Trends in diversity, frequency and complexity of graphoglyptid trace fossils: evolutionary and palaeoenvironmental aspects

Alfred Uchman *

Institute of Geological Sciences, Jagiellonian University, Oleandry 2a, 30063 Kraków, Poland

Abstract

Graphoglyptids, a characteristic component of the *Nereites* ichnofacies, are patterned, mainly meander-, star-, and net-shaped trace fossils, which reveal complex burrow systems used most likely for trapping of meiobenthos or cultivation of microbes in oligotrophic deep-sea environments. They show considerable changes of diversity, frequency and adaptive radiation through Phanerozoic. Rapid radiation and increase of their diversity and density in the Late Cretaceous, probably in the Turonian, is correlated with large-scale biotic changes in marine environments, which are rooted in palaeogeographic and palaeoclimatic changes. The changes of graphoglyptids have been distinctly caused by most of the major biotic crises, especially in the Cretaceous and Cenozoic. Graphoglyptids also display an increase of complexity, which accelerated in the Late Cretaceous, when the farming activity of their trace makers became more common. The distinct changes in development of graphoglyptids challenge the time-stability hypothesis for explanation of their evolution.
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1. Introduction

Graphoglyptids are relatively small, patterned trace fossils of different shapes and complexity, which include spirals, meanders, stars and nets (Figs. 1 and 2), preserved almost exclusively as casts on soles of turbidite beds. They are the most characteristic trace fossils of the *Nereites* ichnofacies, which is typical of deep-sea flysch environments. Graphoglyptids are interpreted as complex agrichnial burrow systems produced by unknown invertebrates, in which they trap meiobenthos or farm microorganisms in generally oligotrophic deep-sea environments (Seilacher, 1977a,b; Miller, 1991).

It is considered that graphoglyptids originated in shallow-marine environments in the Early Cambrian and migrated to the deep-sea after the Middle Cambrian (Crimes and Fedonkin, 1994), probably at or near the Cambrian–Ordovician boundary (Orr, 2001). According to Seilacher

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* Fax: +48-12-4226306.
E-mail address: fred@ing.uj.edu.pl (A. Uchman).

(1974, 1977a,b, 1978) and Frey and Seilacher (1980), diversity and complexity of graphoglyptids increased gradually throughout the Phanerozoic with a rapid acceleration in the Cretaceous. Because of a significant increase of data about new localities of graphoglyptids and their taxonomy, a re-examination of this view is necessary. This paper examines the diversity and complexity of graphoglyptids throughout the Phanerozoic, and an analysis of frequency of their occurrence adds a useful parameter in consideration of long-term palaeoenvironmental or evolutionary changes.

2. Data and methods

Data from about 800 papers concerning deep-sea ichnology and previously unpublished data of the author have been used in this paper. They derive mostly from Jurassic–Miocene flysch formations of the Carpathians and the Mediterranean and Balkan regions. The useful papers are cited in the publications by Uchman (1995, 1998, 1999, 2001) and in the additional literature, including papers by Seilacher (1977a), Wetzel and Uchman (1997, 1998, 2001), Uchman and Wetzel (2001), Löffler and Geyer (1994), Tunis and Uchman (1998), Uchman et al. (1998), Uchman and Demírcan (1999), and Tchoumatchenco and Uchman (1999, 2001).

The source papers contain a lot of taxonomic descriptions of graphoglyptids supplemented commonly by synonymy lists. Several graphoglyptid taxa have been revised there, and it must be said that numerous trace fossils listed in the literature as graphoglyptids, especially those from the Lower Palaeozoic, actually belong to other non-graphoglyptid ichnotaxa, or their determination is doubtful. Determination at the ichnospecies level

among graphoglyptids is commonly wrong, or else poor illustrations of material commonly do not allow for confirmation of the determinations.

The analyses for this paper have been considered at the ichnospecies level, except for *Squamodictyon* and *Paleodictyon*, for which morphometric parameters have been analysed. A revision of all determinations of *Squamodictyon* and *Paleodictyon* ichnospecies from the literature is very difficult because it needs detailed morphometric data. This omission probably does not significantly alter the general picture of evolutionary trends of graphoglyptids outlined in this paper. The differences between ichnospecies of most graphoglyptids are relatively well defined, so the ichnospecific level of consideration provides more precise information. Most ichnotaxa have been ascribed to the geological periods of the Palaeozoic and Triassic, and to the epochs of the Jurassic, Cretaceous and Cenozoic.

Post-Miocene graphoglyptids are not considered in this analysis, because deep-sea flysch deposits of this age are rarely exposed and therefore are undersampled. The problem of undersampling exists also for other periods, especially in the Palaeozoic (Pickerill, 1980). For instance, Devonian and Permian flysch deposits are very poorly known. However, the problem of sampling or preservational potential cannot be overestimated if the diversity pattern is repetitive in several localities. Graphoglyptid lebensspuren referred to *Paleodictyon*, *Urohelminthoida*, *Spirorhaphe* and *Cosmorhaphe* are known from recent deep-sea pelagic deposits (e.g. Rona and Merill, 1978; Ekdale, 1980; Gaillard, 1991). These modern trace data are neither considered.

A few ichnospecies considered as graphoglyptids by Seilacher (1977a) are excluded from this group. *Hormosiroidea grossheimi* should be in-

Fig. 1. Examples of graphoglyptids from the Carpathian Flysch, Poland: (A) *Spirorhaphe involuta* (de Stefani), Szczawnica Formation (Upper Paleocene–Lower Eocene), Magura Unit, Łąkcica, 171P1; (B) *Belorhaphe zickzack* (Heer), Hieroglyphic Beds (Middle Eocene), Magura Unit, Tymbark, 171P2; (C) *Cosmorhaphe gracilis* (Książkiewicz), Lower Godula Beds (Upper Turonian), Silesian Unit, Rzyki, 171P3; (D) *Protopaleodictyon incompositum* (Książkiewicz), Mniszek Shale Member (Middle/Upper Eocene), Magura Unit, Konina, 171P4; (E) *Helicolithus sampelayoi* Azpeitia Moros, Malcov Formation (uppermost Eocene/lowermost Oligocene), Magura Unit, Nowy Targ-Samorody, 171P5; (F) ?*Glockerichnus* cf. *sparsicostata* (Książkiewicz), Beloveža Formation, Magura Unit, (Lower–Middle Eocene), Zbludza, 171P6. All specimens are hypichnial semi-reliefs. Scale bars = 1 cm.
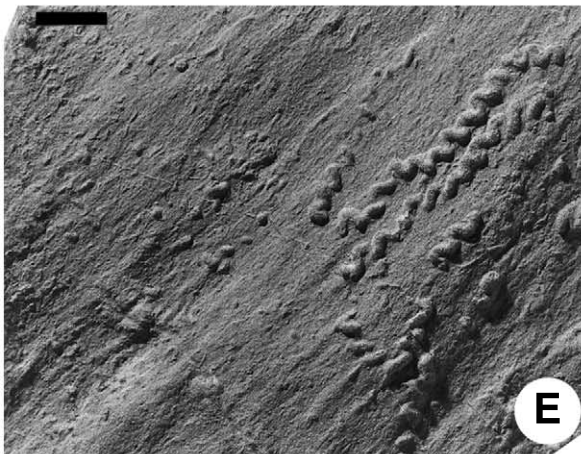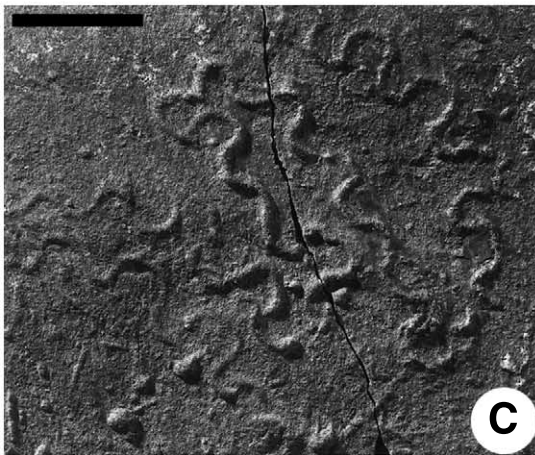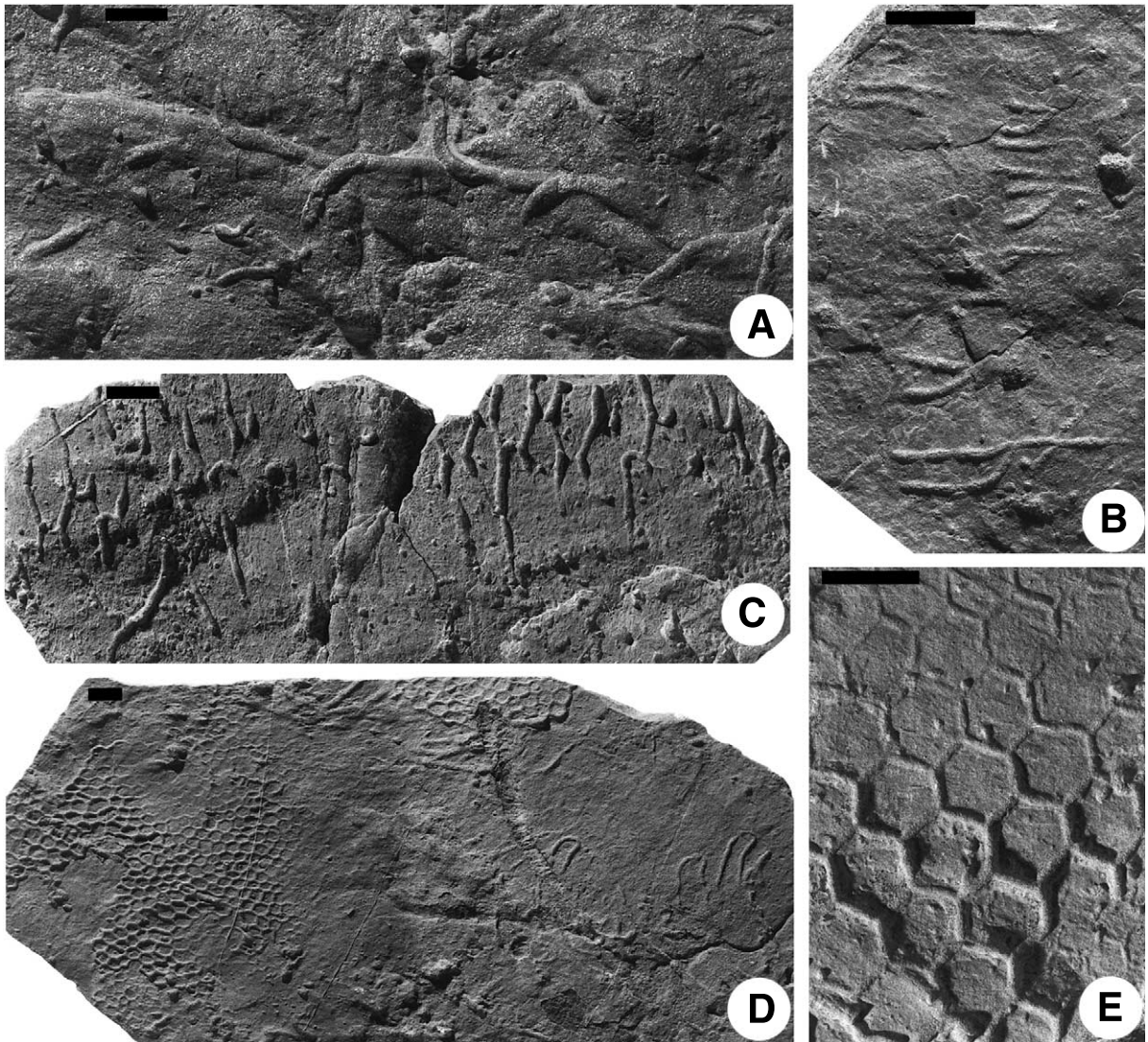
Fig. 2. Other examples of graphoglyptids from the Carpathian Flysch, Poland and Ukraine: (A) *Ubinia alternanas* (Seilacher), Berezna Beds (Upper Cretaceous), Dukla Unit, Luta, Ukraine, 171P7; (B) *Urohelminthoida dertonensis* Sacco, Hieroglyphic Beds (Eocene), Dukla Unit, Liszna, Poland, 171P8; (C) *Desmograpton dertonensis* (Sacco), Beloveža Formation (Lower–Middle Eocene), Magura Unit, Zbludza, Poland, 171P9; (D) *Paleodictyon strozzii* Meneghini (left side) and *Helminthorhaphe flexuosa* Uchman (right side), Szczawnica Formation (Upper Paleocene–Lower Eocene), Magura Unit, Łąkcica, Poland, 171P10; (E) *Paleodictyon majus* Meneghini in Peruzzi, Piwniczna Sandstone Member (Middle Eocene), Magura Unit, Tylmanowa, Poland, 171P11. All specimens are hypichnial semi-reliefs. Scale bars = 1 cm.

cluded in the bivalve locomotion trace fossil *Protovirgularia* (Seilacher and Seilacher, 1994), and *Hormosiroidea florentina* and *H. beskidensis* are regarded as non-graphoglyptid trace fossils of different character (Uchman, 1995).

Graphoglyptid diversity is measured by the total number of ichnospecies and ichnogenera in a given period, and the 'ichnospeciation' rate is represented by a percentage contribution of new ichnospecies in a given period with respect to the

total number of graphoglyptid ichnospecies. The frequency of occurrence is expressed by the number of formations in which the trace fossil occurs. For final considerations, the parameters are related to time, i.e. they were divided by the duration of the respective period or epoch (in million years), whose length is commonly very different.

The complexity is analysed on the basis of reconstructed morphology of the burrow system of graphoglyptids. Most reconstructions are published by Seilacher (1977a, 1986, 1989). The other potential criterion describing the complexity changes is the regularity of the burrow systems or at least their elements, but this is a separate topic for detailed morphometric and statistical analyses, which is not undertaken in this paper.
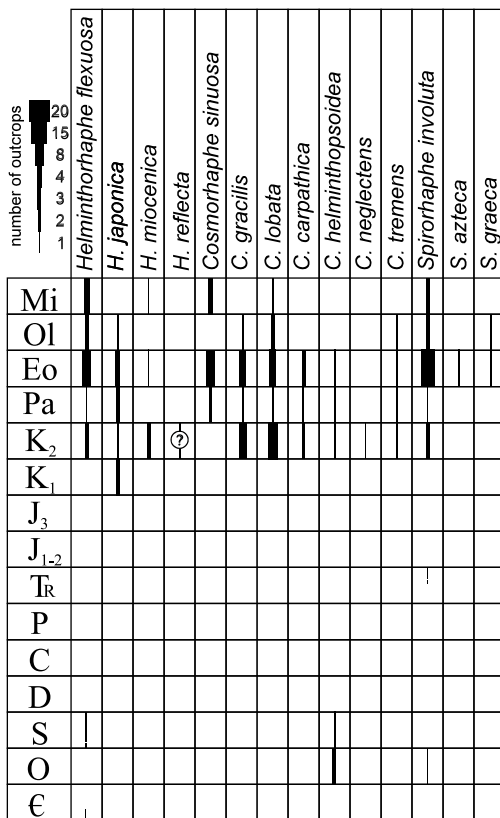

Fig. 3. Stratigraphic ranges and occurrence frequency of the continuous meanders, including the spiral graphoglyptids. The question mark indicates that the stratigraphic position is not sure. Dash lines indicate ranges of ichnospecies, where occurrence determination is questionable.
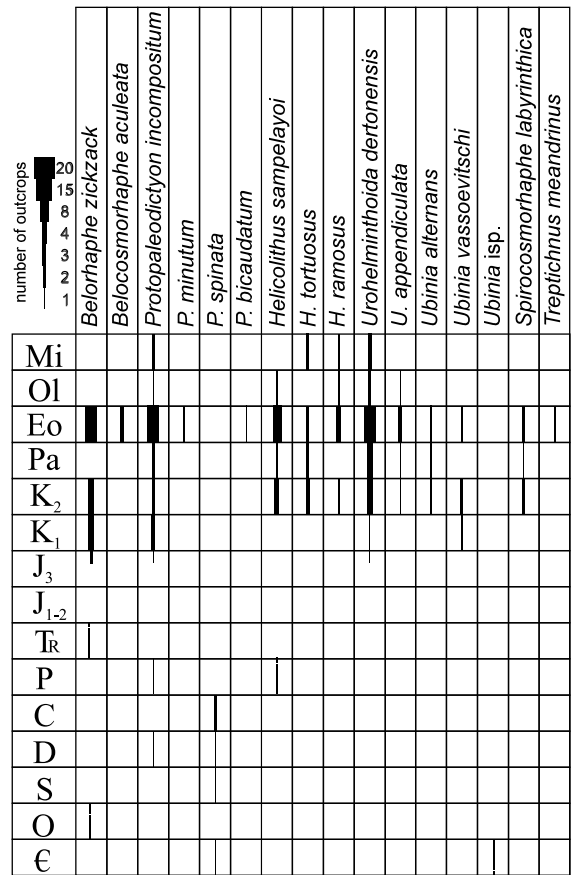

Fig. 4. Stratigraphic ranges and occurrence frequency of the uniramous meanders. Dash lines indicate ranges of ichnospecies, where occurrence determination is questionable.

3. Diversity and frequency

Graphoglyptid diversity and frequency are illustrated in Figs. 3–6, where stratigraphic ranges of individual ichnotaxa and the number of formations for each ichnotaxon in a given period are shown. Following Seilacher (1977a), graphoglyptids are grouped in continuous meanders, which includes also spirals (Fig. 3), uniramous meanders (Fig. 4), radial forms (Fig. 5), biramous meanders, irregular forms and nets (Fig. 6). Miller (1991) distinguished spiral forms as a separate group and joined uniramous and biramous meanders together, but for convenience of this discussion, the former divisions of Seilacher (1977a) are used.
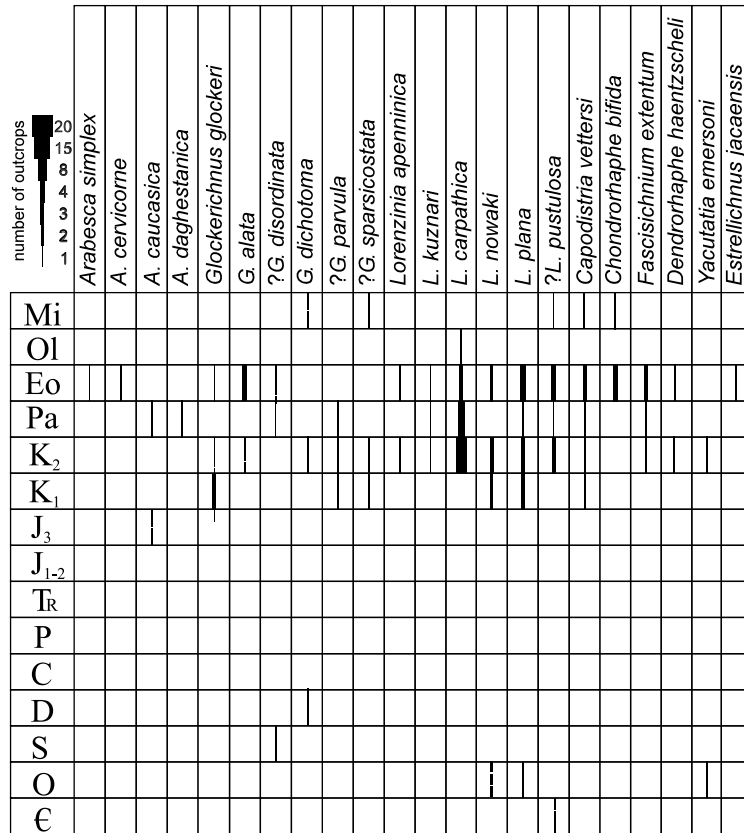
Fig. 5. Stratigraphic ranges and occurrence frequency of the radial graphoglyptids. Dash lines indicate ranges of ichnospecies, where occurrence determination is questionable.

There are 67 ichnospecies and 27 ichnogenera of graphoglyptids, without the inclusion of ichnospecies of *Squamodictyon* and *Paleodictyon*. Most ichnotaxa range from the Late Cretaceous. Only 30.5% of the ichnospecies occur before the Late Jurassic, and among those about 61.5% are only reservedly included in the considered ichnotaxa. Only two ichnospecies, *Protopaleodictyon spinata* and *Desmograpton pamiricus*, occur exclusively before the Late Jurassic.

The total number of ichnospecies is very low before the Cretaceous, with a low peak in the Ordovician (Fig. 7). The number increases considerably in the Early Cretaceous and again in the Late Cretaceous. It drops in the Paleocene and reaches the highest value in the Eocene, drops considerably in the Oligocene and increases in the Miocene. The diversity in time (per million years) shows a different trend in the Tertiary (Fig. 9). It increases in Paleocene, where it reaches the maximum value, and drops gradually to the Miocene. Before the Cretaceous, the number of ichnospecies is almost the same as the number of ichnogenera, but since the Cretaceous the number of ichnospecies has been distinctly larger than the number of ichnogenera.

Very interesting is the percentage contribution of first occurrences of ichnospecies in the stratigraphic context (Fig. 7). Almost 5.8% of the ichnospecies (+2.9% of those included reservedly) occur already in the Cambrian, and 9%(+3%) in the Ordovician, but only 1.5% (reservedly included) in the Silurian. From the Devonian to the Middle Jurassic, appearances of new ichnospecies remain very low, ranging from 0% to 1.5%. There is a distinct increase of first occurrences in the Late
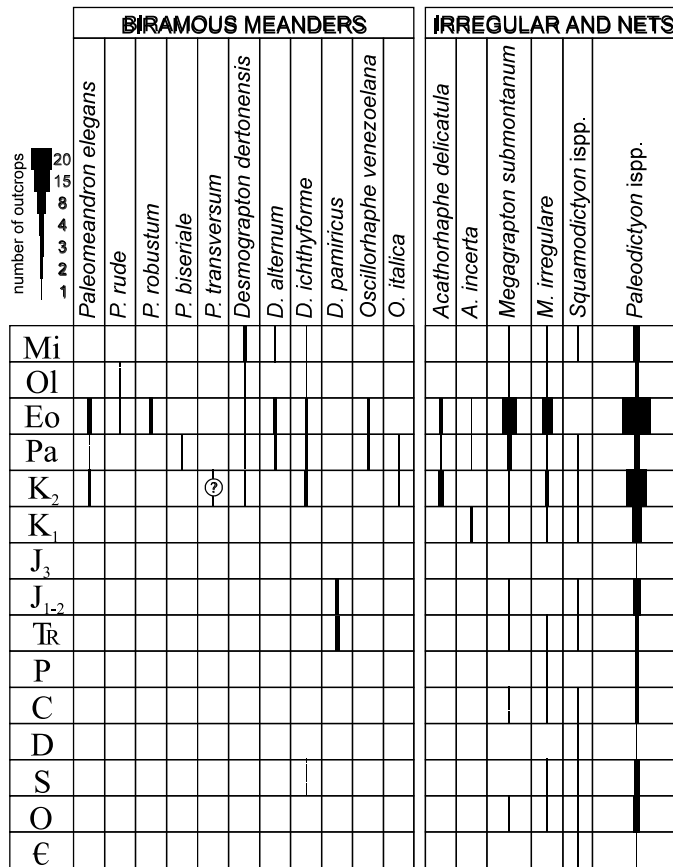
Fig. 6. Stratigraphic ranges and occurrence frequency of the biramous meanders and the remaining graphoglyptids. The question mark indicates that the stratigraphic position is not sure. Dash lines indicate ranges of ichnospecies, where occurrence determination is questionable.

Jurassic and Early Cretaceous, respectively 3%(+3%) and 12%, and an 'explosion' in the Late Cretaceous (36%). In the Paleocene, this coefficient drops to 9% and increases to 19.4% in the Eocene. The same trend is shown when the number of new ichnotaxa in a given period is related to its time duration (Fig. 9). There are no occurrences of new ichnospecies in the Oligocene and Miocene.

The frequency of occurrences measured by total number of formations is very low before the Cretaceous, with low peaks in Ordovician and Silurian (Figs. 8 and 9). The frequency increases in the Early and Upper Cretaceous, and then it drops in the Paleocene. It explodes to a maximum value in the Eocene, drops drastically in the Oligocene,

and increases again in the Miocene (Fig. 8). The frequency of occurrences shows a different pattern in the Tertiary when related to time (Fig. 9). It grows after the Late Cretaceous, reaches a distinct maximum in the Eocene, and drops drastically in the Oligocene and latter in the Miocene. In both cases, the maximum frequency is in the Eocene, and it is followed by the drastic drop in the Oligocene.

4. Complexity

The morphological complexity of graphoglyptids is a problem to assess, because more complex morphologies contain more differently oriented
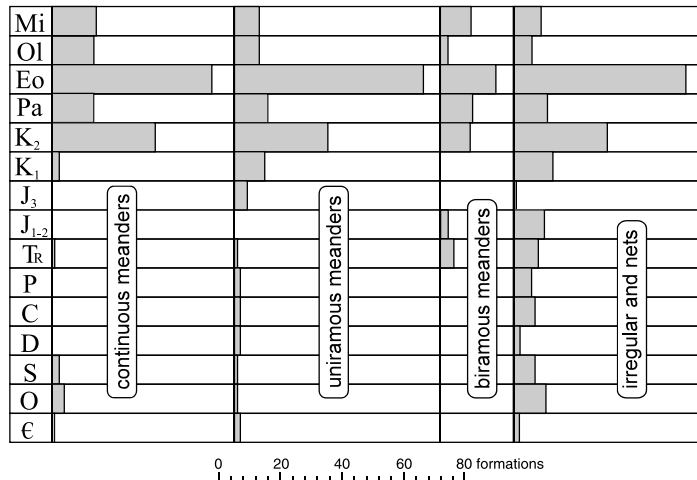
Fig. 7. Changes of graphoglyptid diversity measured by the number of ichnospecies (excluding *Paleodictyon* and *Squamodictyon* ispp.) and ichnogenera per stage or epoch, and the percentage contribution of ichnospecies per stage or epoch.

elements and require more complicated programmes of trace maker behaviour. The continuous meanders are less complex than the uniramous meanders, and the biramous meanders seem to be the most complex. Most of the radial forms are more complex than the continuous meanders, but some of them (e.g. *Lorenzinia nowaki* or *L. plana*) are rather simple. *Paleodictyon* with vertical shafts is more complex than irregular nets (e.g. *Megagrapton* and *Squamodictyon*) or *Paleodictyon* without shafts.

Among the continuous meanders, the simplest *Helminthorhaphe flexuosa* appears already in the Early Cambrian (Fig. 3). More complex ichnospe-
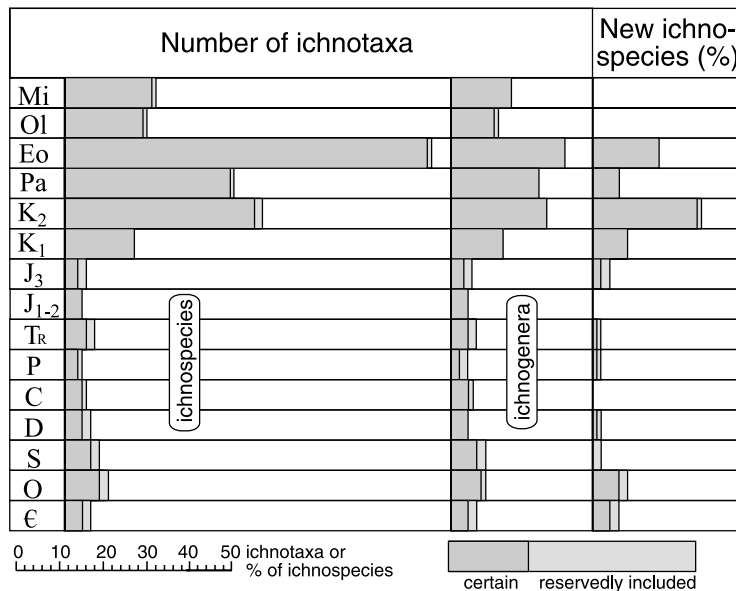

Fig. 8. Frequency of occurrence of graphoglyptids in formations around the world in which they have been studied.
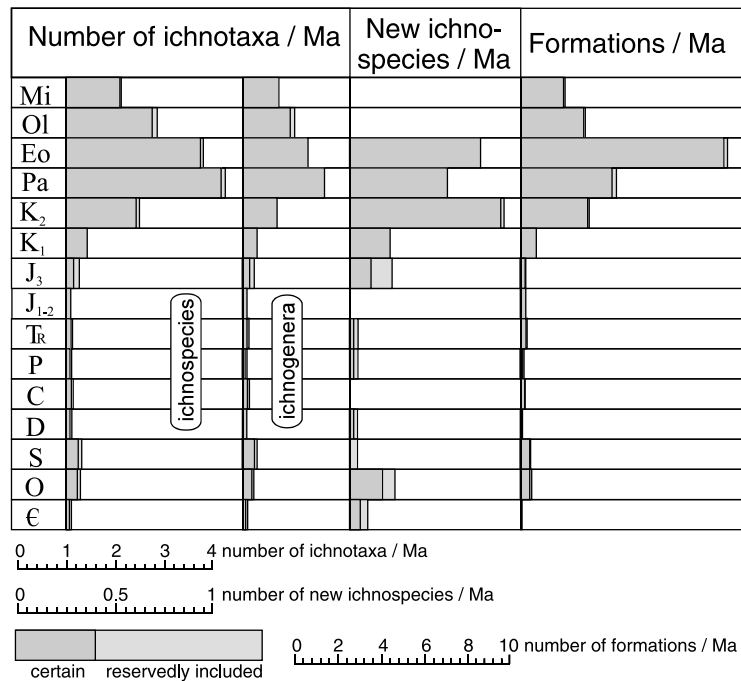
Fig. 9. Number of ichnotaxa (diversity), new ichnospecies (ichnospeciation rate) and frequency of occurrence of graphoglyptids in formations around the world in which they have been studied related to the duration of stages and epochs.

cies of *Cosmorhaphe* occur since the Cretaceous. The Lower Palaeozoic *Cosmorhaphe* described by Crimes and Crossley (1991) and Han and Pickerill (1994) have been excluded from this ichnogenus (Uchman, 1998). *Spirorhaphe*, which seems to be at least as complex as *Cosmorhaphe*, occurs in the Early Palaeozoic.

Among the uniramous meanders (Fig. 4), the relatively simple *Protopaleodictyon spinata* is the first to occur in the Cambrian. More complicated ichnotaxa, such as *Helicolithus* or *Urohelminthoida*, occur latter. The biramous meanders, characterised by several connections to the sea floor, do not occur in the Palaeozoic at all, except for the occurrence of a questionable Silurian *Desmograpton* (McCann, 1989). Only one ichnospecies of *Desmograpton* (i.e. *D. pamiricus*) occurs in the Triassic and Jurassic. The other biramous meanders occur for the first time in the Late Cretaceous and Palaeogene. Irregular and regular net-like graphoglyptids coexist together in the Palaeozoic and Mesozoic, but *Paleodictyon* with vertical shafts connecting the hexagonal net to the sea floor are

known only since the Cretaceous. Thus, morphologic complexity increases within each group and among different groups, but less and more complex forms coexist in the Cretaceous and Tertiary.

Seilacher (1977a,b, 1986) described evolutionary trends among graphoglyptids and depicted the lineages for their morphologic groups. Theoretically, ranges of trace fossils arranged in the lineages, especially their first occurrence, should be in chronologic order. Of course, the vagaries of trace fossil preservation might cause actual first occurrence to go unnoticed in incomplete stratigraphic sections. The lineages described by Seilacher (1977a) are in general agreement with the first occurrences presented in this paper, but there are several exceptions. According to the theoretical scheme, *Ubinia* (= *Dendrotichnium*) *alternans* should occur before *U. llarenai* (Seilacher, 1977a, fig. 6; 1986, figs. 3–11), but their first occurrences (respectively in the Late Cretaceous and Early Cretaceous) are out of chronologic order (Fig. 4). *Protopaleodictyon incompositum* should occur after *Helicolithus sampelayoi*, but the first un-
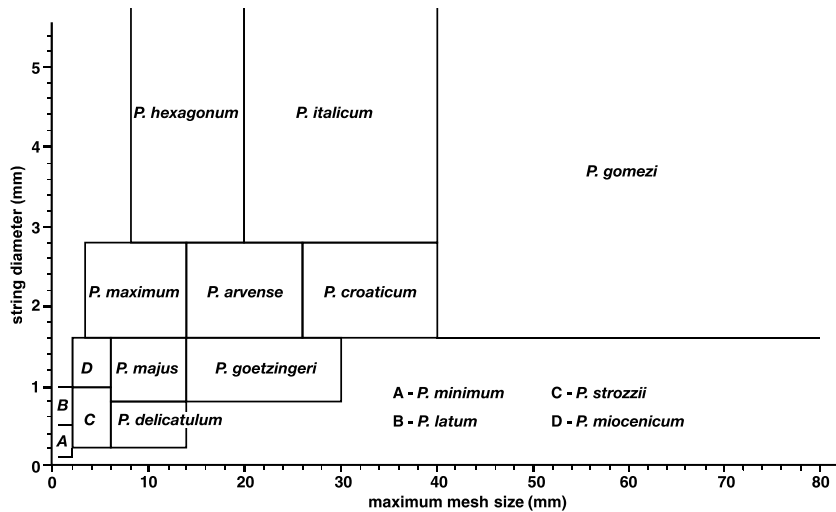
Fig. 10. Objective morphologic distinction of the ichnospecies of *Paleodictyon* based on the morphometric parameters of tunel diameter and maximum mesh size (after Uchman, 1995).

doubted occurrence of the former is in the Tithonian, and the latter occurs since the Late Cretaceous. Problems are posed by the radiating forms (Seilacher, 1977a, fig. 9; 1986, fig. 3.12), where all lineages begin with *Arabesca* (= *Tuapseichnium*) *simplex*, which occurs since the Eocene. It is followed by *Lorenzinia apenninica* and *L. carpathica*, which range since the Late Cretaceous, or *Glockerichnus glockeri*, which ranges since the Late Jurassic, or *Yacutatia emersoni*, which occurs in the Ordovician (Fig. 5). *Helminthorhaphe japonica* should occur after *Helminthorhaphe flexuosa* (= *H. crassa*) (Seilacher, 1977a, fig. 3; 1986, fig. 3.10) but the former ranges since the Early Cretaceous and the latter since the Late Cretaceous. It is clear that at least some of the mentioned lineages of graphoglyptids are not valid. New data may shed new light on this matter and allow a more general assessment of the lineage concept.

5. Trends in morphometric parameters of *Paleodictyon*

Maximum mesh size and maximum tunnel diameter are the basic ichnotaxobases used for distinguishing *Paleodictyon* ichnospecies (Sacco, 1888; Vialov and Golev, 1965; Książkiewicz, 1977). They have been revised by Uchman (1995) by means of a simple diagram (Fig. 10). The ichnotaxonomic parameters commonly overlap, and the distribution of ichnotaxa admittedly is somewhat arbitrary. Detailed stratigraphic analysis of *Paleodictyon* ichnospecies is not undertaken in this paper, but trends in the morphometric parameters are considered. In the Palaeozoic, large *Paleodictyon* nets with narrow tunnels dominate (Fig. 11A). In the Triassic and Jurassic, small- and medium-size forms with wide tunnels occur (Fig. 11B). A similar trend is shown in the Cretaceous (Fig. 12A). In the Palaeogene, *Paleodictyon* nets of different mesh size occur, but with relatively narrow tunnels (Fig. 12B). In the Miocene, forms with broad tunnels are common again (Uchman, 1995, text-fig. 24), similar to those from the Mesozoic. Thus, different morphometric parameters show different trends in the Palaeozoic, Mesozoic, Palaeogene and Neogene (Fig. 13).

The frequency of occurrence of *Paleodictyon* follows the trends of other graphoglyptids (Fig. 6). Regular nets of *Paleodictyon* have occurred since the Early Cambrian (Pacześna, 1985) and have coexisted with more irregular forms including *Squamodictyon* (Fig. 6).

Fig. 11. Morphometric parameters of the *Paleodictyon* specimens occurring in strata of Palaeozoic age (A) and Triassic and Jurassic age (B). For ichnospecies designations, see Fig. 10.

6. Discussion

6.1. Phanerozoic changes

According to Frey and Seilacher (1980, p. 201), the diversity of deep-sea ichnospecies increased gradually through the Phanerozoic until the Cretaceous burst, and it reached 'a point of near-saturation' in the Late Palaeozoic. However, Seilacher (1978) earlier had suggested that deep-sea ichnofauna reached a diversity saturation in the mid-Palaeozoic time. Crimes and Fedonkin (1994)
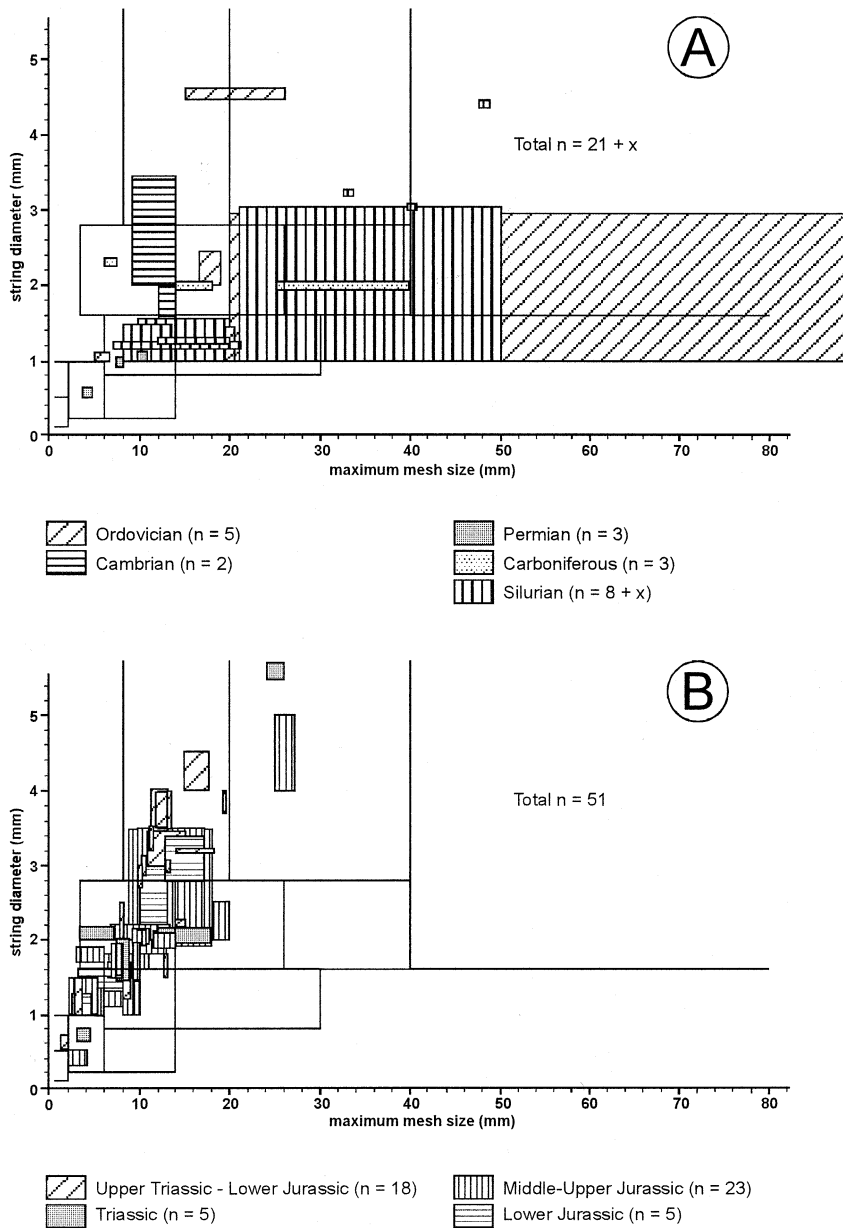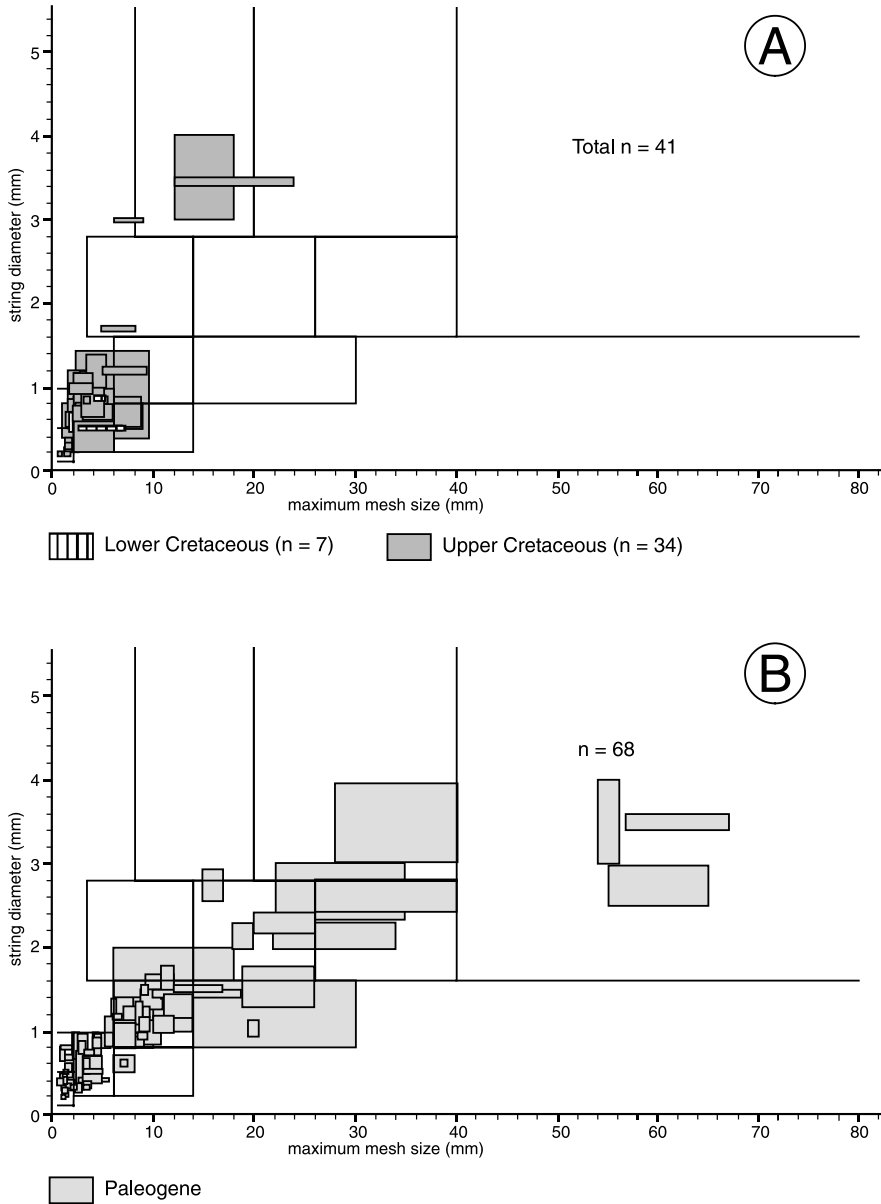
Fig. 12. Morphometric parameters of the *Paleodictyon* specimens occurring in strata of Cretaceous age (A) and Palaeogene age (B). For ichnospecies designations, see Fig. 10.

also suggested a gradual increase of ichnotaxonomic diversity until the Cretaceous. These views are challenged in this chapter, where considerable changes of graphoglyptids throughout the Phanerozoic and their relation to several biotic and abiotic changes are documented (Table 1).

6.1.1. Palaeozoic changes

The trends in diversity of graphoglyptids, especially in the contribution of their first occurrences (Figs. 7 and 9), show that graphoglyptids radiated for the first time in the Cambrian and reached the first peak in the Ordovician and Silurian. How-

Fig. 13. Main trends in the morphometric parameters of *Paleodictyon* for the Palaeozoic (based on Fig. 11A), for the Mesozoic (based on Figs. 11B and 12A) for the Palaeogene (based on Fig. 12B), and for the Miocene (after Uchman, 1995, text-fig. 24).

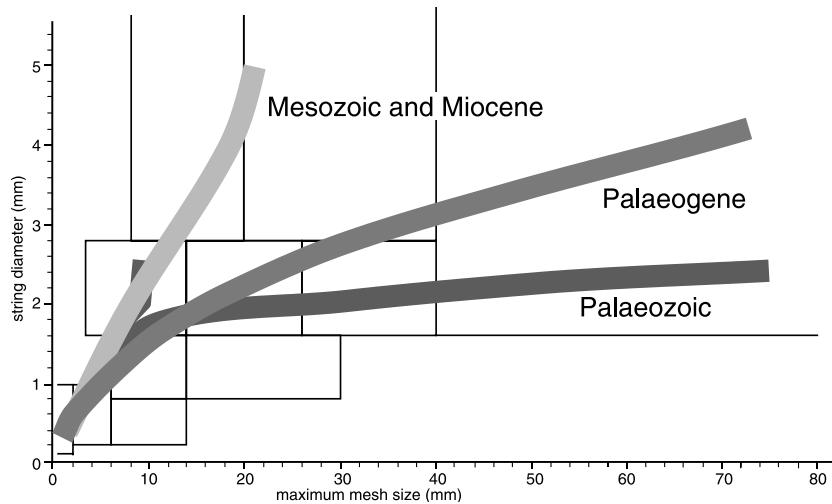ever, occurrences of new ichnospecies drop dramatically after the Ordovician (Fig. 9). The diversity drop of all deep-sea trace fossil taxa in the Welsh Basin was announced by McCann (1990). Crimes et al. (1992, fig. 6) showed a gradual increase of all deep-sea trace fossils from the Late Precambrian (Vendian) to the Early Silurian, but according to Orr (2001) the diversity increased after the Cambrian and dropped slightly after the Ordovician. The terminal Ordovician crisis corresponds to the Upper Ashgill bio-event, which was caused by the Late Ordovician glaciation, which resulted in the decline of diversity of several groups of organisms, including trilobites and graptolites (Barnes et al., 1996).

Pre-depositional trace fossils, represented mainly by graphoglyptids, and post-depositional trace fossils developed independently (Seilacher, 1978). Occurrences of new ichnotaxa of graphoglyptids were rare throughout the rest of the Palaeozoic and first half of the Mesozoic. Thus, graphoglyptids apparently filled the ecological niches in their environments in the Early Palaeozoic (i.e. in the Ordovician). Extensive colonisation of the deep sea by benthos first occurred in the Early Ordovician (Crimes et al., 1992; Crimes and Fedonkin, 1994) or the Cambrian–Ordovician boundary (Orr, 2001). The observed Ordovi-

cian increase of diversity and frequency of graphoglyptids confirms this view.

6.1.2. Mesozoic changes

The diversity of graphoglyptids started to increase again in the Late Jurassic and Early Cretaceous, and it exploded in the Late Cretaceous (Figs. 7 and 9), but the precise timing of this explosion has not been hitherto known before now. Seilacher (1974) wrote that it occurred by the Cretaceous. Seilacher (1977a) also wrote that most graphoglyptids range through the Late Cretaceous and Tertiary, suggesting that the main diversification happened in the Late Cretaceous. Frey and Seilacher (1980, p. 201) also noted the Late Cretaceous burst of diversity of deep-sea trace fossils in general. Seilacher (1986, p. 81) subsequently wrote that this burst began to happen by the mid-Cretaceous. The gradual increase of the diversity of graphoglyptids in the Late Jurassic roughly follows to the significant increase of diversity of foraminifera (Bathonian), calcareous nannoplankton (acme in Upper Callovian–Lower Oxfordian), and dinoflagellates (since the Middle Jurassic) (Hallam, 1996). Deep-sea coccolith oozes have covered large areas of the deep sea since the Late Jurassic (Roth, 1989).

The beginning of graphoglyptid diversification

Table 1
Main stages of evolutionary trends of graphoglyptids and corresponding biotic and abiotic changes

Main stages of the graphoglyptid changes	Selected biotic events and changes	Selected abiotic changes and events
Cambrian–Ordovician radiation	General radiation of biota	–
Post-Ordovician (Silurian) crisis	Upper Ashgill bio-event; decline of diversity in several groups of organisms	Late Ordovician glaciation
Devonian–Middle Jurassic stability	–	–
Late Jurassic and Early Cretaceous slow increase in diversity	Increase in diversity of foraminifera (Bathonian), calcareous nannoplankton (acme in Upper Callovian–Lower Oxfordian), and dinoflagellates (since Middle Jurassic)	Increasing amount of nutrient recycling since the Jurassic; widespread anoxia in the Early Cretaceous
Late Cretaceous explosion of diversity, occurrence frequency, and the maximum number of first occurrences	Rapid radiation of benthic foraminifera by the Turonian and nannoplankton in the early Cenomanian; increase in food competition in the deep-sea habitats; growing amount of terrigenous phytodetritus deposited to the deep sea	Maximum surface sea temperature in the Early Turonian; divergence of continents resulting in enlargement of ocean basins; improving of oxygenation of deep-sea floors
Early Paleocene drop of number of first occurrences	K/T boundary crisis, especially in marine plankton and benthic foraminifera	Temperature drop of deep-sea waters
Late Paleocene–Middle Eocene maximum diversity, occurrence frequency, and a new increase of rate of occurrence of new ichnospecies	Middle Eocene diversity peak of calcareous nannoplankton and benthic foraminifera	Increase of deep-water temperatures, widespread oligotrophy
Oligocene drop of diversity and frequency. Now new ichnotaxa	Eocene/Oligocene boundary crisis; drop of diversity of foraminifera, dinoflagellates and nannoplankton	Temperature drop of deep-sea waters, local anoxia
Miocene reappearance of several ichnotaxa	Increase in diversity of planktonic and benthic foraminifera and nannoplankton	Improving of climate

in the Late Cretaceous is confirmed in this paper (Figs. 7 and 9). Examples from the Carpathians (Książkiewicz, 1977; Uchman, 1998) and the Alps (Uchman, 1999) show that the dramatic increase of diversity of graphoglyptids took place after the Cenomanian, probably in the Turonian. Simultaneously, a rapid radiation of benthic foraminifera by the Turonian is observed in the North Atlantic (Kuhnt, 1992; Kuhnt and Wiedmann, 1995). Similarly calcareous nannoplankton showed a maximum rate of speciation a few million years earlier in the early Cenomanian (Bown et al., 1992; Burnett et al., 2000), and maximum surface sea temperature took place in the Early Turonian (Gale, 2000). Maximum increase of the first occurrences of graphoglyptids happened also in the Late Cretaceous. However, the increase in the frequency of graphoglyptid occurrences is slower. Probably, the speciation of graphoglyptid trace makers, indicated by the increase of the first occurren-

ces, did not result in immediate filling of their niches.

The rapid acceleration of graphoglyptid diversity in the Late Cretaceous may be explained by the increased amount of foraminiferal and coccolith oozes and the growing amount of plant detritus deposited to the deep sea due to the coeval evolution of terrestrial angiosperms. Radiation of the graphoglyptid trace makers may have been a response on the increased amount of non-refractory organic matter, mainly cellulose, into the oligotrophic deep-sea environment, where it could be used by burrowers for microbial farming (Seilacher, 1974, 1977a). Frey and Seilacher (1980) also suggested abiotic causes related to the divergence of continents resulting in enlargement of ocean basins, which in turn might have resulted in increased speciation.

The influence of the input of plant detritus on trace fossil diversity is not easy to explain. Per-

haps, more attention should be paid to the Cretaceous changes of plankton (Miller, 1991), but the influence of plankton upon graphoglyptids also remains unclear. Graphoglyptids are most common in oligotrophic flysch facies containing light-coloured shales (Tunis and Uchman, 1996; Uchman, 2001), which are not rich in phytodetritus. Probably the rapid burst of diversity is also sharpened with other palaeoceanographic and biotic changes in the deep sea. For instance, a slow expansion of graphoglyptid trace makers may have been caused by the widespread anoxia in the Early Cretaceous (Jenkyns, 1980), especially in the Valanginian (Lini et al., 1992) and Upper Barremian–Lower Aptian (Bralower et al., 1994). The poor oxygenation of oceanic bottom water in the Early Cretaceous was an important factor limiting deep-sea faunal diversity (Jacobs and Lindberg, 1998, and references therein).

The end of the major anoxic episodes in the Turonian enabled more extensive colonisation of the deep-sea floor accompanied by radiation of graphoglyptids or their expansion from refuges. At that time, *Ophiomorpha* (produced by larger crustaceans) became common in the deep-sea facies (Bottjer et al., 1987, 1988), as did *Scolicia* (produced by irregular echinoids; Tchoumatchenco and Uchman, 2001). In fact, the migration of these two ichnogenera into deep-sea habitats happened already in the Tithonian, but this migration continued into the mid-Cretaceous because of the frequent intervals of anoxia (Tchoumatchenco and Uchman, 2001). The trace makers of *Ophiomorpha* and *Scolicia* were very effective sediment feeders, and so food competition in the deep-sea habitats increased. This competition was enhanced by the increasing amount of nutrient recycling since the Jurassic (Martin, 1996).

6.1.3. Major biological crises and Cenozoic changes

Seilacher (1974, 1986) suggested that deep-sea trace fossils are not influenced by the major biological crises that affected shallow-marine and terrestrial faunas, but McCann (1990) expressed a different opinion. Ichnologic analyses of the Permian/Triassic (Twitchett and Wignall, 1996) and the Cretaceous/Tertiary (K/T) crises (Ekdale and Bromley, 1984; Ekdale and Stinnesbeck, 1998) in certain sections or regions do not offer meaningful generalisations about the influence of these crises on the general diversity of trace fossils. However, the drop of ichnospeciation rate of graphoglyptids in the Silurian (Fig. 7) might be related to the crisis across the Ordovician/Silurian boundary.

Changes of graphoglyptids at the K/T boundary are not clear. However, the number of ichnotaxa and frequency of occurrences drop in the Paleocene, but the same parameters divided by million years show an increase in comparison to the Upper Cretaceous. Only the first occurrences display a drop in both cases. It is not impossible that the drop was caused by the K/T boundary crisis, which strongly influenced marine plankton (e.g. Thunell, 1981; Canudo et al., 1991; Burnett et al., 2000) and benthic foraminifera (e.g. Speijer, 1994). At least a local crisis of planktonic foraminifera occurred already in the Maastrichtian (Abramovich et al., 1998). The temperature of deep-sea waters dropped in the Paleocene (Barron and Peterson, 1991). This may have disturbed the infaunal farming activity of graphoglyptid trace makers.

The maximum occurrence frequency and a new increase of number of new ichnospecies occur in the Eocene (Fig. 7). The number of graphoglyptid ichnotaxa is highest also in the Eocene, but the diversity related to time drops slightly at the same time (Fig. 9). Ichnologic studies in the Julian Prealps (Tunis and Uchman, 1996), Carpathians (Książkiewicz, 1977; Uchman, 1998) and the Rhenodanubian Flysch (Uchman, 1999) show that the increase of graphoglyptid diversity began already in the Late Paleocene and actually started to decrease in the latest Middle Eocene. This phenomenon is related to the advent of oligotrophic conditions in the Late Paleocene–Early Eocene (Tunis and Uchman, 1996), which is a widespread phenomenon (Hallock et al., 1991) related to an interval of global warming (Savin et al., 1975; Boersma and Premoli Silva, 1991) that resulted in a significant increase of deep-water temperatures (e.g. Brass et al., 1982; Shackleton, 1986). These phenomena are rooted in the global tectonic and palaeoceanographic changes (Rea et al., 1990; Oberhänsli, 1996; Pickering, 2000).

Calcareous nannoplankton diversity displays a second diversity peak in the Middle Eocene (Bown et al., 1992). The generic richness of benthic foraminifera also shows a maximum in the Middle Eocene (Lutetian) (MacLeod et al., 2000). These observations seem to support a relationship between the evolutionary dynamic of plankton and graphoglyptids. It may not be merely a coincidence. Graphoglyptid trace makers, with their infaunal farming activity exploiting short seasonal rains of phytoplankton, were succesfully adapted to the oligotrophic conditions. A predicted supply of organic matter to the deep-sea floor in a short span of time (Tyson, 1995) might have been an evolutionary factor promoting farming activity, which would have allowed a prolonged availability of food during the rest of the year.

A distinct drop in diversity and a drastic drop in frequency of graphoglyptids occurred in the Oligocene, since 72% of the Eocene ichnospecies do not occur in the Oligocene. No new ichnospecies have appeared since that time (Fig. 7), so the niche of graphoglyptids apparently became filled by the Eocene.

This decrease of diversity and cessation of graphoglyptid speciation can be related to the Eocene/Oligocene boundary crisis that also influenced plankton (Corliss, 1979). The diversity of foraminifera, dinoflagellates and nannoplankton dropped drastically after the Eocene (Cavelier et al., 1981). The temperature dropped as well (Buchard, 1978), and the longitudinal Atlantic circulation and connection to the Arctic Ocean was established (Prothero, 1994). Cold polar water entered several deep-sea basins, such as in the Carpathians and in the Alps, and local anoxic conditions occurred (Leszczyński, 1997).

A new increase in total number of graphoglyptids and the occurrence frequency occurred in the Miocene. The parameters in relation to time are not obvious (Fig. 9) because the Oligocene (10.2 Ma) was shorter than the Miocene (18.2 Ma). Nevertheless, the lack of a record of several graphoglyptid taxa in the Oligocene is clear (Figs. 3–6). This shows that the parameters related to time are not always more objective than those expressed by the total numbers. Most likely,

the producers of the graphoglyptids that are not recorded in the Oligocene but occur again in the Miocene are Lazarus taxa (Wignall and Benton, 1999; Twitchett et al., 2000), which had lived in Oligocene refugia and than became widespread once again in the Miocene when palaeoenvironmental conditions improved. This problem concerns also long discontinuities in ranges of several ichnospecies of graphoglyptids (Figs. 3–6).

Similarly to the Oligocene, no new ichnospecies appeared in the Miocene. The climate improved (Savin et al., 1975), but the benthic niches still remained filled with graphoglyptids. Diversity of planktonic and benthic foraminifera increased at the beginning of the Miocene (Thunell, 1981; MacLeod et al., 2000), as did the diversity of the calcareous nannoplankton (Bown et al., 1992).

6.2. Evolutionary considerations

The general increase in the complexity of graphoglyptids through time is supported by this study. However, the general development of behavioural optimisation, as proposed by Seilacher (1967, 1976, 1977a,b, 1986) has been challenged by Crimes and Fedonkin (1994), who showed that the high level of behavioural optimisation already had been reached in the Early Cambrian or even in the Late Precambrian.

The miniaturisation of graphoglyptids through the Phanerozoic as suggested by Seilacher (1974, 1977a,b) is very problematic. Maximum mesh size of the Palaeozoic *Paleodictyon* (Fig. 11A) is generally larger than in the Mesozoic (Figs. 11B and 12A), and in the Palaeogene large and small *Paleodictyon* meshes coexist (Fig. 12B). *Cosmorhaphe heliminthopsoidea* is generally larger in the Palaeozoic (Crimes and Crossley, 1991) than in the Upper Cretaceous and Palaeogene (Książkiewicz, 1977). In other groups of graphoglyptids, a trend of miniaturisation is unclear. Even opposite examples can be invoked. In the Eocene, for example, some giant forms do occur, such as *Paleodictyon gomezi* (Wetzel, 2000), *Glockerichnus alata* (Seilacher, 1977b; Tunis and Uchman, 1998), *Dendrorhaphe haentzscheli* (Seilacher, 1977a; Uchman, 1999), and *Estrellichnus jacaensis* (Uchman and Wetzel, 2001).

Taxonomy of the early graphoglyptids presents a problem, because it has been common for researchers to name them after well-known Cretaceous/Tertiary ichnotaxa. More than half of these taxonomic determinations are questionable (e.g. Uchman, 1998), and so the early graphoglyptids require a careful ichnotaxonomic revision. Several of them probably belong to new ichnospecies of graphoglyptid ichnogenera, and several others probably are preservational variants of meandering, non-graphoglyptid ichnotaxa. In many cases, their meanders show crossings, which generally are not present in graphoglyptids. Seilacher (1977a) suggested that the simplest graphoglyptids (continuous meanders) derive from producers of simple, meandering, locomotion trails, like *Cochlichnus*. *Cochlichnus* sometimes is regarded as a trace fossil of predators (Głuszek, 1998), and this hypothesis fits very well with the trap model, based on the modern annelid worm *Paraonis*, for the Palaeozoic graphoglyptids (Seilacher, 1977a). Precursors of the other major graphoglyptids are not known, but the Lower Cambrian *Phycodes coronatum*, with a ring-like tunnel and a wreath of vertical shafts (Crimes and Anderson, 1985), might have been the precursor of *Lorenzinia*. The Lower Cambrian *Treptichnus* (Crimes, 1992) and *Hormosiroidea canadensis* (Crimes and Anderson, 1985) might have been precursors of uniramous and biramous, meandering graphoglyptids. This was suggested by Crimes (1992, fig. 10).

The different trends in morphometric parameters of *Paleodictyon* through the Phanerozoic (Fig. 13) probably are related to phylogenetic changes of the trace makers, which are thought by some researches to have been small crustaceans (Garlick and Miller, 1993). The early *Paleodictyon* burrow systems, without any evidence of multiple vertical connections to the sea floor, can be considered as traps of meiobenthos. In contrast, those from the Cretaceous and Tertiary, with multiple vertical shafts, are regarded as microbial gardens (Seilacher, 1977a). The evidence shows that the morphometric trends in these burrows changed at least four times throughout the Phanerozoic.

Generally, the increase of diversity, frequency, and ichnospeciation rate were not gradual with a single explosion in the Cretaceous, as inferred by Seilacher (1974, 1977a,b, 1986). These changes exhibit their own dynamics, similar to the changes of diversity of marine plankton, which are related to large-scale palaeoceanographic, tectonic and climatic changes and are influenced by major global biotic crises.

The earlier inference of a long, gradual, predictable evolution of trace fossils in extremely stable deep-sea biotopes by Seilacher (1976, 1978) and Frey and Seilacher (1980) was explained as an example of the time-stability hypothesis of Sanders (1968). According to this view, the long-term stability of the environmental conditions in the deep sea promoted linear trends of gradualitic evolution of the graphoglyptid trace makers. However, departure from the time-stability hypothesis is demonstrated in this paper by the rapid increase in the graphoglyptid diversity in the Late Cretaceous. The changes of graphoglyptid diversity, frequency and ichnospeciation presented in this paper show unpredictable dynamics, not simple linear changes through time. This observation is not in accordance with the time-stability hypothesis of Sanders (1968).

7. Conclusions

(1) The diversity and frequency of graphoglyptid trace fossils display considerable changes throughout the Phanerozoic. Generally, the diversity and frequency of graphoglyptids are low from the Cambrian to the Middle Jurassic, with a low peak in the Ordovician followed by a drop in the Silurian. The diversity and frequency started to increase gradually in the Late Jurassic and increase markedly in the Late Cretaceous, probably during the Turonian. They dropped again in the Paleocene, and then they increased to maximum values in the Eocene. The Oligocene is marked by a sharp decrease in graphoglyptid diversity and frequency, followed by an increase in the Miocene. For the Tertiary, a plot of diversity related to time shows a single peak in the Paleocene, and a plot of frequency related to time shows a single peak in Eocene.

(2) Graphoglyptids radiated morphologically in

the Cambrian and Ordovician. The benthic niches for graphoglyptid trace makers were almost saturated from the Silurian to Middle Jurassic. New radiation started in the Late Jurassic and accelerated suddenly in the Late Cretaceous. Diversification of graphoglyptid burrows dropped in the Paleocene, increased again in the Eocene, and ceased in the Oligocene and Miocene.

(3) The Late Cretaceous radiation of graphoglyptids may be correlated with global changes in plankton and organic matter circulation. The ichnologic radiation probably was delayed from the Lower Cretaceous by the widespread anoxia at that time.

(4) The Eocene (total number of ichnotaxa) or Paleocene (total number of ichnotaxa/Ma) peak of the diversity of graphoglyptids and the Eocene peak of frequency of graphoglyptids are related to the common occurrence of oceanic oligotrophy in the Late Paleocene and Early Eocene.

(5) The biotic crises across the Ordovician/Silurian, Cretaceous/Tertiary, Paleocene/Eocene, and Eocene/Oligocene boundaries influenced the diversity and occurrence frequency of graphoglyptids.

(6) Graphoglyptids display an increase of complexity with time, showing a distinct acceleration in the infaunal Late Cretaceous, when the farming activity of their trace makers became a common feeding strategy.

(7) Morphometric analyses of *Paleodictyon* display trends in size and shape throughout the Phanerozoic, and these changes are related to evolutionary changes of their trace makers.

(8) Application of the time-stability hypothesis of Sanders (1968) to graphoglyptid evolution is not supported by the observed data.

Acknowledgements

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