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Ichnological record of the activity of Anthozoa in the early Cambrian succession of the Upper Silesian Block (southern Poland)

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ABSTRACT:

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A new occurrence of inferred Anthozoa trace fossils from the Lower Cambrian subsurface succession of the Upper Silesian Block is discussed with respect to their ichnotaxonomical variation and some aspects of the palaeoecology. The three ichnogenera *Bergaueria* Prantl, 1945, *Conichnus* Männil, 1966 and *Conostichus* Lesquereux, 1876 have been identified. A relatively diverse assemblage of actinian or cerianthid trace fossils allows recognition of habitats, feeding modes and life strategies of the tracemakers. An example of probable anthozoan-polychaete mutualism is suggested on the basis of the interrelationships of the trace fossils.

Key words: Anthozoa trace fossils; Ichnotaxonomy; Palaeoecology; Lower Cambrian; Upper Silesian Block; Southern Poland.

INTRODUCTION

Trace fossils of Anthozoa are first recorded in the Ediacaran (Fedonkin and Runnegar 1992; Crimes, 1994) but in many cases their ichnological origin remains problematic and they may consist instead of Ediacara-type soft-bodied fossils (Crimes and Fedonkin 1996) or inorganic structures. The first unquestioned ichnogenera that represent dwelling or resting burrows of sea anemone-like organisms occur in the Cambrian (e.g. Alpert 1973; Alpert and Moore 1975; Crimes *et al.* 1977; Crimes and Anderson 1985; Pemberton *et al.* 1988; Hofman *et al.* 1994; Orłowski and Żylińska 1996; Pacześna 1996; Jensen 1997; Seilacher-Drexler and Seilacher 1999). Seilacher-Drexler and Seilacher (1999) suggest sea pens as possible producers of *Bergaueria*-like trace fossils.

Seven ichnospecies of *Bergaueria* Prantl, 1945 and a few specimens of *Conostichus* Lesquereux, 1876 have previously been recognised in the Lower and Middle Cambrian of the Polish part of the East European Craton (Pacześna 1996). In the Lower, Middle and Upper Cambrian of the Holy Cross Mountains Orłowski and Żylińska (1996, 2002) have distinguished three ichnospecies of *Bergaueria.*

Presented in detail in this paper, for the first time at this locality, is an abundant and diverse assemblage of trace fossils that were produced probably by the Cambrian peri-Gondwanan ancestors of recent soft-bodied sea anemones or biologically related organisms (Pacześna 2008).

GEOLOGICAL SETTING

The trace fossils were collected from a subsurface clastic succession in the Goczałkowice IG 1 borehole in the southwestern part of the Upper Silesian Block.

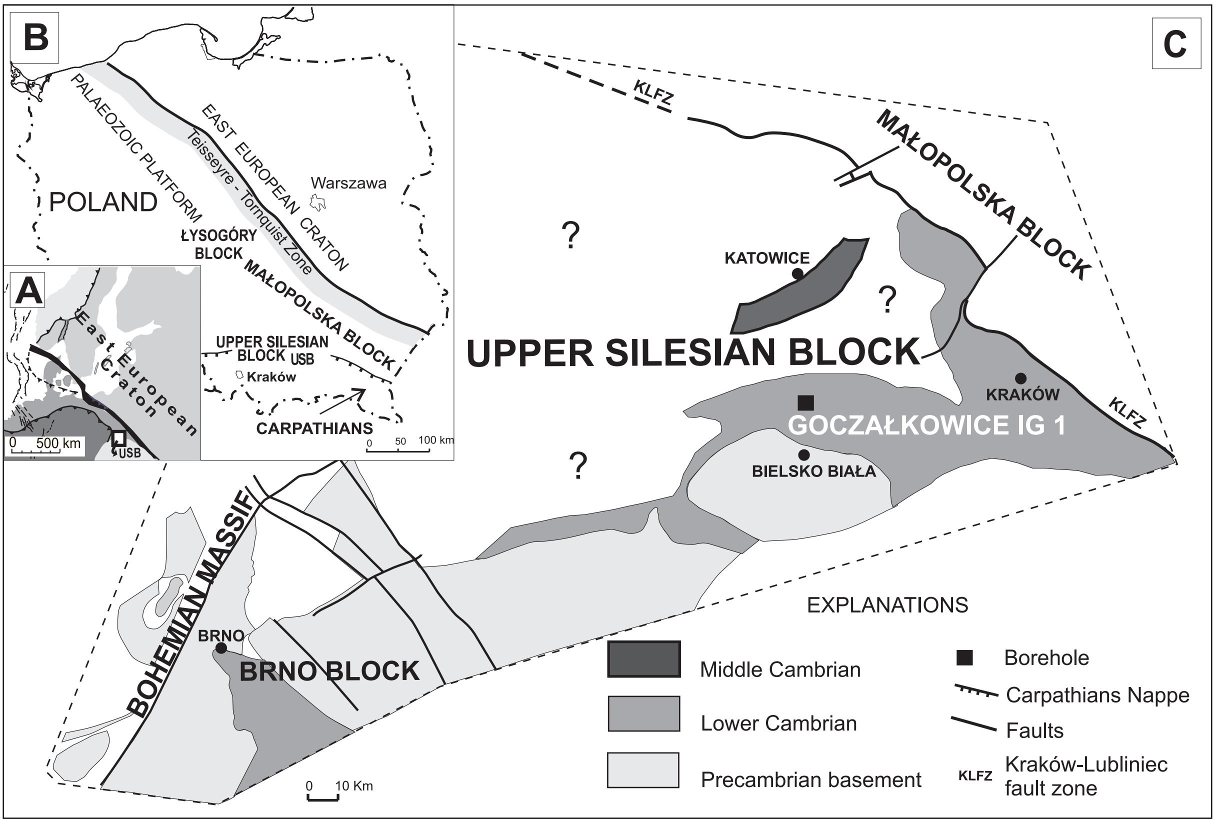
The studied trace fossils comprise a few unusual gregarious accumulations in an interval in the middle part of the Lower Cambrian succession.

The Upper Silesian Block is situated in southern Poland within the central segment of the Trans European Suture Zone, near the southwestern margin of the East European Craton, between the Małopolska Block and the Bohemian Massif (Text-fig. 1). During the early Palaeozoic, together with the Brno Block, it was a part of a larger unit called the Brunovistulicum (Buła and Żaba 2008) or as the Brunovistulian terrane (Nawrocki *et al.* 2004).

Several geotectonic hypotheses interpret the Upper Silesian Block as an allochthonous suspect terrane derived as a fragment of the crust from the peri-Gondwana belt and accreted together with Małopolska Block and Bohemian Massif to the palaeocontinent of Baltica (East European Craton) during the Middle or Late Cambrian (e.g. Leichman and Höck 2001; Nawrocki and Poprawa 2006).

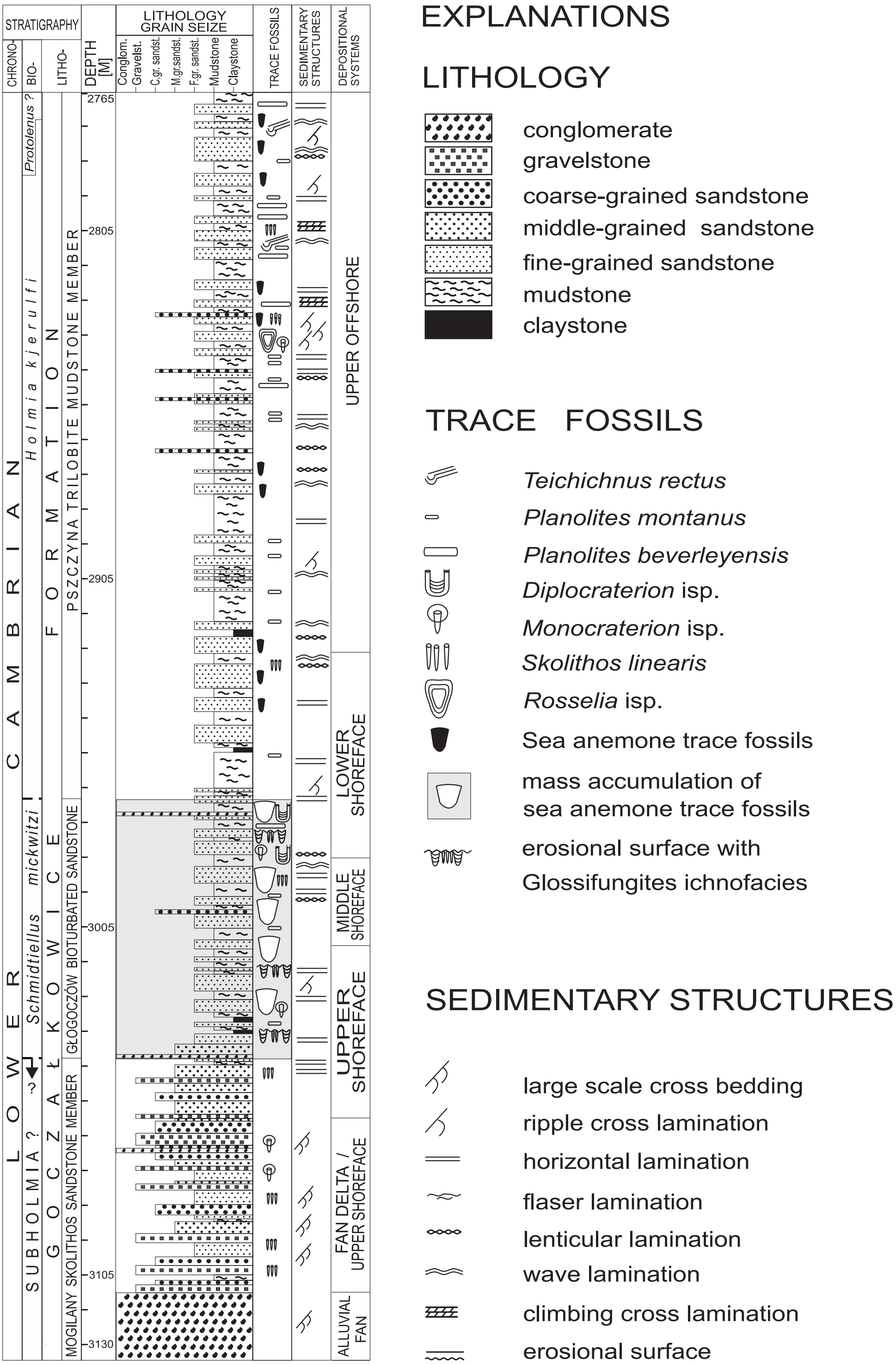
The chronostratigraphy of the Lower and Middle Cambrian clastic sediments is based on distinct acritarch assemblages (Buła and Jachowicz 1996, Jachowicz and Přichystal 1998, Moczydłowska 1998) and a sparse trilobite fauna (Orłowski 1975). The Lower Cambrian succession in the region of the studied Goczałkowice IG 1 borehole is referred to as the Goczałkowice Formation, whose base consists of gravel and polymictic conglomerate with hematitic cement and coarse-grained quartzo-feldspathic sandstone and whose upper part consists of mudstone alternating with fine-grained sandstone (Buła *et al.* 1997a, b; Buła 2000). The lowermost part of the succession was evidently deposited as alluvial fans and fan deltas, but the uppermost part in a shoreface and offshore zone with little tidal influence (Pacześna 2005, 2008).

The trace fossils occur in the core samples recovered from the middle Goczałkowice Formation, referred to the Głogoczów Bioturbated Sandstone Member (Buła 2000) (Text-fig. 2). This part of the Lower Cambrian succession is characterized by a rich and diverse trace fossil assemblage. Any original structure in most alternating thin beds of light-green fine-grained quartz sandstone and greenish-grey siltstone has been completely destroyed as a result of burrowing.



Text-fig. 1. Location maps of the Upper Silesian Block and investigated borehole section. A – Location of the Upper Silesian Block (USB) on the background of simplified tectonic map of central and northeastern Europe; B – Sketch-map indicating the largest tectonic units of Poland with location of the Upper Silesian Block; C – Schematic geological map showing distribution of the Cambrian deposits and location of Goczałkowice IG 1 borehole (generalized from Buła and Żaba 2005)

Accompanying trace fossils are *Monocraterion* isp., *Skolithos linearis* Haldeman, 1840, *Skolithos* isp., *Diplocraterion parallelum* Torell, 1870 *Diplocraterion* isp., very rare *Planolites beverleyensis* (Billings 1862) and *Planolites montanus* Richter, 1937.



Text-fig. 2. Stratigraphic section of the Lower Cambrian in the Goczałkowice IG 1 borehole with occurrence of the investigated trace fossil intervals (shaded). Chrono- and lithostratigraphy according to Buła and Jachowicz (1996) and Buła (2000), biostratigraphy after Buła and Jachowicz (1996) and Moczydłowska (1998). Depositional systems according to Pacześna (2005)

DESCRIPTIONS OF TRACE FOSSILS

Ichnogenus *Bergaueria* Prantl, 1945

TYPE ICHNOSPECIES: *Bergaueria perata* Prantl, 1945

Bergaueria major Palij, 1976
(Text-figs 3Aa, 4Cb)

1976. *Bergaueria major* n. sp.; V.M. Palij, pl. 28, figs 1–6.
1983. *Bergaueria major* Palij: V.M. Palij, E. Posti and M.A. Fedonkin, pl. 55, figs 2–6.
1996. *Bergaueria major* Palij: J. Pacześna, pl. 2, figs 5–7; pl. 3, figs 1–6.

MATERIAL: Three specimens separated from host rock and numerous specimens occurring in concentrations in core samples.

DESCRIPTION: Sandstone-filled traces consisting of a regular, elongated, cylindrical shaft. Surface of a shaft smooth, lacking a central depression, knobs or other sculptural elements. The basal part is hemispherical or smoothly conical with a rounded apex. The shaft height is generally significantly greater than the diameter, ranging from 32 to 56 mm. Its diameter ranges from 8 to 16 mm. The trace fossils are oriented vertically and infrequently a little obliquely, occurring as endichnial or exichnial full reliefs.

REMARKS: The elongated, cylindrical, smooth shaft or hemispherical and slightly conical shape of the basal part relates the described specimens to the typical *Bergaueria major* from the Lower Cambrian of Podolia, Ukraine (Palij 1976) and to trace fossils from the Lower and Middle Cambrian of the Polish part of the East European Craton (Pacześna 1996). Pemberton *et al.* (1988) cautiously included *Bergaueria major* Palij, 1976 in *Bergaueria perata* Prantl, 1945. This interpretation is rejected here because the shaft morphology of the two ichnospecies is different. The features that distinguish *Bergaueria perata* from *Bergaueria major* are the central basal depression and the less elongate shaft of trace fossils relative to diameter. These morphological differences indicate that *Bergaueria major* can be treated as a separate ichnospecies.

Ichnogenus *Conichnus* Männil, 1966

TYPE ICHNOSPECIES: *Conichnus conicus* Männil, 1966

Conichnus cf. *conicus* Männil, 1966
(Text-fig. 3 Ab, Af)

MATERIAL: Three specimens separated from host rocks.

DESCRIPTION: Regular, conical, sandstone-filled trace fossils with unornamented shafts, somewhat elliptical in a transverse section. The shaft height ranges between 15 and 31 mm, and its diameter is 16–26 mm. Basal part smooth, with no apical protuberance. The trace fossils are preserved in full relief as endichnia.

REMARKS: The consistently conical shape and lack of an apical knob distinguish the studied specimens from *Conichnus papillatus* (Männil 1966, pl. 1, figs 1–3, pl. 2, figs 2, 3, 5; Häntzschel 1975, fig. 24.3). A somewhat oval, transverse section of the shaft links described trace fossils to similar trace fossils from the Upper Cretaceous of Utah, USA (Frey and Howard 1981; Howard and Frey 1984).

Conichnus aff. *papillatus* (Männil, 1966)
(Text-figs 3Ae, C, 4Aa, Ba, Ca)

MATERIAL: Five specimens separated from host rocks in various state of preservation, and numerous specimens at specific horizons.

DESCRIPTION: Trace fossils having a barrel, amphora to double cone- in form with a sandstone-filled, vertical, unornamented and thinly lined shaft. The shafts are 16 to 76 mm in height, their diameter ranging from 10 to 30 mm. The lining constitutes a distinct 0.5 to 1 mm thick wall between burrow fill and host sediment. The lining thickness is consistent everywhere. The inner surface of lining is dark. The basal part may be slightly rounded or conical, rarely flattened. The trace fossils are preserved in full relief as endichnia.

REMARKS: Mänill (1966, fig. 2) originally designated simple, conical burrows as the ichnogenera *Conichnus* and *Amphorichnus* on the basis of slightly different shapes of shafts. Frey and Howard (1981) revised these ichnogenera and concluded that such small morphological differences are more significant at the ichnospecies than ichnogenus level and consequently considered the two as synonymous. As the first revisers, they accorded priority to *Conichnus* by virtue of pagination: *Conichnus* is therefore a valid ichnogenus.

The basic morphological feature identifying with some doubt the described specimens as *Conichnus* aff.

papillatus is the barrel to amphora-like shape, which is typical for this ichnospecies (Männil 1966; Pemberton *et al.* 1988). The lack of an apical bump sharply distinguishes the Upper Silesian trace fossils from the type specimens from the Middle and Upper Ordovician of Estonia (Männil 1966). However, the poor state of preservation of most specimens makes exact designation of the studied trace fossils impossible.

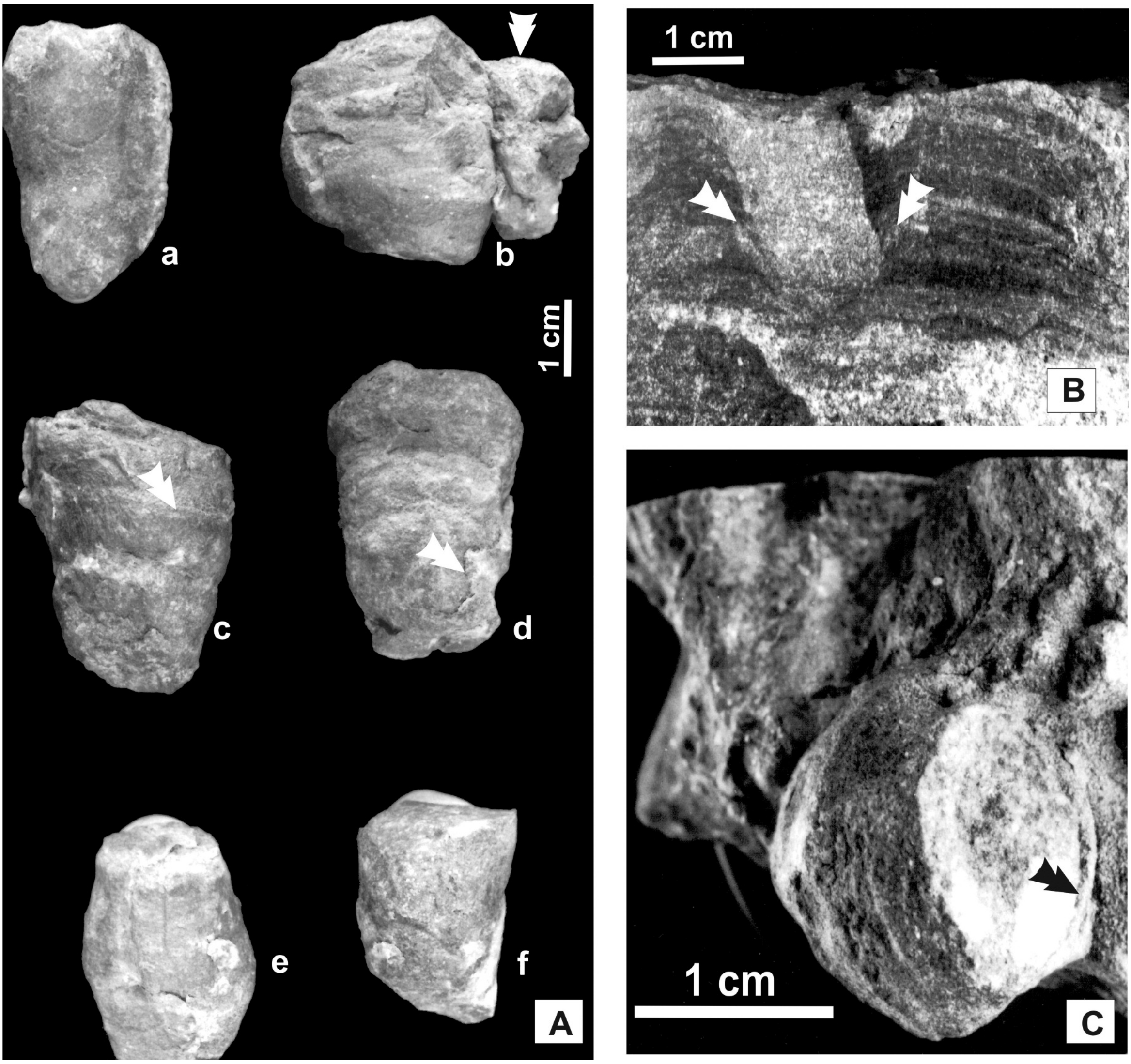
Ichnogenus *Conostichus* Lesquereux, 1876

TYPE ICHNOSPECIES: *Conostichus ornatus* Lesquereux, 1876

Conostichus isp.
(Figs 3Ac, d)

MATERIAL: Two poorly preserved specimens.

DESCRIPTION: Conical, vertical, sandstone-filled trace fossils with transverse constrictions and furrows



Text-fig. 3. Trace fossil specimens separated from host rocks of the Lower Cambrian, Głogoczów Bioturbated Sandstone Member, Goczałkowice Formation, Goczałkowice IG 1 borehole. Aa – *Bergaueria major* Palij, specimen (MUZ. PIG 1730.II 1), depth 2981.3 m; Ab – *Conichnus* cf. *conicus* Männil, burrows of adult and young (arrowed) individuals, specimen (MUZ. PIG 1730.II.2), depth 2981.8 m; Ac – *Conostichus* isp., note subtle ribs at the surface of the shaft (arrowed) – specimen (MUZ. PIG 1730.II.3), depth 2983.6 m; Ad – *Conostichus* isp., note a thinly lined burrow (arrowed) – specimen (MUZ. PIG 1730.II.4), depth 2984.1 m; Ae – *Conichnus* aff. *papillatus* Männil, an amphora-like form, specimen (MUZ. PIG 1730. II.5), depth 2981.9 m; Af – *Conichnus* cf. *conicus* Männil, specimen (MUZ. PIG 1730.II.6) depth 2983.9 m; B – indeterminable sack-like structure, visible in a cross sectional view on the core samples surface, note downward bending of the bedding planes, indicates upward movement of tracemaker, specimen (MUZ. PIG 1730.II.7), depth 2980.1 m; C – *Conichnus* aff. *papillatus* Männil, barrel form, note a thin wall lining (arrowed), specimen (MUZ. PIG 1730.II.8), depth 2978.5 m of indistinctly expressed width on the surface of the shaft. The shaft is distinctly lined. The very thin, dark lining constitutes discontinuity between burrow fillings and the surrounding rock. Height of the shaft ranges between 35 and 40 mm, diameter reaching 26–28 mm. A flattened disc is very weakly developed at the base. The structures are oriented vertically and occur as hypichnial semi-relief.

REMARKS: The generally conical shape and characteristic, although poorly developed, transverse ribbons on the shaft surface allow cautious inclusion of the studied specimens in the ichnogenus *Conostichus* Lesquereux, 1876. The distinct, thin lining (Text-fig. 3Ad) indicates that this is probably the dwelling burrow of a cerianthid anemone (Frey, 1970; Pemberton *et al.* 1988). The presence of transverse ribbons and lack of longitudinal furrows are similar to those of *Conostichus typicus* (King in Harrington and Moore, 1955), illustrated by Pemberton *et al.* (1988). Lack of the evident morphological features does not allow clear distinction of these forms to the ichnospecies level.

Sack-like structure, indeterminable
(Text-fig. 3B)

MATERIAL: 1 poorly preserved specimen.

DESCRIPTION: Slightly obliquely oriented, sandstone-filled trace fossil with a sack-shaped, smooth, subvertical shaft. The shaft widens into a rounded expansion in the basal part.

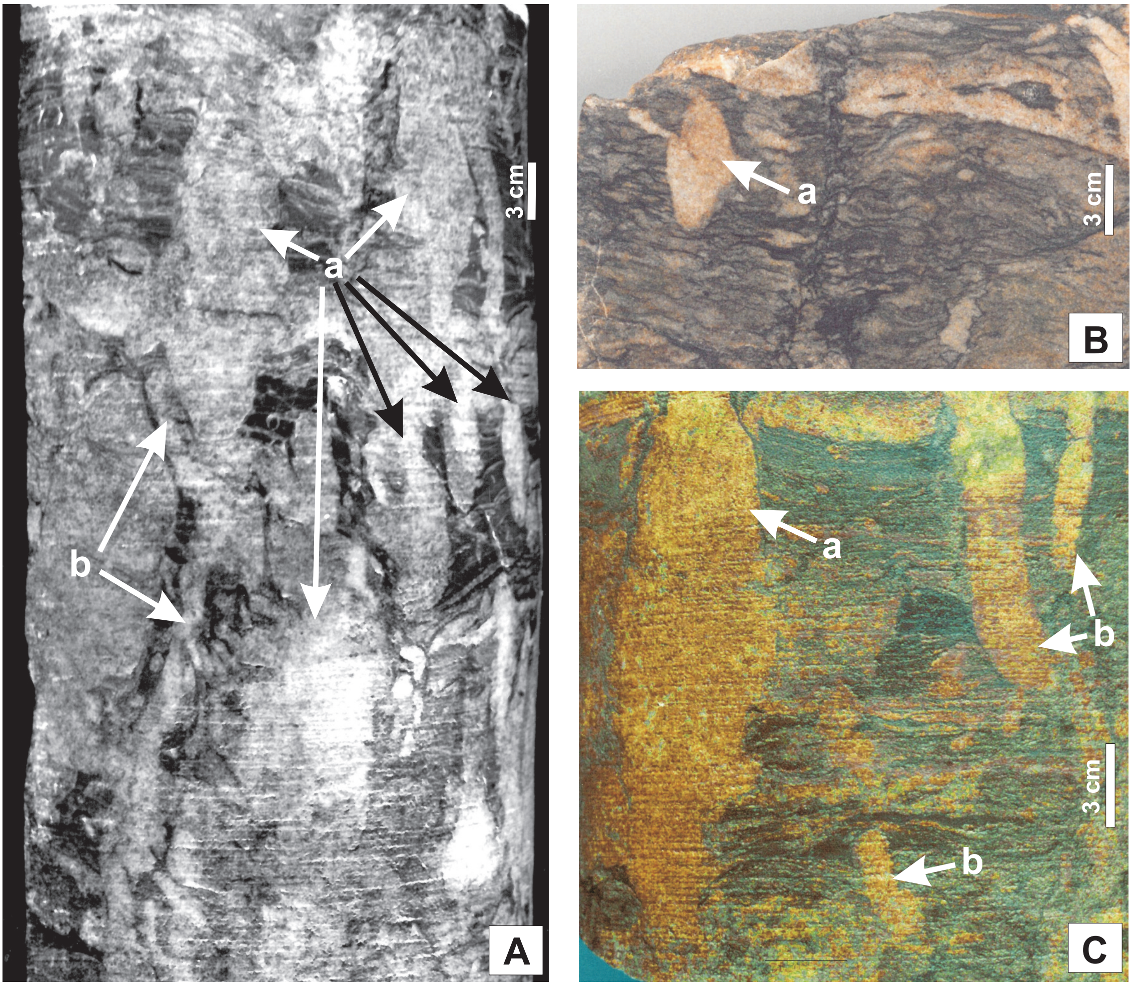
The upper part of the shaft is to some extent destroyed. Maximum observed shaft height reaching 24 mm with a diameter of 21 mm. Near the walls of the structure, sediment layers distinctly bent toward the pit.

REMARKS: The studied specimen somewhat resemble structures described by Hakes (1976) particularly those presented in a cross sectional view presented in his Pl. 8, fig. 1b), but does not exhibit the distinct double ball-shaped structures connected to each other by a vertical or oblique cylindrical shaft. The flexure of sediment layers near the burrow walls suggests upward movement of the producer within the sediment in order to keep up with a rapid increase in sedimentation.

PALAEOECOLOGY OF TRACEMAKERS

Living burrowing sea anemones representing class Anthozoa, subclass Hexacorallia and order Actiniaria or Ceriantharia are solitary, mobile or semi-mobile polyps whose columnar body has radial symmetry. Actinian soft-bodied anemones have a pedal disc that attaches firmly to solid objects like rocks and corals or else anchors the polyp to the sea floor (Bruska and Bruska 1990). Some excavate vertical, unlined burrows. Actinian *Paranthus rapiformis* (Lesueur) in the Beaufort area, North Carolina, USA, digs shallow, unagglutinated burrows. In contrast, cerianthid anemones construct mucous-impregnated tubes. An example of a tube-dwelling sea anemone in this area is *Ceriantheopsis americanus* (Verrill), building Y-shaped, cnidaceous tubes that line their long, vertical burrows (Frey 1970). Very rare occurrences of the early Palaeozoic sea anemone body fossils indicate many morphological similarities with modern sea anemones. The most celebrated fossil example of columnar soft-bodied fossils is the uniquely preserved life assemblage of anemones from the Lower Cambrian Chengjiang biota from the Kunming–Chengjiang area of Yunnan, China (Hou *et al.* 2005). In the many cases where the morphology of the trace fossils has been related to the activity of sea anemones, it has been particularly the columnar shape of the burrows, ornamentation or lining of the shaft walls and the shape or sculpture of the base that confirm their actinian or cerianthid origin.

The presence of the three morphologically differentiated ichnogenera described herein may indicate a taxonomically and ethologically diverse assemblage of anemones in the Lower Cambrian of Upper Silesian Block. A characteristic feature is the relatively high ichnospecies variability and frequency of the ichnogenus *Conichnus,* which is represented by two ichnospecies, and a very high frequency of the amphora-like and similar forms assigned to *Conichnus* aff. *papillatus.* Another fact is the very low ichnospecies differentiation within the ichnogenus *Bergaueria* and the presence of only one ichnospecies *Bergaueria major*. In contrast to the Upper Silesian *Bergaueria* trace fossils, their ichnological counterparts from the Lower and Middle Cambrian successions of the East European Craton show high ichnotaxonomical variability and seven ichnospecies have been described there (Pacześna 1996). With a high degree of probability it can be said that this ichnotaxonomical difference was the result of ethological causes. Most of the *Bergaueria* specimens from the East European Craton are unlined burrows. This fact points clearly to the ethological character of these structures and thereby the most of them represent resting trace fossils of actinian anemones (e.g. Frey, 1970; Hakes 1976; Pemberton *et al.* 1988). The presence of lined and unlined shafts among the studied structures may indicates an etho-

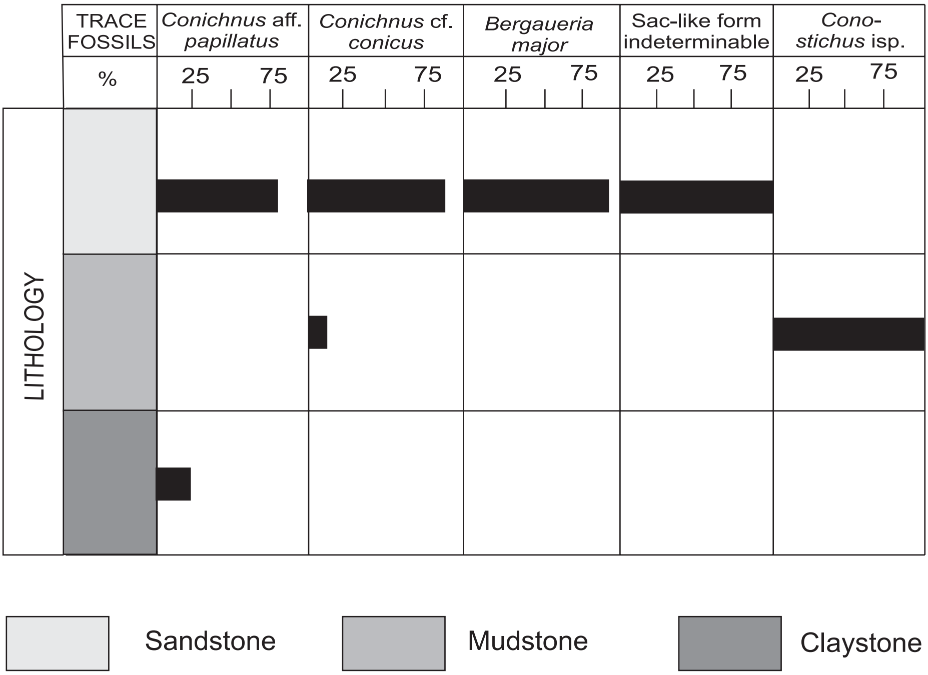


Text-fig. 4. Some trace fossils from Lower Cambrian, Głogoczów Bioturbated Sandstone Member, Goczałkowice Formation, Goczałkowice IG 1 borehole. Aa – *Conichnus* aff. *papillatus* Männil, a double cone form in a gregarious occurrence of trace fossils, Ab – *Diplocraterion* isp., specimen (MUZ. PIG 1730.II.9), depth 2976.0 m; Ba – *Conichnus* aff. *papillatus* Männil, a solitary double cone form, specimen (MUZ. PIG 1730.II.10), depth 2990.6 m; Ca – *Conichnuss* aff. *papillatus* Männil, a double cone form, Cb – *Bergaueria major* Palij in a gregarious occurrence of trace fossils, specimen (MUZ. PIG 1730.II.11), depth 3009.9 m. A-C Lower Cambrian, Głogoczów Bioturbated Sandstone Member, Goczałkowice Formation, Goczałkowice IG 1 borehole

logically mixed ichnoassemblage and an occurrence of dwelling and resting trace fossils of cerianthid and actinian sea anemones.

Numerous living species of anemones burrow into sediment and produce permanent burrows over a long period of time if the environment is suitable; or they can crawl by lifting a small area of the sole and move over a short distance when conditions are unfavourable. The majority of modern sea anemones prefer a sandy bottom for settlement (Schäfer 1962; Pickens 1988). Some can dwell in muddy or gravelly bottoms. Each species has a fairly specific preference. Similarly, the studied tracemakers had fairly narrow grain size preferences and the majority lived in sandy substrates (Text-fig. 5).

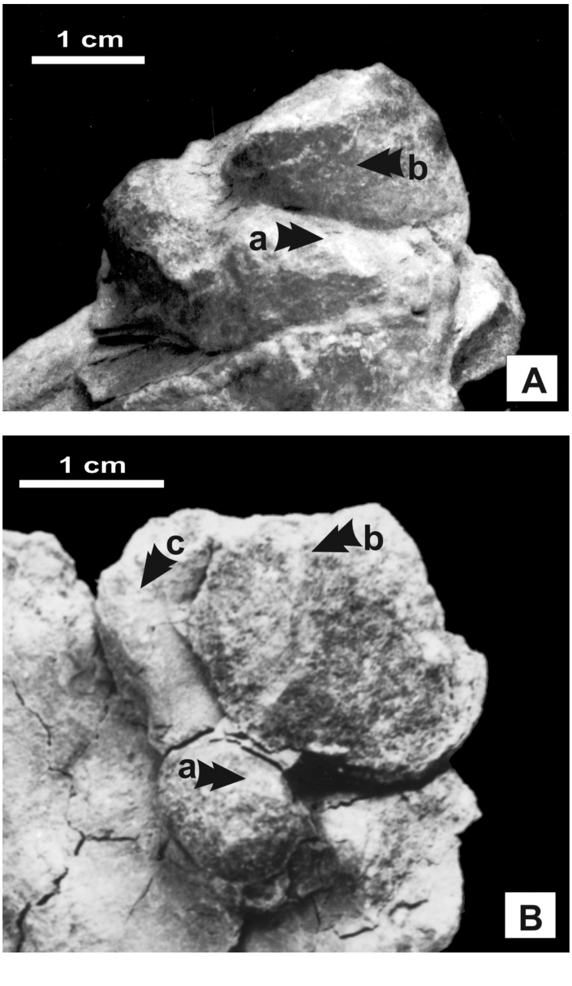
Modern anemones fit into several trophic categories. The majority are carnivorous predators and micropredators that use their tentacles to catch selected food selectively. A victim is paralysed by the tentacles, dragged into the digestive cavity and digested. Some anemones are simultaneously carnivores on small organisms and filter-feeders on very small zoo- and phytoplankton suspended in the sea water (Schäfer 1962; Levinton 1972; Shimek 2004). There is broad agreement among ecologists that the type of sediment controls the feeding mode of recent benthic sea organisms. The apparent dependence may be correlated with the ancient producers of trace fossils (e.g. Craig and Jones 1966; Elders 1975; Begon *et al.* 1996; Pacześna 1996) and has been observed in the analysed



Text-fig. 5. Dependence of ichnotaxa on sediment type

material. Most of the Upper Silesian tracemakers lived in thinly lined dwelling burrows. This mode of habitat is usually characteristic of filter-feeding organisms that commonly prefer sandy bottoms occurring in environments having turbid water rich in suspended food.

The assemblage of studied sea anemone trace fossils and accompanying ichnotaxa is characterised by a high density of trace fossils (Text-fig. 4A) and a very low ichnotaxonomical and ethological diversity. The features mentioned above distinctly indicate an opportunistic life strategy of the tracemakers. The gregarious occurrence of anemone may represent mass reproduction, which is a characteristic biological phenomenon for *r*-ichnostrategists (e.g. Ekdale 1985; Uchman 1992; Bromley 1996; Pacześna 1996). Modern adult sea anemones are solitary polyps that form mass accumulations during asexual reproduction in process of cloning themselves longitudinal or binary fission of the pedal disc. Therefore fossil accumula-



Text-fig. 6. Probable examples of mutualism; all from Lower Cambrian, Głogoczów Bioturbated Sandstone Member, Goczałkowice Formation, Goczałkowice IG 1 borehole. Aa – burrow of a deposit-feeding worm-like organism, Ab – plug-shaped burrow of a sea anemone-like organism, specimen (MUZ. PIG 1730.II.12), depth 2985.6 m; Ba – burrow of a deposit-feeding worm-like organism, Bb – fragment of a plug-shaped burrow of adult sea anemone-like organism, Bc – small burrow of a juvenile sea anemone (clone?), specimen (MUZ. PIG 1730.II.13), depth 2980.2 m tions of their dwelling trace fossils probably represent burrows of asexually reproduced clones.

Some of the recent sea anemone species live together with other sea organisms for their mutual benefit and are examples of symbiosis. A famous modern example of mutualism is the relationship of hermit crabs or clownfish with sea anemone polyps (e.g. Begon *et al.* 1996). Sea anemones may also be associated with polychaetes (e.g. Fuchs 1894). A possible example of fossil evidence of this ecological phenomenon may be recorded in the studied trace fossil suite. In a few specimens collected at different core depths a discernible longitudinal burrow coiled around the cylindrical shaft of a plug-shaped trace fossil has been found. The most likely interpretation of this co-occurrence is mutualism. Evidently, a worm-like deposit-feeder (*Planolites*-like structure; Text-figs 6Aa, 6Ba) stabilised and was protected by a sea anemone dwelling burrow (*Bergaueria*-like structure; Text-figs 6Ab, 6Bb) and gained organic leftovers from the sea anemone's meals.

CONCLUSIONS

The Lower Cambrian subsurface succession of the Upper Silesian Block yields an abundant and diverse suite of trace fossils that are interpreted to be the work of sea anemones-like organisms.

The three ichnogenera *Bergaueria*, *Conichnus* and *Conostichus* together with an indeterminable sack-like structure, have been recognised for the first time in these strata. The generally poor state of preservation of the studied material does not allow exact identification of most specimens but a few diagnostic traits make it possible to distinguish the following ichnospecies: *Bergaueria major, Conichnus* cf. *conicus* and *Conichnus* aff. *papillatus*.

The relatively high ichnotaxonomic diversity of the studied sea anemone dwelling and resting burrows allows some inferences about the mode of life of the soft-bodied tracemakers. The majority of them represent sandy bottom dwelling, filter-feeding opportunists. A probable example of symbiosis between worm-like organisms and sea anemone polyps is suggested.

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