

TAXONOMY AND ETHOLOGY OF FLYSCH TRACE FOSSILS: REVISION OF THE MARIAN KSIĄŻKIEWICZ COLLECTION AND STUDIES OF COMPLEMENTARY MATERIAL

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Abstract: Ichnotaxonomy of 1,840 of flysch trace fossil specimens from the Książkiewicz collection is revised. The specimens derive from diverse Tithonian–Miocene flysch deposits of the Polish Carpathians. Their ichnotaxonomy, based on morphology, was published by Książkiewicz in 1997. In the revision presented in this publication, the ichnotaxonomic subdivisions are based on type of behaviour represented by the considered trace fossil. As a result, several diagnoses are changed and several ichnospecies ascribed to other ichnogenera. Ichnogenera *Hormosiroidea*, *Saerichnites*, *?Parahaentzschelinia*, *Halopoa*, *Nereites*, *Beaconites*, *Cladichnus*, *Protovirgularia*, *Ubinia* and *Oscillorhapse* are used the first time in the Polish Carpathians. The ichnogenera *Pararusophycus*, *Rhabdoglyphus*, *Fucusopsis*, *Traucumichnis*, *Sabularia*, *Granularia*, *Bostricophyton*, *Halymenidium*, *Buthotrephis*, *Tubulichnium*, *Tuberculichnus*, *Helminthoida*, *Muensteria*, *Keckia*, and *Taphrhelminthoida* are not recommended for further use. The new ichnogenus *Belocosmorhapse* n. igen. and the new ichnospecies name *Cosmorhapse carpathica* nom. nov. are proposed. Ichnotaxa *Trichichnus linearis* Frey, *Imponoglyphus torquendus* Vialov, *Palaeophycus tubularis* Hall, *Chondrites ?recurvus* (Brongniart) and *Arenituba* isp. are distinguished for the first time in the Carpathian flysch on the base of Książkiewicz material.

Abstrakt: 1840 okazów fliszowych skamieniałości śladowych z kolekcji Książkiewicza poddano ichnotaksonomicznej rewizji. Okazy te pochodzą z różnych tytońsko-miocenickich utworów fliszowych Karpat polskich. Ichnotaksonomia, oparta na morfologii, była przedstawiona przez Książkiewicza w 1997 roku. W rewizji przedstawionej w niniejszej publikacji, wydzielenia ichnotaksonomiczne oparto na typie behawioru reprezentowanego przez daną skamieniałość śladową. W rezultacie, zmieniono szereg diagnoz. Wiele ichnotaksonów zaliczono do innych niż dotąd ichnorodzajów. Ichnorodzaje *Hormosiroidea*, *Saerichnites*, *?Parahaentzschelinia*, *Halopoa*, *Nereites*, *Beaconites*, *Cladichnus*, *Protovirgularia*, *Ubinia* i *Oscillorhapse* użyto po raz pierwszy w Karpatach polskich. Ichnorodzaje *Pararusophycus*, *Rhabdoglyphus*, *Fucusopsis*, *Traucumichnis*, *Sabularia*, *Granularia*, *Bostricophyton*, *Halymenidium*, *Buthotrephis*, *Tubulichnium*, *Tuberculichnus*, *Helminthoida*, *Muensteria*, *Keckia* i *Taphrhelminthoida* nie są rekomendowane do dalszego używania. Zaproponowano nowy ichnorodzaj *Belocosmorhapse* n. igen. i nową nazwę ichnotaksonomiczną *Cosmorhapse carpathica* nom. nov. Ichnotaksony *Trichichnus linearis* Frey, *Imponoglyphus torquendus* Vialov, *Palaeophycus tubularis* Hall, *Chondrites ?recurvus* (Brongniart), *Arenituba* isp. są wyróżnione po raz pierwszy we fliszu karpaccim, w oparciu o materiał z kolekcji Książkiewicza.

Key words: Ichnotaxonomy, trace fossils, flysch, Cretaceous, Paleogene, Carpathians.

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AIM, MATERIAL, AND METHODS

Imprecisely defined ichnotaxa are still the weak point of ichnology. This problem still negatively influences various applications of trace fossils and is a hinderance in their study. The problem may be ameliorated by ichnotaxonomic revisions using the application of clearly defined principles. Such revision of the Książkiewicz collection is the main aim of this paper.

The Książkiewicz collection, housed in the Institute of Geological Sciences of the Jagiellonian University, Kraków (acronym UJ TF), is one of the largest flysch trace fossil collections in the world. It contains 1,840 specimens including 57 ichnogenera and 147 ichnospecies described by Książkiewicz (1958, 1960, 1961, 1968, 1970, 1977) from almost 220 localities in the Polish Carpathians, from the Tithonian–Miocene flysch formations. Almost all the specimens were labelled. Each full label includes number of specimen, name of locality and lithostratigraphic unit, and ichnotaxonomic determination. A number of the labels appeared to be not readable, having been damaged because of improper housing. For this reason, a lot of important information from labels was lost. As a result of the inventory work connected

with the present revision, the first catalogue of the specimens of the collection was prepared, which comprises the information from the labels and place of housing. The collection contains a few ichnotaxa, which were neither described nor labelled, for instance *Trichichnus* and *Imponoglyphus*, which are included in this study. About a dozen specimens are lost.

In order to resolve certain ichnotaxonomic problems, complementary material was studied. This derives from the author's collection, the collections in the Naturhistorisches Hofmuseum in Vienna, the Sternberg collection in the National Museum in Prague, the Heer collection in the Geological Institute of the ETH, Zürich, and the Fischer-Ooster collection in the Natural History Museum in Bern.

Some specimens from the Książkiewicz collection underwent additional preparation, and/or were cut and studied in polished slabs after treatment with the "Bushinsky oil technique" (Bromley, 1981).

CLASSIFICATION AND PRINCIPLES OF ICHNOTAXONOMY

An extensive discussion of nomenclature/classification problems is beyond the scope of this paper (for reviews see Vialov, 1968b, Häntzschel, 1975; Ekdale *et al.*, 1984a; Pickerill, 1994, with references therein).

The first problem is the definition of trace fossils. I follow the idea that trace fossils are the sedimentary expressions of fossil behaviour (Seilacher, 1986). Thus, the most important questions of ichnotaxonomy are what behaviour is represented by an examined trace fossil and how to clearly define it, not only the exact description of the appearance of the examined trace fossil. Morphology of trace fossils can be strongly dependant on taphonomic processes. Especially, trace fossils preserved as semi-reliefs are incomplete bedding-plane expressions of commonly much more complicated three-dimensional burrows. The numerous difficulties encountered in reconstruction of complete trace fossils and in understanding of the behaviour they represent cannot be arguments that influence principles of ichnotaxonomy.

The other problem is the rank of ichnotaxonomic divisions, especially the hierarchy of features used for diagnoses of ichnogenera and ichnospecies. I tried to follow the idea of Fürsich (1974a), according to which important morphological features (so-called significant features) diagnostic of ichnogenera are these related to distinct behaviour are diagnostic of ichnogenera. Other features related to minor variation of tracemaker behaviour and to some preservational features are regarded as diagnostic of ichnospecies (so-called accessory features). Other features of third-order rank, reflecting mainly preservational aspects, may be used informally at the subichnospecies level as variations (Uchman, 1995). Division of this level is not forbidden by the 1985 International Code of Zoological Nomenclature (Rindsberg, 1990). Examples of their use are given by Ekdale & Lewis (1991b) for *Diplocraterion*. The main principle in the presented ichnotaxonomy is the application of ichnogenetic names only for trace fossils representing distinctly different fossil behaviour. Only ichnogenera diagnosed in this way may be used for further palaeoecological interpretations and compared with other ichnocommunities. Application of accessory or lower-rank features at the ichnogenetic level would give a false picture of behavioural diversity.

In order to recognize the fossil behaviour represented by some trace fossils, their careful ethological interpretation is necessary. Such interpretation was applied for instance to passively filled *Palaeophycus* versus actively filled *Planolites* (Pemberton & Frey, 1982). Purely morphological classification, without references to any ethological model and without taphonomic interpretation, seems to be one of the dead-ends of ichnotaxonomy.

Another problem of ichnotaxonomy is classification of trace fossils above the ichnogenetic rank (cf. Bromley, 1996). Książkiewicz (1977) introduced classification of flysch trace fossils based solely on morphological criteria. He distinguished ten morphological groups, namely: (1) circular and elliptical, (2) simple, (3) branched, (4) rosetted, (5) spreite, (6) winding, (7) spiral, (8), meandering, (9)

branched winding and meandering, and (10) nets. This classification is very simple and easy to apply. It is based more on non-interpretative criteria than other classification schemes. However, it has also several disadvantages. For instance, each group embraces very different ichnotaxa. None of the groups directly addresses vertical trace fossils. Most of trace fossils classified as simple structures have branches (e.g., *Arthropycus*, *Halymenidium*=*Spongeliomorpha*). For this reason the simple and branched structures are united in one group in this paper. In the Książkiewicz, classification genetically close ichnotaxa, such as *Scolicia* and *Taphrohelminthoida* (= *Scolicia* in this paper), belong to different groups. Thus, a classification based on rigid criteria is not satisfactory.

SYSTEMATIC PART

In order to shorten the systematic part, a number of ichnotaxa descriptions provided by Książkiewicz (1977) that have not been changed or have been supplemented only by new diagnoses, are omitted.

CIRCULAR AND ELLIPTICAL STRUCTURES

Mammillichnis Chamberlain 1971a

Emended diagnosis: Hypichnial mound with a convex or concave apex and a teat-like tubercle at the centre of the apex.

Mammillichnis aggeris Chamberlain 1971a Figs. 1–2

- * 1971a *Mammillichnis aggeris* n. ichnog. and sp. – Chamberlain, 238, pl. 30, figs. 6–7.
- 1977 *Mammillichnis aggeris* Chamberlain – Chamberlain, 14, figs. 2b', 7G.
- 1977 *Mammillichnis aggeris* Chamberlain – Stanley *et al.*, 267, fig. 18.
- v 1977 *Mammillichnis aggeris* Chamberlain – Książkiewicz, 53, text-fig. 5a–b, pl. 1, figs. 1–2.
- 1979 *Mammillichnis aggeris* Chamberlain – Chamberlain, 17, fig. 3.
- 1981 *Mammillichnis aggeris* Chamberlain – Crimes *et al.*, 975, pl. 4, figs. 9–10 [specimen from fig. 10 also in Pemberton *et al.*, 1988, fig. 11C].
- 1985 *Mammillichnis* Chamberlain – Eager *et al.*, 140, pl. 1D.
- ?non 1986 *Mammillichnis* ichnosp. – Paczeńska, 32, pl. 5, fig. 2.
- 1993 *Mammillichnis aggeris* Chamberlain – Alexandrescu *et al.*; 10, figs. 2–5.
- ?non 1996 *Mammillichnis* ichnosp. – Paczeńska, 57, pl. 7, figs. 1–2.
- ? 1997 ?*Mammillichnis* ichnosp. – Zagora, 355, fig. 5.3

Diagnosis: As for ichnogenus by its monotypy.

Material: 9 specimens (UJ TF 117–118, 122, 1464, 1470, 1762–1764, 2501).

Description: Small, circular or elliptical hypichnial mounds with apical depression and tubercle at the centre of the depression. Only one specimen does not display the apical depression and the tubercle is located at the convex top of the mound. The mounds are 8–10 mm in diameter and 3–4 mm in height.

Remarks: The specimens with the apical depressions resemble *Laevicyclus* Quenstedt. Some of them (UJ TF 118, 1470) had been labelled by Książkiewicz as *Laevicyclus*

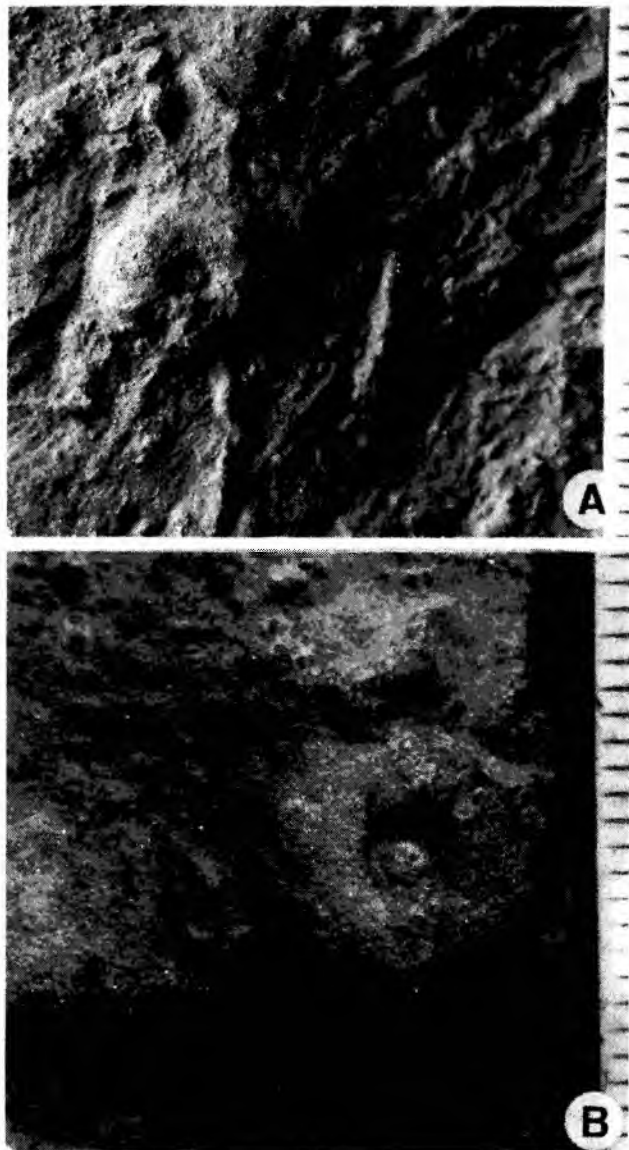


Fig. 1. *Mammillichnis aggeris* Chamberlain, soles of turbiditic sandstone beds. A. UJ TF 1649, Krosno beds (Oligocene), Stonne Góry range near Załuż. B. UJ TF 2501, Krosno beds (Oligocene), Wujskie. Scales in mm

philippi (Wurm), but then the labels were changed to *M. aggeris*. The trace fossils described by Wurm (1911) are distinctly larger and display a double ring.

Origin of *M. aggeris* is not clear. According to Chamberlain (1971a), this is a resting or hiding trace, a fossil egg case (a body fossil), or the upper termination of a burrow. Later, Chamberlain (1977) suggested that *M. aggeris* is a resting or dwelling trace produced by a ?"worm" and that it is probably a preservational variant of *Alcyonidiopsis pharmacus* Richter & Richter. However, it is difficult to find relationships between these two ichnotaxa. Only the granular surface in some specimens of *M. aggeris* (especially in the Chamberlain's material) may be related to the pelletal structure of *Alcyonidiopsis*. However, the morphology of the apex in *M. aggeris* has no relationship to homogeneously faecal-stuffed trace fossil of *Alcyonidiopsis*. Książkiewicz (1977) suggested that *Mammillichnis* is an actinian burrow

ORIGIN OF MAMMILICHNIS

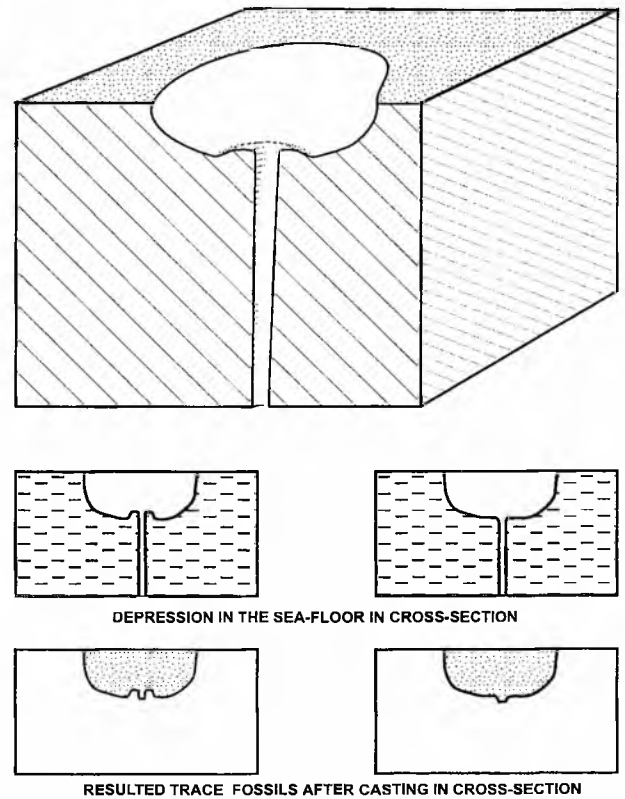


Fig. 2. General model (top) and morphological variations (below) of *Mammillichnis*. The morphological variants depend on the shape of the depression in the sea floor

because of supposed radial symmetry in Chamberlain's (1971a) fig. 7J, which is, however, a drawing of the trace fossil model. Similarly, Crimes *et al.* (1981) referred to supposed radial symmetry of *M. aggeris* in their pl. 4, fig. 9. However, neither the Książkiewicz material nor the specimen in the photograph of Crimes *et al.* (1981) display the radial patterns. The photographs and descriptions published by Chamberlain (1971a) and part of the photographs of Crimes *et al.* (1981) show a granular surface of the trace fossils, and therefore their slightly lobate outline, which cannot be treated as the radial pattern. The Książkiewicz specimens are mostly smooth and display convex or concave apex. Some of them, similarly to the material of Crimes *et al.* (1981), are slightly fluted. This reveals the pre-depositional origin of the trace fossil flange. However, it cannot be excluded that the apical knob is a termination of a vertical burrow that may be also active after deposition of turbidite. Nevertheless, there is no vertical burrow structure in the polished slab of one cross-sectioned Książkiewicz specimen (UJ TF 1762).

In two cases (UJ TF 1763, 2501), the trace fossils display a bulb-like morphology in cross-section, i.e. their diameter is smaller at the base than at the half-way point of their height.

Most probably, *M. aggeris* represents the upper part of a thin vertical or subvertical cylindrical burrow, which displays a hemispherical funnel-like upper termination (Fig. 2).

It is not excluded that the funnel was filled with pellets. Vertical trace fossils with the funnel-like termination are described as *Monocraterion* Torell. However, *Monocraterion* displays a triangular cross section of the funnel and is closely related to *Skolithos* Haldeman, or regarded even as a preservational variant of the latter (Goodwin & Anderson, 1974). Its funnel is produced by sliding of grains in less cohesive sediment. In contrast, the funnel of *M. aggeris* was most probably produced actively by the tracemaker in cohesive mud and possibly it worked as a trap. Thus, the funnel is a record of a unique behaviour and is a basis for separation of *M. aggeris* from other ichnotaxa. However, it is not excluded that *Mammillichnis* and *Laevicyclus* Quenstedt are related. Nevertheless, there is so far no satisfactory explanation of *Laevicyclus* and therefore such comparison cannot be drawn. Probably, the flatter specimens with deeper apical depressions, which resemble *Laevicyclus*, are only preservational variants of the same ichnotaxon. These specimens can occur if the termination of the thin burrow in the funnel was rimmed by a small mound (Fig. 2).

Palaeoenvironment: Deep-sea flysch deposits, except one occurrence in the Carboniferous deltaic deposits (Eager *et al.*, 1985) and on occurrence (?) in the Cambrian shallow-water deposits (Paczeńska, 1986, 1996).

Stratigraphic range: (?) Cambrian (Paczeńska, 1986, 1996), Ordovician (Chamberlain, 1977), Oligocene (Książkiewicz, 1977; Alexandrescu *et al.*, 1993).

Bergaueria Prantl 1945

Diagnosis: Cylindrical or hemispherical, vertical structures having smooth, unornamented walls, circular to elliptical in cross-section; fill essentially structureless; rounded base, with or without shallow, central depression and radial ridges (after Pemberton *et al.*, 1988).

Remarks: *Bergaueria* is probably a cubichnial or domichnial trace fossil produced by suspension-feeders (Fürsich, 1975). These were probably coelenterates, chiefly sea anemones (e.g. Prantl, 1945; Alpert, 1973; Pemberton *et al.*, 1988) similar to living *Cerianthus* or *Edwardsia* (Pemberton *et al.*, 1988). The present-day sea anemones are very widely distributed from estuaries to abyssal plains (e.g. Carney, 1981). However, in the case of non-radiated ?*B. prantli* Książkiewicz (1977) and *B. hemispherica* Crimes *et al.* (1977) that additionally has no apical depression, the comparison with sea-anemone burrows should be treated with caution.

Bergaueria occurs in diverse facies from shallow-water deposits (Narbonne, 1984; Crimes & Anderson, 1985) to flysch deposits (Prantl, 1945; Książkiewicz, 1977; Crimes & Crossley, 1991) from the late Precambrian (e.g. Crimes, 1987) to (?) the Eocene (Książkiewicz, 1977) and Miocene (Uchman, 1995).

?*Bergaueria prantli* Książkiewicz 1977

Fig. 3

- partim 1977 *Bergaueria prantli* n. ichnosp. – Książkiewicz, 53, pl. 1, figs. 3-5, text-fig. 5c-e.
 ? 1996 *Bergaueria prantli* Książkiewicz – Paczeńska, 56, pl. 1, figs. 8-9.

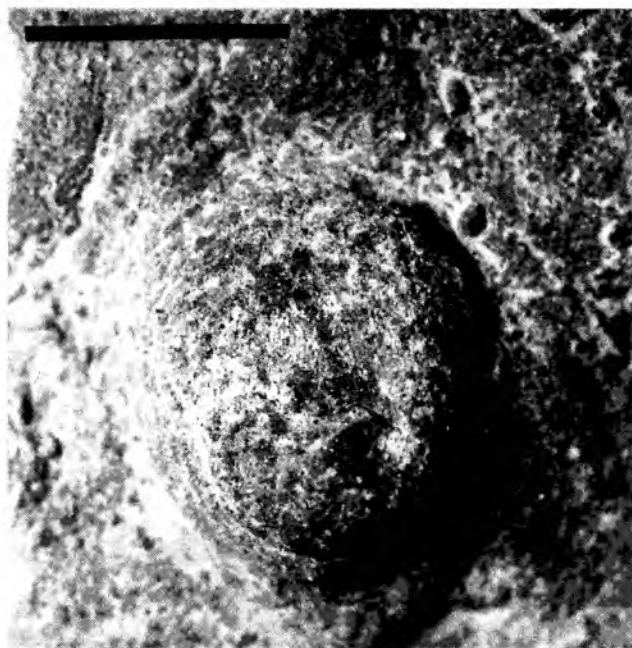


Fig. 3. ?*Bergaueria prantli* Książkiewicz, sole of turbiditic sandstone bed. UJ TF 907, Ropianka beds (Senonian–Paleocene), Kałowa. Scale bar = 1 cm

Emended diagnosis: Bergauerians that display an irregular shape and apical, more or less distinct, irregular depression.

Material: 3 specimens (UJ TF 115 (holotype), 967, 1178).

Remarks: In confrontation with the revised *Bergaueria* (Pemberton *et al.*, 1988), the original Książkiewicz (1977) diagnosis of ?*B. prantli* is too broad and does not sufficiently express differences between this taxon and *B. perata* Prantl. Pemberton *et al.* (1988) reservedly included ?*B. prantli* in *B. perata*. This suggestion cannot be accepted. *B. perata* is more regular, with steeper sides, more or less circular apical depression, and faint radial ridges at the apex. The differences have been noticed by Książkiewicz (1977, p. 53). In contrast, ?*B. prantli* is characterized by an irregular outline and irregular apical depression. Therefore, it should be treated as a separate ichnospecies. However, it is not clear if this trace fossil is a real *Bergaueria*, which is typified by *B. perata* Prantl. It cannot be excluded that some specimens are casts of the upper terminations of some vertical or subvertical partially filled burrows. Therefore, the question-mark is placed in front of the ichnogenetic name.

Some specimens labelled by Książkiewicz as *B. prantli* are undeterminable trace fossils (UJ TF 1471).

SIMPLE STRUCTURES

Arthropycus Hall 1852

Ichnospecies included in *Arthropycus* Hall:

- 1831 *Fucoides alleghaniensis* – Harlan, 393-398.
 1838 *Fucoides Harlani* – Conrad, 113.
 1843 *Fucoides Harlani* – Hall, 46, figs. 1-2.
 1852 *Arthropycus harlani* – Hall, 5, pl. 1, pl. 2, figs. 1a-c.
 1852 *Harlania Hallii* Göpp. – Göppert, 98, pl. 41, fig. 4.

- 1856 *Harlania Hallii* Goepf. – Bronn & Roemer, pl. 4, fig. 1.
 1869 *Harlania* Goepf. – Schimper, 195.
 1874 *Harlania Hallii* Goepf. – Schimper, pl. 2, fig. 6.
 1881 *Harlania Hallii* Goepf. – Saporta, fig. 1.2.
 1882 *Arthropycus Harlani* Hall – Saporta, 49, pl. 7, fig. 2.
 1883 *Arthropycus Harlani* Hall – Saporta & Marion, fig. 21.
 1886 *Arthropycus* cfr. *Harlani* Hall – Delgado, 75, pls. 23, 25-26.
 1887 *Arthropycus* cfr. *Harlani* Hall – Delgado, 66, pls. 9-10.
 1890 *Arthropycus Harlani* Hall – Schimper & Schenk, fig. 41.
 1895 *Arthropycus Harlani* Göpp. – Fuchs, pl. 9, fig. 2.
 1901 *Arthropycus harlani* Conrad – Grabau, 132, pl. 16.
 1908 *Arthropycus Harlani* Hall – Hernandez Pacheco, 84 (lappus calami).
 1918 Problematicum – Zuber, fig. 123.
 1940 *Harlania harlani* (Conrad) – Desio, 68, fig. 7, pl. 6, figs. 1-2, pl. 7, pl. 13, fig. 6.
 non 1942 *Harlania* Goepfert – Picard, 14, pl. 2, figs. 6-8.
 1948 *Arthropycus alleghaniensis* (Harlan) – Shimer & Shrock, 719, pl. 303, figs. 26-27.
 ? 1949 *Fraena* (?) – Gómez de Larena, fig. 1.
 1952 *Arthropycus* – Becker & Donn, 214, figs. 1-2.
 1955 *Harlania harlani* Conrad – Lessertisseur, pl. 74, fig. 11.
 ? 1960 *Arthropycus* – Henbest, fig. 177.1F.
 1961 *Arthropycus alleghaniensis* (Harlan) – Wolfart, 81, pl. 7, fig. 2.
 1963 *Harlania alleghaniensis* (Harlan) – Bender, pl. 13, fig. 3.
 1969 *Arthropycus* – Seilacher, 120, pl. 1.
 non 1970 *Arthropycus*-like burrows – Frey, 23, fig. 4E.
 non 1970 *Arthropycus* (?) sp. – Frey & Howard, 159, fig. 3e.
 1970 *Arthropycus* sp. – Książkiewicz, 285, fig. 1a.
 1970 *Harlania* – Selley, pl. 2, fig. b.
 non 1971 *Arthropycus* – Maberry, 11, fig. 8.
 non 1972 *Arthropycus*-like burrows – Frey, fig. 9A.
 1972 ?*Arthropycus* – Frey & Chows, 37, fig. 5C.
 non 1975 *Arthropycus* sp. – Chiplonkar & Ghare, 72, fig. 1B.
 1977 *Arthropycus alleghaniensis* (Harlan) – Baldwin, 26, pl. 2a.
 ? 1977 ?*Arthropycus* Hall – Kern, 30.
 1977 *Arthropycus strictus* n. ichnosp. – Książkiewicz, 57, pl. 1, figs. 11-12.
 non 1977 *Arthropycus annulatus* n. ichnosp. – Książkiewicz, 56, pl. 1, figs. 8-10 [= *Ophiomorpha annulata* (Książkiewicz)]
 non 1977 *Arthropycus*(?) *dzulynskii* n. ichnosp. – Książkiewicz, 58, pl. 1, figs. 13-14 [= *Protovirgularia dzulynskii* (Książkiewicz)].
 partim 1977 *Bothotrepis* spec. indet. – Książkiewicz, 76, text-fig. 10b [non text-fig. 10d, f-g, i-j, m, o-s, u-y = *Thalassinoides suevicus* (Rieth)].
 1977 *Sabularia tenuis* n. ichnosp. – Książkiewicz, 71, pl. 2, fig. 3.
 1978 *Arthropycus alleghanensis* – Aceñolaza, 40, fig. 25.
 ? 1978 ?*Arthropycus* Hall – Kern, 251.
 ? 1981 *Lorenzina* cf. *moreae* Renz – Crimes *et al.*, 972, pl. 3, figs. 4-5.
 ? 1982 *Arthropycus* cf. *strictus* Książkiewicz – Alexandrescu & Brustur, 36, pl. 3, fig. 4.
 1983 *Arthropycus alleghaniensis* (Harlan) – Turner & Benton, 451, fig. 4A.
 1984 *Arthropycus alleghaniensis* (Harlan) – Liñán, 57, pl. 2, fig. 5.
 1984 *Arthropycus alleghaniensis* (Harlan) – Pickerill, Romano & Meléndez, 251, fig. 2a.
 1985 *Arthropycus alleghaniensis* (Harlan) – Durand, 41, pl. 4, figs. 3-4.
 1985 cf. *Arthropycus* – Eager *et al.*, 137, fig. 10A.
 non 1986 *Arthropycus* – Ghare & Kulkarni, 45, pl. 1, fig. 1.
 1987 *Arthropycus* Hall – Bjerstedt, 875, fig. 8.1.
 1987 *Arthropycus alleghaniensis* (Harlan) – Valle, 26, fig. 5.
 1988 *Arthropycus* – Seilacher & Alidou, fig. 1d-f, fig. 2.
 ?non 1991 *Arthropycus* isp. – Pickerill, Fillion & Branchley, 73, fig. 2.
 ?non 1992b “*Arthropycus*” *corrugatus* (Fritsch) – Mikuláš, 27, pl. 14, fig. 1.
 ? 1993a *Arthropycus* sp. A – Li, 94, pl. 1, fig. 5.
 ?non 1993a *Arthropycus* sp. A – Li, 94, pl. 2, fig. 7.
 ? 1994 *Arthropycus minoricensis* Bourrouilh – Orr, 209, figs. 7, 13, 15 (nomen nudum).
 ?non 1994 *Arthropycus qiongzhusiensis* ichnosp. nov. – Luo *et al.*, 33, pl. 1, fig. 4., pl. 2, fig. 3 [= ?*Torrowangea* isp.].
 1996 *Arthropycus strictus* Książkiewicz – Paczeńska, 59, pl. 10, fig. 3.
 1996 *Arthropycus hunanensis* ichnosp. nov. – Zhang & Wang, 484, pl. 3, fig. 1.

Emended diagnosis: Oblique to horizontal, cylindrical or subcylindrical structures with regular, perpendicular fine ribs and a tendency to plunging into bed surfaces. Commonly, the trace fossils are grouped in bundles.

Remarks: Probably, the above diagnosed *Arthropycus* embraces only three ichnotaxa, i.e. *A. alleghaniensis* (Harlan) and two ichnotaxa lumped so far in *A. strictus* Książkiewicz, which are separated as *A. strictus* Książkiewicz and *A. tenuis* (Książkiewicz) in this paper. Orr (1994) illustrated *Arthropycus minoricensis* Bourrouilh, which was originally described in an unpublished thesis. The description and illustration of this trace fossil is not sufficient for assessment of its diagnostic features. *Arthropycus qiongzhusiensis* described by Luo *et al.* (1994) from the Cambrian of China, is a hypichnial, winding trace fossil with fine transverse striae. A photograph of this trace fossil suggests that the striae can be an external expression of internal sediment pads typical of *Torrowangea* Webby. Relationships between these two ichnotaxa should be explained. Zhang & Wang (1996) described *Arthropycus hunanensis* from Silurian–Devonian deposits of China. It is not excluded that it is a junior objective synonym of *A. alleghaniensis*.

Arthropycus annulatus Książkiewicz and *Arthropycus*(?) *dzulynskii* Książkiewicz (Książkiewicz, 1977), and several other ichnotaxa are excluded from *Arthropycus* as indicated in the above list.

A. alleghaniensis (Harlan) is common in neritic siliclastic facies of the Middle Palaeozoic and regarded as representing a burrow (Sarle, 1906) of feeding arthropods (e.g., Turner & Benton, 1983). However, Schiller (1930) tried to explain it as a tectonic structure, and Becker & Donn (1952) regarded this ichnotaxon as an “algal structure”. *A. alleghaniensis* may occur as linear, protrusive, flat palmate, or deep palmate retrusive trace fossil (Seilacher & Alidou, 1988). The palmate specimens have been included in *Phycodes palmatus* (Hall) (Seilacher, 1955, p. 386) [incorrectly spelled *P. palmatum*; Fillion & Pickerill, 1990]. Similarities of this ichnotaxon to *Phycodes* were pointed out by Beck (1916). *A. strictus* Książkiewicz displays similar tendencies. Thus, grouping in bundles can be regarded as the common feature of *Arthropycus*, which is included in the diagnosis. However, this feature does not occur constantly, and therefore *Arthropycus* cannot be included in *Phycodes* Richter.

Stratigraphic range: Lower Cambrian (Liñán, 1984) – Lower Miocene (Alexandrescu & Brustur, 1984).

Arthropycus strictus Książkiewicz 1977
 Figs. 4, 5A, 6

1970 *Arthropycus* sp. – Książkiewicz, 285, fig. 1a.

*v 1977 *Arthropycus strictus* n. ichnosp. – Książkiewicz, 57, pl. 1, figs. 11-12.

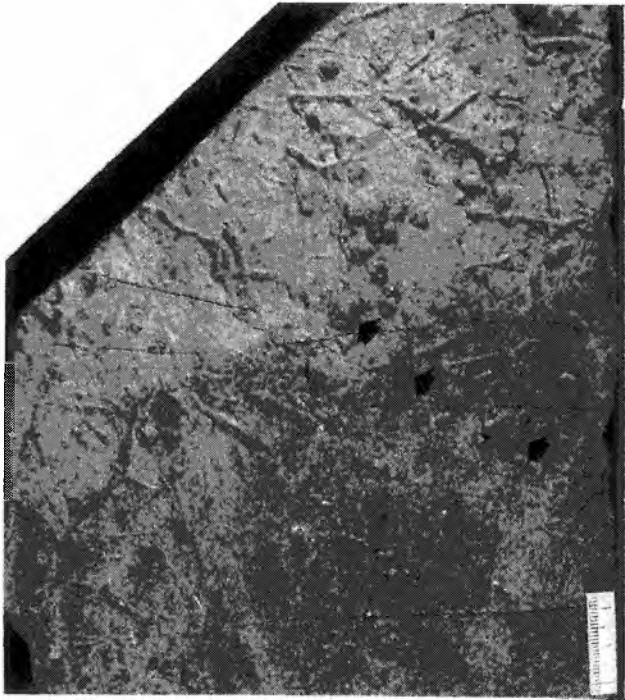


Fig. 4. *Arthrophyucus strictus* Książkiewicz (arrowed) and *Arthrophyucus tenuis* (Książkiewicz). Sole of a turbiditic sandstone bed. UJ TF 131, Lgota beds (Albian), Rzyki near Andrychów. More details are shown in Fig. 5. Scale in mm

- partim 1977 *Buthotrephis* spec. indet. – Książkiewicz, 76, text-fig. 10b [non text-fig. 10d, f-g, i-j, m, o-s, u-y = *Thalassinoides suevicus* (Rieth)].
- ? 1981 *Lorenzina* cf. *moreae* Renz–Crimes *et al.*, 972, pl. 3, figs. 4-5.
- ? 1982 *Arthrophyucus* cf. *strictus* Książkiewicz – Alexandrescu & Brustur, 36, pl. 3, fig. 4.
- non 1996 *Arthrophyucus strictus* Książkiewicz – Paczeńska, 59, pl. 10, fig. 3.

Emended diagnosis: Small *Arthrophyucus*, approximately circular in cross-section, with very fine, delicate perpendicular ribs. Structures are distinctly arcuate in vertical plane and plunge into sole of beds.

Material: 5 slabs (UJ TF 124, 131 (holotype), 1318, 1508, 1523).

Remarks: The holotype of *Arthrophyucus strictus* Książkiewicz (UJ TF 131, Fig. 4) contains two different trace fossils treated by Książkiewicz (1977) as variations of the same ichnospecies. However, these trace fossils display enough different features for their separation at the ichnospecies level. The first trace fossil is represented by short hypichnial, perpendicularly striated, simple ridges, which dip into the bed at both ends (Fig. 5). They are elevated at the middle part and form wide, variably oriented arches, which are 4–6 mm in diameter. Ridges of the same morphology are better and more completely preserved in other specimens (e.g. UJ TF 124), which were determined by Książkiewicz as *A. strictus*. In some more complete specimens, the ridges tend to form bunches, which plunge into the sole of beds (Fig. 6).

The second type is represented by short, horizontal and

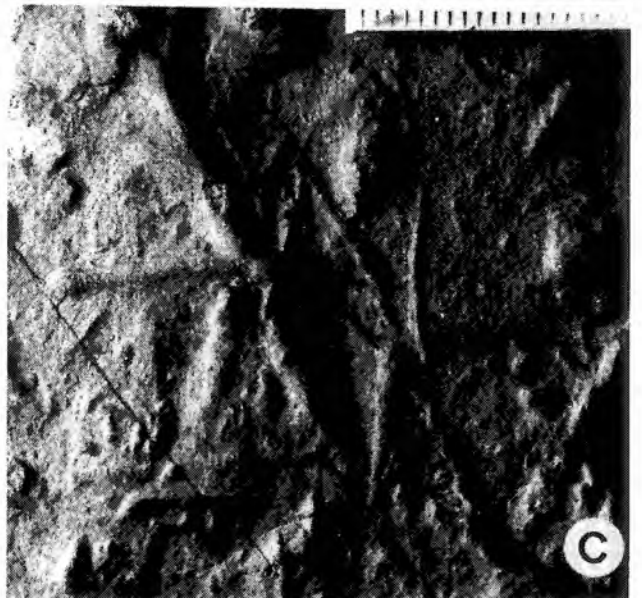
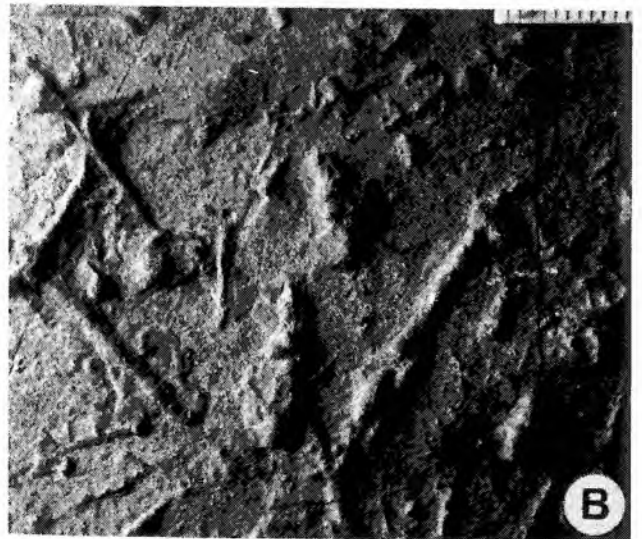
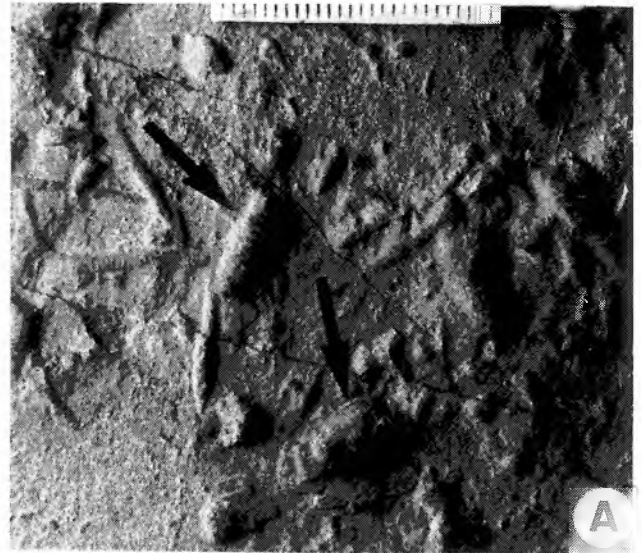


Fig. 5. *Arthrophyucus strictus* Książkiewicz (arrowed) and *Arthrophyucus tenuis* (Książkiewicz). A-C. Details of Fig. 4. Scales in mm

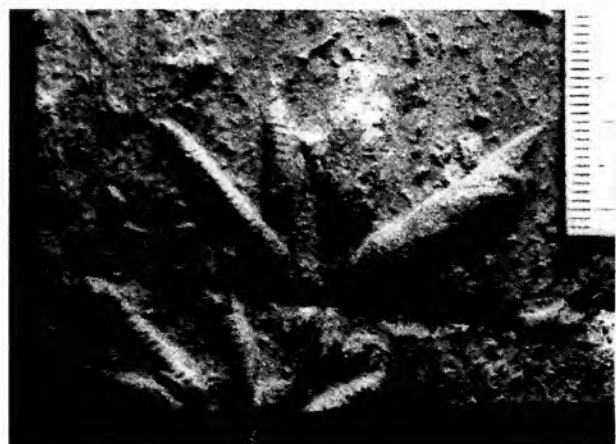


Fig. 6. *Arthropycus strictus* Książkiewicz. Sole of a turbiditic sandstone bed. UJ TF 124, Ropianka beds (Senonian–Paleocene), Mszana Dolna. Scale in mm

commonly branched ridges, which do not form bunches and are not bent in arches (Fig. 5B–C). The ridges are covered with very fine perpendicular striae and are distinctly thinner than the ridges of the first type. Their diameter ranges from 0.4 to 1.2 mm. About half of the ridges are branched, always at a sharp angle. Ridges of the second type are almost identical to *Sabularia tenuis* Książkiewicz. These trace fossils differ only in the lack of the perpendicular striation in most specimens of *S. tenuis*. However, some ridges of the latter ichnotaxon, including the holotype (UJ TF 1686), display faint perpendicular striation, which was noted also by Książkiewicz (1977, p. 71). Preservation of the fine striation depends strongly on cohesion of substrate and weathering. Thus, degree of preservation of the striation is not a sufficient criterion for the ichnotaxonomic separation of these trace fossils and therefore *S. tenuis* is included in *Arthropycus*. The ichnospecies name of *S. tenuis* is retained, as *A. tenuis*, for the second type of ridges. For the first type of ridges the name *A. strictus* is retained.

The specimen UJ TF 1318 indicated by Książkiewicz (1977, text-fig. 10b) as *Buthotrephis* spec. indet. displays distinct features of *A. strictus*.

A. strictus was regarded by Książkiewicz as representing a feeding burrow of polychaetes. It occurs in the Albian–Senonian flysch deposits of the Carpathians (Książkiewicz, 1977). A not well preserved occurrence, treated therefore reservedly, is noted in the Eocene flysch of Romania (Alexandrescu & Brustur, 1982). Brustur & Stoica (1993) reported *A. cf. strictus* from Upper Eocene flysch.

Paczeńska (1996) described *A. strictus* from the shallow-water Cambrian deposits, but it displays a median furrow transecting the perpendicular ribs. Therefore, it is excluded from this ichnospecies.

Arthropycus tenuis (Książkiewicz 1977)
Figs. 4–5, 7

- 1918 [...] drobne hieroglify – Zuber, fig. 3.
*v 1977 *Sabularia tenuis* n. ichnosp. – Książkiewicz, 71, pl. 2, fig. 3.
partim 1977 *Arthropycus strictus* n. ichnosp. – Książkiewicz, 57, pl. 1, figs. 11–12.

- 1984 *Sabularia tenuis* Książkiewicz – Alexandrescu & Brustur, 20, pl. 1, figs. 1–2, pl. 2, fig. 1.
1986 *Sabularia tenuis* Książkiewicz – Alexandrescu, 6, pl. 1, figs. 1–2, pl. 2, figs. 1–2.
1993 *Sabularia* ichnosp. – Alexandrescu *et al.*, pl., figs. 1–3.
?non 1995 *Sabularia tenuis* Książkiewicz – Bąk, fig. 10.
?non 1995 ?*Sabularia tenuis* Książkiewicz – Bąk, fig. 21.

Emended diagnosis: Small, hypichnial, short, straight, rarely branched ridges, covered with very fine perpendicular striae. The striation commonly is not preserved.

Material: 9 slabs (UJ TF 131, 373–374, 1493, 1579, 1583, 1614, 1687 (holotype), 2680).

Remarks: *A. tenuis* is noted only in the flysch deposits of the Carpathians from the Valanginian (Książkiewicz, 1977) to the (?) Lower Miocene (Alexandrescu & Brustur, 1981).

Halopoa Torell 1870

Ichnospecies included in *Halopoa* Torell:

- 1870 *Halopoa imbricata* n. sp. – Torell, 7 [no illustration]
1878b *Trichophycus sulcatum* n. sp. – Miller & Dyer, 4, pl. 4, fig. 5. [also James, 1884, pl. 6, fig. 5].
1932 *Fucusopsis angulatus* Palib. gen. et sp. n. – Vassoevich, 51, pl. 2, figs. 2, 6.
1946 *Fucusopsis angulatus* – Grossheim, fig. 4b (lapsus calami).
? 1949 Pistas de arthropodos – Gómez de Llarena, fig. 8.
?non 1959 *Fucusopsis angulatus* Palibin – Birkenmajer, 229, pl. 22 [non text-fig. 1].
1959 *Fucusopsis angulatus* Palibin – Seilacher, 1070, tab. 2, fig. 30.
1962 *Fucusopsis* – Seilacher, fig. 1, pl. 1, fig. 2.
1964 *Gyrochorda fraeniformis* nov. iscp. – Farrés Malian, 92, pl. 5, fig. 2.
1965 *Halopoa imbricata* Torell – Martinsson, 219, fig. 29.
1965 Halopoaans – Martinsson, 219, figs. 30–32.
v 1970 *Fucusopsis angulata* Palibin – Książkiewicz, 286, fig. 1s.
v 1970 *Fucusopsis annulata* ichnosp. n. – Książkiewicz, 286, fig. 1r.
1970 *Fucusopsis sulcatum* (Miller and Dyer) – Osgood, 380, pl. 64, fig. 1, pl. 70, fig. 1, pl. 71, fig. 5.
?non 1970 *Fucusopsis* cf. *angulatus* Vassoevich – Chiplonkar & Badve, 9, pl. 3, fig. 6.
? 1973 *Feddenichmus feddeni* sp. n. – Chiplonkar & Borkar, 572, figs. 1–2.
1976 *Fucusopsis* – Hakes, 27, pl. 8, fig. 2a–b.
v 1977 *Fucusopsis angulata* Palibin – Książkiewicz, 59, pl. 2, fig. 5 [also Leszczyński, 1992, pl. 15, fig. 1].
v 1977 *Fucusopsis annulata* Książkiewicz, 60, pl. 2, figs. 6–7.
v 1977 *Fucusopsis striata* (Hall) – Książkiewicz, 61, pl. 2, fig. 8.
? 1977 *Fucusopsis* Vassoevich – Kumar *et al.*, 427, pl. 9, fig. 6.
1978 *Fucusopsis angulata* Palibin – Radwański, 51, pl. 1, fig. 2.
?non 1980 *Fucusopsis* – Soudant, pl., figs. C–D.
? 1978 *Halopoa indica* ichnosp. n. – Badve & Ghare, 132, pl. 4, fig. 5.
non 1981 ?*Fucusopsis* sp. – Bradshaw, 639, figs. 38–39 [= *Palaeophycus* isp.].
partim 1981 *Fucusopsis angulata* Palibin – Crimes *et al.*, 968, pl. 2, fig. 1 [?non pl. 2, fig. 2].
1981 *Fucusopsis* sp. – Pickerill, 44, fig. 5b.
non 1982 *Radionereites annulata* (Książkiewicz) – D’Alessandro, 535, pl. 38, fig. 2, pl. 39, fig. 4, pl. 40, fig. 1, pl. 42, fig. 4.
? 1983 *Halopoa* sp. – Singh & Rai, 77, pl. 7, figs. 74–76.
1983 *Halopoa* sp. – Palij *et al.*, pl. 67, figs. 1–2.
? 1986 *Fucusopsis angulatus* Palibin in Vassoevich – Ghare & Kulkarni, 47, pl. 1, fig. 2, pl. 5, fig. 2.
? 1988 *Fucusopsis?* isp. – Yang, 322, pl. 1, fig. 3a.
? 1990 *Palaeophycus striatus?* Hall – Fillion & Pickerill, pl. 11, fig. 1.
1990b *Fucusopsis* – Seilacher, pl. 32.2f.

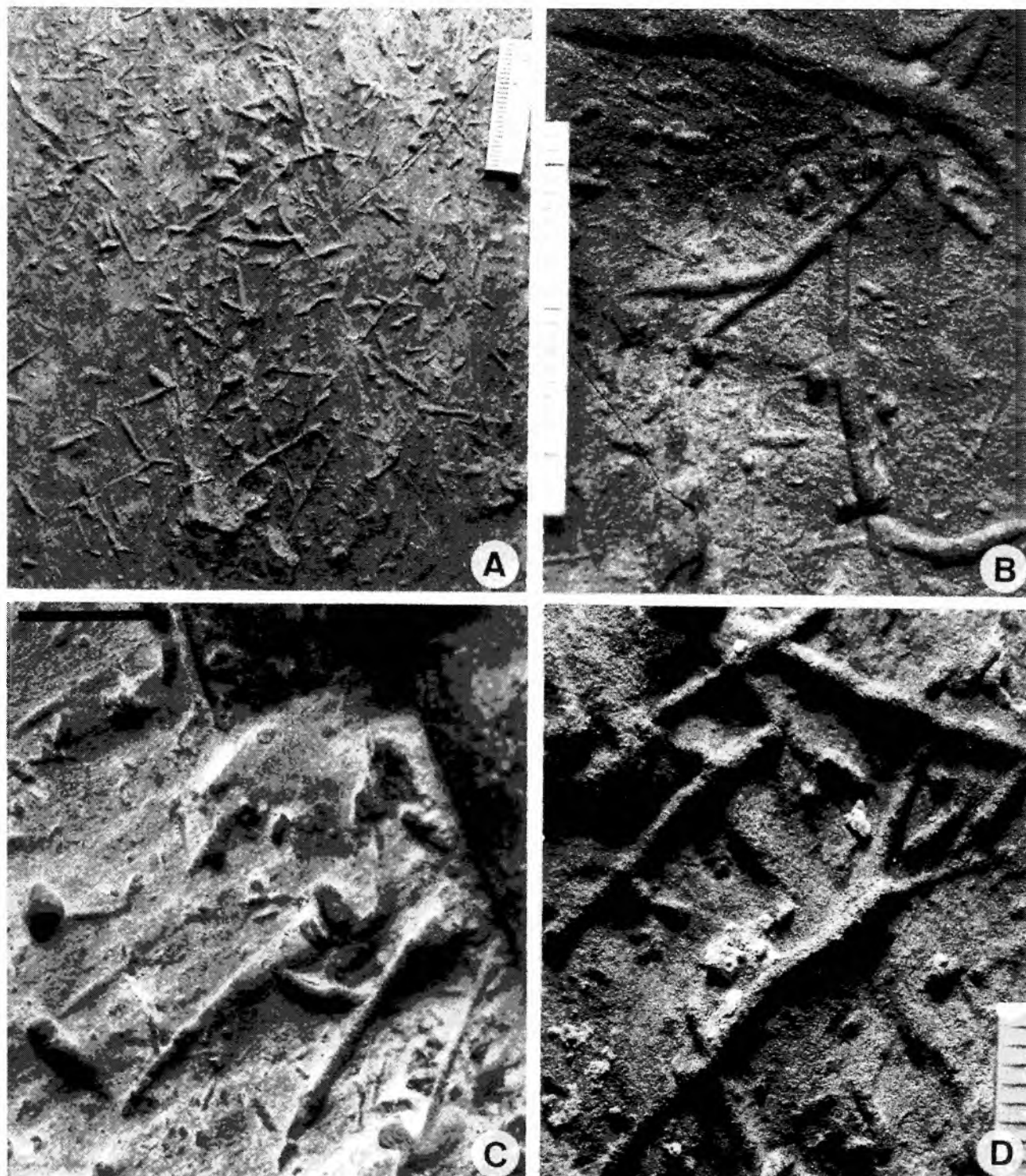


Fig. 7. *Arthrophyucus tenuis* (Książkiewicz). Soles of a turbiditic sandstone beds. A. UJ TF 1687, holotype, Krosno beds (Oligocene), Wujskie. B. UJ TF 2680, label lost. C. UJ TF 374, Kałowa, Ropianka beds (Senonian–Paleocene). Coll. W. Szajnocha. D. UJ TF 373, Krosno beds (Oligocene), Słonne near Załuż. Scale bars = 1 cm, scale in C in mm

- 1993 Bioglife ("Pietrificarea de la Pinsdorf") – Contescu *et al.*, pl. 8, fig. 3.
 ? 1994 *Fucusopsis* isp. – Gong, 487, pl. 6, fig. 4.
 ? 1995 *Palaeophycus (Fucusopsis) angulata* Palibin in Vassovitch – Crimes & McCall, 239, fig. 4a.
 ? 1995 *Palaeophycus striatus* Hall – Crimes & McCall, 239, fig. 4b.

- 1995 *Palaeophycus sulcatus* (Miller & Dyer) – Crimes & McCall, 241, fig. 4c.
 ? 1995 *Fucusopsis* ichnosp. – Bąk, fig. 19.
 1997 *Palaeophycus imbricatus* (Torell) – Jensen, 69, figs. 8D, 45-46, 47B, D, 48B.

Emended diagnosis: Long, generally horizontal trace fos-

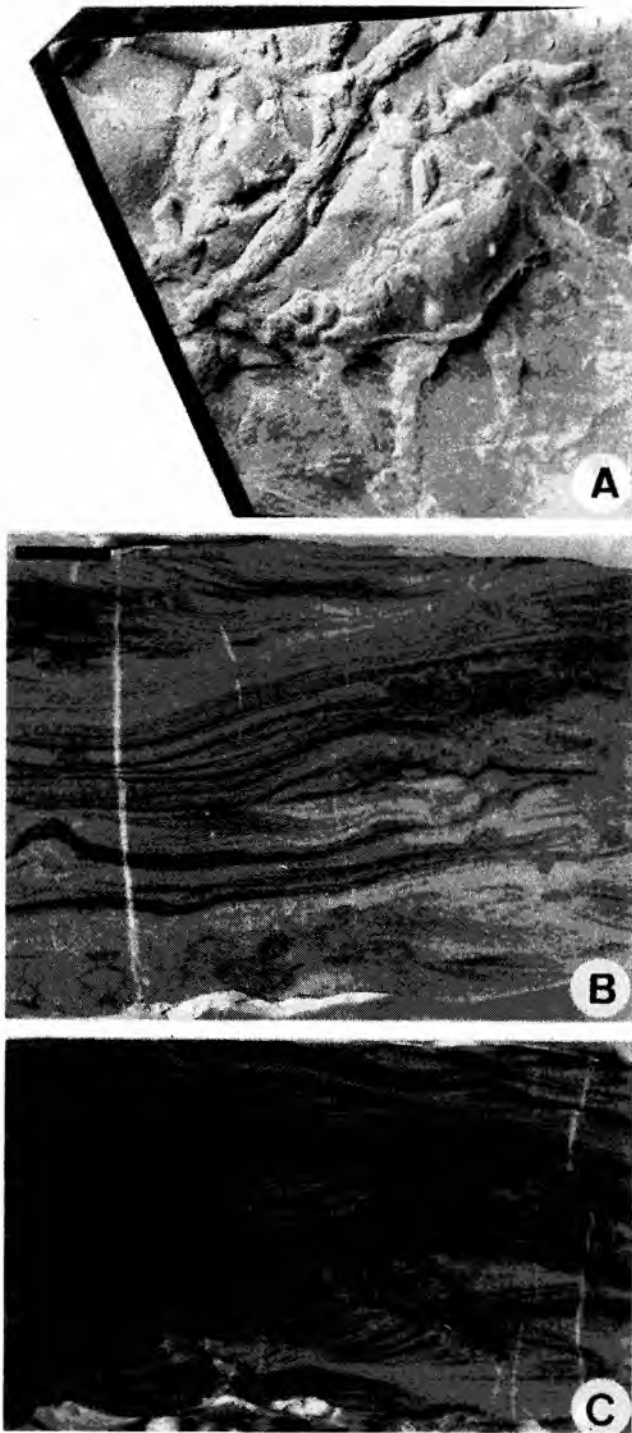


Fig. 8. *Halopoa imbricata* Torell in turbiditic sandstone bed. UJ TF 87, Beloveža Formation (Eocene), Zubrzyca Górna. **A.** Bedding-plane view. **B-C.** Cross-section views. Polished and oiled surfaces. Scale bars = 1 cm

sils covered with longitudinal irregular ridges or wrinkles, which are composed of several imperfectly overlapping cylindrical probes.

Remarks: *Halopoa* was described, but not illustrated by Torell (1870). Andrews (1955) designated *H. imbricata* Torell as the type ichnospecies of this ichnogenus. Martinsen (1965) synonymized *Halopoa composita* Torell (1870),

Scotolithus mirabilis Linnarson (1871) and *Halopoa imbricata*, and illustrated the lectotype of the latter ichnotaxon. He tried to compare *H. imbricata* to *Gyrochorte* Heer. However, Jensen (1997) showed that *H. composita* and *S. mirabilis* are different ichnospecies and that the comparison to *Gyrochorte* cannot be accepted. Hakes (1976) turned his attention to the strong similarities between *Halopoa* Torell and *Fucusopsis* Palibin in Vassoevich (1932). According to the description by Jensen (1977), *Halopoa* displays the same significant features as *Fucusopsis*. However, Jensen included these two ichnogenera in *Palaeophycus*. Also Pemberton & Frey (1982) included *Fucusopsis* in *Palaeophycus*, who related *Palaeophycus* to passively filled, open, walled burrows, including specimens that display longitudinal striation. However, the origin of the longitudinal striation may be diverse and related to diverse tracemaker behaviour or taphonomic processes. The longitudinal striation may be produced actively by locomotory organs and/or passively by body appendages of tracemaker. Its preservation strongly depends on cohesion of the substrate. Other types of longitudinal striation may be produced by microfaulting connected with collapse of burrows or with compressional faulting due to tension caused by tracemaker from interior of burrow. This type of striation is a product of a unique behaviour, which can be interpreted as diagnostic feature at the ichnogeneric level. The latter idea was proposed for *Fucusopsis* (Osgood, 1970, p. 380; Seilacher, 1990b). In the case of the Książkiewicz material, there is no wall and no evidence that the burrows were open, and therefore it does not conform with the idea of *Palaeophycus* sensu Pemberton & Frey (1982). Trace fossils of this type, especially *H. imbricata* (= *F. angulata*) from the Książkiewicz material are commonly densely crowded and they rework the lowermost part of turbiditic beds. They are rather produced by deposit feeding organisms. Their outline is not sharp and diameter is not constant.

The cross-sections of the *Halopoa* specimens display several overlapping probes, which are commonly stacked in vertical plane (Fig. 8B–C). The trace fossils form a *Teichichnus*-like structure, however much less vertically and regularly developed than in *Teichichnus* Seilacher. Some probes of *Halopoa* diverge away from some objects, for instance other fills of burrows of the same ichnotaxon, and join once again behind the object (Fig. 9B). Formation of each new component probe is connected with pushing out of the formerly reworked sediment in the older probe which results in the formation of an irregular longitudinal striation. Deformation of the laminae above the trace fossils (Fig. 8) indicates that the sediment was pushed out of the burrow interior. The burrows were presumably formed by intruding in the sediment by the tracemaker.

Teichichnus is never so long, lacks external sculpture, and is much more extended in the vertical plane. Therefore, *Halopoa* and *Teichichnus* should remain separate. One can conclude that *Halopoa* represents sufficiently unique behaviour for its retention as ichnogenus.

Książkiewicz (1977) regarded the striation of *Fucusopsis* (= *Halopoa*) as resulting from the sculpture of the tracemaker, which probably belonged to priapulid worms. Such explanation does not conform with the trace fossil morphol-

ogy. There is no evidence of dragging of hard or soft objects that may be related to sculpture of the tracemaker body.

Halopoa ranges from Lower Cambrian (Seilacher, 1990b, Jensen, 1997) to Middle Miocene (Crimes & McCall, 1995). In the Carpathian Flysch, it is common in sandstone turbidites. Some beds are heavily bioturbated, including their basal part. Stronger bioturbation along organic-rich laminae can be observed. *Halopoa* exploits rarely occupy tiers in the sandstone part of turbiditic beds.

Halopoa imbricata Torell 1870

Figs. 8–9

- * 1870 *Halopoa imbricata* n. sp. – Torell, 7 [no illustration]
- 1878b *Trichophycus sulcatum* n. sp. – Miller & Dyer, pl. 4, fig. 5 [also James, 1884: pl. 6, fig. 5]
- 1932 *Fucusopsis angulatus* Palib. gen. et sp. n. – Vassoevich, 51, pl. 2, figs. 2, 6.
- 1946 *Fucusopsis angulatus* – Grossheim, fig. 4b (lapsus calami).
- ? 1949 Pistas de arthropodos – Gómez de Llarena, fig. 8.
- ?non 1959 *Fucusopsis angulatus* Palibin – Birkenmajer, 229, fig. 1, pl. 12.
- 1959 *Fucusopsis angulatus* Palibin – Seilacher, 1070, tab. 2, fig. 30.
- 1962 *Fucusopsis* – Seilacher, fig. 1, pl. 1, fig. 2.
- 1962 *Fucusopsis angulatus* Palib. – Dimitrieva *et al.*, pl. 75, fig. 1.
- 1964 *Gyrochorda fraeniformis* nov. iscp. – Farrés Malian, 92, pl. 5, fig. 2.
- 1965 *Halopoa imbricata* Torell – Martinsson, 219, fig. 29.
- 1965 Halopoans – Martinsson, 219, figs. 30–32.
- 1970 *Fucusopsis angulata* Palibin – Książkiewicz, 286, fig. 1s.
- 1970 *Fucusopsis sulcatum* (Miller and Dyer) – Osgood, 380, pl. 64, fig. 1, pl. 70, fig. 1, pl. 71, fig. 5.
- 1976 *Fucusopsis* – Hakes, 27, pl. 8, fig. 2a–b.
- v 1977 *Fucusopsis angulata* Palibin – Książkiewicz, 59, pl. 2, fig. 5 [also Leszczyński, 1992, pl. 15, fig. 1].
- v 1977 *Fucusopsis striata* (Hall) – Książkiewicz, 61, pl. 2, fig. 8.
- 1978 *Fucusopsis angulata* Palibin – Radwański, 51, pl. 1, fig. 2.
- partim 1981 *Fucusopsis angulata* Palibin – Crimes *et al.*, 968, pl. 2, fig. 1 [?non pl. 2, fig. 2].
- ? 1990 *Palaeophycus striatus?* Hall – Fillion & Pickerill, pl. 11, fig. 1.
- 1990b *Fucusopsis* – Seilacher, pl. 32.2f.
- 1993 Bioglife (“Pietrificarea de la Pinsdorf”) – Contescu *et al.*, pl. 8, fig. 3.
- 1995 *Palaeophycus (Fucusopsis) angulata* Palibin in Vassoevich – Crimes & McCall, 239, fig. 4a.
- ? 1995 *Palaeophycus striatus* Hall – Crimes & McCall, 239, fig. 4b.
- 1995 *Palaeophycus sulcatus* (Miller & Dyer) – Crimes & McCall, 241, fig. 4c.

Emended diagnosis: Unbranched *Halopoa* with horizontal, relatively long and continuous furrows and wrinkles.

Material: 9 specimens (UJ TF 69–70, 87, 93, 588, 1158, 1179, (?)1570, 2507).

Description: As in Książkiewicz (1977) description of *Fucusopsis angulata* Palibin.

Remarks: The Carpathian material displays comparable features to *Halopoa imbricata* Torell (1870) and *Trichophycus sulcatum* Miller & Dyer (1877). Pemberton & Frey (1982) included *Trichophycus sulcatum* Miller & Dyer, the type material of *F. sulcatum* (Osgood, 1970), in *Palaeophycus sulcatum* (Miller & Dyer). They also excluded *F. angulata* described by Książkiewicz (1970, 1977) from this ichnospecies; however, these authors included the type mate-

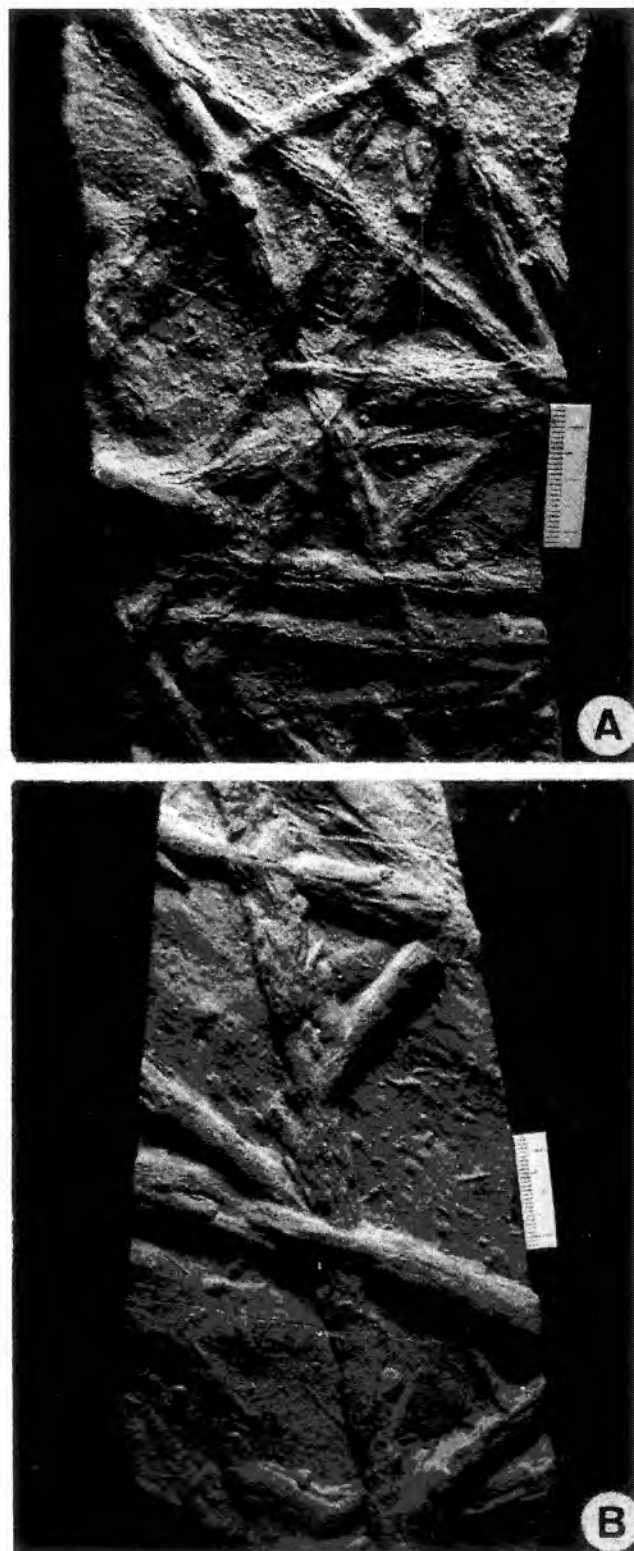


Fig. 9. *Halopoa imbricata* Torell. Soles of turbiditic sandstone beds. A. UJ TF 93, Jarmuta Formation (Senonian), Jaworki. B. UJ TF 1158, Szydłowiec beds (Senonian), Kobielnik. Scales in mm

rial of *F. angulatus* in *P. sulcatum*. They included also, reservedly, the Książkiewicz material in *Palaeophycus striatus*. Nevertheless, the mentioned ichnotaxa display features of *Halopoa*, and are excluded herein from *Palaeophycus*, and described under *H. imbricata*.

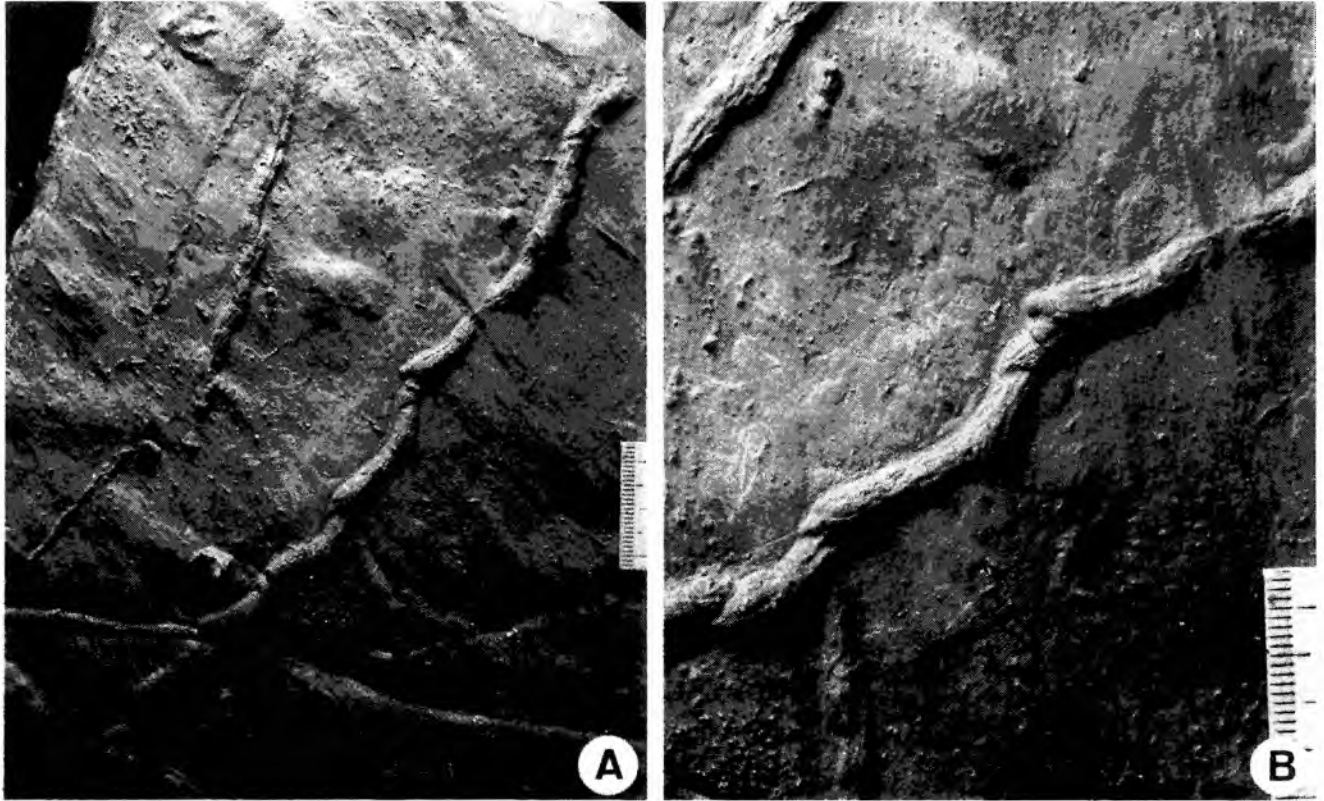


Fig. 10. *Halopoa annulata* (Książkiewicz), the holotype. Sole of a turbiditic sandstone bed. A. UJ TF 1263, Hieroglyphic beds (Eocene), Kamionka Wielka. A. General view. B. Detail of A. Scales in mm

Książkiewicz (1977) distinguished *Fucusopsis striata* (Hall) (labelled also as *Fucusopsis longistriata*) and compared it to *Palaeophycus striatus* described by Hall (1852, p. 22, pl. 10, fig. 1a). Pemberton & Frey (1982) included reservedly the Książkiewicz *Fucusopsis striata* in *Palaeophycus striatus* Hall. One of the Książkiewicz specimens (UJ TF 70) is a hypichnial striated trace fossil on the sole of bioturbated turbiditic sandstone, lacking wall. It displays features of *H. imbricata* and is included in this ichnospecies.

Birkenmajer (1959) considered that *F. angulata* (= *H. imbricata*) was produced by deposit-feeding annelids.

Stratigraphic range: Lower Cambrian (Seilacher, 1990b; Jensen, 1997) – Middle Miocene (Crimes & McCall, 1995).

Halopoa annulata (Książkiewicz 1977)

Figs. 10, 15

*v partim 1970 *Fucusopsis annulata* ichnosp. n. – Książkiewicz, 286, fig. 1r2 (non fig. 1r1).

v 1977 *Fucusopsis annulata* Książkiewicz, 60, pl. 2, figs. 6-7.

Diagnosis: Commonly branched *Halopoa* with perpendicular constrictions.

Material: 10 specimens (UJ TF 71, 587, 767, 1263 (holotype), 1525, 1696, 2503-2504, 2506, 2509).

Remarks: The discussed ichnotaxon, described by Książkiewicz as *Fucusopsis annulata*, is included in *Halopoa* Torell in this paper. *F. annulata* was reservedly included in *Palaeophycus alternus* Pemberton & Frey (1982). In the

same year, D'Alessandro included *F. annulata* Książkiewicz (1970, non 1977) in *Radionereites* Gregory. *Fucusopsis annulata* described by Książkiewicz in 1970 without designation of the holotype, comprises two different trace fossils. In 1977, Książkiewicz designated the holotype, which corresponds only to the specimen illustrated in 1970 in fig. 1r2. The specimen illustrated in fig. 1r1 is related to *Imponoglyphus* Vialov in this paper. Irrespective of these facts, D'Alessandro (1982) included both these specimens of *F. annulata* Książkiewicz 1970 non 1977 in *Radionereites* Gregory. However, D'Alessandro *et al.* (1987) then excluded the material of D'Alessandro (1982) from *Radionereites* and erected for it a new ichnogenus, *Rutichnus*, which lumps certain meniscate trace fossils. They reservedly included *F. annulata* Książkiewicz (1977, non 1970) in *Rutichnus* and suggested the presence of a meniscate internal structure in the Książkiewicz specimens.

The Książkiewicz material, including the holotype, does not display any evidences of internal meniscate structure, including in specimens sectioned along the trace fossils. It displays, however, features of *Halopoa* (see the discussion of this ichnogenus). The morphology of *H. annulata* is due to a special behaviour of tracemaker. Apart from repeatedly reworking of sediment along the same general course and the outward tension of the sediment typical of *Halopoa*, the tracemaker moved by steps searching obliquely in sediment, retreated, and repeated its action along wide, shallow, vertical or oblique, and asymmetrical U-shaped sub-courses. This resulted in the occurrence of per-

pendicular constrictions: the wider parts of the sole expressions are the bases of the U-shape segments. Occasionally, tracemaker changed the general course of its burrowing and this resulted in formation of branchings. The unique behaviour of *H. annulata* resembles the behaviour of *Trichophycus* Miller & Dyer (Geyer & Uchman, 1995).

Stratigraphic range: Paleocene (Książkiewicz, 1977) – Lower Oligocene (personal observations, Malcov Formation, Samorody near Nowy Targ in the Polish Carpathians).

Hormosiroidea Schaffer 1928

Ichnospecies included in *Hormosiroidea* Schaffer:

- ? 1856 *Corallinites rosarium* Massal. – Massalongo, 41, pl. 6, fig. 4.
- partim 1877 *Fucoides Moeschii* Hr. – Heer, 113, pl. 39, fig. 15b, pl. 40, 5a, 6a, 11 [non pl. 40, fig. 7a, ?non pl. 40 fig. 12a].
- ?non 1888 *Taenidium carboniferum* Sacc. – Sacco, 14, pl. 2, fig. 1.
- 1897 *Halimeda Fuggeri* Lor. – Lorenz von Liburnau, 177, pl. 1.
- 1902 *Halimedites Fuggeri* Lor. – Lorenz von Liburnau, 710, pls. 1-2
- 1908 *Spongolithus annulatus* Fr. – Fritsch, 16, pl. 12, fig. 17.
- 1928 *Hormosiroidea florentina* n. gen. n. sp. – Schaffer, 215, fig. 3.
- 1959 *Hormosiroidea* – Seilacher, tab. 2, fig. 20.
- 1962 *Rhabdoglyphus grossheimi* Vassoevich – Bouček & Eliáš, 146, pl. 8, fig. 3 (also Vialov, 1971, 91, fig. 3).
- 1962 *Hormosiroidea florentina* – Häntzschel, W241.
- 1965 *Hormosiroidea florentina* – Häntzschel, 47.
- 1965 *Halimedites fuggeri* – Häntzschel, 42.
- 1970 *Hormosiroidea florentina* Schaffer – Osgood, pl. 78, fig. 7.
- ? 1970 Ichnofossil gen. et sp. indet. – Meiburg & Speetzen, 12, figs. 1-3.
- partim 1970 *Rhabdoglyphus* ichnosp. a – Książkiewicz, 285, fig. 1h, k (non fig. 1i-j).
- 1971 *Fustiglyphus annulatus* gen. et sp. n. – Vialov, 91, fig. 3.
- ? 1972 *Hormosiroidea* – Frey & Chows, 37, pl. 5G-H.
- 1975 *Hormosiroidea florentina* – Häntzschel, 70, fig. 43.3.
- 1975 *Halimedites fuggeri* – Häntzschel, 65, fig. 42.1.
- v 1977 *Rhabdoglyphus caliciformis* n. ichnosp. – Książkiewicz, 66, pl. 3, figs. 6, 11, text-fig. 6c-d.
- v ?non 1977 *Rhabdoglyphus sulcatus* n. ichnosp. – Książkiewicz, 67, pl. 3, fig. 9, text-fig. 6e.
- v 1977 *Rhabdoglyphus spinosus* n. ichnosp. – Książkiewicz, 66, text-fig. 6b, pl. 3, figs. 7-8.
- v ?non 1977 *Rhabdoglyphus compositus* n. ichnosp. – Książkiewicz, 67, pl. 3, fig. 9, text-fig. 6.
- 1977a *Hormosiroidea florentina* Schaffer – Seilacher, 309, fig. 6n.
- non 1977a *Hormosiroidea beskidensis* – Seilacher, 309, fig. 6k-l.
- 1977 *Hormosiroidea florentina* Schaffer – Chamberlain, 14, figs. 2q, 5G.
- 1979 *Hormosiroidea florentina* Schaffer – Chamberlain, 17, part of fig. 3.
- 1979 *Fustiglyphus roselandensis* new species – Boyer, 75, figs. 2-3.
- non 1985 *Hormosiroidea canadensis* n. ichnosp. – Crimes & Anderson, 325, fig. 8.1-9
- ? 1979 *Hormosiroidea* – Powichrowski, fig. 3.4.
- ?non 1989 *Hormosiroidea arumbera* sp. nov. – Walter *et al.*, 244, figs. 14D-E, 15B, D.
- non 1990 *Hormosiroidea* isp. – Bryant & Pickerill, 49, fig. 4.
- non 1991 *Hormosiroidea* (*Saerichnites*) cf. *beskidensis* (Plička) – Crimes & Crossley, 32, fig. 3d-e (= *Saerichnites abruptus* Billings).
- 1993 *Fustiglyphus annulatus* Vialov – Stanley & Pickerill, 58, figs. 2-3A-D.
- partim 1993 *Rhabdoglyphus grossheimi* Vassoevich – Stanley & Pickerill, 62, fig. 5I (copy from Książkiewicz, 1977, fig. 6b).
- v 1995 *Hormosiroidea florentina* Schaffer – Uchman, fig. 15A.
- ?non 1997 *Fustiglyphus* isp. – Jensen, 50, fig. 34B.

non 1997 "*Hormosiroidea*" isp. – Jensen, 56, figs. 37A-B, ?34A.

For synonymy of *Fustiglyphus annulatus* Vialov see Stanley & Pickerill (1993).

Emended diagnosis: Subspherical bodies joined by horizontal string. Additional, usually oblique strings can emerge from the chambers.

Discussion: Separation of trace fossils described herein under *Hormosiroidea* Schaffer at the ichnogenetic level is rather the problem of tradition and minor morphological features than use of significant diagnostic features.

Seilacher (1977a) regarded the spherical "chambers" of *Hormosiroidea* as sectioned vertical burrows that protrude from the horizontal burrow toward the bottom. He included *Saerichnites* Billings and *Rhabdoglyphus* Vassoevich in *Hormosiroidea* Schaffer. This ichnotaxon was tentatively included in the graphoglyptids (Seilacher, 1977a). Such a concept of *Hormosiroidea* cannot be accepted.

The type ichnospecies of *Hormosiroidea*, *H. florentina* Schaffer (1928), consists of a row of small bulbs connected by a string (Schaffer, 1928; Häntzschel, 1975, p. W70, fig. 40.3) (Fig. 11B). This ichnotaxon was tentatively included in the graphoglyptids (Seilacher, 1977a). *Saerichnites* consists of one or two parallel rows of casts of vertical shafts (Uchman, 1995). Relation of *Saerichnites* to *H. florentina* is problematic. Probably, the bulbs of *H. florentina*, which are much greater than the string diameter and which tend to be a little lobate in outline, do not represent vertical burrows, but more likely breeding (?) structures. Thus, single or double rows of vertical or subvertical burrows or single or double rows of casts of their outlets represent a separate ichnogenus *Saerichnites* Billings (Uchman, 1995).

Hormosiroidea Schaffer is proposed as the proper name for the discussed trace fossils. Older names (see the list of ichnotaxa included in *Hormosiroidea*) are either applied for trace fossils recently described under other ichnogenera or can be treated as forgotten (nomen oblitum) (see Stanley & Pickerill (1993).

Stanley & Pickerill (1993) discussed the taxonomy of *Rhabdoglyphus* Vassoevich (= *Protovirgularia* McCoy in this paper) and *Fustiglyphus* Vialov. They kept these ichnotaxa separate, as well as *Hormosiroidea* Schaffer. Nevertheless, similarities between *Fustiglyphus* and *Hormosiroidea* are clearly distinct (Fig. 11), as noticed by Osgood (1970) and Häntzschel (1975), and these ichnotaxa are comparable at the ichnogenetic level and the differences between them can be regarded as these at the ichnospecies level. Therefore, *Fustiglyphus* Vialov is a junior objective synonym of *Hormosiroidea* Schaffer. The chambers of *Fustiglyphus* were interpreted also as possible brood structures, similarly to interpretation of *Hormosiroidea florentina* Schaffer (Uchman, 1995).

Chamberlain (1977) included with hesitation, expressed by "cf.", a few taxa in *Hormosiroidea*. These are: *Halimeda saporta* Fuchs (1894a), *Hormosira moniliformis* Heer (1877), and *Arthroderon difussum* (Ulrich, 1904). However, these forms represent body fossils of large foraminifers and cannot be included in *Hormosiroidea*.

The groove-mound traces, described from deep-sea floor of the Arctic Canada Basin were compared with *Hor-*

mosiroidea and *Rhabdoglyphus* (Kitchell *et al.*, 1978).

Hormosiroidea annulata (Vialov 1971)

Figs. 11–13

- * 1962 *Rhabdoglyphus grossheimi* Vassoevich – Bouček & Eliáš, 146, pl. 7, fig. 1, pl. 8, figs. 2 [copied by Osgood, 1970, pl. 78, figs. 8–9).
- partim 1970 *Rhabdoglyphus* ichnosp. a – Książkiewicz, 285, fig. 1h, k (non fig. li–j).
- * 1971 *Fustiglyphus annulatus* gen. et sp. n. – Vialov, 91, fig. 3.
- v 1977 *Rhabdoglyphus caliciformis* n. ichnosp. – Książkiewicz, 66, pl. 3, figs. 6, 11, text-fig. 6c.
- v 1977 *Rhabdoglyphus* aff. *caliciformis* n. ichnosp. – Książkiewicz, 66, text-fig. 6d.
- v 1977 *Rhabdoglyphus sulcatus* n. ichnosp. – Książkiewicz, 67, pl. 3, fig. 9, text-fig. 6e.
- v? 1977 *Rhabdoglyphus sulcatus* n. ichnosp. – Książkiewicz, 67, pl. 3, fig. 9, text-fig. 6e.
- v *Rhabdoglyphus spinosus* n. ichnosp. – Książkiewicz, 66, text-fig. 6b, pl. 3, figs. 7–8.
- 1979 *Fustiglyphus roselandensis* new species – Boyer, 75, figs. 2–3.
- ? 1993a *Fustiglyphus roselandensis* Boyer – Metz, 170, fig. 2.
- 1993 *Fustiglyphus annulatus* Vialov – Stanley & Pickerill, 58, figs. 2–3A–D.
- partim 1993 *Rhabdoglyphus grossheimi* Vassoevich – Stanley & Pickerill, 62, fig. 5I (copied from Książkiewicz, 1977, fig. 6b).

For additional synonymy of *Fustiglyphus annulatus* Vialov see Stanley & Pickerill (1993).

Emended diagnosis: Straight or rarely winding *Hormosiroidea* with angular, trapezoid, oval, semispherical or arcuate outline of chamber-like bodies, which are regularly or irregularly distributed along the string. Thin strings, locally

branched, may emerge from the chamber-like bodies.

Material: 10 specimens (UJ TF 181–182, 710, 726, 1175, 1505, 1728, 1780, 2018, one specimen in the Naturhistorisches Hofmuseum in Vienna).

Description: As in the diagnosis and in the descriptions of the Książkiewicz (1977) ichnotaxa included in *H. annulata*.

Remarks: Stanley & Pickerill (1993) only partially included the material of Bouček & Eliáš (1962) in *Fustiglyphus annulatus* (Vialov). They retained the Bouček & Eliáš' (1962; pl. 8, fig. 2) specimen in *Rhabdoglyphus grossheimi* Vassoevich. However, this cannot be accepted. Also in Bouček & Eliáš (1962, pl. 7, fig. 1 and pl. 8, fig. 2), are illustrated trace fossils with chambers, however not so well preserved as in pl. 8, fig. 3. The drawing of Bouček & Eliáš' specimen in pl. 8, fig. 2 in Stanley & Pickerill (1993, fig. 5A) is simplified and does not show important details. All these trace fossils are included in *Hormosiroidea annulata* (Vialov) in this paper.

The specimen UJ TF 994 (Fig. 13) probably belongs to *H. annulata*.

Stanley & Pickerill (1993) regarded the chambers of *H. annulata* as brood structures, which is probable. It is difficult to explain the morphology of this trace fossil as a deposit feeding structure as was previously suggested (Bouček & Eliáš, 1962; Chamberlain, 1977). The thin strings that come out from chambers (e.g. Stanley & Pickerill, 1993) and cross bedding, i.e. in the direction of the sea-floor, can be produced by juvenile tracemakers leaving the chambers or by predators (Fig. 11).

Strobilorhappe Książkiewicz 1968

Ichnospecies included in *Strobilorhappe* Książkiewicz:

- v 1968 *Strobilorhappe clavata* n. "sp." – Książkiewicz, 8, pl. 1, figs. 4–5.
- v 1968 *Strobilorhappe pusilla* n. "sp." – Książkiewicz, 8, pl. 1, fig. 6.
- v 1970 *Strobilorhappe clavata* Książkiewicz – Książkiewicz, 288, fig. 1d, e.
- v 1970 *Strobilorhappe pusilla* Książkiewicz – Książkiewicz, 288, fig. 1c.
- v 1977 *Strobilorhappe clavata* Książkiewicz – Książkiewicz, 82, pl. 5, figs. 10–11, text-fig. 11a–r.
- v 1977 *Strobilorhappe pusilla* Książkiewicz – Książkiewicz, 84, pl. 5, fig. 12.
- v partim 1977 *Strobilorhappe glandifer* n. ichnosp. – Książkiewicz, 84, pl. 11, fig. 16, text-fig. 11s–z.
- 1975 *Strobilorhappe clavata* – Hantzschel, W112, fig. 67, 4a.
- 1977 *Strobilorhappe clavata* Książkiewicz – Chamberlain, 18, fig. 2z (copied in Stanley *et al.*, 1977; 268, fig. 18, and in), 7D.
- 1979 *Strobilorhappe clavata* Książkiewicz – Chamberlain, 17, fig. 3.
- ? 1987a *Strobilorhappe* – Pickerill, 129, fig. 3 (copy in: Pickerill, 1987b; 387, fig. 3s).
- ? 1990 *Strobilorhappe* ichnosp. – Mikulaš, 327, pl. 8, fig. 2.
- 1990 *Strobilorhappe pusilla* – Uchman, pl. 1, fig. 5 [lapsus calami].
- ? 1993 *Strobilorhappe* cf. *clavata* Książkiewicz – Miller, 23, fig. 6E.

Emended diagnosis: Horizontal trace fossils consisting of central stem and numerous lateral short, blunt, clavate branches.

Remarks: The smooth version of *Ophiomorpha annulata*

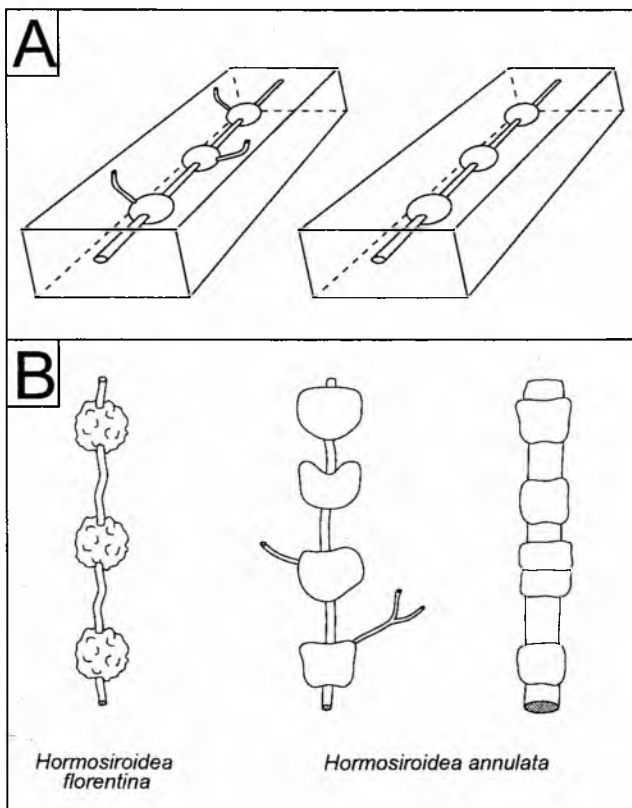


Fig. 11. *Hormosiroidea*. A. General model, with and without side branchings. B. Ichnospecies of *Hormosiroidea*

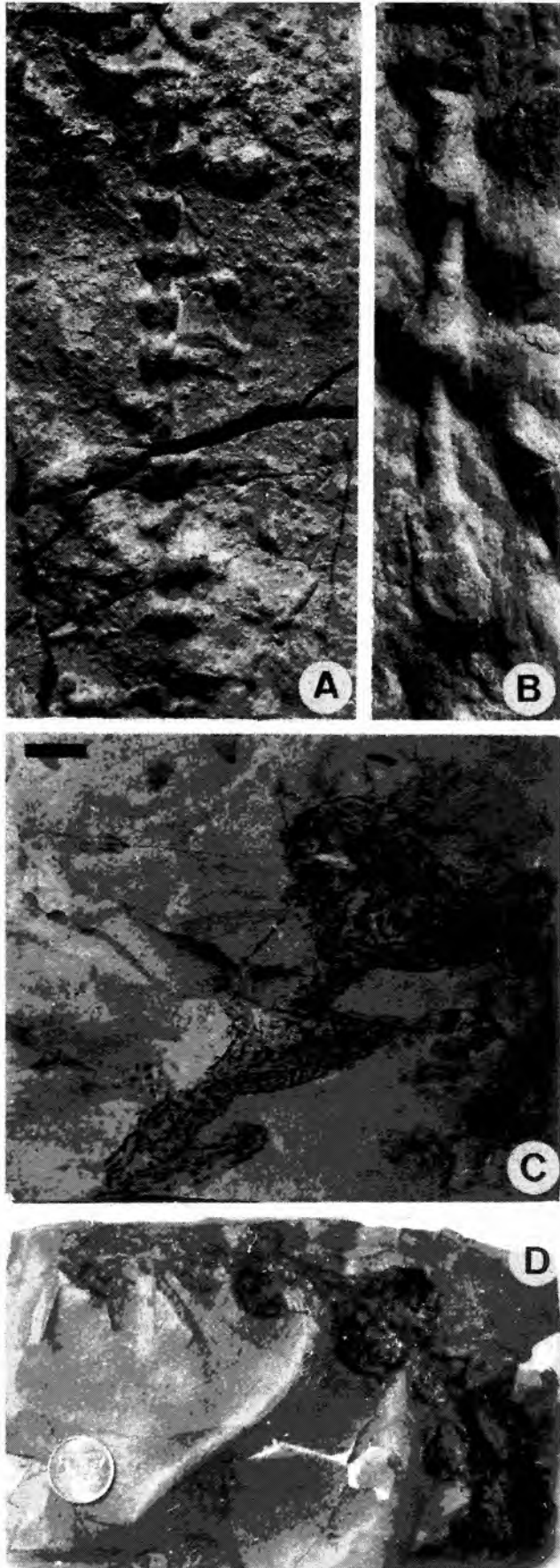


Fig. 12. *Hormosiroidea annulata* (Vialov). A. UJ TF 710, Ropianka beds (Senonian–Palaeocene), Lubomierz. Sole of turbiditic sandstone bed (labelled as *Rhabdoglyphus spinosus*). B. UJ TF 2018, Hieroglyphic beds (Eocene), Dobra Szlachecka. Sole of turbiditic sandstone bed. Coll. B. Gucik (labelled as *Rhabdoglyphus caliciformis*). C. UJ TF 726, Szczawa (part of label lost). Composite endichnial form in marlstone reworked by ?*Chondrites*. D. Specimen in the Naturhistorisches Hofmuseum in Vienna. Cretaceous flysch deposits, marlstone, Muntigl near Salzburg. Endichnial form. Scale bar in A–C = 1 cm; diameter of the coin in D = 19 mm



Fig. 13. ?*Hormosiroidea* isp. UJ TF 994, Siliceous marls (Turonian), Huwniki. Endichnial form in marlstone bed. Scale in mm

(Książkiewicz) described by Książkiewicz (1977) as *Sabularia simplex* Książkiewicz (Uchman, 1995) displays uncommon short side branches, commonly clavate in shape. They are very similar in morphology to *Strobilorhapse glandifer* Książkiewicz (Fig. 14), labelled earlier as *Sabularia glandifer*. Probably, *Strobilorhapse glandifer* is a fragment of *A. annulata* var. *simplex*. However, *S. glandifer* probably represents different behaviour of the same trace-maker. *Strobilorhapse clavata* can be a breeding structure. In contrast, *O. annulata* is a pascichnial-domichnial trace fossil. For this reason, they are separated, as was *Gyrolithes* from *Ophiomorpha* (Bromley & Frey, 1974).

The ichnospecies of *Strobilorhapse*, *S. clavata*, *S. pusilla*, and *S. glandifer* (Fig. 14) are retained without changes as in the Książkiewicz (1977) monograph.

Strobilorhapse is interpreted as a feeding trace (pascichnion) produced by ?worms (Chamberlain, 1977). Książkiewicz (1977) interpreted it in the same way and tentatively indicated polychaetes as their producers. *Strobilorhapse* occurs from Ordovician (Chamberlain, 1977) to Upper Eocene (Książkiewicz, 1977).

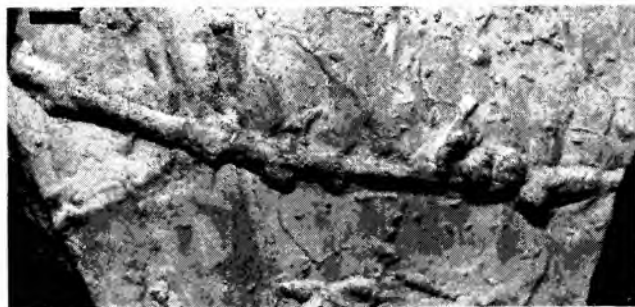


Fig. 14. *Strobilorhaphic glandifer* Książkiewicz. Sole of turbiditic sandstone bed. UJ TF 1510, Tylmanowa (lithostratigraphic unit unknown, label lost). Scale bar = 1 cm

Imponoglyphus Vialov 1971

Ichnospecies included in *Imponoglyphus* Vialov:

- 1970 Ex.aff. *Rhabdoglyphus* – Książkiewicz, 285, fig. 1n.
- partim 1970 *Fucusopsis annulata* ichnosp. nov. – Książkiewicz, 286, fig. 1r1.
- 1971 *Imponoglyphus torquendus* gen. et sp. nov. – Vialov, 89, pl. 2, figs. 1a-b, 2 (copied in Häntzschel, 1975, fig. 45.1a-c).
- ? 1980 *Imponoglyphus kevadiensis* ichnosp. n. – Badve & Ghare, 122, pl. 1, fig. 2, text-fig. 6.
- 1984 *Imponoglyphus* – Mason, 8, fig. 2.
- ? 1988 *Imponoglyphus torquendus* Vialov – Yang, 7, pl. 1, fig. 6a.
- 1989 *Imponoglyphus* – Suarez de Centi *et al.*, 364, pl. 3a-b.

Diagnosis: Horizontal, slightly winding trace fossil composed of invaginated, regularly spaced cones (modified after Teichert in Häntzschel, 1975).

Remarks: It is not excluded that *Imponoglyphus* is a preservational version of *Taenidium* Heer. Chamberlain (1979, fig. 3) drew *Taenidium* as a chain of cone-in-cone structures.

Cone-in-cone horizontal trace fossils, which resemble *Imponoglyphus*, have been described (no ichnotaxonomic name) by Högbom (1925) from the Cambrian of Sweden.

Imponoglyphus torquendus Vialov 1971

Fig. 15

- v 1970 Ex.aff. *Rhabdoglyphus* – Książkiewicz, 285, fig. 1n.
- v partim 1970 *Fucusopsis annulata* ichnosp. nov. – Książkiewicz, 286, fig. 1r1.
- * 1971 *Imponoglyphus torquendus* gen. et sp. nov. – Vialov, 89, pl. 2, figs. 1a-b, 2 (copied in Häntzschel, 1975, fig. 45.1a-c).

Diagnosis: As for the ichnogenus.

Material: 2 specimens (UJ TF 634, 638).

Description: As in the diagnosis, hypichnial trace fossil. Dimensions are: 6–7 mm wide, individual cones are 1.5–3.0 mm long.

Remarks: *I. torquendus* Vialov described by Yang (1988, pl. 1, fig. 6a) is a very small trace fossil, about 1 mm wide, and its cone-in-cone structure can be hardly visible in the photograph.

Planolites Nicholson 1873

Diagnosis: Unlined, rarely lined, rarely branched, straight to tortuous, smooth to irregularly walled or annulated trace fossils, circular to elliptical in cross-section, of variable di-

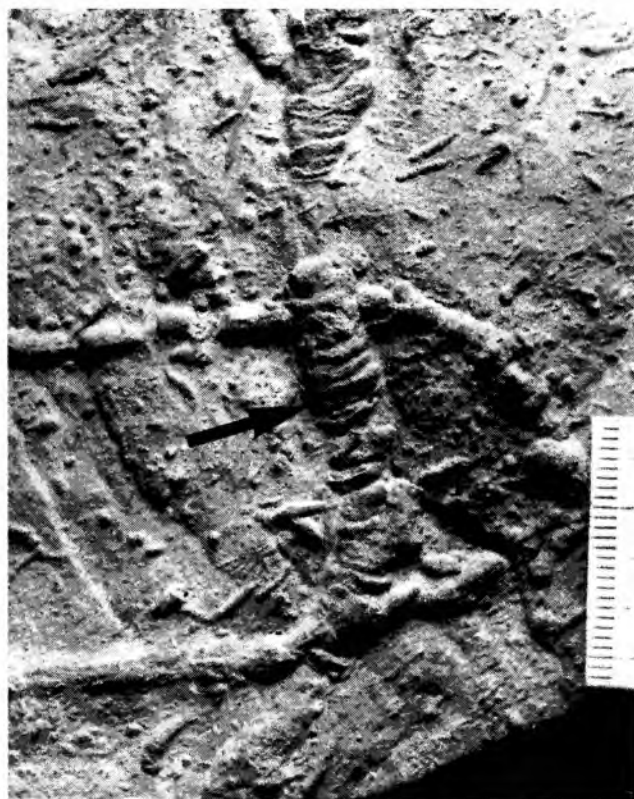


Fig. 15. *Imponoglyphus torquendus* Vialov (arrowed) and *Halopoa annulata* (Książkiewicz). Sole of turbiditic sandstone bed. UJ TF 634, Beloveža Formation (Eocene), Stara Wieś. Scale in mm

mensions and configurations: fill essentially structureless, differing in lithology from host rock (after Pemberton & Frey, 1982 and Fillion & Pickerill, 1984).

Remarks: Differences between *Planolites*, *Palaeophycus*, and *Macaronichnus* were discussed by Pemberton & Frey (1982), Fillion (1989), Fillion & Pickerill (1990), and Bromley (1996, p. 262).

Planolites is an eurybathic, extremely facies-crossing ichnogenus referred to polyphyletic vermiform deposit-feeders producing active backfilling (e.g. Pemberton & Frey, 1982; Fillion & Pickerill, 1990, and references therein).

Planolites occurs from the Precambrian to the Recent (Häntzschel, 1975).

Planolites reinecki Książkiewicz 1977

- *v 1977 *Planolites reinecki* n. ichnosp. – Książkiewicz: 64, pl. 2, fig. 9.
- 1994 *Planolites constriamulatus* isp. n. – Stanley & Pickerill, 120, figs. 2-3.

Material: 1 specimen, the holotype (UJ TF 1015).

Diagnosis: *Planolites* characterized by both longitudinal striations and transverse annulations superimposed in the same specimen (after Stanley & Pickerill, 1994).

Description: As in Książkiewicz (1977) with the following addition: there is no evidence of lining in the cross-section of the holotype.

Remarks: *Planolites reinecki* Książkiewicz was reservedly included in *Palaeophycus alternus* Pemberton & Frey

(1982). However, the holotype of *Planolites reinecki* does not display a lining or any other features of *Palaeophycus*. Stanley & Pickerill (1994) distinguished *Planolites constriannulatus* isp. n. for trace fossils that display the same features as *P. reinecki*. Thus, *P. constriannulatus* is the junior objective synonym of *P. reinecki* Książkiewicz.

Planolites heverleyensis Billings 1862

Fig. 16

- * 1862 *Planolites heverleyensis* (n. sp.) – Billings, p. 97, text-fig. 86.
- v 1977 *Sabularia ramosa* n. ichnosp. – Książkiewicz, 71, text-figs. 8, 9a-d.

Synonymy of this ichnospecies in Pemberton & Frey (1982).

Diagnosis: Relatively large, smooth, straight to gently curved or undulose cylindrical *Planolites* (after Pemberton & Frey, 1982).

Material: 8 specimens (TF UJ 735, 842, 999, 1583-1584, 1752, 1802, 1845).

Description: Cylindrical, horizontal to oblique, unlined trace fossils, circular to elliptical in cross-section, 1.5–5.0 mm in diameter, filled with sediment different in colour and/or lithology from the host rock.

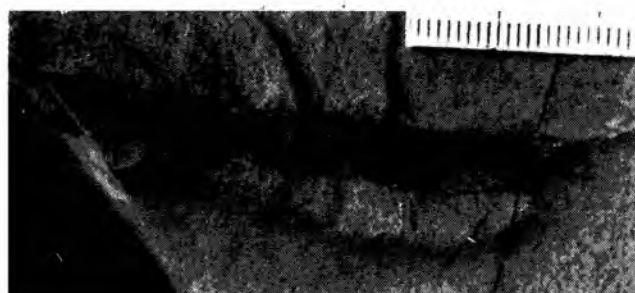


Fig. 16. *Planolites heverleyensis* Billings. Endichnial form in marlstone bed. UJ TF 999. Siliceous marls (Turonian), Huwniki (part of label lost). Scale in mm

Remarks: *Sabularia ramosa* Książkiewicz, including the holotype (UJ TF 842), displays features of *Planolites heverleyensis* Billings. It has no lining, and is actively filled. The active filling is indicated by local faint menisci. However, some specimens originally labeled as *S. ramosa* (UJ TF 383, 384) display features of *Thalassinoides*. One specimen (UJ TF 1583) is labelled as *Sabularia flexuosa*. This name was never used by Książkiewicz in publications. This specimen displays features of *P. heverleyensis*.

Palaeophycus Hall 1847

Diagnosis: Branched or unbranched, smooth or ornamented, lined, essentially cylindrical, predominantly horizontal trace fossils of variable diameter; fill typically structureless, of the same lithology as the host rock (after Pemberton & Frey, 1982).

Remarks: The distinction between *Palaeophycus*, *Planolites*, and *Macaronichmus* is partially controversial (Pemberton & Frey, 1982; Fillion, 1989; Fillion, & Pickerill, 1990). *Palaeophycus* is a eurybathic facies-crossing ichnogenus, produced probably by polychaetes, which occurs from the Precambrian to the Recent (Pemberton & Frey, 1982).

Palaeophycus tubularis Hall 1847

Fig. 17

Diagnosis: Smooth, unornamented *Palaeophycus* of variable diameter, thinly but distinctly lined (modified after Pemberton & Frey, 1982).

Material: 3 specimens (UJ TF 371, 1198, 2017).

Description: Horizontal smooth, straight, rarely curved, distinctly lined, long unbranched trace fossils, 2.8–3.1 mm in diameter, distinctly flattened in cross-section, filled with the same sediment as the host rock.



Fig. 17. *Palaeophycus tubularis* Hall. Sole of turbiditic sandstone bed. UJ TF 1198, ?Hieroglyphic beds (Eocene), Komańcza (part label lost). Scale bar = 1 cm

Chondrites Sternberg 1833

Diagnosis: Regularly branching tunnel systems consisting of a small number of mastershafts open to the surface which ramify at depth to form a dendritic network (after Osgood, 1970; Fürsich, 1974b).

Remarks: *Chondrites* is a feeding system of unknown trace makers related to infaunal deposit feeders (e.g. Osgood, 1970). According to Kotake (1991b), this ichnotaxon is produced by surface ingestors, packing their faecal pellets inside burrows. According to Seilacher (1990a) and Fu (1991), the tracemaker of *Chondrites* may be able to live under dysaerobic conditions as a chemosymbiotic organism.

Chondrites occurs from the Tommotian (Crimes, 1987) to the Holocene (e.g. Werner & Wetzel, 1981).

Chondrites intricatus (Brongniart 1823)

Figs. 18–19

- * 1823 *Fucooides intricatus* Brongniart, 311, pl. 19, fig. 8.
- 1890 *Bostricophyton Pantanellii* n. sp. – Squinabol, 183, pl. 7, fig. 5.
- 1891 *Bostricophyton Pantanellii* Squin. – Squinabol, 16, pl. C, fig. 3.
- v 1977 *Bostricophyton pantanellii* Squinabol Książkiewicz, 86, pl. 5, fig. 5 (lapsus calami).
- v 1977 *Chondrites aequalis* (Brongniart) – Książkiewicz, 78, pl.



Fig. 18. *Chondrites intricatus* (Brongniart) (arrowed). Full relief adherent to the sole of a turbiditic sandstone bed. UJ TF 709A. Siliceous marls (Turonian), Huwniki. Scale in mm

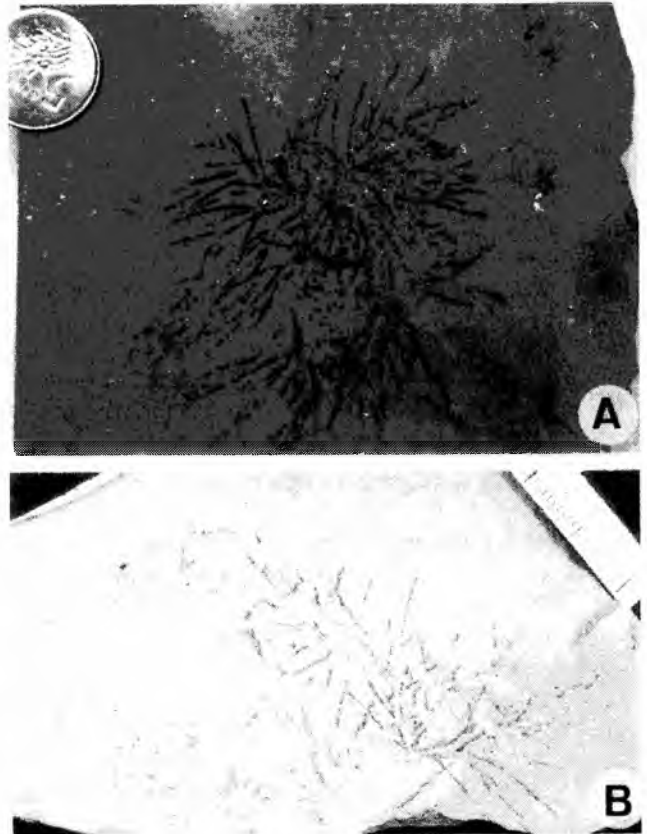


Fig. 19. *Chondrites intricatus* (Brongniart) with deformed filling. **A.** Specimen from the Gebhard's collection in the Naturhistorisches Hofmuseum in Vienna. Bisamberg near Langenersdorf. ?Cretaceous flysch of the Wienerwald. The coin is 19 mm in diameter. **B.** UJ TF 961, endichnial form, Ropianka beds (Senonian–Paleocene), Biała Wyżna (labelled as *Bostricophyton pantanellii*). The coin in A is 19 mm in diameter, scale for B in mm

- 4, fig. 6.
 v partim 1977 *Chondrites expansus* Fischer-Ooster – Książkiewicz, 79, pl. 4, fig. 3.
 v 1977 *Chondrites filiformis* Fischer-Ooster – Książkiewicz, 79, pl. 4, fig. 8.
 v 1977 *Chondrites intricatus* (Brongniart) – Książkiewicz, 80, pl. 4, fig. 5.
 v partim 1977 *Chondrites flexilis* Fischer-Ooster – Książkiewicz, 79, in collection [non pl. 4, fig. 10 = large foraminifer].

Diagnosis: Small trace fossil composed of numerous downward radiating branches. The angle of branching is usually less than 45 degrees (modified after Fu, 1991).

Material: 21 specimens (UJ TF 147, 149, 153, 361, 393, 398, 604, 657, 709A, 889, 895, 960, 962, 1215, 1309, 1654–1655, 2516, 3 specimens in the Gebhard's collection in the Naturhistorisches Hofmuseum in Vienna).

Description: A system of tree-like branching, downward penetrating, markedly flattened tunnels, 0.4–10 mm in diameter. Branches form sharp angles. The tunnels are filled with sediment lighter or darker than the host rock. In cross-section, *Chondrites* appears as patches of small, circular or elliptical spots, 0.5–1.0 mm in diameter (compare e.g. Werner & Wetzel, 1981).

Chondrites intricatus occurs in variable substrates including medium-grained turbiditic sandstone exhibiting Tb lamination of Bouma (1962), but mostly in fine-grained siliciclastic and calcareous rocks. In one case (UJ TF 709A), it occurs on the sole of turbiditic sandstone in full relief filled with dark fine-grained material (Fig. 18).

Remarks: After revision of the systematics of *Chondrites*, only 4 ichnospecies are considered as useful instead of the 170 ichnospecies distinguished in the past (Fu, 1991). The problem of systematics of *Chondrites* was noticed by Książkiewicz (1977), who distinguished 9 ichnospecies. Nevertheless, most of the specimens from the Książkiewicz mate-

rial represent the same pattern referred by Fu (1991) to *Ch. intricatus*, *Ch. targionii*, *Ch. patulus*, or *Ch. recurvus* (see the synonymy list). Many specimens (UJ TF 599, 670, 680, 703, 758, 778, 959, 1181, 1641, 1644, 1650, 1656–1657, 1678, 2023) are poorly preserved and their ichnospecific determination cannot be made.

Several trace fossils referred by Książkiewicz to *Chondrites* belong to other ichnogenera. Some specimens of *Ch. affinis* (eg. UJ TF 1641, 1646) are flattened, branched or unbranched tubes, which may be referred to *Palaeophycus* or small *Thalassinoides*. Some specimens determined as *Ch. expansus* (UJ TF 988, 2516) are radial trace fossils referred to *Glockerichnus* (see description of *Glockerichnus*). In the specimen UJ TF 1659 determined as *Ch. affinis*, there is a radial trace fossil different from *Ch. intricatus*. It displays radial branches with rounded and enlarged terminations. This is probably a new ichnogenus.

Bostricophyton pantanellii Squinabol (1890) is a branched trace fossil, which displays several features of *Chondrites intricatus*. The only difference is the non-continuous guidance of burrow filling. Squinabol indicated that the filling displays spiral pattern. However, this observation may be questioned. The segments of filling may be only arranged in an indistinct chevron pattern. The Książkiewicz

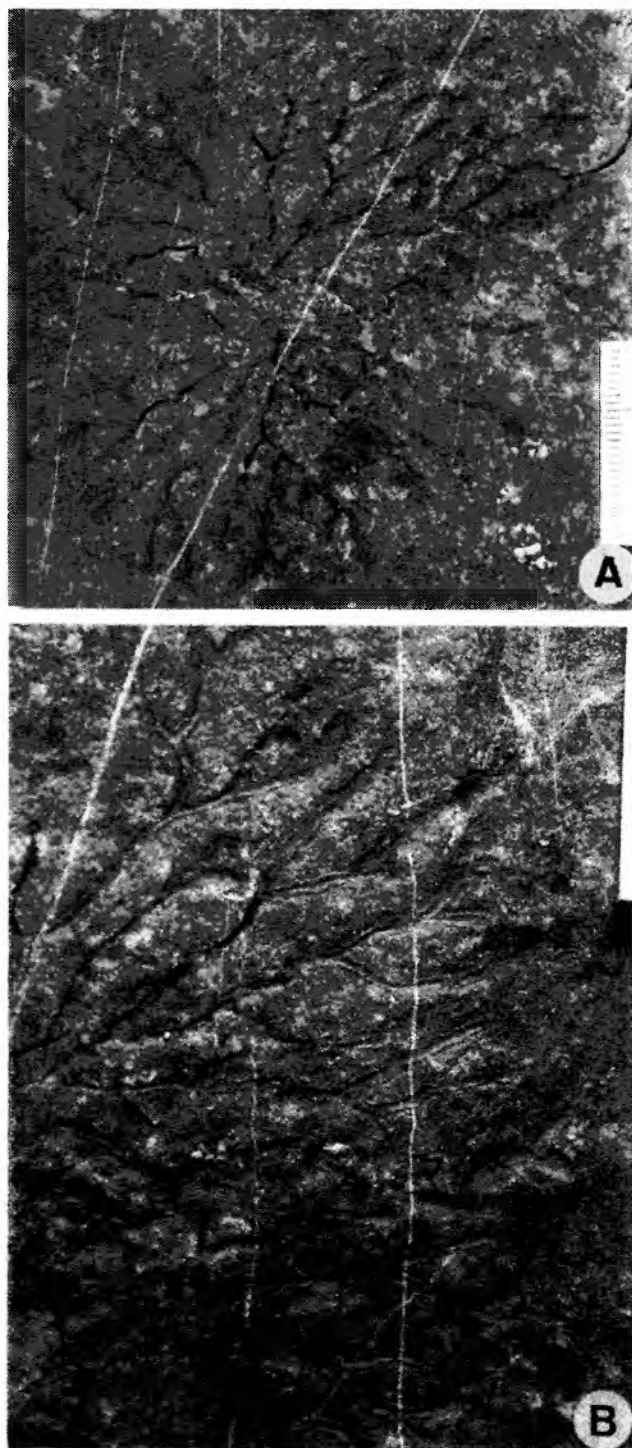


Fig. 20. A large foraminifer on sole of turbiditic sandstone bed (labelled as *Chondrites flexilis*). UJ TF 148, Ropianka beds (Senonian–Paleocene), Wola Brzezińska. A. General view. B. Detail of A. Scale in mm

material (2 specimens) display neither spiral nor chevron pattern of the filling (Fig. 19B). I have observed a few specimens of this type in the Naturhistorisches Hofmuseum in Vienna (Upper Cretaceous marls, flysch of the Northern Alps, Gebhard's collection). They have been also observed by Fuchs (1895, p. 407, 1905). Some of the specimens contain *Chondrites intricatus* with a transition from continuous

burrow fillings to discontinuous fillings. The fragments with the discontinuous fillings are identical to *Bostricophyton pantanellii* Squinabol in the Książkiewicz collection and strongly resemble Squinabol's drawing (1890, pl. 7, fig. 5) of the holotype of this ichnotaxon. Most probably this trace fossil resulted from deformation of *C. intricatus* by flowing of sediment at a certain stage of diagenesis, when burrow filling had become rigid. Fuchs (1895, p. 407), who was the first to include Squinabol's specimen in "fucoids", supposed that the features of *Bostricophyton* resulted from deformation.

The second ichnospecies of *Bostricophyton*, *B. etruscus* Squinabol (1890, p. 184, pl. 11, fig. 5) was compared by Fuchs (1895, 1905) to *Caulerpites eseri* Heer (1877), which is included in *Polykampton eseri* (Unger) (Wetzels & Uchman, 1997).

Książkiewicz (1977, pl. 4, fig. 10) illustrated specimen UJ TF 1031, a large protist, as *Ch. flexilis* (Fig. 20). It resembles *Chondrites*, but the test is visible. Moreover dichotomous branchings occur, which are not present in *Chondrites*. Large protists are commonly mistaken for trace fossils (e.g., Seilacher, 1959, pl. 2, fig. 36; Crimes *et al.*, 1981, pl. 4, fig. 2).

Chondrites targionii (Brongniart 1828)

Figs. 21–22A–B

- * 1828 *Fucoides targionii* Brongniart, 56, pl. 4, figs. 2–6.
- v 1977 *Chondrites arbuscula* Fischer-Ooster – Książkiewicz, 79, pl. 4, fig. 7.
- v ?partim 1977 *Chondrites furcatus* (Brongniart) – Książkiewicz, 79, pl. 4, fig. 1 (?non pl. 4, fig. 2)
- v 1977 *Chondrites affinis* (Brongniart) – Książkiewicz, 78, pl. 4, fig. 11.

Diagnosis: *Chondrites* characterized by well expressed primary successive branchings, which are commonly slightly curved. The angle of branching is usually sharp.

Material: 42 specimens (UJ TF 149–140, 145, 148, 150–151, 593–598, 600, 602–603, 607, 610, 612–614, 617, 619, 686, 707, 930, 994, 997, 1003, 1007, 1053, 1191, 1191A, 1642, 1645, 1648–1649, 1651, 1658, 1736, 1898, 2515A, 2585).

Description: As in the diagnosis, with the following addition: the burrow fillings are 5–6 mm in width.

Chondrites patulus Fischer-Ooster 1858

- * 1858 *Chondrites patulus* F.O. – Fischer-Ooster, 48, pl. 8, figs. 6–7.
- v 1977 *Chondrites patulus* Fischer-Ooster – Książkiewicz, 80, pl. 4, fig. 9.

Diagnosis: Small *Chondrites* system with simple branches, which branches concordantly at an obtuse angle from the main stem (modified after Fu, 1991).

Material: 1 specimen (UJ TF 1214).

Description: As in the diagnosis.

Chondrites ?recurvus (Brongniart 1823)

Fig. 22C

- * 1823 *Fucoides recurvus* – Brongniart, 309, pl. 19, fig. 4.

Diagnosis: *Chondrites* system in which branches arise only on one side of the masterbranch and which are all bent in one direction in a lyre-shaped into two bilaterally opposed directions; there are commonly one or two orders of branching, rarely a third (after Fu, 1991).

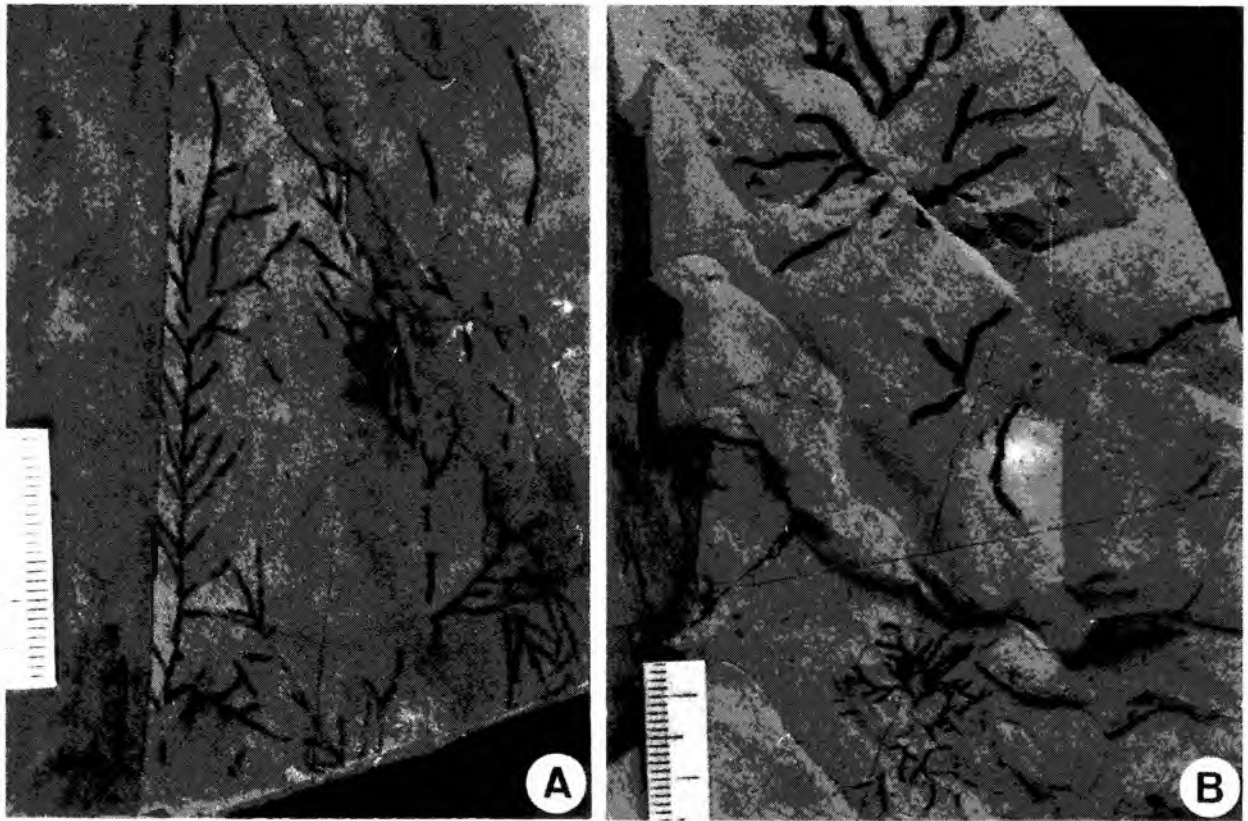


Fig. 21. *Chondrites targionii* (Brongniart). A. UJ TF 619, Inoceranian beds (Senonian–Paleocene), Lubomierz. Parallel laminated (Tb) turbiditic sandstone bed. B. UJ TF 1007, Siliceous marls (Turonian), Huwniki. Turbiditic marlstone bed (labelled as *Chondrites flexilis*). Scale in mm

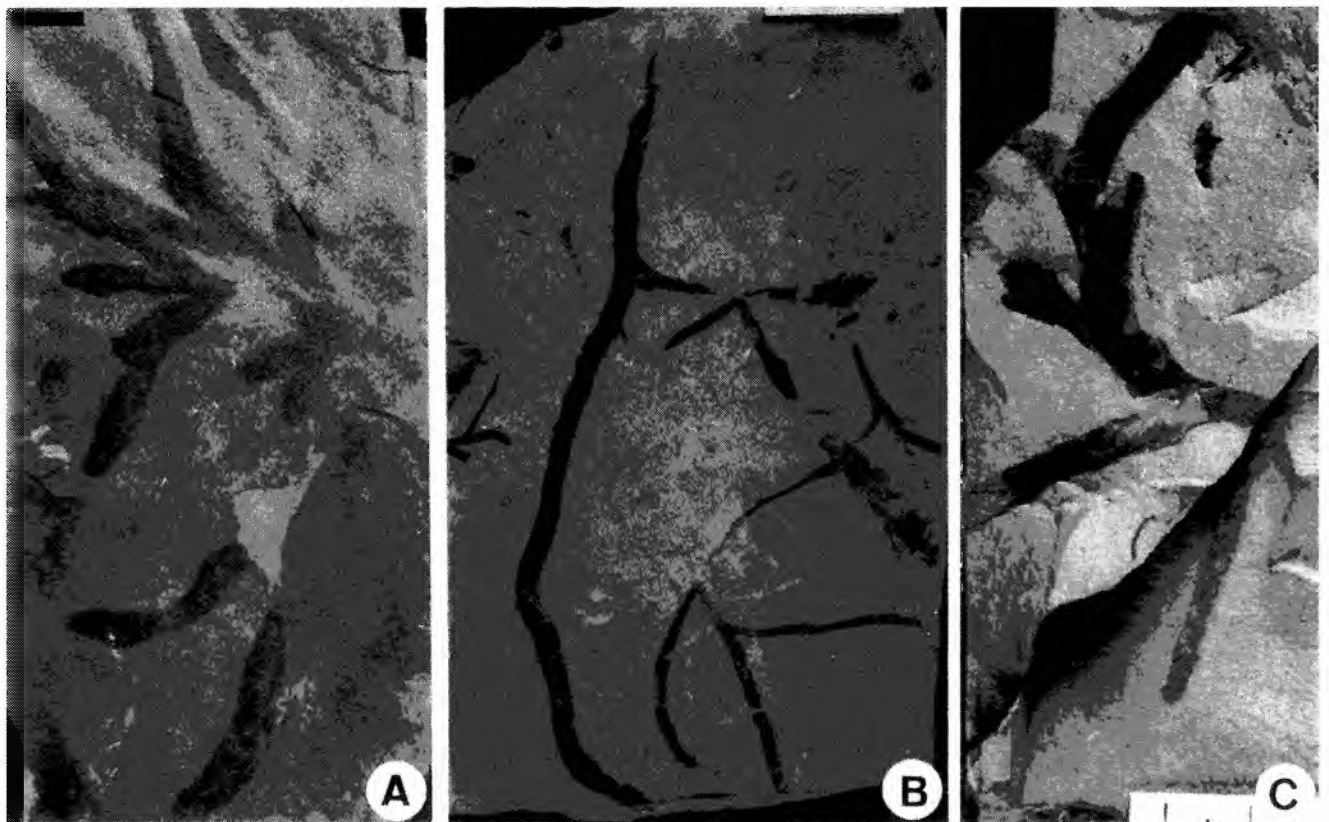


Fig. 22. A–B. *Chondrites targionii* (Brongniart), large forms. A. UJ TF 707, Variegated Shale (Paleocene–Lower Eocene), Szczawa. Turbiditic sandstone bed (labelled as *Chondrites affinis*). B. UJ TF 1003, Siliceous marls (Turonian), Huwniki. Turbiditic marlstone bed (labelled as *Chondrites affinis*). C. *Chondrites recurvus* (Brongniart), UJ TF 994. Siliceous marls (Turonian), Huwniki. Turbiditic marlstone bed. Scale bar in A = 1 cm, scales in B–C in cm

Material: 2 or 3(?) specimens (UJ TF 994, 1001(?), 1737).

Description: As in the diagnosis, with the following remarks: retrusive trace fossil. Only one branch is observed, with flattened tunnels 4–6 mm wide. Additional branches occur on the other side of the masterbranch. Therefore, the question-mark is placed in front of the ichnospecific name.

Trichichnus Frey 1970

Diagnosis: Branched or unbranched, hair-like, cylindrical, straight to sinuous trace fossils, oriented at various angles (mostly vertical) with respect to the bedding. Burrow walls distinct or indistinct, lined or unlined (after Frey, 1970 and Fillion & Pickerill, 1990).

Remarks: *Trichichnus* is present in a few specimens in the Książkiewicz collection. It was neither described nor labelled. It is especially common in marlstone specimens containing *Chondrites*.

This ichnogenus was recently discussed by Fillion & Pickerill (1990) and Uchman (1995).

Trichichnus linearis Frey 1970

Figs. 23

Diagnosis: Lined *Trichichnus* (after Frey, 1970, Fillion & Pickerill, 1990).

Material: 2 specimens (UJ TF 1003, 1007).

Description: ?Lined vertical to horizontal thread-like trace fossils, occasionally branched at sharp angle. The trace fossils are mostly 0.4–1.1 mm in diameter. Usually, the burrows are filled with darker, finer, and pyritised material than the host rock and are commonly impregnated by secondary ferruginous oxides. A ferruginous halo around the trace fossils is also common.

Remarks: Two ichnotaxa of *Trichichnus* were distinguished (Fillion & Pickerill, 1990), namely a lined (*T. linearis*) and unlined (*T. "simplex"*) trace fossil. In the examined material, only the larger specimens seem to be distinctly lined. However, the lack of the lining along the trace fossil may be connected with diagenetic processes. It is highly likely that all exceptionally long and thin *Trichichnus* were primarily lined. Thus, the two species of *Trichichnus* possibly differ only in their degree of lining. Whether this character serves as a useful ichnospecies feature is doubtful (Uchman, 1995).

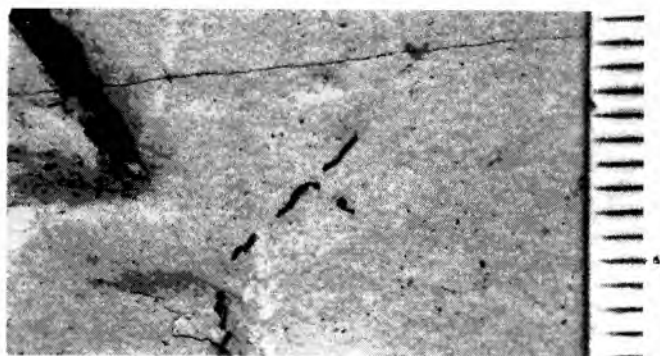


Fig. 23. *Trichichnus linearis* Frey. UJ TF 1003, Siliceous marls (Turonian), Huwniki. Turbiditic marlstone bed, parting surface. Scale in mm

Ophiomorpha Lundgren 1891

Ichnotaxa included in *Ophiomorpha* Lundgren:

- 1962 *Granularia* – Seilacher, 299, pl. 1, fig. 4,
- v 1977 *Arthrophyucus annulatus* n. ichnosp. – Książkiewicz, 56, pl. 1, figs. 8–10.
- v 1977 *Sabularia simplex* n. ichnosp. – Książkiewicz, 68, pl. 2, fig. 2, text-fig. 9e.
- v 1977 *Sabularia rudis* n. ichnosp. – Książkiewicz, 70, pl. 2, fig. 4, text-fig. 7.

Diagnosis: Simple to complex burrow systems lined at least partially with agglutinated pelletoidal sediment (modified after Howard & Frey, 1984).

Remarks: Some horizontal trace-fossil segments lacking the knobby exterior resemble *Thalassinoides* (e.g. Kern & Warme, 1974) but vertical segments are lined. *Sabularia rudis* (Książkiewicz, 1977), including the holotype, displays features of *Ophiomorpha* (Uchman, 1991a) and is included in this ichnogenus.

A certain type of flysch *Granularia* (*Ophiomorpha annulata* in this paper) differs from *Ophiomorpha nodosa* Lundgren mainly in smaller dimensions. This was regarded by Seilacher (1977a) as a small “flysch version” of *Spongeliomorpha* which in turn is closely related to *Ophiomorpha* (Bromley & Frey, 1974; Frey *et al.* 1978).

Flysch *Ophiomorpha* has been discussed by Uchman (1995).

Ophiomorpha annulata (Książkiewicz 1977)

Fig. 24

- 1962 *Granularia* – Seilacher, 299, pl. 1, fig. 4.
- v* 1977 *Arthrophyucus annulatus* n. ichnosp. – Książkiewicz, 56, pl. 1, figs. 8–10.
- v 1977 *Sabularia simplex* n. ichnosp. – Książkiewicz, 68, pl. 2, fig. 2, text-fig. 9e.
- 1982 *Ophiomorpha annulata* – Frey & Howard, figs. 2B, 4A.

Synonymy list: Uchman (1995).

Diagnosis: *Ophiomorpha*, mainly horizontal or subhorizontal, cylindrical, rarely branched, covered with elongate pellets arranged perpendicularly to the long axis of trace fossil. Sharp angles prevail at branching points. Swellings are common. In flysch deposits, commonly hypichnial, smooth and straight small specimens (usually 2–6 mm in diameter) (after Uchman, 1995).

Material: 24 specimens (UJ TF 122 (holotype), 123, 383, 386, 945, 1008, 1189, 1220, 1224, 1293, 1444, 1474, 1502, 1511–1514, 1516–1517, 1618, 1689, 1502, 2510, 2513).

Description: Usually smooth, straight or slightly curved, horizontal or slightly oblique, presumably hypichnial but also rarely endichnial or exichnial cylindrical lined trace fossils, 2–6 mm in diameter. Small indistinct knobs cover the burrow wall only locally. The trace fossils are preserved as full-reliefs. They are usually branched, with swellings (up to 8 mm in diameter) at the branching points. Branches form sharp angles. In places, the branches are very short and represent dead ends.

Remarks: This ichnotaxon was usually described as *Granularia*, but without specific designation. It was also described as *Sabularia simplex* (Książkiewicz, 1977). The latter ichnospecies was defined as a smooth, straight, rarely branched trace fossil (see also Tunis & Uchman, 1993). I observed this ichnotaxon previously in the Eocene flysch of the Istria peninsula, Slovenia (Tunis & Uchman, 1996b). The specific weathering conditions on the seashore resulted in unusually

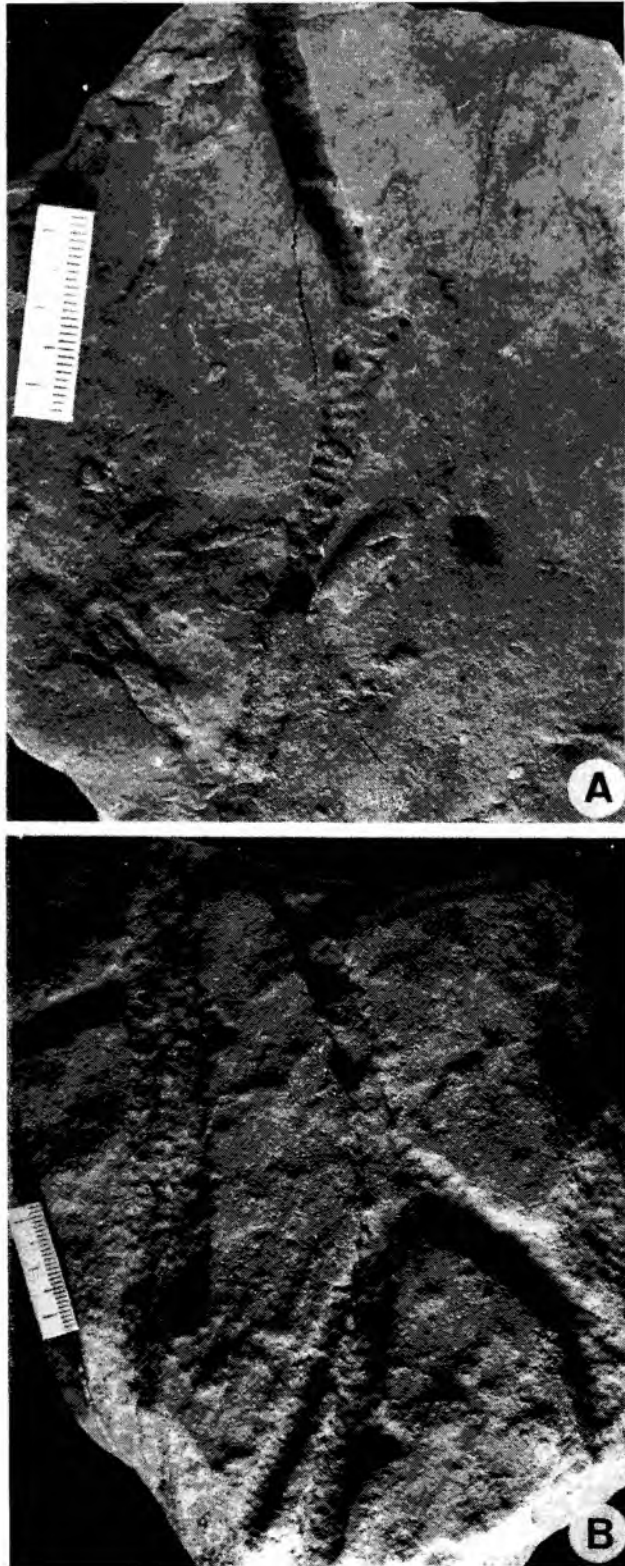


Fig. 24. *Ophiomorpha annulata* (Książkiewicz). Endichnial forms in turbiditic sandstone. **A.** UJ TF 123, Ciężkowice Sandstone (Eocene), Znamirowice. **B.** UJ TF 1444. Beloveža Formation (Eocene), Lipnica Mała. Scale in mm

well preserved details of wall and fill. Well defined elliptical silt pellets cover the walls of some specimens; the long axes of the pellets are perpendicular to the burrow axis (Uchman,

Fig. 25. Fischer-Ooster's (1858) specimens of *Halymenites* (= *Ophiomorpha rectus*). **A.** *H. incrassatus* Fischer-Ooster, holotype (= *Ophiomorpha rectus*), Fähren, Switzerland. Specimen 16/3 in the Natural History Museum, Bern. **B.** *H. flexuosus* Fischer-Ooster, the holotype (= *Ophiomorpha rectus*), Upper Cretaceous Gurnigel Flysch, Sceliggraben near Gurnigelbad, Fribourgian Alps, Switzerland. Specimen 13/2 in the Natural History Museum, Bern. **C.** *H. minor* Fischer-Ooster, holotype (= *Ophiomorpha rectus*) with *Chondrites intricatus*. Drawing based on a photograph. Upper Cretaceous Gurnigel Flysch, Sceliggraben near Gurnigelbad, Fribourgian Alps, Switzerland. Specimen 13/3 in the Natural History Museum Bern. Scale bars = 1 cm

1995). Mostly, the specimens are devoid of pellets and are identical to the material described by Książkiewicz (1977) as *Sabularia simplex*. Preservation and production of pellets is probably related to the consistency of the sediment.

The pelleted segments of *Ophiomorpha annulata* from Slovenia are identical to *Arthropycus annulatus* (Książkiewicz, 1977), recently redescribed as *Ophiomorpha annulata* (Howard & Frey, 1984; Frey & Howard, 1985a, b). However, it is not completely clear, if the material described by the cited authors from shallow-water Cretaceous deposits of North America, and the discussed flysch material are identical. The smooth version of *O. annulata* was described as *O. annulata* var. *simplex* (Uchman, 1995). The problem of *O. annulata* was discussed in the cited publication.

O. annulata occurs from the Valanginian to the Miocene (Uchman, 1995) in deep-sea environment (Książkiewicz, 1977) and probably in shallow-water deposits (e.g. Frey & Howard, 1990)

Ophiomorpha rectus (Fischer-Ooster 1858)

Figs. 25–26

- * 1858 *Halymenites rectus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 2.
- 1858 *Halymenites flexuosus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 1.
- ?partim 1858 *Halymenites minor* F.O. – Fischer-Ooster, 55, 65, pl. 13, fig. 1 (?non 55, pl. 16, fig. 2)
- 1858 *Halymenites incrassatus* F.O. – Fischer-Ooster, 65, pl. 16, fig. 3.
- 1909 *Granularia* cf. *arcuata* Schimp. – Reis, pl. 17, figs. 2-4.
- 1935 agglutinierte Wohnröhre – Abel, figs. 395-396.
- 1936 Grosser Fukoid Krejci-Graf, fig. 3.
- ?non 1941 Agglutinierenden Polychäten (Terebellinen) – Papp, figs. 1-3.
- 1959 Mit ellipsoidischen Kotpillen austapezierter Gang – Seilacher, tab. 3.52.
- v 1977 *Tubulichnium incertum* n. ichnosp. – Książkiewicz, 143, pl. 11, figs. 14-15, text-fig. 29.
- 1978 ?*Granularia* – Kern, 255, fig. 10A.
- partim 1981 *Granularia* sp. – Crimes *et al.*, 969, pl. 2, fig. 5 (non pl. 4, fig. 4).
- v 1991b *Tubulichnium incertum* – Uchman, 289, fig. 2A.
- v 1993 *Tubulichnium incertum* Książkiewicz – Tunis & Uchman, 87 (not figured).
- v 1996a *Tubulichnium incertum* Książkiewicz – Tunis & Uchman, 177, fig. 3J.

Emended diagnosis: Mostly horizontal, rarely branched,

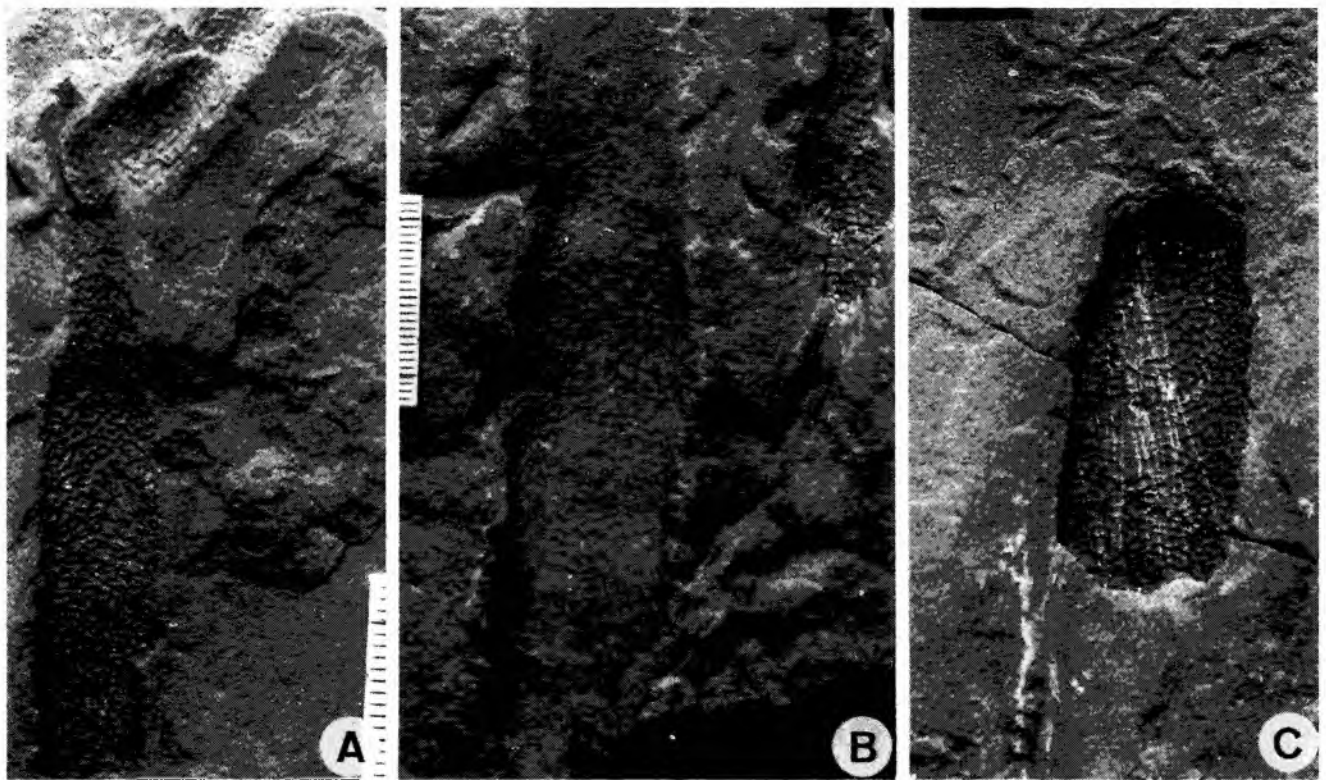
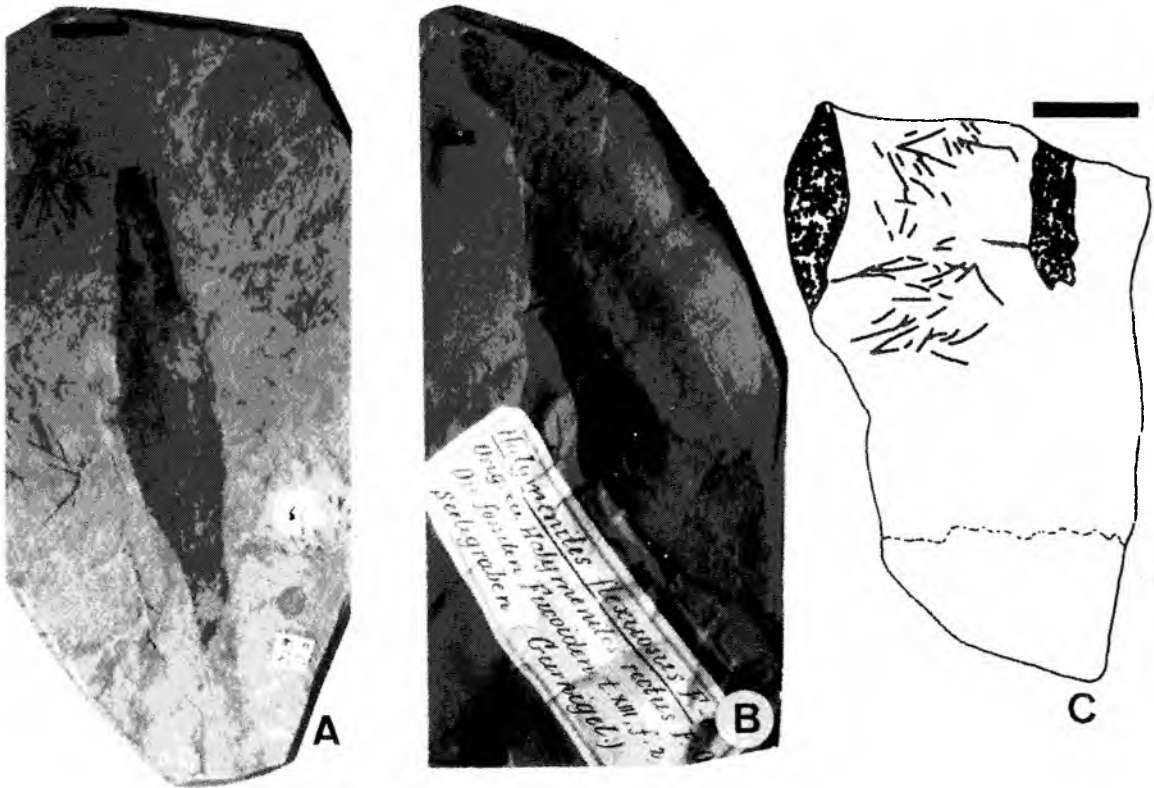


Fig. 26. *Ophiomorpha rectus* (Fisher-Ooster). A. Epichnial forms in turbiditic sandstones. UJ TF 1026, Ropianka beds (Senonian–Paleocene), Wola Brzezińska. B. Specimen from the Gurnigel Flysch (Senonian–Paleocene) in Seeligabern near Gurnigelbad, Fribourgian Alps, Switzerland. The type of *Halymenidium* = *Ophiomorpha rectus* derives from this locality. C. Specimen from the Gurnigel Flysch (Upper Paleocene–Lower Eocene) in Zollhaus, Fribourgian Alps, Switzerland. *Phycosiphon incertum* at the left side. Scale in A–B in mm, scale bar in C = 1 cm

winding *Ophiomorpha* lined with very small muddy pellets.

Material: 7 specimens (UJ TF 938, 1026, 3 specimens from the Fischer-Ooster material, 2 specimens from the Fribourgian Alps).

Description: Horizontal to oblique strongly flattened tubes, which are 4–20 mm wide. Interior of the tube is covered with small, elongate muddy pellets, which are 0.7–2 mm long.

Remarks: Książkiewicz (1977) noticed similarity of the discussed trace fossil to *Ophiomorpha*, but he designated the new ichnogenus. Stratigraphic range: Turonian–Middle Eocene (Książkiewicz, 1977).

Ophiomorpha isp.

Fig. 27

v 1977 *Sabularia rudis* n. ichnosp. – Książkiewicz, 70, pl. 2, fig. 4, text-fig. 7.

Material: 7 specimens (UJ TF 128, 1205, 1509, 1581, 1634, 2511, 2601).

Description: Horizontal, vertical, or subvertical, straight or slightly winding trace fossils, usually smooth or covered with poorly visible knobs. Trace-fossil diameter ranges from 4 to 30 mm, but commonly from 10 to 30 mm. The trace fossils are elliptical to rarely circular in cross-section. They display rare Y-shaped branchings, however, a congestion of branchings is noted in some specimens (UJ TF 1204, Książkiewicz, 1977, pl. 2, fig. 4), which form a kind of knot.

Thalassinoides Ehrenberg 1944

Diagnosis: Three-dimensional burrow systems consisting predominantly of smooth-walled, essentially cylindrical components of variable diameter; branches Y- to T-shaped, enlarged at points

of bifurcation (after Howard & Frey, 1984).

Remarks: *Thalassinoides* is a facies-crossing trace fossil, most typical of shallow-marine environment, and is produced mainly by crustaceans (e.g. Frey *et al.*, 1984). Origin and palaeoenvironmental significance of *Thalassinoides* were summarized lately by Ekdale (1992). According to Föllmi & Grimm (1990), the crustaceans producing *Thalassinoides* may survive transport in turbidity currents and produce burrows under anoxic conditions during a limited number of days.

Apart from widespread Mesozoic and Cenozoic occurrences, *Thalassinoides* was reported from the Palaeozoic from what appears to be shallow water sediments (Palmer, 1978; Archer & Maples, 1984; Sheehan & Schiefelbein, 1984; Stanistreet, 1989; Kulkov, 1991).

Thalassinoides suevicus (Rieth 1932)

Figs. 28

v partim 1977 *Buthotrephis* aff. *palmata* Hall – Książkiewicz, 75, text-fig. 10n [non text-fig. 10h = *Phycodes bilix*].

v partim 1977 *Buthotrephis* aff. *succulens* Hall – Książkiewicz, 75, text-fig. 10c [non text-fig. 10a, e, k-l, t = *Phycodes bilix*].

v partim 1977 *Buthotrephis* spec. indet. – Książkiewicz, 76, text-fig. 10d, o-r [non text-fig. 10f-g, i-j, m, s, u-y = *Phycodes bilix*; non text-fig. 10b = *Arthropycus strictus* Książkiewicz].

Diagnosis: Predominantly horizontal, more or less regularly branched, essentially cylindrical burrow system; dichotomous bifurcations are more common than T-shaped branches (after Howard & Frey, 1984).

Material: 12 specimens (UJ TF 378, 380, 383–384, 703, 902, 1356, 1580, 1582–1583, 2511, 2590).

Description: Horizontal or oblique cylindrical trace fossils, 5–30



Fig. 27. *Ophiomorpha* isp. UJ TF 2601 (original label lost). Scale in mm



Fig. 28. *Thalassinoides suevicus* (Rieth). UJ TF 2590. Sole of turbiditic sandstone bed, Synwódzko Wyżnie, Gorgany Mountains, East Carpathians, Ukraine. Coll. K. Wójcik. Scale in mm

mm in diameter, having Y-shaped branches. T-shaped branching is rare, but may occur together with Y-shaped branching in one and the same trace fossil. Some of the burrows are enlarged at points of bifurcation.

Remarks: Some specimens ascribed to *Thalassinoides* occur among specimens determined by Książkiewicz (1977) as *Buthotrephis* or labelled as *Sabularia rudis* and *Sabularia ramosa*. *Thalassinoides* was noted in the Carpathian Flysch by Uchman (1991a).

Spongiomorpha de Saporta 1887

Diagnosis: Sparsely developed burrow systems; components vertical to horizontal, characterized by sets of longitudinal or oblique, fine, elongate striation on exterior of burrow casts (Fürsich *et al.*, 1981; Frey *et al.*, 1984).

Remarks: Fürsich (1973) included *Thalassinoides* and *Ophiomorpha* in *Spongiomorpha*. Bromley & Frey (1974) suggested that *Spongiomorpha* should be abandoned because of poor definition, and *Thalassinoides* and *Ophiomorpha* should be retained because of their different wall structures. However, material from the type locality of *Spongiomorpha* (*S. iberica*) has since been revised (Calzada, 1981) which has improved definition of this ichnogenus.

The longitudinal striation is interpreted as scratch traces produced in stiff substrate (e.g., Kennedy, 1967; Fürsich, 1973). Książkiewicz (1977, p. 61) supposed that the sculpture of the Carpathian specimens was produced passively by animals (Pholthurians, ?ophiuroids, ?sipunculids) with body appendages and tubercles. This view cannot be accepted because it does not explain why the short ridges are oblique and grouped. If they had been produced by dragging, we would expect more continuous scratches, more concordant to the axis of trace fossil. Fuchs (1895, p. 408) related trace fossils of this type to burrows of annelids like *Terebella*. However, the external ornamentation of the trace fossils strongly resembles scratch traces of crustacean burrows, formed actively by locomotory organs of tracemakers, which are present mainly in *Spongiomorpha*, occasionally in *Thalassinoides*, and in the interior of *Ophiomorpha* (Kennedy, 1967). Some Carpathian examples are enlarged at branching points, similarly to *Thalassinoides*.

Frey *et al.* (1984) speculated that *Spongiomorpha* produced by crabs should have shorter, more stumpy and bulbous sculpting than long sculpting produced by shrimps. On the other hand, enlargement of burrows at branching points is more characteristic of shrimps (Kennedy, 1967; Bromley & Frey, 1974; Fürsich *et al.*, 1981).

Spongiomorpha sublumbrioides (Azpeitia Moros 1933)

Fig. 29

- * 1933 *Halimnites sublumbrioides* Azpeitia, n. sp. Azpeitia Moros, 56, pl. 18, fig. 32 (lapsus calami).
- 1946 *Halimnites sublumbrioides* Azpeitia, n. sp. Gómez de Llarena, 35(143).
- ? 1973 *Halimnidium* Crimes, fig. 11.10.
- 1977 *Halimnidium sublumbrioides* (Azpeitia) Książkiewicz, 62, pl. 3, figs. 1-2.
- ? 1980 *Halimnidium sublumbrioides* (Azpeitia) Alexandrescu & Brustur, 24, pl. 6, fig. 2.

Emended diagnosis: *Spongiomorpha* with short, fine, ir-

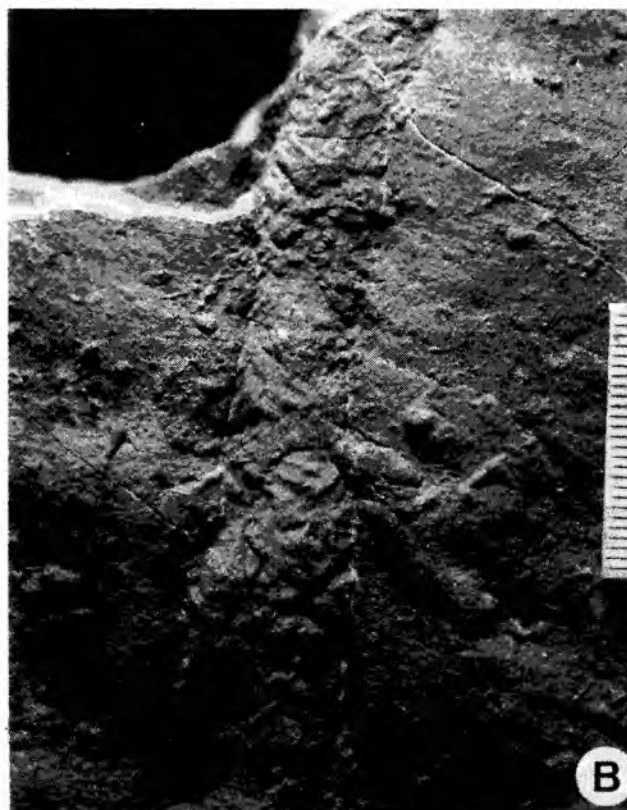


Fig. 29. *Spongiomorpha sublumbrioides* (Azpeitia-Moros). Sole of turbiditic sandstone bed. UJ TF 80, Beloveža Formation (Eocene), Lipnica Mala. **A.** General view. **B.** Detail of A. Scales in mm

regularly, mainly obliquely distributed external ridges.

Material: 5 specimens (TF UJ 80, 297, 458, 1741, 1810).

Remarks: Metz (1993b) distinguished *Spongiomorpha*

milfordensis for nonmarine, probable insect traces, which displays very similar morphology to *S. sublumbricoides*.

Spongiomorpha oraviense (Książkiewicz 1977)

- v* 1961 *Halymenites oraviensis* (n.f.) - Książkiewicz, 884, pl. 2, fig. 1.
- v 1977 *Halymenidium oraviense* (Książkiewicz) - Książkiewicz, 62, pl. 3, figs. 3-4.
- ? 1981 *Halymenidium* - Crimes *et al.*, 970.
- ? 1985 *Halymenidium oraviense* - Sapunov *et al.*, fig. 11.3, fig. 13.6.
- 1992 *Halymenidium oraviense* - Leszczyński, pl. 2, fig. 1.
- ? 1993 *Halymenidium oraviense* - Brustur & Stoica, 64.
- ? 1994 *Halymenidium oraviense* (Książkiewicz) - Löffler & Geyer, 449, fig. 4b.
- v 1996a *Halymenidium oraviense* (Książkiewicz) - Tunis & Uchman, 173, fig. 3F.
- v 1996b "*Halymenidium*" *oraviense* (Książkiewicz) - Tunis & Uchman, 6, fig. 4E-F.
- v 1996 "*Halymenidium*" *oraviense* (Książkiewicz) - Marinčić *et al.*, pl. 1, fig. 7.

Diagnosis: *Spongiomorpha* covered with short, fine, oblique ridges. Ridges are oriented parallel and grouped in small patches. The patches form a plaited design (modified after Książkiewicz, 1977).

Material: 20 specimens (TF UJ 61 (holotype), 62, 161, 456-457, 459, 461-469, 471, 473, 474).

Remarks: The material described by Książkiewicz as *Halymenidium* displays features of *Spongiomorpha* de Saprota. The filling of burrows is covered with short ridges that may be treated as casts of scratch traces.

Phycodes Richter 1850

Emended diagnosis: Densely to loosely packed bundle of tunnels. These are joined as a single stem or tightly packed in the downward-penetrating to horizontal proximal part. The bundle is split and more loose in the upward-penetrating distal part.

Remarks: *Phycodes* Richter, typified by *Ph. circinatum* Richter, was limited only to densely packed bundles (Os-good, 1970; Häntzschel, 1975). A curved, short-branched form, widely known as *Phycodes pedum* (Seilacher, 1955), was recently included in *Trichophycus* Miller & Dyer because the morphology of this trace fossil does not conform with the diagnosis of *Phycodes* (Geyer & Uchman, 1995).

Książkiewicz (1977, p. 82) described only one ichnotaxon of this ichnogenus, namely *Phycodes* aff. *harlani* (Hall). The single specimen of this ichnotaxon comprises vertically stacked cylinders showing faint internal ornamentation, which converge in one direction. The cylinders occur in a single vertical plane as may be observed in cross-section. In contrast, *Phycodes* is a bunch of cylinders (Häntzschel, 1975). In addition the Książkiewicz specimen was compared to *Phycodes harlani* (Hall) (synonym of *A. alleghaniensis* (Harlan), see description of *Arthropycus*). Such comparison is very speculative. The latter ichnotaxon, known from Palaeozoic rocks, is represented by perpendicularly ribbed cylinders having subquadrate cross-section, locally grouped in bunches. One can not exclude that the discussed specimen represents a small *Ophiomorpha* with vertical repetitions, analogous to the trace fossils described by Hester & Pryor (1972).

Książkiewicz (1977), however, described a few trace fossils under *Buthotrephis* Hall, which may be ascribed to *Phycodes* (see below). They are branched structures that penetrate from a single stem in the proximal part. The branchings penetrate slightly upward in the distal part and the branches are arranged in a palmate-like pattern. The branches were produced by successive action of the trace-maker, which withdrew to the main stem after formation of each new branching. This type of behaviour is most similar to *Phycodes*. Distinction between looser and tighter bundles of burrows seems to be problematic. Therefore, a broader diagnosis of *Phycodes* is proposed to cover the differences and unify these trace fossils at the ichnogenetic level. All the differences may be considered at the ichnospecific level. Close comparison to the other *Phycodes* ichnospecies is not feasible, because revision of these ichnospecies is necessary.

Phycodes bilix (Książkiewicz 1977)

Fig. 30

- v* 1977 *Buthotrephis bilix* n. ichnosp. - Książkiewicz, 76, pl. 5, fig. 13.
- v partim 1977 *Buthotrephis* aff. *palmata* Hall - Książkiewicz, 75, text-fig. 10h [non text-fig. 10h = *Thalassinoides suevicus*].
- v partim 1977 *Buthotrephis* aff. *succulens* Hall - Książkiewicz, 75, text-fig. 10a, e, k-l, t [non text-fig. 10c = *Thalassinoides suevicus*].
- v partim 1977 *Buthotrephis* spec. indet. - Książkiewicz, 76, text-fig. 10f-g, i-j, m, s, u-y [non text-fig. 10d, o-r = *Thalassinoides suevicus*; non text-fig. 10b = *Arthropycus strictus* Książkiewicz].

Emended diagnosis: *Phycodes* with a few loosely packed and rarely branched tunnels in the distal part.

Material: 15 specimens (UJ TF 350, 382, 368, 376, 709, 761, 1023, 1173, 1310-1311, 1402, 1726, 1814, 1820, 2016).

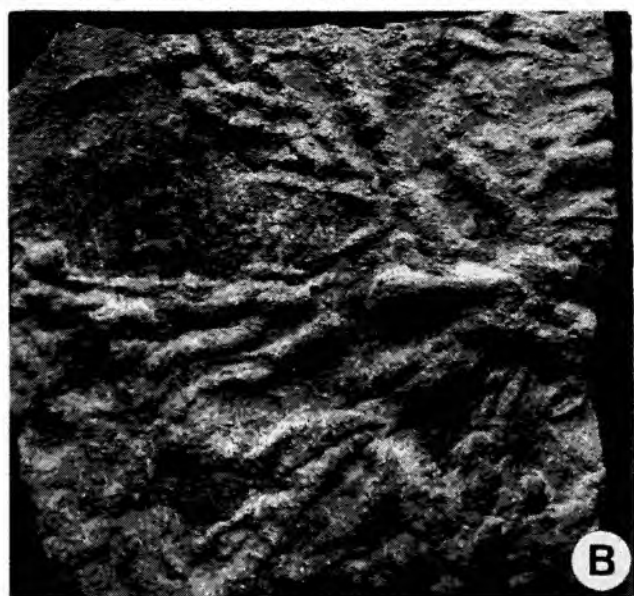
Description: As in the diagnosis and the Książkiewicz (1977) descriptions of ichnotaxa included in this ichnospecies, with the following remarks: two types of preservation are observed. The first type is referred to Książkiewicz *Buthotrephis bilix* (Fig. 30B-C) and connected with a collapse of empty thickly walled tunnels. Edges of the collapsed tunnels are elevated, and therefore Książkiewicz mentioned "median furrows". The second type of preservation is shown in Fig. 30A. This trace fossil is preserved as a washed-out and cast burrow.

Remarks: This ichnospecies occurs in various flysch deposits of the Polish Carpathians from Beriasian to Oligocene (Książkiewicz, 1977).

Saerichmites Billings 1866

Emended diagnosis: Trace fossil comprising at least single parallel rows of semicircular or subquadrate, more or less regularly distributed pits or pustules on bedding planes.

Remarks: This ichnogenus is typified by *S. abruptus* Billings (Billings, 1866; Häntzschel, 1975). Former diagnosis, provided by Uchman (1995), related this ichnogenus to subvertical shafts. According to Bromley (pers. comm., 1997), this trace fossil may be related to a horizontal spirally coiled burrow. Until this problem is further investigated, a less interpretative diagnosis is proposed.



?Saerichnites canadensis (Crimes & Anderson 1985)

v partim 1977 *Tuberculichnus meandrinus* n. ichnosp. – Książkiewicz, 141, pl. 13, fig. 6 [non pl. 13, fig. 5 = *Protovirgularia vagans*, non text-fig. 27a-b].

* 1985 *Hormosiroidea canadensis* n. ichnosp. – Crimes & Anderson, 325, figs. 8.1.

? 1996 *Tuberculichnus meandrinus* Książkiewicz – Paczeńska, 67, pl. 29, fig. 5.

Diagnosis: A meandering line of densely spaced vertical or steeply inclined shafts which appear on the bedding plane as circular or semi-circular knobs (after Crimes & Anderson, 1985).

Material: 1 specimen (UJ TF 917).

Remarks: Single rows of holes produced by unknown organisms were photographed on the deep-sea floor (Eving & Davis, 1967; Hinga, 1981, with ref.). It is possible that they may be referred to *Saerichnites*-like trace fossils. If *Saerichnites* is related to a horizontal spirally coiled burrow (see discussion of this ichnogenus), *?S. canadensis* should be described under other ichnogenus. Therefore, the question-mark is placed in front of the ichnogenetic name.

Parahaentzschelinia Chamberlain 1971a

Diagnosis: Trace fossil composed of numerous vertical shafts radiating vertically from one shaft. It may be expressed on interfaces as groups of oval to circular pits, mounds, bulbs, and spots (modified after Uchman, 1995).

Remarks: *P. ardelia* was identified as an endichnial full-relief trace fossil in Pennsylvanian deep-water deposits of the USA (Chamberlain, 1971a, b). *P. surlyki* was described in Jurassic shallow-water deposits of Greenland (Dam, 1990). The first ichnotaxon was interpreted as a feeding-domichnial structure, the second one as a domichnion.

There are records of Recent grouped holes on the deep-sea floor (Gaillard, 1991).

?Parahaentzschelinia isp.

Fig. 31

v 1977 *Tuberculichnus bulbosus* n. ichnosp. – Książkiewicz, 142, pl. 13, fig. 7, text-fig. 27h.

? 1987 *Tuberculichnus bulbosus* Książkiewicz – Micu *et al.*, 83, pl. 2, fig. 1.

v 1995 *Parahaentzschelinia* isp. – Uchman, 43, pl. 12, figs. 5-8.

Material: 3 specimens (UJ TF 851, 855, 1262).

Remarks: The mounds represent casts of outlets of vertical or inclined burrows.

Anemonichnus Chamberlain & Clark 1973

Anemonichnus concentricus Chamberlain & Clark 1973

Remarks: This ichnotaxon was recorded by Książkiewicz

Fig. 30. *Phycodes bilix* (Książkiewicz). Soles of turbiditic sandstone beds. A. UJ TF 1726, Middle Godula beds (Turonian), Ponikiew (labelled as *Buthotrephis* aff. *succulens*). B. UJ TF 1310, Grodziszczce beds (Hauterivian), Koźmice Wielkie (labelled as *Buthotrephis bilix*). C. UJ TF 1311, the holotype. Grodziszczce beds (Hauterivian), Poznachowice (labelled as *Buthotrephis bilix*). Scale in A in mm, scale bars in B-C = 1 cm

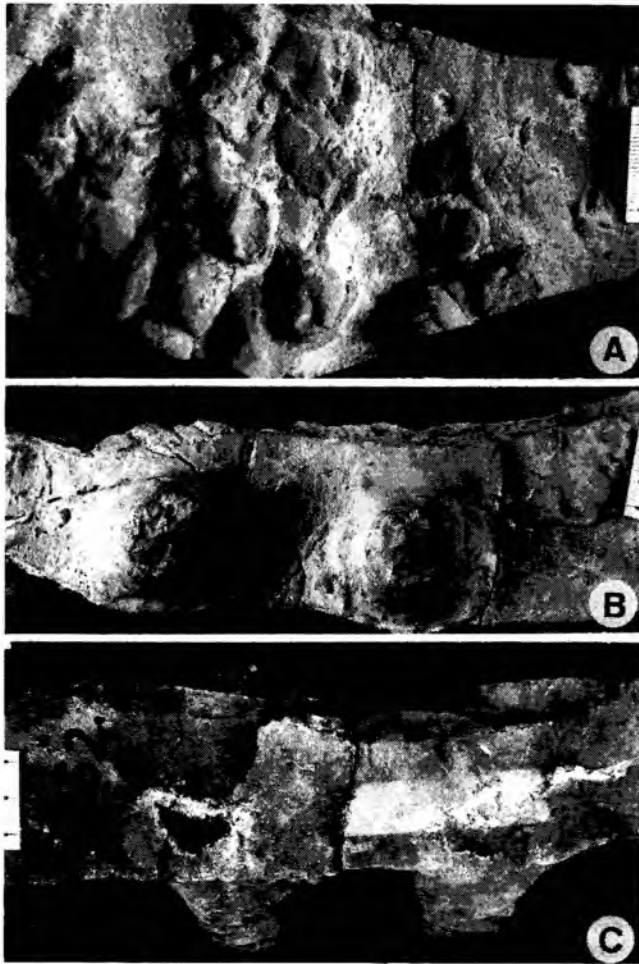


Fig. 31. *Parahaentzschelinia* isp. Hypichnial forms on turbiditic sandstone beds. UJ TF 855, Beloveža beds (Eocene), Berest (labelled as *Tuberculichnus bulbosus*). B. UJ TF 1262, Tokarnia (part of label lost). C. Side view of B. Scale in mm

(1977, p. 112, text-fig. 18) only in the field and documented by a field drawing. For this reason it is impossible to revise the determination.

RADIAL STRUCTURES

Lorenzinia Gabelli 1900

Ichnospecies included in *Lorenzinia* Gabelli:

- ? 1885 *Acanthoceras rhotomagensis* Brug. – Stefani, 89 (after Gortani, 1920, p. 58).
- ? 1890 *Gyrophyllites vestanensis* n. sp. – Squinabol, 189, pl. 11, fig. 2.
- 1900 *Lorenzinia apenninica* n. sp. – Gabelli, 77, pl. 1, fig. 1.
- 1910 *Atollites carpathicus* n. sp. – Zuber, fig. in p. 57.
- 1911 *Atollites carpathicus* Zub. – Kuźniar, 518, fig. D-E.
- 1911 *Atollites kulczynskii* n. sp. – Kuźniar, 519, fig. F.
- 1918 *Atollites carpathicus* – Zuber, 107, fig. 66 (also Vialov, 1968a, pl. 1, fig. 3).
- 1925 *Lorenzinia (Bassaenia) moreae* Renz – Renz, 222, fig. 1.
- partim 1927 *Lorenzinia apenninica* Da Gabelli – Gómez Lluleca, 46, figs. 6, 8-9 [non fig. 7 (= *Glockerichnus* isp.)].
- 1930 *Lorenzinia apenninica* Gabelli – Renz, 298, fig. 1.

- 1933 *Lorenzinia apenninica* Gabelli – Azpeitia Moros, 18, pl. 3, fig. 7.
- 1951 *Atollites bucovinicus* sp. n. – Sandler, 174, figs. 1-2.
- 1951 *Atollites minor* (Maas) – Sandler, 174, fig. 3.
- 1953 *Atollites* – Vassoevich, pl. 3, fig. 2.
- 1957 Traces [...] f la pature des crabes – Nowak, pl. 17, figs. J, L, pl. 18, figs. M-N.
- 1959 *Atollites* sp. – Grossheim, fig. 2.
- 1962 *Lorenzinia* – Seilacher, pl. 2, figs. 1-2.
- 1964 *Lorenzinia apenninica* Gabelli – Farrés Mallian, 125, pl. 7, fig. 2.
- v 1968 *Sublorenzina plana* n. "sp." – Książkiewicz, 10, pl. 5, figs. 1-2.
- ? 1968 cf. *Lorenzinia* – Pfeiffer, 684, text-fig. 3.17.
- 1968a *Lorenzinia prutenensis* sp. nov. – Vialov, 338, pl. 1, fig. 4.
- 1970 *Bifasciculus radiatus* Volk – Crimes, pl. 1a.
- 1970 ?*Lorenzinia* – Crimes, pl. 1e.
- v 1970 *Asterichnus nowaki* ichnosp. n. – Książkiewicz, 310, fig. 7d.
- v 1970 *Bassaenia moreae* Renz – Książkiewicz, 313, fig. 7q.
- v 1970 *Sublorenzina plana* Książkiewicz – Książkiewicz, 313, fig. 7e, f.
- 1971 *Lorenzinia* (?) sp. – Tanaka, 8, pl. 3, fig. 3.
- non 1977 cf. *Sublorenzina* – Kumar *et al.*, 429, pl. 6.2.
- ?non 1976 cf. *Lorenzinia* Da Gabelli – Hakes, 29, pl. 6, fig. 4.
- v 1977 *Sublorenzina nowaki* (Książkiewicz) – Książkiewicz, 95, pl. 7, figs. 1-3, text-fig. 13g, k, m-t. (partim)
- v 1977 *Sublorenzina plana* Książkiewicz – Książkiewicz, 94, pl. 7, figs. 4-8, text-fig. 13q, r.
- v non 1977 *Sublorenzina nowaki* (Książkiewicz) – Książkiewicz, 95, text-fig. 13f, h-j, l.
- v 1977 *Sublorenzina pustulosa* n. ichnosp. – Książkiewicz, 97, pl. 7, fig. 9, text-fig. 13s, t.
- v 1977 *Sublorenzina pusilla* n. ichnosp. – Książkiewicz, 98, pl. 7, figs. 10, 11, text-fig. 13u, w, v, x.
- 1977b *Lorenzinia* cf. *kulczynskii* – Crimes, 594, pl. 4, fig. 1.
- ? 1978 *Sublorenzina plana* Książkiewicz – Radwański, 53, pl. 7, fig. 2.
- 1985 *Bassaenia xaingquanensis* n. ichnosp. – Yang & Song, 7, pl. 3, figs. 3, 5.
- ? 1985 *Phycodes coronatum* n. ichnosp. – Crimes & Anderson, 329, figs. 10.5-10.6.
- non 1986 *Lorenzinia rituensis* Yang new ichnosp. – Yang *et al.*, 227, pl. 2, fig. 8, text-fig. 8.
- non 1988 *Sublorenzina pusilla* Książkiewicz – Yang, pl. 1, fig. 12.
- non 1991 *Lorenzinia* aff. *moreae* Renz – Crimes & Crossley, 36, pl. 3i.
- ?non 1991 *Lorenzinia plana* (Książkiewicz) – Crimes & Crossley, 36, pl. 3j.
- 1992 *Sublorenzina plana* Książkiewicz – Crimes *et al.*, 67, figs. 4C, 5B.
- ? 1993a *Sublorenzina plana* Książkiewicz – Li, 97, pl. 3, fig. 5.
- ? 1993a *Sublorenzina pusilla* Książkiewicz – Li, 98, pl. 3, fig. 4.
- non 1993 *Lorenzinia* cf. *moreae* Renz – Miller, 21, fig. 5C.
- ?non 1993 *Lorenzinia apenninica* da Gabelli – Miller, 21, fig. 5O.
- 1993a *Volkichnium volki* Pfeiffer – Li, 97, pl. 3, figs. 3, 6.
- ? 1994 Sternförmige Lebensspuren indet. – Lobitzer *et al.*, 298, pl. 8, fig. 8.
- ?non 1994 *Sublorenzina nowaki* (Książkiewicz) – Löffler & Geyer, 510, fig. 4a (= ?*Glockerichnus* isp.).
- v 1996 *Lorenzinia* isp. – Marinčić *et al.*, fig. 4G.
- v 1997 *Lorenzinia pustulosa* (Książkiewicz) – Wetzel & Uchman, 145, fig. 4B.

Diagnosis: Simple, short, smooth, hypichnial ridges, arranged in one or two circular rows, radiating from oval or circular central area. The ridges are very similar or different in length and are regularly or irregularly distributed. In some cases, the ridges protrude from a ring surrounding the central area (after Uchman, 1995).

Remarks: *Bassaenia* Renz, regarded by Renz (1925) as a "subgenus" of *Lorenzinia* Gabelli was included in the latter ichnogenus (Książkiewicz, 1977, Seilacher, 1977a).

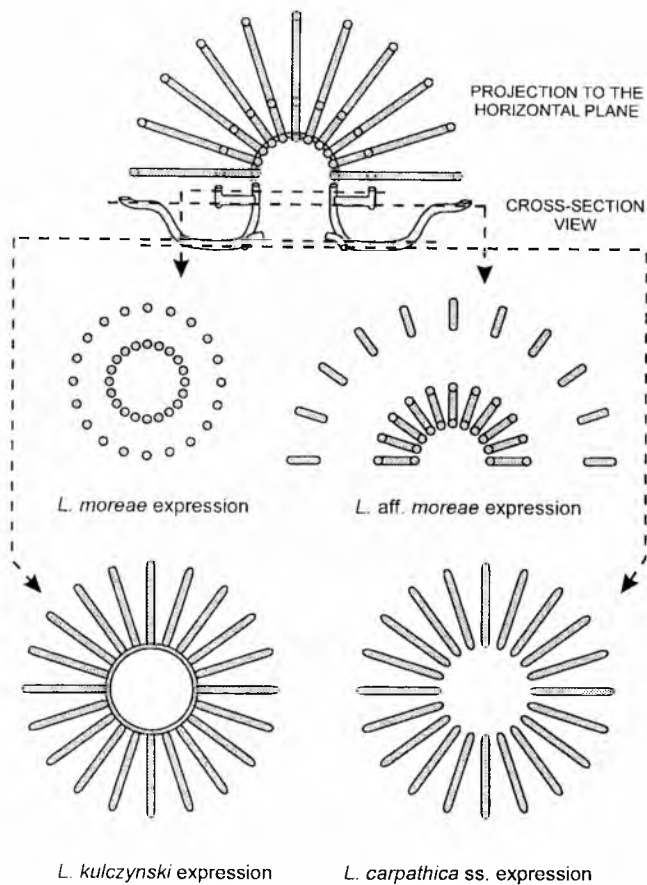


Fig. 32. Model of burrow system integrating *Lorenzina carpathica*, *L. moreae*, *L. peralta*, *L. kulczynskii*, and *L. curticostata* as morphological variants related to depth of erosion

Seilacher (1977a) included *Sublorenzina* Książkiewicz in *Lorenzina* Gabelli. These two ichnogenera differ only in the regularity of the radiating ridges and in the uniformity of their length. These are accessory features and should be considered at the species level. A few *Lorenzina* of different morphologies, ascribed to *L. carpathica* (Zuber), *L. moreae* (Renz), *L. peralta* Książkiewicz, and *L. curticostata* Książkiewicz, were found by Książkiewicz in one turbiditic sandstone bed in the Variegated Shale (Paleocene–Lower Eocene). He supposed (p. 88) that they can be produced by the same animal, however, he separated ichnotaxonomically the morphologically different specimens. Reconsidering the problem, it is possible to integrate all of the ichnospecies within a single burrow system model and explain their differences in morphology by differences in depth of erosion. The erosion exposed different levels of the system before immediate casting on sole of turbiditic bed (Fig. 32). All of the morphological variations, expressed in above accounted ichnospecies are included, together with *L. kulczynskii* (Kuźniar) in *L. carpathica* (Zuber). Differences in morphology between *L. carpathica* (Zuber), *L. apenninica* Gabelli, and *L. kuznari* Książkiewicz can be explained by differences in inclination of the radiating elements (Fig. 33). In general, it seems that *Lorenzina* is a three-dimensional burrow system of various radial elements forming a wreath joined by a central ring (Fig. 32). The ring can be partially

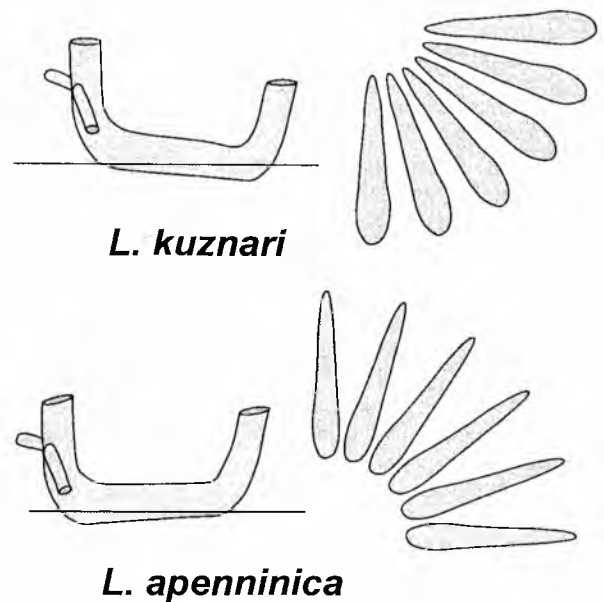


Fig. 33. Model of *Lorenzina kuznari* and *L. apenninica* in relation to inclination of the radiating elements of the burrow system

preserved in some cases (e.g. *L. kulczynskii*). This model should be treated with caution. There is still not enough material for full confirmation of the idea.

Probably, *Phycodes coronatum* described by Crimes & Anderson (1985) from Precambrian/Cambrian deposits of New Foundland represents the oldest, primitive *Lorenzina*.

Taking into account the probably strong influence of preservation on the morphology of *Lorenzina*, the morphometrical classification of Vialov (1968a) cannot be accepted (cf. Książkiewicz, 1977).

Usually, ichnospecies of regular *Lorenzina* display about 20 radiating ridges, and the irregular ichnospecies about 10 ridges.

Lorenzina was included in the graphoglyptids by Seilacher (1977a). It has been interpreted as produced by holothurians (Simonelli, 1905), crabs (Nowak, 1957; Radwański, 1978), annelids (Häntzschel, 1970), or sipunculoids (Heezen & Hollister, 1971). Książkiewicz (1977) regarded *Lorenzina* as a feeding trace of hydromedusae, and *Sublorenzina* (= *Lorenzina*) as produced by polychaetes. The affinity with hydromedusae is hardly likely because it is a complicated burrow system preserved by scour and casting, not a surficial trace produced by tentacles of hydromedusae.

Lorenzina occurs in flysch deposits from the Precambrian/Cambrian (?) (Crimes & Anderson, 1985), the Arenig (Crimes *et al.*, 1992) to the Miocene (Uchman, 1995). Radiating grooves and holes which may be Recent counterparts of *Lorenzina* have been photographed on the deep-sea floor (Heezen & Hollister, 1971, figs. 6.21, 6.24; Gaillard, 1991).

Lorenzina apenninica Gabelli 1900

* 1900 *Lorenzina apenninica* n. sp. – Gabelli, 1, pl. 1, fig. 1 (also Gortani, 1920, pl. 2, fig. 1; Vinassa de Regny, 1924, fig. 51).

1908 *Lorenzina apenninica* – Fucini, fig. 1.

- non 1917 *Lorenzina* aff. *apenninica* Da Gabelli – Jiménez de Cisneros, pl. 5 (= *Lorenzina kuzniari* Książkiewicz).
 1923 *Lorenzina apenninica* Gabelli – Desio, 7, pl. 1, figs. 1-2 [=holotype of Vialov's (1968a) *Lorenzina desioi* sp. nov.].
 1927 *Lorenzina apenninica* Gabelli – Gómez Lluleca, figs. 6-9.
 non 1930 *Lorenzina apenninica* Gabelli – Renz, 298, fig. 1.
 1933 *Lorenzina apenninica* Gabelli – Azpeitia Moros, 18, pl. 3, fig. 7.
 non 1939 *Lorenzina apenninica* Gabelli – Mitzopulos, fig.
 1956 Traces qui se rattachent probablement à la pâture des crabes – Nowak, pl. 17, fig. K.
 ? 1964 *Lorenzina apenninica* Gabelli – Farrés Mallian, 125, pl. 7, fig. 2 (? *L. carpathica*).
 non 1967 *Lorenzina apenninica* Gabelli – Macsotay, 31, pl. 10, figs. 37-38.
 1968a *Lorenzina desioi* sp. nov. – Vialov, 338.
 1977 *Lorenzina* aff. *apenninica* De Gabelli – Książkiewicz, 89, pl. 6, fig. 1.
 ? 1989 *Lorenzina apenninica* – Miller, fig. 2N.
 1992 *Lorenzina apenninica* – Leszczyński, pl. 1, fig. 2 (also Leszczyński, 1993, fig. 5), pl. 10, fig. 2.
 ? 1993a *Volkichnium volki* Pfeiffer – Li, 97, pl. 3, figs. 3, 6.
 non 1993 *Lorenzina apenninica* da Gabelli – Miller, 21, fig. 5.O.

Emended diagnosis: *Lorenzina* with radiating ridges pointed at the outer side and elevated at the inner side.

Material: No material in the Książkiewicz collection.

Lorenzina carpathica (Zuber 1910)

Figs. 32, 34–36

- ? 1885 *Acanthaceras rhotomagensis* Brug. – De Stefani, 89 (after Gortani, 1920, p. 58).
 1905 Unnamed – Simonelli, fig. in p. 5.
 * 1910 *Atollites carpathicus* n. sp. – Zuber, 57, fig. [also Zuber, 1918, p. 107, fig. 66; Vialov, 1968a, pl. 1, fig. 3].
 1911 *Atollites carpathicus* Zub. – Kuźniar, 519, figs. D-E.
 1911 *Atollites kulczynskii* n. sp. – Kuźniar, 519, fig. F.
 1920 *Lorenzina carpathica* Zuber – Gortani, pl. 2, fig. 5, pl. 3.
 1925 *Lorenzina (Bassaenia) moreae* Renz – Renz, 222, fig. 1.
 1930 *Lorenzina apenninica* Gabelli – Renz, 298, fig. 1.
 non 1939 *Lorenzina apenninica* Gabelli – Mitzopulos, fig.
 1941 *Lorenzina carpathica* Zub. – Desio, 8, fig. in p. 8.
 1951 *Atollites bucovinicus* sp. n. – Sandler, 174, figs. 1-2.
 1953 *Atollites* – Vassoevich, pl. 3, fig. 2.
 1956 *Lorenzina* – Harrington & Moore, F42, fig. 32.2d.
 1957 Traces qui se rattachent probablement à la pâture des crabes – Nowak, pl. 17, fig. J, L, pl. 18, fig. M.
 1957 Traces qui se rattachent probablement à la pâture et à l'existence des crabes – Nowak, pl. 18, fig. N [=holotype of Vialov's (1968a) *Lorenzina nowaki*].
 1959 *Atollites* sp. – Grossheim, fig. 2.
 1961 *Lorenzina carpathica* (Zuber) – Grubić, figs. 1-2.
 1961 Hieroglif gwiazdzisty – Koszarski *et al.*, pl. 1, fig. 6.
 1962 Unnamed – Dimitrieva *et al.*, pl. 84, fig. 5.
 1962 *Atollites* sp. – Đurković, pl. 1, fig. 1.
 ? 1964 *Lorenzina apenninica* Gabelli – Farrés Mallian, 125, pl. 7, fig. 2.
 1967 *Lorenzina apenninica* Gabelli – Macsotay, 31, pl. 10, figs. 37-38.
 partim 1968a *Lorenzina gabellii* Vialov, sp. nov. – Vialov, 338, pl. 1, fig. 5 (non pl. 1, fig. 6 = *L. kuzniari* Książkiewicz).
 1968a *Lorenzina* aff. *kulczynskii* (Zuber) – Vialov, pl. 1, figs. 7-8.
 1968a *Lorenzina zuberi* Vialov, sp. nov. – Vialov, 338, pl. 1, fig. 9.
 1968a *Lorenzina nowaki* sp. nov. – Vialov, 338.
 1968 *Lorenzina carpathica* (Zuber) – Książkiewicz, pl. 5, fig. 3 (also Książkiewicz, 1977, pl. 6, fig. 2).
 v partim 1970 *Lorenzina carpathica* (Zuber) – Książkiewicz, 312, fig. 7g-h (non fig. 7i).
 v 1970 *Lorenzina peralta* ichnosp. nov. – Książkiewicz, 313, fig. 7p.
 v 1970 *Bassaenia moreae* Renz – Książkiewicz, 313, fig. 7q.
 v 1977 *Lorenzina peralta* Książkiewicz – Książkiewicz, 92, pl. 6, figs. 9-10.
 v 1977 *Lorenzina carpathica* (Zuber) – Książkiewicz, 89, pl. 6, fig. 1.
 v 1977 *Lorenzina curticosata* n. ichnosp. – Książkiewicz, 91, pl. 6, fig. 11.
 v 1977 *Lorenzina* aff. *moreae* Renz – Książkiewicz, 93, pl. 6, figs. 14-16.
 v 1977 *Lorenzina moreae* Renz – Książkiewicz, 92, pl. 6, figs. 12-13.
 1977b *Lorenzina* cf. *kulczynskii* – Crimes, 594, pl. 4, fig. 1.
 non 1981 *Lorenzina* cf. *moreae* Renz – Crimes *et al.*, 972, pl. 3, figs. 4-5.
 ? 1986 *Lorenzina (Bassaenia) moreae* Renz – Yang, 155, pl. 4, figs. 4-5.
 non 1991 *Lorenzina* aff. *moreae* Renz – Crimes & Crossley, 36, pl. 3i.
 non 1993 *Lorenzina* cf. *moreae* Renz – Miller, 21, fig. 5C.

Emended diagnosis: *Lorenzina* preserved as radiating ridges of constant diameter or as a wreath consisting of a double ring of tubercles, which can be joined by short ridges. One ring can be preferentially preserved.

Material: 13 specimens (UJ TF 84-86, 134, 871, 1030, 1103, 1109, 1111, 1365, 1801, 2022, 2043).

Description: As in the diagnosis and Książkiewicz description of ichnotaxa included in the discussed ichnospecies.

Remarks: *Lorenzina* of various morphologies, ascribed to *L. carpathica* (Zuber), *L. moreae* (Renz), *L. peralta* Książkiewicz, *L. kulczynskii* and *L. curticosata* Książkiewicz are integrated within a single burrow system model (Fig. 32).

Lorenzina kuzniari Książkiewicz 1977

- 1911 *Atollites carpathicus* Zub. – Kuźniar, 518, fig. E. 1917 *Lorenzina* aff. *apenninica* Da Gabelli – Jiménez de Cisneros, pl. 5.
 ? 1951 *Atollites minor* (Maas) – Sandler, 174, fig. 3.
 partim 1970 *Lorenzina carpathica* (Zuber) – Książkiewicz, 312m, fig. 7i (non fig. 7g-h).
 1956 *Lorenzina* – Harrington & Moore, F42, fig. 32.2c.
 partim 1968 *Lorenzina gabellii* Vialov, sp. nov. – 338, pl. 1, fig. 6 (non pl. 1, fig. 5 = *L. carpathica* (Zuber)).
 v 1977 *Lorenzina kuzniari* n. ichnosp. – Książkiewicz, 90, pl. 6, fig. 8.

Diagnosis: *Lorenzina* with radiating ridges tapering gradually toward the centre, with rounded and elevated outer terminations (modified after Książkiewicz, 1977).

Material: No specimens in the Książkiewicz collection.

Remarks: Model of *L. kuzniari* is shown in Fig. 33B.

Lorenzina plana (Książkiewicz 1968)

Figs. 37–38

- ? 1993a *Sublorenzina pusilla* Książkiewicz – Li, 98, pl. 3, fig. 4.
 v 1968 *Sublorenzina plana* n. "sp." – Książkiewicz, 10, pl. 5, figs. 1-2.
 1961 Hieroglif gwiazdzisty – Koszarski *et al.*, pl. 1, fig. 7.
 v partim 1977 *Sublorenzina plana* Książkiewicz – Książkiewicz, 94, pl. 7, figs. 4-8, text-fig. 13q [?non text-fig. 13r].
 v 1977 *Sublorenzina pusilla* n. ichnosp. – Książkiewicz, 98, pl. 7, figs. 10, 11, text-fig. 13u, w, v, x.
 ? 1978 *Sublorenzina plana* Książkiewicz – Radwański, 53, pl. 7, fig. 2.
 non 1988 *Sublorenzina pusilla* Książkiewicz – Yang, pl. 1, fig. 12.
 1970 *Lorenzina* – Simpson, pl. 11, fig. 1.
 non? 1991 *Lorenzina plana* (Książkiewicz) – Crimes & Crossley,



Fig. 34. *Lorenzina carpathica* (Zuber), different types of preservation on sole of turbiditic sandstone bed. UJ TF 134, Beloveža Formation (Eocene), Lipnica Mała. **A.** General view. **B.** Detail of A (labelled as *L. moreae*). **C.** Detail of A (labelled as *L. carpathica*). Scale in A, C in mm, scale bar in B = 1 cm

Emended diagnosis: Irregular *Lorenzina* with short radiating ridges with rounded external terminations, or composed of an irregular wreath of knobs.

Material: 7 specimens (UJ TF 72, 98, 137, 198, 446, 1186, 1301).

Remarks: The specimen UJ TF 939, illustrated by Książkiewicz (1977, text-fig. 13r) may belong to *Glockerichnus*. Several specimens labelled as *Sublorenzina pussila* display features of *L. plana*, except for size, being smaller. However, size cannot be regarded as the diagnostic feature at the ichnospecies level and can be only treated as a variation. The differences between *L. nowaki* and *L. plana* are probably connected with different inclination of the radiating elements within the burrow system (Fig. 39).

Lorenzina nowaki (Książkiewicz 1970)

Fig. 40

- 36, pl. 3j.
 1992 *Sublorenzina plana* Książkiewicz – Crimes *et al.*, 67, figs. 4C, 5B.
 ? 1993a *Sublorenzina plana* Książkiewicz – Li, 97, pl. 3, fig. 5.
 1994 *Sublorenzina plana* Książkiewicz – Löffler & Geyer, 510, fig. 5b.
 v 1996a *Lorenzina plana* (Książkiewicz) – Tunis & Uchman, 177, fig. 4E.

- non 1968a *Lorenzina nowaki* sp. nov. – Vialov, 338 [= *L. carpathica*].
 v non 1970 *Asterichnus nowaki* ichnosp. n. – Książkiewicz, 310, fig. 7d [= *Glockerichnus glockeri*].
 v partim 1977 *Sublorenzina nowaki* (Książkiewicz) – Książkiewicz, 95, pl. 7, figs. 1-3, text-fig. 13k, o [non text-fig. 13f = *Glockerichnus glockeri*; non text-fig. 13g-j, l-n = *Glockerichnus* isp.].
 v non 1977 *Sublorenzina* aff. *nowaki* (Książkiewicz) – Książkiewicz, 95, text-fig. 13p [= *Glockerichnus* isp.].
 1982 *Sublorenzina* cf. *nowaki* (Książkiewicz) – Alexandrescu & Brustur, 37, pl. 3, fig. 1a, plo. 4, fig. 1a.

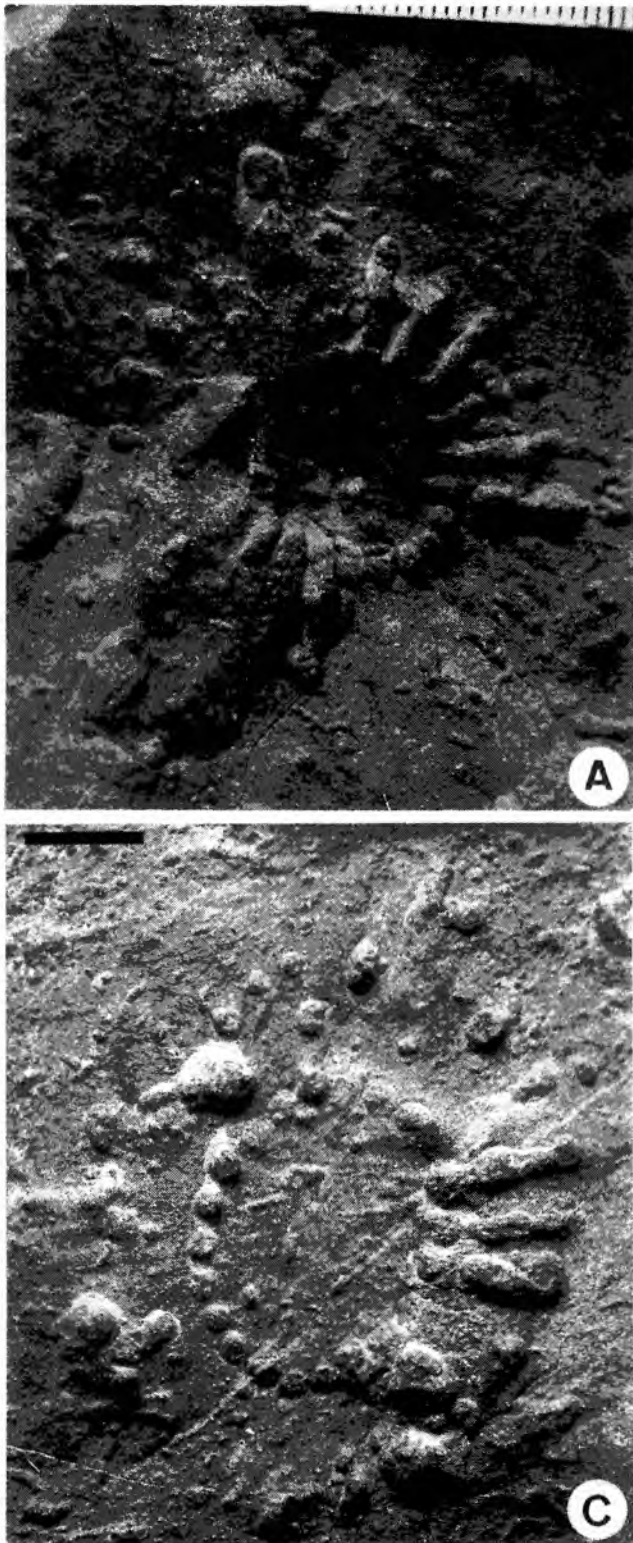


Fig. 35. *Lorenzina carpathica* (Zuber), different types of preservation. **A.** UJ TF 85, Variegated Shale (Paleocene-Eocene), Lipnica Mała (labelled as *L. aff. moreae*). **B.** UJ TF 1109, Variegated Shale (Paleocene-Eocene), Lipnica Mała-Gubernas (labelled as *L. aff. moreae*). **C.** UJ TF 84, Variegated Shale (Paleocene-Eocene), Lipnica Mała-Gubernas (labelled as *L. peralta*). Scale in A in mm, scale bars in B-C = 1 cm

radiating ridges.

Material: 5 specimens (UJ TF 107, 650, 655, 659, 1154).

Remarks: Książkiewicz (1977) mentioned “delicate transverse striation” in ridges of some specimens. These display branched ridges and belong to *Glockerichmus*, and are excluded from *L. nowaki*. Asymmetry in length of the ridges can be partially caused by preferential scouring (cf. Seilacher, 1977a). However, the irregularity of morphology is connected mainly with the primary irregular distribution of elements of the burrow system. The burrow system is interpreted as a wreath of asymmetric, wide U-tubes, which are radially arranged around central area.

?*Lorenzina pustulosa* (Książkiewicz 1977)

Fig. 41

- *v 1977 *Sublorenzina pustulosa* n. ichnosp. – Książkiewicz, 97, pl. 7, fig. 9, text-fig. 13s, t.
- v 1995 *Lorenzina pustulosa* (Książkiewicz) – Uchman, 22, pl. 7, fig. 1.
- v 1996a *Lorenzina pustulosa* (Książkiewicz) – Tunis & Uchman, 177 [not figured].
- v 1996b *Lorenzina* isp. – Tunis & Uchman, 6, fig. 9B.
- v 1997 *Lorenzina pustulosa* (Książkiewicz) – Wetzel & Uchman, 145, fig. 4B.

- ?non 1994 *Sublorenzina nowaki* (Książkiewicz) – Löffler & Geyer, 510, fig. 4a.
- v ? 1996b *Lorenzina ?nowaki* (Książkiewicz) – Tunis & Uchman, 6, fig. 7E.
- v ? 1996 *Lorenzina ?nowaki* (Książkiewicz) – Marinčić *et al.*, pl. 2, fig. 6.

Emended diagnosis: Irregular *Lorenzina*, with pointed external terminations and elevated internal terminations of the

Diagnosis: *Lorenzina* in which a poorly defined central area is surrounded by a wreath of short, wide, and loosely spaced ribs

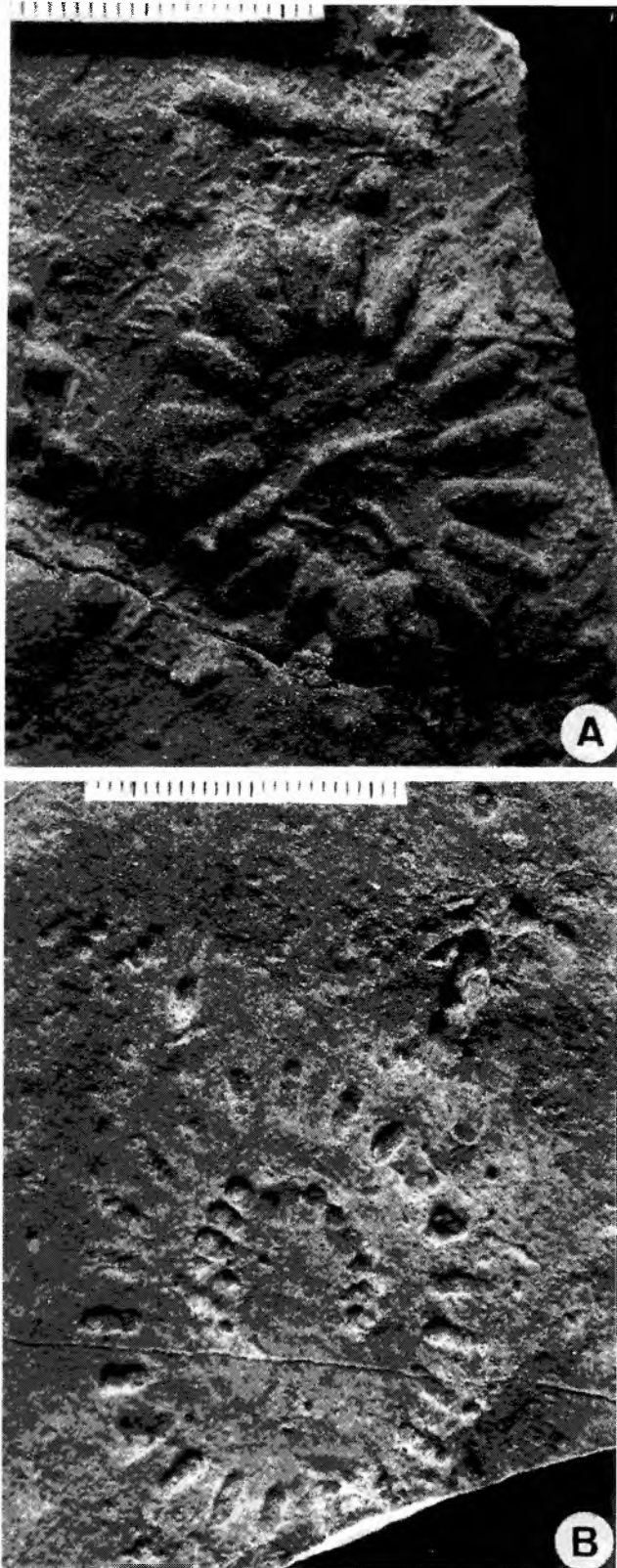


Fig. 36. *Lorenzium carpathica* (Zuber) on sole of turbiditic sandstone beds. A. UJ TF 871, Variegated Shale (Paleocene–Eocene), Lipnica Mała (labelled as *L. carpathica*). B. UJ TF 2022, Ropianka beds (Senonian–Paleocene), Siedkierzyna (labelled as *L. moreae*). Scale in mm

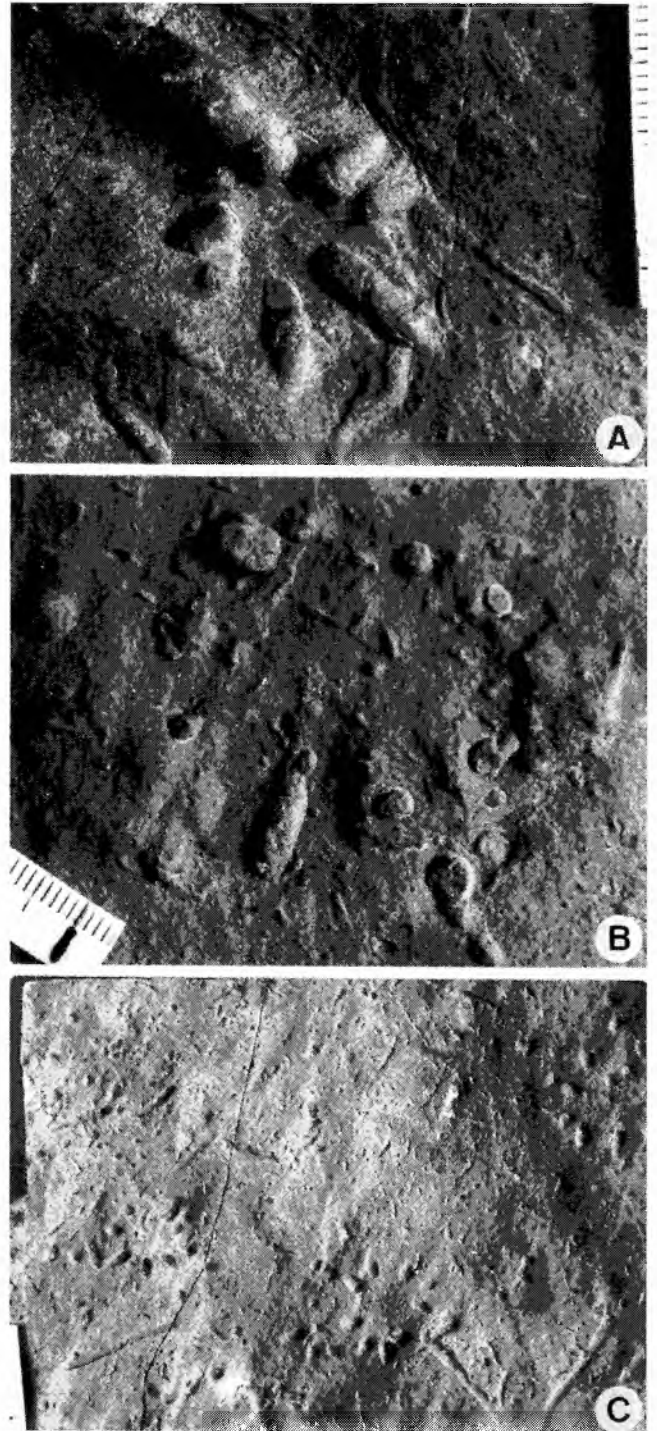


Fig. 37. *Lorenzium plana* (Książkiewicz), soles of turbiditic sandstone beds. A. UJ TF 137, Middle Godula beds (Turonian), Ponikiew. B. UJ TF 198, Beloveža Formation (Eocene), Sidzina (labelled as *Sublorenzium* aff. *pustulosa*). C. UJ TF 98, Cieszyn Limestone (Beriasian), Goleszów. Scale in mm

(modified after Książkiewicz, 1977).

Material: 5 specimens (UJ TF 129, 800, 943, 1177, 1491).

Remarks: Książkiewicz (1977) indicated in his diagnosis that *Sublorenzium* (= *Lorenzium*) *pustulosa* is preserved in full relief. This is regarded as unlikely. The ichnospecies displays a great morphological variability (Książkiewicz,

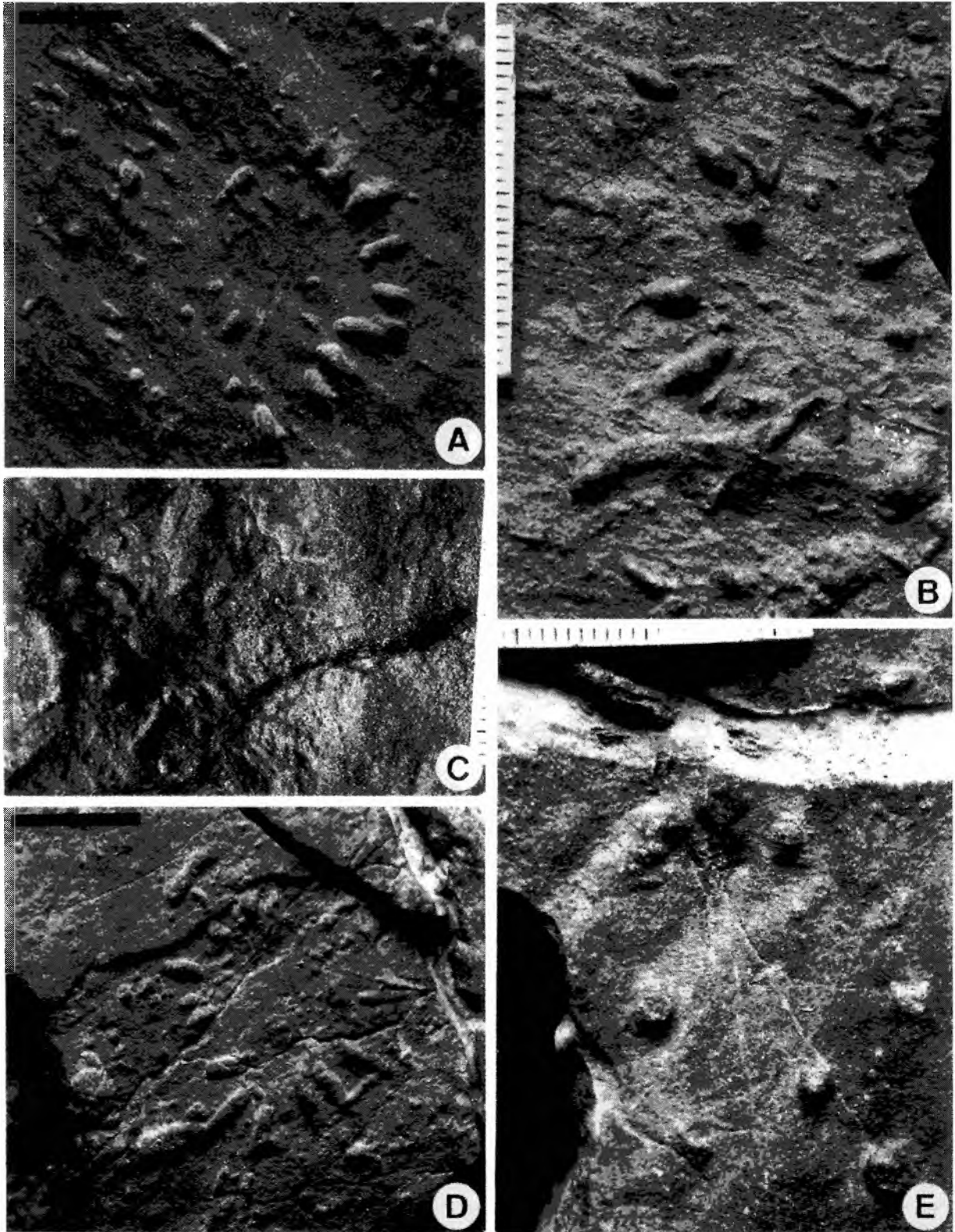


Fig. 38. *Lorenzinia plana* (Książkiewicz), soles of turbiditic sandstone beds. **A.** UJ TF 2588, Jordanów (part of label lost). **B.** UJ TF 971, Ropianka beds (Senonian–Paleocene), Grzechynia near Grybów (labelled as *Sublorenzinia pusilla*). **C.** UJ TF 931, (labelled as *Sublorenzinia pusilla*, part of label lost). **D.** UJ TF 136, Hieroglyphic beds (Eocene), Grzechynia near Grybów (labelled as *Sublorenzinia pusilla*). **E.** UJ TF 1300 (part of label lost, labelled as *Sublorenzinia pusilla*). Scale bars in A, D = 1 cm, scales in B–C, E in mm

1977) and its affinity to *Lorenzinia* may be questioned. Similar sole expressions can also result from uneven scouring of *Glockerichmus*. Therefore, a question mark is placed

before the ichnogenic name. Some specimens (UJ TF 1491, 1557) that display features of ?*L. pustulosa* were labelled by Książkiewicz as *Sublorenzinia nowaki*.

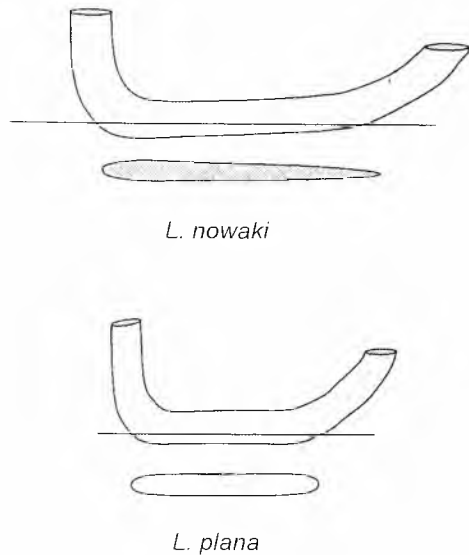


Fig. 39. Model of *Lorenzinia nowaki* and *Lorenzinia plana* in relation to inclination of the radiating elements of the burrow system

?*L. pustulosa* occurs in flysch deposits from the Cenomanian (Książkiewicz) to the Miocene (Uchman, 1995).

Capodistria Vialov 1968a

Diagnosis: Short, simple hypichnial ridges radiating from an oval or circular central area. A distinct knob or a few knobs are situated more or less in the centre. The ridges may differ in length and may be irregularly distributed (modified after Książkiewicz, 1977).

Remarks: Separation of *Capodistria* from *Lorenzinia* at ichnogenetic level may be questioned. In some cases, distinction between irregular *Sublorenzina* (= *Lorenzinia*) and *Capodistria* is difficult. Some specimens of the first ichnotaxon (Książkiewicz, 1977, text-fig. 13l, t) display knobs in the central part, which are, however, not centrally located. These specimens belong probably to strongly scoured *Glockerichnus*. The same concerns the trace fossil illustrated by Książkiewicz (1977, text-fig. 13b) with three central knobs. It displays faint perpendicular striation in one radiating ridge, which is typical of *Glockerichnus* (Fig. 46A). As it is not clear what kind of structure is represented by the central knob, the separation is retained.

On the present-day deep-sea floor, surficial grooves radiating from a central hole were photographed. They were produced by bonnelid echiurians (Ohta, 1984) and may represent behavioural counterparts of *Capodistria*.

This ichnogenus occurs in flysch deposits from the Mid Cretaceous (Książkiewicz, 1977) to the Miocene (Uchman, 1995).

Capodistria vettersi Vialov 1968a

Fig. 42

1910 Hieroglyph aus [...] - Vettors, 131, fig. a (also Książkiewicz, 1977, text-fig. 13a).

? 1961 Zvezdhatiy hieroglif - Grossheim, pl. 2, fig. 2.

1968a *Capodistria vettersi* - Vialov, 337, fig. 4.

*v partim 1977 *Capodistria vettersi* Vialov - Książkiewicz, 99, pl. 7, figs.

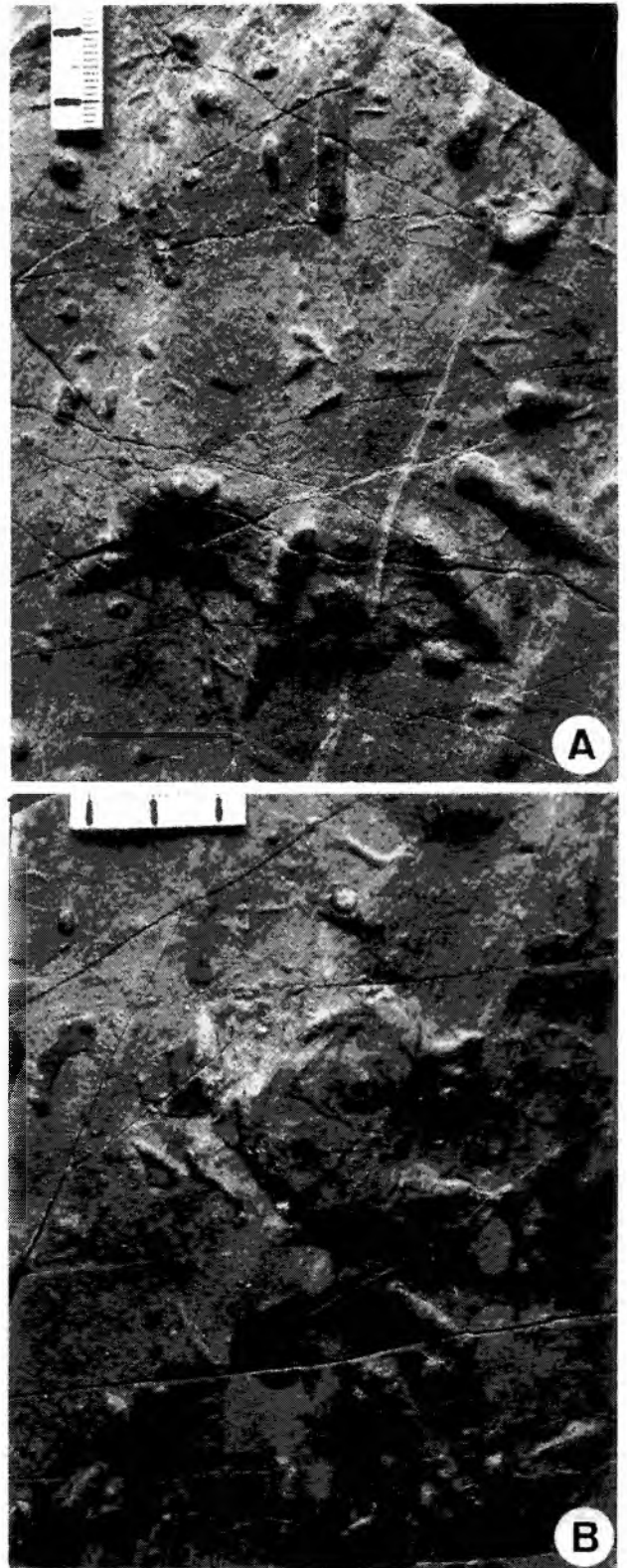


Fig. 40. *Lorenzinia nowaki* (Książkiewicz), soles of turbiditic sandstone beds. A. UJ TF 655, Ropianka beds (Senonian-Paleocene), Limanowa. B. UJ TF 1154, Inoceranian beds (Senonian-Paleocene), Szczawa. Scale in mm

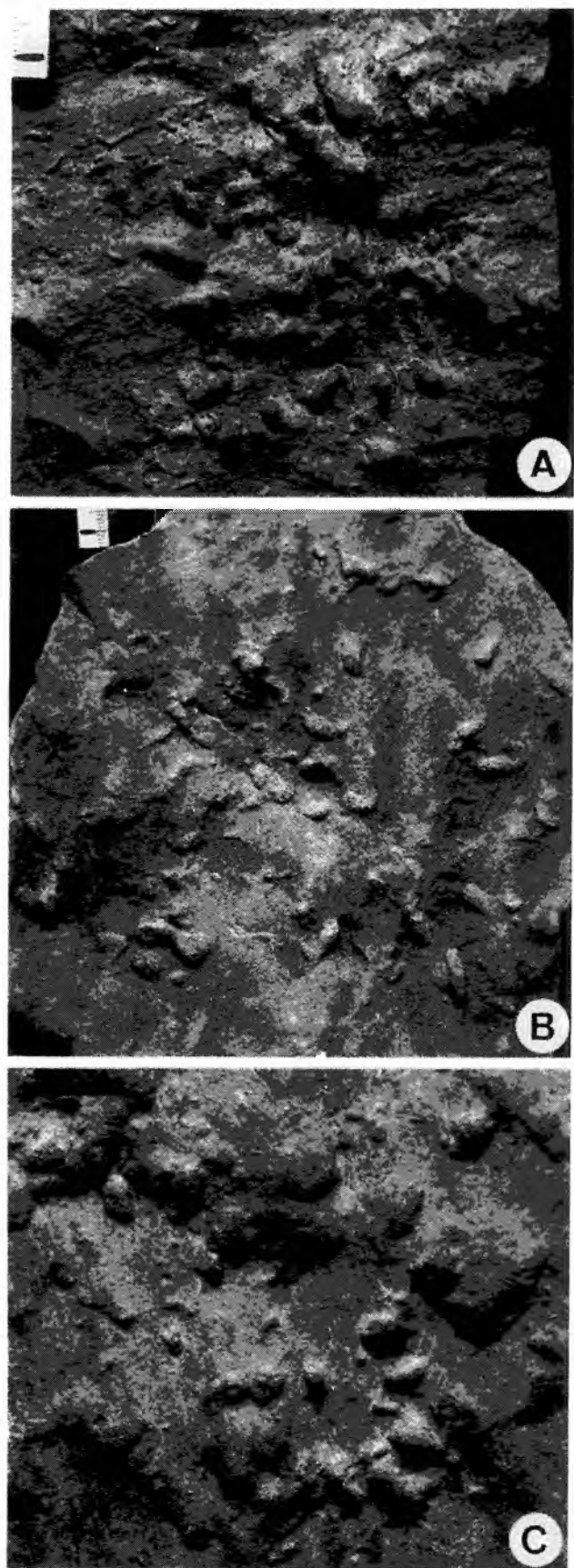


Fig. 41. ?*Lorenzina pustulosa* (Książkiewicz), soles of turbiditic sandstone beds. **A.** UJ TF 1557, Klimkówka (part of label lost, labelled as *Sublorenzina nowaki*). **B.** UJ TF 1491 (labelled as *Sublorenzina pustulosa*, part of label lost). **C.** UJ TF 800, Hieroglyphic beds (Eocene), Tokarnia (labelled as *Sublorenzina plana*). Scale for A-B in mm, scale bar in C = 1 cm

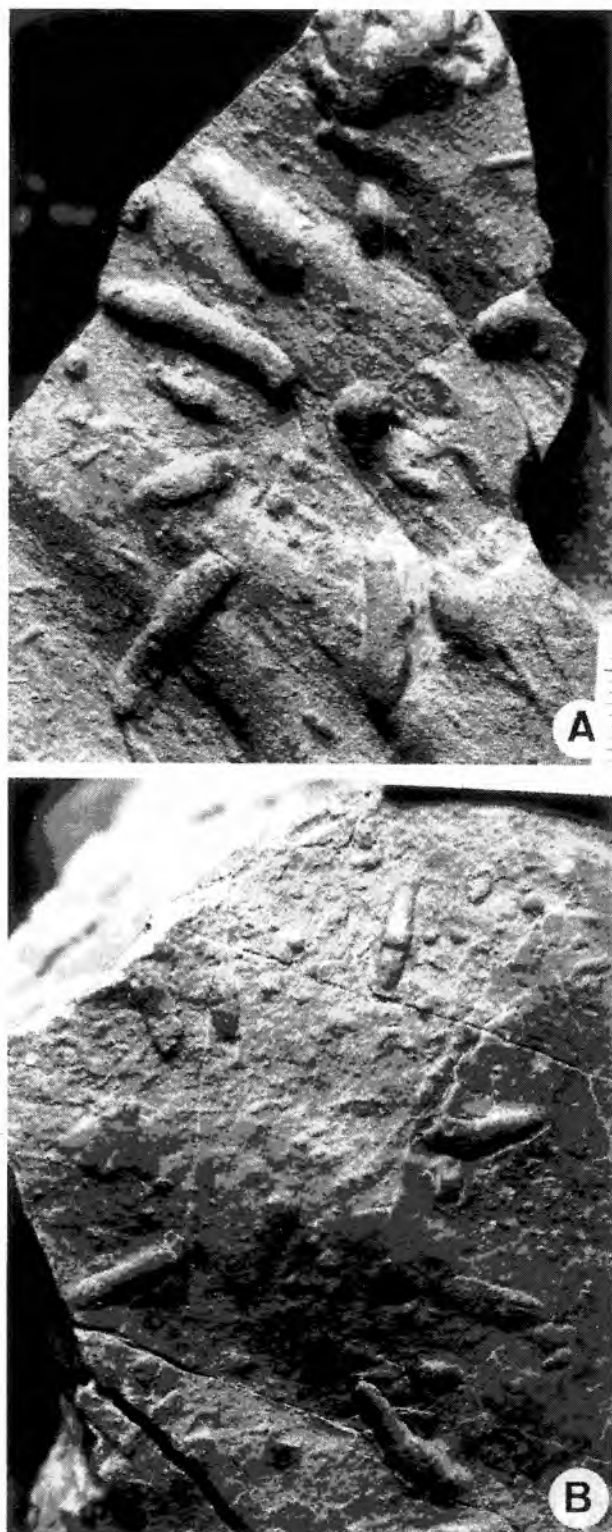


Fig. 42. *Capodistria vettersi* Vialov, soles of turbiditic sandstone beds. **A.** UJ TF 96, Lower Godula beds (Cenomanian), Jaroszewiec. **B.** UJ TF 958, Ropianka beds (Senonian–Paleocene), Kąclowa. Scales in mm

- 12-13, text-fig. 13c-e [not text-fig. 13b = *Glockerichnus* isp.].
- 1990 *Capodistria moldavica* n. ichnosp. - Brustur & Ionesi, 39, text-fig. 2, pl. 1, fig. 1.
- v 1995 *Capodistria vettersi* Vialov - Uchman, 23, pl. 7, fig. 2.
- v 1996b *Capodistria vettersi* Vialov - Tunis & Uchman, 6, fig. 9A.
- v 1996 *Capodistria vettersi* Vialov - Marinčić *et al.*, pl. 2, fig. 5.

Diagnosis: As for ichnogenus.

Material: 5 specimens (UJ TF 96, 109, 671, 958, 1436).

Remarks: *C. vettersi* is based on figured but unnamed material of Veters (1910). The specimen illustrated by Veters (1910) has nine radiating ridges and one central knob; the specimens illustrated by Książkiewicz (1977) have more radiating ridges and one or three central knob(s). However, the number of radiating ridges and central knobs does not appear to be of ichnospecies significance. Brustur & Ionesi (1990) distinguished *Capodistria moldavica* n. ichnosp. on the basis of a double central knob versus the simple knob in Veters' specimen. However, this difference does not appear to be sufficiently significant to justify a separate ichnospecies (Uchman, 1995).

Glockerichnus Pickerill 1982

Ichnospecies included in *Glockerichnus* Pickerill:

- ? 1881 *Sphaerococcytes scharvanus* Göppert - Saporta, fig. 3.2.
- ? 1890 Radiating burrow - Dawson, fig. 9.
- ? 1930 *Nimbus helianthoides* - Bogatchev, 1, fig. 1.
- 1955 Unbenannter sternförmiger Freßbau - Seilacher, fig. 5.89.
- 1956 Traces [...] des Annélides - Nowak, pl. 13, fig. A, pl. 14, figs. C-D, pl. 15, figs. E-F, pl. 16, figs. G-I.
- 1959 Sternförmiger Freßbau - Seilacher, pl. 2, fig. 22.
- 1961 *Asterichnus* n.f. - Nowak, 227 (nomen nudum).
- 1968 *Glockeria glockeri* n. sp. - Książkiewicz, 9.
- ? 1977b *Glockeria* Książkiewicz - Crimes, 594, pl. 4, fig. 2.
- partim 1977 *Sublorenzina nowaki* (Książkiewicz) - Książkiewicz, 95, text-fig. 13f-j, l-n [non pl. 7, figs. 1-3, text-fig. 13k, o = *Lorenzina nowaki*].
- 1977 *Sublorenzina* aff. *nowaki* (Książkiewicz) - Książkiewicz, 95, text-fig. 13p.
- partim 1977 *Capodistria vettersi* Vialov - Książkiewicz, 99, text-fig. 13b [non pl. 7, figs. 12-13, text-fig. 132c-e].
- 1977 *Buthotrephis bifurcata* n. ichnosp. - Książkiewicz, 76, pl. 5, fig. 14, text-fig. 10z.
- ? 1978 *Glockeria* Książkiewicz - Aceñolaza, 24, fig. 9 (also Aceñolaza & Toselli, 1981, fig. 12.4).
- ?non 1980 *Glockeria* sp. - Pickerill, fig. 5c.
- 1982 *Glockerichnus* - Pickerill, 816.
- 1987 *Glockerichnus* isp. - Pickerill *et al.*, 83, fig. 4b.
- 1991 *Glockeria* - Jin & Li, pl. 1, fig. 3a.
- partim 1994 *Glockeria* sp. - Gong, 488, pl. 5, fig. 5 (non pl. 5, fig. 4, ? pl. 5, fig. 6).
- v 1995 *Glockerichnus* isp. - Uchman, 23, pl. 7, fig. 3.
- v 1996a *Glockerichnus* isp. - Tunis & Uchman, 177, fig. 4C.
- ? 1997 *Glockerichnus* isp. - Zagora, 360, fig. 5.4.

Diagnosis: Branched strings, usually dichotomous, radiating from a central point or hollow central area. In some cases, indistinct bilateral symmetry is developed (after Uchman, 1995).

Remarks: *Glockerichnus* was introduced by Pickerill (1982) for *Glockeria* (Książkiewicz, 1968), a name pre-occupied by a phacopid trilobite. According to Vialov (1989), *Glockeria* Książkiewicz and *Glockerichnus* Pickerill are junior synonyms of *Stelloglyphus* Vialov (1964, 1968a) (see also Häntzschel, 1975, p. W111-W112, fig. 69). However, *Stelloglyphus* and *Glockerichnus* display several differences. *Glockerichnus glockeri* (Książkiewicz), the type ich-

nospecies of the ichnogenus, is preserved as hypichnial branched strings, commonly dichotomous, radiating from central point or hollow central area. The strings display more or less the same diameter. The wide, depressed central area and elevation of strings around the points of dichotomy are the characteristic morphological features of this ichnogenus. The central depressed area occurs also in cases where the stellate strings radiate from the central point (Książkiewicz, 1977, pl. 9, fig. 1).

The type ichnospecies of *Stelloglyphus*, *S. turcomanicus* Vialov (1964, fig. 1) (see also Häntzschel, 1975, p. W111-W112, fig. 69.1a) has relatively wide ridges radiating from a distinct shaft, which is visible on photographs in cross section as a small circular or oval vertical shaft. It is not clear if the ridges are branched or not. They are densely spaced and overlap. The ridges are slightly petaloidal in outline. This feature is very distinct in *Stelloglyphus giganteus* Vialov (1968, pl. 2, figs. 1-2) (see also Häntzschel, 1975, p. W111-W112, fig. 69.1b-c). The central depressed area is not present. Both ichnospecies of *Stelloglyphus* derive from Turkestan, where *S. giganteus* Vialov occurs in a dense population of trace fossils at a certain horizon of the Lower Senonian marly-sandy deposits (Atabekan in Vialov, 1968a, 1989). *Glockerichnus* never occurs in dense populations. Probably, *Stelloglyphus* is produced by deposit feeders (fodinichnia). Its producer tried to use the space around the shaft as much as possible. *Glockerichnus* has been included among the graphoglyptids (Seilacher, 1977a), which were probably produced by animals farming microorganisms in morphologically complicated burrow system (agrichnia sensu Ekdale, 1985). Thus, there are enough morphological and probable ethological differences between *Glockerichnus* Książkiewicz and *Stelloglyphus* Vialov for separation of these two ichnogenera.

Glockerichnus occurs in flysch deposits (e.g. Książkiewicz, 1977), from the Ordovician (Pickerill *et al.*, 1987a) to the Miocene (Uchman, 1995). Recent traces morphologically resembling *Glockerichnus* were photographed on the deep-sea floor at 1625 m depth (Ekdale & Berger, 1978). ?*Glockerichnus* ichnosp. has been reported from nonmarine Permian red beds (Mikuláš, 1993b).

Glockerichnus glockeri (Książkiewicz 1968)

Fig. 43

- ? 1930 *Nimbus helianthoides* - Bogatchev, 1, fig. 1.
- 1955 Unbenannter sternförmiger Freßbau - Seilacher, fig. 5.89.
- 1957 Traces [...] des Annélides - Nowak, pl. 13, fig. A, pl. 14, figs. C-D, pl. 15, figs. E-F, pl. 16, fig. G.
- 1959 Sternförmiger Freßbau - Seilacher, pl. 2, fig. 22.
- 1968 *Glockeria glockeri* n. "sp." - Książkiewicz, 9.
- 1970 *Glockeria glockeri* Książkiewicz - Książkiewicz, 312, fig. 7a.
- 1970 *Asterichnus nowaki* ichnosp. nov. - Książkiewicz, 311, fig. 7d.
- partim 1977 *Sublorenzina nowaki* (Książkiewicz) - Książkiewicz, 95, text-fig. 13f.
- 1977 *Glockeria glockeri* Książkiewicz - Książkiewicz, 100, pl. 8, fig. 1, pl. 9, fig. 1.
- ? 1988 *Glockerichnus glockeri* (Książkiewicz) - McCann & Pickerill, 335, fig. 3.11.
- ? 1992c *Glockerichnus glockeri* (Książkiewicz) - Mikuláš, 392, pl. 4, fig. 2, pl. 5, figs. 5-6.
- ?non 1993 *Glockerichnus* cf. *glockeri* (Książkiewicz) - Miller, 20,

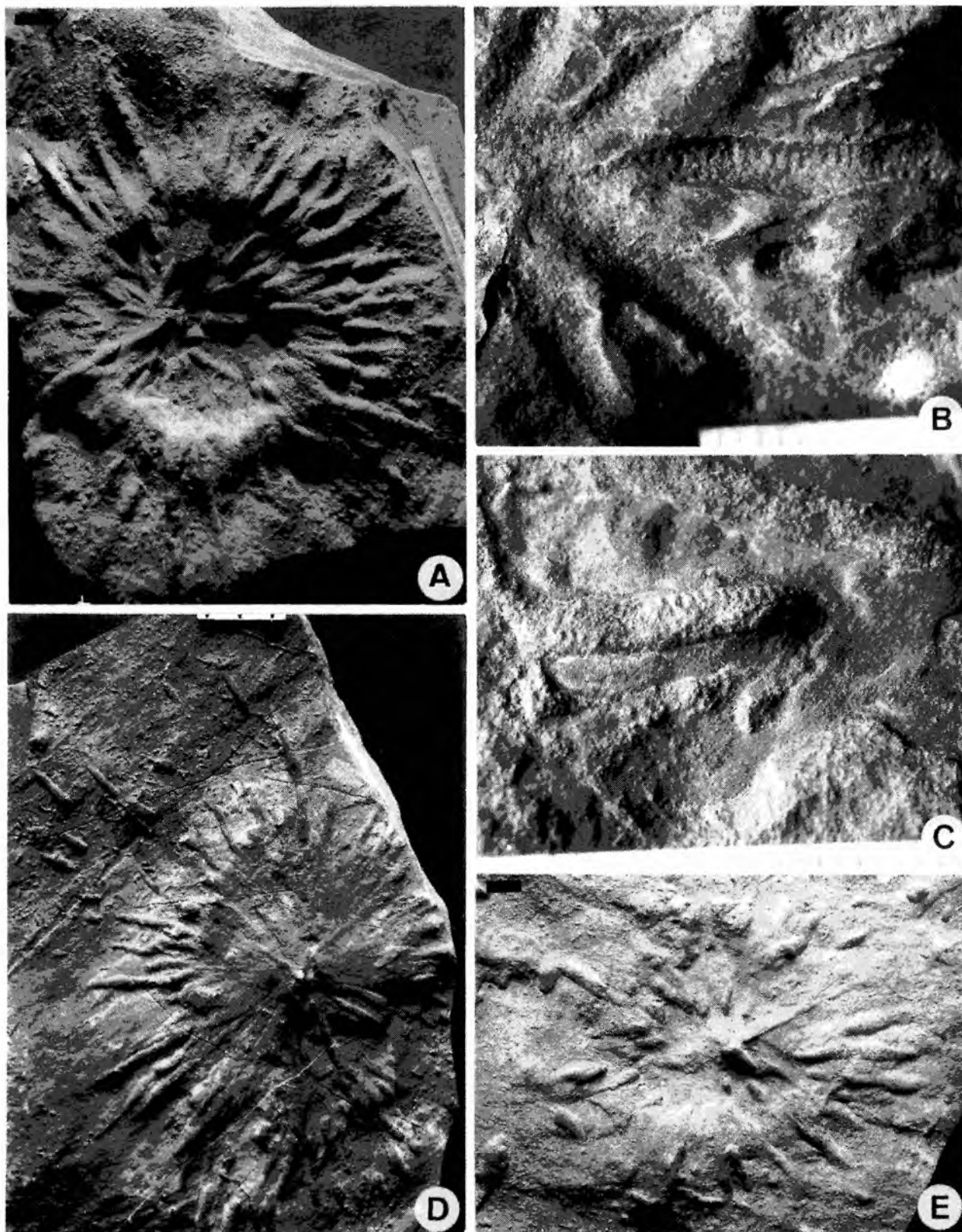


Fig. 43. *Glockerichnus glockeri* (Książkiewicz), soles of turbiditic sandstone beds. **A.** UJ TF 96, Cieszyn Limestone (Beriasian), Golezów. General view. **B-C.** Details of A. **D.** UJ TF 110, Upper Cieszyn Shale (Valanginian), Wilamowice. **E.** UJ TF 1157, Cieszyn Limestone (Beriasian), Golezów (labelled as *Sublorenzinia nowaki*). Scale bars in A, E = 1 cm, scales in B-C in mm, scale in D in mm

fig. 5J.

- ? 1994 *Glockerichnus glockeri* (Książkiewicz) – Mikuláš, pl. pl. 2, figs. 1-2.
 non 1995 *Glockerichnus glockeri* (Książkiewicz) – Crimes & McCall, 235, fig. 2F.

Emended diagnosis: *Glockerichnus* possessing numerous strings, which display narrow U-shaped dichotomy close to the centre. The strings can be elevated in the zone of dichotomy, which encircles the centre. The centre can be eroded.

Material: 3 specimens (TF UJ 95 (holotype), 110, 1157).

Description: Hypichnial branched strings, commonly dichotomous, radiating from central point or hollow central area. The strings display more or less the same diameter. The wide depressed central area and elevation of strings around the points of dichotomy are the characteristic morphological features of this ichnogenus. The central depressed area occurs also in cases where the stellate strings radiate from the central point. The strings display partially preserved, fine, transversal ribbing (Fig. 43B–C).

Remarks: Most occurrences of *G. glockeri* are restricted to Beriasian–Hauterivian flysch deposits. Determinations of the Ordovician (Mikuláš, 1992b, 1994) and the Upper Cretaceous (McCann & Pickerill, 1988) forms can be questioned and therefore they are only reservedly included in *Glockerichnus*.

Glockerichnus alata (Seilacher 1977a)

- 1962 Unnamed large feeding burrow – Seilacher, pl. 2, fig. 5, text-fig. 1 (part).
 v 1970 Unnamed trace related(?) to *Urohelminthoida* – Książkiewicz, fig. 6g1.
 v 1977 *Buthotrephis bifurcata* n. ichnosp. – Książkiewicz, 76, pl. 5, fig. 14, text-fig. 10z.
 1977a *Glockeria alata* n. ichnosp. – Seilacher, 316, pl. 1d, fig. 9e, 10b-c.
 non 1991 *Glockerichnus alata* Seilacher – Crimes & Crossley, 35, fig. 3h.
 1992 *Glockeria alata* – Leszczyński, pl. 8, fig. 2.

Diagnosis: Very large *Glockerichnus*, with a U-bifurcation of the radiating ridges. A new U-element usually occurs at the limb of a former element of similar shape (modified after Seilacher, 1977a).

Material: 1 specimen (UJ TF 1383).

Description: As in the diagnosis and in the description of *Buthotrephis bifurcata* (Książkiewicz, 1977).

Remarks: Książkiewicz collected only fragments of *G. alata* and placed his material under *Buthotrephis* (see comments on *Buthotrephis*). The Książkiewicz (July 1977) ichnospecific name has priority over Seilacher's (August 1977a) ichnospecific name. Nevertheless, the latter name is retained because it refers to more complete material.

?*Glockerichnus disordinata* (Książkiewicz 1977)

Fig. 44

- v* 1977 *Glockeria disordinata* n. ichnosp. – Książkiewicz, 102, pl. 9, fig. 2, text-fig. 13 y, z.
 ? 1987 *Glockeria* aff. *disordinata* Książkiewicz – Micu *et al.*, 82, pl. 1, fig. 1.
 1991 *Glockerichnus alata* Seilacher – Crimes & Crossley, 35, fig. 3h.

Diagnosis: Hypichnial small stellate trace fossil composed of a few short, winding, smooth ridges joined and elevated at the centre, which plunge into the bed at the fringe of the structure (modified after Książkiewicz, 1977).

Material: 3 specimens (UJ TF 1524, 1735 (holotype), 1840).

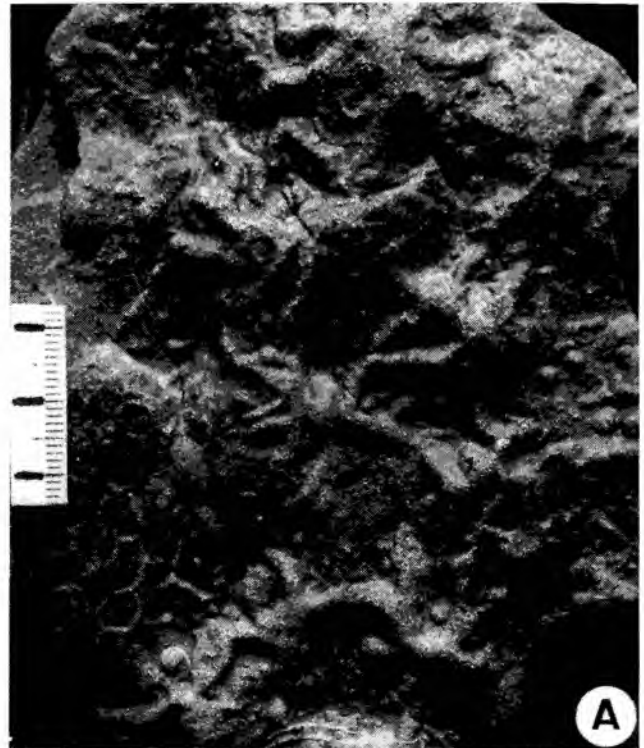


Fig. 44. ?*Glockerichnus disordinata* (Książkiewicz), soles of turbiditic sandstone beds in the Upper Istebna beds (Paleocene). A. UJ TF 1524, Tabaszowa (with *Paleodictyon strozzii*). B. UJ TF 1840, Kamesznica, Janoska stream. Scale in A in mm, in B in cm

Remarks: Dichotomy of the radiating ridges is not clear, which is the significant diagnostic feature of *Glockerichnus*. Therefore, the question mark is placed before the ichnogen-

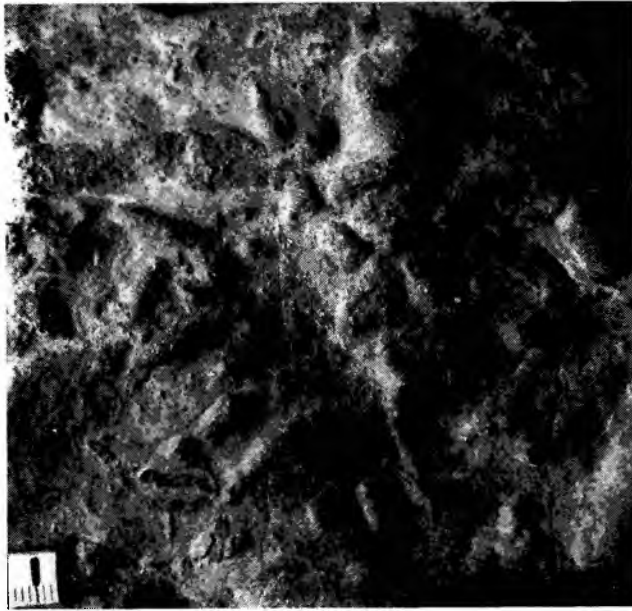


Fig. 45. *Glockerichnus dichotoma* (Seilacher), sole of turbiditic sandstone bed. UJ TF 1705, Wierzbanowa (original label lost). Scale in mm

eric name. Brustur & Stoica (1993) reported *G. aff. disordinata* from Upper Eocene flysch of Romania.

Glockerichnus dichotoma (Seilacher 1977a)

Fig. 45

- 1977a *Glockeria dichotoma* n. ichnosp. - Seilacher, 316, fig. 9d.
 ? 1977b *Glockeria* Książkiewicz - Crimes, 594, pl. 4, fig. 2.
 partim 1994 *Glockeria* sp. - Gong, 488, pl. 5, fig. 5 (non pl. 5, figs. 4, 6).
 v ? 1995 *Glockerichnus* isp. - Uchman, 23, pl. 7, fig. 3.

Diagnosis: Small *Glockerichnus* with V-shape bifurcating narrow ridges, mainly close the central part (modified after Seilacher, 1977a).

Material: 1 specimen (UJ TF 1705).

Description: As in the diagnosis, with the following remarks: whole structure is about 60 mm in diameter. The radiating ridges are fragmentarily preserved. They are 2–3 mm wide and as much as 23 mm long. V-shaped dichotomy is clear in two ridges.

Remarks: Original label of this specimen is lost.

?*Glockerichnus sparsicostata* (Książkiewicz 1968)

- 1957 Traces [...] des Annélides - Nowak, pl. 16, fig. 1.
 1968 *Glockeria sparsicostata* n. "sp." - Książkiewicz, 10, pl. 5, fig. 4.
 1970 *Glockeria sparsicostata* Książkiewicz - Książkiewicz, 312, fig. 7b.
 1977 *Glockeria sparsicostata* Książkiewicz - Książkiewicz, 101, pl. 9, fig. 3.
 ? 1980 *Glockeria* aff. *sparsicostata* Książkiewicz - Alexandrescu & Brustur, 24, pl. 6, fig. 1.
 non 1981 *Glockeria sparsicostata* Książkiewicz - Crimes *et al.*, 972, pl. 3, fig. 3.
 1995 *Glockerichnus glockeri* (Książkiewicz) Crimes & McCall, 235, fig. 2F.

Emended diagnosis: *Glockerichnus* having relatively few, wide ridges radiating from the central point, rarely dichotomous.

Material: 1 specimens (TF UJ 210, holotype).

Remarks: *G. sparsicostata* occurs in flysch deposits from Hauterivian (Nowak, 1957) to Miocene (Crimes & McCall, 1995). It resembles *Stelloglyphus* Vialov (1964, 1968a), especially in its wide rays and gregarious occurrence. Therefore, its ichnogenus affinity may be questioned and a question mark is placed before the ichnogenetic name.

?*Glockerichnus parvula* (Książkiewicz 1970)

- 1960 Rosetted trail - Książkiewicz, 746, pl. 3, fig. 10.
 v* 1970 *Glockeria parvula* ichnosp. nov. - Książkiewicz, 312, fig. 7c.
 1971 *Glockeria parvula* Książkiewicz - Tanaka, 5, pl. 10, fig. 3.
 v 1977 *Glockeria parvula* Książkiewicz - Książkiewicz, 102, pl. 8, fig. 2.
 1981 *Glockeria sparsicostata* Książkiewicz - Crimes *et al.*, 972, pl. 3, fig. 4.

Diagnosis: Hypichnial small stellate cast, consisting of a central cone from which radiate a few short straight thin ribs. A tiny crater-like pit is situated at the top of the cone (after Książkiewicz, 1977).

Material: 1 specimen (UJ TF 108, holotype).

Remarks: Morphology of this trace fossil does not conform to the diagnosis of *Glockerichnus*. There are some similarities with *Asterichnus* Bandel, but this problem needs further study; therefore, the question mark before the ichnogenetic name.

Glockerichnus isp. indet. A

Fig. 46

- v partim 1977 *Sublorenzinia nowaki* (Książkiewicz) - Książkiewicz, 95, text-fig. 13g-j, l-n.
 v partim 1977 *Capodistria vettersi* Vialov - Książkiewicz, 99, text-fig. 13b.

Material: 7 specimens (TF UJ 215-216, 256, 1126, 1137, 1155, 1705).

Description: Variable, irregularly distributed radiating hypichnial ridges and knobs. Dichotomy of the ridges is more or less visible. The ridges are 1–4 mm in diameter and up to 40 mm long.

Glockerichnus isp. indet. B

Fig. 47A–B

Material: 2 specimens (UJ TF 991B).

Description: Endichnial trace fossil, which displays at least about 30 long, radiating, thin, cylindrical rays. The rays are up to 70 mm long and about 1 mm in diameter. They are slightly winding, radiate from a central point, and occur on different levels within about a 2-cm-thick layer. The rays branching dichotomously at sharp angles at a distance of about 3 cm from the centre.

Remarks: This trace fossil was labelled by Książkiewicz as *Chondrites expansus*, but it displays features of *Glockerichnus*. It is not excluded that this is a new ichnospecies. However, comparison to the other ichnospecies of *Glockerichnus* is problematic, because they are only partially preserved semi-reliefs.

Glockerichnus isp. indet. C

Fig. 47C

Material: 1 specimens (UJ TF).

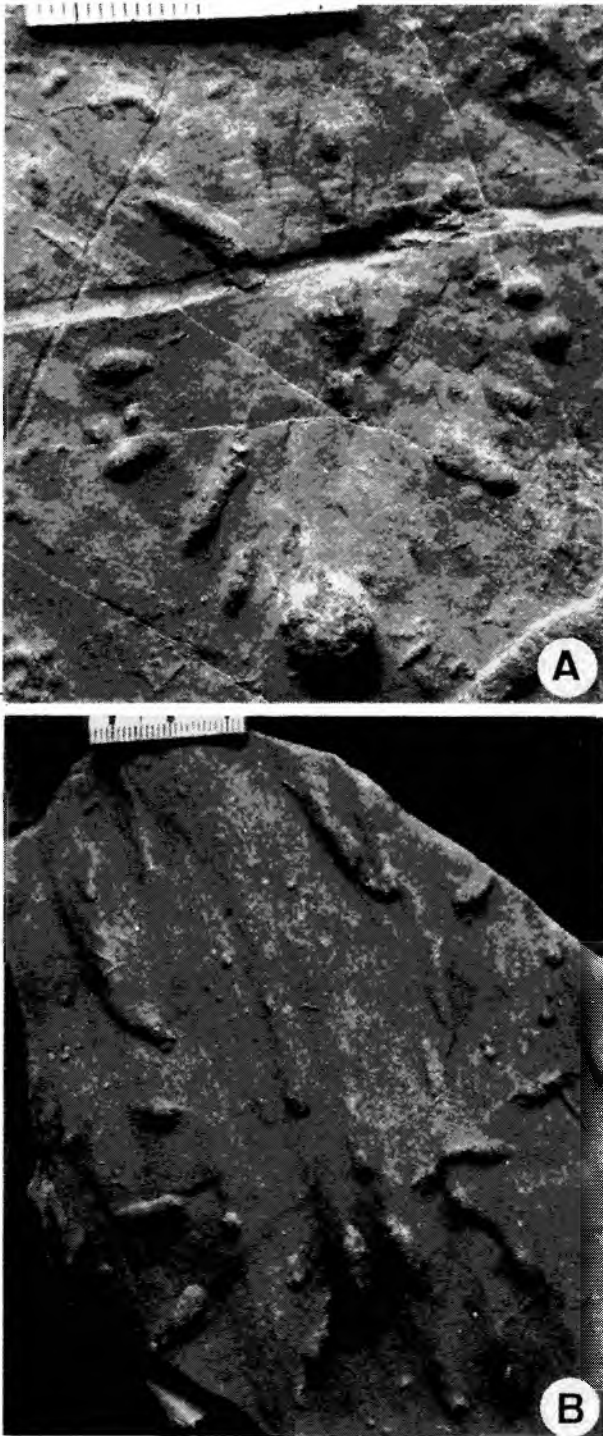


Fig. 46. *Glockerichnus* isp. **A.** strongly eroded forms in soles of turbiditic sandstone beds. UJ TF 1137, Skrzydlina beds (Senonian), Przenosza (labelled as *Capodistria vettersi*). **B.** UJ TF 215, Inoceramian beds (Senonian–Paleocene), Rzeki (labelled as *Sublorenzina nowaki*). Scales in mm

Description: Endichnial trace fossil, which displays structureless strongly flattened fillings of radiating trace fossils with enlarged and rounded terminations. They display dichotomous branchings and occur on different levels. The branchings are 2–7 mm wide and up to 30 mm long.

Remarks: This trace fossil was placed by Książkiewicz in

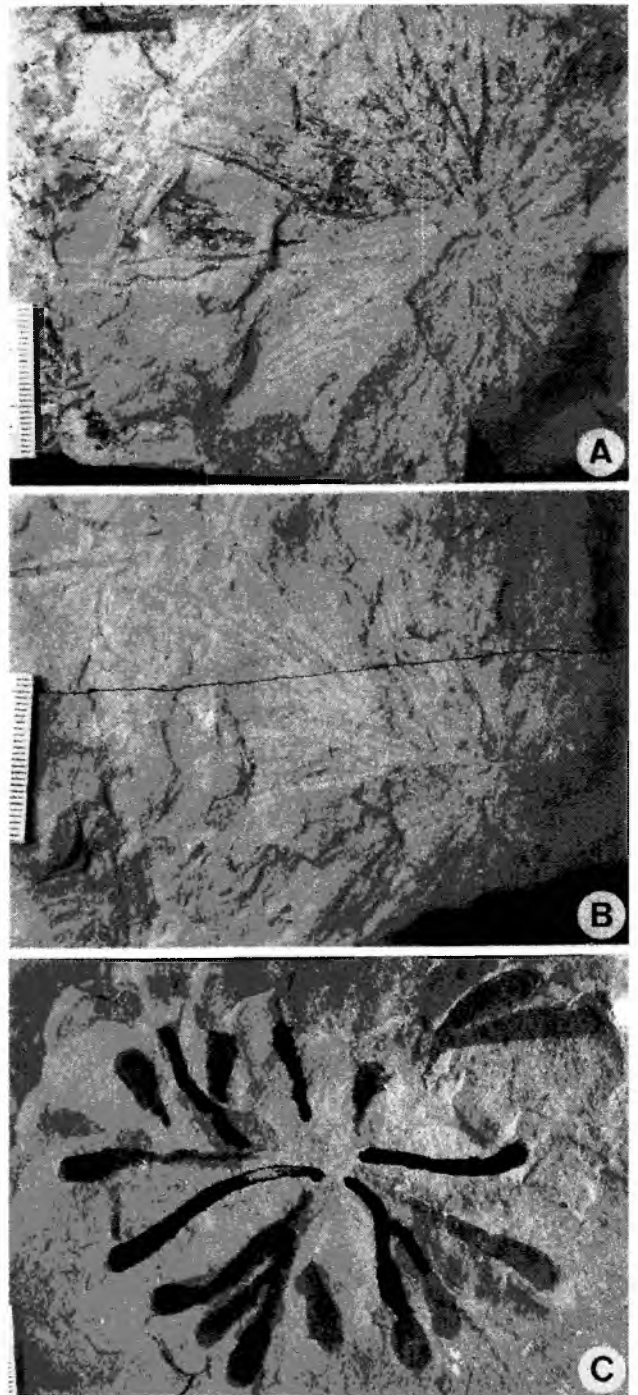


Fig. 47. **A–B.** *Glockerichnus* isp. **B.** endichnial forms in marlstone beds from the Siliceous Marls (Turonian), Krasiczyn. A. UJ TF. **B.** UJ TF 991B. **C.** *Glockerichnus* isp. **C.** endichnial form in a marlstone bed. Ropianka beds (Senonian–Paleocene), Grybów (labelled as *Chondrites affinis*, partially inked specimen). Scales in mm

Chondrites, but it displays features of *Glockerichnus*. One can not exclude that this is a new ichnospecies.

Arenituba Stanley & Pickerill 1995

Diagnosis: Generally irregularly arranged, sometimes branched tubes radiating from a central gallery, single or bunched, straight,



Fig. 48. *Arenituba* isp. Epichnial concave form. UJ TF 665, Ropianka beds (Senonian–Paleocene), Limanowa (labelled as *Chondrites expansus*). Scale in mm

curved, winding or sinuous, smooth to finely annulate, sand-coated or -filled (Stanley & Pickerill (1995) modification after Häntzschel (1975)).

Remarks: *Arenituba* was proposed as the new name for *Micatuba* Chamberlain (1971a), which name was preoccupied by a foraminifer (Stanley & Pickerill, 1995). Similarity of this trace fossil to *Glockerichnus* may be discussed, but this would require further investigation of the type material of *Micatuba*.

Arenituba isp.
Fig. 48

Material: 1 specimen (UJ TF).

Description: Epichnial concave trace fossil composed of 7 slightly winding rays, which come out from central point. The rays are 2 mm wide and as much as 30 mm long. They occasionally display V-shaped branchings in the inner part.

Remarks: The described specimen was housed together with *Chondrites* (original label lost) but displays features of *Arenituba*. For discussion of this ichnogenus see Stanley & Pickerill (1995).

Fascichnium Książkiewicz 1968

Emended diagnosis: Short ridges radially arranged around elongate, open area.

Fascichnium extentum Książkiewicz 1968
Fig. 49

v* 1968 *Fascichnium extentum* n. "sp." – Książkiewicz, 10, pl. 6,



Fig. 49. *Fascichnium extentum* Książkiewicz, sole of turbiditic sandstone bed. UJ TF 1440, Variegated Shale (Paleocene–Lower Eocene), Lipnica Mała-Gubernas. Scale in mm

fig. 1 (also Książkiewicz, 1977, pl. 8, fig. 4).

v 1997 *Fascichnium extentum* Książkiewicz – Wetzel & Uchman, 144, fig. 3F.

?non 1997 ?*Fascichnium* ichnosp. – Zagora, 360, fig. 4.6.

Diagnosis: As for ichnogenus.

Material: 2 specimens (UJ TF 1440, 1567 (holotype)).

Remarks: *Fascichnium* occurs in flysch deposits from Senonian to Eocene (Książkiewicz, 1977). Książkiewicz regarded *Fascichnium* as a trace produced by the inhalant siphon of bivalves or the feeding trace of hydromedusae. However, this ichnotaxon is rather a fossil burrow system produced by a worm-like organism within sediment.

Gyrophyllites Glocker 1841

Diagnosis: Radial trace fossils with numerous, more or less horizontal, swollen leaf-like lobes radiating from a vertical shaft. The radiating lobes occur at one or several levels and are mostly unbranched (modified after Fu, 1991).

Gyrophyllites rehsteineri (Fischer-Ooster 1858)
Fig. 50

* 1858 *Sargassites rehsteineri* F.O. – Fischer-Ooster, 34, pl. 13, fig. 5.

1877 *Gyrophyllites theobaldi* Hr. – Heer, 120, pl. 45, figs. 1–5.

v 1977 *Gyrophyllites kwaszizensis* Glocker – Książkiewicz, 104, pl. 8, fig. 2.

v? 1977 *Asterichnus* aff. *lawrencensis* Bandel – Książkiewicz, 104, pl. 9, fig. 4.

v? 1997 *Gyrophyllites* cf. *rehsteineri* Fischer-Ooster – Wetzel & Uchman, 145, fig. 3H.

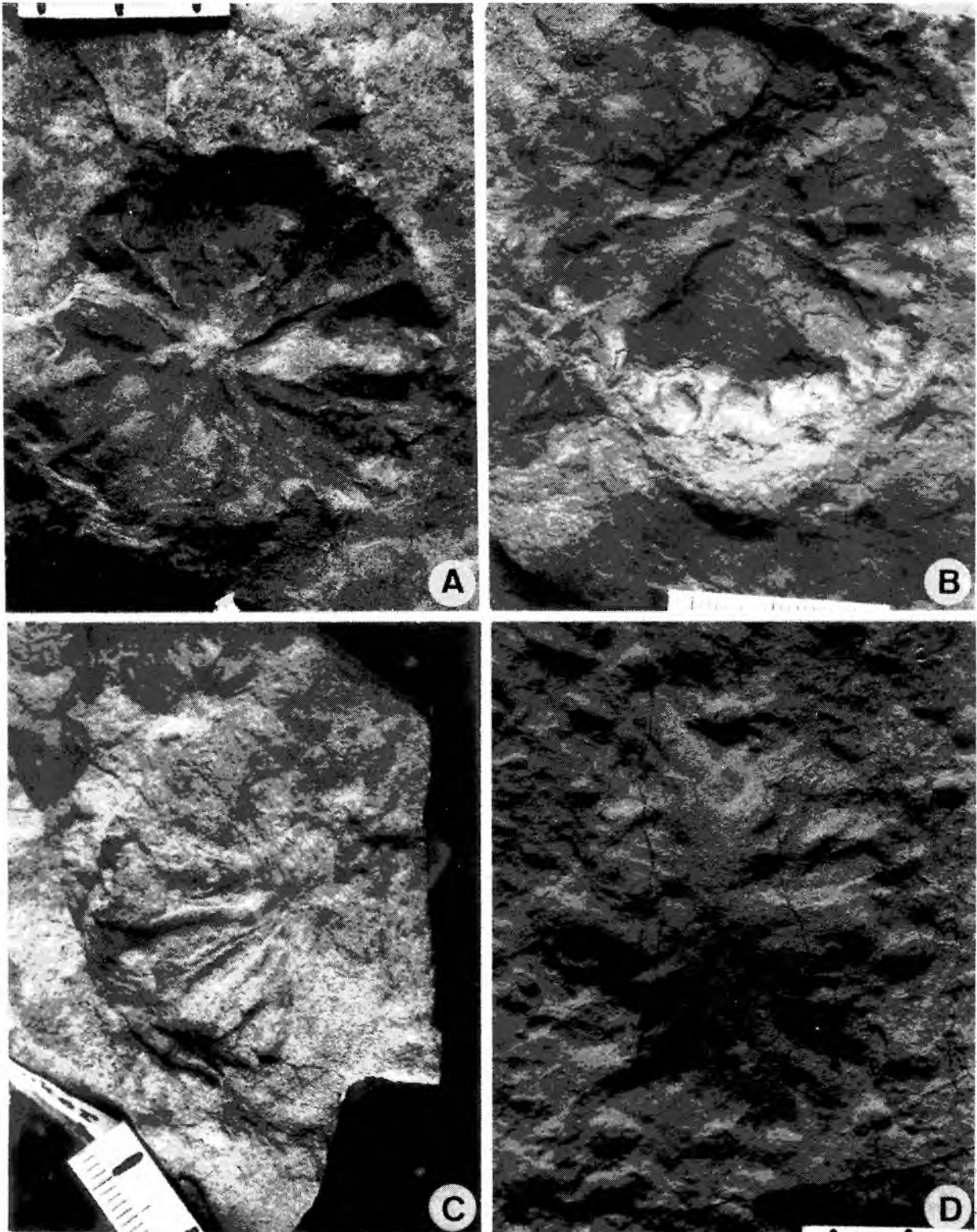


Fig. 50. *Gyrophyllites rehsteineri* (Fischer-Ooster), epichnial forms in turbiditic sandstone beds. A-C. Lower Istebna beds (Senonian), Istebna (labelled as *Gyrophyllites kwassizensis*). A. UJ TF 106. B. UJ TF 259. C. 1794. D. UJ TF 79, hypichnial form, Upper Cieszyn Shale (Valanginian). Poznachowice (labelled as *Asterichnus* aff. *lawrencensis*). Scales in A, D in cm, in B-C in mm

Diagnosis: *Gyrophyllites* with overlapping lobes, which are egg- or drop-like in outline, with rounded distal margin.

Material: 4 specimens (TF UJ 79 (?), 106, 259, 1794).

Description: As in the diagnosis, with the following additions: diameter of the rosette up to 35 mm. The radiating lobes are

maximally 5–7 mm wide.

Remarks: Material ascribed by Książkiewicz to *G. kwassizensis* Glocker differs from the material illustrated by Glocker (1841, p. 322). The latter is characterized by more

elongate, non-overlapping lobes than in the Książkiewicz material, which, in turn, is very similar to the flysch material of *G. rehsteineri* illustrated by Fischer-Ooster (1858). However, morphological diversity of the type material of *G. kwassizensis* is poorly known and transitional forms to the described ichnotaxon are not excluded. In this case, these ichnotaxa would be synonyms. In the present state of knowledge, they are treated as separate ichnospecies. Książkiewicz (1977) described *Asterichnus* aff. *lawrencensis* Bandel on the basis of one, poorly preserved specimen (Fig. 50D). This trace fossil displays rather overlapping lobes and is more similar to *Gyrophyllites* Glocker or *Stelloglyphus* Viarov.

SPREITE STRUCTURES

Zoophycos Massalongo 1855

Diagnosis: Spreite structures composed of numerous small, more or less U- or J-shaped protrusive burrows of variable length and orientation. Spreite arranged in helicoid spirals with an overall outline of circular, elliptical or lobate shape; central vertical tunnel or marginal tube may be present (after Frey, 1970; Häntzschel, 1975; Wetzel & Werner, 1981; Fillion & Pickerill, 1984).

Remarks: Different ichnogenera and/or species have been described under the name *Zoophycos* (Häntzschel, 1975). Recently, the origin of members of the *Zoophycos* group has been extensively discussed (Bromley, 1991; Wetzel, 1992; Gaillard & Olivero, 1993; Olivero, 1994, for review). This group needs to be thoroughly revised. Temporarily, some ichnotaxonomic names are used for description of this group, however, many of them are most likely synonyms.

Zoophycos s.l. is generally assumed to be trace of unknown deposit-feeding organisms. Their producers are possibly found among sipunculoids (Wetzel & Werner, 1981), polychaete annelids, arthropods (Ekdale & Lewis, 1991a), and enteropneust hemichordates (Kotake, 1992). According to Kotake (1989, 1991a), *Zoophycos* is produced by surface ingestors of organic detritus. The origin of this trace fossil is still not clear. Diverse, partially contradicting models of formation of *Zoophycos* have been presented (Seilacher, 1986; Ekdale & Lewis, 1991a; Bromley, 1991; Wetzel, 1992; Gaillard & Olivero, 1993, and references therein), but in most cases, the discussion refers to different taxa or even ichnogenera of the *Zoophycos* group.

According to Bottjer *et al.*, (1987) and Ekdale & Lewis (1991a), *Zoophycos* occurs in shallow-water deposits in the Palaeozoic, and in deep-sea, rarely also in shallow-water deposits after the Palaeozoic. *Zoophycos* s.l. is known from the Precambrian (Crimes, 1987) to the Recent (e.g. Ekdale & Berger, 1978; Wetzel & Werner, 1981).

Książkiewicz (1977) distinguished two ichnotaxa of *Zoophycos*, namely, *Z. brianteus* Massalongo and *Z. insignis* Squinabol. Moreover, he determined several *Zoophycos* spec. indet. *Zoophycos* needs urgent revision but this large problem is beyond the scope of this paper. The Książkiewicz material is insufficient even for a partial solution of the problem. For this reason, the Książkiewicz ichnotaxa are retained as they are. For illustration of the material Fig. 51 is presented.

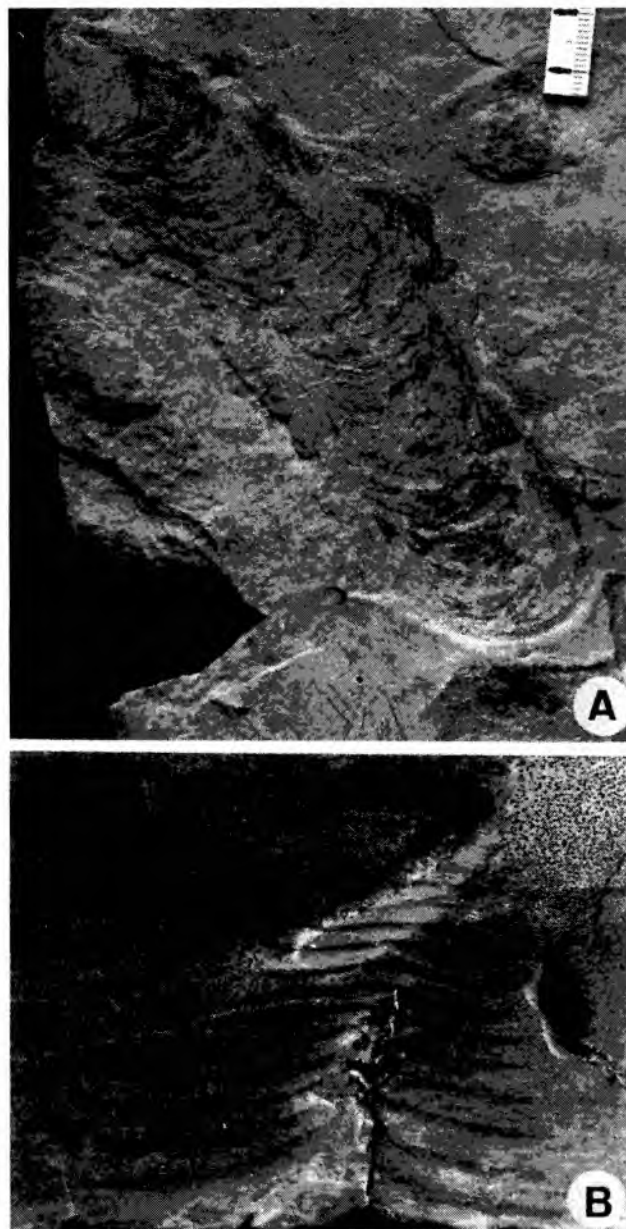


Fig. 51. *Zoophycos* spp. **A.** *Zoophycos insignis* Squinabol, endichnial form in turbiditic sandstone bed. UJ TF 2572, Ropianka beds (Senonian–Paleocene, Wola Brzezińska. **B.** *Zoophycos* isp. (*Spirophyton*-type), endichnial form in cross-section of turbiditic mudstone bed. UJ TF 13, Magura beds (Eocene), Zabrzeż. Scale in A in mm, scale bar in B = 1 cm

Phycosiphon Fischer-Ooster 1858

Emended diagnosis: Planar, horizontal, or oblique lobate spreite structure encircled at least partially by a marginal tunnel. The lobes are protrusive.

Remarks: Hitherto only one ichnospecies, *P. incertum* Fischer-Ooster, was recognised. This ichnospecies was lately analysed by Wetzel & Bromley (1994), who described its morphology in detail. The most characteristic feature of *P. incertum* is the lobate structure filled with protrusive spreite. The same features, expressed in the ichnogenetic diagnosis, occur in larger trace fossils, e.g. *Hydrancylus hamatus* Fis-

cher-Ooster (1858, pl. 5) (Fig. 53) or *Hydrancylus geniculata* (Sternberg) discussed by Fu (1988). For this reason these trace fossils can be described under one ichnogenus and the monotypy of *Phycosiphon* can be broken. *Hydrancylus* was regarded by Fischer-Ooster as a subgenus of *Muensteria* although it has page priority. However, *Phycosiphon* is much more commonly used, as indicated in the synonymy lists supplied by Fu (1991) and Wetzel & Bromley (1994). In interest of ichnotaxonomic stability, therefore *Phycosiphon* is proposed as the generic name of the discussed trace fossils. All the differences between these ichnotaxa correspond to features at the ichnospecies level.

Phycosiphon incertum Fischer-Ooster 1858
Figs. 52, 63

Diagnosis: Extensive small-scale spreite trace fossil comprising repeated narrow, U-shaped lobes enclosing a spreite in millimetre to centimetre scale, branching regularly or irregularly from an axial spreite of similar width. Lobes are protrusive, mainly parallel to bedding/sea floor. However, the plane enclosing the width of individual lobes may lie horizontally, obliquely or even vertically to the bedding/sea floor (Wetzel & Bromley, 1994).

Material: 13 specimens (UJ TF 142, 589-591, 646, 1261, 1485, 1597, 1618, 1676, 1803, 2040, 2517).

Remarks: Recently, Wetzel & Bromley (1994) provided that *Anconichnus horizontalis* Kern is the junior synonym of *Phycosiphon*. *Phycosiphon* is common in poorly oxygenated sediments (e.g. Ekdale & Mason, 1988).

Phycosiphon incertum is correctly described by Książkiewicz (1977). In the analysed collection, especially valuable are well-preserved specimens with well-expressed spreite.

Phycosiphon hamata (Fischer-Ooster 1858)
Figs. 53-55

* 1858 *Münsteria hamata* F.O. (= *Hydrancylus hamatus* F.O.) – Fischer-Ooster, 41, pl. 5.

v 1977 *Münsteria hamata* Fischer-Ooster – Książkiewicz, 122, pl. 13, fig. 3.

1978 *Zoophycos* Kern, 250, fig. 81.

Diagnosis: Large *Phycosiphon* in the scale of centimetres, with well expressed symmetrical lobes filled with spreite.

Material: 4 specimens (UJ TF 154, 738, 2 specimens in the Naturhistorisches Hofmuseum).

Description: As in the diagnosis and in the description of *Muensteria hamata* in Książkiewicz (1977).

Remarks: Although Fischer-Ooster (1858) distinguished *Hydrancylus* as a subgenus of *Muensteria*, it has recently been treated as a separate ichnogenus by Fu (1988), who, however, excluded *Muensteria hamata* F.O. (= *Hydrancylus hamatus* F.O. according to Fischer-Ooster) from *Hydrancylus*. Nevertheless, all the differences between *Hydrancylus geniculata* (Sternberg), which is the only ichnospecies of this ichnogenus recognised by Fu (1988), and *H. hamatus* can be expressed at the ichnospecies level. *Hydrancylus geniculata* (Sternberg) displays smaller size and asymmetry of lobes related to the J-shape burrow. *H. hamatus* Fischer-Ooster displays larger size, and more regular lobes, with deep J-shape or even U-shape burrows (Fig. 53). Nevertheless, both ichnotaxa display the same basic features ex-

pressed in the ichnogenic diagnosis of *Phycosiphon*. This trace fossil is developed only on one level and cannot be confused with *Zoophycos*, which extends to several adjacent levels.

Lophoctenium Richter 1850

Diagnosis: Branches of closely spaced, inwardly bent “twigs” with comb-like branches, joining to form main axis (after Häntzschel, 1975).

Remarks: *Lophoctenium* has lately been studied by Fu (1991). It occurs in flysch deposits (e.g. Książkiewicz, 1977; Kern, 1978, Crimes *et al.*, 1981; Leszczyński, 1992) from the Ordovician (Häntzschel, 1975) to the Miocene (Uchman, 1995).

Książkiewicz (1977, 81) distinguished *Lophoctenium ramosum* (Toula) (pl. 5, figs. 6-8) and *L. aff. comosum* (Richter) (pl. 5, fig. 9). *Lophoctenium* needs a revision but it can not be done without access to several important collections. For this reason, the Książkiewicz ichnospecies are temporally retained as they are.

Rhizocorallium Zenker 1836

Diagnosis: U-shaped spreite burrows, parallel or oblique to bedding plane; limbs more or less parallel and distinct; ratio of tube diameter to spreite width usually 1:5 (after Fürsich, 1974c).

Rhizocorallium jenense Zenker 1836

v 1977 ?*Rhizocorallium* spec. indet. – Książkiewicz, 105, text-fig. 15.

v 1992b *Rhizocorallium* ichnosp. – Uchman, figs. 2-3.

Diagnosis: More or less straight, short U-shaped spreite burrows commonly oblique to bedding plane and sometimes vertically retrusive (after, Fürsich, 1974c).

Material: 2 specimens (UJ TF 1556, 1610).

Remarks: Taxonomic and ethological problems of this ichnogenus were discussed by Fürsich (1974c). Uchman (1992b) discussed its occurrence of this commonly shallow-water trace fossil in the Carpathian flysch.

WINDING AND MEANDERING STRUCTURES

Książkiewicz (1977) regarded winding structures and meandering structures as separate groups. They are here combined because of difficulties in their separation. For instance, according to the Książkiewicz divisions, echinoid trace fossils (*Scolicia* in this paper) are separated (Uchman, 1995).

Nereites MacLeay 1839

Diagnosis: Usually selectively preserved, winding to regularly meandering, more or less horizontal trails, consisting of a median back-filled tunnel (core) enveloped by an even to lobate zone of reworked sediment (mantle). Commonly, only the external part of the mantle is preserved as a densely packed chain of uni- or multi-serial small depressions or pustules (after Uchman, 1995).

Remarks: The list of ichnotaxa included in *Nereites* was presented by Rindsberg (1994) and Uchman (1995). *Scalartuba* Weller, *Neonereites* Seilacher, *Paleohelminthoida*

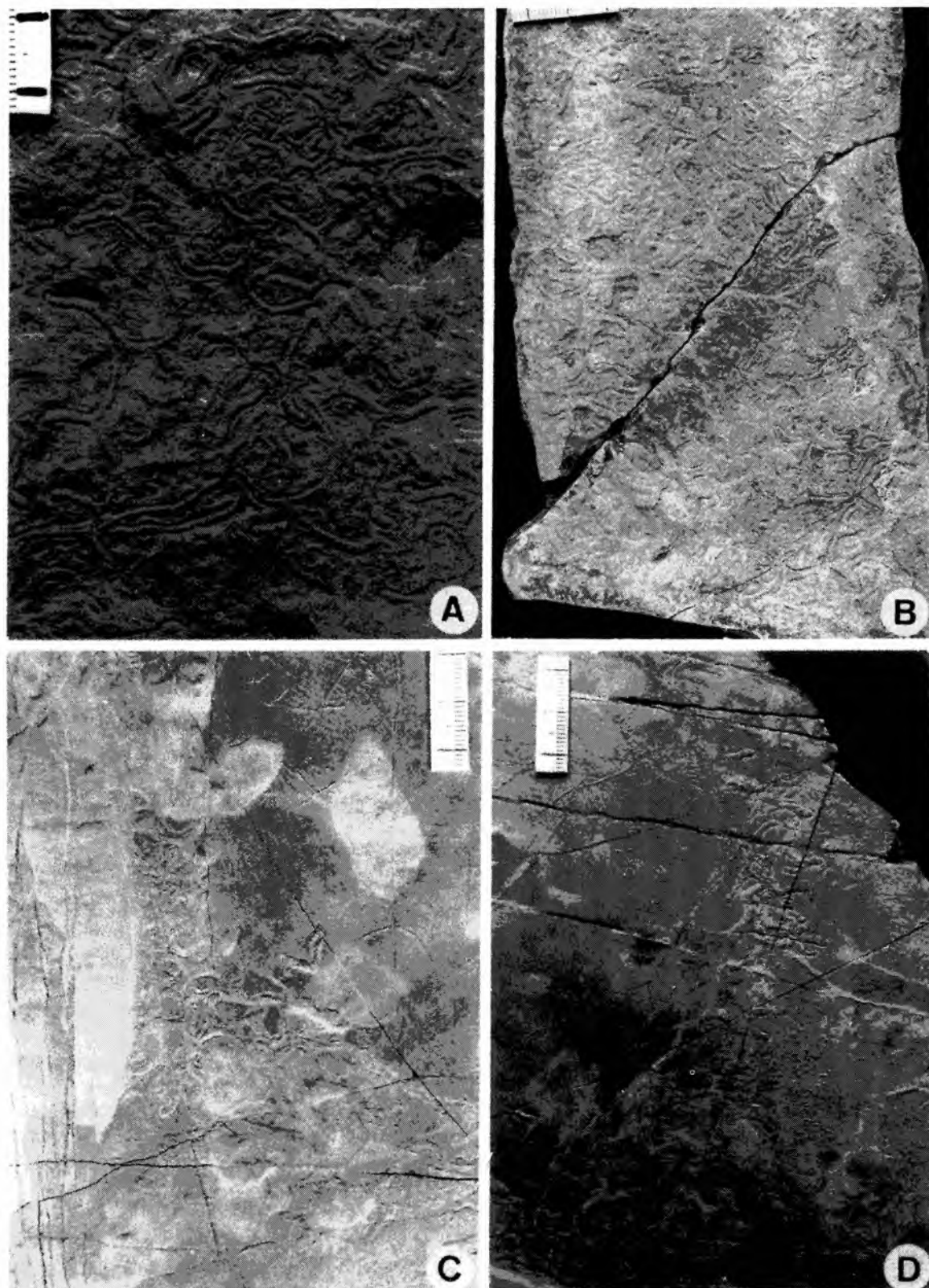
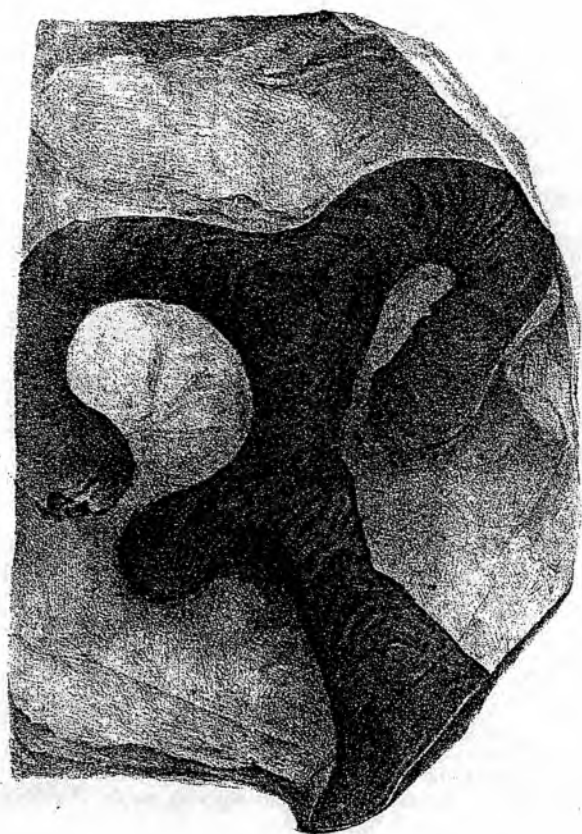


Fig. 52. *Phycosiphon incertum* Fischer-Ooster, endichnial forms in epichnial position. A. UJ TF 646, Ropianka beds (Senonian–Paleocene), Mordarka. B. UJ TF 1261, Variegated Shale (Paleocene–Lower Eocene), Lipnica Mała, Gubernas. C–D. UJ TF 589, Variegated Shale (Paleocene–Lower Eocene), Lipnica Mała, Gubernas. Scales in mm



Hydrancyclus hamatus F. O.

Fig. 53. *Phycosiphon hamata* (Fischer-Ooster). Reproduction of Fischer-Ooster (1858) pl. 5

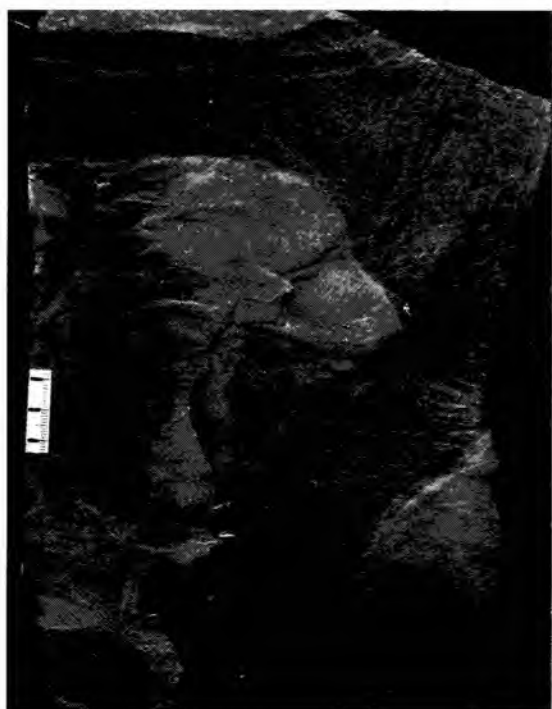


Fig. 54. *Phycosiphon hamata* (Fischer-Ooster), endichnial form in turbiditic sandstone bed, epichnial position. UJ TF 738, Ropianka beds (Senonian-Paleocene), Szczawa. Scale in mm

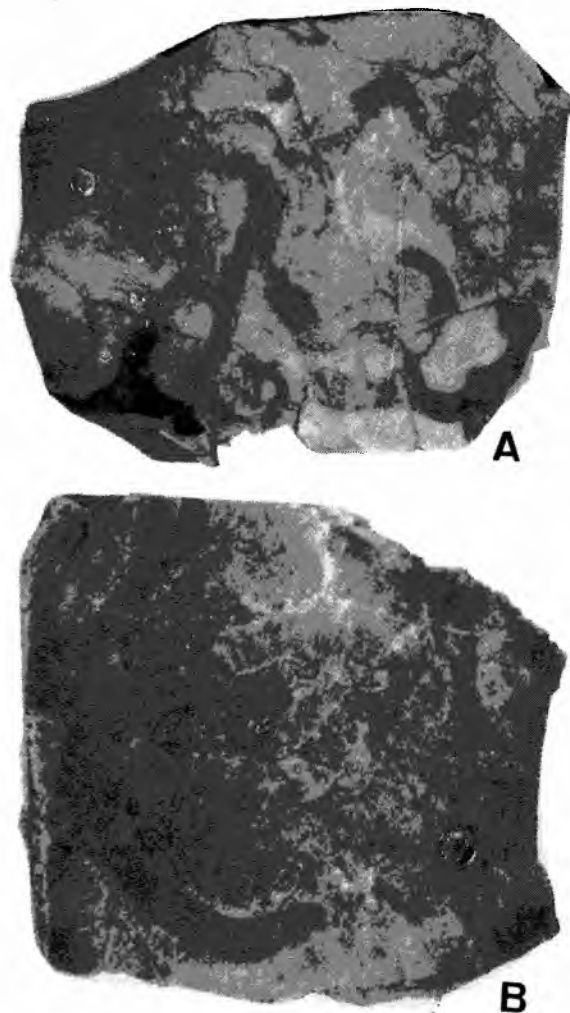


Fig. 55. *Phycosiphon hamata* (Fischer-Ooster) from the Naturhistorisches Hofmuseum in Vienna, endichnial form in turbiditic sandstone bed, epichnial view. A. A specimen in the Gebhard's collection, Sievering Formation (Upper Cretaceous, Mühlberg, Wienerwald). B. "Lengtaler Flysch" between Windhag and St. Leonhard, N of Waidhofen, Austrian Alps. The coins are 19 mm in diameter

Ruchholz, and *Helminthoidea* Schafhäütl were included in *Nereites*.

Nereites irregularis (Schafhäütl 1851)

Figs. 56

For synonymy list: Uchman (1995).

- v 1970 *Helminthoidea labyrinthica* Heer forma *typica* – Książkiewicz, 296, fig. 2g.
- v 1970 *Helminthoidea labyrinthica* Heer forma *lata* – Książkiewicz, 296, fig. 2i.
- v 1970 *Helminthoidea labyrinthica* Heer forma *serrata* – Książkiewicz, 298, fig. 2h.
- v 1977 *Helminthopsis irregularis* (Schafhäütl) – Książkiewicz, 119, pl. 12, fig. 2, text-fig. 22.
- v 1977 *Helminthoidea labyrinthica* Heer – Książkiewicz, 158, pl. 21, fig. 1.
- v 1977 *Helminthoidea serrata* n. isp. – Książkiewicz, 159, pl. 21, fig. 2.

Diagnosis: Relatively small *Nereites* with usually closely packed, multistorey, gregarious, deep meanders which tend to coil. Mean-

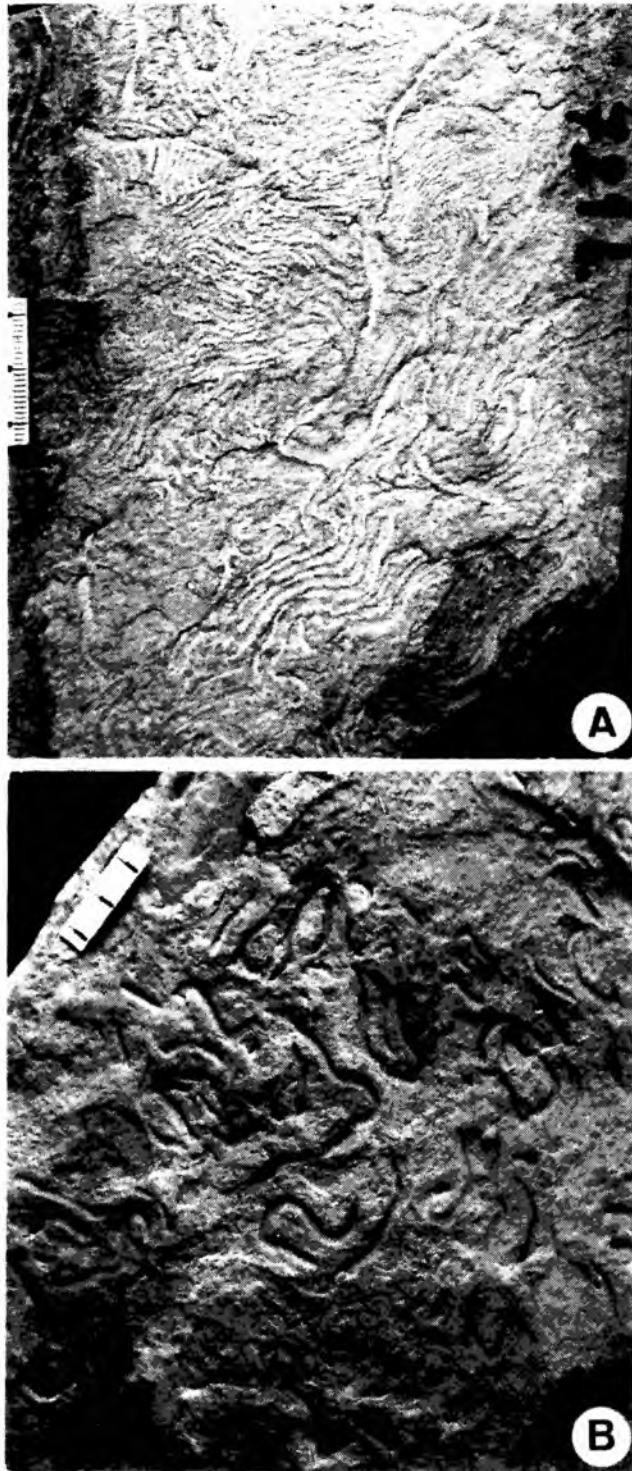


Fig. 56. *Nereites irregularis* (Schafhäütl), endichnial forms, epichnial view. **A.** UJ TF 721 (label lost). **B.** UJ TF 132. Sromowce beds (Senonian), Jaworki, Skalski stream. (Labelled as *Helminthopsis irregularis*). Scales in mm

ders usually of variable dimension and regularity in adjacent levels or even at the same level. Mantle usually thinner than core; where closely packed, meanders touch or overlap with neighboring segments, in looser meanders it displays low lobes. Commonly the mantle is not preserved. Backfill structure is poorly manifested (modified after Uchman, 1995)

Material: 17 specimens (UJ TF 51-58, 105, 132, 236, 721a, b, 734, 797, 1518, 2711).

Description: Meandering epichnial full relief located in shallow furrow, ellipsoidal in cross-section, 3.5–4.0 mm wide. The narrow, irregular meanders occur at adjacent levels, mainly within a 15 mm thick part of a sandstone-mudstone turbidite bed. The lighter-coloured core shows occasionally an indistinct backfill structure appearing as transverse ribs. In some specimens (Fig. 56B), the core is removed by weathering.

Remarks: The holotype of *Helminthoida irregularis* displays all diagnostic morphological features of *Nereites* and was included in the latter ichnogenus, and *Helminthoida labyrinthica* Heer of Książkiewicz is its junior objective synonym (Uchman, 1995).

The Książkiewicz ichnospecies included in *N. irregularis* displays minor differences, which are morphological variations of the same ichnospecies. The differences (lack of core filling, visibility of backfill structure in the core) are controlled mainly by preservation and diagenesis.

Nereites irregularis occurs mainly in deep-sea deposits. It is typical of calcareous planktic sediments (Seilacher, 1986, p. 70). It occurs from (?) the beginning of the Mesozoic (Yang, 1986) to the Miocene (Uchman, 1995) and (?) Quaternary (Ekdale & Lewis, 1991b).

Scolicia de Quatrefages 1849

Ichnospecies included in *Scolicia* de Quatrefages:

- v 1958 trace of creeping gastropods from the *Subphyllochorda* group – Książkiewicz, pl. 2, fig. 3.
- v 1958 *Paleobullia* – Książkiewicz, pl. 3, fig. 1.
- v 1960 Ex. aff. *Climactichnis* Logan – Książkiewicz, 742, pl. 4, fig. 17.
- v 1960 Ex. aff. *Gyrochorte* Heer – Książkiewicz, 742, pl. 3, fig. 11.
- v 1960 Podwójny ślad meandryczny – Książkiewicz, 739, pl. 2, fig. 8.
- v 1968 *Taphrhelminthopsis* Sacco, sp. ind. – Książkiewicz, 8, pl. 6, fig. 3.
- v 1970 *Scolicia prisca* de Quatrefages – Książkiewicz, 289, pl. 1 d.
- v 1970 *Scolicia plana* ichnosp. n. – Książkiewicz, 289, pl. 1c.
- 1970 *Subphyllochorda granulata* ichnosp. n. – Książkiewicz, 289, pl. 1g.
- v 1970 *Subphyllochorda striata* ichnosp. n. – Książkiewicz, 290, pl. 1f.
- v 1970 *Taphrhelminthopsis* aff. *recta* Sacco – Książkiewicz, 290, pl. 2a-d.
- v 1970 *Taphrhelminthopsis auricularis* Sacco – Książkiewicz, 192, pl. 2e-g.
- v 1970 *Taphrhelminthopsis plana* ichnosp. n. – Książkiewicz, 300, pl. 3g-h.
- v 1970 *Taphrhelminthopsis convoluta* (Heer) – Książkiewicz, 300, pl. 3f.
- v 1970 *Subphyllochorda laevis* ichnosp. n. – Książkiewicz, 290, pl. 1e.
- v 1970 *Gyrochorte* isp. B – Książkiewicz, 288, pl. 1b.
- v 1977 *Scolicia prisca* de Quatrefages – Książkiewicz, 126, pl. 11, fig. 12, pl. 14, fig. 8, pl. 15, fig. 6.
- v 1977 *Scolicia plana* Książkiewicz – Książkiewicz, 127, pl. 14, figs. 2-5, 7.
- v non? 1977 *Scolicia vertebralis* n. ichnosp. – Książkiewicz, 128, pl. 14, fig. 1, 6, text-figs. 23j, k, 29.
- v 1977 *Subphyllochorda granulata* Książkiewicz – Książkiewicz, 131, pl. 15, figs. 3, 5, text-fig. 24b-c, e.
- v 1977 *Subphyllochorda striata* Książkiewicz – Książkiewicz, 132, pl. 15, fig. 1, text-fig. 24a.
- v 1977 *Subphyllochorda rudis* n. ichnosp. – Książkiewicz, 133, pl. 15, fig. 2, text-fig. 24d, 25.

- v 1977 *Subphyllochorda laevis* Książkiewicz – Książkiewicz, 134, pl. 16, figs. 1-3, text-fig. 24g-k.
 v 1977 *Taphrhelminthopsis auricularis* Sacco – Książkiewicz, 137, pl. 17, figs. 1-3, text-fig. 26a-j.
 v 1977 *Taphrhelminthopsis vagans* n. ichnosp. – Książkiewicz, 139, pl. 17, figs. 4-5, text-fig. 26l-s.
 v 1977 *Taphrhelminthopsis recta* Sacco – Książkiewicz, 139, pl. 17, fig. 1, text-fig. 26t.
 v 1977 *Taphrhelminthoida convoluta* n. ichnosp. – Książkiewicz, 168, pl. 22, fig. 1, pl. 23, fig. 5.
 v 1977 *Taphrhelminthoida plana* (Książkiewicz) – Książkiewicz, 169, pl. 22, figs. 2-3.
 v 1977 *Pararusophycus oblongus* n. ichnosp. – Książkiewicz, 54, pl. 1, fig. 6.
 v ?non 1977 *Spirorhaphé zumayensis* (Gómez de Llarena) – Książkiewicz, 147, pl. 18, fig. 3.

For additional list of ichnotaxa included in *Scolicia* see Uchman (1995).

Diagnosis: Variably and commonly selectively preserved, simple, winding, meandering to coiling bilobate or trilobate back-filled trace fossils with two parallel, locally discontinuous, sediment strings along their underside. Cross-section approximately oval in outline. Underside between the strings flat or slightly convex up. Backfill laminae composite, may be biserial on the upper side. Washed-out variants preserved as hypichnial bilobate ridges (modified after Uchman, 1995)

Remarks: *Taphrhelminthopsis* Sacco, *Laminites* Ghent & Henderson, *Subphyllochorda* Götzinger & Becker, and *Taphrhelminthoida* Książkiewicz were included in *Scolicia* as taphonomic variants of the same ichnogenus produced by irregular echinoids, and related to the depth of burrowing and to subsequent erosion (Uchman, 1995). Relation of *Laminites* to *Scolicia* was also discussed by Uchman & Krenmayr (1995).

Recently, Goldring *et al.* (1997) questioned inclusion of these ichnogenera in *Scolicia* because, according to their view, names of these ichnogenera bear important toponomic information. This view cannot be accepted, because the toponomic information is not lost, but is removed to the ichnospecies level. On the contrary, the proposed retention of the ichnogenera *Taphrhelminthopsis*, *Subphyllochorda*, and *Taphrhelminthoida* causes loss of information about their common origin and unity of the basic fossil behaviour, and sanctions influence of taphonomy on ichnotaxonomy. Moreover, the cited authors erroneously implied that Uchman (1995) included ichnogenus *Subphyllochorda* in ichnospecies *Scolicia prisca*.

Scolicia prisca de Quatrefages 1849

Fig. 57

Synonymy list: Uchman (1995)

- * 1849 *Scolicia prisca* A. de Qu. – de Quatrefages, 265 (no illustration).
 v 1960 Ex. aff. *Climactichnis* Logan – Książkiewicz, 742, pl. 4, fig. 17.
 v? 1960 Ex. aff. *Gyrochorte* Heer – Książkiewicz, 742, pl. 3, fig. 11.
 v 1970 *Scolicia prisca* de Quatrefages – Książkiewicz, 289, pl. 1d.
 v 1977 *Scolicia prisca* de Quatrefages – Książkiewicz, 126, pl. 11, fig. 12, pl. 14, fig. 8, pl. 15 fig. 6.
 v ?non 1977 *Scolicia vertebralis* n. ichnosp. – Książkiewicz, 128, pl. 14, fig. 1, 6, text-figs. 23j, k, 29.

Diagnosis: *Scolicia* preserved usually as epichnial trilobate furrow with slightly concave, semicircular bottom and oblique slopes,

densely packed fine transverse ribs at the bottom, and looser, asymmetrical and thicker ribs on the slopes. Two parallel strings may occur along the edges of the bottom. Proportion of bottom to slopes may vary in different specimens (after Uchman, 1995).

Material: 28 (?32) specimens (UJ TF 116, 478-479, 483-485, 487-488, 497, 500, 529, 586(?), 624(?), 626, 628-632, 688, 803, 817, 819, 938(?), 952, 1149, 1478(?), 1565, 1702, 1745, 2546, 2548).

Remarks: Probably, *Scolicia vertebralis* is a preservational variant of *S. prisca*. It is underrepresented in the analysed collection and this problem needs further explanation. In the holotype, the furrow has one central narrow string or suture-like structure which passes into the furrow having indistinct trilobate structure, as in *S. prisca* (Fig. 58).

The parallel strings represent the drainage canals of spatangoid echinoids (Kanazawa, 1994, pers. comm.). Densely packed ribs at the bottom are probably produced by locomotion organs of the producer. The asymmetric thicker ribs on slopes are remnants of the edges of backfill menisci. Proportion of bottom to slopes and depth of furrow depend strongly on preservation. When the burrow occupies a deeper position in the sandy portion of a bed, the median ridge is covered, to a variable extent, by the backfill and then appears very narrow; the strings are usually also covered. Substrate properties and degree of weathering may also influence expression of the ribs at the bottom.

This ichnotaxon is usually preserved in the middle part of turbidites (Tc-Td) at the transition from sandstone to mudstone. Only the lowermost part of the burrow is preserved. The upper part, consisting of backfill structures, remains usually in the upper, shaley part of the turbidite bed.

Scolicia plana Książkiewicz 1970

Figs. 59–60

- v* 1970 *Scolicia plana* ichnosp. n. – Książkiewicz, 289, pl. 1c.
 v 1970 *Subphyllochorda striata* ichnosp. n. – Książkiewicz, 290, pl. 1f.
 v 1970 *Subphyllochorda granulata* ichnosp. n. – Książkiewicz, 289, pl. 1g.
 v 1977 *Scolicia plana* Książkiewicz – Książkiewicz, 127, pl. 14, figs. 2-5, 7.
 v ?partim 1977 *Subphyllochorda granulata* Książkiewicz – Książkiewicz, 131, pl. 15, figs. 3, 5 [?non text-fig. 24b-c, e].
 v 1977 *Subphyllochorda striata* Książkiewicz – Książkiewicz, 132, pl. 15, fig. 1, text-fig. 24a.
 v 1977 *Subphyllochorda rudis* n. ichnosp. – Książkiewicz, 133, pl. 15, fig. 2, text-fig. 24d, 25.

Emended diagnosis: *Scolicia* in which the flat medial ridge is longitudinally divided by a shallow furrow or crest.

Material: 36 specimens (UJ TF 143, 135, 480-481, 489, 492-494, 496, 498, 501-503, 508, 535-536, 543, 582, 585 (holotype), 622, 635, 776, 970, 1125, 1153, 1211, 1233, 1241, 1298, 1542, 1700-1701, 2044, 2543, 2545, 2664).

Description: As in the diagnosis and in Książkiewicz description of the ichnotaxa included in *S. plana*.

Remarks: *S. prisca* displays a convex up, arcuate, median ridge, arcuate in cross section, without a central furrow or crest. The division of the main ridge may also be expressed in the hypichnial *Subphyllochorda* type of preservation as a faint crest or furrow in the middle lobe, between the strings. This feature is recognised in some specimens of *Subphyllo-*

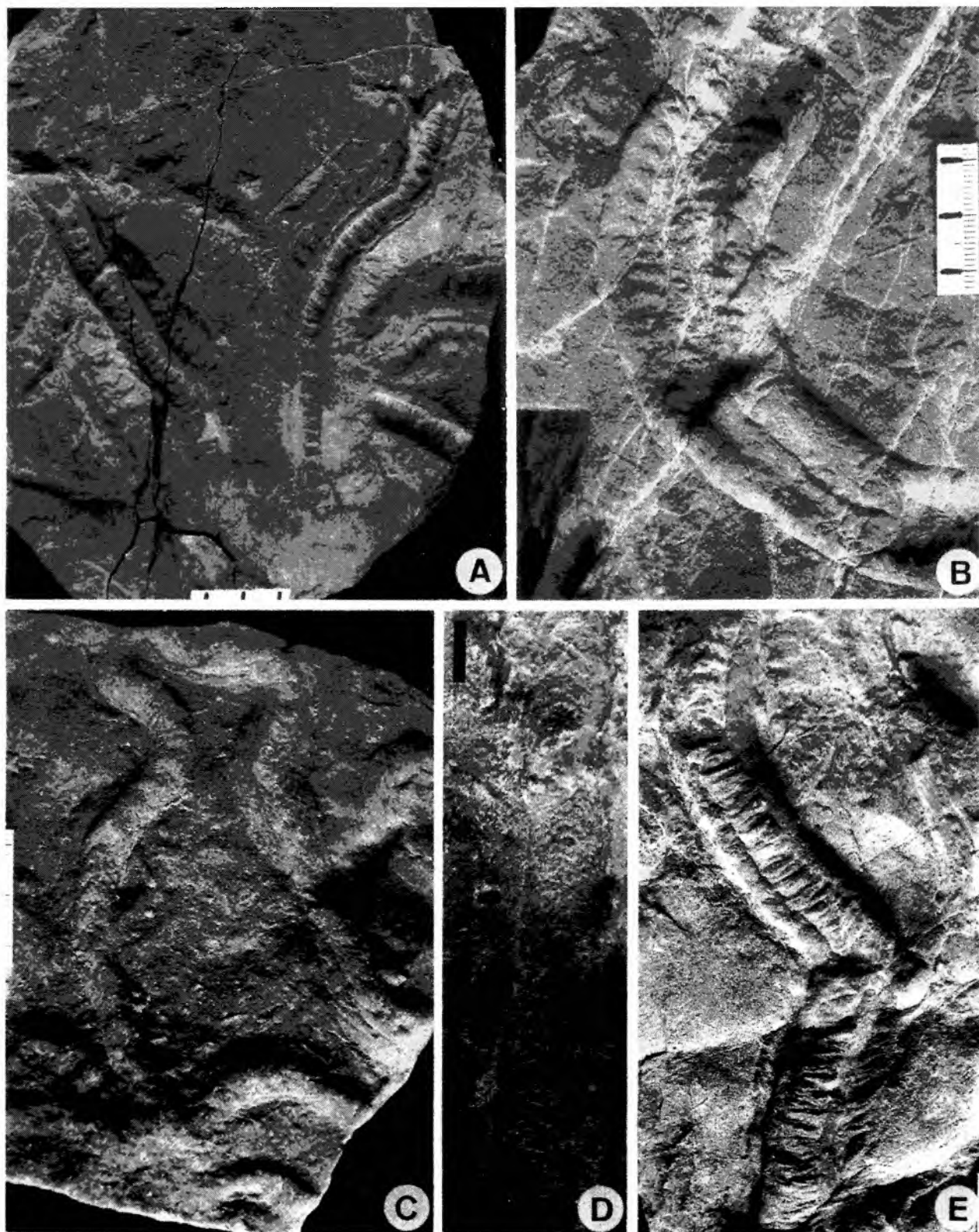


Fig. 57. *Scolicia prisca* de Quatrefages in turbiditic sandstone beds. **A.** UJ TF 626, Beloveža Formation (Eocene), Zubrzyca Górna. Epichnial view of ventral interior. **B.** UJ TF 1565, Hieroglyphic beds (Eocene), Zawoja, Końskie. Epichnial view of dorsal interior (upper part) and dorsal exterior (lower part). **C-D.** Hypichnial view of ventral exterior (slightly eroded). **C.** UJ TF 2548 (label lost). **D.** UJ TF 2546, Variegated Shale (Paleocene–Eocene), Kałowa. **E.** UJ TF 631, Hieroglyphic beds (Eocene), Juszczyń. Epichnial view of interior. Scale in A in cm, scales in B–C in mm, scale bar in D = 1 cm, scale bar in E = 16 mm

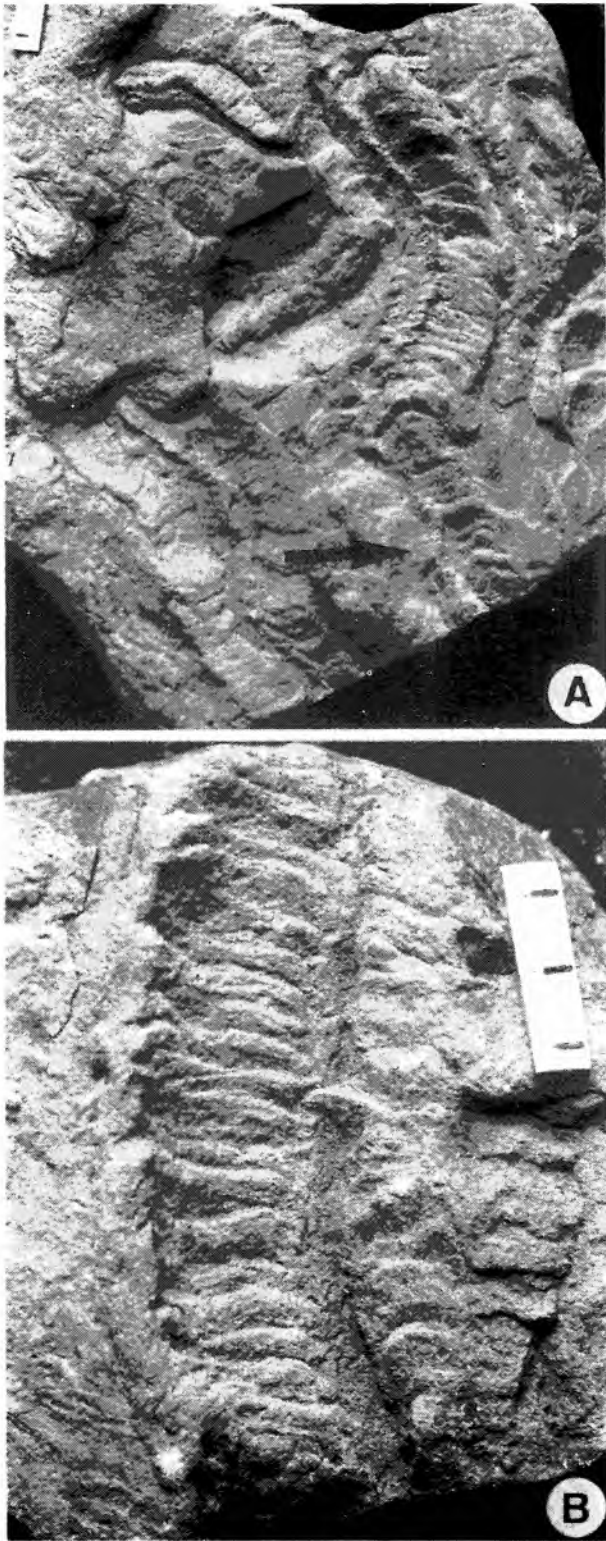


Fig. 58. *Scolicia vertebralis* Książkiewicz (= *Scolicia ?prisca*) in turbiditic sandstone beds. **A.** UJ TF 1478, holotype, Inoceranian beds (Senonian–Paleocene), Bachów. Transition to *S. prisca* arrowed. **B.** UJ TF 624, Lower Istebna beds (Senonian), Czchów. Scales in mm

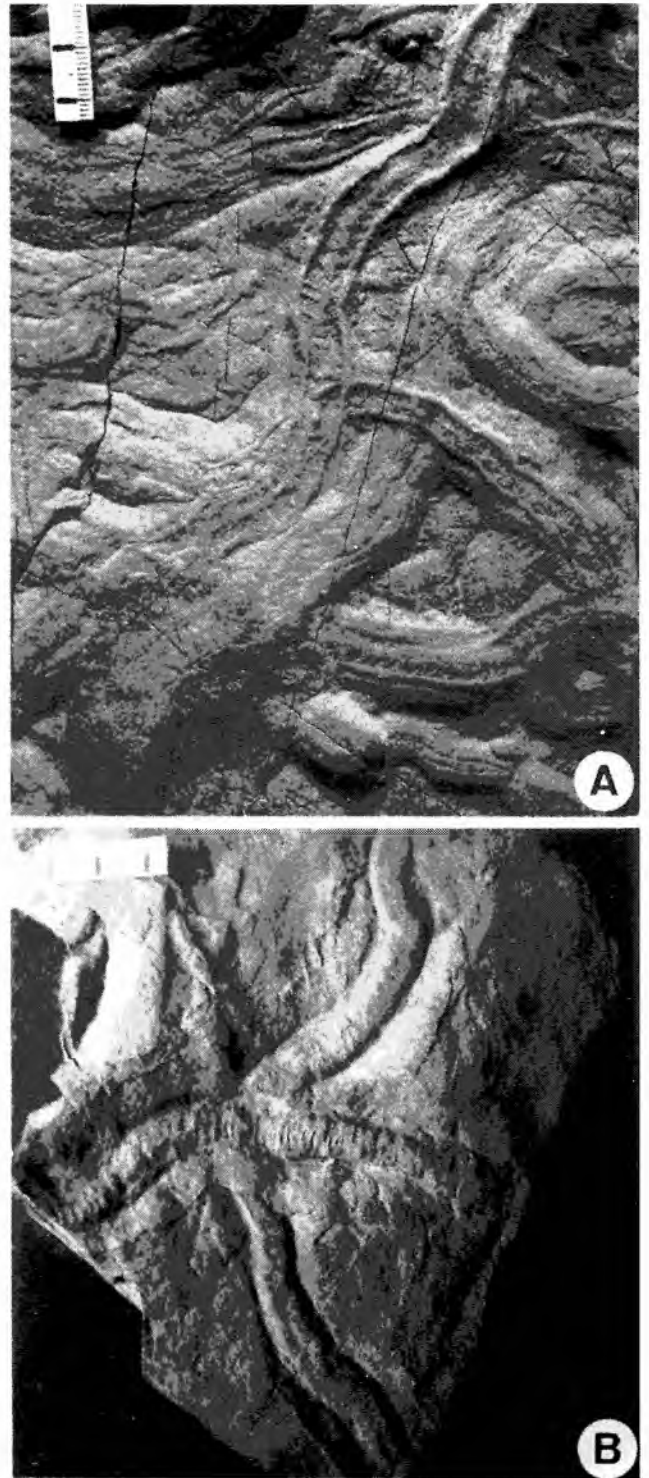


Fig. 59. *Scolicia plana* Książkiewicz in turbiditic sandstone beds. **A.** UJ TF 481, Cenomanian–Lower Senonian), Rzyki. Epichnial view of ventral interior. **B.** UJ TF 635, Variegated Shale (Paleocene–Eocene), Lubomierz (labelled as *Subphyllochorda striata*). Hypichnial view of ventral exterior. Scales in mm

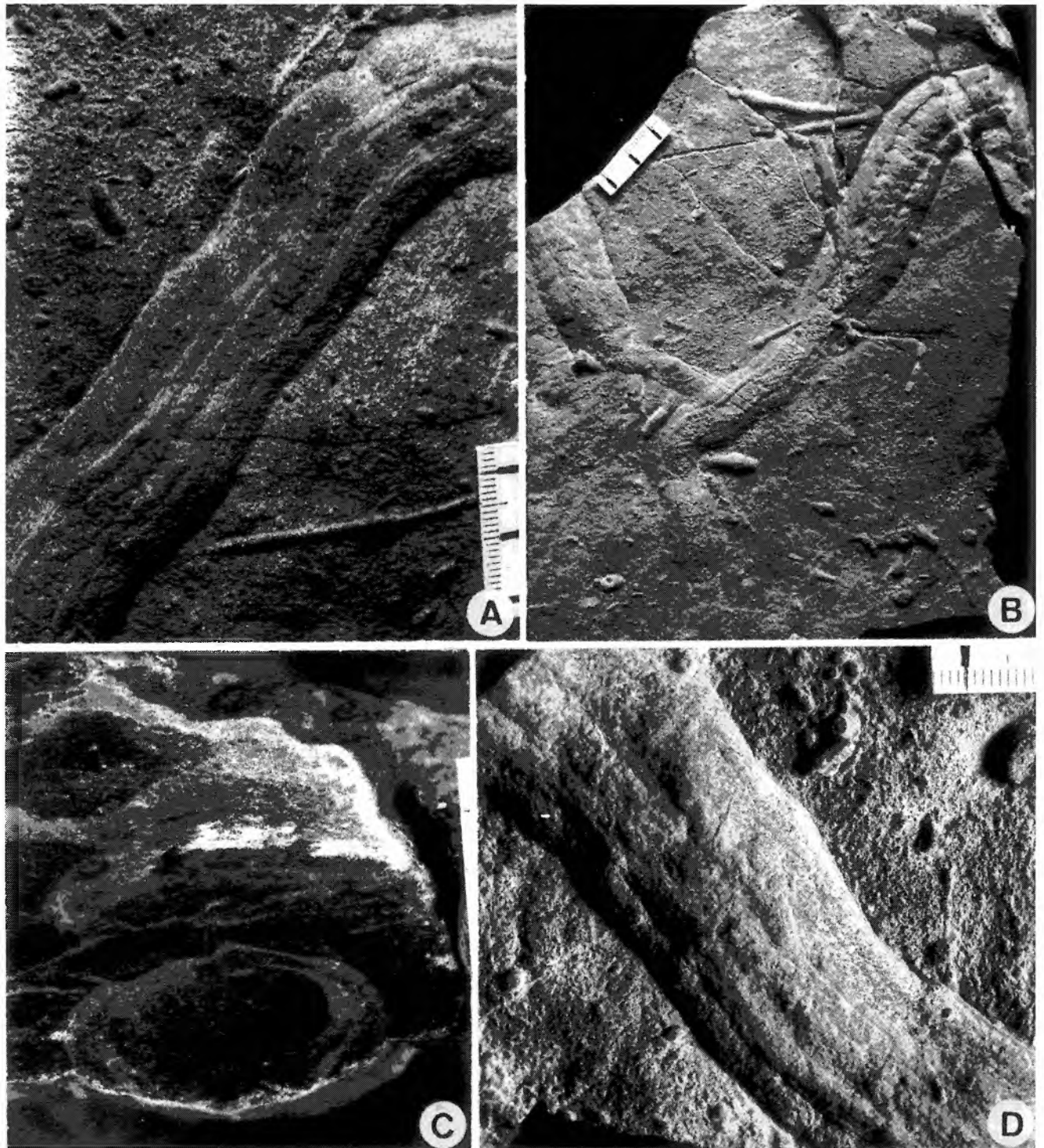


Fig. 60. *Scolicia plana* Książkiewicz in turbidite sandstone beds. A-C. Hypichnial views of ventral exterior. A. UJ TF 2545, Variegated Shale (Paleocene–Eocene), Kałowa. B. UJ TF 1542, Beloveža Formation (Eocene), Lipnica Wielka (labelled as *Subphyllochorda granulata*). C-D. UJ TF 2543, Variegated Shale (Paleocene–Eocene), Kałowa. C. Cross-section view. D. Hypichnial view. Scales in mm

chorda granulata and *S. striata* (Figs. 59B, 60B). There is transition of *S. striata* of this type to *S. rudis* in the same trace fossil. Typical *S. striata* and *S. rudis* occur together on the same bedding plane (Fig. 59B). This suggests that these trace fossils are only preservational variants of the same burrow, and they can be included in *S. plana*. However, some *Subphyllochorda* (but not *S. laevis*, which belongs to

Scolicia strozzii) distinctly do not display the median furrow or crest in the median lobe, and these should be included in *S. prisca* (Fig. 57C–E). In cases where the features are not clear, the considered *Subphyllochorda*-like specimen should be slightly polished at the lowermost part in order to expose the structure of the median lobe for proper determination.

Scolicia strozzii (Savi & Meneghini 1850)

Figs. 61–62

- * 1850 *Nemertilites strozzii* nob. – Savi & Meneghini, 421.
- v 1958 trace of creeping gastropods from the *Subphyllochora* group – Książkiewicz, pl. 2, fig. 3.
- v 1960 Podwójny ślad meandryczny – Książkiewicz, 739, pl. 2, fig. 8.
- v 1968 *Taphrhelminthopsis* Sacco, sp. ind. – Książkiewicz, 8, pl. 6, fig. 3.
- 1970 *Taphrhelminthopsis* aff. *recta* Sacco – Książkiewicz, 290, 292, pl. 2a-d.
- v 1970 *Taphrhelminthopsis auricularis* Sacco – Książkiewicz, 192, pl. 2e-g.
- v 1970 *Taphrhelminthopsis plana* ichnosp. n. – Książkiewicz, 300, pl. 3g-h.
- v 1970 *Taphrhelminthopsis convoluta* (Heer) – Książkiewicz, 300, pl. 3f.
- v 1970 *Subphyllochora laevis* ichnosp. n. – Książkiewicz, 290, pl. 1e.
- v 1977 *Subphyllochora laevis* Książkiewicz – Książkiewicz, 134, pl. 16, figs. 1-3, text-fig. 24g-k.
- v 1977 *Taphrhelminthopsis auricularis* Sacco – Książkiewicz, 137, pl. 17, figs. 1-3, text-fig. 26a-j.
- v 1977 *Taphrhelminthopsis vagans* n. ichnosp. – Książkiewicz, 139, pl. 17, figs. 4-5, text-fig. 26l-s.
- v 1977 *Taphrhelminthopsis recta* Sacco – Książkiewicz, 139, pl. 17, fig. 1, text-fig. 26t.
- v 1977 *Taphrhelminthoida convoluta* n. ichnosp. – Książkiewicz, 168, pl. 22, fig. 1, pl. 23, fig. 5.
- v 1977 *Taphrhelminthoida plana* (Książkiewicz) – Książkiewicz, 169, pl. 22, figs. 2-3.

Diagnosis: Straight to tightly meandering hypichnial bilobate ridge, preserved as semi-relief. A median groove separates the prominent zones of the ridge. The prominent zones and the groove are more or less arcuate in cross-section. Tendency to meandering: width, depth, height, and proportions of the morphological elements may vary from specimen to specimen (after Uchman, 1995).

Material: 74 specimens (UJ TF 126, 504-509, 511-513, 515, 517-518, 520, 522-523, 525-528, 530-531, 538, 541-544, 546-549, 554, 580, 693, 703, 737, 744, 746, 750, 780, 784-785, 813, 862-864, 867, 869, 898, 937, 1367-1370, 1386-1387, 1482, 1588, 1734, 1749-1750, 2580, 2602-2605a, 2606a, 2621, 2627, 2637, 2687, 2655a, 2689, 2698).

Description: As in the diagnosis and in the Książkiewicz (1977) description of *Taphrhelminthopsis* and *Taphrhelminthoida* ichnospecies.

Remarks: This ichnotaxon is a cast of the furrow formed after washing-out of the *Scolicia* burrow by erosion. Height, depth of the median ridge, and width of the trace depend strongly on small differences in depth of burrowing, depth and strength of erosion, and properties of substrate. If the burrow is cut by erosion in the middle part, its cast is higher and wider, the slope of the ridge is more gentle, and the median groove seems to be narrower. If erosion cuts the base of the burrow, its cast is lower, the median groove is shallow and wide, and the prominent parts of the ridge are narrow. Erosional currents flowing through the excavated furrow may strongly influence its shape and some tool marks may be produced by small objects being dragged along it. Indistinct longitudinal ridges or striae typical of *Taphrhelminthopsis recta* (see Książkiewicz, 1977) are most probably such tool marks. Modification by erosion may strongly depend on geotechnical properties of the sediment, influenced by large production of mucus by the burrowing echinoids. However, some differences in trace fossil shape depend on biological

factors. They include the taxa involved. Preservational factors seem to dominate the shape of the ridge, which, in consequence, cannot be regarded as an accessory diagnostic feature at the ichnospecies level. In the past, such criteria were mainly used for distinguishing taxa of *Taphrhelminthopsis*.

Subphyllochora laevis distinguished by Książkiewicz (1970, 1977), including the holotype, is a hypichnial semi-relief, which displays all features of *S. strozzii* and is included in that ichnospecies.

Książkiewicz (1977) differentiated (1) gently winding, usually single *T. vagans*, meandering, (2) usually gregariously occurring *T. auricularis*, and (3) tightly meandering *Taphrhelminthoida*. The first ichnospecies may correspond to locomotion activity (repichnia), and the latter to feeding activity (pascichnia). However, some transitional forms occur (e.g. Książkiewicz, 1977, pl. 17, fig. 2; Crimes, 1977a, pl. 6b). Brustur & Alexandrescu (1992) showed transitions between different ichnospecies of *Taphrhelminthopsis* and *Taphrhelminthoida* in one trace fossil, and concluded that they should be regarded as synonyms of *Taphrhelminthopsis auricularis* Sacco (1888). However, *Scolicia strozzii* (Savi & Meneghini, 1850) has a priority.

Scolicia prisca and *Subphyllochora* (= *Scolicia* isp.) also commonly display meanders, which potentially may be preserved as *Taphrhelminthopsis* or *Taphrhelminthoida* (= *Scolicia strozzii*). The tendency to meandering depends most probably on the nutritional value of the substrate. Thus, differentiating between meandering and non-meandering forms is problematic at the species level. Nevertheless, after exclusion of transitional forms, some informal differentiation at ichnosubspecies level may be proposed, i.e., *Scolicia strozzii* (Savi & Meneghini) var. *convoluta* for the distinctly meandering forms (after *Taphrhelminthoida convoluta* Książkiewicz) and *S. strozzii* var. *vagans* (after *Taphrhelminthopsis vagans* Książkiewicz) (Text-fig. 13).

S. strozzii was produced at shallow tiers as indicated by the co-occurrence of *Paleodictyon strozzii* (Fig. 62) (Książkiewicz, 1977; Seilacher, 1977a). One cannot exclude that its Mesozoic–Caenozoic producers (spatangoid echinoids) feed on microbial gardens of graphoglyptids (Seilacher, 1986). The Palaeozoic specimens are probably casts of washed out burrows of *Cruziana* and *Curvolithus* (Uchman, 1995). There are no diagnostic features which allow separation of Palaeozoic and post-Palaeozoic forms.

Scolicia isp. indet.

Fig. 63

v 1970 *Gyrochorte* isp. B – Książkiewicz, 288, pl. 1b.v 1977 *Subphyllochora* indet. – Książkiewicz, pl. 15, fig. 4.**Material:** 3 specimens (UJ TF 116, 817, 1358).

Description: A (Fig. 63A). Endichnial trace fossils in epichnial view visible as a winding belts, which are 8–12 m wide, with zigzag-like design. This is the epichnial view of a deeper full relief structure B (Fig. 63B). Epichnial convex meandering belts with median crest. The belt is 35–40 mm wide. This is again the epichnial view of a deeper full relief structure.

Remarks: The preservation as above described does not allow specific determination.

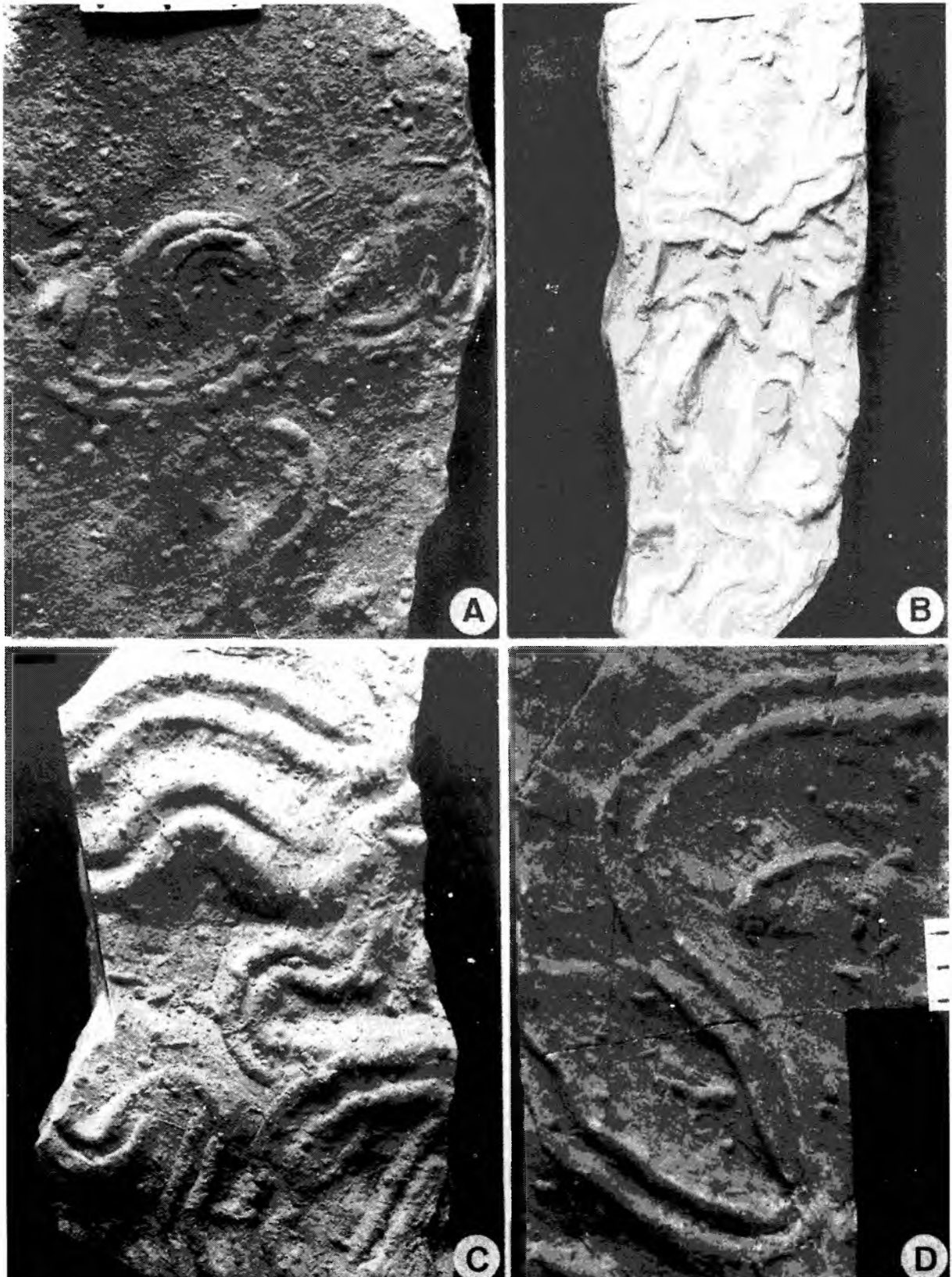


Fig. 61. *Scolicia strozzii* (Savi & Meneghini). Hypichnial forms in turbiditic sandstone beds. **A.** UJ TF 780, Beloveža Formation (Eocene), Sidzina. **B.** UJ TF 1750, Krosno beds (Oligocene), Sowina (labelled as *Taphrhelminthopsis vagans*, part of label lost). **C.** UJ TF 525, Beloveža Formation (Eocene), Lipnica Mała (labelled as *Taphrhelminthopsis auricularis*). **D.** UJ TF 937, Szczawnica Formation (Paleocene–Lower Eocene), Krościenko (labelled as *Taphrhelminthoida convoluta*). Scale in A in cm, scales in B, D in mm, scale bar in C = 1 cm



Fig. 62. *Scolicia strozzii* (S) with *Palcoedictyon strozzii* (P) and *Palcomacandron robustum* (M). UJ TF 1482. Beloveža Formation (Eocene), Sidzina. Scale in mm

Scolicia isp.

Fig. 64

1977 *Pararusophycus oblongus* n. ichnosp. – Książkiewicz, 54, pl. 1, fig. 6.

Material: 1 specimen (UJ TF 114).

Remarks: This trace fossil strongly resembles an oblique structure of the *Subphyllochorda*-type. *Subphyllochorda* is included in *Scolicia* (Uchman, 1995). Książkiewicz (1977) interpreted it as a pre-depositional burrow of a crustacean. However, the elevated part of structure, separated from the sandstone sole by a layer of mudstone, suggests a post-depositional origin. Two strings along its lower part, and a tuberculous sculpture on its sides are identical to *Scolicia* of the *Subphyllochorda*-type. The strings are broken off at the most elevated part of this specimen. This suggest a continuation of the trace fossil downward.

Naviculichnium Książkiewicz 1977

Diagnosis: Epichnial depressions in the shape of a elongated ellipse (modified after Książkiewicz, 1977).

Naviculichnium marginatum Książkiewicz 1977

Fig. 65

1957 Unnamed Dżułyński & Kinle, pl. 27.

* 1977 *Naviculichnium marginatum* n. ichnosp. Książkiewicz, 123, pl. 11, fig. 6.

1977a *Pelecypodichmus* sp. – Crimes, pl. 3c.



Fig. 63. *Scolicia* isp. (original labels lost). Epichnial forms in turbiditic sandstone beds. A. UJ TF 817. Beloveža beds (Eocene), Berest. Chevron design of the double menisci of the upper part of interior. B. UJ TF 116. *Phycosiphon incertum* at the upper right side. Dorsal exterior view. Scales in mm

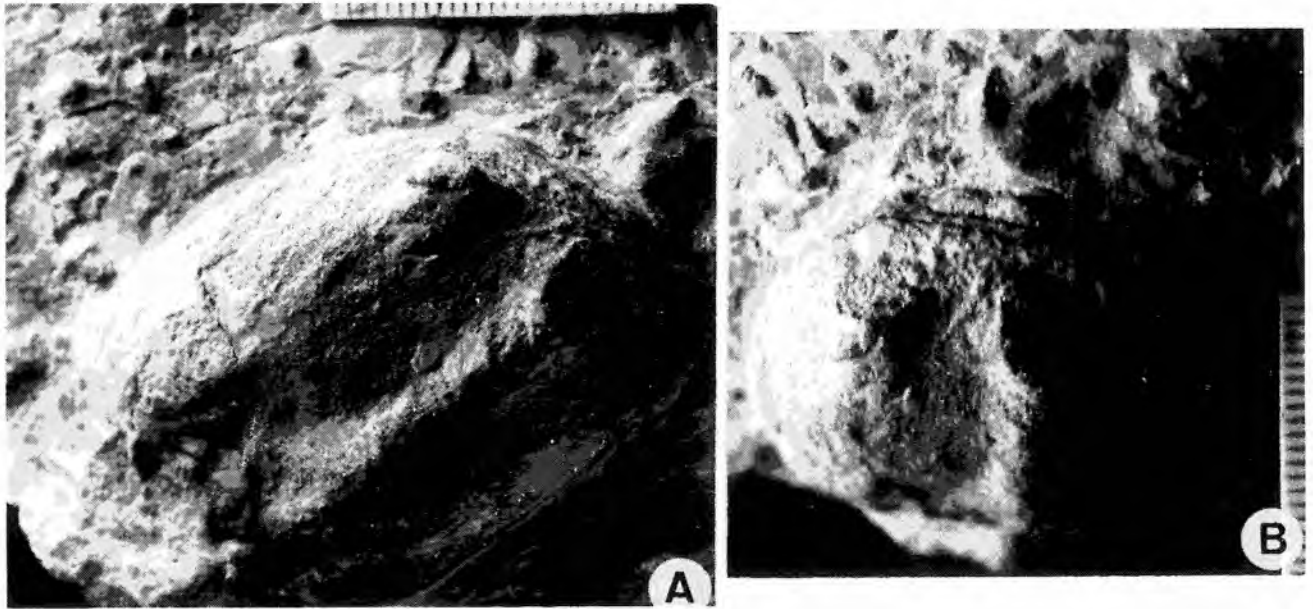


Fig. 64. *Pararusophycus oblongus* Książkiewicz (= *Scolicia* isp. properly), the holotype. Sole of turbiditic sandstone bed. UJ TF 114. Hieroglyphic beds (Eocene), Liszna. A. Bedding-plane view. B. Front view. Scales in mm

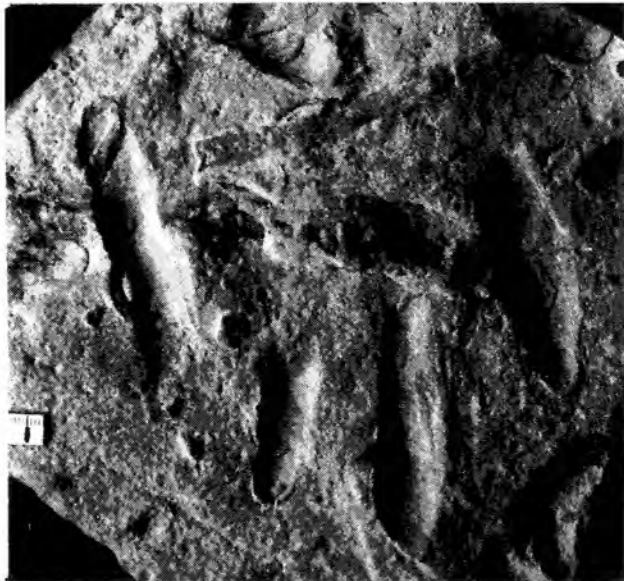


Fig. 65. *Naviculichnium marginatum* Książkiewicz. Epichnial form in turbiditic sandstone beds. UJ TF 1589 (label lost). Scale in mm

Diagnosis: As for ichnogenus.

Material: 4 slabs (TF UJ 760 (holotype), 1025, 1589, 2009).

Description: As in the diagnosis, with the following additions: This trace fossil occurs exclusively at the top of the sandy part of thin turbiditic beds. The depressions are commonly rimmed elevated rims. The depressions commonly overlap. In some cases, the depressions are filled with finer sediment.

Remarks: The rim around the depressions is caused by the tracemaker active pressing the sediment. Full morphology of this trace fossil is not well understood. This is mostly owing to weathering of the shale part of turbiditic beds were the

main part of the trace fossil occurs. What we observe are the deepest parts of the trace fossils. Probably, it represents a cylindrical burrow meandering in a vertical plane or several single burrow probes. The depressions are the lowermost parts of the meanders or the deepest parts of the probes. Książkiewicz (1977) regarded that *N. marginatum* was produced by burrowing ?polychaetes along sand/clay interfaces and stuffed immediately by faecal string. Stratigraphic range: Senonian–Middle Eocene flysch deposits (Książkiewicz, 1977).

Taenidium Heer 1877

Ichnospecies included in *Taenidium* Heer:

- v ? 1977 *Taenidium amulatum* (Schalhäutl) – Książkiewicz, 85, pl. 5, fig. 4.
- v ? partim 1977 *Taenidium isseli* (Squinabol) – Książkiewicz, 85, pl. 5, fig. 1 [non pl. 5, fig. 2 = *Cladichmus fischeri* (Heer)].
- v non 1977 *Taenidium fischeri* Heer – Książkiewicz, pl. 5, fig. 3 [= *Cladichmus fischeri* (Heer)].
- v 1977 *Keckia* aff. *hoessii* (Sternberg) – Książkiewicz, 64, pl. 3, fig. 15.
- v 1977 *Muensteria planicostata* n. ichnospl. – Książkiewicz, 122, pl. 13, fig. 1.
- v ? 1977 *Muensteria geniculata* Sternberg – Książkiewicz, 122, pl. 13, fig. 2.

Diagnosis: Unlined or very thinly lined, simple, straight to sinuous, cylindrical trace fossils with a fill of meniscus-shaped segments (modified after D'Alessandro & Bromley, 1987).

Remarks: Taxonomic problems of *Taenidium* and other meniscate trace fossils and their formation were discussed by D'Alessandro & Bromley (1987) and Keighley and Pickerill (1994).

Książkiewicz (1977) described under *Taenidium* among others radiating meniscated trace fossils, namely *T. fischeri* Heer and one incomplete specimen included in *Taenidium isseli* (Squinabol) (pl. 5, fig. 2). The first ichnospecies was included in *Cladichmus fischeri* (Heer) (D'Alessandro &

Bromley, 1987). The second specimen could be also included in this ichnotaxon. Moreover, trace fossils described under *Muensteria* can be partially included in *Taenidium*. *Muensteria geniculata* Sternberg illustrated by Książkiewicz (1977) in pl. 13, fig. 2 (Fig. 66C) is reservedly included in *Taenidium*. It is possible that this form is a *Scolicia* in horizontal section.

Taenidium occurs from the Lower Cambrian (Crimes *et al.*, 1992) to the ?Quaternary [Wetzel, 1983b (in synonymy by D'Alessandro & Bromley, 1987)].

Taenidium ispp.

Fig. 66

- ✓ 1977 *Keckia* aff. *hoessii* (Sternberg) Książkiewicz, 64, pl. 3, fig. 15.
- ✓ 1977 *Muensteria planicostata* n. ichnosp. Książkiewicz, 122, pl. 13, fig. 1.
- ✓ ? 1977 *Muensteria geniculata* Sternberg Książkiewicz, 122, pl. 13, fig. 2.
- ✓ partim 1977 *Taenidium isseli* (Squinabol) Książkiewicz, 85, pl. 5, fig. 1 [non pl. 5, fig. 2 = *Cladichmus fischeri* (Heer)].

Material: 3, reservedly 5 specimens (UJ TF 133, 780(?), 833, 1002, 1004(?)).

Description: As in the Książkiewicz (1977) description of the ichnotaxa included in the discussed trace fossils.

Remarks: These trace fossils do not conform with any of the three ichnospecies of *Taenidium* revised by D'Alessandro & Bromley (1987). The most similar, *T. serpentinum* Heer, displays thick meniscate segments, dissimilar to densely packed menisci of the discussed trace fossils. *T. satanassi* has pellets and its menisci are thick and composed of two different types of sediment.

Beaconites Vialov 1962

Diagnosis: Small, cylindrical, unbranched, walled, meniscate trace fossil. Straight or sinuous, horizontal or more rarely inclined or vertical. Weakly to strongly arcuate meniscate packets or segments enclosed by distinct, smooth and unornamented wall linings (after Keighley & Pickerill, 1994).

cf. *Beaconites capronus* (Howard & Frey 1984)

- ✓ 1977 *Keckia hoessii* (Sternberg) Książkiewicz, 64, pl. 3, figs. 16.
- * 1984 *Ancorichmus capronus* n. ichnosp. Howard & Frey, 201, figs. 2-3A, B.

Synonymy list: Keighley & Pickerill (1994, p. 319).

Diagnosis: Thinly lined, smooth walled, rarely branched, predominantly horizontal cylindrical trace fossils having distinct, chevron-laminated fills (modified after Howard & Frey, 1984).

Material: Three specimens (UJ TF 677, 1806, 1696).

Description: Endichnial, thinly walled, unbranched cylinders filled with chevron meniscated sediment. This trace fossil was traced for 10 cm.

Remarks: Książkiewicz (1977, p. 64, pl. 3, figs. 16) compared his material to *Muensteria hoessii* Sternberg, described and illustrated in Fischer-Ooster (1858, p. 38, pl. 7, fig. 3 and pl. 16 (non 6), fig. 4) under *Keckia*, which was treated as a subgenus of *Muensteria*. This comparison, however may be questioned. First of all, clarification of this problem needs comments to Sternberg's (1833) type mate-

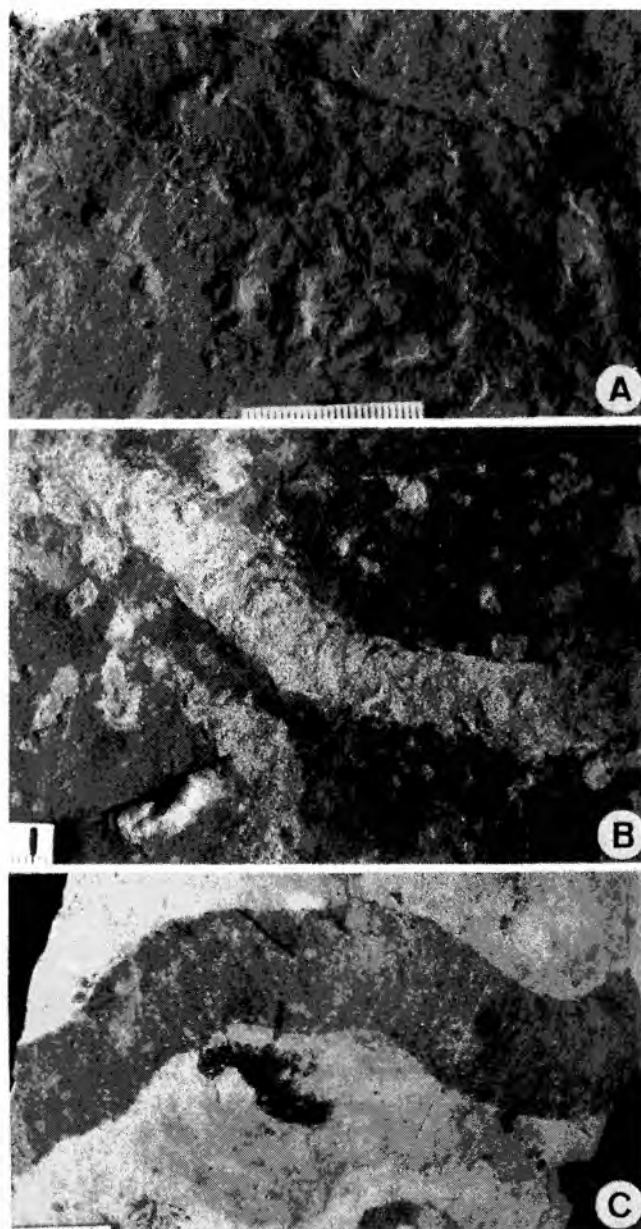


Fig. 66. *Taenidium* ispp. A. UJ TF 833, hypichnial form in mudstone. Ropianka beds (Senonian-Palaeocene), Limanowa-Marciszówka (labelled as *Keckia* aff. *hoessii*). B. UJ TF 1002, endichnial form in a marlstone bed. Siliceous marls (Turonian), Huhniki (labelled as *Muensteria geniculata*). C. ?*Taenidium* ispp., endichnial form in a marlstone bed. UJ TF 1004. Siliceous marls (Turonian), Huhniki (labelled as *Muensteria geniculata*). Scales in mm

rial of *Muensteria* housed in the National Museum in Prague (Uchman & Mikuláš, 1996). The following results were obtained: *Muensteria* Sternberg is a heterogenous taxon. *M. clavata* and *M. vermicularis* are fossil plants. *M. lacunosa* is a cast of a coprolite. The lectotype of *M. hoessii* (not found) is probably a plant fragment. The paralectotype of *M. hoessii* may be referred reservedly to *Keckia* Glocker sensu Fu (1991). The next two specimens of *M. hoessii* belong to *Chondrites* Sternberg and *Hydrancylus* Fischer-Ooster, respectively. The third specimen (*M. flagellaris* according to

the text, labelled as *M. hoessii* is an unidentifiable trace fossil. *M. flagellaris* is a *Chondrites*. *M. geniculata* is the type form of *Hydrancylus* Fischer-Ooster. Thus, because of its heterogenous nature, and confusing mislabelling of specimens, the "genus" *Muensteria* is not recommended for further use as ichnotaxon (cf. D'Alessandro and Bromley, 1987; Keighley & Pickerill, 1994).

In conclusion, the Książkiewicz material comprises walled meniscate trace fossils, which can be much better compared to *Beaconites* Vialov and its features conform with *B. capronus* (Howard & Frey). However, chevron meniscate filling of *Thalassinoides* is comparable to *B. capronus* and separation of these two trace fossils is impossible in small incomplete specimens (Howard & Frey, 1984). This problem concerns the Książkiewicz material and therefore the determination is retained.

Cladichnus D'Alessandro & Bromley 1987

Diagnosis: Annulated or moniliform burrow fills composed of meniscus-shaped segments, comprising primary successively branched and radiating systems; wall lining lacking or very thin (after D'Alessandro & Bromley, 1987).

Cladichnus fischeri (Heer 1877)

- v 1977 *Taenidium fischeri* Heer – Książkiewicz, pl. 5, fig. 3
v ? partim 1977 *Taenidium isseli* (Squinabol) – Książkiewicz, 85, pl. 5, fig. 2 [non pl. 5, fig. 1 = ? *Taenidium* isp.].

Diagnosis: Radiating and primary successively branched *Cladichnus* (after D'Alessandro & Bromley, 1987).

Material: 2 specimens (UJ TF 1489, 1694).

Remarks: Specimen UJ TF 1694 derives from the Coniacian "Carbonate flysch" in Achmata, Caucasus.

Protovirgularia McCoy 1850

Ichnospecies included in *Protovirgularia* McCoy:

- 1850 *Protovirgularia dichotoma* McCoy – McCoy, 272.
1851 *Protovirgularia dichotoma* McCoy – McCoy, 10, pl. 1B, figs. 11-12.
1853 ?*Cladograpsus nereitarum* n. sp. – Richter, 450, pl. 12, figs. 1-2.
1860 *Caulerpites pennatus* m. – Eichwald, 47, pl. 1, fig. 1.
1878a *Walcottia rugosa* n. sp. – Miller & Dyer, 39, pl. 2, figs. 11 and 11a.
? 1878b *Walcottia ? cocana* n. sp. – Miller & Dyer, 27, pl. 3, figs. 12 and 12a.
1885 *Pennatulites longespicata* Cocchi – De Stefani, 99, pl. 2, fig. 2.
1885 *Paleosceptron meneghini* (Cocchi) – De Stefani, 101, pl. 2, fig. 2.
1887 *Chrossochorda tuberculata* Will. – Williamson, 22, pl. 1, fig. 1. [lapsus calami].
? 1924 *Climactichnites mathieui* Sun (sp. nov.) – Sun, 16, pl. 1, fig. 2.
1937 Koproolithen – Dahmer, 536, pl. 35, figs. 5-10.
1941 *Ichnia spicosa* – Richter, 229, figs. 4-7.
? 1948 undetermined fossil – Bartrum, pl. 76, figs. 4-5.
1949 *Biformites insolitus* n.g. n. sp. – Linck, 40, text-fig. 1, pl. 4, figs. 1-(?)2.
1955 *Virgularia presbyteres* n.sp. – Bayer, 300, fig. 2a-c.
1955 *Pterocoides argenteum* (Ellis & Solander) – Bayer, 300, fig. 2f-g.
1960 *Nereites tosaensis* Katto, new species – Katto, 324, pl. 34, figs. 6, 12, pl. 35, fig. 17.
1960 *Nereites murotoensis* Katto, new species – Katto, 326, pl. 35, figs. 3, 14-15.

- 1962 Unnamed – Dimitrieva *et al.*, pl. 80, fig. 4.
1965 *Caulerpites pennatus* Eichw. – Hecker, pl. 11, fig. 5.
1966 *Nereites* – Gupta *et al.*, 624, fig. 1.
1967 *Nereites* sp. – Macsotay, 32, figs. 11-14.
1967 *Uchirites triangularis* sp. n. – Macsotay, 37, figs. 15, 15A.
partim 1967 *Pelecypodichnus ornatus* Bandel, n. sp. – Bandel, 8, pl. 5, fig. 1.
1969 *Crossopodia* sp. – Hattin & Frey, 1435, text-fig. 2A-L.
1969 variant (?) of *Scolicia* – Gregory, pl. 3, fig. 2.
1969 *Nereites tosaensis* Katto – Katto, pl. figs. 1-2, 5-6.
1969 *Nereites murotoensis* Katto – Katto, pl., figs. 3-4.
? 1969 *Scolicia* (?) – Gregory, pl. 3, fig. 2.
1970 *Imbrichnus wattonensis* ichnosp. nov. – Hallam, 197, pl. 2b-c (also Häntzschel, 1975, fig. 46B.1a-b).
1970 *Biformites* cf. *insolitus* Linck – Chiplonkar & Badve, 8, pl. 3, figs. 2, 2a.
v 1970 *Rhabdoglyphus* (?) sp. – Książkiewicz, 286, fig. 1m.
1970 *Walcottia rugosa* Miller & Dyer – Osgood, 379, pl. 67, fig. 6, pl. 69, fig. 5.
1971a *Sustergichnus lenadumbratus* n. ichnogen. and sp. – Chamberlain, 231, pl. 31, figs. 8, 11 (also Häntzschel, 1975, fig. 68.1a-b).
non 1971a *Biformites insolitus* Linck – Chamberlain, 234, pl. 31, figs. 16-18.
1973 *Nereites murotoensis* Katto – Katto, fig. 17.
1973 *Nereites* – Katto, figs. 15, 19.
1973 *Nereites tosaensis* Katto – Katto, fig. 16.
1974b *Scolicia* sp. – Fürsich, 44, figs. 35-36.
non 1975 *Imbrichnus* (?) – Ward & Lewis, 892, fig. 12.
1976 *Chevronichnus imbricatus* ichnosp. nov. – Hakes, 22, pl. 3, figs. 1a-b, pl. 4, figs. 1a-b.
v 1977 *Keckia annulata* Glocker – Książkiewicz, 63, pl. 3, fig. 14.
v 1977 *Gyrochorte hurtani* n. ichnosp. – Książkiewicz, 113, pl. 11, figs. 1-5, text-fig. 19.
v 1977 *Gyrochorte imbricata* n. ichnosp. – Książkiewicz, 114, pl. 11, figs. 6-8.
v ? 1977 *Gyrochorte oblitterata* n. ichnosp. – Książkiewicz, 115, pl. 11, fig. 9, text-fig. 20.
v 1977 *Arthroplycus* (?) *dzulynskii* n. ichnosp. – Książkiewicz, 58, pl. 1, figs. 13-14.
1977 Ladder trail – Hakes, 222, pl. 1a.
non 1979 cf. *Biformites* – Pickerill & Forbes, 2025, fig. 4a.
1979 *Biformites* sp. – Boyer, 74, fig. 1.
1981 *Walcottia devilsdingli* ichnosp. nov. – Benton & Gray, 686, figs. 11d-g - 12.
1981 *Ichnospica guptai*, sp. nov. – Chiplonkar *et al.*, 147, fig. 1.
1982 *Nereites tosaensis* Katto – Noda, pl. 7, fig. 6.
non 1982 *Imbrichnus protuberans* n. sp. – Marintsch & Finks, 1074, pl. 5, figs. 1-3; text-fig. 4E-G.
1982 *Pennatulites* (?) *corrugata* ichnosp. n. – D'Alessandro, 531, pl. 36, figs. 1-2, pl. 39, fig. 1, 3, pl. 43, fig. 2.
1984 *Oniscoidichnus sintanensis* ichnosp. nov. – Yang, 711, pl. 2, figs. 9-11.
partim 1984 *Oniscoidichnus hubeiensis* ichnosp. nov. – Yang, 712, pl. 2, figs. 13-14 (?non pl. 2, fig. 12).
?non 1985 *Imbrichnus wattonensis* Hallam – Durand, 59, pl. 9, figs. 7-9.
1985 *Biformites* Linck – Miller & Knox, 83, pl. 2, fig. H.
non 1985 *Imbrichnus* sp. – Pieńkowski, 41, pl. 2F.
1985 *Isopodichnus* sp. – Pieńkowski, 43, fig. 2H.
? 1988 *Sustergichnus* Chamberlain – Bjerstedt, 517, fig. 11.9.
? 1989 *Helminthopsis* sp. – Martino, 396, figs. 6.6-6.7.
? 1989 *Biformites* sp. – Metz, 212, fig. 1A.
1990 *Uchirites triangularis* Macsotay – Fillion & Pickerill, 63, pl. 17, figs. 9-11.
1994 *Uchirites implexus* n. isp. – Rindsberg, 55, pl. 15B-D, 20D-E, 22A, C-D.
1994 *Walcottia rugosa* Miller & Dyer – Rindsberg, 56, pl. 16A-C.
1994 *Walcottia imbricata* Hakes – Rindsberg, 57, pl. 16D-E.
1994 *Protovirgularia dichotoma* McCoy – Seilacher & Seilacher, 10.
1994 *Protovirgularia triangularis* (Macsoy) – Seilacher & Seilacher, 10.

- 1994 *Protovirgularia tuberculata* (Williamson) – Seilacher & Seilacher, 10.
 1994 *Protovirgularia rugosa* (Miller & Dyer) – Seilacher & Seilacher, 11, figs. f-h.
 1994 *Protovirgularia longespicata* (DeStefani) – Seilacher & Seilacher, 11, pl. 2, figs. a-f.

Additional ichnotaxa included in *Protovirgularia* are listed by Han & Pickerill (1994b) and Seilacher & Seilacher (1994).

Emended diagnosis: Horizontal or subhorizontal cylindrical trace fossil, trapezoidal, almond or triangular in cross-section, distinctly or indistinctly bilobate. Internal structure can be preserved: it is formed by successive pads of sediment which can be expressed on the exterior as ribs. The ribs are arranged in a chevron-like biserial pattern along the external or internal dorsal part. Exterior smooth mantle covering the structure and/or oval mound-like terminations of the trace fossil can be present.

Remarks: Recently, Seilacher & Seilacher (1994) revised *Protovirgularia* as a molluscan trace fossil, and proved its origin by neoichnological experiments. They expanded the previous diagnosis of this ichnogenus, limited to keel-like trace fossils covered with chevron markings open in one direction (Han & Pickerill, 1994b), and included in *Protovirgularia* also full-relief trace fossils described under several ichnogenera (see the list above). Similarities between these ichnogenera were noted earlier. Rindsberg (1994) more closely discussed *Uchirites* Macsotay (= *Protovirgularia*) and *Walcottia* Miller & Dyer (= *Protovirgularia*). He confirmed the view of Seilacher (1977b, p. 363) that *Sustergichnus* Chamberlain is the junior objective synonym of *Uchirites*. This idea was subsequently suggested partially by Maples (1988), who observed epichnial *Uchirites* in association with *Lockeia* and related it to the traces of bivalves. He suggested that *Sustergichnus* Chamberlain, *Chloephyucus* Miller & Dyer, and *Imbrichnus* Hallam are potential synonyms. However, *Chloephyucus* Miller & Dyer (1878b) is probably an inorganic structure (Nathorst, 1881; James, 1884; Häntzschel, 1962). Rindsberg (1994) considered *Walcottia* as a separate ichnogenus, which is the senior synonym of *Biformites* Linck, *Imbrichnus* Hallam, and *Chevronichnus* Hakes. Bayer (1955) illustrated a specimen from the Eocene/Oligocene deposits of Mollukks Islands, which is very similar to *Sustergichnus* Chamberlain. He interpreted it as a body fossil of sea pen of the genus *Pteroeides*. All the mentioned ichnotaxa are included in *Protovirgularia* McCoy by Seilacher & Seilacher (1994). This idea is confirmed in this paper. Moreover, *Caulerpites pennatus* Eichwald, of which a photograph is presented by Hecker (1965) displays the diagnostic features of *Protovirgularia*. Katto (1960) described a Miocene trace fossil under *Nereites* and presented its almond-like cross-section (Katto, 1969) typical of *Protovirgularia*. Additionally, *Rhabdoglyphus* Vassoevich (see discussion of this ichnigenus) is partially included in *Protovirgularia*.

Hypichnial expression of *Crossopodia* sensu Hattin & Frey (1969, text fig. 2K) is very similar to the hypichnial expression of *Chevronichnus* Hakes (1976, pl. 3, fig. 1b). These two ichnotaxa display features of *Protovirgularia* and were included in this ichnogenus.

Trace fossils included in *Protovirgularia* display very

strong morphological variation and particular elements of their exterior and interior. Hallam (1970) illustrated a very nice example of *Imbrichnus* (= *Protovirgularia*) that displays a gradation of preservation from smooth ridges with a keel (*Uchirites* aspect) to ridges with chevron ribs (*Sustergichnus* aspect). The same concerns *Walcottia rugosa* illustrated by Rindsberg (1994, Pl. 16, fig. C). It can be concluded that the appearance of trace fossils considered here under *Protovirgularia* strongly depends on preservation and details of their morphology should be treated with caution as potential diagnostic features.

Historically views concerning the origin of *Protovirgularia* are diverse. For instance, *Walcottia rugosa* described by Miller & Dyer (1878a) was regarded by James (1886) as the imprint of the under side of a star-fish arm, and *W. cocana* Miller & Dyer as the impression of a crinoid. James (1886) mentioned *W. sulcata* James as a trace fossil, but I did not find any description or bibliographic data for this taxon.

The modern views on the origin of the trace fossils included subsequently in *Protovirgularia* have been presented since 30 years. *Imbrichnus* (= *Protovirgularia*), described as *I. wattonensis* Hallam, was related to action of bivalves as was deduced from similar trace fossils associated with the bivalve trace fossil *Lockeia* (= *Pelecypodichnus*) illustrated by Bandel (1967, pl. 5, fig. 1). The imbricated structure is related to the action of the bivalve foot and the smooth mantle to the shell (Hallam, 1970). *Uchirites* (= *Protovirgularia*) and *Walcottia* (= *Protovirgularia*) were regarded as the locomotion traces of bivalves (Rindsberg, 1994), however he suggested that gastropods can produce the first ichnotaxon. Molluscan origin of *Protovirgularia* was documented by Seilacher & Seilacher (1994), who observed structures produced by a few bivalve taxa in aquaria.

Several trace fossils, included herein in *Protovirgularia*, were described by Książkiewicz (1977) as *Gyrochorte*. Brustur & Stoica (1993) reported Książkiewicz ichnospecies of *Gyrochorte* as *Pseudogyrochorte*. However, no further discussion was provided. *Gyrochorte* is typified by *G. comosa* Heer, which is a bilobed ribbon-like trace fossil, composed of small sediment pads, with extensive vertical repetitions (e.g., Heinberg, 1973; Powell, 1992). Similarity of the Książkiewicz material to *G. comosa* is superficial only. The material corresponds well to *Protovirgularia* and is included in this ichnogenus.

Stratigraphic range: Arenig (Fillion & Pickerill, 1990) – Miocene (Bayer, 1955; D'Alessandro, 1982).

Protovirgularia dichotoma McCoy 1850

- * 1850 *Protovirgularia dichotoma* McCoy – McCoy, 272.
- 1851 *Protovirgularia dichotoma* McCoy – McCoy, 10, pl. 1B, figs. 11-12.
- 1951 *Rhabdoglyphus grossheimi* n. sp. Wass. – Vassoevich, pl. 6, fig. 4 (also Dimitrieva *et al.*, pl. 91, fig. 1; Vialov, 1971, fig. 2).
- 1953 *Rhabdoglyphus grossheimi* Wssw. – Vassoevich, fig. 16.
- v 1977 *Rhabdoglyphus grossheimi* Vassoevich – Książkiewicz, 65, pl. 3, fig. 5, text-fig. 6a.

Synonymy list in Stanley & Pickerill (1993).

Emended diagnosis: *Protovirgularia* preserved as a keel-

like axis and paired, lateral, wedge-shaped short appendages or a series of invaginated calices tapering along their length.

Material: 1 specimen (TF UJ 82).

Remarks: Ichnogenus *Rhabdoglyphus* Vassoevich, revised by Stanley & Pickerill (1993) (see discussion of *Rhabdoglyphus* as an ichnogenus not recommended for further use), is included in *Protovirgularia dichotoma* McCoy because of strong morphological affinity between these ichnotaxa. Especially, *P. dichotoma* from the Devonian of Canada (Han & Pickerill, 1994b, figs. 3-4, 5A) displays invaginated calices typical of *Rhabdoglyphus grossheimi*. Figures 3A and 4A in the cited publication show a transition from the lateral appendages to the calices in the same specimen of *P. dichotoma*. The deeper part displays the calices and the shallow part the lateral appendages. Thus, the differences are related to subtle changes of the burrowing depth.

Protovirgularia pennatus (Eichwald 1860)

Fig. 67A

- * 1860 *Caulerpites pennatus* m. – Eichwald, 47, pl. 1, fig. 1.
- 1965 *Caulerpites pennatus* Eichw. – Hecker, pl. 11, fig. 5.
- 1967 *Uchurtes triangukaris* sp. n. – Macsotay, 37, figs. 15, 15A.
- 1971a *Susterigichnus lenadumbratus* n. ichnogen. and sp. – Chamberlain, 231, pl. 31, figs. 8, 11 (also Häntzschel, 1975, fig. 68.1a-b).
- partim 1977 *Gyrochorte burtani* n. ichnosp. – Książkiewicz, 113, pl. 11, fig. 4 (non pl. 11, figs. 1-3, 5 = *P. rugosa*).

Diagnosis: *Protovirgularia* with deeply impressed, carinate cross section. Chevron markings faint and densely spaced (modified after Seilacher & Seilacher, 1994).

Material: 1 slab (UJ TF 1165) with 4 specimens.

Remarks: Probably, different substrate properties and preservation caused the differences in morphology of *P. pennatus*, especially the state of the fine oblique ribs.

Seilacher & Seilacher (1994) interpreted *P. pennatus* as a molluscan repichnial undertrace. They described it as *Protovirgularia triangularis* (Macsoyay), but the Eichwald (1860) material has priority.

P. pennatus occurs from Devonian (Eichwald, 1860) to Oligocene (Książkiewicz, 1977).

Protovirgularia rugosa (Miller & Dyer 1878a)

Figs. 67C–D, 68B, D.

- * 1878a *Walcottia rugosa* n. sp. – Miller & Dyer, 39, pl. 2, figs. 11 and 11a.
- 1937 Koproolithen – Dahmer, 536, pl. 35, figs. 5-10.
- 1949 *Biformites insolitus* n.g. n. sp. – Linck, 40, text-fig. 1, pl. 4, figs. 1-(?)2 [also Häntzschel, 1975, fig. 29.3].
- 1966 *Nereites* – Gupta *et al.*, 624, fig. 1.
- partim 1967 *Pelecypodichnus ornatus* Bandel, n. sp. – Bandel, 8, pl. 5, fig. 1.
- 1970 *Imbrichnus wattonensis* ichnosp. nov. – Hallam, 197, pl. 2b-c (also Häntzschel, 1975, fig. 46B.1a-b).
- 1970 *Biformites cf. insolitus* Linck – Chiplonkar & Badve, 8, pl. 3, figs. 2, 2a.
- 1970 *Walcottia rugosa* Miller & Dyer – Osgood, 379, pl. 67, fig. 6, pl. 69, fig. 5.
- 1977 Ladder trail – Hakes, 222, pl. 1a.
- v partim 1977 *Gyrochorte burtani* n. ichnosp. – Książkiewicz, 113, pl. 11, figs. 2-3, 5 (non pl. 11, fig. 1 = *P. ?longespicata*; non pl. 11, fig. 4 = *P. pennatus*).
- v partim 1977 *Gyrochorte imbricata* n. ichnosp. – Książkiewicz, 114, pl. 11, fig. 7 (pl. 11, figs. 6, 8 = *P. ?rugosa*).

- 1981 *Ichnospica guptai*, sp. nov. – Chiplonkar *et al.*, 147, fig. 1.
- 1982 *Pemmatulites (?) corrugata* ichnosp. n. – D'Alessandro, 531, pl. 36, figs. 1-2, pl. 39, fig. 1, 3, pl. 43, fig. 2.
- 1985 *Biformites* Linck – Miller & Knox, 83, fig. 2H.
- 1994 *Walcottia rugosa* Miller & Dyer – Rindsberg, 56, pl. 16A-C.
- 1994 *Protovirgularia rugosa* (Miller & Dyer) – Seilacher & Seilacher, 11, figs. f-h.

Diagnosis: Commonly short *Protovirgularia* terminated by smooth *Lockeia*-like body. Chevron markings strong (modified after Seilacher & Seilacher, 1994).

Material: 5 specimens (UJ TF 175, 178, 687, 689, 936), reservedly 1 additional specimen (UJ TF 176).

Remarks: One specimen (UJ TF 178, Fig. 68D) is labelled as *Rhabdoglyphus bisculdatus*. This ichnospecies name was never used in publications. Two specimens, determined by Książkiewicz (1977, pl. 11, figs. 6, 8) as *Gyrochorte burtani*, are reservedly included in *Protovirgularia rugosa*, because they do not have the *Lockeia*-like termination. One can not exclude that they represent a new ichnospecies, but the material is underrepresented.

Seilacher & Seilacher (1994, p. 11) interpreted this ichnospecies as “cubichnial version of *Protovirgularia* [...] always found at the bases of sandy tempestites. So it makes sense that escape was in response to storm sand sedimentation”. The examined material suggests that turbidite sedimentation also should be considered.

P. rugosa occurs from Devonian (Dahmer, 1937) to Miocene (D'Alessandro, 1982).

Protovirgularia obliterated (Książkiewicz 1977)

Figs. 68C, 69

- v ? 1977 *Gyrochorte obliterated* n. ichnosp. – Książkiewicz, 115, pl. 11, fig. 9, text-fig. 20.

Material: 2 specimens (UJ TF 127, 1169).

Diagnosis: *Protovirgularia* having poorly expressed median groove and chevron markings (modified after Książkiewicz, 1977).

Remarks: *P. pennatus* (Eichwald) and *P. vagans* (Książkiewicz) have much stronger carinate profile. *P. tuberculata* (Williamson) displays more distinct median groove and chevron markings.

This ichnospecies occurs in the Barremian–Aptian flysch deposits in the Carpathians (Książkiewicz, 1977).

Protovirgularia ?longespicata (De Stefani 1885)

- * 1885 *Pemmatulites longespicata* Cocchi – De Stefani, 99, pl. 2, fig. 2.
- 1885 *Paleosceptron maneghim* (Cocchi) – De Stefani, 101, pl. 2, fig. 2.
- 1955 *Virgularia presbytes* n.sp. – Bayer, 300, fig. 2a-c (also Häntzschel, 1958, fig. 4).
- 1960 *Nereites tosaensis* Katto, new species – Katto, 324, pl. 34, figs. 6, 12, pl. 35, fig. 17.
- 1960 *Nereites murotoensis* Katto, new species – Katto, 326, pl. 35, figs. 3, 14-15.
- 1969 *Nereites tosaensis* Katto – Katto, pl., figs. 1-2, 5-6.
- 1969 *Nereites murotoensis* Katto – Katto, pl., figs. 3-4.
- 1973 *Nereites murotoensis* Katto – Katto, fig. 17.
- 1973 *Nereites* – Katto, figs. 15, 19.
- 1973 *Nereites tosaensis* Katto – Katto, fig. 16.
- v ? partim 1977 *Gyrochorte burtani* n. ichnosp. – Książkiewicz, 113, pl. 11, fig. 1 (non pl. 11, figs. 2-3, 5 = *P. rugosa*; non pl. 11,

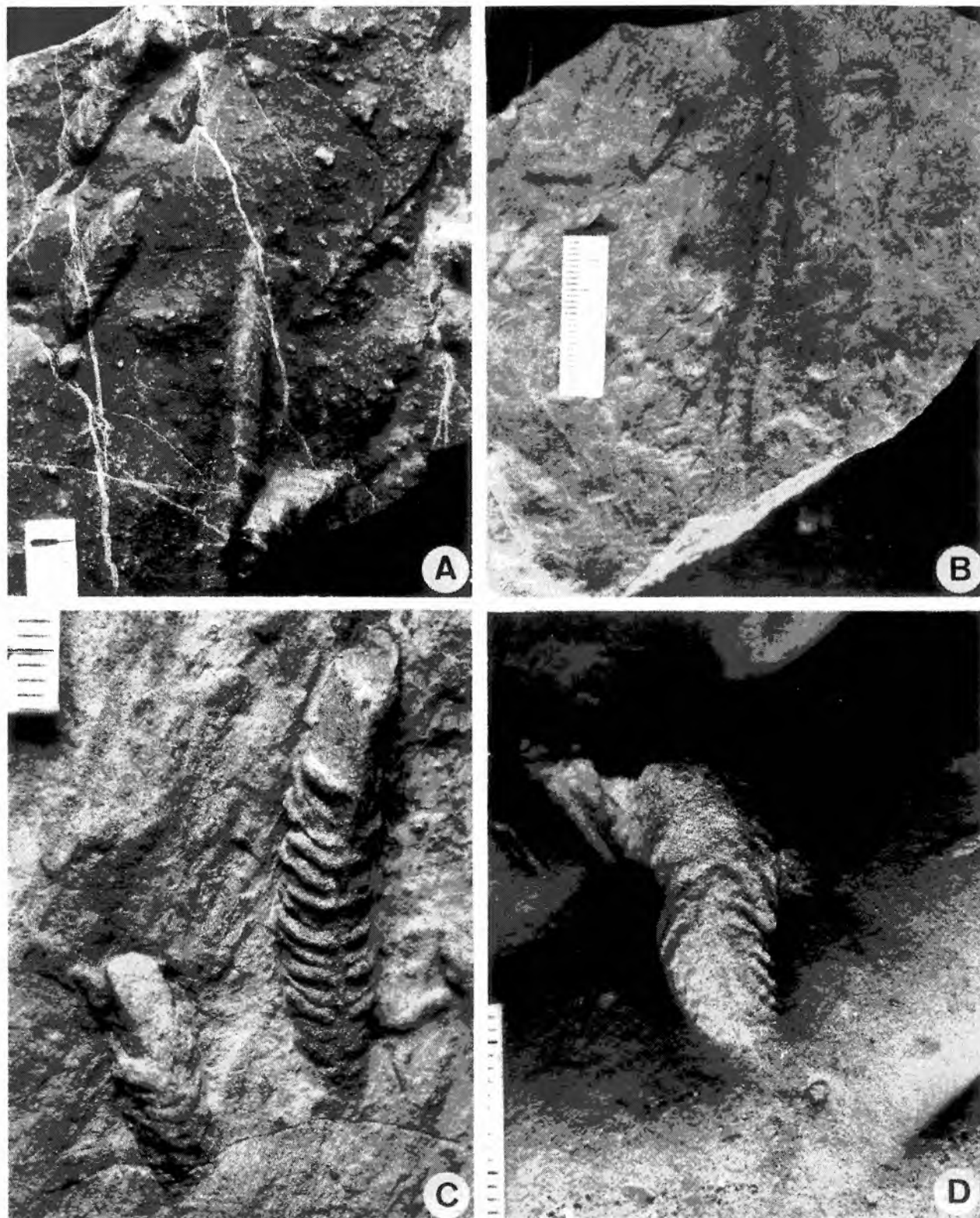


Fig. 67. *Protovirgularia* spp. Soles of turbiditic sandstone beds. A. *Protovirgularia pennatus* (Eichwald), UJ TF 1165, Verovice beds (Barremian–Aptian), Wiśniowa (labelled as *Gyrochorte burtani*). B. *Protovirgularia* isp. UJ TF 893, Szczawnica Formation (Paleocene–Lower Eocene), Szczawnica (labelled as *Keckia annulata*). C–D. *Protovirgularia rugosa* Miller & Dyer. C. UJ TF 175, Ciężkowice Sandstone (Eocene), Gródek (labelled as *Gyrochorte imbricata*). D. UJ TF 687, Krosno beds (Oligocene), Dębna (labelled as *Gyrochorte burtani*). Scales in mm

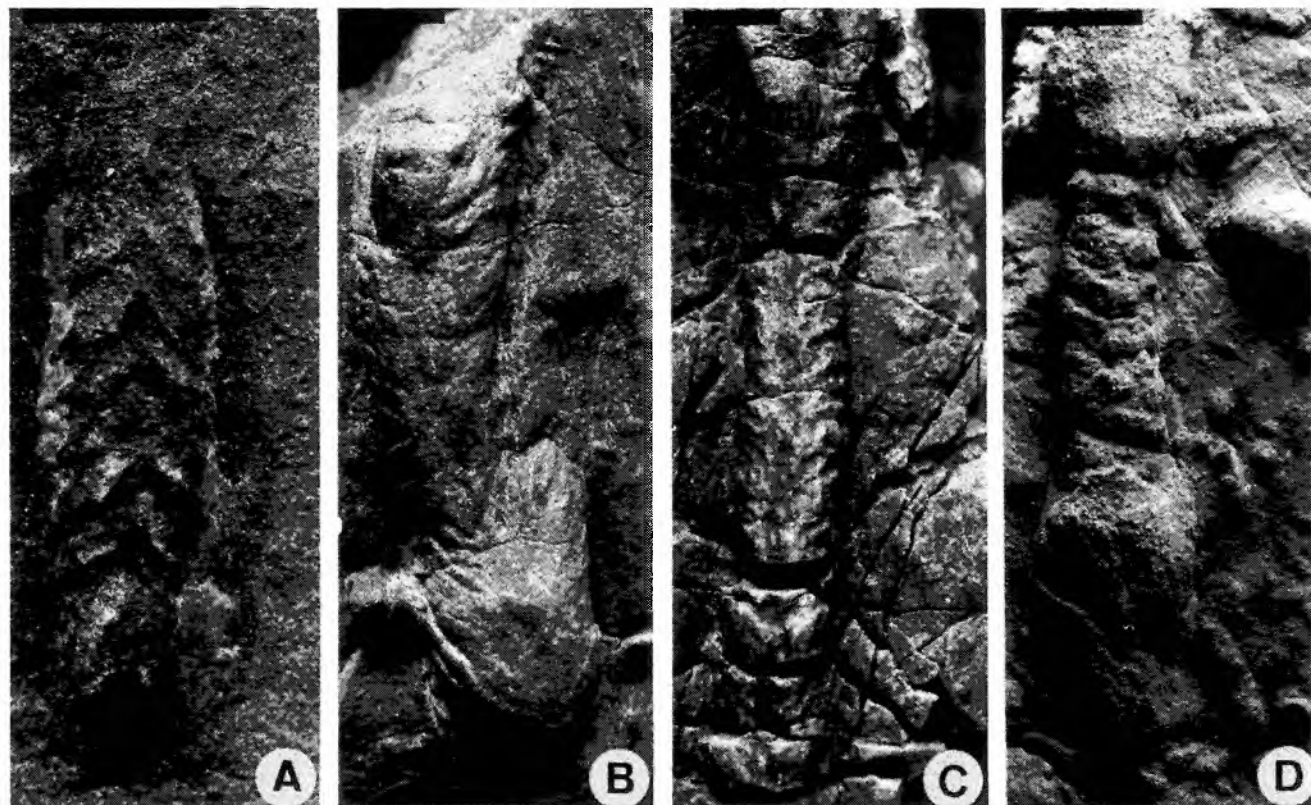


Fig. 68. *Protovirgularia* ispp. Soles of turbiditic sandstone beds. **A.** *Protovirgularia ?longespicata* (De Stefani). UJ TF 679, Grodziszcze beds (Hauterivian), Lipnik (labelled as *Gyrochorte burtani*). **B.** *P. rugosa* Miller & Dyer. UJ TF 936, Inoceramian beds (Senonian–Paleocene), Wierzbanowa (labelled as *Gyrochorte burtani*). **C.** *P. obliterated* (Książkiewicz) UJ TF 1169, Verovice beds (Barremian–Aptian), Wiśniowa (labelled as *Gyrochorte burtani*). **D.** *P. rugosa*. UJ TF 178, Sromowce Formation (Senonian), Szaflary (labelled as *Rhabdoglyphus bisculdatus*). Scale bars = 1 cm

fig. 4 – *P. pectatus*).

1994 *Protovirgularia longespicata* (De Stefani) – Seilacher & Seilacher, 11, pl. 2, figs. a-f.

Material: 2 specimens (UJ TF 679, 1475).

Diagnosis: Relatively large *Protovirgularia* with strong, papillate chevrons. Several probings may form a palmate system with spire-like backfill (modified after Seilacher & Seilacher, 1994).

Remarks: None of the discussed specimens displays the palmate probings. Specimen UJ TF 1475 is relatively large, but its chevrons do not display the papillate aspect. On the other hand this aspect of morphology can be strongly controlled by the substrate properties. Specimen UJ TF 679 is distinctly smaller than typical specimens of this ichnospecies.

Protovirgularia vagans (Książkiewicz 1977)

Fig. 70

v*?partim 1977 *Tuberculichnus vagans* n. ichnosp. – Książkiewicz, 140, pl. 13, fig. 4, text-fig. 27d-e [non text-fig. 27c, f-g].

v partim 1977 *Tuberculichnus meandrinus* n. ichnosp. – Książkiewicz, 141, pl. 13, fig. 5 [non pl. 13, fig. 6 = *Saerichnites canadensis*, non text-fig. 27a-b].

?non 1996 *Tuberculichnus vagans* Książkiewicz – Paczeńska, 67, p. 29, fig. 8, pl. 30, figs. 1-3.

? 1996 *Tuberculichnus vagans* Książkiewicz – Buatois *et al.*, 296, fig. 10c-d.

Diagnosis: Smooth *Protovirgularia* having strong carinate profile,

undulating in the vertical plane, and therefore preserved as hypichnial disrupted ridges.

Material: 4 specimens (UJ TF 76, 255, 773, 1036 (holotype)).

Remarks: The holotypes of *T. vagans* and *T. meandrinus* display the characteristic carinate (amygdaloid) cross-section, which is the typical feature of *Protovirgularia* McCoy and is described under this ichnogenus as *P. vagans* in this paper.

Stratigraphic range: Senonian–Eocene (Książkiewicz, 1977). Jurassic lacustrine trace fossil described as *Tuberculichnus vagans* Książkiewicz (Buatois *et al.*, 1996) is reservedly included in this ichnospecies.

Protovirgularia dzulynskii (Książkiewicz 1977)

Fig. 71

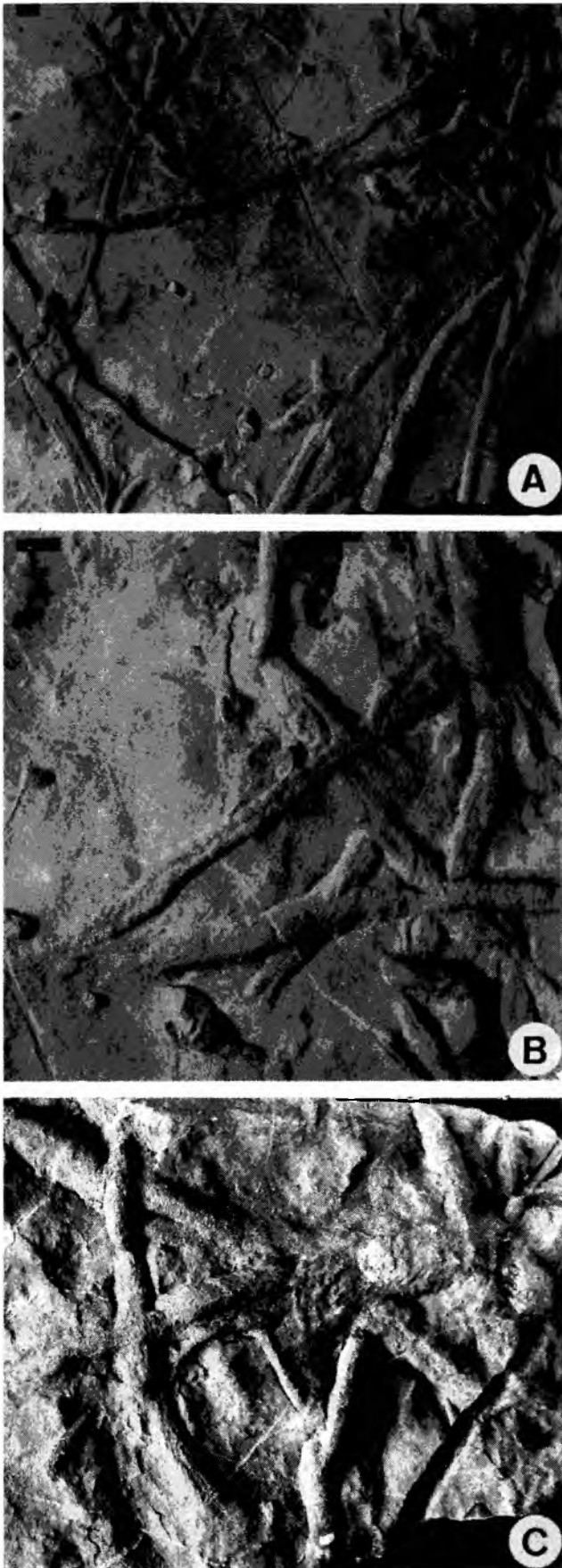
v 1970 *Rhabdoglyphus* (?) sp. – Książkiewicz, 286, fig. 1m.

v * 1977 *Arthroplycus* (?) *dzulynskii* n. ichnosp. – Książkiewicz, 58, pl. 1, figs. 13-14.

Diagnosis: Hypichnial, cylindrical rope-sized full-relief structure, or hypichnial furrow. The sculpture of the full-relief trace fossil consists of tuberculated transversal narrow ribs slightly bent in one direction. The furrows are transversely grooved (after Książkiewicz, 1977).

Material: One slab, the holotype (UJ TF 177).

Description: This trace fossil is preserved in different ways. However, Książkiewicz (1977) focused on the transversely ribbed



ridge. The ribbed ridge displays features mentioned in the diagnosis. Moreover, it is terminated by an elevated oval smooth body and has a thin wall. The grooves are semicircular in cross-section and display transverse arcuate faint ridges, which are edges of menisci. One groove is terminated by an elongate oval body, which is very similar to that which terminates the ridge. Another groove passes into a low, flat, non-ribbed ridge. The ridge is subdivided by a narrow, shallow median groove. The ribbed ridge is the interior of the trace fossil. The flat ridge is probably an exterior of the ventral side of the trace fossil.

Remarks: Superficially, the ribbed ridge resembles *Climactichnites* Logan 1860, but the latter is a large surface trail known from the Lower Palaeozoic marginal marine deposits of North America (Yochelson & Fedonkin, 1993). It is not impossible that *Climactichnites* mentioned by Nowak (1961) from the Lower Cretaceous flysch deposits of the Grodziszczce beds is a similar or identical trace fossil. Also Contescu *et al.* (1993) mentioned an occurrence of *Climactichnites* in the Eocene flysch deposits of the Romanian Carpathians.

The ribs mentioned in the diagnosis are edges of cross-sectioned menisci. The trace fossil has a thin wall. However, the elliptical termination at the oval termination of the trace fossil is the characteristic feature of *Protovirgularia*. The termination is probably a place where the tracemaker shifted to another level or was suddenly pressed to escape. The tubercles on the "ribs" are probably sandy pellets. The menisci are not perfectly arcuate. Part of them are bent in an obtuse angle and form a chevron pattern which is an additional feature of *Protovirgularia*.

This trace fossil does not conform with the definitions or appearance of known *Protovirgularia* ichnospecies. Therefore Książkiewicz's species name is retained. However the material is too scarce for more pronounced ichnotaxonomic evaluation.

Protovirgularia isp.

v 1977 *Keckia annulata* Glocker – Książkiewicz, 63, pl. 3, fig. 14.

Material: 1 specimen (UJ TF 893).

Description: *Protovirgularia* having strong carinate profile and rare chevron markings.

Remarks: Książkiewicz (1977) described the discussed material under *Keckia annulata* Glocker. Similarity of the material to *Keckia* is impossible to accept (see comments to *Keckia*). It displays features of *Protovirgularia*, similar to *P. pennatus*, but the latter ichnotaxon have distinctly densely spaced chevron markings. The material is underrepresented and therefore determination at the ichnospecific level is not proposed.

Fig. 69. *Protovirgularia obliterata* (Książkiewicz). Soles of turbiditic sandstone beds. Verovice beds (Barremian–Aptian), Lipnik near Myślenice (labelled as *Gyrochorte obliterata*). **A.** UJ TF 1456. **B-C.** UJ TF 127, holotype of *Gyrochorte obliterata*. **B.** General view. **C.** Detail of B. Scale bars = 1 cm

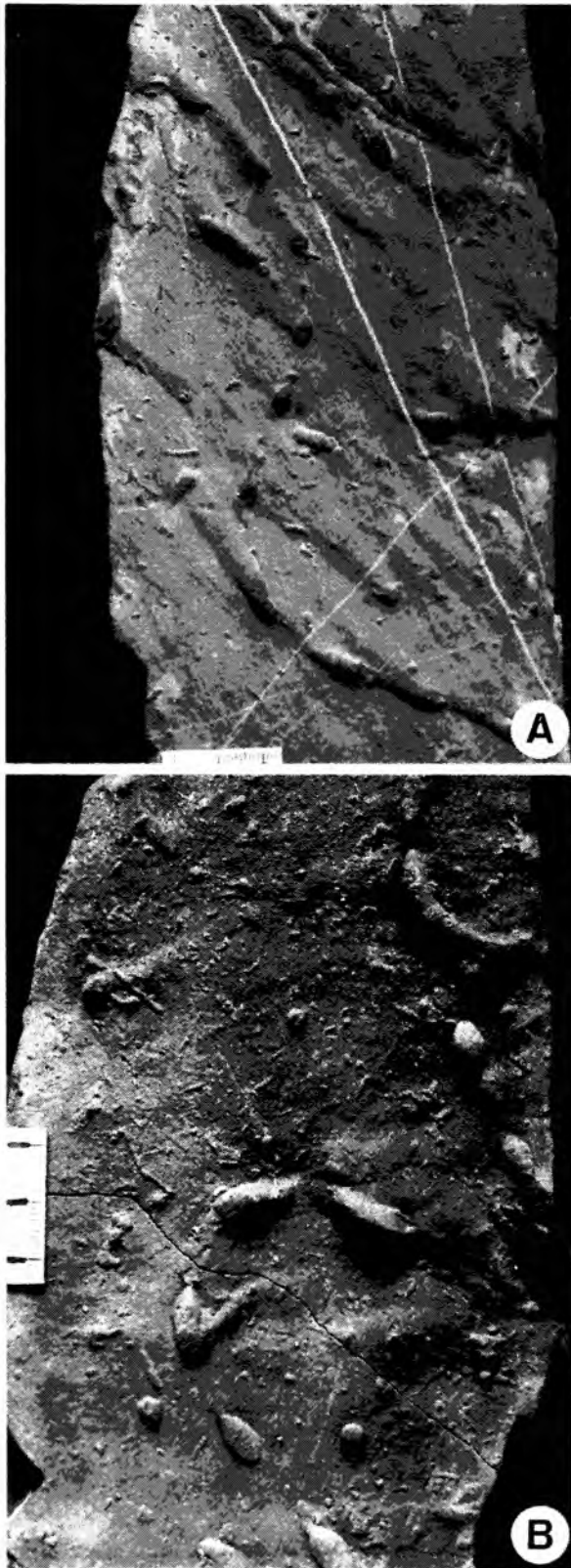


Fig. 70. *Protovirgularia vagans* (Książkiewicz) on sole of turbiditic sandstone. **A.** UJ TF 76, Beloveža beds (Eocene), Sidzina (labelled as *Tuberculichnus meandrinus*). **B.** UJ TF 255, Ropianka beds (Senonian–Palaeocene), Lipnica Wielka-Kiczora (labelled as *Tuberculichnus vagans*). Scales in mm

Oniscoidichnus Brady 1949

Oniscoidichnus carpathicus Książkiewicz 1977

Fig. 72

v 1977 *Oniscoidichnus carpathicus* n. ichnosp. – Książkiewicz, 124, pl. 11, fig. 11.

Material: 2 specimens (UJ TF 1471, 1472a).

Remarks: It is not clear, if the discussed structures are trace fossils. One can not exclude that they are mechanical artifacts and their morphology remains enigmatic.

Gordia Emmons 1844

Diagnosis: Unbranched, horizontal, winding, or irregularly meandering trace fossils, predominantly horizontal, that tend to form loops (modified from Pickerill & Peel, 1991 and Fillion & Pickerill, 1990).

Remarks: Ichnotaxonomic problems of *Gordia* Emmons have been recently discussed by Fillion & Pickerill (1990) and Pickerill & Peel (1991). Książkiewicz (1977) distinguished two ichnospecies of *Gordia*: *G. molassica* (Heer) and *G. arcuata* Książkiewicz. The first ichnospecies is regarded as the junior synonym of *Gordia marina* Emmons (Pickerill, 1981; Fillion & Pickerill, 1990). This is confirmed in this paper. *G. arcuata* Książkiewicz is regarded as a useful and valid ichnotaxon.

Gordia marina Emmons 1844

Fig. 73

* 1844 *Gordia marina* – Emmons, 24, pl. 2, fig. 2.

v 1977 *Gordia molassica* (Heer) – Książkiewicz, pl. 20, figs. 4–7, text-fig. 36s–x.

v partim 1977 *Helminthopsis hieroglyphica* Heer – Książkiewicz, pl. 12, fig. 3 [non text-fig. 2li, k–o].

Diagnosis: *Gordia* in which level crossing is fully developed and meanders are unguided (after Miller, 1889 and Fillion & Pickerill, 1990).

Material: 8 specimens (TF UJ 245, 1082, 1184, 1197, 1249, 1253, 1353, 1520).

Remarks: *Helminthopsis hieroglyphica* Heer illustrated by Książkiewicz (1977) in pl. 12, fig. 3 (UJ TF 1082, Fig. 73A) displays features of *Gordia marina* and is included in this ichnospecies.

Gordia arcuata Książkiewicz 1977

Fig. 74

*v 1977 *Gordia arcuata* n. ichnosp. – Książkiewicz, 156, pl. 20, fig. 8, text-fig. 36y.

Diagnosis: *Gordia* in which only apical arcuate bends are developed in hypichnial reliefs (modified after Książkiewicz, 1977).

Material: 3 specimens (UJ TF 1219, 1222, 1225).

Cosmorhapse Fuchs 1895

Ichnospecies excluded from *Cosmorhapse* Fuchs reservedly included in this ichnogenus:

non 1964 *Cosmorhapse sinuosus* Azpeitia – Farrés Malian, 86, pl. 5, fig. 1.

?non 1964 *Cosmorhapse* Volk, fig. 12.

non 1968 *Cosmorhapse timida* n. sp. – Pfeiffer, 667, pl. 2, figs. 1–2.

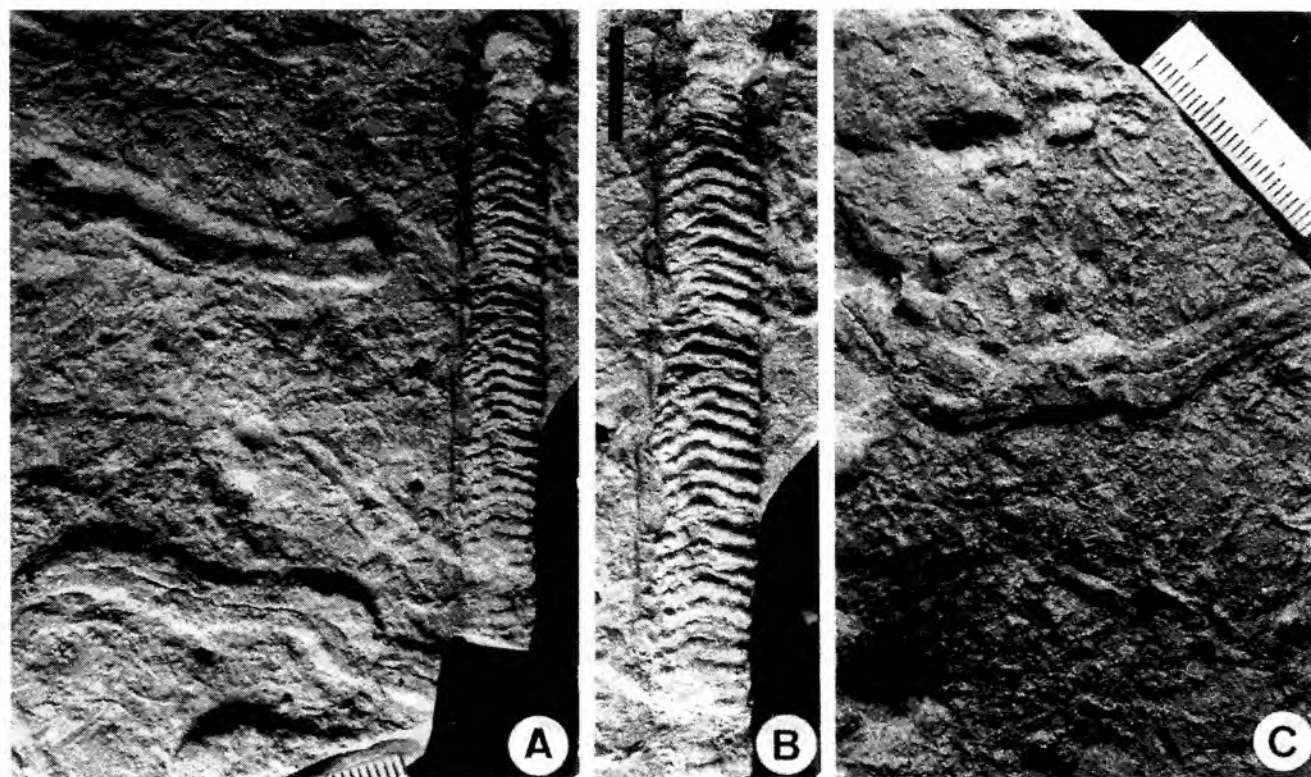


Fig. 71. *Protovirgularia dzulynskii* (Książkiewicz). UJ TF 177 (the holotype), Krosno beds (Oligocene), Dębna. Hypichnial form in fine-grained turbiditic sandstone. A. General view. B-C. Details of A. Scales in A, C in mm, scale bar in B = 1 cm

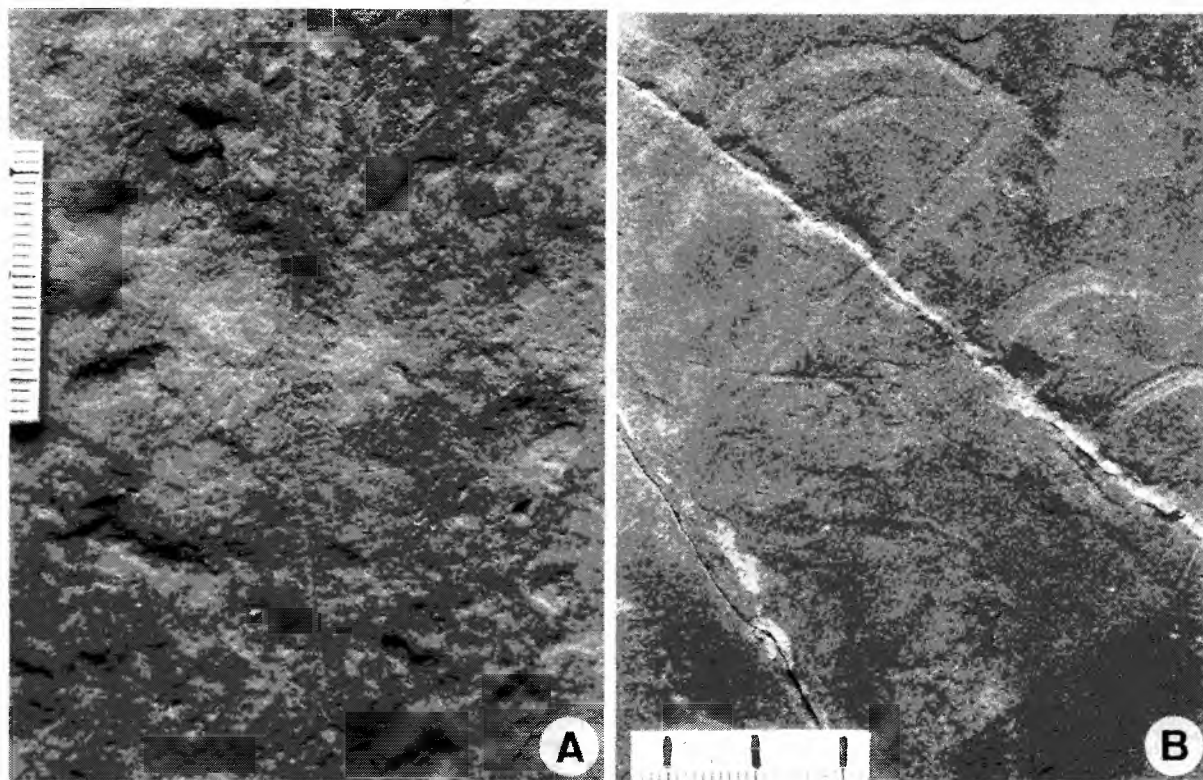


Fig. 72. *Oniscoidichmus carpathicus* Książkiewicz. Epichnial forms in marly siltstone beds, Krosno beds (Oligocene), Lubomierz. A. UJ TF 1741, holotype. B. UJ TF 1472a. Scales in mm

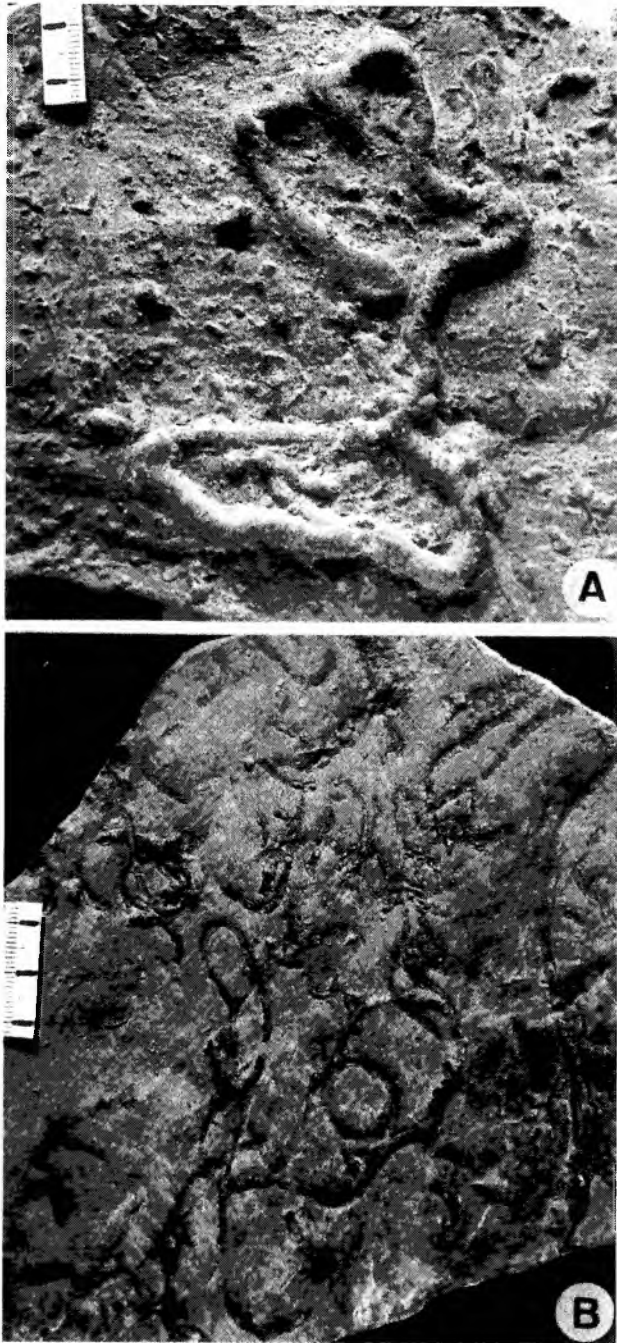


Fig. 73. *Gordia marina* Emmons. UJ TF 1082, sole of turbiditic sandstone bed, Sidzina, Beloveža beds (Eocene), Sidzina (labelled as *Helminthopsis hieroglyphica*). **B.** UJ TF 1353, Krościenko (label lost). Scale in mm

- text-fig. 3.1 [= *Phycosiphon*].
- non 1968 *Cosmorhapse* sp. - Pfeiffer, 669, pl. 2, fig. 2.
- non 1969 cf. *Cosmorhapse* - Roberts, 231, pl. 1, fig. 1.
- non 1970 *Cosmorhapse* (?) *tortuosa* ichnosp. n. - Książkiewicz, 294, pl. 3c.
- non 1971 ?*Cosmorhapse* sp. - Jerzykiewicz, pl. 11, fig. 6.
- non 1975 *Cosmorhapse filiformis* sp. nov. - Chiplonkar & Ghare, 77, fig. 2C.
- ?non 1975 *Cosmorhapse ketneri* n. ichnosp. - Pek & Zapletal, 56, fig. 1.
- ?non 1990 *Cosmorhapse ketneri* Pek & Zapletal - Zapletal & Pek,



Fig. 74. *Gordia arcuata* Książkiewicz. UJ TF 2581, hypichnial form in turbiditic sandstone bed (label lost). Scale in mm

- 56.
- non 1976 *Cosmorhapse* - Garcia Ramos, 139, pl. 1g.
- non 1977 *Cosmorhapse* (?) *tortuosa* Książkiewicz - Książkiewicz, 155, pl. 19, fig. 9 [= *Helicolithus tortuosus*].
- non 1977a *Cosmorhapse helicoidea* n. ichnosp. - Seilacher, 299, fig. 3g.
- ? 1977a *Cosmorhapse* - Crimes, pl. 7c.
- non 1979 *Cosmorhapse dyoraki* sp. n. - Lang *et al.*, 69, pl. 6, fig. 1, text-fig. 5 [= *Gordia* isp.].
- non 1988 *Cosmorhapse helicoidea* Seilacher - McCann & Pickerill, 334, fig. 3.6 [= *Spirocsmorhapse* Seilacher].
- ? 1991 *Cosmorhapse* - Jin & Li, pl. 1a-b.
- ? 1992 *Cosmorhapse* ichnosp. - Kim *et al.*, 319, fig. 2.7.
- ? 1993 ?*Cosmorhapse* ichnosp. - Miller, 17, fig. 5B.
- ?non 1994 *Cosmorhapse* - Gong, pl. 4, fig. 4.
- non 1994a *Cosmorhapse fuchsi* Książkiewicz - Han & Pickerill, 227, fig. 4C.
- non 1994a *Cosmorhapse sinuosa* (Azpeitia Moros) - Han & Pickerill 229, fig. 4G.
- ? 1994 cf. *Cosmorhapse* - Lobitzer *et al.*, pl. 4, fig. 3.

Diagnosis: Unbranched graphoglyptid trace fossil with two orders of meanders or undulations (modified after Seilacher, 1977a).

Remarks: *Cosmorhapse* is a graphoglyptid trace fossil that occurs in Cretaceous and Tertiary flysch deposits. Large Palaeozoic forms occur also in the Ordovician and Silurian (Pickerill, 1980; McCann, 1990). *Cosmorhapse* ? isp. was reported from the Cambrian (Narbonne *et al.*, 1987). Present-day shallow-tier traces of *Cosmorhapse*-morphology were found on the deep-sea floor below 4,000 m (Ekdale & Berger, 1978; Ekdale, 1980; Ekdale *et al.*, 1984b; Miller, 1991).

Cosmorhappe sinuosa (Azpeitia Moros 1933)

- * 1933 *Helminthopsis sinuosa* Azpeitia n. sp. – Azpeitia Moros, 45, fig. 24B.
 1935 *Spirorhappe* – Abel, fig. 263.
 1954 *Helminthopsis sinuosa* Azpeitia – Gómez de Llarena, pl. 46, fig. 1.
 1959 *Helminthopsis sinuosa* – Seilacher, tab. 1, fig. 8.
 non 1964 *Cosmorhappe sinuosus* Azpeitia – Farrés Malian, 86, pl. 5, fig. 1.
 1967 *Cosmorhappe* – Macsotay, 27, pl. 6, fig. 22.
 v non 1970 *Cosmorhappe sinuosa* (Azpeitia) – Książkiewicz, 292, text-fig. 2a, pl. 3a.
 v 1970 *Cosmorhappe fuchsi* ichnosp. nov. – Książkiewicz, 294, text-fig. 2b, pl. 3b.
 v non 1977 *Cosmorhappe sinuosa* (Azpeitia) – Książkiewicz, 153, pl. 19, figs. 3-5, text-fig. 33g-j [= *Cosmorhappe lobata*].
 v 1977 *Cosmorhappe fuchsi* Książkiewicz – Książkiewicz, 154, pl. 19, fig. 7, text-fig. 33 n-s.
 1978 *Cosmorhappe* sp. – Fukuda & Hayasaka, 18, pl. 1, fig. 2.
 1978 *Cosmorhappe sinuosa* – Montenat & Seilacher, fig. 1c.
 non 1980 *Cosmorhappe sinuosa* (Azpeitia) – Alexandrescu & Brustur, 21, pl. 6, figs. 3-4.
 ? 1980 *Cosmorhappe sinuosa* (Azpeitia Moros) – D'Alessandro, 372 [not figured].
 non 1988 *Cosmorhappe sinuosa* Azpeitia Moros – McCann & Pickerill, 334, fig. 3.5 [= *C. lobata*].
 non 1991 *Cosmorhappe* aff. *sinuosa* (Azpeitia Moros) – Crimes & Crossley, 44, fig. 8c.
 1991a *Cosmorhappe* – Leszczyński, figs. 9-10.
 1991b *Cosmorhappe* – Leszczyński, fig. 5.
 1991 *Cosmorhappe sinuosa* (Azpeitia Moros) – Leszczyński & Seilacher, 296, figs. 3-6, 8.
 1992 *Cosmorhappe sinuosa* – Leszczyński, pl. 3, fig. 2.
 v ? 1992a *Cosmorhappe* ichnosp. – Uchman, fig. 4.4.
 ? 1993 *Cosmorhappe* cf. *sinuosa* – Leszczyński, fig. 7.
 non 1993 *Cosmorhappe sinuosa* Azpeitia Moros – McCann, 43, fig. 4D [= *C. helminthopsoidea*].
 v ? 1993 *Cosmorhappe* ? *sinuosa* Azpeitia Moros – Tunis & Uchman, 90, figs. 6F, 8D.
 ? 1994 *Cosmorhappe helminthopsida* Fuchs – Giese *et al.*, 82, fig. 4.
 non 1994a *Cosmorhappe sinuosa* (Azpeitia Moros) – Han & Pickerill 229, fig. 4G.
 v ? 1995 *Cosmorhappe sinuosa* (Azpeitia Moros) – Uchman, 40, pl. 11, fig. 4.

Diagnosis: First-order meanders widely spaced; second-order undulations of greater wave length than amplitude. Occasional shortcuts may connect successive turns (after Seilacher, 1977a).

Material: 5 specimens (UJ TF 11, 243, 2048-2050).

Remarks: Książkiewicz (1977) included specimens with deep, lobate second-order meanders within *Cosmorhappe sinuosa*, but this ichnotaxon is characterised by shallow, wide second-order meanders (Azpeitia Moros, 1933; Seilacher, 1977a). On the other hand, the wide second-order meanders indicate *C. fuchsi*, and the specimens with the deep, lobate second-order meanders conform with the diagnosis of *C. lobata* Seilacher (1977a). In consequence, these specimens were included in these ichnotaxa, according to their affinity.

Stratigraphic range: Senonian (Książkiewicz, 1977) – Upper Miocene (Montenat & Seilacher, 1978).

Cosmorhappe gracilis Książkiewicz 1977

- 1895 *Cosmorhappe* – Fuchs, pl. 6, fig. 1.
 1924 *Cosmorhappe* – Richter, fig. 6.
 1955 *Cosmorhappe* – Lessertisseur, pl. 74, fig. 1.
 1959 *Cosmorhappe* – Seilacher, fig. 1.8.
 v * 1977 *Cosmorhappe gracilis* n. ichnosp. – Książkiewicz, 152, pl.

19, figs. 1-2, text-fig. 33a-f.

- 1977a *Cosmorhappe parva* n. ichnosp. – Seilacher, 297, fig. 3c.
 ? 1978 *Cosmorhappe* – Kern, 254, fig. 9L.
 ? 1982 *Cosmorhappe* cf. *gracilis* Książkiewicz – Alexandrescu & Brustur, 39, pl. 4, fig. 2a.
 1987 *Cosmorhappe* – Yeh, 50, fig. 2A.
 ? 1989 *Cosmorhappe* – Powichrowski, fig. 3.5.
 1993 *Cosmorhappe* cf. *gracilis* Książkiewicz – Pickerill *et al.*, 62, fig. 2a.
 v 1993 *Cosmorhappe lobata* Seilacher – Tunis & Uchman, 90, fig. 8A.
 ? 1994 *Cosmorhappe gracilis* Książkiewicz – Löffler & Geyer, 497 (only description).
 v 1996a *Cosmorhappe* ? *gracilis* Książkiewicz – Tunis & Uchman, 181, fig. 9A.

Diagnosis: First order meanders widely spaced, containing 15–18 turns of regular second order undulations, which are slightly higher than wide and interlock like a jig-saw puzzle (after Seilacher, 1977a).

Material: 7 specimens (TF UJ 91, 1022, 1138, 1162 (holotype), 1613, 1755, 1853).

Remarks: Książkiewicz (July 1977) created *C. gracilis* with the lectotype illustrated by Fuchs (1895, pl. 6, fig. 1). In the same year Seilacher (August 1977a) created *C. parva* and designated the same Fuchs' specimen for the holotype as was selected by Książkiewicz as lectotype. Thus, *C. parva* is the junior objective synonym of *C. gracilis*.

Stratigraphic range: Senonian–Eocene–?Oligocene (Książkiewicz, 1977).

Cosmorhappe lobata Seilacher 1977a

Fig. 75

- 1895 *Cosmorhappe* – Fuchs, pl. 6, fig. 5.
 1904 *Helminthopsis*? *labyrinthica* Heer – Ulrich, 144, pl. 20, figs. 2-3.
 1932 *Spyrorhappe* – Buoi, pl. 4, fig. 8 (lapsus calami).
 ? 1935 Kriechspur – Abel, fig. 261B.
 1949 *Magarikume akkestiensis* sp. nov. – Minato & Suyama, 277, figs. 1-2.
 1955 *Cosmorhappe* – Seilacher, fig. 5.66.
 1959 *Cosmorhappe* – Seilacher, fig. 1.9.
 1963 *Cosmorhappe* – Müller, fig. 837.
 v 1970 *Cosmorhappe sinuosa* (Azpeitia) – Książkiewicz, 292, text-fig. 2a, pl. 3a.
 * 1977a *Cosmorhappe lobata* n. ichnosp. – Seilacher, 299, fig. 3d.
 v 1977 *Cosmorhappe sinuosa* (Azpeitia) – Książkiewicz, 153, pl. 19, figs. 3-5, text-fig. 33g-j.
 1978 *Cosmorhappe* sp. – Fukuda & Hayasaka, 18, pl. 1, fig. 1.
 non 1980 *Cosmorhappe sinuosa* (Azpeitia) – Alexandrescu & Brustur, 21, pl. 6, figs. 3-4.
 1982 *Cosmorhappe* – Scholle & Spearing, fig. 120.
 1988 *Cosmorhappe sinuosa* Azpeitia Moros – McCann & Pickerill, 334, fig. 3.5.
 v 1993 *Cosmorhappe lobata* Seilacher – Tunis & Uchman, 90, fig. 8A.
 ? 1994 *Cosmorhappe helminthopsidea* (Sacco) – Löffler & Geyer, 495, fig. 3e (lapsus calami).
 ? 1995 *Cosmorhappe* cf. *lobata* Seilacher – Crimes & McCall, 234, figs. 2C-2D.
 v ? 1996a *Cosmorhappe* ? *lobata* Seilacher – Tunis & Uchman, 181, fig. 9B.
 v 1996a *Cosmorhappe lobata* Seilacher – Tunis & Uchman, 181 [not figured].

Diagnosis: First order meanders fairly dense, containing 15–20 turns of regular second order meanders, which are 2–3 times higher than wide and interlock strongly (after Seilacher, 1977a).

Material: 9, reservedly 10 specimens (TF UJ 7, 74-75, 224, 243, 672, 754(?), 1107, 1118, 1872).

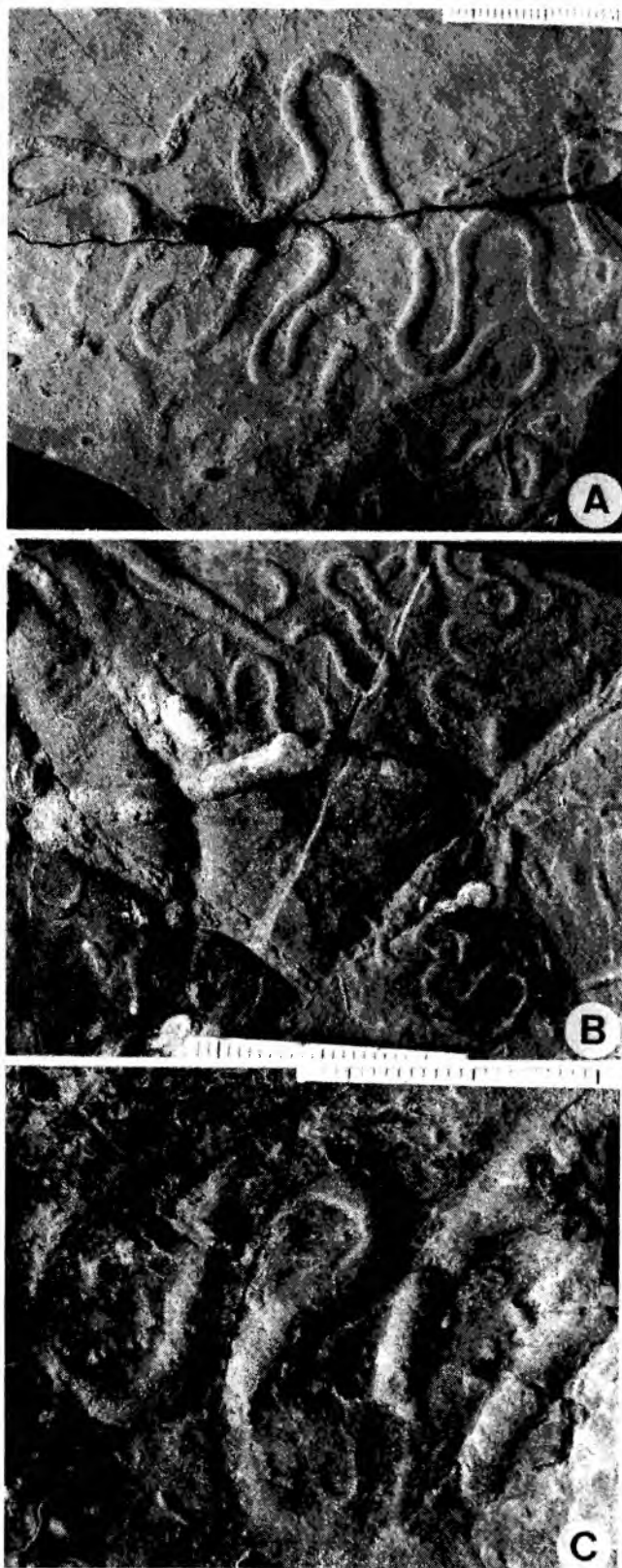


Fig. 75. *Cosmorhaphes lobata* Seilacher on soles of turbiditic sandstone beds (labelled as *Cosmorhaphes sinuosa*). A. UJ TF 74, Variegated Shale (Paleocene–Eocene), Lipnica Wielka. B. UJ TF 75, Inoceranian beds (Senonian–Paleocene), Szczepanowice. C. (?) UJ TF 754, full relief, Pólrzeczeki (part of label lost). Scales in mm

Remarks: Relatively thick *Cosmorhaphes* (Fig. 75C), preserved in full relief, is reservedly included in *C. lobata*.

Stratigraphic range: Senonian (Książkiewicz, 1977; Alexandrescu & Brustur, 1980) – Middle Eocene (Książkiewicz, 1977).

Cosmorhaphes carpathica nom. nov.

- * 1898 *Helminthoidea helminthopsioidea* Sacco – Paul, pl. 3, fig. 1.
- v 1958 *Cosmorhaphes* Książkiewicz, pl. 3, fig. 2.
- ? 1962 Pista de reptatie de verinij tip *Helminthoidea* – Dnbian & Dimian, pl. 7, fig. 4.
- v* 1970 *Cosmorhaphes helminthopsioidea* (Sacco) – Książkiewicz, 294, fig. 2c.
- 1975 *Cosmorhaphes* sp. – Hantzschel, W53, fig. 34.3.
- v 1977 *Cosmorhaphes helminthopsioidea* (Sacco) – Książkiewicz, 153, pl. 19, fig. 6 (*), text-fig. 33k-m.
- 1977a *Cosmorhaphes helminthopsioidea* (Sacco) – Seilacher, 299, fig. 3e (lapsus calami).

Origin of the name: From the Carpathians.

Diagnosis: First order meanders fairly dense; second order meanders of 2–3 times greater amplitude than wavelength, but suppressed for long stretches (after Seilacher, 1977a).

Material: 4 specimens (TF UJ 77 (lectotype), 249, 828–829).

Remarks: Książkiewicz (1977) created *C. helminthopsioidea* n. isp. and selected a specimen (Książkiewicz, 1958, pl. 3, fig. 2) for the holotype. He compared the holotype to the specimen illustrated by Paul (1898) and indicated as *Helminthoidea helminthopsioidea* Sacco. Seilacher (1977a) included Sacco's (1888) *Helminthoidea helminthopsioidea* and Książkiewicz holotype in *Cosmorhaphes helminthopsioidea* (Sacco). Sacco's specimen was treated by Książkiewicz (1977) as a separate ichnospecies of *Helminthoidea*, although it displays first- and second-order meanders typical of *Cosmorhaphes*. There are distinct differences between the specimen illustrated by Sacco (1888) and the Książkiewicz material. The first Sacco's specimen displays relatively shallow, fairly dense first-order meanders and irregular, very shallow second-order meanders. The Carpathian material displays second-order meanders which have 2–3 times greater amplitude than wave length. The long, winding stretches are a very characteristic feature of this material, which do not conform with other ichnospecies of *Cosmorhaphes*. For this reason the new name *Cosmorhaphes carpathica* is proposed for the Książkiewicz material. Sacco's specimen belongs also to *Cosmorhaphes* and its specific name should be retained.

Stratigraphic range: Senonian–Middle Eocene (Książkiewicz (1977).

Cosmorhaphes helminthopsioidea (Sacco 1888)

- * 1888 *Helminthoidea helminthopsioidea* Sacc. – Sacco, 32, pl. 2, fig. 7.
- v non 1898 *Helminthoidea helminthopsioidea* Sacco – Paul, pl. 3, fig. 1.
- 1969 *Cosmorhaphes* sp. – Webby, 83, pl. 10, figs 1–2.
- v non 1970 *Cosmorhaphes helminthopsioidea* (Sacco in Paul) – Książkiewicz, 294, fig. 2c.
- v non 1977 *Cosmorhaphes helminthopsioidea* (Sacco in Paul) Książkiewicz, 153, pl. 19, fig. 6, text-fig. 33k-m.
- v 1977 *Helminthoidea helminthopsioidea* Sacco – Książkiewicz, 163, pl. 20, fig. 3, pl. 21, fig. 9, text-fig. 36k-n.
- non 1977a *Cosmorhaphes helminthopsioidea* (Sacco) – Seilacher, 299,

- fig. 3e (lapsus calami).
 1980 *Cosmorhapse* sp. – Pickerill, fig. 4a.
 non 1986 *Cosmorhapse helmithopsidea* (Sacco) – Miller, fig. 2c (lapsus calami).
 1986 *Cosmorhapse changhuaensis* ichnosp. nov. – Yang, 153, pl. 1, fig. 6.
 1990 *Cosmorhapse* – McCann, fig. 4d.
 1991 *Cosmorhapse* aff. *sinuosa* (Azpeitia Moros) – Crimes & Crossley, 44, fig. 8c.
 1993 *Cosmorhapse sinuosa* Azpeitia Moros – McCann, 43, fig. 4D.
 non 1994 *Cosmorhapse helmithopsidea* (Sacco) – Löffler & Geyer, 495, fig. 3e (lapsus calami).

Emended diagnosis: *Cosmorhapse* with first order meanders relatively shallow, fairly dense; second order meanders irregular, very shallow.

Material: 5 specimens (TF UJ 2. 102, 339, 1013, 2030).

Remarks: The holotype described by Sacco (1888) derives from the Eocene Flysch del Grivò (G. Tunis, pers. comm., 1994). The Palaeozoic (Pickerill, 1980; Yang, 1986; McCann, 1990) specimens are distinctly larger, up to 10 mm in string diameter.

Stratigraphic range: Ordovician (McCann, 1993) – Lower Eocene (Sacco, 1888).

Cochlichnus Hitchcock 1858

Diagnosis: Regular, sinusoidal, horizontal trails and burrows resembling a compressed and stretched corkscrew. The overall width of an individual trace may change progressively (after modification from Gluszek (1995)).

Remarks: This ichnogenus was recently discussed by Filion & Pickerill (1990) and Gluszek (1995).

Cochlichnus anguineus Hitchcock 1858

Fig. 76

- v 1977 *Cochlichnus* aff. *anguineus* Hitchcock – Książkiewicz, 151, pl. 20, fig. 1, text-fig. 36 p-q.

Diagnosis: As for the ichnogenus.

Material: 4 specimens (UJ TF 1203, 1230, 1316, 1635).

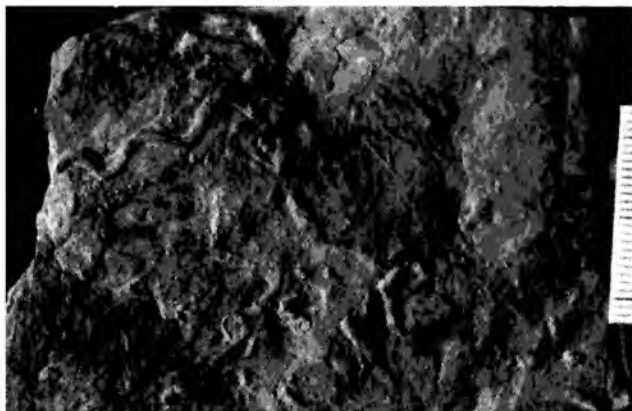


Fig. 76. *Cochlichnus anguineus* Hitchcock on sole of turbiditic sandstone bed. UJ TF 1316, Beloveža beds (Eocene), Sidzina. Scale in mm



Fig. 77. ?*Helicorhapse* isp. on sole of turbiditic sandstone bed. UJ TF 1378, Lipnica Wielka (part of label lost). Scale in mm

Helicorhapse Książkiewicz 1961

Diagnosis: Strings helicoidally twisted along a horizontal axis (after Książkiewicz, 1977).

Remarks: This ichnogenus is represented only by a few specimens, which makes understanding of its affinity to other ichnogenera difficult. *Helicolithus* Azpeitia Moros displays meanders and changing of the twisting direction at the turning points of the meanders. These features are enough for the ichnogenic separation.

One specimen (Fig. 77) is a short, helicoidally twisted hypichnial trace fossil situated between two short strings. It probably belongs to *Helicorhapse*.

Helicorhapse tortilis Książkiewicz 1970

Fig. 78

- ? 1915 Unnamed – Hogbom, pl. 2, fig. 1.
 1961 *Helicorhapse* (n.f.) – Książkiewicz, 885, pl. 2, fig. 3.
 * 1970 *Helicorhapse tortilis* ichnosp. n. – Książkiewicz, 286, fig. 1t.
 1975 *Helicorhapse tortilis* Książkiewicz – Häntzschel, W70, fig. 43.4.
 1977 *Helicorhapse tortilis* Książkiewicz – Książkiewicz, 116, pl. 11, fig. 10.
 non 1981 *Helicorhapse* – Tanaka & Sumi, pl. 6, fig. 1.
 non 1989 *Helicorhapse meandriformis* sp. n. – Plička & Kokolusová, 113, text-fig. 2, pl. 64, fig. 2.
 1995 *Helicorhapse tortilis* Książkiewicz – Crimes & McCall, 236, fig. 3a.

Diagnosis: As for the ichnogenus.

Material: 2 specimens (UJ TF 277 (holotype), 499).



Fig. 78. *Helicorhaphé tortilis* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 277, the holotype. Beloveža beds (Eocene), Lipnica Mała. Scale in mm

Remarks: Müller (1971) compared *Helicorhaphé* Książkiewicz and *Helicodromites* Berger to recent helicoidal traces of insects observed in coastal sand environment. Crimes & McCall (1995) described a trace fossil compared to *Helicorhaphé tortilis* Książkiewicz from the Miocene flysch of Iran, however it is much larger.

Helicorhaphé Książkiewicz (1961) was defined as helicoidally twisted string according to helicoidal axis.

Helicolithus Azpeitia Moros 1933

- 1933 *Helicolithus sampelayoi* Azpeitia, n. sp. – Azpeitia Moros, 48, pl. 4, fig. 11, pl. 13, fig. 24A.
- non 1933 *Helicolithus fabregae* Azpeitia, n. sp. – Azpeitia Moros, 52, pl. 3, fig. 10, pl. 10, fig. 21A [= *Belorhaphé*].
- ? 1986 *Helicolithus sampelayoi* Azpeitia Moros – Yang, 154, pl. 2, fig. 4.
- ? 1988 *Helicolithus sampelayoi* Azpeitia Moros – Yang, 6, pl. 2, fig. 3.
- ? 1991 *Helicolithus* ichnosp. – Crimes & Crossley, 47, fig. 8k.
- non 1992 *Helicolithus tortuosus* (Książkiewicz) – Yang & Hu, 389, pl. 3, fig. 5.

Diagnosis: Small, horizontal, meandering trace fossils with, horizontal, second order helicoidal turns. Changes of screw direction at every turn of first order meanders (modified after Seilacher, 1977a).

Remarks: It is possible that *Paleomeandron transversum* Seilacher is a helicoidal trace fossil that can be compared with *Helicolithus*. However, this ichnotaxon is known only from one drawing (Seilacher, 1977a, fig. 7c) and its evalu-

ation is problematic.

Helicolithus sampelayoi Azpeitia Moros 1933

Fig. 79

- * 1933 *Helicolithus sampelayoi* Azpeitia, n. sp. – Azpeitia Moros, 48, pl. 4, fig. 11, pl. 13, fig. 24A.
- 1954 *Helicolithus sampelayoi* Azpeitia – Gómez de Llarena, pl. 45, fig. 1.
- 1954 *Helicolithus sampelayoi* Azpeitia – Seilacher, fig. 2.15.
- 1955 *Helicolithus sampelayoi* Azpeitia – Seilacher, fig. 5.67.
- 1959 *Helicolithus sampelayoi* Azpeitia – Seilacher, tab. 1, fig. 12.
- 1961 *Helicolithus sampelayoi* Azpeitia – Książkiewicz, 885, pl. 2, fig. 2.
- 1962 Pista de reptatie de tip *Belorapha* – Dimin & Dimin, pl. 7, fig. 3 (lapsus calami).
- 1967 *Helicolithus sampelayoi* Azpeitia – Macsotay, 31, figs. 7, 14.
- 1968 *Helicolithus sampelayoi* Azpeitia – Książkiewicz, pl. 3, fig. 2.
- 1970 *Helicolithus sampelayoi* Azpeitia – Książkiewicz, 300, fig. 3i.
- 1975 *Helicolithus sampelayoi* Azpeitia Moros – Häntzschel, W67, fig. 42.2a-c.
- v 1977 *Helicolithus sampelayoi* Azpeitia – Książkiewicz, 157, pl. 23, fig. 4.
- 1977a *Helicolithus* sp. – Crimes, pl. 6, fig. c.
- 1977b *Helicolithus* – Crimes, 593, pl. 3, figs. 1-2.
- partim 1977b *Paleomeandron* [...] and *Belorhaphé* – Crimes, 593, 594, pl. 1, fig. 1.
- 1978 *Helicolithus* – Kern, 251, fig. 9H.
- ? 1978 *Helicolithus sampelayoi* Azpeitia – Radwański, 58, pl. 9, fig. 2.
- 1982 *Helicolithus* – Scholle & Spearing, fig. 117.
- ? 1986 *Helicolithus sampelayoi* Azpeitia Moros – Yang, 154, pl.



Fig. 79. *Helicolithus sampelayoi* Azpeitia-Moros on sole of turbiditic sandstone bed. UJ TF 226. Beloveža beds (Eocene), Lipnica Mała. Scale in mm



Fig. 80. *Helminthorhapse flexuosa* Uchman on sole of turbiditic sandstone bed. UJ TF 1362, Krosno beds (Oligocene), Dźwiniacz Dolny-Królów stream (labelled *Helminthoida crassa*). Scale in mm

2, fig. 4.

? 1987 *Helicolithus* cf. *sampelayoi* Azpeitia – Alexandrescu & Brustur, 12, pl. 5, fig. 2.

? 1988 *Helicolithus sampelayoi* Azpeitia Moros – Yang, 6, pl. 2, fig. 3.

1992 *Helicolithus sampelayoi* – Leszczyński, pl. 2, fig. 2.

Diagnosis: *Helicolithus* with simple, short, regular helicoidal undulations (modified after Seilacher, 1977a).

Material: 20 specimens (TF UJ 20, 22-23, 26-31, 71, 226-227, 798, 847, 894, 920, 1131, 1856, 2595, 2686).

Remarks: Stratigraphic range: Senonian-Oligocene (Książkiewicz, 1977). It is difficult to assess the material described by Yang (1986, 1988) from the Permian flysch. It may belong to *Helicolithus*.

Helicolithus tortuosus (Książkiewicz 1970)

1959 Unnamed – Seilacher, tab. 1, fig. 13.

* v 1970 *Cosmorhapse* (?) *tortuosa* ichnosp. n. – Książkiewicz, 294, pl. 3c.

v 1977 *Cosmorhapse* (?) *tortuosa* Książkiewicz – Książkiewicz, 155, pl. 19, fig. 9.

1977a *Helicolithus tortuosus* (Książkiewicz) – Seilacher, 306, fig. 6d.

1977b *Cosmorhapse?* *tortuosa* Książkiewicz – Crimes, 601, pl. 4, fig. 3, pl. 5, figs. 1-2.

partim 1977b *Belorhapse* [...] *Protopalaeodictyon* [...] *Paleodictyon* – Crimes, pl. 1, fig. 2.

partim 1977b *Paleodictyon* [...] *Paleomeandron* – Crimes, pl. 2, fig. 1.

1980 *Helicolithus tortuosus* (Książkiewicz) – D'Alessandro, 373, pl. 36, fig. 1, pl. 41, fig. 1.

non 1992 *Helicolithus tortuosus* (Książkiewicz) – Yang & Hu, 389,

pl. 3, fig. 5.

v 1993 *Helicolithus tortuosus* (Książkiewicz) – Tunis & Uchman, 91, fig. 8B.

v 1996a *Helicolithus tortuosus* (Książkiewicz) – Tunis & Uchman, 181, fig. 9H.

Diagnosis: *Helicolithus* with long, sigmoidal helicoidal turns (modified after Seilacher, 1977a).

Material: This ichnospecies is not present in the Książkiewicz collection.

Remarks: Stratigraphic range: Senonian (Książkiewicz, 1977) – Miocene (D'Alessandro, 1980).

Helminthorhapse Seilacher 1977a

Diagnosis: Non-branching trace fossil of small string diameter with only one order of smooth systematic meanders of very high amplitude, usually preserved as hypichnial semi-relief strings (modified after Seilacher, 1977a; Uchman, 1995).

Remarks: The separation of *Helminthoida* and *Helminthorhapse* (Seilacher, 1977a) was discussed by Uchman (1995), who included *Helminthoida* Schafhäütl within *Nereites* MacLeay.

Regularity of meanders, distance between meanders, and lack or presence of a bulge in the curved parts of meanders are diagnostic features at the ichnospecies level (Seilacher, 1977a). However, these features have not been considered by several authors. Besides the ichnotaxa described by Seilacher (1977a), *Helminthorhapse miocenica* (Sacco), re-defined by Książkiewicz (1977) as *Helminthoida*, appears to be a useful ichnotaxon.

Helminthorhapse flexuosa Uchman 1995

Fig. 80

non 1970 *Helminthoida*(?) aff. *molassica* Heer – Książkiewicz, 298, fig. 2j.

v 1970 *Helminthoida crassa* – Książkiewicz, 296, fig. 2d-f.

v 1977 *Helminthoida crassa* Schafhäütl – Książkiewicz, 159, pl. 21, figs. 3, 5, text-fig. 34b-c, f, h, k-l, m-n, q-r, m [non pl. 21, figs. 4, 6-8, text-fig. 34d-e, g, i, o-p, s = *H. japonica*, non text-fig. 21j = *Helminthorhapse* isp.].

For synonymy see Uchman (1995).

Diagnosis: *Helminthorhapse* with relatively deep, commonly irregular and poorly guided meanders lacking distinct bulges in the curved portions.

Material: 7 specimens (TF UJ 42, 99, 103, 238, 722, 1361-1362).

Description: As in Książkiewicz (1977), with the following additions: convex hyporeliefs consisting of a string that follows narrow and high amplitude regular meanders. Bulges in the turning portion are very rare and are poorly expressed.

Remarks: In contrast to Seilacher's (1977a) diagnosis of *H. crassa* (= *H. flexuosa*), the meanders of the described material are relatively tightly spaced. However, distance between meanders is a variable feature, also in the holotype (see also Leszczyński & Seilacher, 1991). Thus, it is not regarded as a diagnostic feature at the species level.

Helminthorhapse japonica (Tanaka 1970)

Fig. 81

partim 1977 *Helminthoida crassa* Schafhäütl – Książkiewicz, 159, pl. 21, figs. 4, 6-8, text-fig. 34d-e, g, i, o-p, s [non pl. 21, figs. 3, 5, text-fig. 34b-c, f, h, k-l, m-n, q-r = *H. flexuosa*, non text-fig. 21j = *Helminthorhapse* isp.].

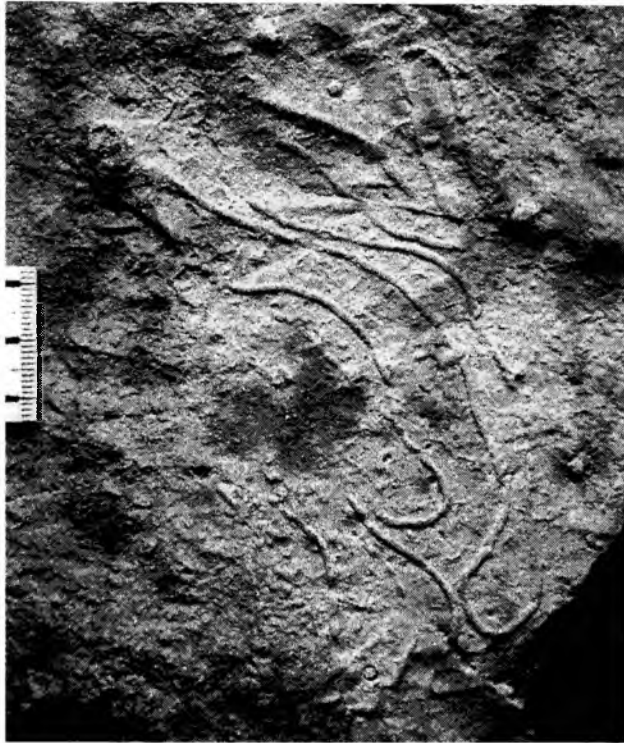


Fig. 81. *Helminthorhapha japonica* (Tanaka) on sole of turbiditic sandstone bed. UJ TF 104, Ciężkowice Sandstone (Eocene). Znamirowice (labelled as *Helminthoidea crassa tenuis*). Scale in mm

For synonymy see Uchman (1995).

Diagnosis: Meanders of very high amplitude and densely guided, at least part of the meanders with rounded and often bulging turns (modified after Seilacher, 1977a).

Material: 10 specimens (TF UJ 38, 49, 103-104, 750, 828, 1244, 1361, 1495, 1812).

Description: As in Książkiewicz (1977), with the following additions: convex hyporeliefs consisting of a string forming narrow and high regular meanders and showing characteristic bulges in the turning portions of meanders.

Helminthorhapha miocenica (Sacco 1886)

- * 1886 *Helminthoidea miocenica* Sacc. – Sacco, 310 (16), fig. 2.
- v 1977 *Helminthoidea miocenica* Sacco – Książkiewicz, 160, pl. 21, figs. 10-11, text-fig. 36a-j.

Diagnosis: Meanders of relatively low amplitude and widely guided, with rounded turns.

Material: 7 species (TF UJ 652, 714, 1022, 1127, 1133, 1174, 1403).

Helminthopsis Heer 1877

Diagnosis: Simple, unbranched, clongate, cylindrical tube with curves, windings, or irregular open meanders (after Wetzel & Bromley, 1996).

Remarks: Examination of the type material of *Helminthopsis* revealed that the type species, *Helminthopsis magna* (Heer, 1877, pl. 47, fig. 1-2), is in fact *Taphrhelminthopsis* Sacco [= *Scolicia strozzii* (Savi & Meneghini) in this paper] (Książkiewicz, 1977; see also Seilacher, 1977a, p. 297; Han & Pickerill, 1995). Moreover, *Helminthopsis labyrinthica*

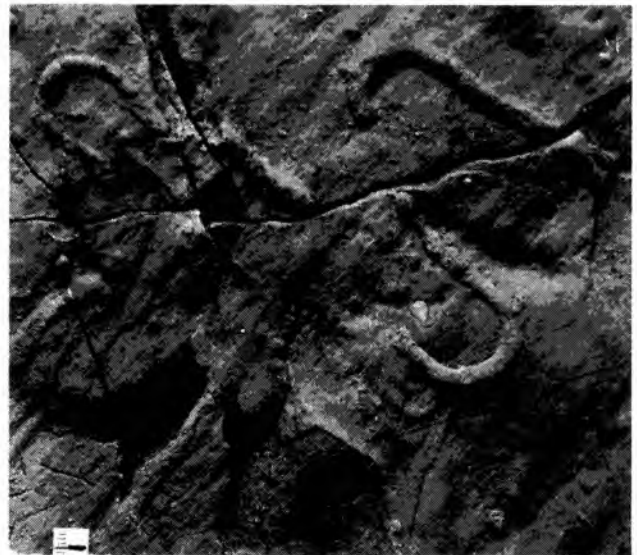


Fig. 82. *Helminthopsis abeli* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 255, Inoceranian beds (Senonian–Paleocene), Łodzinka. Scale in mm

Heer (1877, pl. 47, figs. 3-4), the species-name bearing-type of *Helminthopsis labyrinthica* Heer in Maillard, is identical to *Spirocormorhapha* Seilacher (Wetzel & Bromley, 1996). In order to retain *Helminthopsis* as ichnogenus, Wetzel & Bromley selected one of specimens from

Heer's collection (not previously illustrated) determined as *Helminthopsis hieroglyphica* as the type ichnospecies of *Helminthopsis*.

Recent review of ichnospecies of *Helminthopsis* was provided by Han & Pickerill (1995) and Wetzel & Bromley (1996).

Helminthopsis is a eurybathic facies-crossing trace fossil, common in flysch deposits, and produced probably by polychaetes or priapulids (Książkiewicz, 1977; Fillion & Pickerill, 1990). It occurs from the Cambrian (Crimes, 1987) to the Recent (Swinbanks & Murray, 1981; Wetzel, 1983a, b).

Helminthopsis abeli Książkiewicz 1977

Fig. 82

- ? 1935 Kriechspur – Abel, fig. 261B.
- v partim 1977 *Helminthopsis abeli* n. ichnosp. – Książkiewicz, 117, pl. 12, fig. 5 (*), text-fig. 21a-b, f [?non text-fig. 21c-d (= *Cosmorhapha* isp.), ?non text-fig. 21e (= *Thalassinoides* isp.), non text-fig. 21h (also Książkiewicz, 1970, p. 299, fig. 3a (= *Helminthopsis* isp.))].
- v partim 1977 *Helminthopsis tenuis* Książkiewicz – Książkiewicz, 120, text-fig. 21q, t-x [non pl. 12, fig. 1, text-fig. 21p, r-s].
- v partim 1977 *Helminthopsis hieroglyphica* Heer – Książkiewicz, 119, text-fig. 21k-l [non pl. 12, fig. 3 = *Gordia marina*, non text-fig. 21m-p].

Emended diagnosis: *Helminthopsis* that commonly displays deep and bulged or horseshoe meanders.

Material: 11 specimens (UJ TF 33, 100, 233, 252, 255, 1290, 1302, 1321 (lectotype), 1615, 1631, 1661).

Remarks: Książkiewicz (1977) designated the specimen illustrated by Abel (1935, fig. 261B) as the lectotype of *H.*

abeli. In the same year, Seilacher (1977a) included Abel's specimen in *Cosmorhapse lobata* Seilacher. Abel's specimen is a deeply meandering hypichnial trace fossil. Its course cannot be traced along sufficient distance for unambiguous assessment of the trace fossil taxonomy because the specimen is incomplete. In this state it is impossible to assess whether this is a *Helminthopsis* or *Cosmorhapse*. Nevertheless, the Książkiewicz (1977, pl. 12, fig. 5) lectotype of *H. abeli* belongs to *Helminthopsis*.

Han & Pickerill (1995) concluded that separation of *H. abeli* and *H. tenuis* is difficult and they regarded them as synonyms. Książkiewicz (1977) also noted the problem, but argued that the style of winding is different in these ichnotaxa. Moreover, he used size as the diagnostic criterion. However, size alone cannot be accepted as a taxobase (also Han & Pickerill, 1995). Thus, the style of winding should be regarded as the only diagnostic feature for these ichnotaxa. This prompts an emendation of the diagnosis. Han & Pickerill (1995) emended the diagnosis of *H. abeli* and formulated it as: "*Helminthopsis* that is loosely winding or meandering. Meanders irregular and variable in shape, mostly deep, but also shallow, with bell-shaped and, or, horseshoe-shaped segments, but no straight segments or loops. The axes of the meanders are not parallel. Diameter is variable and generally constant within a single specimen." Nevertheless, contrary to the diagnosis, the co-type of *H. abeli* displays straight segments (Książkiewicz, 1977, pl. 12, fig. 5). Most specimens of *H. tenuis*, including the holotype, display repeated, wide, shallow meanders and deeper narrow but obtuse meanders. On the other hand, *H. abeli* commonly displays relatively deep, bulged (horseshoe) meanders. In the light of this differentiation and neglecting the size criteria, some of the Książkiewicz specimens ascribed to *H. tenuis* and *H. hieroglyphica* should be placed in synonymy with *H. abeli*. Nevertheless, these two ichnospecies are eligible for separation and should be retained. The same conclusion is presented by Wetzel & Bromley (1996).

Wetzel & Bromley (1996) included *H. abeli* from Książkiewicz pl. 12, fig. 5 and text-fig. 21a in *Cosmorhapse helminthopsoidea* (Sacco). However, in the next pages they regarded the specimen from pl. 12, fig. 5 as the co-type of *H. abeli*. Possible removal of these specimens from *Helminthopsis* cannot be accepted. The specimen in pl. 12, fig. 5 displays no first-order meanders and therefore cannot be included in *Cosmorhapse*. Moreover, it displays deep meanders, which are not present in *C. helminthopsoidea* (described also in this paper). The specimen in text-fig. 21a is too short to allow assessment as to whether it has first-order meanders or not, and therefore it is retained in *Helminthopsis*.

Some of the Carpathian specimens ascribed by Książkiewicz to *H. abeli* belong probably to *?Cosmorhapse* isp., *?Thalassinoides* isp., and to *Helminthopsis* isp. (see the synonymy list).

Helminthopsis tenuis Książkiewicz 1968

Fig. 83

- *v 1968 *Helminthopsis tenuis* n. "sp." - Książkiewicz, 7, pl. 4, fig. 1 (also *Helminthopsis tenuis* Książkiewicz - Książkiewicz, 1970, 299, fig. 3b).

partim 1977 *Helminthopsis tenuis* Książkiewicz - Książkiewicz, 120, pl. 12, fig. 1, text-fig. 21r-s [non text-fig. 21q, t-x (= *H. abeli*)].

Emended diagnosis: *Helminthopsis* with co-occurring wide, shallow meanders and deeper, narrow, but obtuse meanders.

Material: 3 specimens (UJ TF 1465 (holotype), 1631, 1661).

Remarks: The differences between *H. tenuis* and *H. abeli* are explained under remarks for *H. abeli*.

"*Helminthopsis granulata*" Książkiewicz 1968

Fig. 84

- ? 1850 *Platyrhynchus problematicus* - Glocker, pl. 73, fig. 2.
* 1968 *Helminthopsis granulata* n. "sp." - Książkiewicz, 7, 15, pl. 4, fig. 2, text-fig. 4 (also Książkiewicz, 1970, p. 300, fig. 3c, Książkiewicz, 1977, 121, pl. 12, fig. 6).

Diagnosis: Hypichnial string at least partially covered with warts and ridges arranged parallel to the axis of the trace fossil (modified after Książkiewicz, 1977).

Material: 5 specimens (UJ TF 224 (the holotype, 1373-1374, 2574, 2578).

Remarks: Wetzel & Bromley (1996) suggested that ichnospecies of *Helminthopsis* should be based solely on geometry of meanders. Therefore, they concluded that *H. granulata*, which is distinguished on the basis of surface character, is not a useful ichnospecies. They stressed that the surface ornamentation strongly depends on substrate properties and suggested that *H. granulata* might be stuffed with pellets, and concluded that *H. granulata* should be ascribed to



Fig. 83. 83. *Helminthopsis tenuis* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 1661, Beloveža beds (Eocene), Sidzina-Mała Głaza. Scale in mm

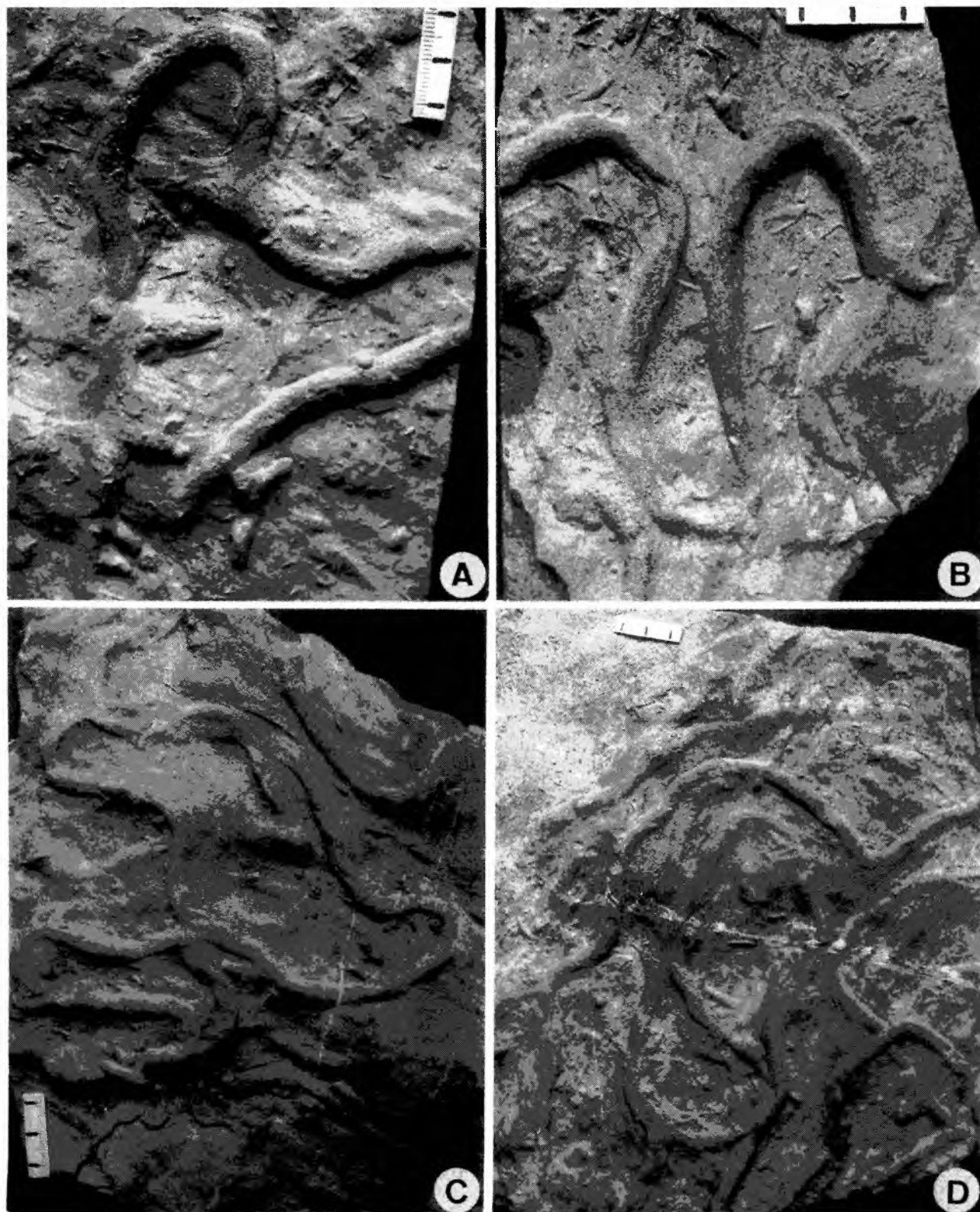


Fig. 84. "*Helminthopsis granulata*" Książkiewicz on soles of turbiditic sandstone beds. A. UJ TF 1373 (label lost). B. UJ TF 2578a, Cieszyn Limestone (Beriassian), Golezów quarry (labelled *Helminthopsis* aff. *hieroglyphica*). C. UJ TF 1374 (label lost). D. UJ TF 2574 (label lost). Scales in mm

other ichnospecies of *Helminthopsis* or regarded as *Alcyonidiopsis*.

Surface ornamentation of "*H. granulata*" cannot be accidental. Their filling is massive. Therefore, relation of *H. granulata* to *Alcyonidiopsis* is excluded. However, transition to smooth forms is very common. The smooth forms were labelled as *Helminthopsis* aff. *hieroglyphica*. Generally, the pattern of the meandering is similar to *H. abeli*, but, the trace fossils intersect at different levels, and locally display branchings. However, the nature of the branchings needs further study of material which should be collected at the type locality. The branchings suggest some similarity to *Thalassinoides*. Thus, the ichnotaxonomic status of the discussed material remains uncertain. For this reason, the ichnotaxonomic name is retained, but in quotation marks.

"*H. granulata*" is represented by a few specimens from the Lower Cretaceous flysch of the Silesian Nappe.

Problem of *Helminthopsis hieroglyphica*

Książkiewicz used the photograph of Heer's specimen in the publication of Maillard (1887, pl. 2, fig. 4) as the type of *Helminthopsis hieroglyphica*. The ichnogenetic and ichnospecific names were already used by Maillard (pl. 1, fig. 2) for another Heer specimen, which was excluded by Książkiewicz (1977, p. 119) from *H. hieroglyphica*. This specimen is similar to the other specimens originally described by Heer (1877), under the same name, from the Eocene Ganei Slate in the Swiss Alps. These belong to *Spirocosmorhaphé* Seilacher (A. Wetzel & R.G. Bromley, 1996, comm., and personal observations of the Heer's specimens and specimens from Heer's type locality by A. Wetzel & A. Uchman). Incomplete *Spirocosmorhaphé* can display features of *Helminthopsis*. The Carpathian material can be easily ascribed to *H. tenuis* and *H. abeli* (see their synonymy lists). Therefore, *Helminthopsis hieroglyphica* Heer in Maillard is not recommended for further use, and Heer's material can be included in *Spirocosmorhaphé* Seilacher (cf. Wetzel & Bromley, 1996). Nevertheless, for retaining *Helminthopsis*, Wetzel & Bromley selected one of Heer's specimens (not illustrated), determined by Heer as *Helminthopsis hieroglyphica*, as the type ichnospecies of *Helminthopsis*. The name should be used only in the sense outlined by Wetzel & Bromley (1996) as in the case described below.

Helminthopsis hieroglyphica Wetzel & Bromley 1996

Fig. 85

v partim 1977 *Helminthopsis hieroglyphica* (Heer) Książkiewicz, 119, text-fig. 21i, n-o [non pl. 12, fig. 3 = *Gordia marina* text-fig. 21 k-l = *H. abeli*].

* 1996 *Helminthopsis hieroglyphica* isp. nov. - Wetzel & Bromley, 15, text-figs. 5, 7.

Diagnosis: Strings 5–10 mm in diameter with irregular windings of low amplitude; the windings are composed of low-angle kinks and straight sections giving the trace a box-shaped fold appearance.

Material: 4 specimens (UJ TF 354, 920, 1320, 1587).

Remarks: Wetzel & Bromley (1996) included *Helminthopsis hieroglyphica* (Heer) from the Książkiewicz (1977) text-fig. 21k-l and pl. 12, fig. 3 in *Helminthopsis hieroglyphica*



Fig. 85. *Helminthopsis hieroglyphica* Wetzel & Bromley on sole of turbiditic sandstone bed. UJ TF 354, Ropianka beds (Senonian–Paleocene), Poręba Wielka (labelled as *Helminthopsis* sp.). Scale in mm

Wetzel & Bromley. However, the specimens from text-fig. 21k-l display deep meanders and should be included in *H. abeli* as in this paper, and the specimen from pl. 12, fig. 3 displays crossing of string and should be included in *Gordia marina* Emmons (Fig. 73A).

Helminthopsis irregularis (Schafhäütl 1851)

Remarks: Many erroneous opinions were expressed by different authors concerning *Helminthopsis irregularis* (Schafhäütl, 1851) (see Han & Pickerill, 1995). Irrespective of the opinions based only on the original drawing, the holotype of this ichnotaxon, rediscovered in München, displays features of *Nereites* and was described under this ichnogenus (Uchman, 1995). Książkiewicz (1977) ascribed this ichnotaxon erroneously to *Helminthopsis*. His Carpathian material represents irregular forms of *Helminthoidea*, which, in turn, is included within *Nereites irregularis* (Schafhäütl) (Uchman, 1995) and are placed under this name in this paper.

SPIRAL STRUCTURES

"*Spirophycus*" Häntzschel 1962

Ichnospecies reservedly included in and excluded from "*Spirophycus*" Häntzschel:

partim 1955 *Spirorhaphé* - Lessertisseur, pl. 74, fig. 6 [non pl. 74, fig. 4 = *Spirorhaphé*].

1961 Unnamed - Logvinenko, fig. 8.

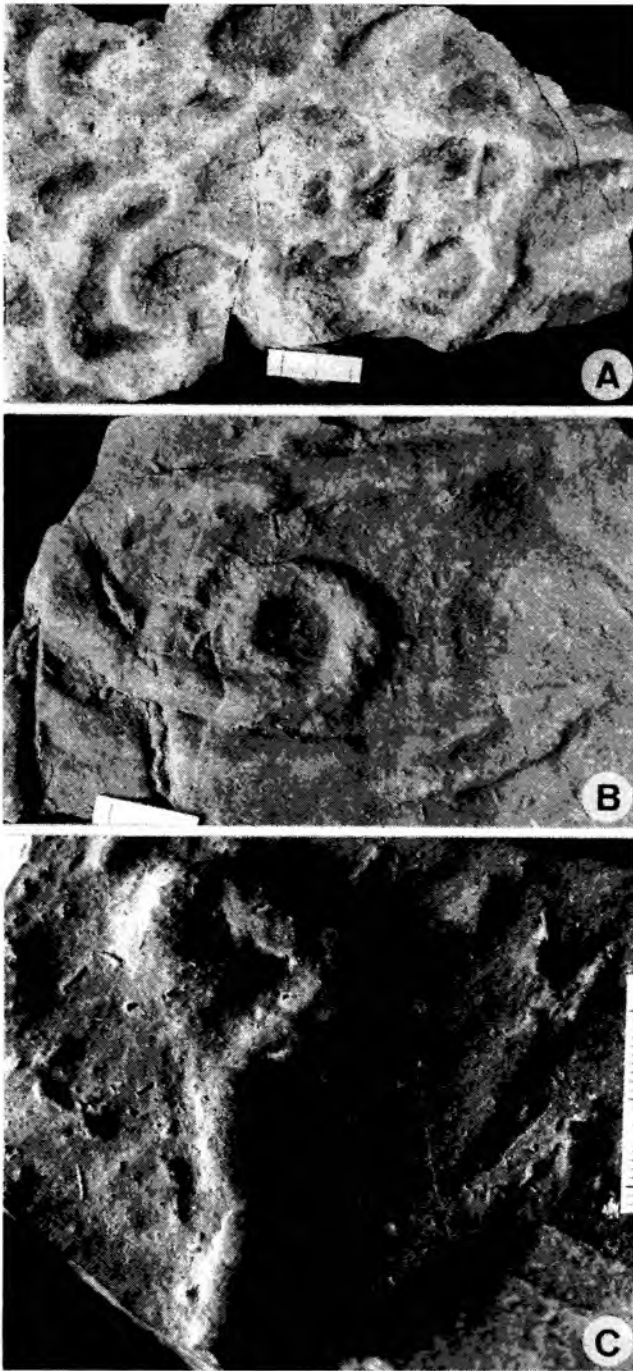


Fig. 86. “*Spirophyucus*” *bicornis* (Heer) on soles of turbiditic sandstone beds. **A.** UJ TF 590, Hieroglyphic beds (Eocene), Grzechynia (labelled as *Spirophyucus convolutus*). **B.** UJ TF 1024 (labelled as *Spirophyucus caprinus*, part of label lost). **C.** UJ TF 796, Hieroglyphic beds (Eocene), Tokarnia (labelled as *Spirophyucus caprinus*). Scales in mm

- 1971a *Spirophyucus bicornis* (Heer) – Chamberlain, 231 pl. 32, fig. 1.
 1971b *Spirophyucus* – Chamberlain, fig. 6.33.
 1973 *Spirophyucus bicornis* (Heer) – Chamberlain & Clark, 680, pl. 2, fig. 1, text-fig. 5.
 1981 *Spirophyucus* – Tanaka & Sumi, pl. 4, fig. 2.
 1987 *Spirophyucus minimus* n. ichnosp. – Plička, 168, pl. 44, fig. 2, text-fig. 26.
 ?non 1987 *Spirophyucus* (?) *sinesis* ichnosp. n. Yang et Hu – Yang et

- al.*, 3, pl., fig. 9.
 ?non 1991 *Spirophyucus* – Bruton & Link, fig. 7e, g.
 1991 *Spirophyucus* ichnosp. – Crimes & Crossley, 43, fig. 7c-f.
 1993 *Spirophyucus bicornis* (Heer) – McCann, 49, fig. 61.
 ?non 1993a *Spirophyucus* cf. *bicornis* (Heer) – Mikuláš, 174, pl. 2, fig. 1.
 1996 *Spirophyucus bicornis* (Heer) – Paczeńska, 61, pl. 18, fig. 5.
 v 1997 *Spirophyucus bicornis* (Heer) – Wetzel & Uchman, 150, fig. 4F.

Emended diagnosis: Horizontal strings bent at one end in a spiral.

Remarks: Recently, “*Spirophyucus*” has been regarded as a preservational variant of *Nereites* MacLeay (A. Wetzel, pers. comm.). This requires further study. Aware of this problem, I tentatively retain the former ichnogenic name, but in quotation marks.

“*Spirophyucus*” *bicornis* (Heer 1877)

Fig. 86

- ? partim? 1868 *Keckia ambigua* n. – Eichwald, 11, pl. 4, fig. 13 (non. fig. 14).
 1869 *Münsteria* – Ooster, 29, pl. 8, fig. 2.
 1877 *Münsteria bicornis* Hr. – Heer, 165, pl. 66, figs. 1b, 2.
 non 1877 *Münsteria caprina* Hr. – Heer, 163, pl. 65, fig. 1.
 1885 *Ceratophycus bicornis* Schimper – Fugger & Kastner, 73 [no illustration].
 ? 1885 *Ceratophycus caprinus* Schimper – Fugger & Kastner, 73 [no illustration].
 1888 ?*Münsteria bicornis* Heer – Sacco, 166 (21), pl. 2, figs. 4, 12.
 1898 *Ceratophycus* Sch. – Paul, pl. 5, fig. 1.
 1900 *Ceratophycus* – Toulou, fig. 161.
 1919 Unnamed – Kindelan, fig. 20.
 partim 1933 *Münsteria bicornis* Heer – Azpeitia Moros, 54, pl. 16, figs. 29-30 (non pl. 17, fig. 31).
 1955 *Ceratophycus* – Seilacher, fig. 5.74.
 v 1958 Hieroglif organiczny – Książkiewicz, pl. 2, fig. 2.
 1959 Unnamed – Seilacher, tab. 2, fig. 2.
 v 1960 *Ceratophycus* Schimper – Książkiewicz, pl. 2, fig. 6.
 1962 *Ceratophycus* – Seilacher, fig. 1.
 1967 *Spirophyucus* cf. *Spirophyucus bicornis* (Heer) – Macsotay, 37, fig. 23.
 ? non 1971a *Spirophyucus bicornis* (Heer) – Chamberlain, 231 pl. 32, fig. 1.
 non 1973 *Spirophyucus bicornis* (Heer) – Chamberlain & Clark, 680, pl. 2, fig. 1, text-fig. 5.
 v 1977 *Spirophyucus caprinus* (Heer) – Książkiewicz, 148, pl. 18, figs. 4-5, text-fig. 31a-o.
 v 1977 *Spirophyucus caprinus* (Heer) – Książkiewicz, 148, pl. 18, figs. 6, 7, text-fig. 31 p. q, r.
 1980 *Spirophyucus* – Kern, fig. 3C, G.
 1981 *Spirophyucus caprinus* (Heer) – Crimes et al., 972, fig. 10e.
 1982 *Spirophyucus bicornis* (Heer) – Alexandrescu & Brustur, 37, pl. 2, figs. 1-2, pl. 3, fig. 3.
 1987 *Spirophyucus bicornis* (Heer) – Micu et al., 82, pl. 1, fig. 2.
 1988 *Spirophyucus bicornis* (Heer) – McCann & Pickerill, 341, fig. 4.11.
 1988 *Spirophyucus qinhatensis* ichnosp. nov. – Yang, 10, pl. 1, fig. 11.
 1991a *Spirophyucus caprinus* – Leszczyński, fig. 12.
 ? 1993 *Spirophyucus* cf. *caprinus* (Heer) – Miller, 23, fig. 5M.
 v 1993 *Spirophyucus bicornis* (Heer) – Tunis & Uchman, 88, not figured.
 1995 *Spirophyucus bicornis* (Heer) – Crimes & McCall, 246, fig. 7B.
 ? non 1996 *Spirophyucus bicornis* (Heer) – Paczeńska, 61, pl. 18, fig. 5.
 v 1997 *Spirophyucus bicornis* (Heer) – Wetzel & Uchman, 150, fig. 4F.

Diagnosis: Thick “*Spirophyucus*” with one or two spiral whorls.

Material: 19 specimens (TF UJ 81, 193-194, 203-205, 208, 555,

557, 565, 570, 575, 590, 796, 932, 1024, 2004, 2046, 2715).

Remarks: Seilacher (1967a, fig. 4) drew internal meniscate structure and a knobby exterior for “*Spirophycus*”. This confirms the idea of its affinity to *Nereites*. However, I have not found a specimen with internal meniscate structure, all of them being structurless semi-reliefs. The knobby exterior is the main feature of *S. caprinus*. This feature seems to be strongly influenced by preservation and therefore this ichnospecies is included in *Spirophycus bicornis*.

S. bicornis occurs from the Aptian (Alexandrescu & Brustur, 1980) to the Upper Eocene (Książkiewicz, 1977).

“*Spirophycus*” *involutissimus* (Sacco 1888)

Fig. 87

- 1858 *Cylindrites convolutus* F.O. - Fischer-Ooster, 58, pl. 15, fig. 1.
 ? 1885 *Cylindrites convolutus* F.O. - Fugger & Kastner, 71 [no illustrated].
 1888 *Münsteria involutissima* Sacc. - Sacco, 168 (20), pl. 2, fig. 14.
 1895 *Ceratophycus* - Fuchs, pl. 6, fig. 6.
 partim 1933 *Münsteria bicornis* Heer - Azpeitia Moros, 54, pl. 17, fig. 31 [non pl. 16, figs. 29-30].
 1935 *Spiralgänge* - Abel, fig. 262.
 partim 1955 *Spirorhaphé* - Lessertisseur, pl. 74, fig. 6 [non pl. 74, fig. 4 = *Spirorhaphé*].
 1969 *Spirophycus* - Simpson, 42, figs. 3-4.
 1970 *Spirophycus* aff. *involutissimus* (Sacco) - Książkiewicz, 305, fig. 5d.
 v 1977 *Spirophycus involutissimus* (Sacco) - Książkiewicz, 149, pl. 18, fig. 8, text-fig. 31s-w.
 v 1993 *Spirophycus involutissimus* (Sacco) - Tunis & Uchman, 88, fig. 7C.
 1995 *Spirophycus involutissimus* (Sacco) - Crimes & McCall, 248, fig. 7C.

Diagnosis: Thin “*Spirophycus*” with two or more whorls.

Material: 3 specimens (UJ TF 196, 596, 2047).

Remarks: This ichnospecies occurs in flysch deposits from Senonian to the Middle Eocene (Książkiewicz, 1977).

Spirorhaphé Fuchs 1895

Diagnosis: Thin, spirally coiled trace fossil, supposedly multi-floored (modified after Seilacher, 1977a).

Remarks: Ichnotaxonomy of *Spirorhaphé* Fuchs was revised by Seilacher (1977a), who distinguished three ichnospecies: *S. involuta* (De Stefani), *S. azteca* Seilacher, and *S. graeca* Seilacher. Książkiewicz distinguished *S. involuta* (De Stefani) and *S. zumayensis* (Gómez de Larena). The latter ichnospecies is identical with *S. minuta*, which had been distinguished by Książkiewicz (1970) as a new ichnospecies, and which was included later (1977) by him in *S. zumayensis*. The trace fossil described as *S. zumayensis*, however, does not display features of *Spirorhaphé*. It is composed of spirally coiled oblique ribbons, which are inclined toward the centre of the spiral and which locally display perpendicular striation. Seilacher (1977b, 1978) included this trace fossil in *Scolicia*. However, Plička (1989) distinguished a new ichnogenus, *Rotundusichnium*, for this trace fossil. Features of *Scolicia* are hardly visible in the examined material and the problem of ichnogenetic affinity still exists. The discussed trace fossil is provisionally de-



Fig. 87. “*Spirophycus*” *involutissimus* (Sacco) on sole of turbiditic sandstone bed, covered with tests of large foraminifers. UJ TF 179. Hicroglyphic beds (Eocene), Zawoja-Końskie. Scales in mm

scribed under *Rotundusichnium* Plička.

Spirorhaphé involuta (De Stefani 1895)

Fig. 88

- * 1895 *Helminthopsis involuta* n. - De Stefani, 168(16), pl. 14, fig. 1.
 1898 Unnamed - Paul, pl. 3, figs. 3-4.
 1927 Geführte Spirale - Richter, pl. 2, fig. 2.
 1954 *Spirorhaphé involuta* (De Stefani) - Seilacher, fig. 2.9.
 1955 *Spirorhaphé* - Papp, fig. 2.
 partim 1955 *Spirorhaphé* - Lessertisseur, pl. 74, fig. 4 [non pl. 74, fig. 6 = *Spirophycus*].
 v 1960 *Spirorhaphé* Fuchs - Książkiewicz, 738, pl. 2, fig. 6.
 1967b *Spirorhaphé* - Seilacher, fig. 6.
 v 1970 *Spirorhaphé involuta* de Stefani - Książkiewicz, 304, fig. 5a.
 1973 *Spirorhaphé concentrica toyensis* Katto - Katto, fig. 28.
 v 1977 *Spirorhaphé involuta* (De Stefani) - Książkiewicz, 144, pl. 18, figs. 1-2, text-fig. 30a-d.
 1977 *Spirorhaphés* - Pendón, pl. 2, figs. 1-2 (lapsus calami).
 1978 *Spirorhaphé* sp. a - Fukuda & Hayasaka, 16, pl. 1, fig. 12.
 1978 *Spirorhaphé* - Kern, 254, fig. 6J.
 1978 *Spirodesmos* sp. b - Fukuda & Hayasaka, 17, pl. 1, fig. 11.
 ? 1980 *Spirorhaphé* sp. - Pickerill, fig. 2b.
 1982 *Spirorhaphé* sp. - Noda, pl. 7, fig. 2.
 ? 1987a *Spirorhaphé* - Pickerill, 388, fig. 3b.
 1988 *Spirorhaphé involuta* (De Stefani) - McCann & Pickerill, 341, fig. 5.7.
 1991 *Spirorhaphé involuta* (De Stefani) - Leszczyński & Seilacher, 298 (no illustrations).
 1992 *Spirorhaphé involuta* - Leszczyński, pl. 12, fig. 2 (also Leszczyński, 1993, fig. 6).
 1995 *Spirorhaphé involuta* (De Stefani) - Crimes & McCall, 249, figs. 7D-F-8A-C.

The above placed synonymy list is complementary to the syno-



Fig. 88. *Spirorhapse involuta* (De Stefani) on sole of turbiditic sandstone. UJ TF 552 (label lost). Scale in mm

nymy list of Seilacher (1977a).

Diagnosis: Two-way spirals consisting of an inward spiral, a central loop and an outward spiral, guided between the turns of the inward one (after Seilacher, 1977a).

Material: 5 specimens (TF UJ 210-211, 552, 1519, 1850).

Remarks: Pickerill (1980, 1987a) illustrated an Ordovician *Spirorhapse* with identical central part as in the typical *S. involuta*, but with only a few whorls. It is reservedly included in *S. involuta*.



Fig. 89. "*Rotundusichnium*" *zumayensis* (Gómez de Llarena), epichnial form in turbiditic mudstone. UJ TF 2656. Beloveža beds (Eocene), Szczawa-Głębieniec. Scale in mm

"*Rotundusichnium*" Plička 1989

Emended diagnosis: Spirally coiled, partially overlapping ribbons inclined toward the center of spiral. The ribbons may be perpendicularly striated.

Remarks: *Rotundusichnium* was erected by Plička (1989) for *Spirorhapse zumayensis* (Gómez de Llarena). He properly noted that this trace fossil differs of *Spirorhapse* typified by *S. involuta* De Stefani. Seilacher (1977b, 1978) included this trace fossil in *Scolicia*. Features of *Scolicia* are hardly visible in the examined material and the problem of ichnogenetic affinity still exists.

"*Rotundusichnium*" *zumayensis* (Gómez de Llarena 1946) Fig. 89

- * 1946 *Helminthoidea zumayensis* n. sp. – Gómez de Llarena, 37, pl. 1, fig. 12.
- v 1977 *Spirorhapse zumayensis* (Gómez de Llarena) – Książkiewicz, 147, pl. 18, fig. 3.
- 1977b *Scolicia* – Seilacher, fig. 6H.
- 1978 *Scolicia zumayensis* – Seilacher, fig. 2c.
- 1980 *Scolicia zumayensis* – Frey & Seilacher, fig. 15.
- 1986 *Scolicia* – Seilacher, fig. 3.6d.
- 1989 *Rotundusichnium zumayensis* – Plička, 74, pls. 43-44, 46, text-figs. 3A-C, 4, 6-7.
- 1989 *Rotundusichnium magnum* ichnosp. n. – Plička, 76, pl. 45, 46, text-fig. 3D.
- v 1991c *Spirorhapse zumayensis* Llarena – Uchman, fig. 4.1.

Diagnosis: As for the ichnogenus.

Material: 6 specimens (UJ TF 202, 212, 2656, 2660-2662).

Branched winding and meandering traces

Belorhapse Fuchs 1895

Ichnospecies excluded from *Belorhapse* Fuchs:

- non 1955 *Belorhapse kochi* (Ludwig) – Michelau, 306, pls. 1-4 [= *Cochlichnus*].
- 1963 *Belorhapse fulgur* sp. nov. – Vialov, 104, fig. 2.
- non 1973 *Belorhapse protopalcoedictyum* n. sp. – Bandel, 166, pl. 37, fig. 6, pl. 38, fig. 2, text-fig. 6 [= *Treptichnus*].
- non 1978 *Belorhapse* sp. – Fukuda & Hayasaka, 18, pl. 1, fig. 6 [= ? *Cochlichnus*].

Emended diagnosis: Horizontal trace fossil with fine, angular zigzag second order meanders, which are thicker around points of curvature. Short lateral protrusions extending from the curved points can occur. The first order meanders very wide.

Remarks: *Belorhapse* is rare in Palaeozoic, in Ordovician (?) (Pickerill, 1980) and Silurian (Vialov, 1963), and was recorded mainly from Cretaceous and Tertiary from Beriasian (Książkiewicz, 1977) to Oligocene (Nowak, 1970).

Belorhapse zickzack (Heer 1877)

Figs. 90-91

- * 1877 *Cylindrites zickzack* Hr. – Heer, 159, pl. 68, fig. 10.
- 1895 *Belorhapse* – Fuchs, pl. 4, fig. 4.
- 1900 *Belorhapse* – Toulou, fig. 162.
- 1933 *Helicolithus fabregae* Azpeitia, n. sp. – Azpeitia Moros, 52, pl. 3, fig. 10, pl. 10, fig. 21A.
- 1951 *Belorhapse* – Vassoevich, pl. 6, fig. 2.
- 1955 *Belorhapse* – Seilacher, fig. 5.68.
- 1959 Unnamed – Seilacher, tab. 2, fig. 10.
- v 1961 *Belorhapse fabregae* (Azpeitia) – Książkiewicz, 885, pl. 2, fig. 5.

- 1961 *Belorhapse psesuapse* nov. sp. – Grossheim, pl. 1, fig. 2.
 1962 *Belorhapse* – Dimitrieva *et al.*, pl. 82, fig. 4.
 1963 *Belorhapse* – Vialov, fig. 3b.
 v 1970 *Belorhapse zickzack* (Heer) – Książkiewicz, 303, fig. 4g.
 v 1970 *Belorhapse fabregae* (Azpeitia) – Książkiewicz, 303, fig. 4f.
 1970 *Belorhapse zickzack* (Heer) – Nowak, 153, pl. 1, fig. 4, pl. 2, fig. 6.
 1970 *Belorhapse fabregae* (Azpeitia) – Nowak, 158, pl. 2, fig. 5.
 1974 *Belorhapse* – Kern & Warme, 898, fig. 7g.
 v 1975 *Belorhapse* – Hantzschel, 45, fig. 29.2.
 1977 *Belorhapse zickzack* (Heer) – Książkiewicz, 172, pl. 24, fig. 1, text-fig. 39a-j.
 v 1977 *Belorhapse fabregae* (Azpeitia) – Książkiewicz, 173, pl. 24, fig. 2, text-fig. 39 i, k.
 partim? 1977b *Belorhapse* – Crimes, 593, pl. 2, fig. 2 (?) (non pl. 1, figs. 1-2, pl. 3, fig. 1).
 ? 1980 *Belorhapse* sp. – Pickerill, fig. 5e.
 1987 *Belorhapse zickzack* (Heer) – Alexandrescu & Brustur, 14, pl. 6, fig. 3.
 ?partim 1987 *Belorhapse zickzack* (Heer) – Plička, 173, pl. 45, figs. 3, 5, pl. 46, figs. 1-3, text-fig. 30.1-7.
 non? 1987 *Belorhapse fabregae* (Azpeitia) – Plička, 173, text-fig. 30.8.
 1989 *Desmograpton* cf. *geometricum* – Miller, fig. 2D.
 1993 *Belorhapse zickzack* (Heer) – Miller, 16, fig. 5B.
 1993 *Belorhapse zickzack* (Heer) – Brustur & Stoica, 59, pl. 2, fig. 6.
 1994 *Belorhapse* – Lobitzer *et al.*, 298, pl. 4, figs. 1-2.
 v 1996a *Belorhapse zickzack* (Heer) – Tunis & Uchman, 181, fig. 9D.
 v 1996b *Belorhapse zickzack* (Heer) – Tunis & Uchman, 10 [not figured].

Diagnosis: As for ichnogenus.

Material: 25 specimens (TF UJ 653, 792, 822, 1016, 1018-1019, 1027, 1037, 1168, 1226, 1414, 1445, 1665, 1666-1668a, 1669-1671, 1672, 1858a, 1874, 1889, 2025a, 2560).

Description: See Książkiewicz (1977) with the following additions: occasionally, repetitions of the zigzag occur and two zigzags are arranged parallel and are joined (Fig. 90A). In some cases, the zigzag passes into a stretched string (Fig. 91B).

Remarks: Książkiewicz (1977) distinguished *B. zickzack* (Heer) and *Belorhapse fabregae* (Azpeitia Moros). However, these ichnospecies seem to be varieties of the same ichnospecies, controlled by depth of erosion and minor differences in behaviour of the tracemaker. They are thus regarded as synonyms and *B. zickzack* (Heer) has priority. Irregularity of the strings, which typifies *B. fabregae*, is not constant in these trace fossils. It seems that the tracemaker made a few occasional mistakes, which resulted in the irregularities.

Stratigraphic range: Flysch deposits from the Beriasian (Książkiewicz, 1977) to Oligocene (Nowak, 1970).

Belocosmorhapse n. igen.

Origin of the name: from the ichnogenera *Belorhapse* and *Cosmorhapse*.

Diagnosis: Hypichnial string with first- and second-order meanders with short lateral knobby appendages.

Remarks: This ichnogenus is monotypical, typified by *Helminthoida aculeata* Książkiewicz. Its morphology does not conform to *Helminthoida*, which was separated in *Nereites* and *Helminthorhapse*. These trace fossils display only first-order meanders and display some similarities to *Cosmorhapse* and *Belorhapse*. However, the first ichnogenus is



Fig. 90. *Belorhapse zickzack* (Heer) on soles of turbiditic sandstone beds. A. UJ TF 1414, Gorzeń Górny (part of label lost). B. UJ TF 1670, Beloveža beds (Eocene), Lipnica Mała (labelled as *Belorhapse fabregae*). Scale in A in mm, scale in B in cm

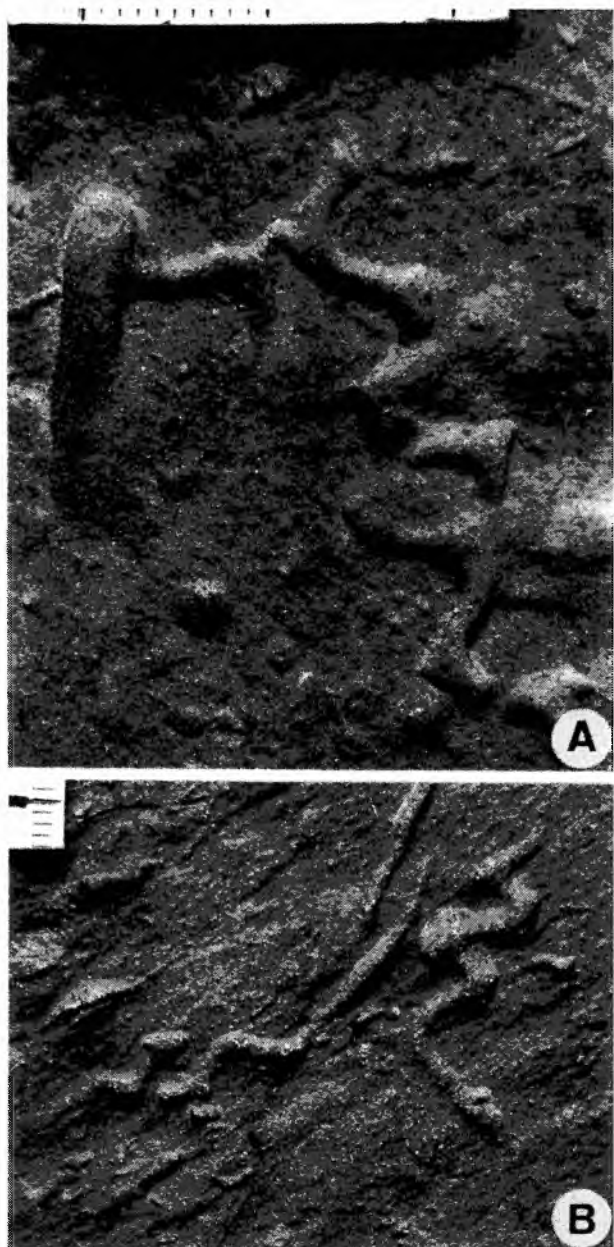


Fig. 91. *Belorhaphé zickzack* (Heer) on soles of turbiditic sandstone beds. A. UJ TF 1666, Beloveža beds (Eocene), Sidzina. B. UJ TF 2445, Jaworki (part of label lost). Scales in mm

smooth, without any appendages, and latter ichnogenus displays zigzag pattern and lacks first-order meanders. For these reasons, the new ichnogenus is created.

Belocosmorhaphé aculeata (Książkiewicz 1977)
Fig. 92

v* 1977 *Helminthoida aculeata* n. ichnosp. – Książkiewicz, 163, pl. 19, fig. 8, text-fig. 36o.

Diagnosis: As for the ichnogenus.

Material: 2 specimens (UJ TF 716, 1360 (holotype)).

Paleomeandron Peruzzi 1880

Emended diagnosis: Meandering string, with small, more



Fig. 92. *Belocosmorhaphé aculeata* (Książkiewicz) on sole of a turbiditic sandstone bed. UJ TF 716, Beloveža beds (Eocene), Szczawa-Głębieniec stream. Scale in mm

or less regular, three-dimensional, rectangular second-order meanders.

Remarks: Seilacher (1977a) distinguished *P. elegans* Peruzzi, *P. biseriale*, and *P. transversum*. Książkiewicz (1968, 1970, 1977) described *P. elegans* Peruzzi, *P. rude* Peruzzi, and *P. robustum* Książkiewicz. Seilacher (1977a) included *P. rude* Peruzzi described by Książkiewicz (1970, fig. 3e) in *P. elegans* Peruzzi. Nevertheless, these trace fossils display ample differences for their separation, which are expressed in their emended diagnoses.

Paleomeandron elegans Peruzzi 1880

Fig. 93

- * 1880 *Paleomeandron elegans* – Peruzzi, 8, pl. 1, figs. 2, 5.
- 1895 *Paleomeandron elegans* Peruzzi – Fuchs, pl. 5, fig. 7.
- ? 1967 *Paleomeandron* cf. *Paleomeandron elegans* Peruzzi – Macsotay, 35, fig. 6.
- 1968 *Paleomeandron elegans* Peruzzi – Książkiewicz, 3, pl. 1, fig. 1 [also Książkiewicz, 1977, pl. 23, fig. 1].
- v 1970 *Paleomeandron elegans* Peruzzi – Książkiewicz, 301, fig. 3d.
- 1970 *Paleomeandron* – Simpson, pl. 10, fig. 4.
- 1977a *Paleomeandron elegans* Peruzzi – Seilacher, 310, fig. 7a.
- v 1977 *Paleomeandron elegans* Peruzzi – Książkiewicz, 163, pl. 23, fig. 1.
- partim 1977 *Paleomeandron rude* Peruzzi – Książkiewicz, 165, pl. 23, fig. 2 (non pl. 22, fig. 4 = *Paleomeandron rude*).
- non? 1977b *Paleomeandron* – Crimes, 594, pl. 2, figs. 1-2, pl. 3, fig. 1.
- 1978 *Paleomeandron* sp. – Fukuda & Hayasaka, 19, pl. 1, figs. 7-8.

Emended diagnosis: *Paleomeandron* with second order undulations in one plane with sharp and regular corners. The

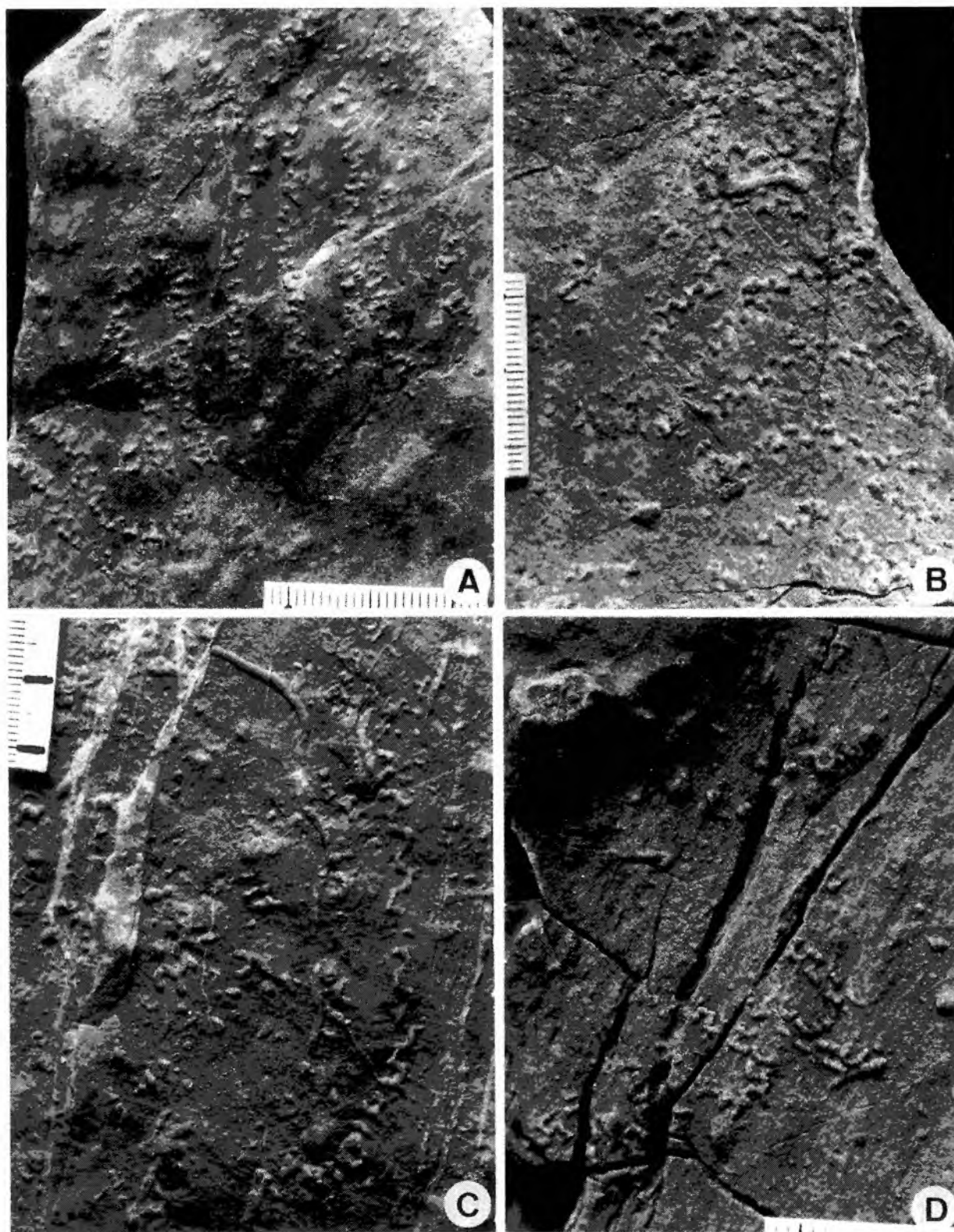


Fig. 93. *Paleomeandron elegans* Peruzzi on soles of turbiditic sandstone beds. A. UJ TF 221, Szczawa (part of label lost). B. UJ TF 1423, Osielec (part of label lost). C. UJ TF 219, Sidzina-Glaza stream (part of label lost, labelled as *Paleomeandron intermedium*). D. UJ TF 1176, Wierzbanowa (part of label lost). Scales in mm



Fig. 94. *Acanthorhaphhe delicatula* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 1745, Ropianka beds (Senonian–Paleocene), Smrekowice. Scale bar = 1 cm

Acanthorhaphhe Książkiewicz 1970

Diagnosis: Winding or arcuate thin strings with short appendages usually on the convex side (modified after Książkiewicz, 1977).

Acanthorhaphhe delicatula Książkiewicz 1977

Fig. 94

- v 1970 *Acanthorhaphhe* – Książkiewicz, 301, fig. 4b1–b3.
- v* 1977 *Acanthorhaphhe delicatula* n. ichnosp. – 170, pl. 23, figs. 8–10, text-fig. 38a–o.
- 1977a *Acanthorhaphhe pectinata* n. ichnosp. – Seilacher, 321, fig. 11c.
- non 1977b *Acanthorhaphhe* – Crimes, 601, pl. 5, figs. 1–2.
- 1988 *Acanthorhaphhe* ichnosp. – McCann & Pickerill, 331, fig. 3.1.
- v 1997 *Acanthorhaphhe delicatula* Książkiewicz – Wetzel & Uchman, 142, figs. 3C, 4A.

Diagnosis: Hypichnial, short arcuate ridges with appendages on the convex side (modified after Książkiewicz, 1977).

Material: 19 specimens (TF UJ 877, 972 (holotype), 1322–1330, 1332–1334, 1364, 1499, 1740, 1745, 2001).

Remarks: Książkiewicz (July 1977) erected *A. delicatula* on the basis of earlier, but unnamed *Acanthorhaphhe* material described by him (Książkiewicz, 1970). On the same basis of Książkiewicz specimen, Seilacher (August 1977a) distinguished *A. pectinata*, which is, therefore, regarded as the junior synonym of *A. delicatula*.

Stratigraphic range: Senonian–Middle Eocene (Książkiewicz, 1977).

Acanthorhaphhe incerta Książkiewicz 1970

Fig. 95

- 1961 *Acanthorhaphhe* (n.f.) – Książkiewicz, 883, pl. 1, fig. 4.
- v* 1970 *Acanthorhaphhe incerta* ichnosp. n. – Książkiewicz, 301, fig. 4a1–a4.
- v 1977 *Acanthorhaphhe incerta* Książkiewicz – Książkiewicz, 171, pl. 23, figs. 6–7.
- 1977a *Acanthorhaphhe incerta* Książkiewicz – Seilacher, 320, fig. 11b.
- ? 1982 *Acanthorhaphhe* cf. *incerta* Książkiewicz – Alexandrescu & Brustur, 42, pl. 4, fig. 2b.

Diagnosis: Winding, rarely branched strings with short side appendages, mainly on the convex side (modified after Książkiewicz, 1977, and Seilacher, 1977a).

Material: 1 slab (UJ TF 1441, the holotype) and UJ TF 1017.

Description: See Książkiewicz (1977) with the following additions: the specimen UJ TF 1017 displays long, side appendages, unlike the holotype.

Remarks: Stratigraphic range: Beriasian (Książkiewicz) – Paleocene (Seilacher, 1977a). Brustur & Stoica (1993) reported *Acanthorhaphhe* cf. *incerta* from Upper Eocene.

Desmograpton Fuchs 1895

Diagnosis: trace fossil preserved usually as hypichnial double rows of string-like U-, J-shaped, or angular semi-meanders. Their curved segments are inwardly oriented, in alternating position, and two opposite semi-meanders are joined by short bars. Orientation of the bars variable. Some axial elements of the system may be elevated or depressed (after Uchman, 1995).

Remarks: Ichnotaxonomic problems and revisions of ichnospecies of *Desmograpton* have been recently discussed by Uchman (1995). As a result, *D. fuchsi* Książkiewicz was

first order meanders are deep.

Material: 8 specimens (UJ TF 138, 219–221, 787, 1176, 1423, 2714).

Description: See description of Książkiewicz (1977) ichnotaxa.

Remarks: Specimen UJ TF 219 is labelled as *Paleomeandron intermedium*. This name was never used in the literature.

Paleomeandron rude Peruzzi 1880

- * 1880 *Paleomeandron rude* – Peruzzi, 8, pl. 1, fig. 4.
- v 1968 *Paleomeandron rude* Peruzzi – Książkiewicz, 3, pl. 1, fig. 2 [also Książkiewicz, 1977; pl. 22, fig. 4].
- v 1970 *Paleomeandron rude* Peruzzi – Książkiewicz, 301, fig. 3e.
- partim 1977 *Paleomeandron rude* Peruzzi – Książkiewicz, 165, pl. 22, fig. 4 (non pl. 23, fig. 2 = *Paleomeandron elegans*).

Emended diagnosis: *Paleomeandron* with second order undulations in one plane with irregular corners. The first order meanders are relatively shallow.

Material: 2 specimens (TF UJ 25, 218).

Description: See description of Książkiewicz (1977) ichnotaxa.

Paleomeandron robustum Książkiewicz 1968

- * 1968 *Paleomeandron robustum* n. "sp". – Książkiewicz, 4, pl. 1, fig. 3 [also Książkiewicz, 1977, pl. 23, fig. 3].
- v 1970 *Paleomeandron robustum* Książkiewicz – Książkiewicz, 301, fig. 3f–h.
- 1977 *Paleomeandron robustum* Książkiewicz – Książkiewicz, 165, pl. 23, fig. 3, text-fig. 37a–c.

Emended diagnosis: Large *Paleomeandron* with second-order undulations in one plane and with irregular corners. The first-order meanders very wide.

Material: 8 specimens (TF UJ 228–229, 231 (holotype), 834, 1481–1482, 1807, 1479).

Description: See description of the Książkiewicz (1977) ichnotaxa.



Fig. 95. *Acanthorhapha incerta* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 1017, Zegocina (label lost). Atypical form with long appendages. Scale in mm



Fig. 96. *Desmograption dertonensis* (Sacco) on sole of turbiditic sandstone bed. UJ TF 1452, Beloveža beds (Eocene), Sidzina-Głaza stream. Scale in mm

partially included in *D. dertonensis* (Sacco) and partially in *D. ichthyforme* (Macsoyay). *Helminthoida alterna* Książkiewicz was included in *Desmograption* as *D. alternum* (Książkiewicz).

Desmograption is interpreted as a three-dimensional graphoglyptid trace fossil (Seilacher, 1977a). It occurs in flysch deposits from the Silurian (McCann, 1989, 1993) to the Miocene (D'Alessandro, 1980; Uchman, 1995).

Desmograption dertonensis (Sacco 1888)

Fig. 96

- * 1888 *Nemertilites? dertonensis* Sacc. – Sacco, 42, pl. 2, fig. 19.
- v 1970 *Desmograption fuchsi* n. Książkiewicz, 305, fig. 6a1.
- v partim 1977 *Desmograption fuchsi* n. ichnosp. – Książkiewicz, 182, text-fig. 43g [non pl. 29, fig. 5, text-fig. 43 = *Desmograption ichthyforme*].

Diagnosis: *Desmograption* with narrow U- or J-shaped semi-meanders, commonly elevated in the curved segments. The connecting bars are parallel or sub-parallel (Uchman, 1995).

Material: 1 specimen (UJ TF 1452).

Remarks: McCann (1989) included *D. inversum* in *D. fuchsi* Książkiewicz (1977), but the definition of the ichnospecies given by McCann (1989) is too broad (see details in the discussion of the ichnogenus).

Desmograption alternum (Książkiewicz 1977)

Fig. 97

- *v 1977 *Helminthoida alterna* n. ichnosp. – Książkiewicz, 162, pl. 20, fig. 2 text-fig. 35a-m.
- 1977a *Desmograption geometricum* n. ichnosp. – Seilacher, 312, 7e, 8e.

Diagnosis: *Desmograption* which displays U- or J-shaped semi-meanders of moderate width, elevated in the curved portions. The connecting bars are obliquely oriented to the trace-fossil axis and form a zigzag pattern (Uchman, 1995).

Material: 13 specimens (UJ TF 246-248, 656, 790, 806, 815-816, 843 (holotype), 975, 1081, 1232, 1432).

Remarks: The connecting bars of *Desmograption geometricum* Seilacher are looser than in the described material (Seilacher, 1977a), but the morphological variability of *D. geometricum* is poorly known.

Desmograption ichthyforme (Macsoyay 1967)

Fig. 98

- v partim 1977 *Desmograption fuchsi* n. isp. – Książkiewicz, 182, pl. 29, fig. 5, text-fig. 43a-f, h-i [non text-fig. 43g = *Desmograption dertonensis*].

Diagnosis: *Desmograption* which displays angular narrow semi-meanders which appear as parallel ridges joined by short perpendicular bars. Axial part of trace fossil commonly elevated. Perpendicular bars may be not preserved.

Material: 8 specimens (TF UJ 396, 644, 898, 1119, 1350, 1433, 1591, 2002).

Urohelminthoida Sacco 1888

Ichnospecies reservedly included in *Urohelminthoida* Sacco:

- ? 1965 Helminthoids – Hecker, pl. 11, fig. 4.
- 1967 *Urohelminthoida* cf. *U. appendiculata* (Heer) – Macsoyay, 38, fig. 21.
- non 1986 *Urohelminthoida* – Yang et al., pl. 2, fig. 2.
- ? 1996 ?*Urohelminthoida* ichnosp. – Mikuláš & Pek, 83, pl. 1,

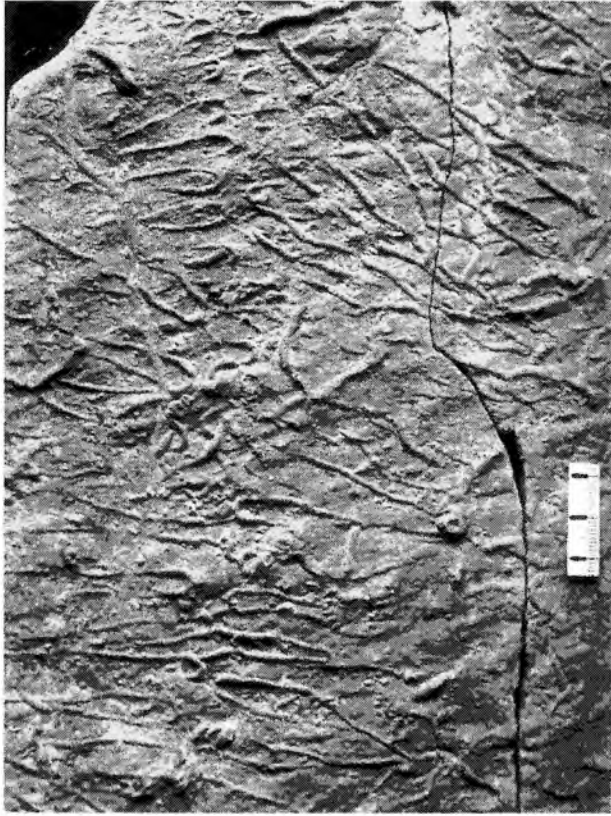


Fig. 97. *Desmograpton alternum* (Książkiewicz) on sole of turbiditic sandstone bed. UJ TF 816, Beloveža beds (Eocene), Berest. Scale in mm

figs. 1-2.

1997 *Urohelinthoida* ichnosp. Zagora, 362, figs. 4.1-2, 5.5, 7.1-2, 6.

Diagnosis: Trace fossil preserved usually as string-sized, deep hypichnial meanders. Lateral appendages protrude outwardly from the curved segments of the meanders (after Uchman, 1995).

Remarks: *Urohelinthoida* is a typical graphoglyptid trace fossil (Seilacher, 1977a). Apart from numerous flysch occurrences it was found in Mesozoic shallow-water deposits (Fürsich & Heinberg, 1983; Gierlowski-Kordesch & Ernst, 1987). Modern traces of *Urohelinthoida* were photographed on the deep-sea floor (Gaillard, 1991). Fossil forms occur from the Jurassic (Fürsich & Heinberg, 1983) to the Miocene (D'Alessandro, 1980; Uchman, 1995). Questionable forms occur from Ordovician (Zagora, 1997).

Urohelinthoida dertonensis Sacco 1888

Fig. 98B

- * 1888 *Urohelinthoida dertonensis* Sacc. – Sacco, 36, pl. 2, figs. 8, 16.
- 1895 *Hercorhaphé* Fuchs, pl. 5, fig. 3.
- 1933 *Urohelinthoida dertonensis* Sacco – Azpeitia Moros, 61, pl. 5, fig. 15B.
- v partim 1960 *Hercorhaphé* Fuchs – Książkiewicz, 735, pl. 1, figs. 3 (?) [non pl. 1, fig. 2 = *U. appendiculata*], (also *Urohelinthoida* in Sacco, 1899, pl. 1, fig. 10).
- 1964 *Helminthoida* aff. *appendiculata* Heer – Farrés Malian, 88, fig. 3b, c.
- v 1970 *Urohelinthoida dertonensis* Sacco – Książkiewicz, 310, fig. 6e.
- v 1970 *Urohelinthoida* aff. *appendiculata* Heer – Książkiewicz,

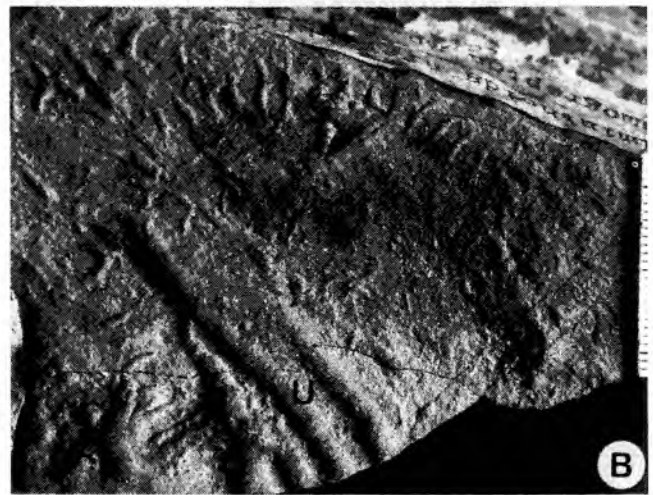


Fig. 98. *Desmograpton ichthyforme* (Macsoy) on soles of turbiditic sandstone beds. A. UJ TF 1350, Hangau beds, Valle de Langu, Romania. B. UJ TF 1591 (together with *Urohelinthoida dertonensis* (U). Ropianka beds (Senonian–Paleocene), Lipnica Wielka-Kiczora stream. C. UJ TF 898, Szczawnica Formation (Paleocene–Lower Eocene), Krościenko. Scales in mm

310, fig. 6f.

- v partim 1977 *Urohelinthoida appendiculata* Heer – Książkiewicz, 179, pl. 26, fig. 3 (?); text-fig. 42a-c. [non pl. 26, figs. 1-2 = *U. appendiculata*].
- v 1977 *Urohelinthoida dertonensis* Sacco – Książkiewicz, 179, pl. 26, figs. 4-5, text-fig. 42e-w.
- v 1977 *Urohelinthoida* aff. *dertonensis* Sacco – Książkiewicz, 181, text-fig. 42x-y (non pl. 26, fig. 6 = *Oscillorhaphé*).
- 1977a *Urohelinthoida dertonensis* Sacco – Seilacher, 307, fig. 6f.
- 1980 *Urohelinthoida dertonensis* Sacco – D'Alessandro, 375, pl. 42, fig. 1, pl. 43, fig. 3, text-fig. 11.
- ? 1981 *Urohelinthoida* aff. *appendiculata* Heer – Tanaka & Sumi, pl. 2, fig. 1.
- 1982 *Urohelinthoida* – D'Alessandro, fig. 11.

- ? 1983 *Urohelminthoidea* – Fürsich & Heinberg, fig. 10a.
 1989 *Urohelminthoidea* – Powichrowski, fig. 3.6.
 1990 *Urohelminthoidea* isp. – Uchman, pl. 1, fig. 6.
 1995 *Urohelminthoidea appendiculata* Heer – Crimes & McCall, 252, fig. 9C.
 v 1995 *Urohelminthoidea dertonensis* Sacco – Uchman, 47, pl. 13, figs. 6-7, pl. 14, figs. 1-4, text-fig. 20A-E.
 v 1996a *Urohelminthoidea dertonensis* Sacco – Tunis & Uchman, 183, fig. 9K.
 v 1996b *Urohelminthoidea dertonensis* Sacco – Tunis & Uchman, 10, fig. 14A.
 v 1996 *Urohelminthoidea dertonensis* Sacco – Marinčić *et al.*, fig. 5E.

Diagnosis: *Urohelminthoidea* with lateral appendages which pass straight into one arm of meander, but form an angle with the second arm (after Uchman, 1995).

Material: 24 specimens (UJ TF 141, 144, 344, 346, 348, 351-352, 355, 358, 702, 732, 749, 768, 823, 974, 1134, 1150, 1172, 1486, 1591, 1593, 1599, 1862, 2052).

Remarks: Seilacher (1977a) indicated that one of the characteristic features of *U. dertonensis* is the wide spacing of the meanders. However, the distance between meanders varies in the examined material from tight to widely spaced (cf. Uchman, 1995). Consequently, this feature is not regarded as diagnostic. The lateral appendages which pass straight into one arm of the meanders, but form an angle with the second arm are the most pronounced feature of this ichnotaxon. *U. appendiculata* Heer is characterised by lateral appendages, which protrude from the apical part of meanders, and by very deep, slightly winding meanders (Uchman, 1995; Tunis & Uchman, 1996b, fig. 12). These differences were not consistently applied by Książkiewicz (1977) and Seilacher (1977a). Książkiewicz (1977) applied *U. appendiculata* to specimens having deep meanders, but showing characteristic *U. dertonensis* protrusions. Seilacher (1977a) included in the synonymy of *U. appendiculata* specimens that display the same features. Recently, Crimes & McCall (1995) lumped these to ichnotaxa under *U. appendiculata*. However, they display enough features for separation.

Urohelminthoidea appendiculata Heer 1877

- * 1877 *Urohelminthoidea appendiculata* Hr. – Heer, 168, pl. 66, fig. 1a.
 v ?partim 1960 *Hercorhaphé* Fuchs – Książkiewicz, 735, pl. 1, figs. 2 [non pl. 1, fig. 3 = ?*U. dertonensis*].
 v partim 1977 *Urohelminthoidea appendiculata* Heer – Książkiewicz, 179, pl. 26, figs. 1-2 [non pl. 26, fig. 3 (?); text-fig. 42a-c = *U. dertonensis*].
 1977a *Urohelminthoidea appendiculata* Heer – Seilacher, 308, fig. 6g.
 v 1993 *Urohelminthoidea appendiculata* Heer – Tunis & Uchman, 92, figs. 7D, 8C.
 v 1996a *Urohelminthoidea appendiculata* Heer – Tunis & Uchman, 183 [not figured].
 v 1996b *Urohelminthoidea appendiculata* Heer – Tunis & Uchman, 10, figs. 12, 13C, 17G.
 v 1996 *Urohelminthoidea appendiculata* Heer – Marinčić *et al.*, pl. 4, fig. 3.

Emended diagnosis: *Urohelminthoidea* with very deep, narrow meanders. The string is usually slightly winding, and the appendages can be long and can turn towards meanders.

Material: 2 specimens (UJ TF 120, 1592).

Ubinia Grossheim 1961

Diagnosis: Trace fossils preserved as a hypichnial, straight or slightly winding, axial string with arcuate or straight simple branches (after Wetzel & Uchman, 1997).

Remarks: *Ubinia* Grossheim was revised by Wetzel & Uchman (1997). It occurs in flysch or flysch-like deposits.

Ubinia alternans (Seilacher 1977a)

- 1967 *Chondrites* [...] no es típico – Macsotay, pl. 5, fig. 16.
 1970 *Rhabdoglyphus* aff. *grossheimi* Vassoevich – Książkiewicz, 285, fig. 1g.
 1977 *Rhabdoglyphus* aff. *spinosus* n. ichnosp. – Książkiewicz, 66, pl. 3, fig. 13 [redrawn by Stanley & Pickerill, 1993, fig. 5J].
 v non 1977 *Rhabdoglyphus spinosus* n. ichnosp. – Książkiewicz, 66, text-fig. 6b, pl. 3, figs. 7-8 (= *Hormosiroidea annulata* (Vialov)).
 * 1977a *Dendrotichnium alternans* n. ichnosp. – Seilacher, 308, fig. 6h.
 ? 1981 *Dendrotichnium häntzscheli* Farrés – Crimes *et al.*, 968 [not figured].
 ? 1992 *Dendrotichnium haentzscheli* (Farrés) – Kim *et al.*, 319, pl. 2, fig. 2.
 * 1994a *Dendrotichnium häntzscheli* (Farrés) – Han & Pickerill, 229, fig. 4E.
 ? 1996 *Dendrotichnium* – Twitchett & Wignall, 142.
 v 1997 *Ubinia alternans* (Seilacher) – Wetzel & Uchman, 152, figs. 3C-D.

Diagnosis: *Ubinia* with zigzag-shaped axial part; branches alternate on either side along the length of the central axis (after Wetzel & Uchman, 1997).

Material: 1 specimen in J. Burtan's collection.

Remarks: *Rhabdoglyphus* aff. *spinosus* (Książkiewicz, 1977) displays features of *Ubinia alternans*. The same morphology of this ichnospecies was observed by Wetzel & Uchman (1997). The material corresponds very well with the type material from the Upper Cretaceous flysch of N Spain (photographs kindly provided by A. Seilacher).

Stratigraphic range: Devonian (Han & Pickerill, 1994a) – Paleocene (Macsoy, 1967; Crimes *et al.*, 1981).

Oscillorhaphé Seilacher 1977a

Diagnosis: Hypichnial strings arranged in high amplitude meanders, whose sharp turning points are marked by a distinct cross bar (modified after Seilacher, 1977a).

Oscillorhaphé venezuelana Seilacher 1977a Fig. 99

- * 1977a *Oscillorhaphé venezuelana* n. ichnosp. – Seilacher, 313, fig. 8d.
 v 1977 *Urohelminthoidea* aff. *dertonensis* Sacco – Książkiewicz, 181, pl. 26, fig. 6 [non text-fig. 42x-y = *U. dertonensis*].
 v 1996a *Oscillorhaphé venezuelana* Seilacher – Tunis & Uchman, 183, fig. 9F.

Diagnosis: As for the ichnogenus.

Material: 1 specimen (UJ TF 144).

Description: As in the diagnosis, with the following remarks: the meanders are at least 40 mm deep. The string is 1.2 mm wide.

Remarks: This is a very rare ichnotaxon, which occurs in Paleocene–Eocene flysch deposits.



Fig. 99. *Oscillorhaphis venezuelana* Seilacher on sole of turbiditic sandstone bed. UJ TF 144, Ciężkowice Sandstone (Eocene), Znamierowice. Scale in mm

Protopalaeodictyon Książkiewicz 1958

Ichnotaxa included in *Protopalaeodictyon* Książkiewicz:

- 1867 *Palaeophycus spinatus* Geinitz – Geinitz, 16, pl. 6, fig. 4.
- 1927 Trugdoldig verzweigte Fährte – Richter, 199, pl. 1, fig. 5.
- ? 1931 Wurmsspuren – Hundt, 26, fig. 3.
- 1958 *Protopalaeodictyon* – Książkiewicz, pl. 2, fig. 1 (nomen nudum).
- 1960 *Protopalaeodictyon* (n. f.) – Książkiewicz, 737, pl. 1, fig. 5 (nomen nudum).
- 1968 *Spinorhaphis spinata* (Geinitz) – Pfeiffer, 682, pl. 6, fig. 4.
- 1968 *Spinorhaphis rubra* n. sp. – Pfeiffer, 682, pl. 6, figs. 5-6.
- partim 1970 *Protopalaeodictyon incompositum* ichnogen. nov. – Książkiewicz, 303, figs. 4e1-4e2 [non fig. 4e3] (fig. 4e1-3 reproduced in Häntzschel, 1975, fig. 60.1b).
- v* partim 1977 *Protopalaeodictyon incompositum* Książkiewicz – Książkiewicz, 174, pl. 24, figs. 3-4, text-fig. 40a-h, j-q [non text-fig. 40i = *Megagraption submontanum*].
- 1991 *Protopalaeodictyon incompositum* Książkiewicz – Crimes & Crossley, 51, fig. 10g-i.
- v 1996 *Protopalaeodictyon incompositum* Książkiewicz – Marinčić *et al.*, fig. 5B.

Ichnotaxa reservedly included in or excluded from *Protopalaeodictyon* Książkiewicz:

- non 1977b *Protopalaeodictyon* – Crimes, 593, pl. 1, fig. 2, pl. 4, figs. 2-3, pl. 5, fig. 2.
- non 1986 *Protopalaeodictyon incompositum* Książkiewicz – Yang *et al.*, 225, pl. 2, fig. 3 [= *Phycosiphon incertum*].
- non 1985 *Protopalaeodictyon* cf. *incompositum* Książkiewicz – Crimes & Anderson, 331, fig. 6.18.
- ? 1980 *Protopalaeodictyon* – Pickerill, 1270, fig. 4b [?= *Paleodictyon* isp.].
- ? 1981 *Protopalaeodictyon* sp. – Pickerill, 50, fig. 5a.
- ? 1983a ?*Protopalaeodictyon* – Wetzel, 291, fig. 2.6.
- non 1985 *Protopalaeodictyon* cf. *submontanum* (Azpeitia) – Crimes & Anderson, 331, fig. 6.19.
- ?non 1985 *Protopalaeodictyon* Książkiewicz – Eager *et al.*, 143, pl.

6D.

- ?non 1987a *Protopalaeodictyon* – Pickerill, 388, fig. 5f. Pickerill, 341, fig. 4.8.
- ?non 1988 *Protopalaeodictyon incompositum* Książkiewicz – McCann & Pickerill, 341, fig. 4.8.
- non 1959 *Protopalaeodictyon* – Nowak, pl. 5, fig. a, pl. 6, fig. b (lapsus calami) [= *Paleodictyon* isp.].
- non 1993 *Protopalaeodictyon* cf. *incompositum* Książkiewicz – McCann, 49, fig. 6G.
- non 1993 *Protopalaeodictyon submontanum* (Azpeitia Moros) – McCann, 49, fig. 6H.
- non 1994 *Protopalaeodictyon* ? sp. – Löffler & Geyer, 506, fig. 5a.
- v non 1997 *Protopalaeodictyon submontanum* (Azpeitia Moros) – Wetzel & Uchman, 150, fig. 5E [= *Megagraption submontanum*].

Diagnosis: Hypichnial, wide first-order meanders and more or less regular second-order meanders with one or two appendages usually branching from the apex of the second-order meanders (modified after Książkiewicz, 1977, and Seilacher, 1977a).

Remarks: Książkiewicz (1977) distinguished *P. incompositum* Książkiewicz, *P. minutum* Książkiewicz, and *P. submontanum* (Azpeitia Moros). However, only the first ichnospecies displays features of *Protopalaeodictyon* as expressed in the diagnosis. The last two ichnospecies are rather more irregular hypichnial nets than meanders with appendages. For this reason they are excluded from *Protopalaeodictyon* and included in *Megagraption* Książkiewicz, which is re-defined as an irregular hypichnial net in this paper. Kern (1980, tab. 1) informally included *Protopalaeodictyon submontanum* in *Megagraption*.

Probably, only four ichnospecies of *Protopalaeodictyon* can be distinguished: *P. incompositum* Książkiewicz, *P. minutum* Książkiewicz, *P. bicaudatum* Seilacher, and *P. spinata* (Geinitz). They are distinguished on the basis of shape of the second-order meanders and number of appendages.

Protopalaeodictyon occurs almost exclusively in flysch deposits. Only Gierlowski-Kordesch & Ernst (1987) noted its occurrence in the Cretaceous shallow-water deposits of East Africa.

Protopalaeodictyon incompositum Książkiewicz 1958

Fig. 100

- v 1958 *Protopalaeodictyon* – Książkiewicz, pl. 2, fig. 1 (nomen nudum).
- 1959 unnamed – Seilacher, tab. 1, fig. 11.
- v 1960 *Protopalaeodictyon* (n. f.) – Książkiewicz, 737, pl. 1, fig. 5 (nomen nudum).
- *v partim 1970 *Protopalaeodictyon incompositum* ichnogen. nov. – Książkiewicz, 303, figs. 4e1-4e2 [non fig. 4e3] [fig. 4e1-3 reproduced in Häntzschel, 1975, fig. 60.1b].
- 1970 *Anapaleodictyon irregulare* n. sp. – Tanaka, 53, pl. 10, fig. 1 [also Noda, 1982, pl. 5, fig. 1].
- 1971 *Protopalaeodictyon* sp. – Tanaka, 16, pl. 9, figs. 1-4.
- 1975 *Protopalaeodictyon incompositum* – Häntzschel, W97, fig. 60.1a.
- v* partim 1977 *Protopalaeodictyon incompositum* Książkiewicz – Książkiewicz, 174, pl. 24, figs. 3-4, text-fig. 40a-h, j-q [non text-fig. 40i = *Megagraption submontanum*].
- 1977a *Protopalaeodictyon incompositum* Książkiewicz – Seilacher, 305, fig. 6b.
- 1982 *Protopalaeodictyon incompositum* Książkiewicz – D'Alessandro, 537, pl. 43, fig. 3, text-fig. 13.
- non 1986 *Protopalaeodictyon incompositum* Książkiewicz – Yang, 157, pl. 4, fig. 6.
- non 1988 *Protopalaeodictyon incompositum* Książkiewicz – Yang, 9, pl. 1, figs. 9-10.

- non 1991 *Protopaleodictyon incompositum* Książkiewicz – Crimes & Crossley, 51, fig. 10g-i [= *Protopaleodictyon spinata*].
- v non 1993 *Protopaleodictyon incompositum* Książkiewicz – Tunis & Uehman, 92, fig. 8F [= *Megagraption submontanum*].
- ? 1994a *Protopaleodictyon incompositum* Książkiewicz – Han & Pickerill, 237, fig. 7F.
- v 1996a *Protopaleodictyon incompositum* Książkiewicz – Tunis & Uehman, 183, fig. 7D.
- v 1996a *Protopaleodictyon incompositum* Książkiewicz – Tunis & Uehman, 11, fig. 13E.
- v 1996 *Protopaleodictyon incompositum* Książkiewicz – Marinčić *et al.*, fig. 5B.

Emended diagnosis: *Protopaleodictyon* with sinuous second-order meanders and one appendage per undulation.

Material: 15 specimens (UJ TF 130, 336-338, 342-343, 395, 709, 723, 763, 900, 955, 1484 (holotype), 1554, 2501).

Remarks: *P. incompositum* occurs reservedly since Devonian (Han & Pickerill, 1994a), and certainly from the Albian (Książkiewicz, 1977) to the Miocene (D'Alessandro, 1982) in marine turbidites.

Protopaleodictyon minutum Książkiewicz 1977

Fig. 101

- v * 1977 *Protopaleodictyon minutum* n. ichnosp. – Książkiewicz, 177, pl. 24, fig. 5.

Diagnosis: *Protopaleodictyon* with fine sinuous meanders and short appendages or small tubercles on the apices.

Material: 2 specimens (UJ TF 121 (holotype), 334).

Remarks: Short appendages and distinctly smaller meanders are the main diagnostic feature of this ichnospecies. The appendages and tubercles are probably casts of oblique to vertical shafts, which connected the meandering burrow system to the sea-floor. The shafts were much more inclined than in the other ichnospecies of *Protopaleodictyon*.

Protopaleodictyon spinata (Geinitz 1867)

Fig. 102

- * 1867 *Palaeophycus spinatus* Geinitz – Geinitz, 16, pl. 6, fig. 4.
- 1927 Trugdoldig verzweigte Fährte – Richter, 199, pl. 1, fig. 5.
- ? 1931 Wurmsspuren – Hundt, 26, fig. 3.
- 1968 *Spinorhapha spinata* (Geinitz) – Pfeiffer, 682, pl. 6, fig. 4.
- ?partim 1968 *Spinorhapha rubra* n. sp. – Pfeiffer, 682, pl. 6, figs. 5-6).
- 1982 *Protopaleodictyon* sp. – Pickerill *et al.*, 28, fig. 2c.
- 1982b *Protopaleodictyon spinata* (Geinitz) – Benton, 121, fig. 6s.
- 1991 *Protopaleodictyon incompositum* Książkiewicz – Crimes & Crossley, 51, fig. 10g-i.

Emended diagnosis: *Protopaleodictyon* with zigzag-shaped second-order meanders and one appendage per undulation.

Material: This ichnotaxon is not present in the Książkiewicz collection.

Remarks: Benton (1982b) properly included trace fossils of this type in *Protopaleodictyon*. *P. spinata* differs from *P. incompositum* by its zigzag-shaped guidance of second-order meanders. It has been followed only over short distances and it is not clear if it displays the first-order meanders, which are common in *P. incompositum*.

P. spinata occurs in deep water-deposits, mainly turbidites, from Cambrian (Pickerill *et al.*, 1982) to Lower Carboniferous (Geinitz, 1867).

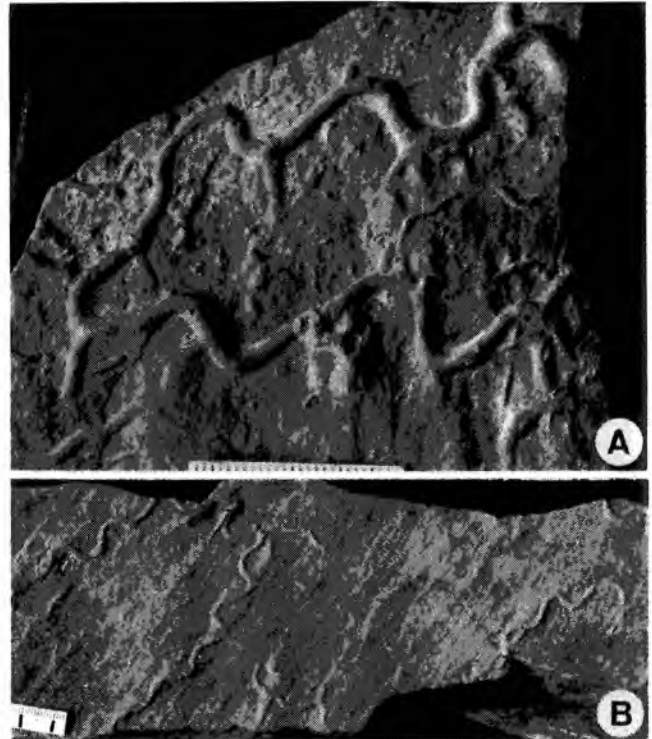


Fig. 100. *Protopaleodictyon incompositum* Książkiewicz on soles of turbiditic sandstone beds. A. UJ TF 709, Variegated Shale (Paleocene–Lower Eocene), Stara Wieś. B. UJ TF 342, Hieroglyphic beds (Eocene), Jordanów-Przykrzyc. Scale in mm



Fig. 101. *Protopaleodictyon minutum* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 121, holotype. Magura Sandstone (Eocene), Marcówka near Sucha Beskidzka. Scale in mm

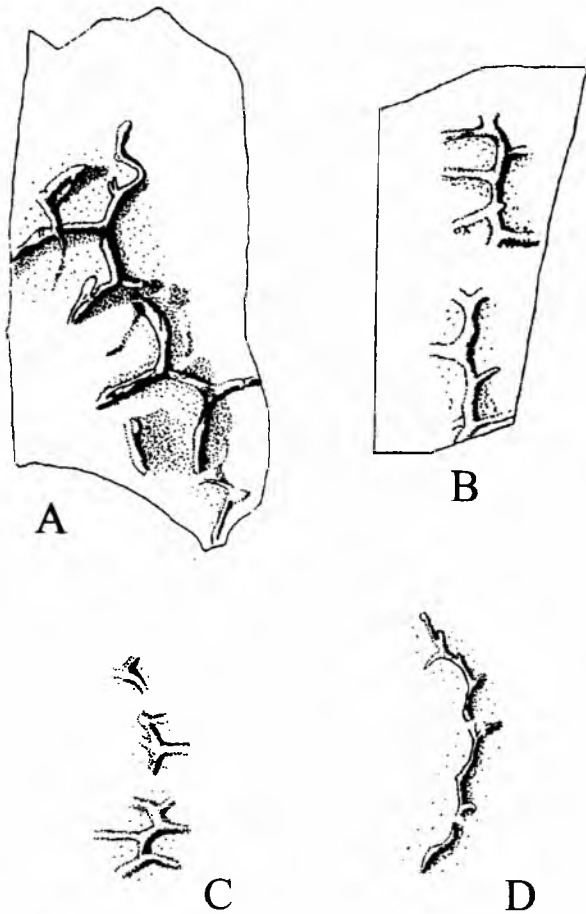


Fig. 102. *Protospaleodictyon spinata* (Geinitz). **A.** Redrawn from Geinitz (1867), pl. 6, fig. 4 (labelled as *Palaeophycus spinatus*). Tentaculitenschiefer, Zederhügel near Schleiz, Germany. **B.** Redrawn from Richer (1927), pl. 1, fig. 5 (labelled as "Trugdoldig verzweigte Fährte"). Upper Devonian quartzit, Saalfeld, Thuringia, Germany. **C.** Redrawn from Pfeiffer (1968), pl. 6, fig. 4 (labelled as *Spinorhapha spinata*), neotype, Kulm (Lower Carboniferous), Koselstein, Germany. **D.** Redrawn from Pfeiffer (1968), pl. 6, fig. 6 (labelled as *Spinorhapha rubra*), Kulm (Lower Carboniferous), Koselstein, Germany

Protospaleodictyon bicaudatum Seilacher 1977a

* 1977a *Protospaleodictyon bicaudatum* n. ichnosp. – Seilacher 313, figs. 7h, 8b.

?non 1981 *Protospaleodictyon bicaudatum* Seilacher Crimes, 974, pl. 4, fig. 4.

?non 1993b *Protospaleodictyon bicaudatum* Seilacher – Li, pl. 1, fig. 3.

Diagnosis: *Protospaleodictyon* with two appendages per undulation (modified after Seilacher, 1977a).

Remarks: This ichnotaxon is not present in the Książkiewicz or the studied complementary collections. *P. bicaudatum* is so far known only from the Eocene flysch deposits of Wienwerwald and of Pyrenees.

Networks

Megagraption Książkiewicz 1968

Ichnospecies reservedly included in or excluded from *Megagraption* Książkiewicz:

- ?non 1969 (?) *Megagraption* – Roberts, 231, pl. 1, fig. 3 (? pl. 1, fig. 2).
- non 1977 *Megagraption* – Stanley *et al.*, fig. 18.
- ?non 1977 *Megagraption regulare* ichnosp. nov. – Ghare & Badve, 210, pl. 7, fig. 2 (=physical structure).
- ?non 1986 *Megagraption* sp. – Yang, 226, pl. 2, fig. 4.
- non 1981 *Megagraption irregulare* Książkiewicz – Crimes *et al.*, 974, pl. 4, fig. 2 [=large foraminifer].
- ? 1982a *Megagraption* isp. – Benton, 78, fig. 8c.
- non 1986 *Megagraption irregulare* Książkiewicz – Ghare & Kul-karni, 48, pl. 2, fig. 1, pl. 8, fig. 1.
- non 1986 *Megagraption irregulare* Książkiewicz – Ghare & Kul-karni, fig. 2b.
- non 1987 *Megagraption tenue* Książkiewicz – Plička, 179, text-fig. 33.1-4.
- non 1988 *Megagraption irregulare* Książkiewicz – Pickerill & Harland, 125, fig. 6c [=Pseudopaleodictyon hartungi (Geinitz)].
- ? 1989 *Megagraption aequale* Seilacher – Miller, fig. 2o.
- ?non 1992 *Megagraption irregulare* Książkiewicz – Kim *et al.*, 320, fig. 3.2.
- ? 1992 *Megagraption aequale* Seilacher – Kim *et al.*, 320, fig. 3.3.
- non 1994 *Megagraption* isp. – Gong, 489, pl. 6, fig. 1.
- non 1995 *Megagraption irregulare* Książkiewicz – Gámez Vintaned & Mayoral, 225, pl. 1, fig. 3.
- non 1996 *Megagraption* isp. – Bi *et al.*, 722, pl. 3, fig. 5.
- ?non 1997 ?*Megagraption* ichnosp. – Zagora, 362, fig. 6.3.
- non 1997 *Megagraption?* sp. – Zhou, 156, fig. 4.

Emended diagnosis: Trace fossils commonly preserved as hypichnial irregular nets.

Remarks: Książkiewicz (1977), as well as Seilacher (1977a) defined *Megagraption* as curved or meandering trace fossil bearing lateral appendages, which tend to form irregular nets. However, their definitions do not conform with the appearance of the trace fossils illustrated by these authors. In fact, they are hypichnial irregular nets and the supposed meanders are apparent. It is possible to imagine some meanders in partially eroded forms, where only some parts of the net are preserved; however, in more complete specimens they pass in distinct irregular nets. Moreover, some specimens ascribed by Książkiewicz to *Protospaleodictyon*, particularly the specimens determined as *P. submontanum* (Azpeitia) (Fig. 105), are also hypichnial irregular nets and can be included in *Megagraption*.

Mikuláš (1992a) distinguished *Neodictyon bouckeii* ichnosp. nov. from the Silurian deposits of Bohemia. This ichnotaxon differs from *Megagraption* only by granular structure of the strings. The structure can result from preservational conditions. In this case *Neodictyon* would be the junior objective synonym of *Megagraption*, but the problem should be studied more closely. Therefore, *Megagraption* and *Neodictyon* are retained as separate ichnogenera.

Several authors reported *Megagraption* from the Palaeozoic. However, these determination seems to be problematic. Benton (1982b) and Stepanek & Geyer (1989) regarded *Palaeophycus hartungi* Geinitz from Kulm of Thuringia (Geinitz, 1867, 16, pl. 8, fig. 3) (Fig. 103) as *Megagraption*. Pfeiffer (1968, p. 674) erected *Pseudopaleodictyon hartungi* on the base of Geinitz's specimen. In the same year, Or-



Fig. 103. *Pseudopaleodictyon hartungi* (Geinitz) redrawn from Geinitz (1867), pl. 8, fig. 3. Lobenstein, Germany

lowski (1968) erected *Multina magna* for a Cambrian trace fossil of the same morphology. On the other hand, Häntzschel (1975, p. W97) reservedly included *Pseudopaleodictyon* in *Protopaleodictyon* Książkiewicz. Pemberton & Frey (1982, p. 851) also included *Ps. hartungi* in *Protopaleodictyon*. Nevertheless, Geinitz's and several other Palaeozoic specimens display well expressed overcrossings of strings, also at different levels, in very irregular polygons. This feature is extremely rare or absent in the Caenozoic



Fig. 104. *Megagraption irregulare* Książkiewicz on sole of turbiditic sandstone bed. UJ TF 1137, Beloveža beds (Eocene), Zubrzyca Górna-Ochlipów. Scale bar = 1 cm

specimens. Hence, differences between *Pseudopaleodictyon* (or *Multina*) and *Protopaleodictyon* are obvious and these two ichnogenera should be treated separately. Ichnotaxon *Pseudopaleodictyon* (or *Multina*) seems to be useful for the Palaeozoic material with common overcrossings of the string. *Protopaleodictyon submontanum* described by Crimes & Crossley (1991) from Silurian of Wales may be also included in *Pseudopaleodictyon*. Similarity of related Cambrian ichnotaxon *Olenichmus* Fedonkin (? junior synonym of *Pseudopaleodictyon*) to *Megagraption* was discussed by Jensen (1997).

Häntzschel (1975, p. W97) reservedly included *Unarites suleki* Macsotay (1967) in *Protopaleodictyon*. However this ichnotaxon displays polygons bordered by winding strings, which are typical of *Megagraption submontanum* (formerly *Protopaleodictyon submontanum*), and therefore it is included in this ichnospecies.

Megagraption irregulare Książkiewicz 1968

Fig. 104

- v 1961 *Megagraption* (n. f.) – Książkiewicz, 882, pl. 1, figs. 1-2 (nomen nudum) [fig. 1 reproduced in Häntzschel, 1975, 60.3a].
- v* 1968 *Megagraption irregulare* n. "sp." – Książkiewicz, 5, text-fig. 3.
- v 1968 *Megagraption tenue* n. "sp." – Książkiewicz, 5, pl. 3, fig. 1.
- 1969 "irregular *Paleodictyon*" – Simpson, pl. 43, fig. 1.
- v 1970 *Megagraption irregulare* Książkiewicz – Książkiewicz, 305, fig. 6b.
- v 1970 *Megagraption tenue* Książkiewicz – Książkiewicz, 305, fig. 6c.
- 1971 *Megagraption* sp. – Tanaka, 9, pl. 5, fig. 1.
- 1972 *Iredictyon chaos* sp. n. – Vialov, 79, pl. 3, fig. 1, pl. 4, figs. 1-2.
- v partim 1977 *Protopaleodictyon submontanum* (Azpeitia) – Książkiewicz, 177, pl. 25, fig. 3, text-fig. 41a, o [non pl. 25, figs. 1-2, 4-5, text-fig. 41b-n, p = *Megagraption submontanum*].
- v partim 1977 *Megagraption irregulare* Książkiewicz – Książkiewicz, 185, pl. 25, figs. 6-8, text-fig. 44b-g [non text-fig. 44a = *Thalassinoides* isp.].
- v non 1977 *Megagraption* aff. *irregulare* Książkiewicz – Książkiewicz, pl. 25, fig. 9 [= *Thalassinoides* isp.].
- v 1977 *Megagraption tenue* Książkiewicz – Książkiewicz, 185, pl. 25, fig. 10.
- non 1977a *Megagraption irregulare* Książkiewicz – Seilacher, 321, fig. 11a, d [= *Megagraption submontanum*].
- 1977a *Paleodictyon* – Crimes, pl. 4, fig. c.
- non 1977 *Megagraption irregulare* Książkiewicz – Chamberlain, 14, figs. 2d', 3H, 4E [= *Pseudopaleodictyon hartungi* (Geinitz)].
- 1980 *Megagraption* – Kern, fig. 3C (no description).
- 1982 *Megagraption irregulare* Książkiewicz – D'Alessandro, 537, text-fig. 14.
- ? 1986 *Megagraption irregulare* Książkiewicz – Yang, 155, pl. 3, fig. 3.
- 1986 *Megagraption irregulare* Książkiewicz – Miller, fig. 2c.
- 1987 *Megagraption irregulare* Książkiewicz – Plička, 179, text-fig. 33.5.
- ? 1988 *Megagraption irregulare* Książkiewicz – Yang, 7, pl. 2, fig. 5.
- 1989 *Megagraption* – Powichrowski, fig. 3.2.
- partim 1989 *Megagraption angulare* n. ichnosp. – Stepanek & Geyer, 22, pl. 3, figs. 19, 21-24, text-fig. 6a-e, g [non. fig. 20, text-fig. 6f = *Megagraption submontanum*].
- ? 1991 *Megagraption irregulare* Książkiewicz – Crimes & Crossley, 52, fig. 11a-e.
- 1991 *Megagraption tenue* Książkiewicz – Crimes & Crossley, 52, fig. 11f.

- ? 1991a *Megagraption irregulare* Książkiewicz – Leszczyński, fig. 13 (also Leszczyński, 1993, fig. 7).
 non 1991 *Megagraption irregulare* Książkiewicz – Leszczyński & Seilacher, 299, figs. 2, 7-8 [= *Megagraption submontanum*].
 partim 1992 *Megagraption irregulare* – Leszczyński, pl. 7, fig. 1 [non pl. 2, fig. 2 = *Megagraption submontanum*].
 ? 1992c *Megagraption irregulare* Książkiewicz – Mikuláš, 393, text-fig. 3.
 v 1993 *Megagraption* isp. – Tunis & Uchman, 93 [not figured].
 ? 1993b *Megagraption irregulare* Książkiewicz – Li, pl. 1, fig. 5.
 non 1995 *Megagraption irregulare* Książkiewicz – Gámez Vintaned & Mayoral, 225, pl. 1, fig. 3.
 v 1996a *Megagraption irregulare* Książkiewicz – Tunis & Uchman, 183, fig. 7F-G.
 ? 1996 *Palaeochorda submontana* Azpeitia – Twitchett & Wignall, 142, fig. 3b.
 ? 1997 *Protopalaeodictyon* ichnosp. Zagora, 362, figs. 6.4, 7.7.

Emended diagnosis: *Megagraption* with meshes bordered by only slightly winding strings, which commonly branch at approximately right angle.

Material: 9 specimens (UJ TF 80, 387, 391, 809 (holotype), 985, 1137, 1343, 1345, 2053).

Remarks: *M. irregulare* occurs reservedly from Silurian (Crimes & Crossley, 1991) to Miocene (D'Alessandro, 1982) in deep-water, mainly flysch deposits. Li (1993b) illustrated not fully convincing *M. irregulare* from the Ordovician of China.

Megagraption submontanum (Azpeitia Moros 1933)

Fig. 105

- 1877 *Cylindrites vermicularis* Hr. – Heer, 115, pl. 45, figs. 12-13 (nomen oblitum).
 ? 1877 *Cylindrites montanus* Hr. – Heer, 159, pl. 68, fig. 11 (nomen oblitum).
 * 1933 *Cylindrites submontanus* n. sp. – Azpeitia Moros, 44, fig. 21b.
 ? 1939 *Palaeodictyon tenue* sp. nov. – Koriba & Miki, 61, pl. 5, fig. 4.
 1959 unnamed – Seilacher, tab. 1, fig. 19.
 v 1961 *Palaeochorda submontana* (Azpeitia) – Książkiewicz, 883, pl. 1, fig. 3.
 1967 *Unarites suleki* sp. n. – Macsotay, 38, figs. 27, 29, 36.
 v 1970 *Palaeochorda submontana* (Azpeitia) – Książkiewicz, 302, fig. 4d.
 v partim 1970 *Protopalaeodictyon incompositum* ichnogen. nov. – Książkiewicz, 303, fig. 4e3 [non fig. 4e1, 4e2].
 v ?partim 1970 *Palaeophycus* – Książkiewicz, 303, fig. 4c1 (?non fig. 4c2).
 1971 reticulate trail – Tanaka, 20, pl. 7, figs. 3-4.
 v partim 1977 *Protopalaeodictyon incompositum* Książkiewicz – Książkiewicz, 174, text-fig. 40i [non pl. 24, figs. 3-4, text-fig. 40a-h, j-q = *Protopalaeodictyon incompositum*].
 v partim 1977 *Protopalaeodictyon submontanum* (Azpeitia) – Książkiewicz, 177, pl. 25, figs. 1-2, 4-5, text-fig. 41b-n, p [non pl. 25, fig. 3, text-fig. 41a, o = *Megagraption irregulare*].
 1977a *Megagraption irregulare* Książkiewicz – Seilacher, 321, fig. 11a, d.
 1978 *Palaeochorda submontana* (Azpeitia) – Radwański, 57, pl. 4, fig. 1.
 1978 *Protopalaeodictyon* Książkiewicz – Kern, 253, fig. 9F.
 1988 *Helminthoidae* – Leshukh, pl. 1, figs. g-e.
 1988 *Protopalaeodictyon submontanum* (Azpeitia Moros) – McCann & Pickerill, 341, fig. 4.9.
 ? partim 1989 *Megagraption angulare* n. ichnosp. – Stepanek & Geyer, 22, pl. 3, fig. 20, text-fig. 6f [non pl. 3, figs. 19, 21-24, text-fig. 6a-e, g = *Megagraption irregulare*].
 1991 *Megagraption irregulare* Książkiewicz – Leszczyński & Seilacher, 299, figs. 2, 7-8.

- non 1991 *Protopalaeodictyon submontanum* (Azpeitia Moros) – Crimes & Crossley, 51, fig. 10j-k [= *Pseudopalaeodictyon* isp.].
 1992 *Megagraption irregulare* – Leszczyński, pl. 2, fig. 2.
 v 1993 *Protopalaeodictyon incompositum* Książkiewicz – Tunis & Uchman, 92, fig. 8F.
 v 1993 *Protopalaeodictyon submontanum* (Azpeitia Moros) – Tunis & Uchman, 92 [not figured].
 ?non 1993 *Protopalaeodictyon submontanum* (Azpeitia Moros) – McCann, 49, fig. 6H [indicates as *Protopalaeodictyon* in

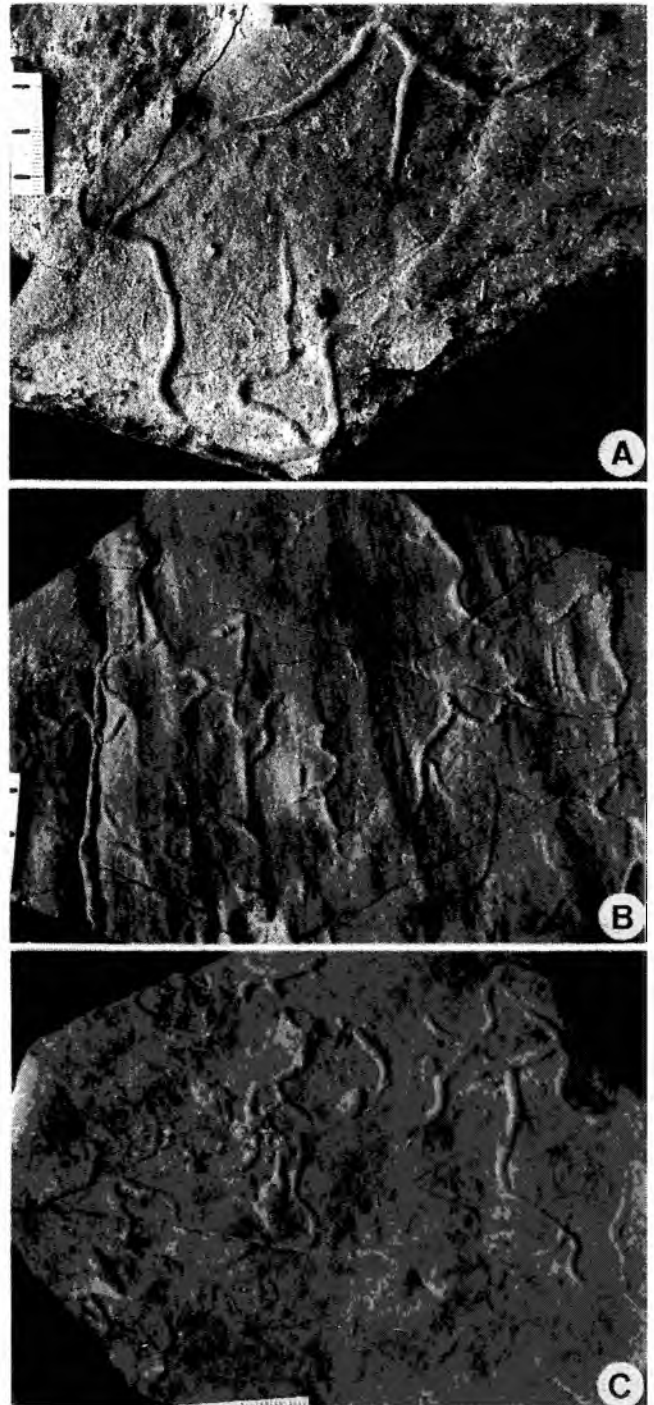


Fig. 105. *Megagraption submontanum* (Azpeitia Moros) on soles of turbiditic sandstone beds. A. UJ TF 1190, Hieroglyphic beds (Eocene), Komańcza. B. UJ TF 2575 (label lost). C. UJ TF 765, Jordanów-Munkacz stream (part of label lost). Scales in A, C in mm, scale in B in cm

- McCann, 1990, 248, fig. 5e].
 ? 1993 *Megagraption irregulare* Książkiewicz – Miller, 21, fig. 5P.
 v 1996a *Protopalaeodictyon submontanum* (Azpeitia Moros) – Tunis & Uchman, 183, figs. 4F, 7E.
 v 1996b *Protopalaeodictyon submontanum* (Azpeitia Moros) – Tunis & Uchman, 11, fig. 13D.
 v 1996 *Protopalaeodictyon submontanum* (Azpeitia-Moros) – Marinčić *et al.*, fig. 5C.
 v 1997 *Protopalaeodictyon submontanum* (Azpeitia Moros) – Wetzell & Uchman, 150, fig. 5E.

Emended diagnosis: *Megagraption* with meshes bordered by distinctly winding strings. Acute angles of branchings are common.

Material: 16 specimens (UJ TF 340, 388, 454, 635, 637, 640, 657, 765, 793, 1123, 1148, 1156, 1190, 1255, 1258, 2575).

Remarks: *M. submontanum* occurs exclusively in deep water, mainly in flysch deposits, reservedly from Lower Carboniferous (Stepanek & Geyer, 1989), surely from Cenomanian to Eocene (Książkiewicz, 1977).

Paleodictyon Meneghini in Sari & Meneghini 1850

Diagnosis: Three-dimensional network trace fossil consisting of horizontal net composed of regular to irregular hexagonal meshes and vertical outlets. Preferentially, the net is preserved (after Uchman, 1995).

Remarks: The Książkiewicz collection contains several ichnotaxa of *Paleodictyon*, which are revised in this paper according to the morphometric scheme devised by Uchman (1995), where the reader can find a review of this ichnogenus.

Ichnosubgenus *Glenodictyum* Van der Marck 1863

Paleodictyon (Glenodictyum) minimum Sacco 1888

- * 1888 *Paleodictyon minimum* Sacc. – Sacco, 11, pl. 1, fig. 6.
 v 1970 *Paleodictyon minutissimum* ichnosp. n. – Książkiewicz, 306, pl. 4a-b.

Diagnosis: Very small *Glenodictyum*, mesh-size up to 2 mm, string diameter up to 0.5 mm (Uchman, 1995).

Material: 8 specimens (UJ TF 89b, 161b, 155b, 307b, 317, 849, 1158, 1196).

Paleodictyon (Glenodictyum) latum Vialov & Golev 1965

- 1965 *Paleodictyon latum* sp. nova – Vialov & Golev, 100, pl. 2, fig. 2.

Diagnosis: Very small *Glenodictyum*, mesh-size up to 2 mm, string diameter from 0.5 to 1.0 mm (modified Uchman 1995).

Material: 11 specimens (UJ TF 111, 168, 170, 172, 318, 321, 324, 333, 584, 894, 1258).

Paleodictyon (Glenodictyum) strozzii Meneghini 1850 Figs. 44A, 62

- * 1850 *Paleodictyon strozzii* nob. – Meneghini in Savi & Meneghini, 484.
 v 1970 *Paleodictyon intermedium* ichnosp. nov. – Książkiewicz, 306, fig. 4g.
 partim 1977 *Paleodictyon tellini* Sacco – Książkiewicz, 197, pl. 28, fig. 3.

Diagnosis: Small *Glenodictyum*, net 2–6 mm in size and 0.2–1.0 mm in string diameter (Uchman, 1995).

Material: 32 specimens (UJ TF 18, 63 67–68, 101, 214, 273, 301, 316, 319–320, 322–324, 326, 328, 330–332, 307a-b, 373, 978, 1102, 1259, 1496, 1524, 1560, 1713, 1715, 1761, 1800).

Paleodictyon (Glenodictyum) miocenicum Sacco 1886

- * 1886 *Paleodictyon miocenicum* Sacc. – Sacco, 301, fig. 4.

Diagnosis: Small *Glenodictyum*, mesh-size 2–6 mm, string diameter 1.0–1.6 (Uchman, 1995).

Material: 2 specimens (UJ TF 64–65).

Paleodictyon delicatulum Uchman 1995

Diagnosis: Small *Paleodictyon*, mesh-size 6–14 mm, string diameter up to 0.8 mm (Uchman, 1995).

Material: 6 specimens (UJ TF 187–188, 262, 307a, 811, 1162 (holotype)).

Paleodictyon (Glenodictyum) majus Meneghini in Peruzzi 1880

- * 1880 *Paleodictyon majus* Mgh. – Peruzzi, 7, pl. 1, fig. 1.

Diagnosis: Medium-sized *Glenodictyum*, mesh-size 6–14 mm, string diameter 0.8–1.6 mm (Uchman, 1995).

Material: 50 specimens (UJ TF 89a, 155a, 158–161a, 163–164, 167, 174, 184, 186, 229, 260, 264–272, 280–283, 285, 287–289, 292–295, 297, 300, 304, 305–306, 308, 491, 660, 756, 787, 840, 857, 976–977, 979, 982, 1016, 1638).

Paleodictyon (Glenodictyum) maximum (Eichwald 1868)

- * 1868 *Cephalites maximus* – Eichwald, 82, pl. 7, fig. 12.

Diagnosis: Medium-sized *Glenodictyum* with thick string; mesh-size up to 14 mm, string diameter 1.6–2.8 mm.

Material: 1 specimen (UJ TF 92).

Paleodictyon (Glenodictyum) gomezii Azpeitia Moros 1933

- * 1933 *Paleodictyon gomezii* n. sp. – Azpeitia Moros, 43, pl. 9, fig. 20.
 v 1977 *Paleodictyon* aff. *gomezii* Azpeitia Moros – Książkiewicz, 197, pl. 29, fig. 4.

Diagnosis: Very large *Glenodictyum*, mesh-size more than 40 mm, string diameter more than 1.6 mm (Uchman, 1995).

Material: 1 specimen (UJ TF 2005).

(ICHO)TAXA NOT RECOMMENDED FOR FURTHER USE

Pararusophycus Książkiewicz 1977 Fig. 64

The ichnogenus *Pararusophycus* Książkiewicz (1977, p. 54, pl. 1, fig. 6), represented by only one ichnospecies, *P. oblongus* Książkiewicz, which is based on only one specimen (UJ TF 114), displays features of *Scolicia* and is included in and discussed under *Scolicia* isp. in this paper. Therefore, it is not recommended for further use.

Rhabdoglyphus Vassoevich 1951

This ichnogenus was defined by Vassoevich for hypichnial cylinders composed of dense, partially invaginated calices. Bouček & Eliáš (1962) described under this ichnogenus hypichnial cylinders with rosary-like swellings.

These specimens were separated from *Rhabdoglyphus* by Vialov (1971) as ichnogenus *Fustiglyphus*.

Książkiewicz (1977) distinguished only *Rhabdoglyphus* also for specimens of the *Fustiglyphus* morphology. He distinguished *Rhabdoglyphus grossheimi* Vassoevich and new ichnospecies *Rh. spinosus*, *caliciformis*, *compositus*, and *sulcatus*. *Rhabdoglyphus* and *Fustiglyphus* were recently revised by Stanley & Pickerill (1993) and they separated the Książkiewicz ichnospecies into *Fustiglyphus annulatus* Vialov, *Rhabdoglyphus grossheimi* Vassoevich, and *R. spinosus* Książkiewicz. This separation, with some correction (see discussion below), can be accepted at the ichnospecies level. However, all these trace fossils can be ascribed to other ichnogenera, which display the same type of morphology and fossil behaviour. For this reason, *Fustiglyphus* is included in *Hormosiroidea* Schaffer and part of the Książkiewicz material is considered under this ichnogenus. *Rhabdoglyphus grossheimi* Vassoevich is included in *Protovirgularia dichotoma* McCoy, and *Rhabdoglyphus* aff. *spinosus* Książkiewicz in *Ubinia altrenans* (Seilacher). For this reason *Rhabdoglyphus* is not recommended for further use.

Stanley & Pickerill (1993) excluded Książkiewicz (1977) *Rhabdoglyphus sulcatus* (pl. 3, fig. 9) from *Rhabdoglyphus* and included it in *Palaeophycus annulatus*. Its inclusion in *Palaeophycus* is also very problematic. It is represented by one specimen and its affinity remains enigmatic. The same authors excluded *Rhabdoglyphus compositus* (pl. 3, fig. 10) from *Rhabdoglyphus* and included it also in *Palaeophycus annulatus*. Its inclusion in *Palaeophycus* is also very problematic. Książkiewicz (1977) drew *Rh. compositus* in fig. 6e and referred it to pl. 3, fig. 10. He drew also *Rh. sulcatus* in fig. 6f and referred it to pl. 3, fig. 9. However, the fig. 6e fits better to pl. 3, fig. 10, and fig. 6f to pl. 3, fig. 10. Probably, the figures are misplaced. Nevertheless, Stanley & Pickerill (1993, p. 62) compared the specimen in text-fig. 6f to *Imponoglyphus torquendus*. However, similarity of this specimen and that from pl. 3, fig. 10 is very problematic. The discussed specimens are too poorly represented for their sufficient explanation.

Fucusopsis Palibin in Vassoevich 1932

Ichnogenus *Fucusopsis*, represented by three ichnospecies (*F. angulata*, *F. annulata*, *F. striata*) was included in *Halopoa* Torell in this paper, and can be regarded as its junior objective synonym. Therefore, it is not recommended for further use.

Traucumichnis Książkiewicz 1977

Ichnogenus *Traucumichnis* Książkiewicz, represented only by one ichnospecies, *T. glaber* Książkiewicz (1977, p. 55, pl. 1, fig. 7) (two specimens), is an inorganic structure. This is a group of hemispherical pits on the upper side of a sandstone bed. The depressions are weathering structures of the tafoni type. For this reason, the ichnogenus *Traucumichnis* is not recommended for further use.

Zhang & Wang (1996) described *Traucumichnis zhongguensis* from the Silurian–Devonian deposits of China, but this trace fossil is probably a synonym of some *Bergaueria*

ichnospecies.

Non-organic structures were commonly and are occasionally described as trace fossils (Boyd, 1975; Häntzschel, 1975, Ekdale *et al.*, 1984a, for partial review). Discrimination between organic and inorganic structures is not easy in some cases.

Sabularia Książkiewicz 1977

This ichnogenus was introduced by Książkiewicz (1977) for various cylindrical trace fossils, which can be included in other well-defined ichnogenera which have priority. *Sabularia simplex* was included in *Ophiomorpha annulata* (Książkiewicz) (Uchman, 1995). *Sabularia rudis* is included in *Ophiomorpha* isp., *Sabularia tenuis* is considered as *Arthropycus tenuis* (Książkiewicz), and *Sabularia ramosa* is included in *Planolites beverleyensis* (Billings). For this reason, this ichnogenus is not recommended for further use.

Granularia Pomel 1849

Książkiewicz (1977, p. 80) mentioned the probable occurrence of this ichnogenus in the Carpathians. However, he did not illustrate any specimens. In the collection, he labelled one specimen as *Granularia fuchsi* Książkiewicz. This is a composite trace fossil consisting of ?*Palaeophycus* reworked by ?*Chondrites*. Nonetheless, *Granularia* is poorly defined and is not recommended for further use (Uchman, 1995).

Bostricophyton Squinabol 1890

This ichnogenus was used by Squinabol (1890) who distinguished two ichnospecies. *Bostricophyton pantanellii* is a branched trace fossil, which displays several features of *Chondrites intricatus* and is included in this ichnotaxon in this paper. The second ichnospecies of *Bostricophyton*, *B. etruscus* Squinabol (1890, p. 184, pl. 11, fig. 5) displays features of "*Caulerpites*" *eseri* (Unger) (Fuchs, 1905). Therefore, *Bostricophyton* is not recommended for further use.

Halymenites Sternberg 1833 and *Halymenidium* Schimper 1879

Halymenidium Schimper (1879, p. 37) was established (as algae) for *Halymenites flexuosus* and *H. minor* described by Fischer-Ooster (1858), *Halymenites lumbricoides* described by Heer (1877), and *Phymatoderma Dienalli* Watelet (1866) [the latest ichnotaxon was included in *Ophiomorpha nodosa* Lundgren (Häntzschel, 1952)]. These forms, according to Schimper, are characterized by distinct sporangia. For discussion of these forms, it is necessary to return to *Halymenites*.

Halymenites was erected by Sternberg (1833), who distinguished several taxa under this genus on the basis of a material from the Solnhofen Limestone, which represents various plant remains. I had the opportunity to see several holotypes of the Sternberg's species in the National Museum in Prague, Czech Republic, and can confirm that they are in fact plant body fossils, for instance that illustrated in Fig. 106. Sternberg included *Achilleum dubium* Goldfuss



Fig. 106. *Halymenites stockii* Sternberg from the Solnhofen Limestone (= a plant body fossil). Specimen no 380 in the Sternberg collection. The National Museum in Prague. Scale in mm. Courtesy of R. Mikuláš

(1831), which derives also from the Solnhofen Limestone, in *Halymenites*. Most probably, it is also a plant body fossil. The list of *Halymenites* taxa from the Solnhofen Limestone is as follows:

- 1831 *Achilleum dubium* nobis. – Goldfuss, 221, pl. 1, fig. 2.
 1833 *Halymenites vermiculatus* – Sternberg, 29, pl. 8, fig. 3 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 14].
 1833 *Halymenites cactiformis* – Sternberg, 29, pl. 2, fig. 2 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 15].
 1833 *Halymenites varius* – Sternberg, 29, pl. 2, fig. 4 [also Unger, 1845, 12; Bronn, 1848, 4; Bronn & Roemer, 1850-56: pl. 14, fig. 3; Zingo, 1856, 15].
 1833 *Halymenites subarticulatus* – Sternberg, 29, pl. 4, fig. 2 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 16].
 1833 *Halymenites secundus* – Sternberg, 29, pl. 4, fig. 3 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 17].
 1833 *Halymenites schnitzelini* – Sternberg, 30, pl. 5, fig. 1 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 18].
 1833 *Halymenites cernuus* – Sternberg, 30, pl. 7, fig. 4 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 19].
 1833 *Halymenites stockii* – Sternberg, 30 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 19].
 1833 *Halymenites goldfussii* – Sternberg, 30 [also Unger, 1845, 12; Bronn, 1848, 8; Bronn & Roemer, 1849, 43; Zingo, 1856, 20].
 1833 *Halymenites cylindricus* – Sternberg, 30 [also Unger, 1845, 13; Bronn, 1848, 8].
 1833 *Halymenites brongniarti* – Sternberg, 30 [also Unger, 1845, 12; Bronn, 1848, 8; Zingo, 1856, 20; Schimper, 1869, 193].
 1833 *Halymenites concatenatus* – Sternberg, 30, pl. 2, fig. 1 [also Unger, 1845, 13; Bronn, 1848, 8; Zingo, 1856, 21].
 1833 *Halymenites ramulosus* – Sternberg, 31 [also Unger, 1845, 13; Bronn, 1848, 43].

All of the taxa were erected by Sternberg, and then they were used by Unger (1845), Bronn (1848), and Zingo (1856) and others, exclusively in respect to the material from the Solnhofen Limestone. Only Zingo (1856) used *H. ramulosus* Sternberg for the material from the Jurassic of England. It can be concluded that the type material of *Ha-*

lymenites comprises plant body fossils and does not represent trace fossils.

Massalongo (1859, pp. 8-9) erected the following taxa of *Halymenites* Sternberg: *H. aglaophyllum* Massal., *H. gratelupia* Massal., *H. sarniensis*, *H. undulatus*, *H. callyblepharoides*, *H. linzoides*, *Halymenites elisae*, and *H. antoniae*. The last two forms had been described earlier under the genus *Gastridiopsis*, and *H. linzoides* under the genus *Solenopsis* (Massalongo, 1851). Subsequently, they were re-described by Meschinelli & Squinabol (1892, pp. 69-71). Moreover, these authors discussed *Halymenites crinatus* Massalongo. All of these derive from “calcare marnoso di Salcedo” and are presumably trace fossil. Unfortunately, they are not illustrated and it is impossible to assess their affinity.

Fischer-Ooster (1858) distinguished the following taxa of *Halymenites*:

- 1858 *Halymenites rectus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 2 [also Schimper, 1869, 193].
 1858 *Halymenites flexuosus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 1 [also Schimper, 1869, 193].
 1858 *Halymenites minor* F.O. – Fischer-Ooster, 56, pl. 13, fig. 3; 65, pl. 16, fig. 2 [also Schimper, 1869, 194].
 1858 *Halymenites incrassatus* F.O. – Fischer-Ooster, 65, pl. 16, fig. 3 [also Schimper, 1869, 194].
 1858 *Halymenites dubius* F.O. – Fischer-Ooster, 66, pl. 12, fig. 4.

All of these forms are trace fossils from the Gurnigel Flysch deposits of Switzerland. I have examined these forms, which are housed in the Natural History Museum in Bern. They represent simple or branched, flattened cylindrical trace fossils covered with small granular muddy pellets.

Halymenites incrassatus Fischer-Ooster (1858, pl. 16, fig. 3, Fischer-Ooster coll. 16/3, Bern) (Fig. 25A) is an endichnial, horizontal, straight, strongly flattened tube, observed in the epichnial position in a gray marly mudstone. The tube is 6–7 mm wide, and has a swelling at the central part, which is observed at the distance of about 70 mm. The swollen part is up to 18 mm wide. The central part of the tube displays a preserved lining consisting of small, oval, dark, strongly flattened, densely packed pellets. The outline of the pellets is indistinct. They are 0.5–1 mm in diameter. The segments of the tube where pellets are not preserved are smooth and have a slightly darker colour. *Chondrites intricatus* occurs together with the described trace fossil at the same level. The specimen derives from the flysch deposits in Föhnern in the Swiss Alps.

Halymenites flexuosus Fischer-Ooster (1858, pl. 13, fig. 2, Fischer-Ooster coll. 13/2, Bern) (Fig. 25B) is an epichnial, endichnial, horizontal, straight, strongly flattened tube, in a light brown massive marlstone. The tube is 16–19 mm wide. It is lined with dark, flattened pellets, which are 1–2 mm in diameter. Commonly, the pellets are poorly outlined, especially at the places where they are most densely packed. The described trace fossil occurs together with *Chondrites targionii* at the same level on the same slab. The latter trace fossil is labelled originally as *Chondrites furcatus* Sternberg. Close to the edge of the specimen, *H. flexuosus* is cross cut by a specimen of the same morphology at a slightly shallower level. The specimen derives from the Upper Cretaceous Gurnigel Flysch, Seeliggraben near Gurnigelbad, the

Fribourgian Alps, Switzerland.

Halymenites minor Fischer-Ooster (1858, pl. 13, fig. 3, Fischer-Ooster coll. 13/3, Bern) (Fig. 25C) is referred to a specimen that is a piece of grey marlstone containing *Chondrites intricatus* and two slightly oblique endichnial, strongly flattened tubes dipping into the rock and observed at the epichnial position. The first tube is 4 mm in diameter and it is observed for the distance of 13 mm. It is lined with very small, about 0.5 mm, indistinct pellets, and filled with dark sediment. The second tube occurs on the edge of the specimen and is incomplete. It is at least 7 mm wide and lined with flattened pellets, which are about 0.5 mm in diameter. The pellets in both tubes display indistinct arcuate arrangement. The described specimen derives from the Upper Cretaceous Gurnigel flysch, Seeligraben near Gurnigelsbad, Fribourgian Alps, Switzerland.

The above described trace fossils, especially *H. flexuosus* and *H. minor*, are identical to *Tubulichnium incertum* Książkiewicz (1977), which is included together with the Fischer-Ooster's species in *Ophiomorpha rectus* (Fischer-Ooster) in this paper. Ettinghausen (1863) recognized the first three of Fischer-Ooster's forms in the Cretaceous-Eocene flysch deposits of Wienerwald, but he was not able to separate them taxonomically and suggested that they belong to a single taxon.

Pelleted filling or lining, which are features of *Alcyonidiopsis* Massalongo and *Ophiomorpha* Lundgren, respectively, can be also recognized in the taxa of *Halymenites* described by Ooster (1869), Heer (1865, 1877), Squinabol (1890) and Fuchs (1894b, lacking species designation). They are listed below.

Saporta (1882) described *Halymenites arnaudi* Saporta & Marion from Cretaceous deposits of France. It is a branched form with irregular margins. It is difficult to discuss this enigmatic form in detail without access to specimens.

Rothpletz (1896) included two taxa of *Halymenites*, *H. lumbricoides* Heer and *H. minor* Fischer-Ooster, in *Granularia* Pomel. Nonetheless, poorly defined, heterogenous *Granularia* Pomel is not recommended for further use (Uchman, 1995). Vialov (1966) reservedly included *Halymenites rectus*, *H. incrassatus*, and *H. flexuosus* Fischer-Ooster in *Ophiomorpha*. The same was also proposed in respect to *H. flexuosus* (Häntzschel, 1975, p. W85). However, according to Häntzschel (1952), these trace fossils which were included in *Halymenidium* Schimper (1879), cannot be included in *Ophiomorpha*, mainly because of smaller dimension. Nevertheless, such argument based solely on size cannot be accepted. Trace fossils of this type can be listed as follows:

- 1865 *Halymenites lumbricoides* – Heer, 245, pl. 10, fig. 11.
- 1869 *Halymenites rectus* Fischer-Ooster – Ooster, 29, pl. 6, fig. 5, pl. 7.
- 1877 *Halymenites minutus* Hr. – Heer, 118, pl. 45, figs. 10-11.
- 1877 *Halymenites flexuosus* Fisch.-Oost. – Heer, 165, pl. 64, fig. 10.
- 1877 *Halymenites minor* Fisch.-Oost. – Heer, 165.
- 1877 *Halymenites lumbricoides* Hr. – Heer, 166, pl. 64, figs. 11-12.
- 1885 *Halymenidium lumbricoides* Heer – Fugger & Kastner, 74 [no illustration].
- 1890 *Halymenides Taramelli* n. sp. – Squinabol, 184, pl. 8, figs. 5-6.
- 1890 *Halymenides Grateloupiaformis* n. sp. – Squinabol, 185, pl. 7, fig. 7.

1894b *Halymenites* – Fuchs, pl. 2, fig. 4.

Lesquereux (1873, 1878) described a few Upper Cretaceous and Tertiary taxa of *Halymenites*, which in fact represents *Ophiomorpha* (Häntzschel, 1952); *H. striatus* probably belongs to *Spongiomorpha*. These forms, including those described by latter authors, are listed below.

- 1873 *Halymenites major* – Lesquereux, 373 [= *Ophiomorpha*, Häntzschel, 1952].
- 1878 *Halymenites striatus* Lesqx. – Lesquereux, 37, pl. 1, fig. 6.
- 1878 *Halymenites major* Lesqx. – Lesquereux, 38, pl. 1, figs. 7-8 [= *Ophiomorpha nodosa* Lundgren].
- 1878 *Halymenites minor*? F.O. – Lesquereux, 39, pl. 1, fig. 9.
- 1937 *Halymenites major* Lesquereux – Carter, 257, pls. 43-44.
- 1939 *Halymenites major* Lesquereux – Brown, 253, pl. 62, figs. 1-7, pl. 63, figs. 1-2 [= *Ophiomorpha*].
- 1942 *Halymenites* – Patterson, 271, fig. 1 [= *Ophiomorpha* isp.].
- 1948 *Halymenites major* Lesquereux – Shimer & Shrock, 717, pl. 303, fig. 20.
- 1967 *Halymenites* sp. – Macsotay, 30, figs. 45, 47, 50, 56.
- 1971 ?*Halymenites* sp. – Jerzykiewicz, 174, pl. 4, fig. 7.

It can be concluded that ichnogenus *Halymenites* includes heterogenous ichnospecies (Häntzschel, 1952, with references). The type material represents plant remains. The forms described later, which are trace fossils, can be ascribed to the well-defined ichnogenera *Alcyonidiopsis* or *Ophiomorpha*, including ichnotaxa used for definition of *Halymenidium* Schimper (1869). Thus, *Halymenites* Sternberg and *Halymenidium* Schimper are not recommended for further use. Therefore, ichnospecies described by Książkiewicz (1977) under *Halymenidium* should be placed in another ichnogenus. They are placed in *Spongiomorpha* de Saporta in this paper.

Buthotrephis Hall 1847

Buthotrephis Hall (1847) is included in *Chondrites* Sternberg (Häntzschel, 1975; Fu, 1991) as was previously suggested by Osgood (1970, p. 342). *Buthotrephis palmatus* distinguished by Hall (1852) is included in *Phycodes* Richter (Seilacher, 1955). For these reasons *Buthotrephis* is not recommended for further use. The Książkiewicz (1977) material described as *Buthotrephis* mostly belongs to *Thalassinoides* Ehrenberg or *Phycodes* Richter.

Tubulichnium Książkiewicz 1977

This ichnogenus was distinguished for flattened tubes lined with small pellets. Książkiewicz (1977) distinguished only one ichnospecies, *T. incertum*. This trace fossil is identical to the *Halymenites* described by Fischer-Ooster from the flysch deposits of Switzerland (personal observations). *Tubulichnium* displays features of *Ophiomorpha* and is assigned to *Ophiomorpha rectus* (Fischer-Ooster) in this paper. Therefore, *Tubulichnium* is not recommended for further use.

Tuberculichnus Książkiewicz 1977

Książkiewicz (1977) distinguished three ichnospecies of *Tuberculichnus*: *T. vagans*, *T. meandrinus* (Fig. 70), and *T. bulbosus*. The holotypes of *T. vagans* and *T. meandrinus*

display the characteristic carinate (amygdaloid) cross-section, which is the typical feature of *Protovirgularia* McCoy and are described as *Protovirgularia vagans* in this paper. The holotype of *T. bulbosus* displays features of *?Parahaentzschelinia* isp. and is included in this paper in this ichnogenus. Moreover, some specimens labelled as *Tuberculichnus* are casts of the upper terminations of row of vertical burrows, typical of *Saerichnites* Billings *sensu* Uchman (1995), and *T. bulbosus* is included in this ichnogenus in this paper. Therefore the ichnogenus is not recommended for further use.

Helminthoida Schafhäütl 1851

This commonly used ichnogenus has in fact a weak basis. Schafhäütl (1851) distinguished two species: *H. crassa* and *H. irregularis*. The holotype of the second ichnotaxon displays all features of *Nereites* and is included in this ichnogenus (Uchman, 1995). *H. crassa*, the holotype of which is known only from a drawing, is considered as the synonym of *Helminthoida labyrinthica*, and both are included in *Nereites irregularis* (Schafhäütl). Heer (1877) described under *H. crassa* hypichnial trace fossils which are different from Schafhäütl's forms and which were recently included in *Helminthorhapha* Seilacher. Similar problems concern several 19th century trace fossils described under *Helminthoida* (Uchman, 1995). Therefore, *Helminthoida* is not recommended for further use.

Książkiewicz distinguished *Helminthoida labyrinthica* (Heer), *H. serrata* Książkiewicz, *H. crassa* Schafhäütl, *H. miocenica* Sacco, *H. alterna* Książkiewicz, *H. helminthopsoidea* Sacco, and *H. aculeata* Książkiewicz. The two first ichnospecies are included in *Nereites irregularis* Schafhäütl; *H. crassa* and *H. miocenica* are regarded as *Helminthorhapha*; *H. alterna* is included in *Desmograpton alternum* (Książkiewicz) (Uchman, 1995). *H. helminthopsoidea* is included in *Cosmorhapha helminthopsoidea* and *H. aculeata* in *Belocosmorhapha aculeata* in this paper.

Muensteria Sternberg 1833

The type material of *Muensteria* Sternberg comprises different forms, which partially are plant body fossils or different trace fossils. For this reason, *Muensteria* Sternberg is not recommended for further use (Mikuláš & Uchman, 1996). The problem is partially discussed in this paper under *Beaconites*.

Książkiewicz (1977) described *M. geniculata* Sternberg, *M. hamata* Fischer-Ooster, and *M. planicostata* n. ichnosp. The type material of *M. geniculata* Sternberg is included in *Hydrancylus geniculata* (Sternberg) (Fu, 1988). The Książkiewicz material contains unwallled meniscate trace fossils, which can be included in *Taenidium* Heer (cf. D'Alessandro & Bromley, 1987).

M. hamata is described as *Phycosiphon hamata* in this paper.

The *M. planicostata* is based on one specimen, which represent a horizontal, unwallled meniscate trace fossil and can be ascribed to *Taenidium* Heer (cf. D'Alessandro & Bromley, 1987).

Keckia Glocker 1841

This ichnogenus is poorly defined. D'Alessandro & Bromley (1987) regarded it as a nomen dubium. The type material of Glocker from the shallow-water Cretaceous deposits of Moravia, Czech Republic, although very poor, was analysed by Fu (1991). She presented *Keckia annulata* Glocker as a tightly spaced series of horizontal burrows with half-moon menisci, branching at an acute angle from a stem-like converged area, and concluded that it represents the unique behaviour within the "Muensterioiden".

Several authors have used this ichnogenus, but commonly for different structures. Häntzschel (1975; fig. 47.2) illustrated *K. annulata* with references to the original publication of Glocker. However, the publication (Glocker, 1841, pl. 4) contains drawings of different material. The specimen was illustrated by von Otto (1852, pl. 1) and its photograph (properly referred to the von Otto's publication) was used by Häntzschel (1938, fig. 4). This is rather a meniscate *Thalassinoides*. Similarly, *K. cylindrica* von Otto (1852, p. 5, pl. 2) is most probably a smooth *Thalassinoides*. These trace fossils derive from shallow marine Cretaceous sandstones, as does Glocker's the type material. *Keckia andina* Borello (1966), from Jurassic deposits of Argentina, resembles *Thalassinoides*. According to Häntzschel (1975, p. W75), *K. häntzscheli* Hundt (1940) does not belong to *Keckia*. It is a narrow winding, ?meniscate trace fossil from the Devonian of Thuringia. Häntzschel (1938) regarded *Muensteria annulata* Schafhäütl (1851) as ichnotaxon of *Keckia* but, according to Heer (1877), it belongs to *Taenidium fischeri*, and, according to Keighley & Pickerill (1994), to (?) *Cladichnus* isp.

Książkiewicz (1977) described *Keckia annulata* Glocker and *K. hoessii* (Sternberg). Without analysis of the specimens, Keighley & Pickerill (1994) included *K. annulata* Glocker from Książkiewicz (1977, pl. 3, fig. 14) material (Fig. 67B) in *Taenidium* isp., and *K. hoessii* (Sternberg) (Książkiewicz, 1977, p. 64, pl. 3, figs. 15-16) in *Taenidium* spp. However, after studying of the specimens, this view cannot be accepted. *K. hoessii* (Sternberg) from the Książkiewicz material was partially included in *Beaconites capronus* (Howard & Frey), *Keckia* aff. *hoessii* (Sternberg) in *Taenidium* isp., and *K. annulata* in *Protovirgularia* McCoy (see description of these ichnotaxa). None of the specimens described or labelled by Książkiewicz as *Keckia* resembles Glocker's material.

Most probably, *Keckia* as an ichnogenus is only useful in the sense presented by Fu (1991), however this problem needs a separate examination.

Taphrhelminthoida Książkiewicz 1977

Taphrhelminthoida was erected by Książkiewicz for systematically meandering trace fossils of the *Taphrhelminthopsis*-morphology. All ichnospecies of *Taphrhelminthoida* were included in *Scolicia strozzii* (Uchman, 1995) because of continuous pasasage from meandering and non-meandering forms. The differences in the shape of the ridge in those trace fossils is strongly controlled by preservational processes. For these reasons *Taphrhelminthoida* is not recommended for further use.

MISCELLANEA

The Książkiewicz collection contains a few trace fossils, which belong to undetermined ichnotaxa. They are represented by single specimens and commonly are incompletely preserved. For this reason they are not included in the main part of ichnotaxonomic description. They may be useful for further ichnotaxonomic investigations.

Form A
Fig. 107

v 1977 *Helminthoida crassa* (Schalhäutl) – Książkiewicz, text-fig. 34j.

Material: 1 specimen (UJ TF 788).

Description: Hypichnial, convex, spirally coiled meandering string, about 1 mm in diameter. The structure covers an area of about 40 mm in diameter.

Remarks: The internal part of the structure is identical to *Spirorhaphé involuta*, however the outermost parts display meanders as in *Helminthorhaphé*. It seems to be a transitional form between *Spirorhaphé* and *Helminthorhaphé*.



Fig. 107. Form A. Sole of a turbiditic sandstone bed. UJ TF 788, Hieroglyphic beds (Eocene), Tokarnia (labelled as *Helminthoida crassa*). Scale in mm

Form B
Fig. 108

Material: 1 specimen (UJ TF 1797).

Description: Hypichnial, convex, spirally arranged short ridges and knobs, which are about 1 mm wide. The structure covers an



Fig. 108. Form B. Sole of a turbiditic sandstone bed. UJ TF 1797, Zawoja-Końskie (part of label lost). Scale in mm

area of about 30 mm in diameter.

Remarks: Arrangement of the structure resembles *Spirorhaphé*. However, the presence of knobs suggests occurrence of vertical shafts connecting the horizontal elements and sea-floor. This feature is not known in *Spirorhaphé*.

Form C
Fig. 109

Material: 1 specimen (UJ TF 2029).

Description: Hypichnial full relief composed of pads of sediment arranged in winding and branched strings. The strings are 5–8 mm in diameter.

Remarks: This structure is produced by a deposit-feeder. It belongs maybe to *Nereites* or *Lophoctenium*. The preservation of the structure does not allow for more detailed determination.

Form D
Fig. 110

Material: 1 specimen (UJ TF 2583).

Description: Hypichnial structure composed of tightly spaced, slightly arcuate branchings, which emerge obliquely from a central axis. The branchings are about 1.8 mm wide, 9–12 mm long, and about 1 mm apart. The structure is about 16 mm wide.

Remarks: It is not impossible that this is a fragment of *Lophoctenium minimum* Fu (1991), which is known from flysch deposits.

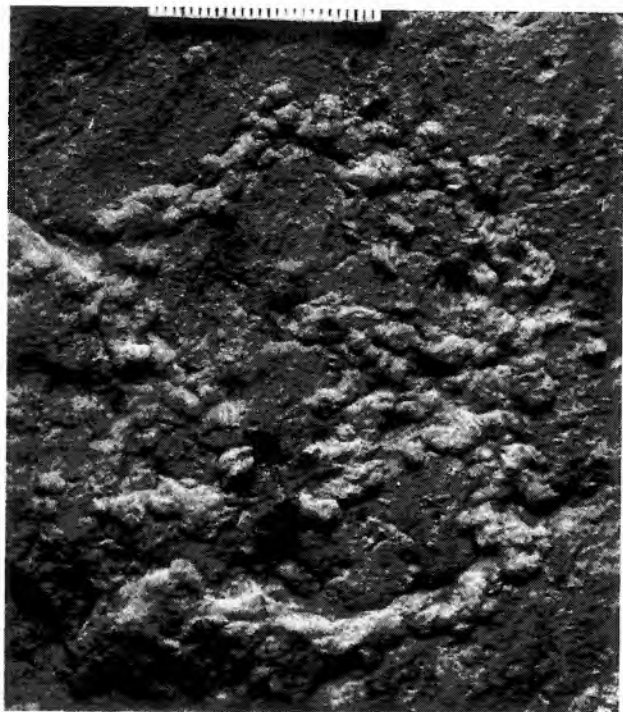


Fig. 109. Form C. Sole of a turbiditic sandstone bed. UJ TF 2029, Ciężkowice Sandstone (Eocene), Gródek (part of label lost). Scale in mm



Fig. 111. Form E. Sole of a turbiditic sandstone bed. UJ TF 2617, (label lost). Scale in mm



Fig. 110. Form D. Sole of a turbiditic sandstone bed. UJ TF 2583, Zwaoja-Końskie (part of label lost). Scale in m



Fig. 112. Form F. Sole of a turbiditic sandstone bed. UJ TF 1380, Lipnica Mała (part of label lost). Scale in mm

Form D

Fig. 111

Material: 1 specimen (UJ TF 2617).

Description: Hypichnial short ridge, 32 mm long, 5 mm wide, from which arcuate elevations diverge about 5 mm apart.

Form E

Fig. 112

Material: 1 specimen (UJ TF 1380).

Description: Hypichnial short ridge, about 2 mm wide, which passes into a single row of tubercles, which are located about 1 mm apart.

Remarks: This is a semi-relief. The tubercles are probably remnants of cross-sectioned oblique shafts, which emerge from a basal tunnel. This resembles the arrangement of *Trichophycus* Miller & Dyer (Geyer & Uchman, 1995).

ICHNOTAXONOMY OF THE KSIĄŻKIEWICZ COLLECTION AFTER REVISION

Comparison of Książkiewicz ichnotaxa and after revision is summarised in Table 1

Table 1

| Książkiewicz ichnotaxa before revision | Książkiewicz ichnotaxa after revision |
|--|---|
| <i>Mammillichnis aggeris</i> Chamberlain | <i>Mammillichnis aggeris</i> Chamberlain |
| <i>Bergaueria prantli</i> Książkiewicz | ? <i>Bergaueria prantli</i> Książkiewicz |
| <i>Pararusophycus oblongus</i> Książkiewicz | <i>Scolicia</i> isp. |
| <i>Traucumichnis glaber</i> Książkiewicz | inorganic structure |
| <i>Arthropycus annulatus</i> Książkiewicz | <i>Ophiomorpha annulata</i> (Książkiewicz) |
| <i>Arthropycus strictus</i> Książkiewicz | <i>Arthropycus strictus</i> Książkiewicz |
| <i>Arthropycus dzułyński</i> Książkiewicz | <i>Protovirgularia dzułyński</i> (Książkiewicz) |
| <i>Fucusopsis angulata</i> Palibin | <i>Halopoa imbricata</i> Torell |
| <i>Fucusopsis annulata</i> Książkiewicz | <i>Halopoa annulata</i> (Książkiewicz) |
| <i>Fucusopsis striata</i> (Hall) | <i>Halopoa imbricata</i> Torell |
| <i>Halymenidium sublumbroides</i> (Azpeitia) | <i>Spongiomorpha sublumbroides</i> (Azpeitia Moros) |
| <i>Halymenidium oraviense</i> Książkiewicz | <i>Spongiomorpha oraviense</i> (Książkiewicz) |
| <i>Keckia annulata</i> Glocker | <i>Protovirgularia</i> isp. |
| <i>Keckia hoessii</i> (Sternberg) | cf. <i>Beaconites capronus</i> (Howard & Frey) |
| <i>Planolites reinecki</i> Książkiewicz | <i>Planolites reinecki</i> Książkiewicz |
| <i>Rhabdoglyphus grossheimi</i> Vassoevich | <i>Protovirgularia dichotoma</i> McCoy |
| <i>Rhabdoglyphus spinosus</i> Książkiewicz | <i>Hormosiroidea annulata</i> (Vialov) |

| | |
|--|---|
| <i>Rhabdoglyphus</i> aff. <i>spinosus</i> Książkiewicz | <i>Ubinia alternans</i> (Seilacher) |
| <i>Rhabdoglyphus caliciformis</i> Książkiewicz | <i>Hormosiroidea annulata</i> (Vialov) |
| <i>Rhabdoglyphus</i> aff. <i>caliciformis</i> Książkiewicz | <i>Hormosiroidea annulata</i> (Vialov) |
| <i>Rhabdoglyphus sulcatus</i> Książkiewicz | <i>Hormosiroidea annulata</i> (Vialov) |
| <i>Rhabdoglyphus compositus</i> Książkiewicz | ?non <i>Hormosiroidea</i> isp. |
| <i>Sabularia simplex</i> Książkiewicz | <i>Ophiomorpha annulata</i> (Książkiewicz) |
| <i>Sabularia rudis</i> Książkiewicz | <i>Ophiomorpha</i> isp. |
| <i>Sabularia tenuis</i> Książkiewicz | <i>Arthropycus tenuis</i> (Książkiewicz) |
| <i>Sabularia ramosa</i> Książkiewicz | <i>Planolites beverleyensis</i> Billings |
| <i>Buthotrephis</i> aff. <i>palmata</i> Hall | <i>Thalassinoides suevicus</i> (Rieth), <i>Phycodes bilix</i> (Książkiewicz) |
| <i>Buthotrephis</i> aff. <i>succulens</i> Hall | <i>Thalassinoides suevicus</i> (Rieth), <i>Phycodes bilix</i> (Książkiewicz) |
| <i>Buthotrephis bifurcata</i> Książkiewicz | <i>Glockerichnus alata</i> (Seilacher) |
| <i>Buthotrephis bilix</i> Książkiewicz | <i>Phycodes bilix</i> (Książkiewicz) |
| <i>Chondrites aequalis</i> Sternberg | <i>Chondrites intricatus</i> (Brongniart) |
| <i>Chondrites affinis</i> (Brongniart) | <i>Chondrites targionii</i> (Brongniart) |
| <i>Chondrites arbuscula</i> Fischer-Ooster | <i>Chondrites targionii</i> (Brongniart) |
| <i>Chondrites expansus</i> Fischer-Ooster | <i>Chondrites intricatus</i> (Brongniart) |
| <i>Chondrites filiformis</i> Fischer-Ooster | <i>Chondrites intricatus</i> (Brongniart) |
| <i>Chondrites flexilis</i> Fischer-Ooster | <i>Chondrites intricatus</i> (Brongniart), large foraminifer |
| <i>Chondrites furcatus</i> (Brongniart) | <i>Chondrites targionii</i> (Brongniart) |
| <i>Chondrites intricatus</i> (Brongniart) | <i>Chondrites intricatus</i> (Brongniart) |
| <i>Chondrites patulus</i> Fischer-Ooster | <i>Chondrites patulus</i> Fischer-Ooster |
| <i>Granularia</i> indet. | ? <i>Palaeophycus</i> isp. |

| | |
|--|--|
| <i>Lophoctenium ramosum</i> (Toula) | <i>Lophoctenium ramosum</i> (Toula) |
| <i>Lophoctenium</i> aff. <i>comosum</i> Richter | <i>Lophoctenium</i> aff. <i>comosum</i> Richter |
| <i>Phycodes</i> aff. <i>harlani</i> Hall | ichnosp. indet. |
| <i>Strobilorhaphe clavata</i> Książkiewicz | <i>Strobilorhaphe clavata</i> Książkiewicz |
| <i>Strobilorhaphe pusilla</i> Książkiewicz | <i>Strobilorhaphe pusilla</i> Książkiewicz |
| <i>Strobilorhaphe glandifer</i> Książkiewicz | <i>Strobilorhaphe glandifer</i> Książkiewicz |
| <i>Taenidium annulatum</i> (Schafhäütl) | ? <i>Taenidium</i> isp. |
| <i>Taenidium isseli</i> (Squinabol) | <i>Taenidium</i> isp., <i>Cladichnus fischeri</i> (Heer) |
| <i>Bostricophyton pantanellii</i> Squinabol | <i>Chondrites intricatus</i> (Brongniart) |
| <i>Lorenzina</i> aff. <i>apenninica</i> Gabelli | <i>Lorenzina apenninica</i> De Gabelli |
| <i>Lorenzina carpathica</i> (Zuber) | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Lorenzina kuznari</i> Książkiewicz | <i>Lorenzina kuznari</i> Książkiewicz |
| <i>Lorenzina curticosata</i> Książkiewicz | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Lorenzina kulczynskii</i> Kuźniar | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Lorenzina peralta</i> Książkiewicz | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Lorenzina moreae</i> Renz | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Lorenzina</i> aff. <i>moreae</i> Renz | <i>Lorenzina carpathica</i> (Zuber) |
| <i>Sublorenzina plana</i> Książkiewicz | <i>Lorenzina plana</i> (Książkiewicz) |
| <i>Sublorenzina nowaki</i> (Książkiewicz) | <i>Lorenzina nowaki</i> (Książkiewicz), <i>Glockerichnus glockeri</i> , <i>Glockerichnus</i> isp. |
| <i>Sublorenzina pustulosa</i> Książkiewicz | ? <i>Lorenzina pustulosa</i> (Książkiewicz) |
| <i>Sublorenzina pusilla</i> Książkiewicz | <i>Lorenzina plana</i> (Książkiewicz) |
| <i>Capodistria vetersi</i> Vialov | <i>Capodistria vetersi</i> Vialov, <i>Glockerichnus</i> isp. |
| <i>Glockeria glockeri</i> Książkiewicz | <i>Glockerichnus glockeri</i> (Książkiewicz) |
| <i>Glockeria sparsicostata</i> Książkiewicz | ? <i>Glockerichnus sparsicostata</i> (Książkiewicz) |

| | |
|---|---|
| <i>Glockeria disordinata</i> Książkiewicz | ? <i>Glockerichnus disordinata</i> (Książkiewicz) |
| <i>Glockeria parvula</i> Książkiewicz | ? <i>Glockerichnus parvula</i> (Książkiewicz) |
| <i>Fascichnum extantum</i> Książkiewicz | <i>Fascichnum extantum</i> Książkiewicz |
| <i>Asterichnus</i> aff. <i>lawrencensis</i> Bandel | ? <i>Gyrophyllites rehsteineri</i> (Fischer-Ooster) |
| <i>Gyrophyllites kwassizensis</i> Glocker | <i>Gyrophyllites rehsteineri</i> (Fischer-Ooster) |
| <i>Phycosiphon incertum</i> Fischer-Ooster | <i>Phycosiphon incertum</i> Fischer-Ooster |
| ? <i>Rhizocorallium</i> indet. | <i>Rhizocorallium jenense</i> Zenker |
| <i>Zoophycos brianteus</i> Massalongo | <i>Zoophycos brianteus</i> Massalongo |
| <i>Zoophycos insignis</i> Squinabol | <i>Zoophycos insignis</i> Squinabol |
| <i>Anemonichnus concentricus</i> Chamberlain | <i>Anemonichnus concentricus</i> Chamberlain |
| <i>Gyrochorte burtani</i> Książkiewicz | <i>Protovirgularia pennatus</i> (Eichwald), <i>Protovirgularia rugosa</i> (Miller & Dyer), <i>Protovirgularia ?longispicata</i> (De Stefani) |
| <i>Gyrochorte imbricata</i> Książkiewicz | <i>Protovirgularia rugosa</i> (Miller & Dyer), <i>Protovirgularia ?rugosa</i> (Miller & Dyer), |
| <i>Gyrochorte oblitterata</i> Książkiewicz | <i>Protovirgularia oblitterata</i> (Książkiewicz) |
| <i>Helicorhaphe tortilis</i> Książkiewicz | <i>Helicorhaphe tortilis</i> Książkiewicz |
| <i>Helminthopsis abeli</i> Książkiewicz | <i>Helminthopsis abeli</i> Książkiewicz, ? <i>Thalassinoides</i> isp., <i>Helminthopsis</i> Isp. |
| <i>Helminthopsis hieroglyphica</i> Książkiewicz | <i>Helminthopsis abeli</i> Książkiewicz, <i>Gordia marina</i> Emmons |
| <i>Helminthopsis irregularis</i> (Schafhäütl) | <i>Nereites irregularis</i> (Schafhäütl) |
| <i>Helminthopsis tenuis</i> Książkiewicz | <i>Helminthopsis tenuis</i> Książkiewicz, <i>Helminthopsis abeli</i> Książkiewicz |
| <i>Helminthopsis granulata</i> Książkiewicz | " <i>Helminthopsis granulata</i> " Książkiewicz |
| <i>Muensteria geniculata</i> Sternberg | ? <i>Taenidium</i> isp. |

| | |
|--|---|
| <i>Muensteria hamata</i> Fischer-Ooster | <i>Phycosiphon hamata</i> (Fischer-Ooster) |
| <i>Muensteria planicostata</i> Książkiewicz | <i>Taenidium</i> isp. |
| <i>Naviculichnium marginatum</i> Książkiewicz | <i>Naviculichnium marginatum</i> Książkiewicz |
| <i>Oniscoidichnus carpathicus</i> Książkiewicz | ?trace fossil, ?inorganic structure |
| <i>Scolicia prisca</i> de Quatrefages | <i>Scolicia prisca</i> de Quatrefages |
| <i>Scolicia plana</i> Książkiewicz | <i>Scolicia plana</i> Książkiewicz |
| <i>Scolicia vertebralis</i> Książkiewicz | ? <i>Scolicia prisca</i> de Quatrefages |
| <i>Subphyllochorda granulata</i> Książkiewicz | <i>Scolicia plana</i> Książkiewicz |
| <i>Subphyllochorda striata</i> Książkiewicz | <i>Scolicia plana</i> Książkiewicz |
| <i>Subphyllochorda rudis</i> Książkiewicz | <i>Scolicia plana</i> Książkiewicz |
| <i>Subphyllochorda laevis</i> Książkiewicz | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Taphrhelminthopsis auricularis</i> Sacco | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Taphrhelminthopsis vagans</i> Książkiewicz | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Taphrhelminthopsis recta</i> Sacco | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Tuberculichnus vagans</i> Książkiewicz | <i>Protovirgularia vagans</i> (Książkiewicz) |
| <i>Tuberculichnus meandrinus</i> Książkiewicz | <i>Protovirgularia vagans</i> (Książkiewicz), ? <i>Saerichnites canadensis</i> (Crimes & Anderson) |
| <i>Tuberculichnus bulbosus</i> Książkiewicz | ? <i>Parahaentschelinia</i> isp. |
| <i>Tubulichnium incertum</i> Książkiewicz | <i>Ophiomorpha rectus</i> (Fischer-Ooster) |
| <i>Spirorhapse involuta</i> (De Stefani) | <i>Spirorhapse involuta</i> (De Stefani) |
| <i>Spirorhapse zumayensis</i> Llarena | " <i>Rotundusichnium</i> " <i>zumayensis</i> (Gómez de Llarena) |
| <i>Spirophycus bicornis</i> (Heer) | " <i>Spirophycus</i> " <i>bicornis</i> |
| <i>Spirophycus caprinus</i> (Heer) | " <i>Spirophycus</i> " <i>bicornis</i> |
| <i>Spirophycus involutissimus</i> (Sacco) | " <i>Spirophycus</i> " <i>involutissimus</i> (Sacco) |
| <i>Cochlichnus</i> aff. <i>anguineus</i> Hitchcock | <i>Cochlichnus anguineus</i> Hitchcock |

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| <i>Cosmorhapse gracilis</i> Książkiewicz | <i>Cosmorhapse gracilis</i> Książkiewicz |
| <i>Cosmorhapse sinuosa</i> (Azpeitia) | <i>Cosmorhapse lobata</i> Seilacher |
| <i>Cosmorhapse helminthopsoidea</i> Książkiewicz | <i>Cosmorhapse helminthopsoidea</i> (Sacco) |
| <i>Cosmorhapse fuchsi</i> Książkiewicz | <i>Cosmorhapse sinuosa</i> (Azpeitia Moros) |
| <i>Cosmorhapse</i> (?) <i>tortuosa</i> Książkiewicz | <i>Helicolithus tortuosus</i> (Książkiewicz) |
| <i>Gordia molassica</i> (Heer) | <i>Gordia marina</i> Emmons |
| <i>Gordia arcuata</i> Książkiewicz | <i>Gordia arcuata</i> Książkiewicz |
| <i>Helicolithus sampelayoi</i> Azpeitia | <i>Helicolithus sampelayoi</i> Azpeitia Moros |
| <i>Helminthoida labyrinthica</i> Heer | <i>Nereites irregularis</i> (Schafhäütl) |
| <i>Helminthoida serrata</i> Książkiewicz | <i>Nereites irregularis</i> (Schafhäütl) |
| <i>Helminthoida crassa</i> Schafhäütl | <i>Helminthorhapse flexuosa</i> Uchman, <i>Helminthorhapse japonica</i> (Tanaka), <i>Helminthorhapse</i> isp. |
| <i>Helminthoida miocenica</i> Sacco | <i>Helminthorhapse miocenica</i> (Sacco) |
| <i>Helminthoida alterna</i> Książkiewicz | <i>Desmograption alternum</i> (Książkiewicz) |
| <i>Helminthoida helminthopsoidea</i> Sacco | <i>Cosmorhapse carpathica</i> nom. nov. |
| <i>Helminthoida aculeata</i> Książkiewicz | <i>Belocosmorhapse aculeata</i> (Książkiewicz) |
| <i>Paleomeandron elegans</i> Peruzzi | <i>Paleomeandron elegans</i> Peruzzi |
| <i>Paleomeandron rude</i> Peruzzi | <i>Paleomeandron rude</i> Peruzzi, <i>Paleomeandron elegans</i> Peruzzi |
| <i>Paleomeandron robustum</i> Książkiewicz | <i>Paleomeandron robustum</i> Książkiewicz |
| <i>Taphrhelminthoida convoluta</i> Książkiewicz | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Taphrhelminthoida plana</i> (Książkiewicz) | <i>Scolicia strozzii</i> (Savi & Meneghini) |
| <i>Acanthorhapse delicatula</i> Książkiewicz | <i>Acanthorhapse delicatula</i> Książkiewicz |
| <i>Acanthorhapse incerta</i> Książkiewicz | <i>Acanthorhapse incerta</i> Książkiewicz |
| <i>Belorhapse zickzack</i> (Heer) | <i>Belorhapse zickzack</i> (Heer) |

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| <i>Belorhapha fabregae</i> (Azpeitia) | <i>Belorhapha zickzack</i> (Heer) |
| <i>Protopaleodictyon incompositum</i> Książkiewicz | <i>Protopaleodictyon incompositum</i> Książkiewicz, <i>Megagraption submontanum</i> (Azpeitia Moros) |
| <i>Protopaleodictyon minutum</i> Książkiewicz | <i>Protopaleodictyon minutum</i> Książkiewicz |
| <i>Protopaleodictyon submontanum</i> (Azpeitia) | <i>Megagraption submontanum</i> (Azpeitia Moros), <i>Megagraption irregulare</i> Książkiewicz |
| <i>Urohelminthoidea appendiculata</i> (Heer) | <i>Urohelminthoidea dertonensis</i> Sacco, <i>Urohelminthoidea appendiculata</i> (Heer) |
| <i>Urohelminthoidea dertonensis</i> Sacco | <i>Urohelminthoidea dertonensis</i> Sacco |
| <i>Urohelminthoidea</i> aff. <i>dertonensis</i> Sacco | <i>Oscillorhapha venezuelana</i> Scilacher |
| <i>Desmograption fuchsi</i> Książkiewicz | <i>Desmograption dertonensis</i> (Sacco), <i>Desmograption ichthyforme</i> (Macsotay) |
| <i>Megagraption irregulare</i> Książkiewicz | <i>Megagraption irregulare</i> Książkiewicz, <i>Thalassinoides</i> isp. |
| <i>Megagraption tenue</i> Książkiewicz | <i>Megagraption irregulare</i> Książkiewicz |
| <i>Paleodictyon minutissimum</i> Książkiewicz | <i>Paleodictyon minimum</i> Sacco |
| <i>Paleodictyon minimum</i> Sacco | <i>Paleodictyon minimum</i> Sacco |
| <i>Paleodictyon latum</i> Vialov & Golev | <i>Paleodictyon latum</i> Vialov & Golev |
| <i>Paleodictyon intermedium</i> Książkiewicz | <i>Paleodictyon strozzii</i> Meneghini |
| <i>Paleodictyon strozzii</i> Meneghini | <i>Paleodictyon strozzii</i> Meneghini |
| <i>Paleodictyon miocenicum</i> Sacco | <i>Paleodictyon miocenicum</i> Sacco |
| <i>Paleodictyon carpathicum</i> Matyasovszky | <i>Paleodictyon majus</i> Meneghini |
| <i>Paleodictyon regulare</i> Sacco | <i>Paleodictyon maximum</i> (Eichwald) |
| <i>Paleodictyon majus</i> Meneghini | <i>Paleodictyon majus</i> Meneghini |
| <i>Paleodictyon tellini</i> Sacco | <i>Paleodictyon strozzii</i> Meneghini |
| <i>Paleodictyon</i> aff. <i>gomezi</i> Azpeitia | <i>Paleodictyon gomezi</i> Azpeitia Moros |

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| | <i>Trichichnus linearis</i> Frey |
| | <i>Imponoglyphus torquendus</i> Vialov |
| | <i>Palaeophycus tubularis</i> Hall |
| | <i>Chondrites ?recurvus</i> (Brongniart) |
| | <i>Arenituba</i> isp. |
| 148 ichnospecies | 116 ichnospecies |
| 57 ichnogenera | 55 ichnogenera |

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