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TRACE FOSSILS FROM STRESS ENVIRONMENTS IN CRETACEOUS–PALEOGENE FLYSCH OF THE POLISH OUTER CARPATHIANS

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Abstract: Trace fossil diversity and density was studied in the Senonian-Oligocene flysch sequence of the southern part of the Magura Nappe, and intervals poor in ichnotaxa have been identified. This paper presents the trace fossil assemblages which are characteristic of these intervals. They were probably produced by opportunistic tracemakers in stress environments. Poor oxygenation and changes in sedimentation rate were probably the main factors of ecological stress. The group of the most opportunistic trace fossils includes: *Chondrites, Sabularia, simplex, Planolites, Helminthoida labyrinthica, Zoophycos, Tubulichnium incertum, Phycosiphon incertum, and Spirorhaphe zumayensis*

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INTRODUCTION

About 160 ichnospecies have been described from flysch deposits (Tithonian-Miocene) of the Polish Outer Carpathians (Książkiewicz, 1977). They exibit horizontal as well as vertical changes in diversity and density. According to the present author's experience, about 40 ichnotaxa may be collected in sections several hundred metres thick, e.g. in the Beloveža Beds (Middle Eocene), whereas in other sections, similar in lithology and exposure, e.g., in the Inoceramian Beds (Senonian-Paleocene) or the Szczawnica Formation (Paleocene-Lower Eocene), usually no more than 10 ichnotaxa can be collected. It seems that this differences are connected with diversified conditions of benthic life. As a rule, the sections poor in ichnotaxa are dominated by a few, usually densely occurring forms. This situation typically occurs when factors unfavourable for benthic life (stress) appear in the environment (cf. Ekdale, 1985; Vossler & Pemberton, 1988).

This paper presents the trace fossils association characteristic of the sections which are poor in ichnotaxa. For this purpose, more than 40 good exposures have been examined in the southern part of the Magura Nappe. In most

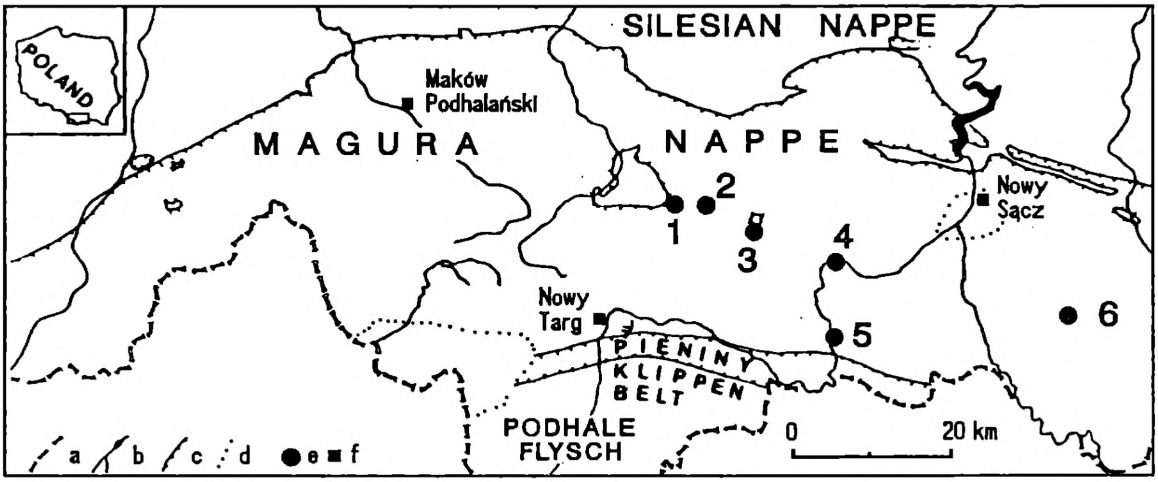

Fig. 1 Index map of studied sections. *a* – state boundary; *b* – rivers and lakes; *c* – main overthrusts; *d* – Neogene post-tectonic cover; *e* – studied sections (*1* – Lubomierz, *2* – Białe, *3* – Szczawa-Głębieniec, *4* – Łącko-Zarzecze, *5* – Krościenko-Łąkcica, *6* – Łabowa), *f* – main towns

cases, the exposures are located in stream valleys and nearly all examined sections are more than 50 m thick.

Ichnotaxonomic names are used according to Książkiewicz (1977), and in case of *Planolites*, according to Pemberton & Frey (1982).

Trace fossils are not so rich in thick-bedded and shaly flysch as in thin-bedded and medium-bedded flysch, mainly due to the low preservation potential (e.g., Książkiewicz, 1970, 1977, p. 14-15; Roniewicz & Pieńkowski, 1977). Hence, the examples presented here are related to occurrences of thin-bedded and medium-bedded flysch. Probably, the trace fossils in this kind of flysch better reflect the primary distribution of tracemakers.

In this publication, "rare" means occurrence of a few ichnotaxa, each represented by single specimens, in a section about 100 m thick, where at least a minimum of 0.5 m^2 of bed surface is available for observations. "Common" and "frequent" mean numbers one and two orders of magnitude greater, respectively.

GEOLOGICAL SETTING

The studied area is located within two facies zones of the Magura Nappe, i.e. the Krynica (Čerhov) zone and Nowy Sącz (Bystrica) zone. The zones consist of Upper Cretaceous-Paleogene flysch deposits which are about 3 000 m thick. The Krynica zone borders on the south with the Pieniny Klippen Belt. Its formal lithostratigraphical division is described by Birkenmajer & Oszczypko (1988, 1989) (Table 1). A more northerly position is occupied by the Nowy Sącz zone which is distinguished mainly by the presence of the so called Łącko marls in the Eocene. Lithostratigraphical division of the zone has been described by Cieszkowski & Oszczypko (1986) and Oszczypko *et al.* (1990) (Table 1).

Table 1
Lithostratigraphy of the Senonian-Oligocene of the Krynica Zone and the Nowy Sącz Zone in the Magura Nappe (according to Birkenmajer & Oszczypko, 1989; Oszczypko *et al.*, 1990, simplified).

Formation and age	Lithology and other divisions
KRYNICA ZONE	
Malcov Formation (Uppermost Eocene-Oligocene)	thin and medium bedded siliciclastic flysch; marly shales, olive and red marls (Leluchów Marl Member); black shales with cherts (Smereczek Shale)
Magura Formation (Eocene)	thick bedded sandstones with packages of thin and medium bedded flysch (Piwniczna Sandstone Member); variegated shales (Mniszek Shale Member); thick bedded sandstones (Poprad Sandstone Member)
Zarzecze Formation (Paleocene-Eocene)	conglomerates, pebble mudstones (Krynica Member); thin and medium bedded flysch, quartz sandstones, marly shales
Szczawnica Formation (Paleocene-Eocene)	conglomerates (Rzyczanów Member); thin and medium bedded siliciclastic flysch with black shales
NOWY SĄCZ ZONE	
Division and age	Lithology
Magura Sandstones (Upper Eocene)	thick bedded sandstones
Jazowsko Beds (Upper Eocene)	thin bedded flysch and variegated shales
Maszkowice Beds (Middle-Upper Eocene)	thick bedded sandstones, packages of thin bedded flysch, thick beds of marls
Beloveža Beds (Middle Eocene) (Łącko Marls)	thin and medium bedded siliciclastic flysch with beds of marls
Variegated Shales (from Łabowa) (Paleocene-Lower Eocene)	variegated shales
Inoceramian Beds (Senonian-Paleocene)	thin, medium and thick bedded flysch with black, marly mudstones

SELECTED EXAMPLES OF THE SECTIONS POOR IN ICHNOTAXA

Five basic types of the sections poor in ichnotaxa may be distinguished in the investigated area. This types are presented on the following examples:

1. Thin-bedded flysch of the Inoceramian Beds (Senonian-Paleocene), Lubomierz, Białe (Fig. 1, outcrops 12 and 15), sandstones interbedded with black mudstones (Fig. 2 A, C-D). Trace fossil assemblage consists of *Chondrites* alone and *Chondrites* and *Helminthoida* (*Helminthoida labyrinthica*). The ichnotaxa occur at the upper parts of sandstones (Fig. 2, A, C-D). The Inoceramian Beds to the east of the studied area (vicinity of Grybów and Gorlice) comprise very diverse ichnofauna (Książkiewicz, 1977).

2. Thin-bedded flysch of the Inoceramian Beds (Senonian-Paleocene), Lubomierz, Białe (Fig. 1, outcrops 12 and 15) consisting of sandstones interbedded with black mudstones (Figs. 2B, 3A). Following ichnotaxa have beennoted: very frequent *Chondrites* ichnosp. (small form), *Chondrites affinis* (large form), common to frequent *Helminthoida labyrinthica, Planolites*, and *Sabularia simplex*. The first two ichnotaxa are connected exclusively with upper parts of sandstone beds (Fig. 3 A). *Urohelminthoida* ichnosp. and *Muensteria* ichnosp. are very rare (outside the illustrated parts of section). The examples 1 and 2 are representative of most studied outcrops of the Inoceramian beds.

3. Thick, structureless beds of light-grey marls and marly claystones (so called Łącko marls) separated by packages of black-grey, slightly calcareous-mudstones. This is a part of the Beloveža Beds section (Middle Eocene) at Łabowa (Fig. 1, outcrop 32). Only the small form of *Chondrites* occurs in this section. Basides it, only a single specimen of *Spirorhaphe zumayensis* has been noted. (Fig. 3 B). Occurrence of *Chondrites* is limited to mudstones and a few centimetres in the highest parts of the marl beds. Trace fossils were not observed in the remaining part of the marls. This example is typical of most outcrops of the Beloveža Beds.

4. Thin-bedded and medium-bedded flysch of the Zarzecze Formation, 300 m thick (Paleocene-Lower Eocene) (Oszczypko, 1979; Oszczypko *et al.*, 1990), Łącko-Zarzecze (Fig. 1, outcrop 21). The section could be subdivided into 4 subsections A, B, C, D (Fig. 4), according to trace fossil distribution. Subsections B and D stand out by their low ichnotaxonomic diversity. Subsection A includes frequent *Sabularia simplex*, *Chondrites* ichnosp., and rare ?*Bergaueria* ichnosp. and *Scolicia* ichnosp. Frequent *Sabularia simplex*, *Chondrites* ichnosp., as well as rare *Megagrapton* ichnosp. and *Helicolithus sampelayoi* are noted in subsection B. Similar subdivison is possible in most sections of the investigated area.

5. Thin-bedded and medium-bedded flysch of the Szczawnica Formation (Paleocene-Lower Eocene) at Krościenko-Łąkcica (Fig. 1, outcrop 26) and thin-bedded to medium-bedded flysch of the Inoceramian Beds (Senonian) at Szczawa (Głębieniec stream) (Fig. 1, outcrop 16), sandstones interbedded with black mudstones. These sections are dominated by frequent *Chondrites* ichnosp. and *Chondrites affinis*. Such ichnotaxa as: *Planolites* ichnosp., *Sabularia simplex, Tubulichnium incertum, Helminthoida labyrinthica, Phycosiphon incertum, Spirorhaphe zumayensis* and *Zoophycos* are also common.

Frequently occurring *Chondrites* is replaced by *Zoophycos* and *Helminthoida* in some parts of the section (Fig. 3 C). Very rare are: *Urohelminthoida, Paleodictyon, Taphrhelminthopsis*. This section is representative of the outcrops of the Szczawnica Formation and partly also the Inoceramian Beds.

GENERAL PATTERN OF TRACE FOSSIL DISTRIBUTION

The following rules of trace fossil distribution in thin bedded flysch may be observed (Fig. 5):

1. *Chondrites* is frequent in sections with reduced number of ichnotaxa and infrequent in sections rich in ichnotaxa. When *Chondrites* occurs as a single ichnotaxon it is represented by small forms. The occurrence of large forms is usually connected with the presence of other ichnotaxa as in the Inoceramian Beds (Figs. 2 B, 3 A) and Szczawnica Formation.

2. *Sabularia simplex*. and *Planolites* ichnosp. occur in almost all investigated sections and they are the most frequent ichnotaxa in the investigated area. They occur in high density in the sections rich in ichnotaxa. Their density is slightly reduced in the sections poor in ichnotaxa.

3. Graphoglyptids, e.g., *Paleodictyon*, *Protopaleodictyon*, *Cosmorhaphe* are rare in the sections poor in ichnotaxa (Inoceramian Beds). The Beloveža Beds are very rich in graphoglyptids, and they are one of the units richest in trace fossils in the Carpathians (Książkiewicz, 1977; Uchman, 1990).

4. Locally, in some sections of the Inoceramian Beds (Szczawa) and in the Szczawnica Formation (Fig. 1), the decrease in density of *Helminthoida labyrinthica* and *Zoophycos* is correlated with the increased density of *Chondrites* (Fig. 3 C).

5. *Taphrhelminthopsis* and related forms, i.e., *Scolicia* and *Taphrhelminthoida*, are comparatively rare in the sections poor in ichnotaxa (Inoceramian Beds, Szczawnica Formation), but frequent in intermediate situations (e.g., some parts of the Beloveža Beds).

6. *Tubulichnium incertum* and *Phycosiphon incertum* are frequent only in the sections poor in ichnotaxa (Inoceramian Beds, Szczawnica Formation). These ichnotaxa occur together with abundant *Chondrites*.

7. *Helminthoida labyrinthica* are frequent in the sections poor in ichnotaxa and less frequent in the sections rich in ichnotaxa.

DISCUSSION

Trace fossils in flysch deposits may be subdivided in two groups – predepositional and postdepositional ones (e.g. Książkiewicz, 1970, 1977; Kern, 1980). Quick colonizers of newly deposited turbidite layers produce usually postdepositional forms, and they are more tolerant to unfavourable environmental conditions. They frequently occur in high density. Tracemakers which are late colonizers are active mainly during comparatively long periods be-

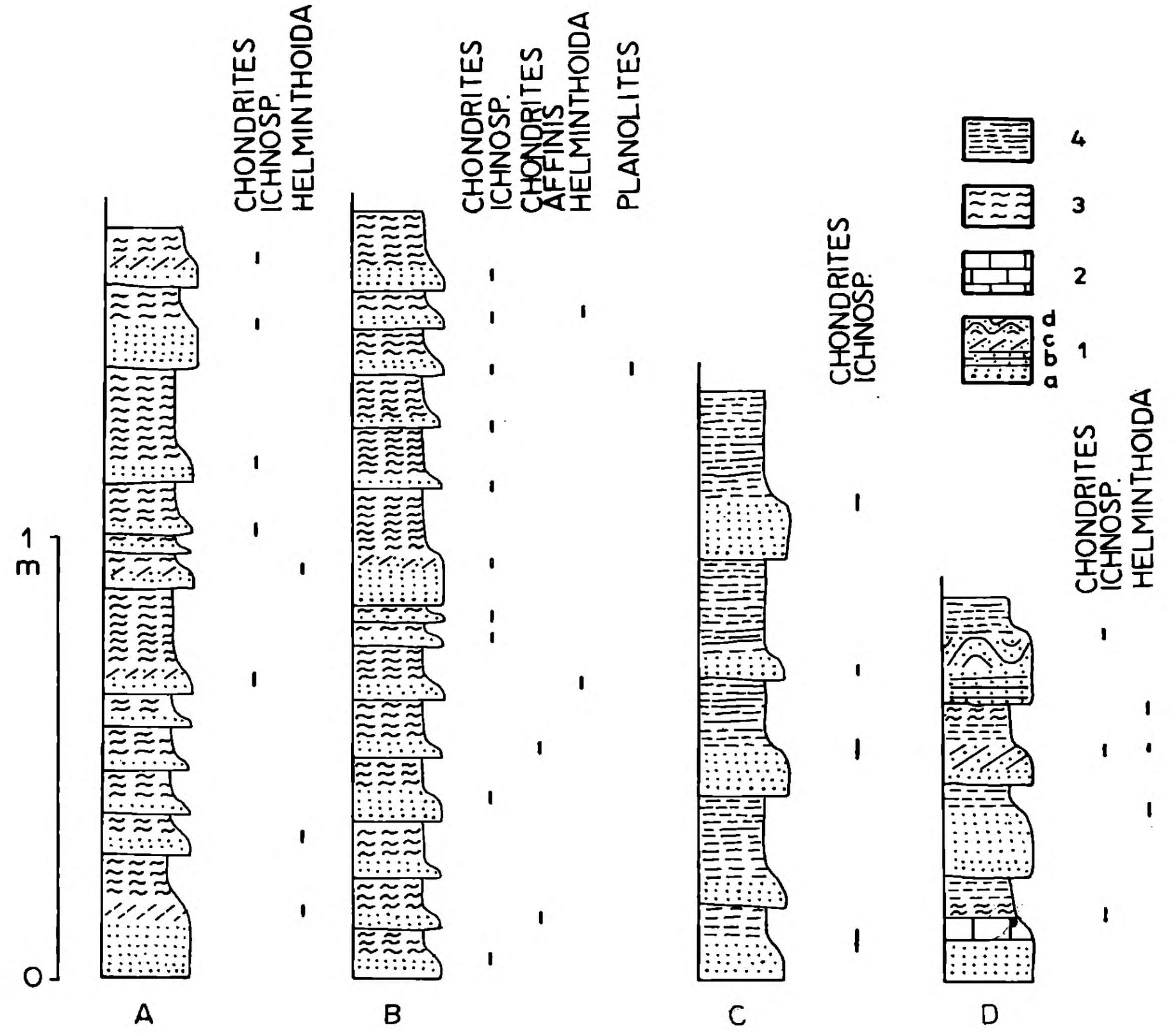

Fig. 2 Trace fossil distribution in selected sections. *A* – Lubomierz (Inoceramian Beds, Senonian-Paleocene), *B* – Łabowa (Beloveža Beds, Eocene), *C* – Krościenko-Łąkcica (Szczawnica Formation, Paleocene-Eocene). *1* – sandstones (*a* – graded bedding, *b* – horizontal lamination, *c* – cross lamination, *d* – convolute lamination), *2* – allodapic limestones, *3* – green mudstones, *4* – black mudstones

tween turbiditic events and they produce usually predepositional forms. They are not resistant to unfavourable conditions (stress) of environment (cf. Ekdale, 1985).

It can be predicted that with increased influence of stress factors in the environment, the sensitive forms are eliminated first, i.e. the predepositional tracemakers before the postdepositional ones. Elimination of the sensitive forms may be followed by development of opportunistic, highly tolerant forms.

The occurrence of dense but not diverse populations in stress environments is a known rule in ecology (e.g., Ekdale, 1985; Rhoads & Boyer, 1982, Vossler & Pemberton, 1988 with references). According to this rule, it may be

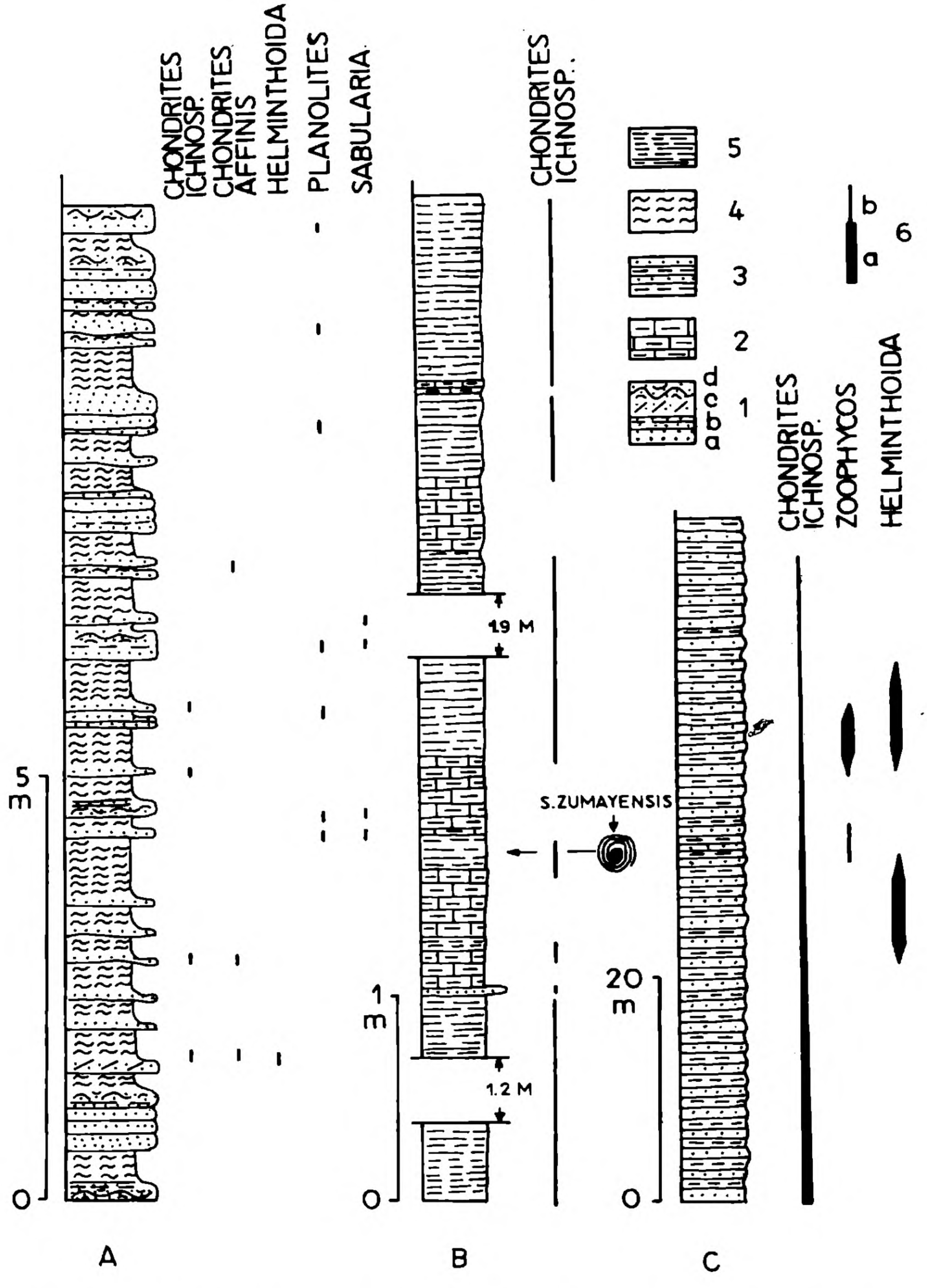

Fig. 3 Trace fossil distribution in selected sections. *A* – Lubomierz (Inoceramian Beds, Senonian-Paleocene), *B* – Łabowa (Beloveža Beds, Eocene), *C* – Krościenko-Łąkcica (Szczawnica Formation, Paleocene-Lower Eocene). *1* – sandstones (*a* – graded bedding, *b* – horizontal lamination, *c* – cross lamination, *d* – convolute lamination), *2* – marls, *3* – thin-bedded and medium-bedded flysch, *4* – grey-green mudstones, *5* – black mudstones, *6* – thickness of the range lines proportional to the relative frequency of forms (*a* – rare, *b* – common to frequent), S. ZUMAYENSIS – *Spirorhaphe zumayensis*

suggested that *Chondrites*, *Planolites*, *Sabularia simplex*, *Zoophycos*, *Helminthoida labyrinthica*, *Tubulichnium incertum*, *Phycosiphon incertum*, and *Spirorhaphe zumayensis*, belong to ichnotaxa reflecting the occurrence of

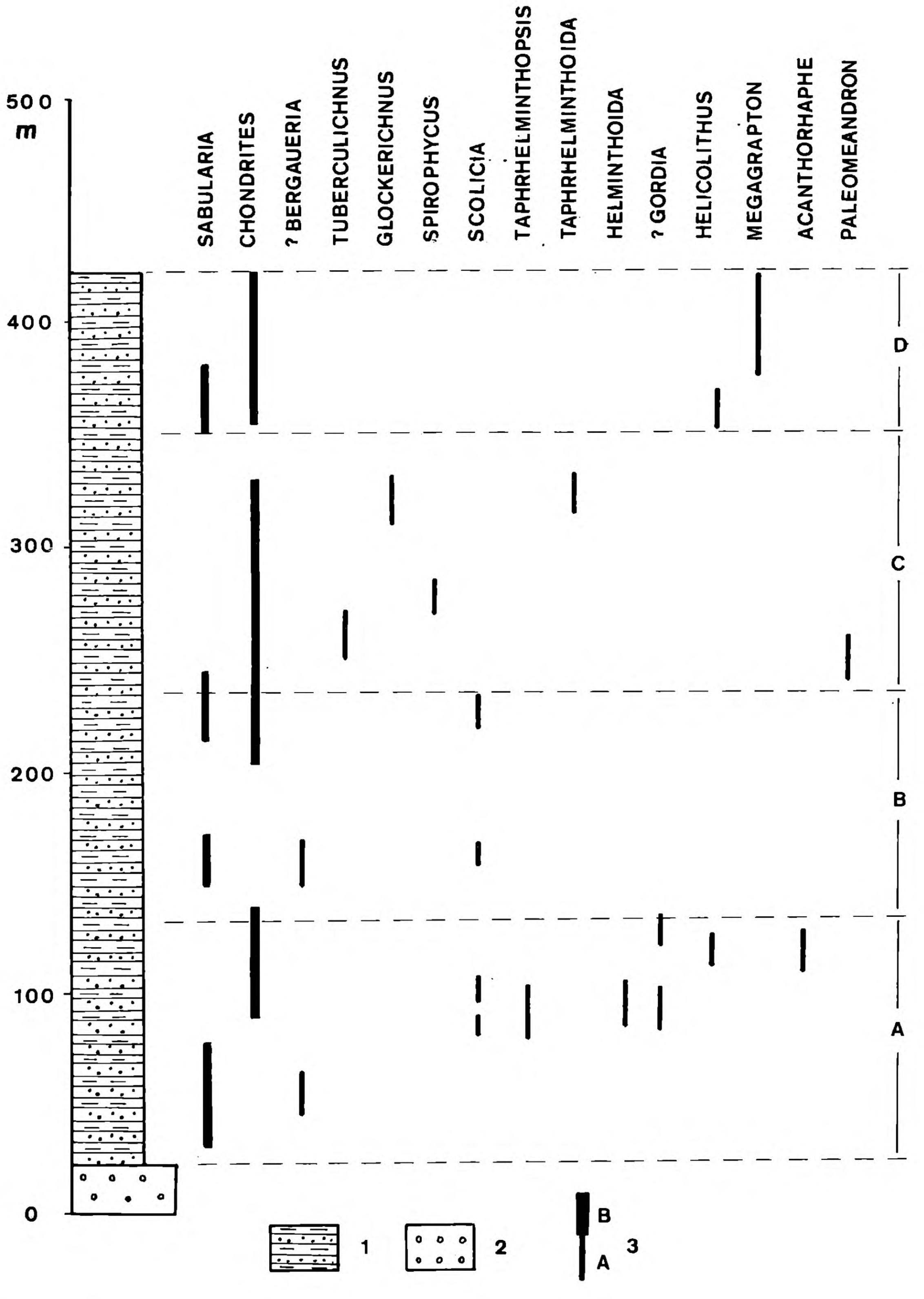

Fig. 4 Trace fossil distribution in the Zarzecze Formation (Paleocene-Lower Eocene) at Łącko-Zarzecze. *1* – thin-bedded and medium-bedded flysch, *2* – conglomerates (Rzyczanów Member), *3* – thickness of the range lines proportional to the relative frequency of forms (*a* – rare, *b* – common or frequent), *A*, *B*, *C*, *D* – units distinguished according to trace-fossil distribution (detailed explanation in the text)

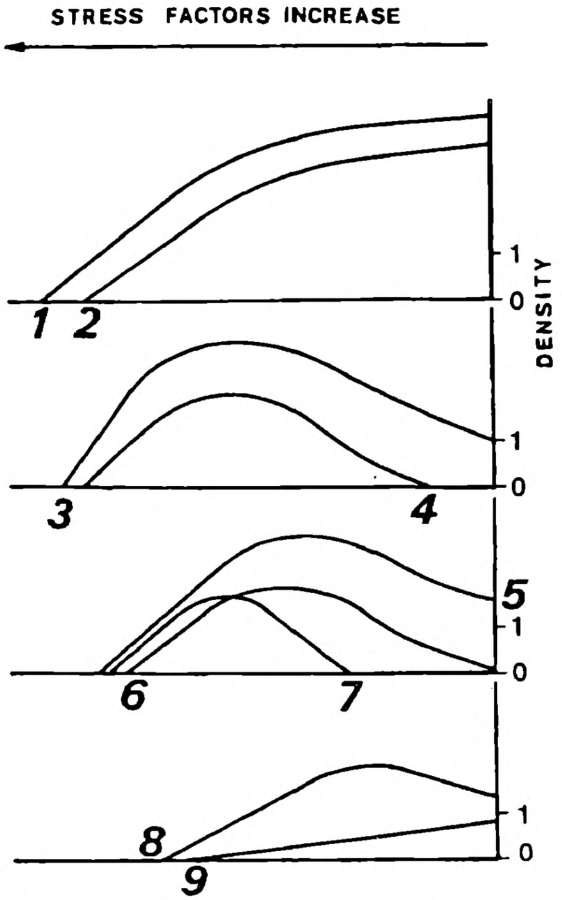

Fig. 5 Approximate relation of selected trace fossils to the increase of stress factors. *1* – *Planolites*, *2* – *Sabularia simplex*, *3* – *Chondrites* (small form), *4* – *Chondrites affinis* (large form), *5* – *Helminthoida labyrinthica*, *6* – *Zoophycos*, *7* – *Phycosiphon incertum*, *8* – *Taphrheminthopsis*, *Subphyllochorda*, *Scolicia*, *9* – graphoglyptids

environmental stress in the studied sections. It seems that *Chondrites*, *Tubulichnium*, *Zoophycos*, and *Phycosiphon* prefer stress environments and occur abundantly there. The remaining ichnotaxa occur frequently in stress environments as well as outside them. Various ichnotaxa are influenced by stress factors in different ways (Fig. 5).

It seems that poor oxygenation of sediment and changes in sedimentation rate were the most important stress factors. However, the reduced diversity of ichnotaxa could be related to other factors.

For example, it is known that the number of traces decreases donward in the sediment (cf. Crimes, 1973, 1977; Bromley & Ekdale, 1986). In a case when the near-bottom sediment, potentially rich in traces, is removed by erosion, many ichnotaxa are eliminated. Finally, a poorly diversified ichnoasso-ciation is observed (cf. Crimes, 1973, Książkiewicz, 1970, 1977, p. 14-15). When erosional structures are rare and when shallow burrows occur, e.g., graphoglyptids (cf. Ekdale, 1980), *Taphrhelminthopsis*, *Helminthoida* (most examples discussed herein), the influence of sediment erosion seems to be insignificant. In this case, the poor oxygenation of sediment and changes in sedimentation rate are the main factors reducing the number of ichnotaxa. In most of the discussed sections poor in ichnotaxa, the dysaerobic or anoxic conditions are marked by black colour of sediment. When anaerobic zone is shallow, only the most tolerant organisms were able to burrow in the thin near-bottom layer.

The amount of burrowers increases following an increase in oxygenation and deepening of anaerobic zone (Figs. 2 B, 3 A, examples 1 and 2). Succession of newly appearing ichnotaxa after an increase in oxygenation has been reported by Bromley and Ekdale (1984). They determined *Chondrites* as the ichnogenus the most tolerant to poor oxygenation. *Zoophycos* and *Phycosiphon* were included to the group of the most resistant ichnotaxa (Frey & Seilacher, 1980; Ekdale & Mason, 1988). The lithostratigraphic horizon with

Planolites from the Podhale Basin Flysch (Oligocene, Polish Inner Carpathians), standing out by its reduced number of ichnotaxa and black colour of mudstones, is related to lower oxygenation of sediment than in a horizon with *Taphrhelminthopsis* (Pieńkowski & Westwalewicz-Mogilska, 1986).

Turbidity currents can bring well oxygenated water into oxygen depleted environment (e.g., Sholkovitz & Soutar, 1975); organic matter is accumulated in the upper parts of turbidites. In this case, an increased number of trace fossils can be observed in the upper parts of sandstone beds (Figs. 2-3, example 2). The fragments of sections enriched in ichnotaxa can be related to the episodes of better oxygenation (Fig. 4, example 4) (cf. Bromley & Ekdale, 1984, Savrda & Bottjer, 1986, 1989). The fragments of sections without trace fossils may be interpreted in two ways: as reflecting a decrease in sediment oxygenation (anaerobic conditions at the bottom), or as a dramatic increase in sedimentation rate. The occurrence of *Chondrites* exclusively in the uppermost few centimetres of the Łącko Marls beds (Fig. 3 B) is connected with changes in sedimentation rate. Continuous reworking of sediment by *Chondrites* was interrupted by incidental, rapid turbiditic deposition of the layers of the Łącko Marls, which are up to a dozen metres thick. So, only the uppermost parts of the turbiditic marls were colonized. If changes in sedimentation rate are limited to the regular deposition of thin- and medium-bedded flysch, and we observe black colour of mudstones, the breaks in trace fossil occurrence may be related to anaerobic conditions at the bottom (Fig. 3 B).

When *Chondrites* occurs as the single ichnogenus, it is represented by small forms. Larger forms occur following the appearrance of other ichnotaxa which need better oxygenation (cf. Rhoads & Morse, 1971; Savrda & Bottjer, 1986). The scarce occurrence of graphoglyptids observed in the sections poor in ichnotaxa, is probably related to their connection with ecologically stable, non-stress environments (cf. Ekdale, 1985). The same prediction can be related to *Taphrhelminthopsis*, a form produced by irregular echinoids (e.g., Frey & Seilacher, 1980; Smith & Crimes, 1983). Most of echinoids and other organisms with calcareous skeleton need better oxygenation (Thompson *et al.*, 1985; Pieńkowski & Westwalewicz-Mogilska, 1986).

Influence of bathymetry (Seilacher, 1967; Książkiewicz, 1977) on trace fossil distribution in the environment of flysch sedimentation seems to be insignificant (Uchman, in press). According to new investigations, *Chondrites* occurs in both, extremely shallow-water sediments (e.g., Archer, 1984), and at depths of several thousands metres (e.g., Werner & Wetzel, 1982). Many "shallow water" forms were reported occurring in deep-water flysch together with deep-water forms (e.g., Crimes *et al.*, 1981, Uchman, in press), and the "deep-water" forms are found in shallow-water sediments (Archer & Maples, 1984). Trace fossils as paleodepth indicators have been critically discussued by Byers (1982), Ekdale (1988), and others.

According to Książkiewicz (1977), *Chondrites* and a few other forms are connected with calcareous sediments. However, this ichnogenus occurs also in non-calcareous mudstones in the Piwniczna Sandstone member, while many calcareous sediments, e.g., fragments of the Beloveža Beds sections lack *Chondrites*.

It can be concluded that poor oxygenation of sediment and changes in sedimentation rate were the main factors controlling the trace-fossil distribution in the studied sections.

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Streszczenie

SKAMIENIAŁOŚCI ŚLADOWE ŚRODOWISK STRESOWYCH WE FLISZU POŁUDNIOWEJ CZĘŚCI PŁASZCZOWINY MAGURSKIEJ, POLSKIE KARPATY ZEWNĘTRZNE

Alfred Uchman

W przebadanych ponad 40 profilach utworów fliszowych (senon - oligocen) w południowej części płaszczowiny magurskiej, polskie Karpaty zewnętrzne (Fig. 1, Tab. 1), wyróżniono skamieniałości śladowe najczęściej występujące, niekiedy w dużej ilości, w profilach najuboższych w ichnorodzaje. Należą do nich: *Chondrites, Planolites* ichnosp., *Sabularia simplex, Zoophycos, Tubulichnium incertum, Phycosphon incertum, Helminthoida labyrinthica i Spirorhaphe zumayensis.* Wymienione ichnotaksony wykazywały zróżnicowaną odporność na czynniki stresogenne (Fig. 5). Przypuszczać można, że wyżej wymienione skamieniałości śladowe reprezentują środowiska stresowe, które charakteryzowały się dużą ilością osobników i małą różnorodnością gatunków producentów skamieniałości śladowych (por. Ekdale, 1985). Wydaje się, że *Chondrites, Tubulichnium, Zoophycos i Phycosiphon* szczególnie preferują środowiska stresowe i w przeciwieństwie do pozostałych ichnogatunków z tej grupy, najliczniej w nich występują. Bardzo często zmniejszanie się ilości *Chondrites* rekompensowane jest zwiększeniem się ilości *Zoophycos* i *Helminthoida* (Fig. 3 C).

Najważniejszymi czynnikami stresogennymi były prawdopodobnie niedotlenienie osadu i zmiany tempa sedymentacji.

O niedotlenieniu osadów świadczą na ogół ciemne barwy utworów, które przeważają w większości profili ubogich w ichnorodzaje. W warunkach silnego niedotlenienia, prądy zawiesinowe przynosiły wraz z osadem więcej tlenu oraz materii organicznej. Było to powodem rozwoju mało zróżnicowanych organizmów związanych z górną powierzchnią ławic piaskowców (Fig. 2). W miarę poprawy natlenienia, ilość organizmów, a co za tym idzie, ilość produkowanych przez nie skamieniałości śladowych wzrastała (Fig. 2 B, 3 A) (por. Bromley & Ekdale, 1984). Fragmenty profilu o zwiększonej ilości ichnorodzajów (Fig. 4) mogą być interpretowane jako epizody lepszego natlenienia (por. Bromley & Ekdale, 1984, Savrda & Bottjer, 1986). Fragmenty profilu bez skamieniałości śladowych (Fig. 3 A) mogą być wiązane z pogorszeniem warunków tlenowych lub z gwałtownym wzrostem tempa sedymentacji. Np. *Chondrites*, często występujący w ciemnoszarych mułowcach i tylko w kilku centymetrach najwyższej części przeławicających je jasnoszarych ławic margli (tzw. margle łąckie) we fragmencie profilu warstw beloweskich (eocen środkowy) (Fig. 3 B), wskazuje na gwałtowną depozycję ławic margli, w których tylko najwyższa część ławic mogła być skolonizowana.

Nieliczne występowanie większości form zaliczanych do graphogliptydów (agrichnia), np. *Paleodictyon*, w profilach ubogich w ichnorodzaje, wiąże się z przystosowaniem tych form do równowagi ekologicznej środowiska (por. Ekdale, 1985). To samo dotyczy *Taphrhelminthopsis*, formy produkowanej przez jeżowce, które jako organizmy o szkielecie wapiennym wymagają lepszych warunków tlenowych (np. Thompson *et al.*, 1985; Pieńkowski & Westwalewicz-Mogilska, 1986). Obserwuje się, że większe formy *Chondrites* związane są zwykle z pojawieniem się innych ichnorodzajów. Jest to spowodowane tym, że organizmy większe wymagają lepszego natlenienia (por. Rhoads & Morse, 1971; Savrda & Bottjer, 1986, 1989).

Przyczyną ubóstwa ichnorodzajów w niektórych profilach nie muszą być jednak wyłącznie czynniki ekologiczne. Ichnozespół może być wtórnie uszczuplony przez erozję powierzchniowej warstwy osadu, potencjalnie najbogatszej w skamieniałości śladowe (por. Crimes, 1973; Książkiewicz, 1977, s. 14-15). Jeżeli jednak struktury erozyjne są rzadkie, ponadto występują skamieniałości śladowe związane z płytkimi penetracjami (np. należące do kategorii agrichnia, *Taphrhelminthopsis* i inne) to rola erozji wydaje się być podrzędna.