Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland

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During the Middle and Late Cambrian in the area of the present-day Holy Cross Mountains all the traces of infaunal activity were produced by animals burrowing parallel to and immediately below the sediment surface, deeper infaunal burrowers being missing. Deeper penetration was probably not possible due to anoxic conditions within the sediment. This was not the case in the Early Cambrian, where numerous deep vertical burrows with spreite structures are known in the area. Diversity of the Middle and Late Cambrian trace fossil assemblages of the Holy Cross Mts is low, with only six ichnogenera of non-arthropod traces in the Middle Cambrian and eight ichnogenera in the Late Cambrian, compared with 24 ichnogenera in the Early Cambrian. The most unusual is a large hemispherical burrow, possibly of actinian origin, for which the name *Bergaueria elliptica* isp. n. is proposed. *Treptichnus rectangularis* isp. n. represents horizontal burrows with stiff walls, being systems of short units connected with one another. Some of the units contain faecal pellets produced by the host animal.

Key words: Cambrian, Poland, trace fossils.

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Introduction

The Cambrian strata are represented in the Holy Cross Mountains by fine and coarse clastic sediments. Most of the trace fossils occurring here are the results of epifaunal activity of trilobites and other arthropods, especially well known from the Wiśniówka ichnocoenosis (Radwański & Roniewicz 1960, 1963, 1967) as well as from other horizons and localities (Orłowski *et al.* 1970; Orłowski 1992).

Early Cambrian trace fossils of non-trilobite origin have been described by Kowalski (1978, 1987), Orłowski (1989), and Paczeŝna (1985, 1986).

The present paper deals with Middle and Late Cambrian trace fossils of non-arthropod origin. These are almost exclusively shallow burrows, probably in response to anoxic conditions within the sediment.

The specimens are housed in the Institute of Geology of Warsaw University (abbreviated as IGPUW).

Taxonomy of trace fossils

Classification schemes constructed for trace fossils refer either to sedimentological (preservational, stratinomic), behavioural (ethological) or phylogenetic (taxonomic) aspects (Häntzschel 1962, 1975; Simpson 1975). There have been several attempts to introduce names and classifications linking trace fossils to zoological taxonomy, but the main problem that precludes this is the lack of direct correspondence between trace and body fossils.

The International Code of Zoological Nomenclature (Ride *et al.* 1985) validates ichnotaxonomy, acknowledging the fact that animals representing different biological taxa can produce quite similar traces, and at the same time several traces can be produced by a single animal (Seilacher 1953; Bromley 1990). In other words, the Code separates ichnotaxa (reflecting animal behaviour) from biotaxa (referring to phylogenetic relationships between organisms) (Rindsberg 1990; Magwood 1992; Pickerill 1994). This approach is followed in the present paper.

The ichnotaxa described herein have been classified into groups according to their general morphological characteristics. Vernacular names without being capitalised or italicised (following a suggestion of Martinsson 1970) are here used to these higher rank units.

Naturally, the important task of naming and formally describing trace fossils from a given region or strata is the first step in ichnological analysis. The next problem is to determine the producers of particular traces. A tremendous increase in knowledge of soft-bodied Cambrian organisms in the last decades allows us to guess which groups of organisms were responsible for some kinds of traces and which can be excluded from considerations as being unlikely to occur in the Cambrian. Organisms very different and not necessarily related to Recent ones occupied ecological niches of infaunal filter- or detritus-feeders during the early Phanerozoic, for instance priapulid worms instead of annelids, probably not present among Cambrian infaunal organisms at all (Conway Morris 1977; Jensen 1990).

Stratigraphy and localities

The studied trace fossils have been collected from several outcrops (Fig. 1) within the Middle and Late Cambrian deposits of the Holy Cross Mountains in Central Poland (Fig. 2).

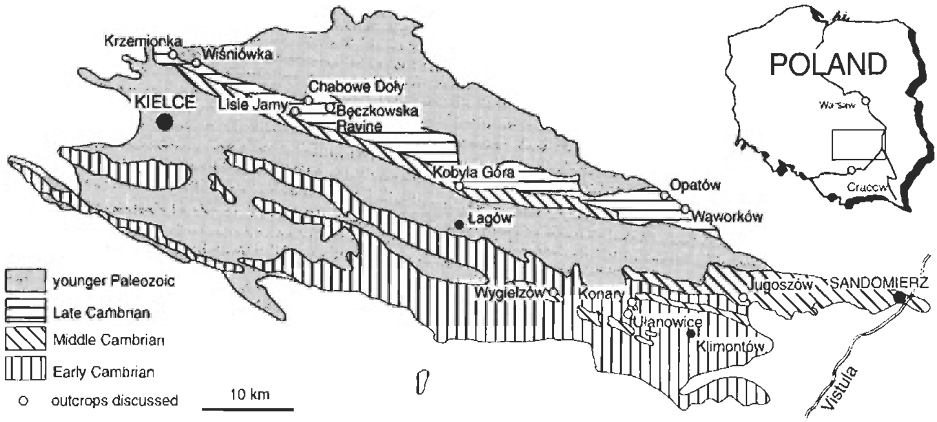


Fig. 1. Geological sketch map of the Holy Cross Mountains.

The oldest traces have been found in two small outcrops (Jugoszów 11 and 23 according to Orłowski 1964) along an unnamed stream near Jugoszów, about 8 km NE from Klimontów in the eastern part of the area. The outcrops are placed within the Usarzów Sandstone Formation, about 400 m thick and comprising sandstones with subordinate clay and silt shale intercalations. The body fossils are represented by numerous trilobites (Orłowski 1964, 1985). Trace fossils are rather scarce being represented by cruzianae, *Planolites beverleyensis* (Billings, 1862) and *Arcuatichnus wimani* Kowalski, 1978.

A little younger is the Słowiec Sandstone Formation composed of medium-grained, medium-bedded sandstones and poorly sorted, often coarse-grained, thick-bedded sandstones of light grey, light yellow and reddish colours, and up to 100 m in thickness. The outcrops which yielded trace fossils are mainly small pits situated usually on the peaks of hills of the Wygiełzów range, WNW from Klimontów in the eastern part of the area, that is in the vicinity of Wygiełzów, Ułanowice and Konary. Trilobites in the formation are common (Orłowski 1985); non-trilobite skeletal fauna is represented by the eldonioid *Velumbrella czarnockii* Stasińska, 1963 (Masiak & Żylińska 1994). Trace fossils are rare; only cruzianae, *Planolites beverleyensis* and *Planolites montanus* Richter, 1937 have been recorded.

The Góry Pieprzowe Shale Formation is poor in trace fossils, only *Bergaueria perata* Prantl, 1945 was found on Kobyla Góra, a hill situated about 8 km north of Łagów in the eastern part of the area. The formation is represented by clay and siltstone shales and siltstones, black or dark grey in colour with thin sandstone intercalations and is up to 400 m thick. Body fossils are rare (Orłowski 1964, 1985) with the exception of the brachiopod *Lingulella vistulae* (Gürich, 1901) (Orłowski 1964).

Trace fossil localities occurring within the Middle to Late Cambrian Wiśniówka Sandstone Formation are placed in the westernmost and easternmost part of the area, that is near Wiśniówka in the west and

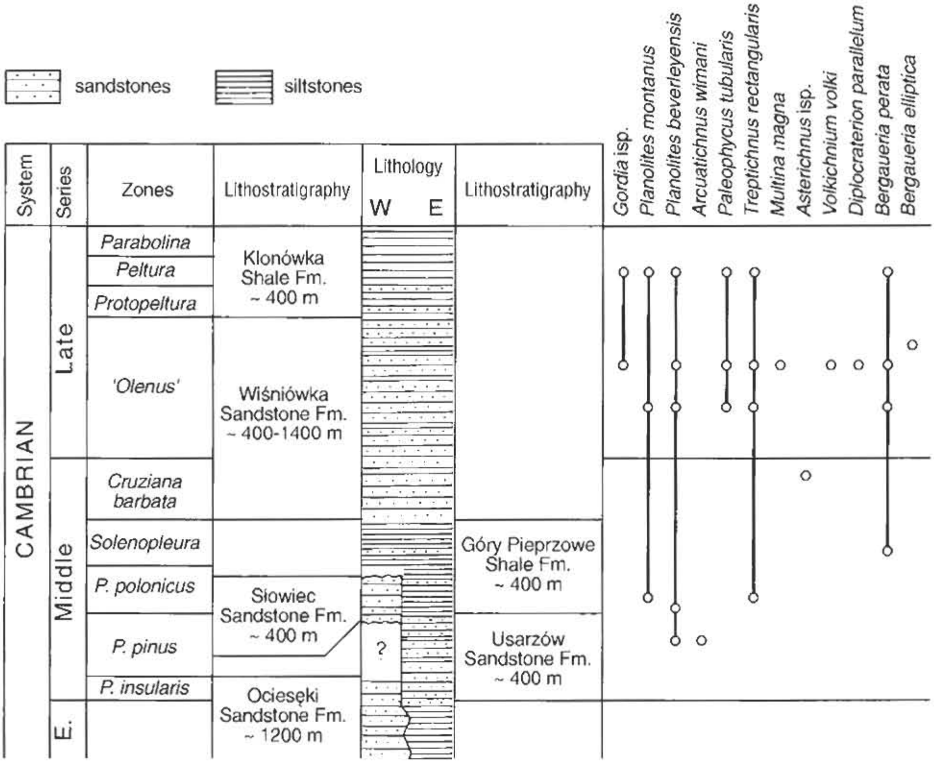


Fig. 2. Stratigraphic position of horizons with trace fossils in the Middle and Late Cambrian of the Holy Cross Mountains. *P.* — *Paradoxides*.

Wąworków in the east. The Wiśniówka outcrops comprise three large quarries, of which one is worked out (Mała Wiśniówka) and in course of being filled up, and the remaining two are in operation (Duża Wiśniówka and Podwiśniówka). The most westernmost outcrop, at present almost creeped, is situated 1 km west of Wiśniówka, on the slopes of Krzemionka hill, in a cross-cut of the Cracow–Warsaw road. The eastern outcrops of the formation are situated in Opatów in a pit near the old cemetery and within an abandoned quarry near Wąworków, 2 km east of Opatów. The Wiśniówka Sandstone Formation consists of thick bedded, hard sandstones, light grey to blue in colour, with numerous intercalations of siltstones and silty and clayey shales. The sandstone beds display numerous well-preserved sedimentary structures typical for shallow water environments, as well as a particularly rich trilobite ichnocoenosis (Radwański & Roniewicz 1960, 1963, 1967). The thickness of the formation varies from 400 to 1400 m. Body fossils include trilobites, brachiopods and eocrinoids (Orłowski 1968b; Dzik & Orłowski 1993). Trace fossils are very common, the most typical being cruzianae and rusophyci, *Bergaueria perata*, *Diplocraterion parallelum*, *Planolites montanus*, *Planolites beverleyensis*, *Paleophycus tubularis* and *Treptichnus rectangularis* isp. n.

The youngest trace fossils come from the Klonówka Shale Formation. It crops out in the northern part of the Duża Wiśniówka quarry (along an old road cut), and in several ravines perpendicular to the strike of Cambrian deposits, that is in Lisie Jamy, Chabowe Doły and the Bęczkowska Ravine. The formation comprises shales and siltstones with sandstone intercalations and is about 400 m thick. Body fossils are represented by trilobites, occurring in local, nest-like associations (Orłowski 1968b; Tomczykowa 1968). Trace fossils are common, including cruzianae and rusophyci, *Planolites montanus*, *Planolites beverleyensis*, *Paleophycus tubularis*, *Bergaueria perata* and *Treptichnus rectangularis* isp. n.

Descriptions

Nonbranching cylindrical burrows

Gordia isp.

Fig. 8C.

Material. — Four specimens.

Description. — These are long, irregularly bent, smooth narrow burrows exposed to the surface in portions. The largest cast is 10 cm long and 2 mm in diameter. Shorter burrows have smaller diameters and are strongly bent, while the longer ones are more regular. Convex epireliefs.

Remarks. — Part of the discussed material has been previously described as *Gordia* sp. A by Orłowski (1968a).

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation at Mała Wiśniówka and Duża Wiśniówka quarries and Late Cambrian Klonówka Shale Formation at Duża Wiśniówka and Chabowe Doły.

Planolites montanus Richter, 1937

Fig. 3A–C, E.

Material. — Fourteen specimens.

Description. — Horizontal burrows, straight or gently curved, with smooth walls, oval in cross section, diameter from 1 to 5 mm. They were produced close to the surface of the clay and follow very complex surfaces modelled by other burrowers. The burrow was apparently open to the surface along its whole length and is completely filled with sand from the overlying bed. Convex epireliefs.

Remarks. — According to Pemberton & Frey (1982) this ichnospecies includes *Planolites ballandus* Webby, 1970, which is its younger synonym. *Planolites nematus* Kowalski, 1987 (Kowalski 1987) can also be included into this ichnospecies, as the specimens are 1 mm in diameter.

Occurrence. — Middle Cambrian Słowiec Sandstone Formation in the vicinity of Ułanowice, Late Cambrian part of the Wiśniówka Sandstone Formation at Wiśniówka and Wąworków quarries, Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry, Bęczkowska ravine and Chabowe Doły.

Planolites beverleyensis (Billings, 1862)

Fig. 3C–E.

Material. — Thirteen specimens.

Description. — Burrows cylindrical to flattened, with smooth walls, straight to slightly curved, very regular with insignificant variations in shape or diameter. They occur either isolated or densely cover bedding surfaces, overlapping each other. Their diameter ranges from 4 to 8 mm, length reaches up to 9 cm. Sometimes they occur within the sandstone bed being infilled with clay and differing in colour from the host rock; occasionally they remain empty. Convex epireliefs.

Remarks. — This ichnotaxon was identified in Early Cambrian strata of the Holy Cross Mts by Orłowski (1989).

Occurrence. — Middle Cambrian Usarzów Sandstone Formation in exposures Jugoszów 11 and 23, Middle Cambrian Słowiec Sandstone Formation near Wygiełzów and Ułanowice, Late Cambrian part of the Wiśniówka Sandstone Formation at Duża Wiśniówka quarry, Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry and Lisie Jamy.

Nonbranching flat bottom burrows

Arcuatichnus wimani Kowalski, 1978

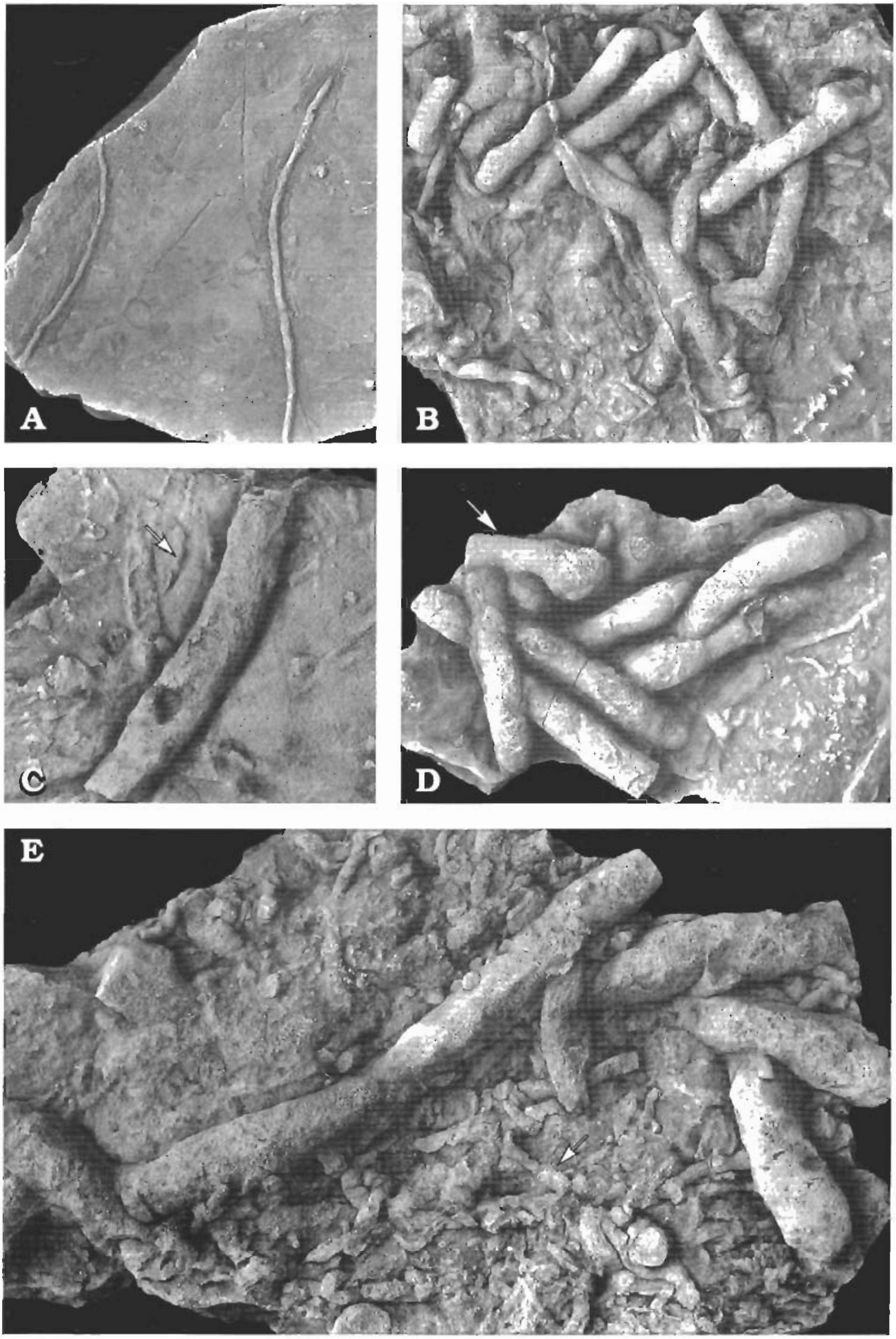
Fig. 4C.

Material. — One specimen.

Description. — Straight burrow, about 15 cm long and 3 cm wide, regular, convex, with many arcuate ridges, each about 1 cm long. Convex epirelief.

Remarks. — This trace fossil differs from the earliest Cambrian *Plagiogmus arcuatus* Roedel, 1929 (see Jaeger & Martinsson 1980) in lacking smooth walls (Kowalski 1978), thus probably being originally only weakly stiffened by an organic wall. The ridges at the bottom of the furrow, similar to those in *Plagiogmus arcuatus*, are perhaps portions of sediment scraped from the bottom by the retrograde peristaltic wave of the animals foot, when it was pushed against the sediment penetrated at its front. According to Glaessner (1969) the extreme form of such action is expressed in trace fossil morphologies referred to as *Psammichnites* Torell, 1870 (see Hofmann & Patel 1989). They apparently represent mollusc burrows or burrows created by the bulldozing action of large unknown soft-bodied animals (Seilacher & Gámez-Vintaned 1995). When free of backward pressure, such a peristaltic wave produced smooth transverse depressions

Fig. 3. **A–B**. *Planolites montanus* Richter, 1937 from the Late Cambrian Klonówka Shale Formation; × 1. **A**. Specimen IGPUW/Tf/1/503 from Bęczkowska ravine. **B**. Specimen IGPUW/Tf/1/505 from Duża Wiśniówka quarry. **C–E**. *Planolites beverleyensis* (Billings, 1862); × 1. **C**. Specimen IGPUW/Tf/1/515 with *Planolites montanus* (arrowed) from the Middle Cambrian Słowiec Sandstone Formation, Ułanowice. **D**. Specimen IGPUW/Tf/1/519 from the Late Cambrian part of Wiśniówka Sandstone Formation, Duża Wiśniówka quarry, superimposed on *Treptichnus* (arrowed). **E**. Specimen IGPUW/Tf/1/525 with *Planolites*



montanus (arrowed) from the Middle Cambrian Usarzów Sandstone Formation, exposure Jugoszów 11.

and elevations, well exemplified by the large Late Cambrian *Climactichnites* Logan, 1860. The end of the body, drawn behind, left there arcuate transverse striae (see Yochelson & Fedonkin (1993) for different interpretation). The trace in some ways resembles Pennsylvanian protobranch trace fossils, resulting from push-and-pull burrowing of the sediment with a cleft-foot (Seilacher & Seilacher-Drexler 1994).

Arcuatichnus was thought to be created by an arthropod (Kowalski 1978) and the ichnotaxon established on the basis of Early Cambrian material (Ocieseki Sandstone Formation) of the Holy Cross Mountains. The Middle Cambrian trail is more elevated above the surface of the sandstone bed.

Occurrence. — Middle Cambrian Usarzów Sandstone Formation, exposure Jugoszów 11.

Branching cylindrical burrows

Paleophycus tubularis Hall, 1847

Fig. 4A–B.

Material. — Four specimens.

Description. — Cylindrical burrows branching dichotomously, varying in shape, unornamented. In cross section they are oval, 2–5 mm in diameter. Convex hyporeliefs.

Remarks. — This ichnotaxon has been described from Early Cambrian strata of the area by Orłowski (1989).

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation at Duża Wiśniówka and Wąworków quarries and Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry.

Ichnogenus *Treptichnus* Miller, 1889

Type ichnospecies: *T. bifurcus* Miller, 1889.

Treptichnus rectangularis isp. n.

Figs 3D, 5–6.

Holotype: Specimen No. IGPUW/Tf/1/601.

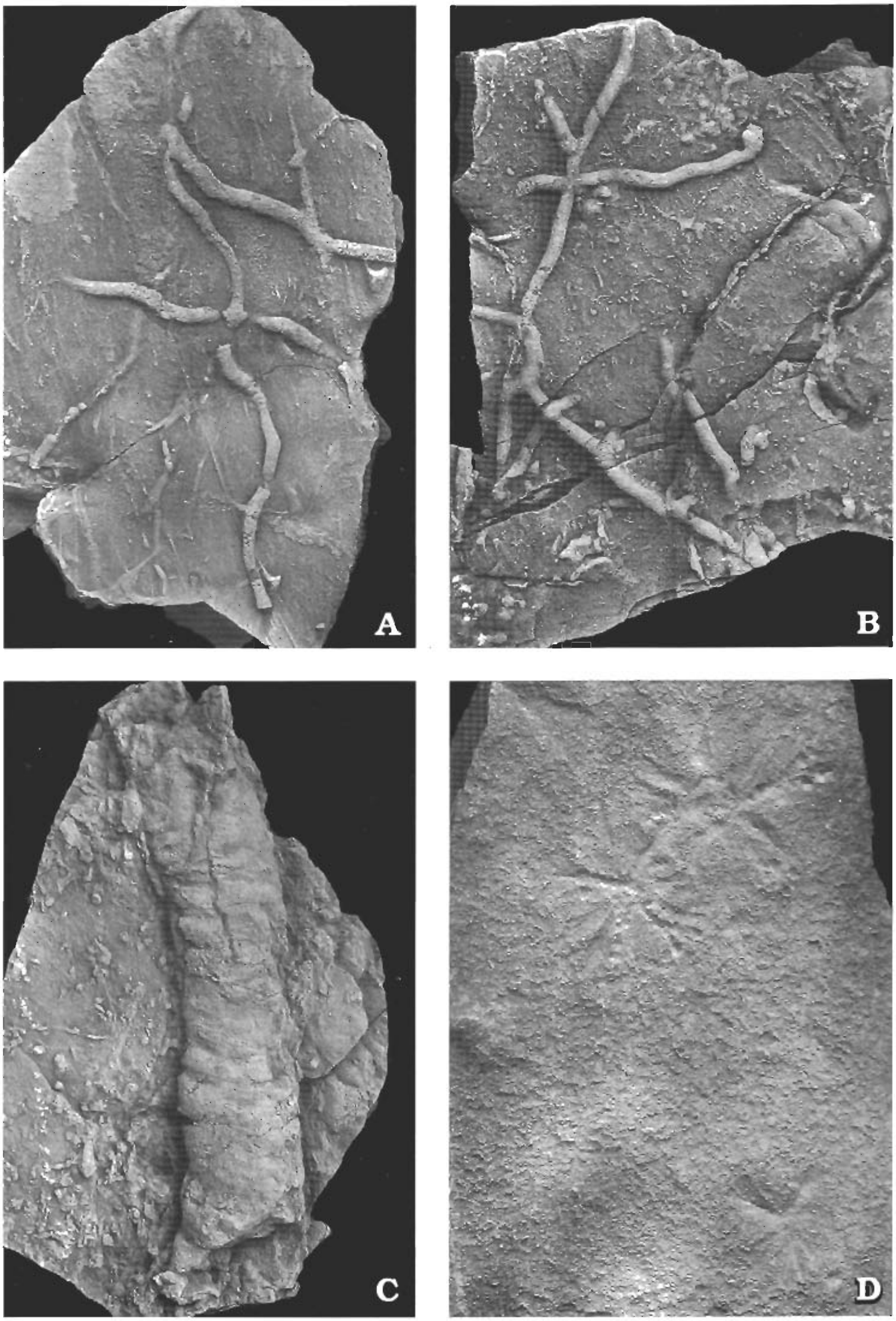
Type locality: Duża Wiśniówka quarry.

Type horizon: Late Cambrian, Klonówka Shale Formation.

Derivation of name: From Latin *rectangularis* — containing right angles; some of the specimens have a strictly right angled mode of branching.

Diagnosis. — Horizontal burrows consisting of a system of short units, 3–5 mm in diameter and up to 40 mm long each, emerging alternately or on the same side from the periapertural part of the preceding unit and opening vertically to the surface. Units are irregularly shaped and almost devoid of ornamentation, they were created parallel and right below the

Fig. 4. **A–B**. *Paleophycus tubularis* Hall, 1847 from the Late Cambrian part of the Wiśniówka Sandstone Formation; × 1. **A**. Specimen IGPUW/Tf/1/530 from Wąworków quarry. **B**. Specimen IGPUW/Tf/1/531 from Duża Wiśniówka quarry. **C**. *Arcuatichnus wimani* Kowalski, 1978. Specimen IGPUW/Tf/1/534 from the Middle Cambrian Usarzów Sandstone Forma-



tion, exposure Jugoszów 11; × 0.5. **D**. *Asterichnus* isp. Specimen IGPUW/A/III/2 from the Late Cambrian part of the Wiśniówka Sandstone Formation, Mała Wiśniówka quarry; × 1.

water/sediment interface. The walls of burrows were stiffened; the organisms produced faecal pellets 0.3 mm in diameter and up to 1 mm long.

Material. — 23 specimens.

Description. — Horizontal burrows being a system of cylindrical units, oval in diameter, elongated or slightly curved. Minor units were created either on one side (Fig. 5A) or, more commonly, alternately on both sides (Fig. 5B); the angle of branching is variable, in some forms a tendency of right angled branching is observed (Fig. 6C–D). The longest set is 14 cm long and consists of 9 units (Fig. 5A). The distal ends of the units are slightly thicker and are directed towards the sediment surface. In some units half-way between their ends an area with fairly distinct longitudinal furrows and ridges is visible (i.e. on Fig. 5B–C). Some of the units contain empty spaces left from faecal pellets. Convex hyporeliefs.

Remarks. — Although particular units differ in shape, diameter and length, there is no apparent gradient in their size along the whole set (Fig. 7B). This means that if all the units were produced by the same individual, it had to construct them quite quickly. Otherwise some growth in size should be recognisable. The alternative interpretation may be offered that each next unit was occupied by a host of a next generation, perhaps as an effect of asexual reproduction, which would suggest burrows of colonial organisms. In fact there is no regular pattern reflected in the change of angle of branching (Fig. 7A) or in unit length and the two parameters are independent (Fig. 7C) — unlike in superficially similar colonies of boring ctenostome bryozoans (Gardiner & Taylor 1982) or monoserial graptolites (Urbanek 1973). However primitive the producers of the burrows might seem, the angle of branching is relatively stable (generally between 70 and 140°), and the most frequent angles are 90 and 135°.

The marking occurring in some units about half-way between their ends may have been left by spines attached to one end of the animal during its peristaltic motion within the sediment. Common representatives of Cambrian infauna, the priapulids, had a spined proboscis and (in *Ottoia* Walcott, 1911) a ring of hooks at the posterior end of the body (Conway Morris 1977; Jensen 1990). Recent priapulids use the proboscis as an anchor to move within the sediment (Bromley 1990), they do not however produce burrows, occupying mainly watery mud substrates.

The pellets which occur at the bottom of some units suggest that they were empty at the moment of being passively filled with sand. The wall of the burrow was apparently stiff, probably owing to impregnation with a mucus. The number of pellets varies and again is not controlled by any gradient. Pellets of similar morphology to those occurring in the *Treptichnus rectangularis* units are associated with the Pennsylvanian echiuroid *Coprinoscolex* Jones & Thompson, 1977 (Jones & Thompson 1977). Echiuroids generally have abilities to dig U-shaped burrows, although *Coprinoscolex* lacking hooks or anal setae was incapable of doing so. Such a general similarity in morphology of pellets and shapes of burrows is not enough to prove an echiuroid nature of the Cambrian burrows and a

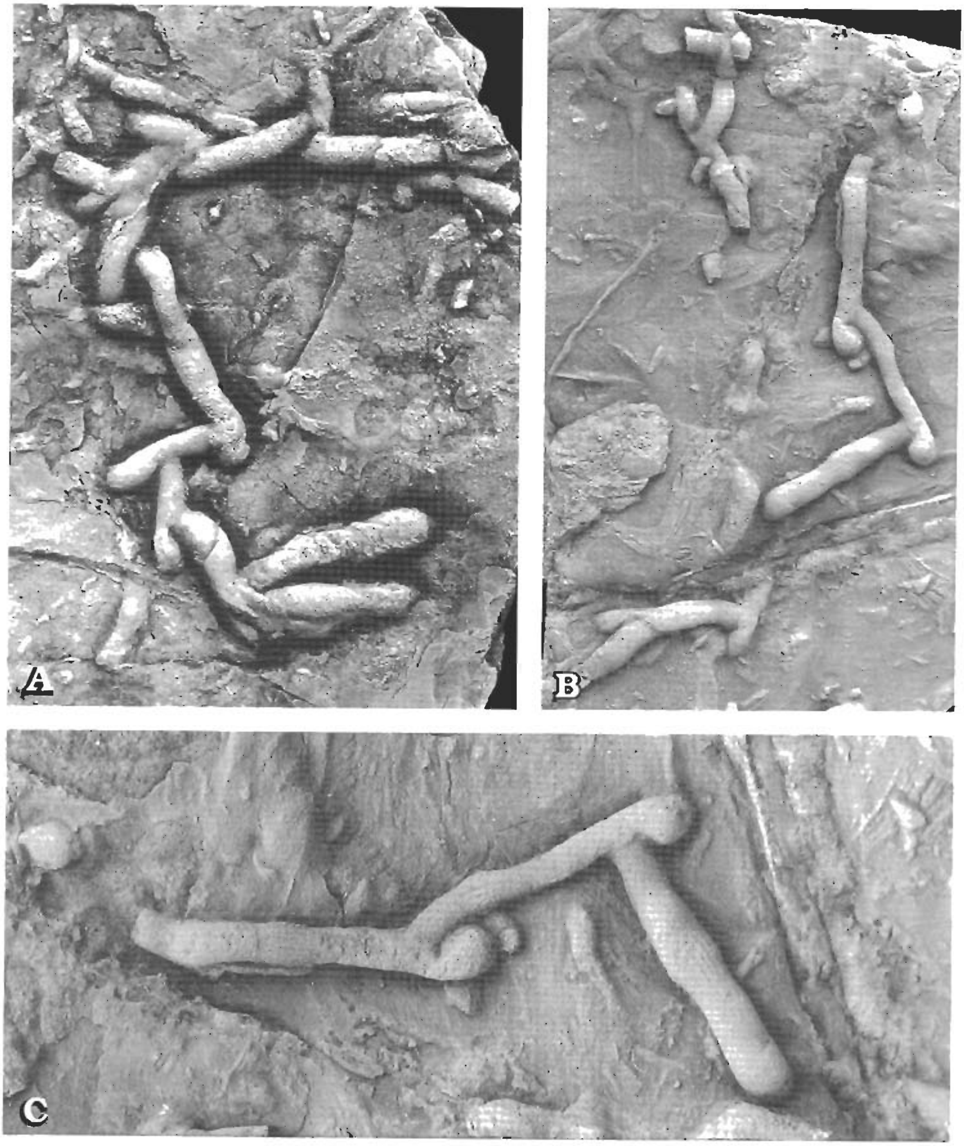


Fig. 5. *Treptichnus rectangularis* isp. n.: Late Cambrian Klonówka Shale Formation, Duża Wiśniówka quarry; × 1 except for C which is × 1,5. **A**. Specimen IGPUW/Tf/1/597. **B**. Specimen IGPUW/Tf/1/592. **C**. Enlarged fragment of B with longitudinal furrows.

priapulid relationship of the animal remains possible. Both these affiliations would make asexual budding rather unlikely.

If the new generations were produced sexually within the substrate another problem arises — why only a single successor was produced each time. It seems thus that the trace is a result of sediment foraging by the same individual.

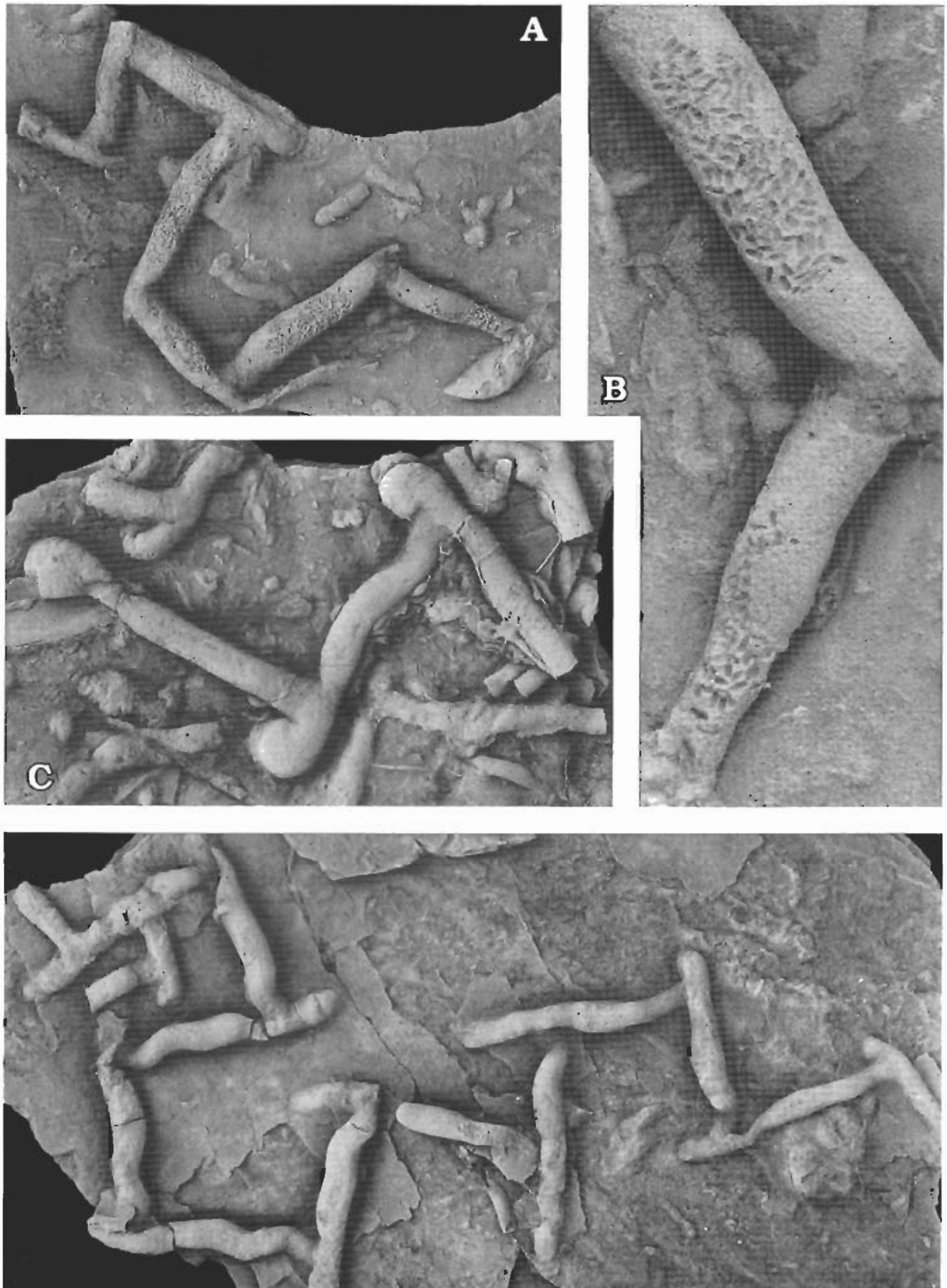


Fig. 6. *Treptichnus rectangularis* isp. n.; Late Cambrian Klonówka Shale Formation, Duża Wiśniówka quarry; × 1 except for B, which is × 3. **A**. Specimen IGPUW/Tf/1/605. **B**. Enlarged fragment of the same specimen with faecal pellets. **C**. Specimen IGPUW/Tf/1/602. **D**. Holotype IGPUW/Tf/1/601.

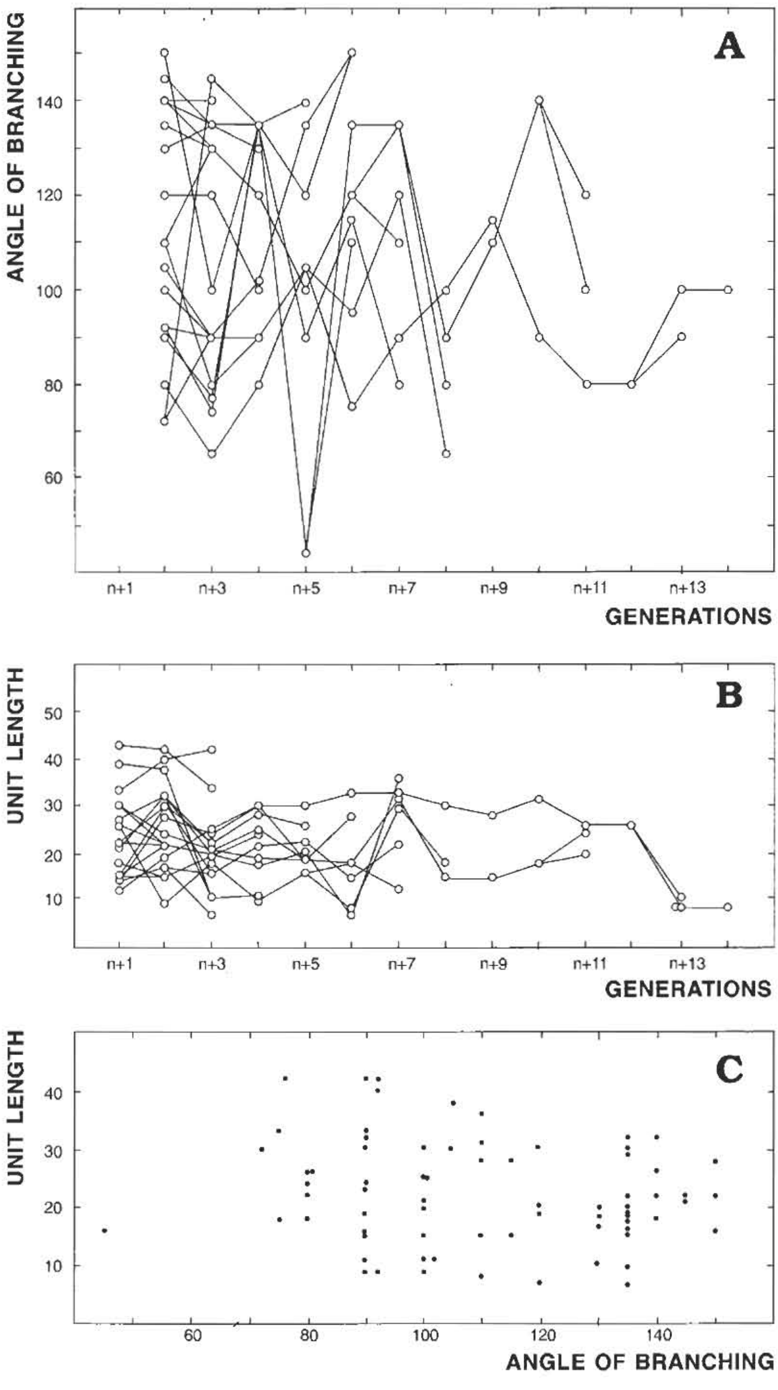


Fig. 7. *Treptichnus rectangularis* isp. n. from the Late Cambrian part of the Duża Wiśniówka quarry. changes in angle of branching (**A**) and length of particular units (**B**) during development of burrow system; **C**. relations between angle of branching and length of particular units.

Burrows of *Treptichnus rectangularis* differ from those of other *Treptichnus* species from Cambrian strata in a rather small diameter of particular units versus unit length as well as different ornamentation. In *Treptichnus lublinensis* Paczeŝna, 1986 (Paczeŝna 1986, 1989, 1996) the units are thicker and more densely packed; *Treptichnus triplex* Palij,1976 has much thicker units with two distinct grooves on each of them (Fedonkin 1985), while *Treptichnus* isp. 6 of Buatois & Mángano (1993) has thicker, unornamented units. Some of the *Treptichnus rectangularis* burrows are similar to burrows identified as *Phycodes pedum* Seilacher, 1955 in the Early Cambrian of the Holy Cross Mountains (Orłowski 1989). The animals responsible for the creation of *Phycodes circinatus* Richter, 1853 (type species of *Phycodes*) foraged by burrowing repeatedly in close contact with the preceding unit, producing in effect a spreite structure. This was not the case with *Treptichnus rectangularis*, where the particular units were stiffened within the clay, therefore being empty (or filled occasionally with faecal pellets) for some time before being passively filled with sand.

According to recent assignments, *Phycodes pedum* has been placed in the *Trichophycus* Miller & Dyer, 1878 group of traces (Geyer & Uchman 1995), representing a system of teichichnoid structures in form of crescents apparently branching from an axial cylinder, while suggestions of Jensen & Grant (1993) and Seilacher (personal communication) stress the resemblance of *Phycodes pedum* to *Treptichnus*.

Occurrence. — Middle Cambrian Słowiec Sandstone Formation at Konary near Klimontów (only one specimen), Late Cambrian part of the Wiśniówka Sandstone Formation at Duża Wiśniówka, Mała Wiśniówka and Wąworków quarries and Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry and Chabowe Doły.

Irregular networks

Multina magna Orłowski, 1968

Fig. 8A–B.

Material. — Four specimens.

Description. — The grooves on the upper surface of sandstones beds are about 1 mm wide, semioval in cross section, straight or slightly curved. They bifurcate and cross each other forming irregular polygons. Indistinct transverse furrows on some specimens resemble the backfill type of burrow infilling and are suggestive of peristaltic locomotion mechanism of the animal. Width of a single polygon varies from 2 to 5 cm. Occasionally networks of grooves overlap and particular grooves follow irregularities of the sandstone surface. Small, oval cavities, perhaps after clay pebbles, occur on the same rock slabs. Concave epireliefs.

Remarks. — The discussed specimens have been previously described by Orłowski (1968a). *Multina* is similar to the ichnogenus *Megagrapton* Książkiewicz, 1968 (Książkiewicz 1977), but the latter is situated on the lower surface of sandstones. The ichnogenus is also similar to *Paleodictyon* Meneghini in Murchison, 1850, however the latter is more regular, the

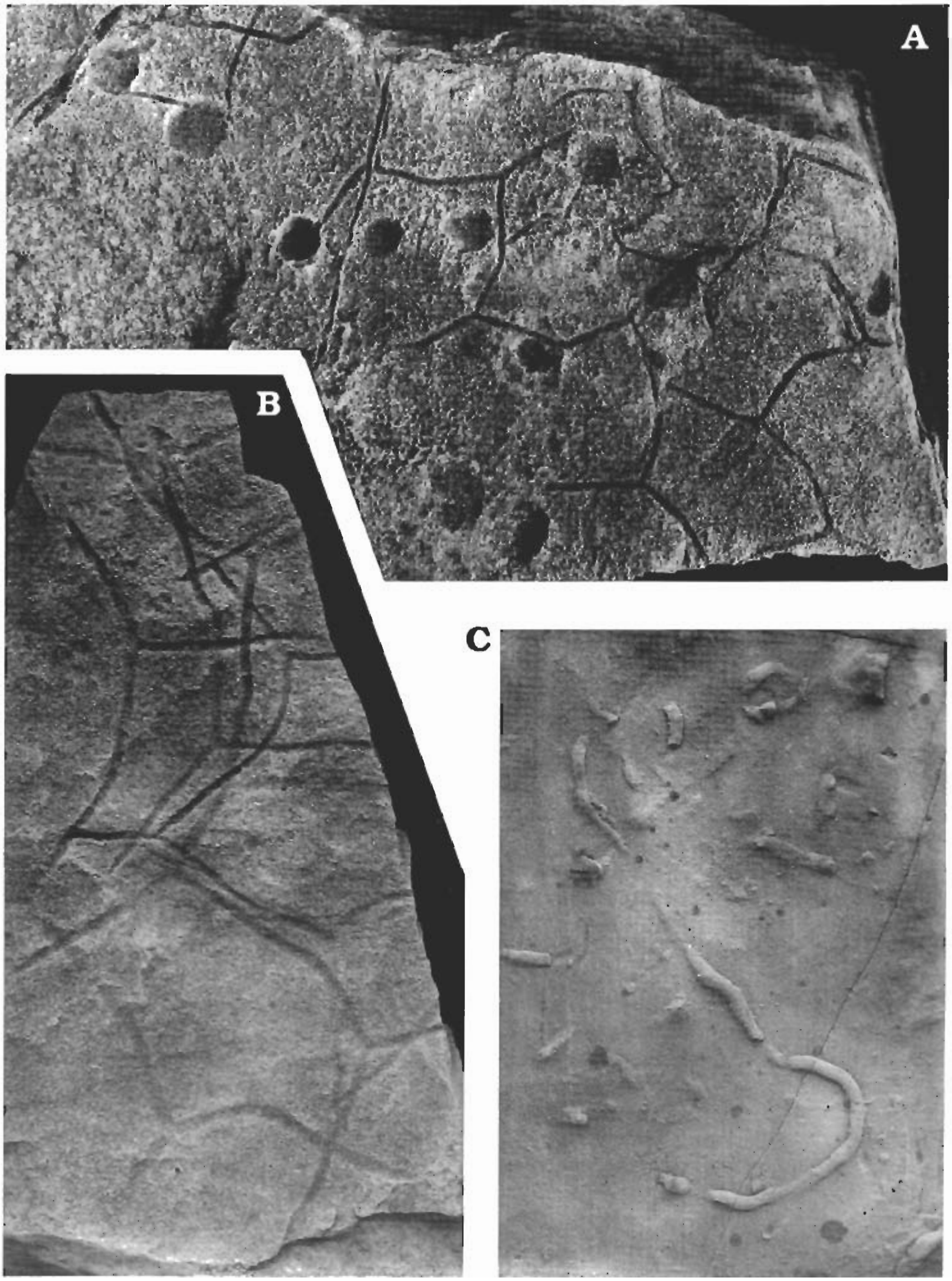


Fig. 8. **A–B**. *Multina magna* Orłowski, 1968; Late Cambrian part of the Wiśniówka Sandstone Formation. Duża Wiśniówka quarry. **A**. Specimen IGPUW/Tf/1/548; × 1. **B**. Specimen IGPUW/Tf/1/550; × 1. **C**. *Gordia* isp.; Specimen IGPUW/Tf/1/537; Late Cambrian Klonówka Shale Formation. Duża Wiśniówka quarry; × 1.

polygons are smaller and is situated in form of a hypichnial cast (Seilacher 1977).

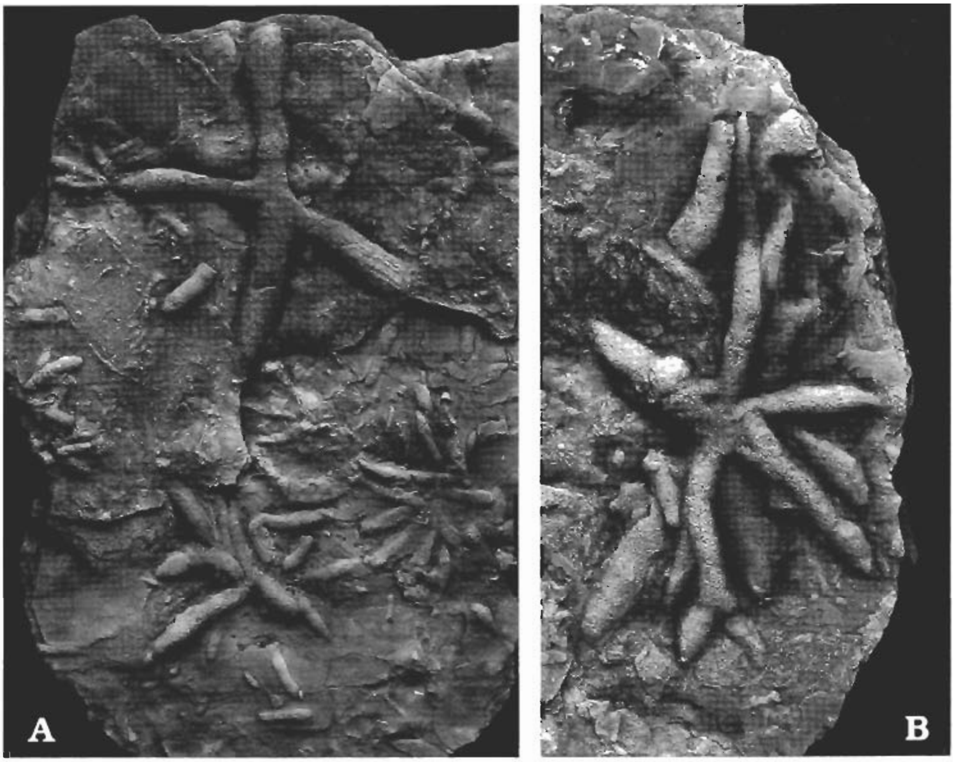


Fig. 9. *Volkichnium volki* Pfeiffer, 1965. **A**. Specimen IGPUW/Tf/1/545, Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka quarry; × 0.5. **B**. Specimen IGPUW/Tf/1/546, Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka quarry; × 1.

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation in Duża Wiśniówka and Mała Wiśniówka quarries.

Radial surface feeding traces

Asterichnus isp.

Fig. 4D.

Material. — Three specimens on one slab.

Description. — The traces, preserved in concave epirelief, are 17–26 mm in diameter. They consist of up to 10 usually non-branching radial grooves that probably represent impressions after rows of faecal pellets, circular in cross section. The areas in between are slightly smoother than the surrounding rough bedding surface of the sandstone, perhaps being smoothened by the organism body. The central part possibly represents the end of a vertical tube.

Remarks. — The discussed specimens were described by Orłowski (1968b) as Problematicum B. These traces were probably a product of a mud eater. Their morphologic features are comparable to *Asterichnus lawrencensis* Bandel, 1967 from the Carboniferous of Kansas (Bandel 1967), although few grooves bifurcate.

Occurrence. — Middle Cambrian part of the Wiśniówka Sandstone Formation at Mała Wiśniówka quarry.

Volkichnium volki Pfeiffer, 1965

Fig. 9.

Material. — Three specimens.

Descriptions. — Irregular star-like systems of cylindrical shallow burrows, oval in cross section and with smooth walls, that radiate from a centre and open to the surface at the ends. Six to eight 'rays', straight or slightly curved or even branching, are present. The diameter of each burrow is slightly larger in the distal part; their ends directed upwards. Length of a single 'ray' ranges from 25 to 45 mm, diameter 4 to 10 mm; the biggest specimen is 9 cm across. Convex hyporeliefs.

Remarks. — Similar trace fossils have been described by Pfeiffer (1965) from the Ordovician rocks of Germany but the Cambrian material differs in a larger number of 'rays' and their smaller diameter.

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka and Wąworków quarries.

Shallow U-shaped burrows

Diplocraterion parallelum Torell, 1870

Fig. 10A–C.

Material. — Seven rock specimens with many individuals

Description. — Shallow U-shaped burrows, semicircular in profile, of variable diameter, ranging from 2 to 5 mm. The preserved parts of tubes are up to 40 mm long. Convex hyporeliefs.

Remarks. — The specimens present only casts of the lowest part of U-shaped *Diplocraterion* burrows. At first glance the traces resemble lower parts of *Arenicolites* Salter, 1857, but typical *Arenicolites* from the Early Cambrian of the area (Orłowski 1989) have a much wider U than the discussed specimens. The expected spreite structures being a result of *Diplocraterion* producer activities are not distinguishable, probably due to their removal by erosion. Similar specimens from the same strata in the Duża Wiśniówka quarry were discussed by Radwański & Roniewicz (1963).

In the Early Cambrian rocks of the Holy Cross Mountains occur complete *Diplocraterion parallelum* specimens with spreite structures (Kowalski 1987; Orłowski 1989).

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation at Duża Wiśniówka and Wąworków quarries, Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry.

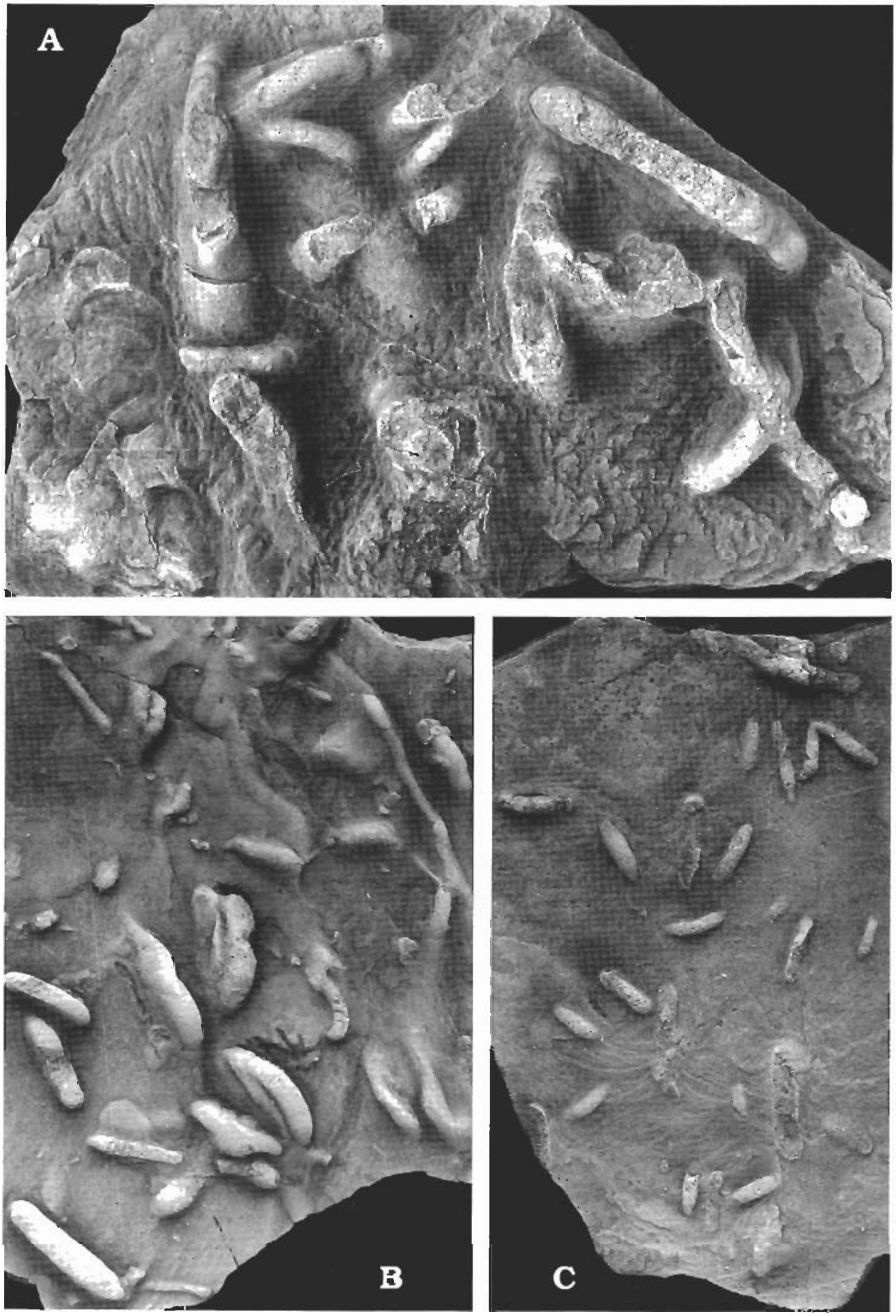


Fig. 10. *Diplocraterion parallelum* Torell, 1870; Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka quarry; × 1. **A**. Specimen IGPUW/Tf/1/540. **B**. Specimen IGPUW/Tf/1/539. **C**. Specimen IGPUW/Tf/1/538.

Short vertical resting burrows

Ichnogenus *Bergaueria* Prantl, 1945

Type ichnospecies: *B. perata* Prantl, 1945.

Bergaueria elliptica isp. n.

Figs 11A–B.

Holotype: Specimen No. IGPUW/Tf/1/607.

Type locality: Duża Wiśniówka quarry.

Type horizon: Late Cambrian part of the Wiśniówka Sandstone Formation.

Derivation of the name: After the elliptical shape of the specimen.

Diagnosis. — Large (more than 5 cm in diameter) oval loaf-like resting places with distinct longitudinal furrow.

Material. — One specimen.

Description. — The holotype and only specimen is oval in shape with a furrow along the axis. A delicate striation parallel to the furrow covers the surface; the ends of the structure are wrinkled. The border of the structure is clearly delimited, probably corresponding in its course to the irregularly waved surface of the bedding plane. Length is 65 mm, width 55 mm, depth 20 mm. The wrinkles may be results of deformation of the burrow preceding diagenesis of the sediment. Convex hyporelief.

Remarks. — The specimen is much larger than other *Bergaueria* type traces known from the Holy Cross Mountains. Its mode of preservation is probably similar to that discussed by Orłowski & Radwański (1986) for *Alpertia sanctacrucensis* Orłowski & Radwański, 1986 from the Early Devonian of the Holy Cross Mountains. It cannot be entirely excluded that the described specimen represents in fact a body fossil similar in origin to those typical for the Ediacaran faunas.

Occurrence. — Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka quarry.

Bergaueria perata Prantl, 1945

Fig. 11C–F.

Material. — Thirty-five slabs with many individuals.

Description. — Shallow cylindrical burrows with hemispherical lower end bearing a small central depression. Largest specimens may reach diameter of 55 mm, the smallest are just 2 mm wide; their depth ranges from 7 to 15 mm. The smaller forms are usually much deeper than the bigger forms. Their walls were stiff enough, probably owing to organic mucus. In some burrows, emptied by the host, mud accumulated before filling with sand. This indicates some wall stiffness. Numerous specimens of different diameter may be associated on the same slab. Convex hyporeliefs.

Remarks. — Similar specimens were discussed by Radwański & Roniewicz (1960, 1963) and Orłowski (1968a) from Duża Wiśniówka quarry and in the vicinity of Opatów; the ichnotaxon is also known from Early Cambrian strata of the area (Orłowski 1989).

Either a catastrophic sand sedimentation killed a population with various growth stages represented or particular specimens changed position producing successive burrows of larger and larger size that did not collapse owing to their stiff walls. The type species of the genus is Ordovician in age; similar structures, possibly attributable to actinian activity and named as *Alpertia sanctacrucensis*, occur also in the Early Devonian of the Holy Cross Mountains (Orłowski & Radwański 1986).

Occurrence. — Middle Cambrian Góry Pieprzowe Shale Formation at Kobyla Hill, Late Cambrian part of the Wiśniówka Sandstone Formation at Duża Wiśniówka quarry and Krzemionka Hill, Late Cambrian Klonówka Shale Formation at Duża Wiśniówka quarry and Lisie Jamy.

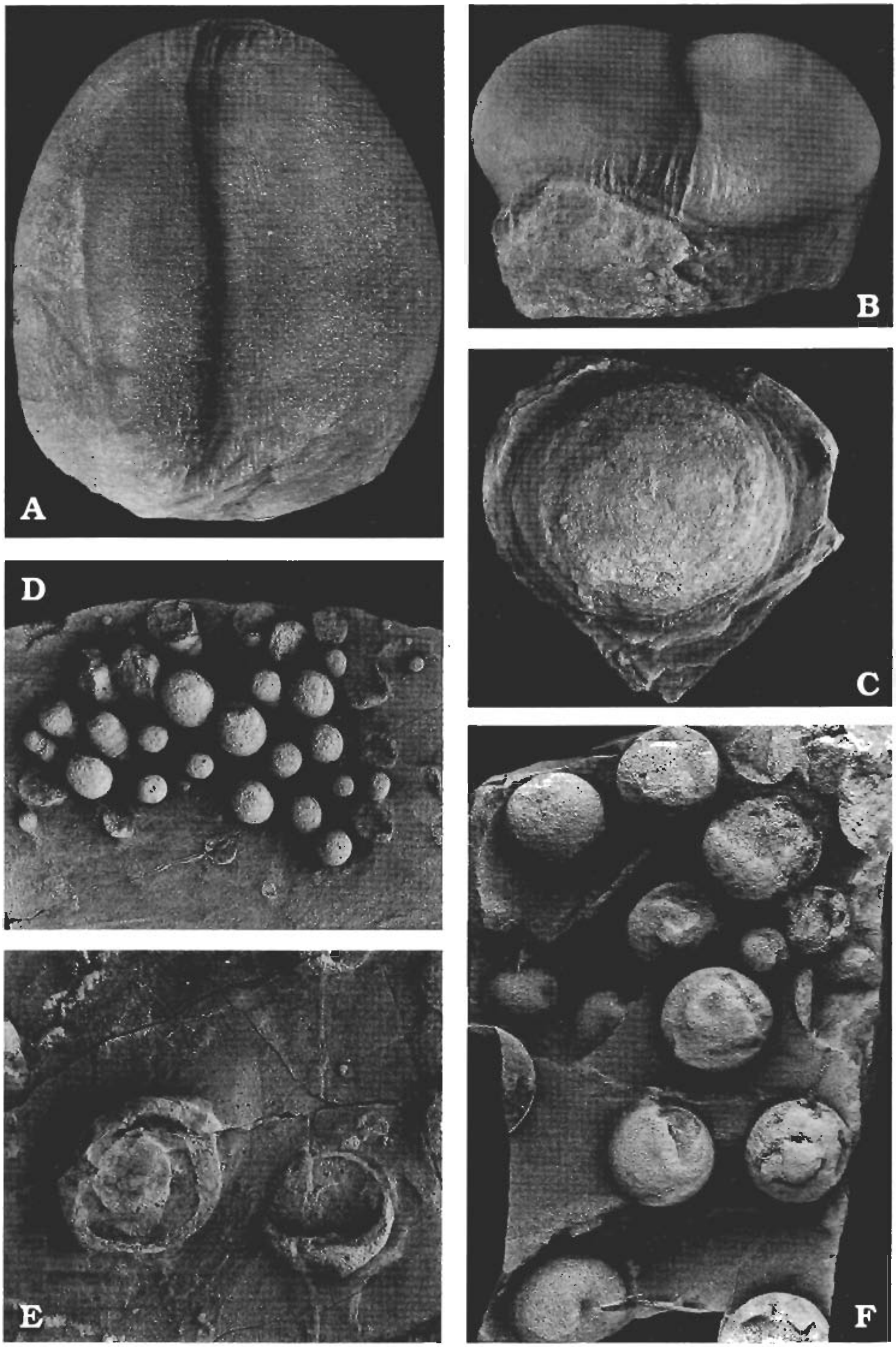
Diversity of trace fossils

The most striking feature of the Middle and Late Cambrian assemblages of trace fossils in the Holy Cross Mountains is the complete lack of traces left by deep infaunal feeders. Virtually all the traces preserved belonged to organisms burrowing parallel to and immediately below the sediment surface. Apparently there was a factor making deeper penetration impossible — most probably anoxic conditions within the sediment. This was not the case in the Early Cambrian, when numerous deep vertical burrows with spreite structures are known (Kowalski 1987; Orłowski 1989).

The Holy Cross Mountains trace fossil assemblages of Middle and Late Cambrian age show also a rather low taxonomic diversity, with only six ichnogenera of non-arthropod traces in the Middle Cambrian and eight ichnogenera in the Late Cambrian (summarised in this paper) when compared with 24 ichnogenera in the Early Cambrian of the area (Kowalski 1978, 1987; Orłowski 1989; Paczeŝna 1985). This confirms the general pattern, with high diversity of behaviours among Early Cambrian shallow water infaunal organisms (Crimes & Anderson 1985; Hofmann & Patel 1989) followed by a decrease in diversity at the beginning of the Middle Cambrian (Crimes 1992).

The Middle and Late Cambrian traces of the Holy Cross Mts represent simple unbranched (*Planolites* and *Arcuatichnus*) and branching burrows (*Paleophycus*, *Treptichnus*), resting traces (*Bergaueria*), radiating traces (*Asterichnus*, *Volkichnium*) and shallow spreite traces (*Diplocraterion*). Networks are represented by *Multina*. There is a lack of regular meandering

Fig. 11. **A–B**. *Bergaueria elliptica* isp. n., holotype IGPUW/Tf/1/607 from the Late Cambrian part of the Wiśniówka Sandstone Formation, Duża Wiśniówka quarry; basal and lateral views, × 1. **C–F**. *Bergaueria perata* Prantl, 1945. **C**. Group of small individuals IGPUW/Tf/1/578 from the Late Cambrian part of the Wiśniówka Sandstone Formation, Krzemionka hill; × 1. **D**. Specimen IGPUW/Tf/1/555 from the Late Cambrian Klonówka Shale Formation, Duża Wiśniówka quarry; × 1. **E**. Burrows partially filled with clay IGPUW/Tf/1/552 from the Late Cambrian part of the Wiśniówka Sandstone Formation, Duża



Wiśniówka quarry; × 1. **F**. Specimen IGPUW/Tf/1/553 from the Middle Cambrian Góry Pieprzowe Shale Formation, Kobyla Hill; × 1.

traces (*Helminthopsis* and *Cochlichnus* are present in the Early Cambrian), vertical traces (like *Monocraterion* and *Cylindrichnus* in the Early Cambrian) and vertical spreite traces (*Syringomorpha* in the Early Cambrian) (Orłowski 1989). Of the mentioned traces *Planolites* is most common and facies-independent, while *Treptichnus*, *Multina* and *Gordia* are less common and facies-specific.

The distinct decrease in trace fossil number in the Middle Cambrian formations of the Holy Cross Mountains may also result from environmental changes: the Góry Pieprzowe Shale Formation was deposited in deeper waters, below the littoral zone, with oxygen deficiency at the sea-bottom, while the underlying Słowiec Sandstone Formation was formed in high energy environments. Also, in the coeval Usarzów Sandstone Formation mainly facies-specific and therefore less common trace fossils are present.

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Nory ze środkowego i późnego kambru Gór Świętokrzyskich

STANISŁAW ORŁOWSKI i ANNA ŻYLIŃSKA

Streszczenie

Profil kambru Gór Świętokrzyskich składa się z naprzemianległych piaskowców i łupków tworzących formacje o znacznej miąższości. W skałach tych właściwym skamieniałościom towarzyszą ślady działalności życiowej

organizmów. Oprócz znanych i wcześniej notowanych śladów działalności organizmów zostały opisane dwa nowe ichnogatunki, tj. *Bergaueria elliptica* i *Treptichnus rectangularis*. Pierwsza z tych form, opisana na podstawie jednego okazu, jest wyjątkowo dużym śladem spoczynku, prawdopodobnie ukwiała. Istnieją przypuszczenia, że mógłyby to być jednak organizm zbliżony do przedstawicieli fauny ediakarańskiej. Nory *Treptichnus rectangularis* są efektem penetrowania osadu przydennego przez organizm zbliżony bądź do priapulidów bądź do echiuroidów, który pozostawił w otwartych norach grudki fekalne.

Większość znanych po-kambryjskich śladów działalności życiowej organizmów miała swój początek w płytkich wodach mórz kambryjskich, przy czym większość z nich pojawiła się już we wczesnym kambrze. Na omawianym obszarze w porównaniu z wczesnym kambrem (24 ichnorodzaje) liczba ichnorodzajów w środkowej i późnej epoce jest niższa i wynosi odpowiednio 6 i 8 ichnorodzajów, przy czym obserwuje się brak śladów głębokiej penetracji w obrębie osadu, jak też skomplikowanych sieci i meandrów. Dane z Gór Świętokrzyskich potwierdzają ogólną regułę o spadku zróżnicowania śladów działalności organizmów z początkiem środkowego kambru. Brak głębokiej penetracji osadu wynikać może ponadto z anoksycznych warunków panujących płytko pod jego powierzchnią.

Najbardziej pospolity ichnorodzaj *Planolites* występuje w całym profilu i jest w zasadzie niezależny od facji, chociaż jego frekwencja w profilu jest bardzo zróżnicowana. *Treptichnus*, *Multina* i *Gordia* są rzadsze i zależne od facji. Natomiast skrajne ubóstwo śladów organicznych w obrębie formacji łupków z Gór Pieprzowych potwierdza wcześniejsze ustalenia o osadzaniu się skał tej formacji w strefie głębszej niż litoralna a ponadto z deficytem tlenu w wodach przydennych.