Miaolingian of Poland, preserved as a positive hypichnial semirelief and assigned to *Arcuatichnus wimani* Kowalski, 1978 by Orłowski and Żylińska (1996: fig. 4C), displays intermediate features between an arcuate surface and transverse ladder-like bars. This specimen is exceptionally well-preserved due to its occurrence at the boundary between a sandy and a muddy layer of the Jugoszów Formation. It is noteworthy that in the reconstruction proposed by Seilacher-Drexler and Seilacher (1999) and Seilacher (2007), both elements are present, with the arcuate surface located at the base of the burrow and the transverse bars situated above it. The preservation of the lower arcuate surface is therefore dependent on a soft, fine-grained substrate.

There is also a difference between the specimens studied here, which typically have a sandy fill similar to the surrounding sediment, and the specimens described by McIlroy and Heys (1997), whose fill is enriched with clay minerals. The latter authors interpreted this as material ingested during the animal's foraging on the substrate surface. However, the Ociesęki specimens mostly show a distinct backfill, clearly resulting from the organism wedging itself into the sand (Seilacher, 2007), rather than from the passive filling of an open burrow with faecal material, as suggested by McIlroy and Heys (1997).

Glaessner (1969) noted that *Psammichnites gigas arcuatus* (then referred to as *Plagiogmus*) occurs in medium- to coarse-grained sandstones, where the burrows are resistant to deformation. However, various forms of *Psammichnites gigas*, including *P. gigas arcuatus*, also occur in fine-grained sandstones and siltstones, where they may be deformed and the features characteristic of this ichnosubspecies obscured (Runnegar et al., 2024). This creates additional difficulties in the classification of trace fossils within the ichnogenus *Psammichnites* Torell, 1870.

DISCUSSION

TRACEMAKER PROBLEM OF *PSAMMICHNITES GIGAS ARCUATUS*

Orłowski (1975b, 1992b) identified specimens of this trace fossil from the Holy Cross Mountains as *Cruziana* sp. and interpreted them as burrows produced by the trilobite *Kingaspidoides santacrucensis*. According to his later interpretation (Orłowski, 1992b), this trace fossil was produced by a trilobite with delicate appendages, and the animal regularly rested between bouts of burrowing. The similarity of *Psammichnites* to an inverted *Cruziana* cast had previously been noted by Fenton and Fenton (1937) based on specimens from the Cambrian of Sweden illustrated by Hadding (1929). The co-occurrence of the trace fossil *Psammichnites gigas arcuatus* and trilobite remains was likely the reason why Orłowski attributed this trace fossil to trilobite activity. Furthermore, the width of *P. gigas arcuatus* specimens (16–44 mm, commonly 25–30 mm; Fig. 7) corresponds to the width of accompanying trilobite remains (cf. Orłowski, 1975b, 1985). The sharp turns of the burrow (Fig. 3C) suggest a short animal burrowing through the sediment rather than a long worm (Rindsberg and Martin, 2003; Seilacher, 2007). Seilacher (2007) noted the gigantic size of Tommotian (Cambrian Age 2) *Psammichnites*, which is unusual for pre-trilobite times, as well as the searching behaviour that resembles scribbling. Both of these characteristics match large trilobites of Cambrian Age 4. However, the two elements mentioned do not fully support a trilobite origin for *Psammichnites gigas*. First, the trilobite would have had to plough upside-down through the sediment to leave some of the trace fossils illustrated here. While this burrowing orientation is not unknown in arthropods (e.g., some amphipods; Nicolaisen and Kanneworff, 1969), it is unusual. Second, and more to the point, most of the trace fossils preserved as epichnial ridges are smooth, without scratch traces made by legs, despite having been made in a substrate suitable for the preservation of striae.

Further evidence on the tracemaker comes from the taphonomy of *Psammichnites* in the Ociesęki Formation and elsewhere. Jaeger and Martinsson (1980) and McIlroy and Heys (1997) argued for the importance of mucus in the lining of burrow walls, which is thought to enhance the integrity of the preserved burrows. McIlroy and Heys (1997) discussed in detail the problem of animal movement and the creation of a mucus-lined burrow, assuming a soft-bodied tracemaker. Locomotion was evidently somewhat slow and halting, as suggested by the menisci. Undulatory motion is indicated by the lower surface of the trace, which can show transverse ridges and valleys suggestive of the motion of a muscular foot as in some molluscs. If the tracemaker of *Psammichnites* used small additional appendages or spines to dig with, they must have been very short, as deep striae are absent in specimens studied to date (Seilacher-Drexler and Seilacher, 1999; Seilacher and Hagadorn, 2010). Long, subhorizontal meniscate burrows are generally attributed to a combination of locomotion and feeding, as in modern spatangoid echinoid burrows (Bromley and Asgaard, 1975), though it is possible that some were made by a combination of locomotion and searching for prey, as perhaps by modern carnivorous gastropods (cf. Howard, 1968), though we suspect that these traces may not have such regular menisci as in *Psammichnites*. McIlroy and Heys (1997) argued against a skeletal animal as the creator of *Psammichnites* (their *Plagiogmus*) because of the lack of any longitudinal sculpture on the wall, but some specimens from the Cambrian Ociesęki Formation do have distinct, multiple striae (Figs. 4B–G and 5A–C, E), and at least some must have been formed by an animal with hard elements. Some transverse and oblique grooves occurring on specimens from the Ociesęki Formation (Figs. 3D–G, 4B–G and 5C–E) appear to be wrinkles formed in sand covered with the animal's mucus. In these cases, the mechanism of trace formation was likely similar to that responsible for the wrinkles in *Climactichnites*, which were produced on the sediment surface by a mucus-covered mollusc (Getty and Hagadorn, 2008, 2009). However, the longitudinal grooves and ridges in the material from the Ociesęki Formation (Figs. 3G and 5A, B) seem to be unequivocal scratches made by hard skeletal elements. It is possible that some small grooves and ridges resembling scratches of *Cruziana* in a specimen associated with *P. gigas arcuatus* (Fig. 4B–G) are, in fact, impressions of skeletal elements, and that they represent a body fossil of the tracemaker.

In the older literature, *Psammichnites gigas* and similar ichnospecies were interpreted as traces of "worms" (Matthew, 1890; Hadding, 1929), gastropods (Fenton and Fenton, 1937; Häntzschel, 1975) or molluscs in general (McIlroy and Heys, 1997; Mángano et al., 2002), and rarely arthropods (Yochelson and Schindel, 1978) or halkieriids (Seilacher-Drexler and Seilacher, 1999). In the case of specimens from the Ociesęki Formation, the tracemakers must have been animals possessing hard skeletal elements. Of course, the specimens described by different authors may have been produced by animals different from those from the Ociesęki Formation.

The typical keel-like median structure was evidently made by a narrow part of the animal that protruded upwards, such as a fin or respiratory appendage. The median structure can be parallel to the axis of the structure, or wavy. Since the work of Seilacher-Drexler and Seilacher (1999), this has been widely accepted as a siphonal trace that connected the tracemaker to the seafloor as it burrowed beneath. Although Seilacher and Hagadorn (2010) considered *Psammichnites* to be a shallow bulldozing trace, we do not certainly know how deeply its tracemaker burrowed, though it seems likely that it was no more than a few centimetres. It is possible that all known specimens of the "siphonal trace" are incomplete. Based on the interpretation of the upper "snorkel" part of the trace, *Psammichnites gigas* was interpreted as made by molluscs or some kinds of halkieriids, Cambrian animals of uncertain affinity (e.g., Seilacher-Drexler and Seilacher, 1999; Seilacher, 2007). Halkieriids had small skeletal elements (e.g., Conway Morris and Peel, 1995; Álvaro et al., 2004) that might have been capable of producing striae similar to those made by trilobites. Attention is drawn to the similarity between the specimens illustrated here (Fig. 4B–G) and fossils attributed to *Halkieria* (Conway Morris and Peel, 1995: fig. 12e, g). According to Conway Morris (1998), halkieriids possessed ventral and lateral sclerites, which have been interpreted as precursors of the bundles of neurochaetae responsible for locomotion in modern polychaetes. According to Mángano et al. (2002), the presence of a siphon in halkieriids is unlikely; therefore, their production of *Psammichnites* is questionable. On the other hand, according to these authors, densely packed meniscate backfill is not known from mollusc burrows. The cited authors emphasised, however, that their considerations concern Carboniferous forms of *Psammichnites* and do not necessarily apply to Cambrian ichnospecies. Nevertheless, in cases where the burrow forms beneath the sediment surface, its upper, bilobed part may have been formed by the animal's convex carapace and not by a flexible siphon (Yochelson and Schindel, 1978; see also Mángano et al., 2002). It is also noteworthy that the median groove on the upper surface of the burrow, formed as a result of the collapse of a circular burrow (McIlroy and Heys, 1997) may be absent for taphonomic reasons (Runnegar et al., 2024).

Regardless of the taxonomic affiliation of the tracemaker, *Psammichnites* is commonly interpreted as a structure produced by animals moving and foraging in the sediment and having a connection with the surface of the sediment through a tubular "snorkel" (McIlroy and Heys, 1997; Seilacher, 1997, 2007; Mángano et al., 2002). In Seilacher-Drexler and Seilacher (1999) and Seilacher's (2007) interpretation, the sinusoidal groove in the upper part of the burrow is a trace left by a snorkel, its amplitude increasing upwards, that is, as it became more distant from the tracemaker's body. In this model, the snorkel swayed from side to side like a pendulum and served both in a respiratory role and as a tool for collecting food from the surface of the sediment. The snorkel must therefore have been sufficiently strong to penetrate through a substantial layer of sand. The wide groove on the upper part of the burrow was caused by its collapse, which suggests the considerable size of the tracemaker.

According to Hofmann and Patel (1989), *Psammichnites* was formed by an animal that made a rhythmically spaced axial groove in its movement through the sediment. Such locomotion is typical of worms, which Matthew (1890) indeed suggested as the *Psammichnites* tracemaker, but wormlike animals do not match the twisted grooves with alternating transverse ridges and depressions (Hofmann and Patel, 1989). Moreover, they do not fit the abrupt turns indicative of a short-bodied organism, observed by Seilacher (2007) and also seen in the Ociesęki specimens. According to Seilacher (2007), there are two possibilities regarding the producer of *Psammichnites*: flatworms (*Platyhelminthes*) or infaunal molluscs possibly related to halkieriids. However, flatworms do not have a long tubular siphon, unlike some molluscs. Seilacher (2007) specified that infaunal molluscs related to halkieriids, but lacking armour, appear to be the most likely tracemakers of *Psam-*

michnites. (Halkieriids are thought to be molluscs, but the relationships of these Cambrian animals are not certainly known). The occurrence in *Psammichnites* specimens from the Ociesęki Formation of both mucus-related wrinkles and scratches produced by hard elements suggests that the tracemakers of these burrows may have been halkieriids or similar animals with exposed, soft body parts but bearing isolated sclerites. This clearly aligns with Seilacher's (2007) concept of halkieriids that had reduced rigid armour. McIlroy and Heys' (1997) analysis of the direction of animal movement suggested that the arcs preserved under the surface of the Cambrian burrows were directed forwards, but Seilacher (2007) suggested motion in the opposite direction. According to McIlroy and Heys (1997), such arcs were the result of muscle contractions observed in molluscs and annelids (see also Lissmann, 1945).

McIlroy and Heys (1997) posed an important question: Why would the "*Plagiogmus*" (now *Psammichnites gigas arcuatus*) tracemaker expend energy digging when it collected food on the surface of the sediment? One possible reason, cited by these authors, is the high-energy palaeoenvironment during the deposition of the Arumbera Sandstone, which could have made it difficult for organisms to function on the surface of the sediment. Another reason, also suggested by these authors, was termed by Dzik (2007) as the Verdun strategy, that is, burial in the sediment for protection against predators while using the siphon for respiration. As McIlroy and Heys (1997) noted, there should be significant evolutionary pressure for biomineralisation in burrowing organisms to reduce tissue damage. Protective armour was indeed developed by halkieriids, which remain as potential creators of *Psammichnites*, although no siphon has ever been recorded in their body fossils. McIlroy and Heys' statement that no definitive conclusions can be drawn about the biological kinship of the animal producing their "*Plagiogmus*" is still valid today. However, relatively young *Psammichnites gigas arcuatus* from the Cambrian Stage 4 of the Ociesęki Formation were presumably created by organisms capable of scratching the sediment, in the lower and upper parts of the burrow. It can therefore be assumed that their distinctive morphology (i.e., arcuate moulds instead of transverse bars and longitudinal ridges), compared to other common Cambrian specimens, results from the evolution of the Cambrian tracemakers and perhaps even the formation of the Ociesęki trace fossil by a different group of organisms. In sum, we do not know what kind of animal(s) made Cambrian *Psammichnites* from the Ociesęki Formation, but the evidence is consistent with a short-bodied animal having a muscular body and hard elements, perhaps an early mollusc restricted to the Cambrian, such as a halkieriid. Like most previous authors, we may conjecture that they burrowed beneath the surface to feed on organic matter while hiding from predators and maintaining minimal contact with the overlying water.

STRATIGRAPHICAL SIGNIFICANCE

The specimens of *Psammichnites gigas arcuatus* illustrated here from the Cambrian Stage 4 of the Ociesęki Formation represent a relatively late occurrence of this ichnosubspecies. In addition, an even younger specimen, representing the Miaolingian, was described from the Jugoszów Formation in this area (Orłowski and Żylińska, 1996). Meanwhile, most documented occurrences of this ichnosubspecies come from older Cambrian strata, ranging from the Terreneuvian to Cambrian Stage 3 (see the compilation in Mángano et al., 2022). According to that summary, the oldest pre-trilobite, i.e., Terreneuvian, specimens originate from Siberia, whereas Cambrian Stage 2 specimens are known from Siberia and Laurentia. Cambrian Stage 3 specimens occur in Gondwana, Laurentia, and Baltica, whereas Cambrian Stage 4 specimens are known only from Baltica. The specimens described in the present paper, together with the Miaolingian specimens from the Holy Cross Mountains (Orłowski and Żylińska, 1996), suggest that the youngest occurrence of *Psammichnites gigas arcuatus* was in the Baltica region. This trace fossil also occurs in Cambrian Series 3 of the Holy Cross Mountains (Stachacz, 2016). The occurrence of *P. gigas arcuatus* in the Miaolingian of Gondwana (Tethyan Himalaya), described by Verma et al. (2023), does not fit this pattern. However, the specimens illustrated by those authors and assigned to *P. gigas arcuatus* do not, in our opinion, display the diagnostic features of this ichnosubspecies, but only exhibit a backfill typical of various ichnospecies of *Psammichnites* (cf. McIlroy and Heys, 1997). Nevertheless, the possibility of migration of Cambrian forms between Gondwana and Baltica cannot be excluded, as was the case for trilobites (cf. Żylińska, 2013).

CONCLUSIONS

● *Psammichnites gigas arcuatus* from the Ociesęki Formation is preserved in several taphonomic variants, which include horizontal sections displaying meniscate backfill ("*Arcuatichnus wimani*"), bilobate furrows or ridges with a median furrow and V-shaped pattern ("*Cruziana* sp."), concave furrows with a U-shaped pattern ("*Plagiogmus*") resembling *Climactichnites*, and complex structures being combinations of these forms.

● The slightly different morphology of this trace fossil compared to other common Cambrian specimens may be the result of evolution, as it represents a relatively late occurrence of *P. gigas*.

● *Psammichnites* dominates the beds characteristic of the high-energy sands of the *Skolithos* ichnofacies.

● The evidence for a halkieriid maker of *Psammichnites* is inconclusive. The currently favoured interpretation of *Psammichnites gigas arcuatus* from Ociesęki points to halkieriids as makers, rather than arthropods and soft-bodied animals, particularly if certain moulds represent sclerites, but the issue has not been definitively resolved.

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Data availability. Supplementary material is available here: https://drive.google.com/drive/folders/1-s4R1Z6-4ChAk-F0kZ0S57DIq3q7xDbrK?usp=drive_link

The material will be made also available on request.

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