

Oligocene trace fossils from temporary fluvial plain ponds: An example from the Freshwater Molasse of Switzerland

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Key words: Trace fossils, ichnofacies, plant remains, continental environment, fluvial plain, Oligocene, Freshwater Molasse

ABSTRACT

Numerous invertebrate trace fossils and small rare vertebrate tracks are reported and described from the Upper Oligocene deposits of the Lower Freshwater Molasse in eastern Switzerland. They are commonly accompanied by mud-cracks, raindrops, and plant remains, mostly leaves. The invertebrate trace fossils were produced by different animals, mostly insect larvae, nematodes, and probably by molluscs, in desiccating pools on a fluvial plain of a braided river. The trace fossil assemblage differs from the *Scoyenia* ichnofacies which is typical for terrestrial fluvial plain environment. Instead, it resembles the impoverished *Mermia* ichnofacies which is probably common but poorly known in this environment. This ichnofacies corresponds to a low energy environment, most probably to fluvial plain ponds.

ZUSAMMENFASSUNG

Aus der oberoligozänen Süßwasser-Molasse der Ostschweiz werden zahlreiche Spurenfossilien von Invertebraten und einige Spuren kleiner Vertebraten beschrieben. Diese Spuren sind häufig mit Trockenrissen, Abdrücken von Regentropfen und Pflanzenresten, vor allem Blättern, assoziiert. Verschiedene Organismen, meist Insektenlarven, Nematoden und möglicherweise Mollusken, haben die Invertebraten-Spuren in austrocknenden Tümpeln auf einer Schwemmlandebene hinterlassen. Die beschriebene Assoziation von Spurenfossilien unterscheidet sich von der *Scoyenia* Ichnofazies, die für Ablagerungen im Bereich von Schwemmlandebenen typisch ist. Statt dessen gleicht sie einer verarmten *Mermia* Ichnofazies, die aus diesem Ablagerungsraum wenig bekannt ist, aber wahrscheinlich häufig auftritt. Diese Ichnofazies entspricht einem Ablagerungsraum geringer Energie, wie er in Tümpeln auf einer Flussebene vorkommt.

Introduction

Continental ichnology has experienced a rapid development during the last decade. Trace fossils are critical tools to recognize environmental parameters in non-marine settings, as they are in marine palaeoenvironments. They provide detailed information about life in the past (Tevesz & McCall 1982; Hasiotis & Bown 1992; Donovan 1994; Buatois & Mángano 1995, 1998; Buatois et al. 1998; Genise et al. 2000; Hasiotis 2002). Almost every continental environment displays its own ichnological record, which changes through geological time. However, data from continental environments are very sparse. The described trace fossils are an example of traces from desiccating ponds, which are rarely observed in the fossil state.

A relatively rich assemblage of invertebrate and small vertebrate trace fossils were discovered in Upper Oligocene mudstones of the Lower Freshwater Molasse from a locality in the Wägital, in central Switzerland (Fig. 1). Sedimentary structures, including mud cracks and raindrop imprints are preserved on mudstone slabs. Their sedimentological context suggests a desiccating pond environment in a fluvial plain of a braided river. Most of the reported ichnospecies have never been reported from the continental Freshwater Molasse of Switzerland. From this area Bräm (1954), Clercq & Holst (1971), Weidmann & Reichel (1979), Keller (1982), and Bolliger (1998, 1999) described trace fossils of vertebrates, whereas Speck (1945), Bolliger & Gubler (1997) and Bolliger (1999) published trace fossils of invertebrates.

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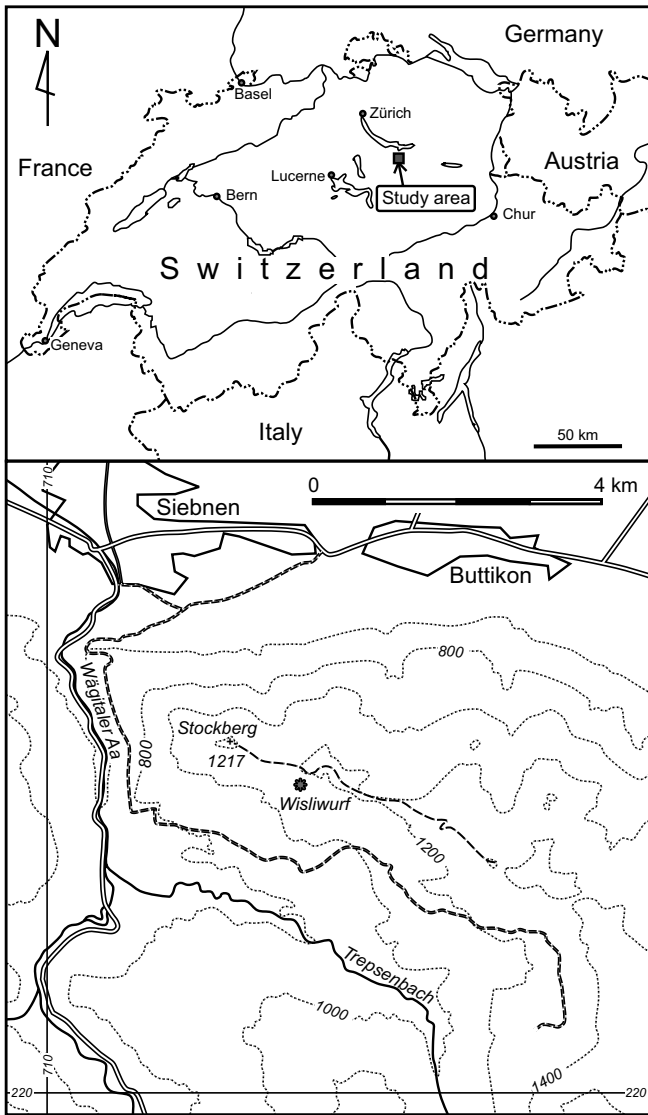


Fig. 1. Location map.

Location and material

The trace fossils described in this paper were collected over several years (1967–1969) by F. Schneider at the location Wisliwurf (N47 09.139 / E08 55.439) near the township of Lachen, Canton Schwyz, Switzerland (location map see Fig. 1). They are now housed in the Geological Collection of the Swiss Federal Institute of Technology in Zürich, Switzerland.

The fossiliferous site is situated in a syncline structure termed “Ruebergschwaend syncline” (Ochsner 1975) which represents a displaced unit of the Lower Freshwater Molasse (allochthonous Subalpine Molasse), 2 km north of the main overthrust of the Alpine Helvetic nappes. The section of Late Oligocene age is composed of an alternation of conglomerates,

sandstones and mudstones. The dominant conglomerates consist essentially of Jurassic and Cretaceous limestone clasts (see profile 4 in Ochsner 1975) and dip southwards with an inclination between 40° and 80°.

The trace fossil bearing horizon is part of an interval of grey fine-grained sediments, about 3 m thick, intercalated between thick sequences of coarse-grained sediments, including conglomerates. The fine-grained sediments are generally thin-bedded and mottled. Lamination can be observed in the immediate vicinity of the trace fossils. On some bedding planes plant debris and some larger plant compressions are common. Most of the plant remains are strongly degraded and only the more resistant leaves, needles and fruits are preserved. The plants are generally concentrated in more sandy horizons. In these beds trace fossils are rare and rather poorly preserved, and root structures prevail.

Plant remains

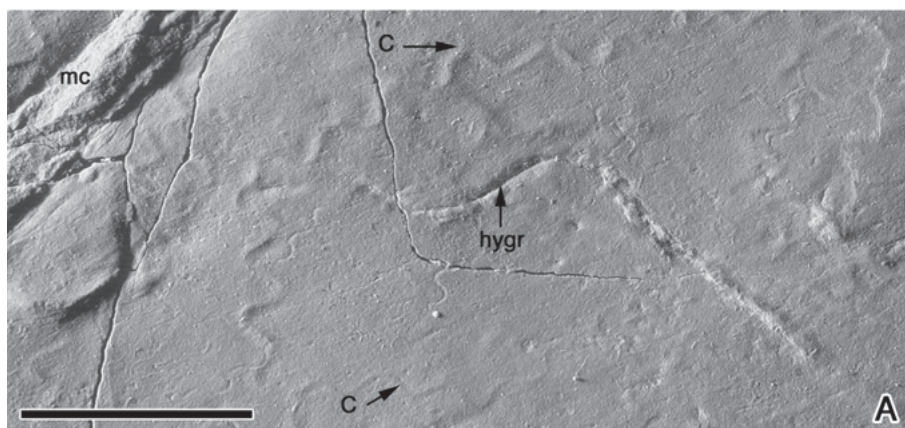
Plant remains are commonly associated with the trace-bearing horizon. The preservation of the leaves varies considerably. They are preserved as compressions or as impressions. Some casts of fruit remains have also been observed. The surface pattern of most leaves is strongly disturbed by roots and animal trace fossils masking in some cases the nervation patterns. Epidermal structures are preserved in some specimens.

The assemblage of fossil plants is relatively poorly diversified. Compared to other plant associations of similar age (Baumberger & Menzel 1914) the percentage of laurophyllous leaves and pine needles is exceptionally high. The remaining part of the plant assemblage consists essentially of leaves of *Salix* and *Populus*. These two groups are also represented by fruit remains similar to *Salix varians* HEER (1856, pl. 65, figs. 8–12) and to *Populus mutabilis* HEER 1856 (pl. 61, figs. 4–5). Paired pine needles of considerable length are very similar to those described as *Pinus hepios* HEER (1855, pl. 21, fig. 7). All the laurophyllous leaves are characterised by typically developed secondary nerves and, as in *Cinnamomum polymorphum* (cf. HEER 1856, pl. 44, figs. 21–25), by a considerable variation in shape. Some of them have pronounced leaf tips (Träufelspitze). Most of the leaves comparable with *Salix* are elongate, some have an entire margin comparable to *Salix angusta* HEER 1856 (pl. 69, figs. 1–11), others have toothed margins (cf. *Salix varians* HEER 1856, pl. 65, figs. 1–3).

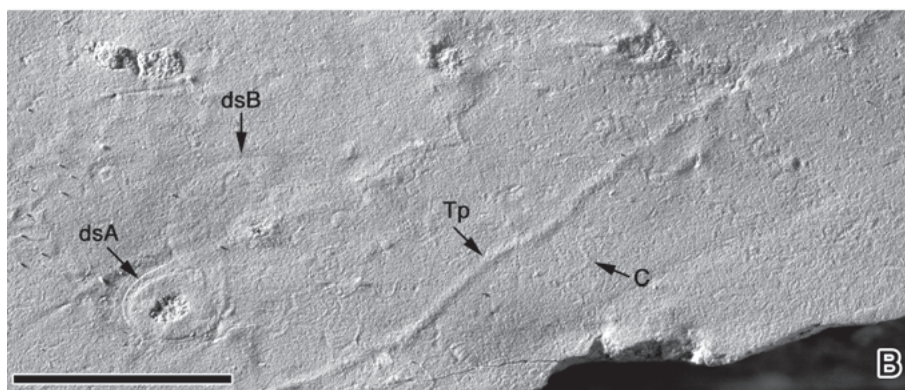
The relatively poorly diversified assemblage may reflect local conditions or its composition may be biased by seasonal or preservation effects.

Invertebrate trace fossils

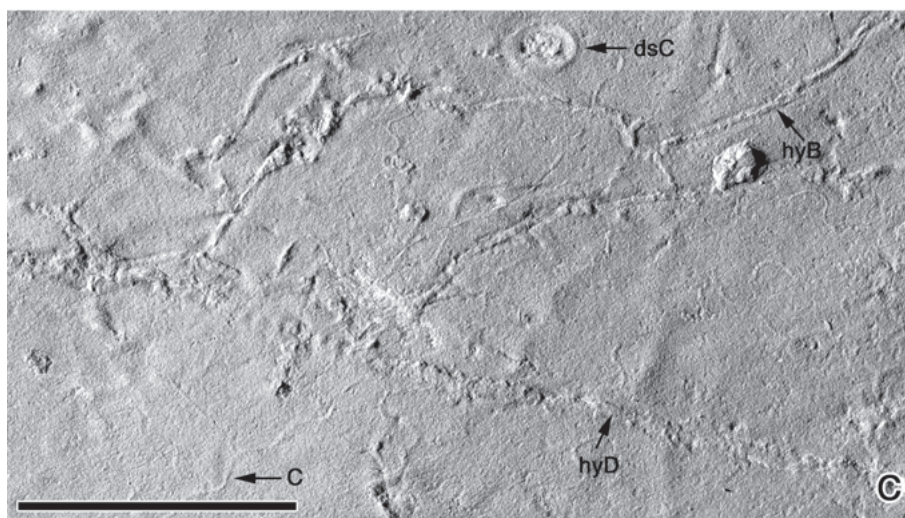
The invertebrate trace fossils are preserved on the lower and upper surfaces of the studied slabs. Several forms have been determined according to the rules of ichnotaxonomy, others are left in open nomenclature because of their poor preservation



5341



5343



5343

Fig. 2. Trace fossils on the lower surface of mudstone slabs. A: *Cochlichnus anguineus* (C), the hypichnial groove-ridge structure (hygr) and a mud-crack (mc), 5341. B: *Treptichnus pollardi* (Tp), *Cochlichnus anguineus* (C), discoid structure A (dsA) and discoid structure B (dsB), 5343. C: *Cochlichnus anguineus* (C), discoid structure C (dsC), hypichnial ridge B (hyB) and hypichnial ridge D (hyD), 5343. Scale bars = 1 cm.

Cochlichnus HITCHCOCK 1858

Cochlichnus anguineus HITCHCOCK 1858

Figs. 2A–C, 4B–D, 5A–C, 6C, 9C

non 1858 *Cochlichnus anguineus* (nov. sp.) - Hitchcock, 161–162, pl. 26, fig. 6 [left and middle].

? 1858 *Cochlichnus anguineus* (nov. sp.) - Hitchcock, 161–162, pl. 26, fig. 6 [right].

1858 *Cochlichnus anguineus* (nov. sp.) – Hitchcock, 161–162, pl. 37, fig. 4.

1940 [unnamed] – Schwarzbach, 569, pl. 20, fig. 8.

1970 nematode trail – Moussa, 304, text-fig. 2 [copied by Tevesz & McCall 1982, fig. 2].

1974 insect larva trail – Gibbard & Stuart, 73, fig. 7.

1977 insect larval trace – Gibbard, 56, figs. 4–5.

1978 *Cochlichnus* – Gibbard & Dreimanis 1972, fig. 3c.

1980 probable nematode trace – Fordyce, 121, fig. 1.

1980 morphotype H, sinusoidal trace – Merta, 168, pl. 4, figs. 4–6.

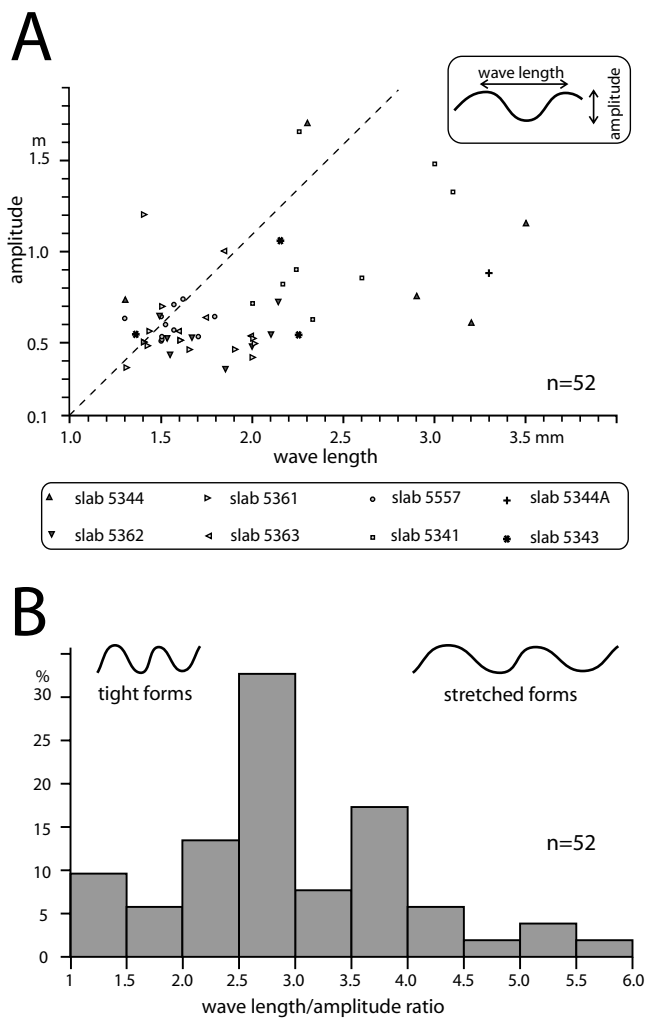


Fig. 3. Morphometric parameters of *Cochlichnus anguineus*.

1998 *Cochlichnus* sp. – Walter & Suhr, pl. 3, 317–318, figs. 2–5.

1998 *Cochlichnus* – Metz, 304, fig. 2.

? 1999 *Cochlichnus* – Bolliger, 526, fig. 4.

1999 *Gracilichnus sinualis* igen. nov., isp. nov. – Yang & Shen, 38, fig. 4, pl. 2, fig. 5.

? 1999 *Gracilichnus sinualis* igen. nov., isp. nov. – Yang & Shen, 38, pl. 2, figs. 2–4, pl. 3, fig. 6.

Description. – Very thin, epichnial, meandering grooves or hypichnial meandering ridges, which display only first-order sinuous meanders. Width of the grooves or ridges ranges between 0.05 and 0.45 mm, but the majority is between 0.1 and 0.25 mm. Most of the meanders are regular. The wavelength of the sinuous meanders in 52 specimens ranges between 1.3 and 3.5 mm, and the amplitude between 0.4 and 1.7 mm. The ratio of the wavelength to amplitude ranges between 1.3 and 5.8. It shows one maximum between 2.5 and 3, and two minor peaks between 1 and 1.5, and 3.5 and 4 (Fig. 3).

Remarks. – *Cochlichnus anguineus* is the type ichnospecies of *Cochlichnus*, but its type specimens from the Triassic of Cincinnati are known only from drawings (Hitchcock 1858). *Cochlichnus* was discussed by several authors (e.g., Fillion & Pickerill 1990; Głuszek 1995). Only surface traces have been included in *Cochlichnus* by Rindsberg (1994). The subsurface forms have been distinguished by the latter author as a new ichnogenus *Cymatulus*. However, Stanley & Pickerill (1998) argued that the distinction is very subtle and regarded *Cymatulus* a junior synonym of *Cochlichnus*. The here described forms are all epichnial grooves, thus their casts belong to *Cochlichnus* HITCHCOCK.

Cochlichnus anguineus displays specific morphometric parameters (Fig. 3) and preservation typical of non-marine environments. Specimens of *C. anguineus* that display the same or very similar features are included in the synonymy list. Forms of *C. anguineus* from marine or brackish settings are larger (see Stanley & Pickerill 1998, and references therein). The ratio wavelength to amplitude displays three peaks (Fig. 3). This is probably related to different producers or to changing substrates. It is possible that the morphometric parameters will help in further taxonomic reassessment of *Cochlichnus*.

Different organisms are regarded as producers of non-marine *Cochlichnus*. Hitchcock (1858) suggested annelids; however, recent traces of this morphology are produced mainly by insect larvae (Toula 1908). Larvae of biting midge (family Ceratopogonidae) and dipteran larvae (family Therevidae) have been found to produce such traces (Metz 1987a and Michealis 1972, respectively). The dipterous insect *Chironomus motilator* is also suspected to produce this kind of trace (Emerson in Tarr 1935). Other authors regarded it as nematode trails (Moussa 1970; Chamberlain 1975; Metz 1998). Indeed, experiments with nematodes confirm the latter idea (Sandstedt et al. 1961; Rode & Staar 1961).

Steinsfjordichnus WHITAKER 1979

Steinsfjordichnus brutoni WHITAKER 1979

Fig. 4A

Description. – Hypichnial, slightly winding row of short bars. The bars are 0.9 mm long, about 0.4 mm wide and about 0.5 mm apart. The row is traced over a distance of about 20 mm.

Remarks. – This trace fossils corresponds to the diagnosis of *Steinsfjordichnus* by Whitaker (1979), who described the monospecific *S. brutoni* WHITAKER which occurs in a rippled sandstone bed in the Lower Devonian fluvial to lacustrine Old Red Sandstone of southern Norway. However, the type material of *S. brutoni* is distinctly larger (9–11 mm wide) than the forms described here. Gibert et al. (2000) recorded a smaller (1–6 mm, typically 2–3 mm wide) *S. brutoni* from Lower Cretaceous lacustrine deposits of Spain. This shows that *S. brutoni* displays a wide size range. Therefore, we include the described material in this ichnospecies.

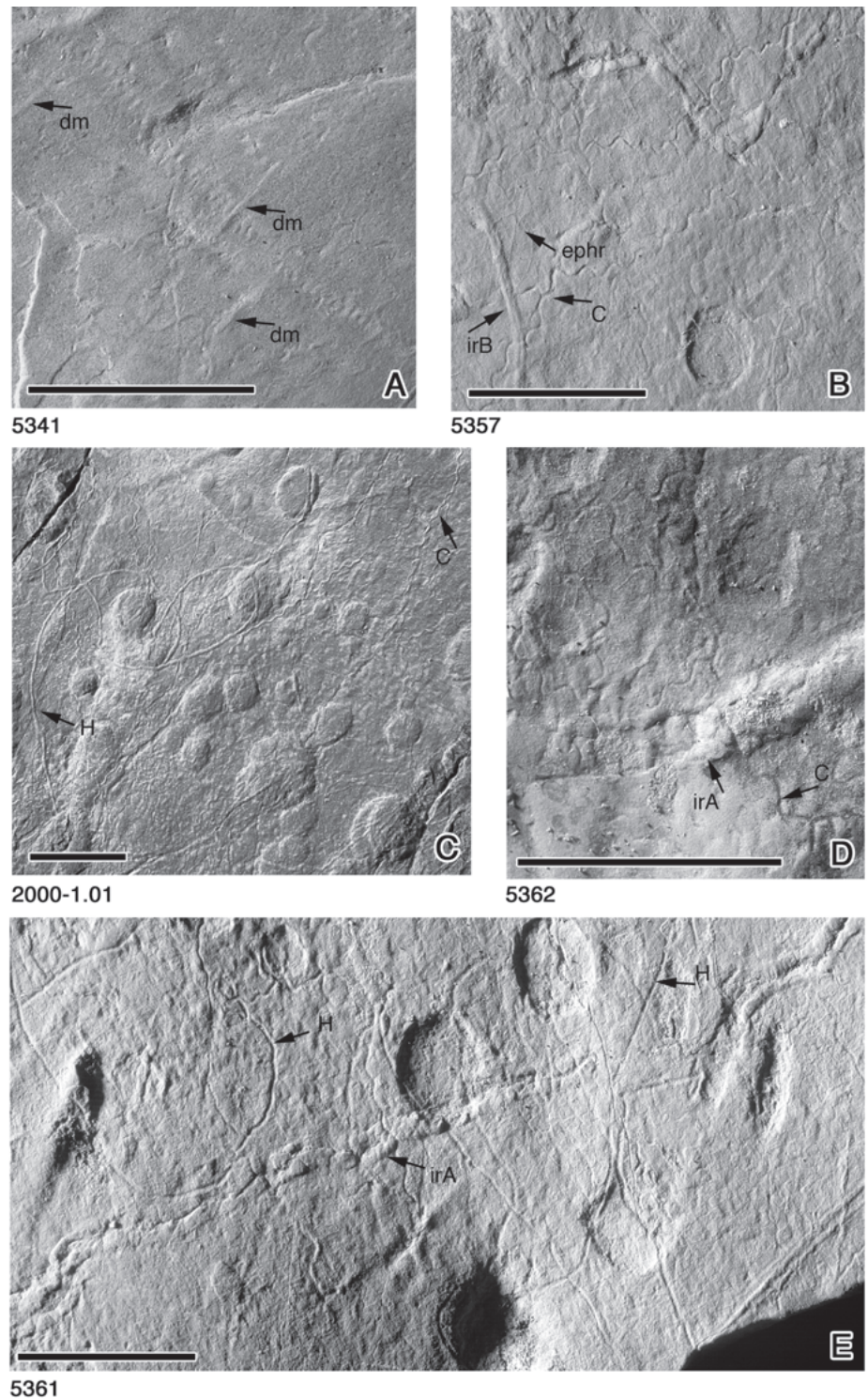
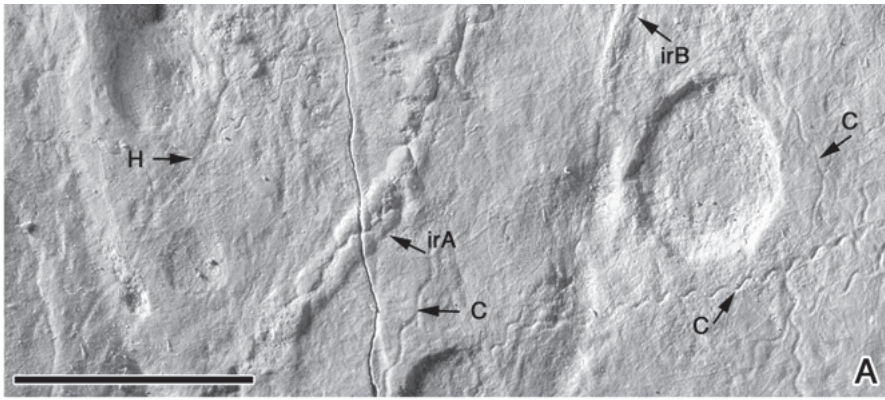


Fig. 4. Trace fossils on the lower surfaces (A) and on the upper surfaces (B-E) of mudstone slabs. A: *Steinsfordichnus brutoni* and drag-marks (dm), 5341. B: *Cochlichnus anguineus* (C), irregular ridge B (irB), epichnial hair ridge (ephr) and rain drop imprints, 5357. C: *Helminthoidichnites* isp. and rain drop imprints, 2000-1.01. D: *Cochlichnus anguineus* (C) and irregular ridge A (irA), 5362. E: *Helminthoidichnites* isp. (He), irregular ridge A (irA) and rain drop imprints, 5361. Scale bars = 1 cm.

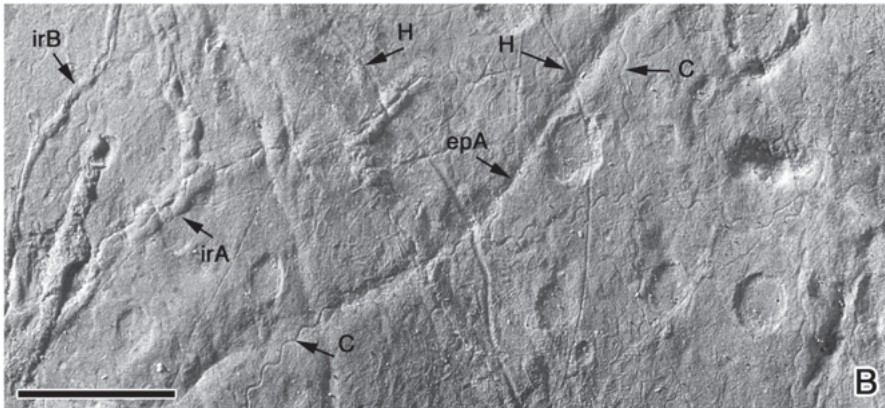
Whitaker (1979) interpreted *Steinsfordichnus* as a locomotion trace of either segmented animals such as annelids, or less likely as a trace of animals with muscular feet, moving rhythmically like a mollusc. Gibert et al. (2000) proposed molluscs,

especially gastropods, as the most probable producers, however, they did not exclude insect larvae or annelids.

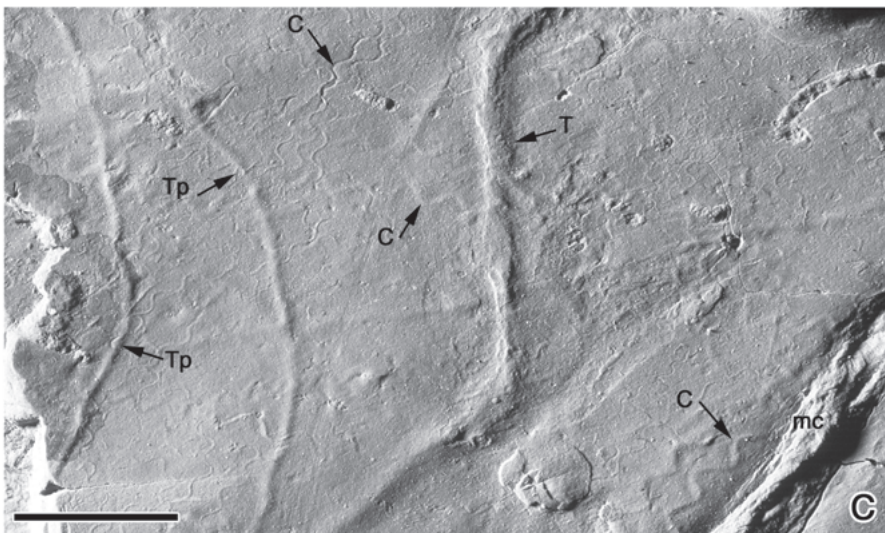
The here described forms represent the youngest record of this ichnogenus.



5361



5357



5341

Fig. 5. Trace fossils on the lower surface of mudstone slabs. A: *Helminthoidichnites* isp. (H), irregular ridge A (irA), *Cochlichnus anguineus* (C) and rain drop imprints, 5361. B: irregular ridge A (irA), irregular ridge B (irB), *Helminthoidichnites* isp. (H), epichnial groove A (epA), *Cochlichnus anguineus* (C) and rain drop imprints, 5357. C: *Treptichnus pollardi* (Tp), *Treptichnus* isp. (T), *Cochlichnus anguineus* (C), and mud-crack (mc), 5341. Scale bars = 1 cm.

Helminthoidichnites FITCH 1850

Helminthoidichnites isp.

Figs. 4C, E, 5A–B, 6F

Description. – Epichnial, slightly winding, very thin, smooth grooves, 0.15 to 0.25 mm wide forming rare, local loops.

Remarks. – *Helminthoidichnites* displays only occasional loops, whereas in *Gordia* EMMONS 1844 loops are the most characteristic feature. In contrast to these genera *Helminthopsis* has no loops (Hofmann & Patel 1989). The differences between *Helminthoidichnites* and *Gordia* were confirmed by

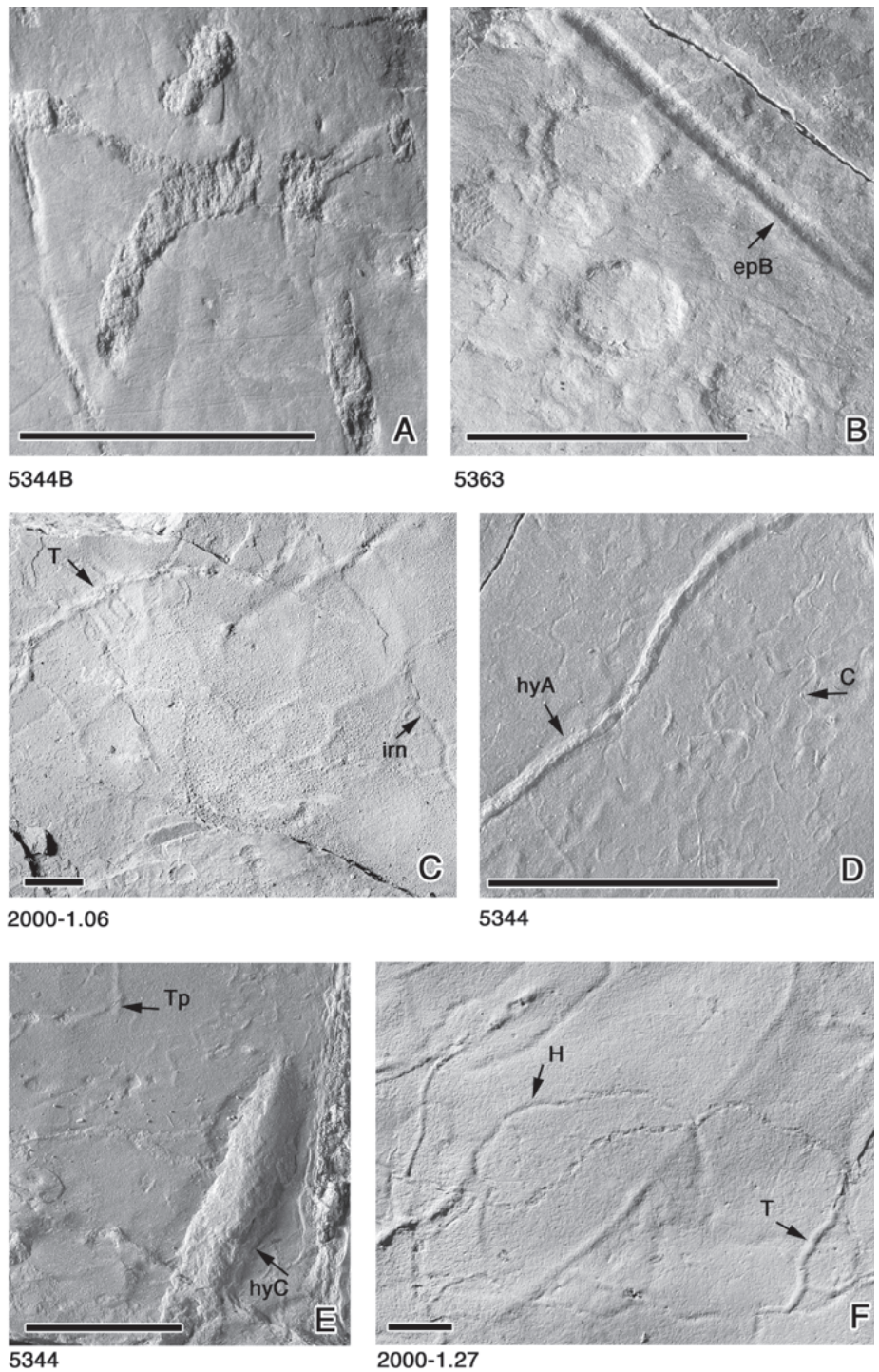


Fig. 6. Trace fossils on the lower surface (A, C-F) and on the upper surface (B) of mudstone slabs. A: ?*Planolites* isp., 5344. B: Epichnial groove B (epB) and rain drop imprints, 5363. C: irregular network (irn) and *Treptichnus* isp. (T), 2000-1.06. D: Hypichnial ridge A (hyA) and *Cochlichnus anguineus* (C), 5344. E: Hypichnial ridge C (hyC) and *Treptichnus pollardi* (Tp), 5344. F: *Treptichnus* isp. (T) and *Helminthoidichnites* isp. (H), 2000-1.27. Scale bars = 1 cm.

computer analysis (Hofmann 1990). *Helminthoidichnites* is known to range from Precambrian (Narbonne & Aitken 1990) to Lower Cretaceous (Fregenal Martínéz et al. 1995). Thus, the here described forms represent the youngest record of this ichnogenus. *Helminthoidichnites* is known from marine and

non-marine settings. In the latter case, it has probably been produced by nematomorphs or insect larvae (Buatois et al. 1997).

?*Planolites* isp.

Fig. 6A

Description. – Endichnial, straight to curved, simple or branched cylindrical trace fossils filled with material coarser than the host rock. They penetrate the rock in different directions and only short segments are traced on the surface of the slabs. The cylinders are 1.8 mm wide in slab 5344 and 1.0 to 1.5 mm wide in 5341 and 3562.

Remarks. – Details of the trace fossil margins are modified by erosion. For this reason a closer determination is impossible. This ichnogenus was discussed by Pemberton & Frey (1982) and by Keighley & Pickerill (1995). The typical *Planolites* represents the traces of deposit feeders in various environments. It is common in non-marine settings.

Treptichnus MILLER 1889

Treptichnus pollardi BUATOIS & MÁNGANO 1993

Figs. 2B, 5C

Description. – Hypichnial thin ridges, 0.18 to 0.25 mm wide, composed of straight to slightly curved segments joined by small oval knots. The segments are 3.5 to 11 mm long and the knots are up to 0.5 mm wide. Some knots display short side protrusions. The overall course of the trace fossil is arcuate or winding.

Remarks. – *Treptichnus pollardi* was first described from Carboniferous lacustrine sediments of Argentina and interpreted as deposit-feeding structures formed by vermiform organisms (Buatois & Mángano 1993).

Treptichnus isp.

Figs. 5C, 6F, 9B

Description. – Hypichnial ridge, 1.8–2.0 mm wide, composed of straight segments joined by elongate knots. The segments are about 30 mm long, and the knots are up to 3 mm wide. In the slab 2000–1.06 (Fig.6C), the ridge displays two short side branches of similar morphology, 7 and 10 mm long, which plunge into the slab.

Remarks. – The form shown in Fig. 5C resembles *T. pollardi*, but it is distinctly larger than the typical *T. pollardi* occurring on the same slab and it displays a distinct zigzag course. However, Metz (1995) included similar forms, but with a sharper zigzag course, from an Upper Triassic lake–margin deposit of Pennsylvania in *T. pollardi*.

Irregular ridge A

Figs. 4D–E, 5A–B

Description. – Epichnial, slightly irregularly curved to winding ridges, 1.3 to 2.0 mm wide. Commonly, a discontinuous slightly wavy thin groove occurs along their axis resulting

in bilobate pattern. In some segments the groove is observed only over a distance of 1 cm. The ridge displays also transverse gentle irregularities, wrinkles and depressions. The latter are interpreted as collapsing structures. A filling, coarser-grained than the host rock, can be observed in the eroded segments of the ridges. Commonly, their slopes pass gradually into the surrounding bedding surface. Locally, the ridges gradually disappear into the beds.

Remarks. – Similar traces are produced by dragonfly (Odonata) larvae on mud surfaces in shallow ponds (Chamberlain 1975, fig. 19.2V). However, the traces of these larvae are larger and display a mantle along the burrow. After collapsing, mole cricket (Gryllotalpidae) burrows can show similar patterns, but they are also larger (Chamberlain 1975, fig. 19.4D; Metz 1989, 1990). Dipteran larvae produce very similar shallow subsurface traces in drying-out mud in various non-marine settings (A.U., personal observations).

Irregular ridge B

Figs. 4B, 5A–B

Description. – Epichnial winding ridges, 0.6 to 0.95 mm wide. Locally, they show sharp turns. The ridges display a median, commonly discontinuous thin groove or short wrinkles and transverse gentle irregularities. Locally they are collapsed or change into short shallow grooves. Their margins are locally irregular and often pass gradually into the surrounding bedding surface. In some places the ridges gradually plunge into the beds.

Remarks. – Most probably, this ridge represents a shallow, subsurface trace, produced by small invertebrates, possibly insect larvae.

Epichnial hair ridge

Fig. 4B

Description. – Epichnial, very thin (< 0.1 mm wide), straight to slightly winding simple ridges. They are very common and cross each other.

Remarks. – This ridge possibly represents a very shallow subsurface trace, which may have been produced by nematodes under a microbial film.

Irregular network

Fig. 6C

Description. – Indistinct, poorly preserved epichnial, winding ridges about 2 mm wide, forming an irregular network of 10 to 20 mm wide meshes. The ridges are not sharply bounded, they pass gradually into the surrounding surfaces.

Remarks. – This structure occurs in laminae just below the surface which bear raindrop imprints. They possibly represent

large overlapping *Cochlichnus*, similar to those described by Buatois et al. (1997, fig. 5.4). Alternatively, they could belong to the ichnogenus *Labyrinthichnus* UCHMAN & ÁLVARO 2001, known from Miocene terrestrial deposits of Spain or to *Mulina anayo* (Wu 1985) described from deep lacustrine Jurassic deposits of China, which form irregular polygons. The poor preservation of these traces does not allow for a more precise determination.

Epichnial grooves Figs. 5B, 6B

Description. – Two types of epichnial grooves can be distinguished:

Type A (Fig. 5B). Shallow, straight to slightly curved, carinate, smooth grooves, 1.0 to 1.6 mm wide.

Type B (Fig. 6B). Straight, slightly curved or semicircular grooves, about 0.5 mm wide in slab 5357 and about 1 mm wide in slab 5363.

Remarks. – The grooves are probably surface trails. The carinate shape in type A suggests a mollusc as the trace maker. However, some insects could leave similar traces (Brustur 1996). Several small invertebrates produce semicircular surface grooves in soft mud, similar to type B. For the present material insect larvae and small oligochaetes are the most probable trace makers.

Hypichnial ridges Figs. 2C, 6D–E

Description. – Four types (A, B, C, D) of slightly winding hypichnial ridges can be distinguished.

Type A (Fig. 6D). Smooth, slightly carinate and winding ridges covered by indistinct longitudinal wrinkles, of 0.9 to 1.0 mm width (slab 5344).

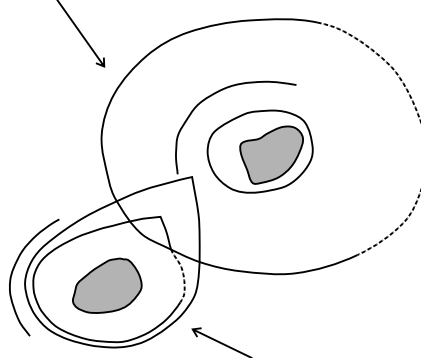
Type B (Fig. 2C). Almost straight 0.9 mm wide ridges with distinct margins, covered with very fine, irregular, oblique wrinkles resembling a rope surface. They are preserved in full relief (slab 5344).

Type C (Fig. 6E). A straight, 20 mm long and 3.5 mm wide, smooth ridge, which plunges into the bed at both terminations.

Type D (Fig. 2C). A 0.6 to 1.2 mm wide, low smoothly winding ridge with indistinct margins. Locally, it is covered with very low irregularities. In some segments, the ridge plunges slightly into the sediment, and it is replaced by a shallow furrow.

Remarks. – These ridges were produced by various invertebrates. Type A may be a cast or an undertrack of a surface trail. Its carinate shape suggests the trace of a small mollusc foot. Type D is probably also a cast of surface trail, whereas the types B and C represent rather shallow burrows. The surface traces may have been left by earthworms on damp substrate (Schmidt 1926).

discoid structure B



discoid structure A



Fig. 7. Discoid structures A and B redrawn from a photograph, 5343 (see also Fig. 2B).

Hypichnial groove-ridge structure Fig. 2A

Description. – About 1 mm wide, hypichnial, winding or slightly curved, shallow carinate grooves, passing into ridges.

Remarks. – Most probably, this trace represents a shallow, slightly undulating burrow produced on the sediment surface.

Discoid structures Figs. 2B–C, 7

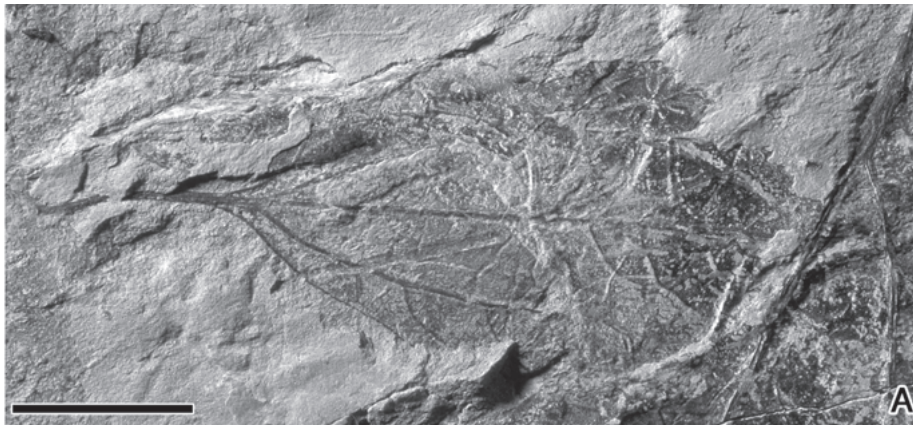
Description. – Three types of hypichnial disc structures are distinguished.

Type A (Figs. 2B, 7). An extremely low-relief disc, 3 mm wide with a circular central depression, 1.7 mm wide. The disc is surrounded by a fan-like elevation, the pointed termination of which overlaps the disc of type B.

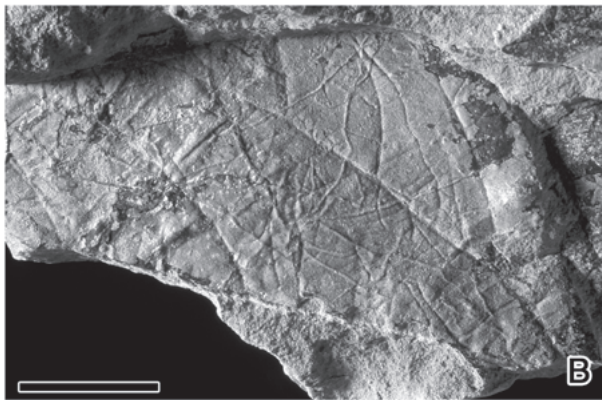
Type B (Figs. 2B, 7). An extremely low-relief disc, 7.8 mm wide, with a central low knob, 2.6 mm wide.

Type C (Fig. 2C). A disc 2.5 mm wide, with a central depression, an elevated central knob (1.2 mm) and distinct edges.

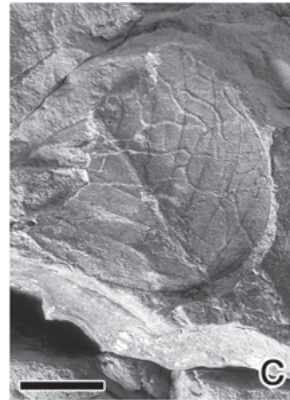
Remarks. – The above mentioned structures resemble scratch circles produced by plants swirled by flowing water or wind (Metz 1991; Jensen et al. 2002). Similar structures have been described from non-marine Permian deposits of Germany (Boy 1976, fig. 34b). Larger traces of the same type have been described as cf. *Cylindrichnus concentricus* HOWARD by



2000-1.26



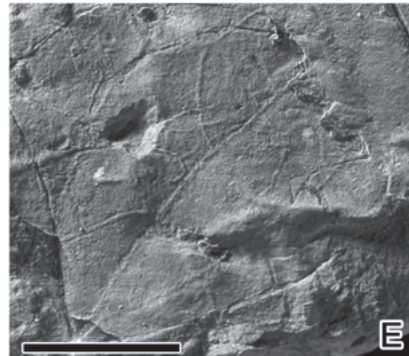
2000-1.12



2000-1.09



2000-1.23



2000-1.11

Fig. 8. Leaf underminings A: Underminings under a compression of a laurophyllaceous leaf (*Cinnamomum scheuzeri* type, HEER 1855), 2000-1.26. B: Undermining under an indeterminate leaf impression, 2000-1.12. C: Undermining under an impression of a fragmentary leaf (*Rannus gaudini* type, HEER 1855), 2000-1.09. D: Undermining under a laurophyllaceous leaf impression (*Cinnamomum polymorphum* type, HEER 1855), the distinct primary and secondary nerves are crossed by the impression of a pine needle, 2000-1.23. E: Undermining under an indeterminate leaf impression, 2000-1.11. Scale bars = 1 cm.

Brustur & Alexandrescu (1993) from Miocene molasse deposits of Romania. The downward continuation of the described forms is unknown, therefore they are left in open nomenclature.

In recent ponds, some insect (?dipteran) larvae located in small vertical shafts produce shallow depressions around them (A.U., personal observation). The discussed trace fossils may represent casts of such traces.

Leaf underminings

Fig. 8A-E

Description. – Straight, curved or irregularly winding, single or possibly branched ridges and grooves 0.3 to 0.5 mm wide, preserved on the underside of fossil leaves. They have been observed associated with leaves on the slabs 2000-1.09, 2000-1.11, 2000-1.12, 2000-1.23 and 2000-1.26.

Remarks. – The size and course of the burrows correspond to those of *Helminthoidichnites* sp. The supposed branches may be primary successive or false branches sensu D’Alessandro & Bromley (1987). The latter are produced when a trace-maker follows a trace of its own type and then continues in a different direction. The described traces may be assigned to *Helminthoidichnites*. However, they are maintained separate because they occur below the leaves. This trace fossil was probably produced by insect larvae under fallen leaves which provided protection and nutrients. Similar traces have been found by Boyd (1993) in a backswamp lake environment in the Cretaceous of Greenland.

Vertebrate tracks

The vertebrate tracks (Figs. 8–9) are preserved as undertracks sensu Goldring & Seilacher (1971). They represent deformations formed under the feet of moving animals and are preserved in layers below the surface on which the tracks were traced. This type of preservation does not reflect the exact morphology of the tracks and does not allow for a closer determination. For convenience these undertracks are treated here as tracks.

Pecoripeda (Ovipeda) VIALOV 1965

Pecoripeda (Ovipeda) isp.

Figs. 9A–B, 10

Description. – Undertracks of artiodactyl hoof tracks forming symmetrical pairs of asymmetrical hypichnial mounds separated by slightly cleft depressions. Each mound is about 26 to 30 mm long and the whole structure is up to 37 to 45 mm wide. The mounds represent undertracks of hoofs separated by interdigital septa. One mound (? inner hoof) is distally slightly shifted. The mounds are elevated in the proximal part and decline gradually towards the heel. The inner edges of the hoofs are almost straight, whereas the outer edges are slightly convex. The tips of the hoofs are 22 mm apart and slightly rounded. The surface of the structure is covered with longitudinal wrinkles. Their slopes pass gradually into the surrounding bedding surface without discontinuity.

Remarks. – Size and overall shape of the described trace fossil are very similar to those described from the Oligocene Molasse at Goldau, Switzerland (Bräm 1954, p. 412, fig. 4). This author ascribed them to tracks of *Traugulidae* or *Cervidae*, an interpretation which seems justified. The pressure of the *Pecoripeda* tracemaker hoofs probably produces the wrinkles.

Track A

Figs. 9C, 10

Description. – Two isolated hypichnial undertracks of four-toed tracks. The toes are preserved as irregular ridges. They

are slightly curved, about 4 mm long and less than 1 mm wide. The second left toe displays a small bulb-like enlargement at its termination. There are oval areas next to the inner side of the most distal part of the outermost toes. The angle between the outermost toes is about 30°. The terminations of the toes are arranged in an asymmetrical arc. This structure is 6.5 to 9 mm wide.

Remarks. – A small vertebrate with long, narrow toes produced this trace fossil. Several lizard species have similar toes, and are considered the possible producers.

Track B

Figs. 9D, 10

Description. – Hypichnial, single undertrack of a four- or five-toed track. They are preserved as irregular, straight ridges, 3.5 to 4.5 mm long and less than 1 mm wide. The toes are slightly radially arranged and their terminations form a deep arc. The angle between the outermost toes is about 40°, the median toes protrude. The structure is about 9 mm wide and 9 mm long.

Remarks. – As for track A.

Track C

Figs. 9E, 10

Description. – Hypichnial undertrack of a four-toed track. The toes are 3.0 to 4.2 mm long and about 1 mm wide. The entire structure is 3.0 to 3.5 mm long and 7 to 9 mm wide. The toes are radially arranged and their tips enlarged. The angle between the first and third toe is about 65°.

Remarks. – A very small vertebrate produced this trace fossil. Small amphibians, reptiles or rodents are possible producers. Reptile tracks with five digits known from the Paleogene of Spain display similar bulb-like terminations (Prats & López 1995).

Track D

Figs. 9F, 10

Description. – Hypichnial, single trapezoid undertrack of a four-toed track. The toes are preserved as narrow ridges. The 5 mm long second toe is strongly shifted forward and terminated by a small hook. The remaining toes are pointed, but distinctly shorter. The heel is indicated by a small oval figure. The angles between the toes are very acute.

Remarks. – A small, short-toed vertebrate, probably a small rodent or amphibian, produced this trace fossil. It falls into the great variation of tracks of recent salamanders reported by Brand (1996).

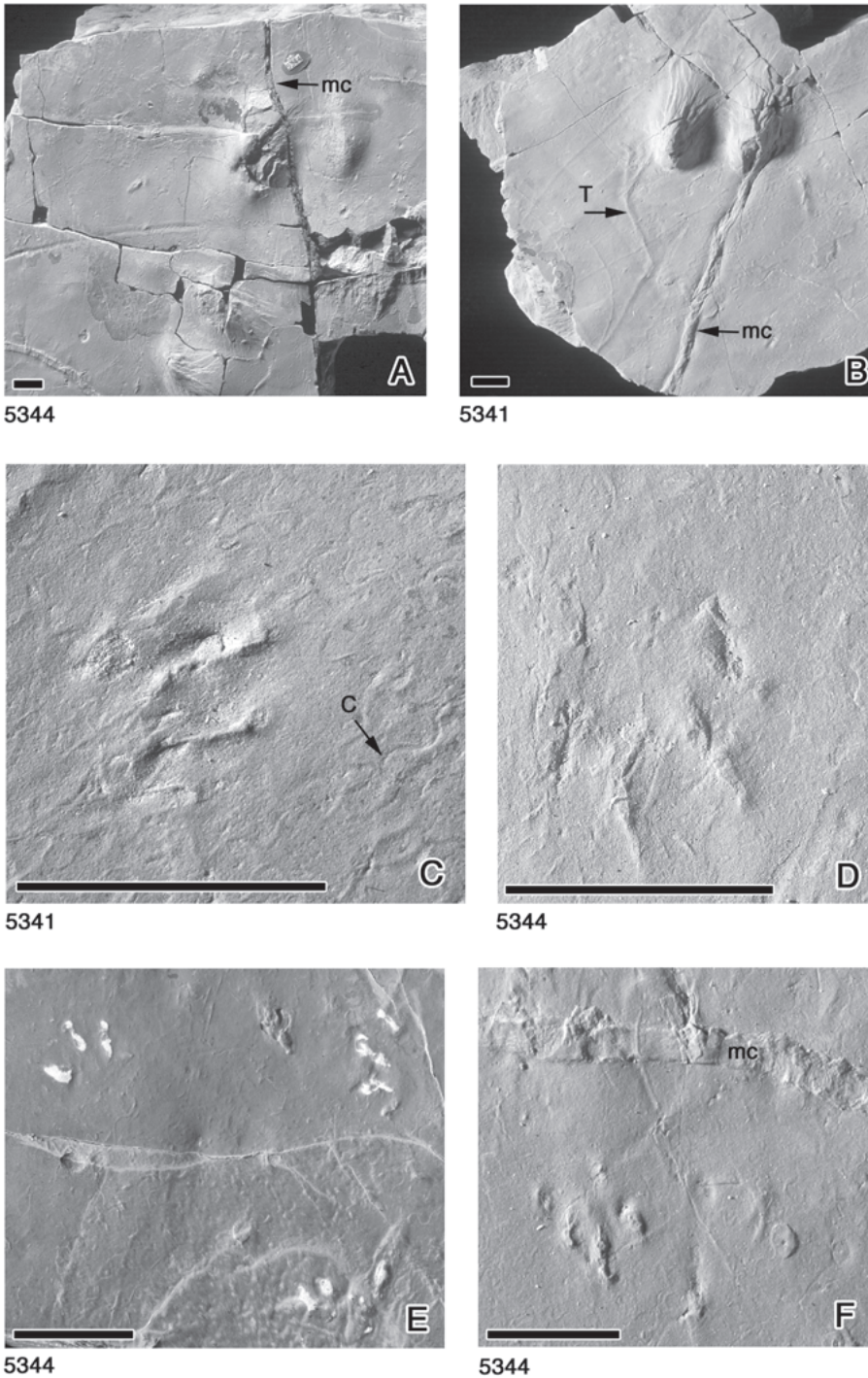


Fig. 9. Tetrapod tracks and other trace fossils on the lower surface of mudstone slabs. A: *Pecoripeda* isp. and a mud-crack (mc), 5344. B: *Pecoripeda* isp., *Treptichnus* isp. (T), and a mud-crack (mc), 5341. C: Track A, *Cochlichnus anguineus* (C), 5341. D: Track B, 5344. E: Track C, 5344. F: Track D, and a mud-crack (mc), 5344. Scale bars = 1 cm.

Physical structures

The physical structures are represented by raindrops, drag-marks, and mud-cracks. Most of the raindrops are elliptical flat-bottom depressions. Their longer axes range from 5.5 to 6 mm and the shorter ones from 3 to 5 mm. They are isolated or grouped in patches; some of them overlap. *Helminthoidichnites*, *Cochlichnus* and the irregular ridge A cross some raindrop imprints (Figs. 4C, E, 5B).

The drag-marks are hypichnial, straight isolated ridges without sharp boundaries (Fig. 4A). They are up to 0,3 mm wide and up to 12 mm long. They were probably produced by wind-dragged objects, possibly plant remains.

The mud-cracks are represented by straight to slightly winding, 2–3 mm-wide fissures filled with coarser sediment (Figs. 2A, 5C, 8A, B, F). Commonly, laminae are wrapped out

close to the fissures, which are most probably part of a mud-crack system larger than the examined slabs. It cannot be excluded that the slabs cracked along this system during collection.

Distribution

The distribution of trace fossils and some sedimentary structures in the investigated specimens is shown in Table 1. *Cochlichnus anguineus* is the most common species occurring in all samples. Irregular ridges A and B occur in more than 50% of the slabs. *Helminthoidichnites* isp. and epichnial hair ridges have been found in at least one third of the examined slabs. The other trace fossils are present only on one or two slabs.

Discussion

Sedimentary structures, especially raindrop imprints and mud-cracks, as well as the overall lithology, suggest that the investigated trace fossils were produced in muddy bottom ponds characterized by shallow, low-energy water and temporal desiccation. Similar environments are common in most of the recent muddy flood plains. These ponds can be filled with water for a long time, especially during prolonged wet seasons. Temporal desiccation is proven by the presence of mud-cracks.

Only a few ichnological studies are available concerning pond environments. Fiege (1949) proposed such an environment for an assemblage of simple traces from the Upper Triassic of Germany. Traces in recent pools have been studied by Fiege (1961), Chamberlain (1975), Ratcliffe & Fagerstrom (1980), Metz (1987b), and Mángano et al. (1996). In recent ponds most of the traces are produced by insects and their larvae. Some of these animals are adapted to life in ponds, others are only occasionally and accidentally present. The producers of most of the investigated invertebrate trace fossils were probably adapted to such an environment. This is certainly true for the most common forms, i.e. *Cochlichnus anguineus*, and for all shallow-subsurface burrows. The trace fossils have been produced under thin films of water (*Cochlichnus*) or in emerged sediments (irregular ridges A and B). Preservation of the very thin trace fossils was probably assured by a thin microbial film, which protected the traces after their formation. Afterwards, the traces were quickly covered by a new influx of mud from adjacent areas. Microbial mats are very common in recent ponds. Water flow is suggested by the occurrence of very delicate drag-marks, which may have been produced by wind-dragged objects, like plant debris. The vertebrate tracks have been produced under similar conditions, as preservation of small vertebrate tracks is possible only in plastic, water-saturated sediments (Scrivner & Bottjer 1986; Cohen et al. 1991).

Several authors have described ichnofacies from non-marine environments. Seilacher (1967) proposed a single ichnofacies for this type of environment, namely the *Scoyenia* ichnofacies.

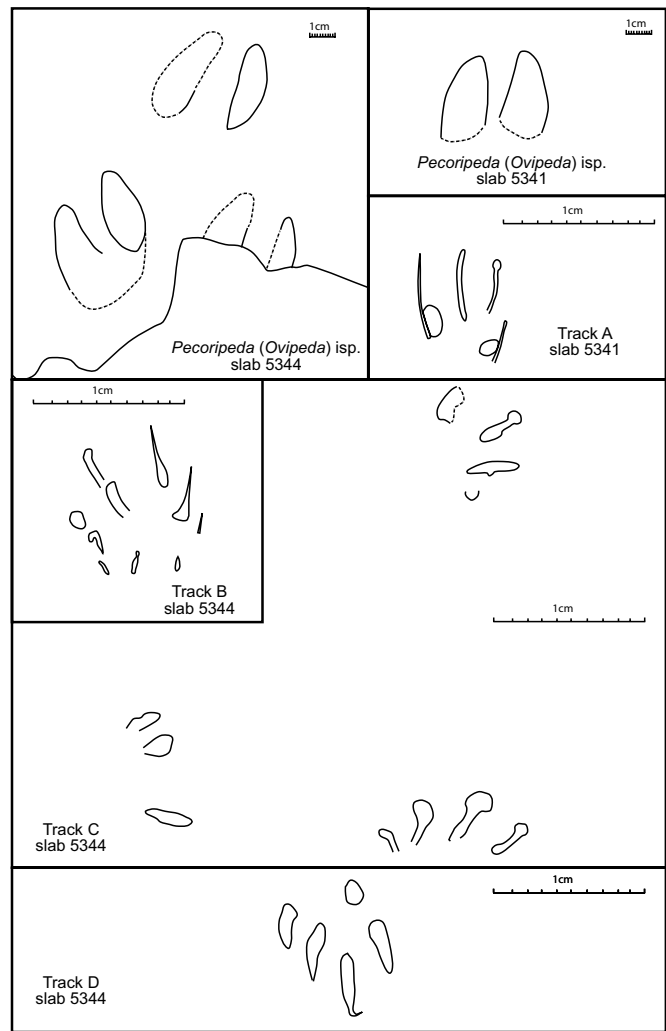


Fig. 10. Vertebrate tracks drawn from photographs.

ciés. Buatois & Mángano (1998) restricted the *Scoyenia* ichnofacies to transitional terrestrial to non-marine aquatic environments, and distinguished a new *Mermia* ichnofacies for permanent lakes. The *Termitichnus* and *Coprinisphaera* ichnofacies have also been defined for terrestrial environments by Smith et al. (1993) and Genise et al. (2000), respectively.

In desiccating ponds we expect the *Scoyenia* ichnofacies. According to the previously cited authors this ichnofacies, recorded in continental formations of different ages, is characterized by meniscate burrows (e.g., *Scoyenia*, *Beaconites*, *Taenidium*), arthropod trackways (e.g., *Umfolzia*, *Merosotomichnites*, *Diplichnites*), bilobate forms (e.g., *Cruziana*, *Rusophycus*) and vertebrate tracks. Surprisingly, the most typical trace fossils of the *Scoyenia* ichnofacies are absent or poorly represented in the investigated material since both meniscate burrows and bilobate forms are absent. Only the presence of vertebrate tracks indicates the *Scoyenia* ichnofacies. The investigated assemblages are dominated by meandering and

Table 1. Distribution and frequency of trace fossils and sedimentary structures in the investigated slabs: A – abundant, C – common, R – rare. The numbers represent the counts of the rare specimens.

Specimens	5341	5343	5344	5344 A	5344 B	5357	5361	5362	5363
Trace fossils				A	B				
invertebrate trace fossils									
<i>Cochlichnus anguineus</i>	A	A	A	C	R	A	A	A	A
<i>Steinsfjordichnus brutoni</i>	1								
<i>Helminthoidichnites</i> isp.			1			5	C		1
? <i>Planolites</i> isp.	1				3				
<i>Treptichnus pollardi</i>	2	2							
<i>Treptichnus</i> isp.	1								
Irregular ridge A	1		1			1	1	2	
Irregular ridge B			1			5	4	4	6
Epichnial hair ridges			1			C	C		
Epichnial groove A						1			
Epichnial groove B						1			1
Hypichnial ridge A				1					
Hypichnial ridge B			1						
Hypichnial ridge C		1							
Hypichnial ridge D		1							
Hypichnial groove-ridge structure	1		1						
Discoid structures		1							
Vertebrate trace fossils									
<i>Pecoripeda</i> (<i>Ovipeda</i>) isp.	1		3						
Track A	2								
Track B			1						
Track C				4					
Track D			1						
Sedimentary structures									
raindrop imprints						x	x		x
Mud-cracks	x		x		?				
Drag-marks			x			x	x	x	

winding surface trails as well as shallow subsurface trace fossils. The latter are considered typical for the *Mermia* ichnofacies which corresponds to rather deep lacustrine environments (Buatois & Mángano 1995, 1998). According to these authors, *Helminthoidichnites* and *Cochlichnus* are typical for the *Mermia* ichnofacies and are regarded as unspecialised grazing and feeding structures. Another characteristic species for this ichnofacies is *Treptichnus pollardi*. However, Metz (1996) described it from lake margin deposits in the Upper Triassic of Pennsylvania together with *Scoyenia gracilis* and *Spongiomorpha milfordensis*, which are typical for the *Scoyenia* ichnofacies. The representative traces of the *Mermia* ichnofacies such as *Undichna* are also absent in the investigated material. The *Scoyenia* ichnofacies seems to be restricted to lake margins and to ponds on dry floodplains. Buatois et al. (1997) de-

scribed a similar assemblage from ponds in Permian fluvial plain deposits from Patagonia which compares better to the *Mermia* ichnofacies than to the *Scoyenia* ichnofacies. These authors suggested that the flood plain remained under water for a long time.

Buatois & Mángano (2002) discussed the above outlined problem and distinguished two communities of trace fossils in flood plains. The first one is the typical *Scoyenia* ichnofacies. The second is dominated by simple, superficial to very shallow, grazing, locomotion and dwelling trace fossils of low diversity, associated with rare tetrapod or arthropod forms. Here meniscate forms are absent. The cited authors ascribed the latter community to the impoverished *Mermia* ichnofacies. The assemblage from the Freshwater Molasse also belongs to this ichnofacies.

Conclusions

The studied trace fossils from Lower Freshwater Molasse are closely comparable to the *Scoyenia* ichnofacies. This ichnofacies is related to a low energy environment, most probably to ponds on a fluvial plain. The section containing these traces is a three meter thick sequence of fine-grained sediments intercalated between coarse sandstones and conglomerates. Although closely associated with plant and root remains most of the trace fossils are perfectly preserved. This means that these fine-grained sediments were deposited in a relatively short time and that the plants had no time to get established and well rooted. The sedimentary environment proposed for this trace-bearing horizon is a floodplain with braided rivers. The over- and underlying coarse sediments represent channel fills deposited during major floods, whereas the horizons containing the trace fossils correspond to a quiet environment, most probably a desiccating pond. Desiccation phases are testified by the presence of mud cracks and rain drops. In the general context of the high-energy depositional environment of the Subalpine Freshwater Molasse the preservation of sediments deposited in a temporary quiescent phase has to be considered exceptional.

Acknowledgements

We thank U. Gerber for the excellent photographic work, and E. Morlotti for the critical reading of the manuscript. We also thank Richard G. Bromley, who provided several improvements and useful remarks. Jagiellonian University (DS funds) gave an additional support.

REFERENCES

- BAUMBERGER, E. & MENZEL, P. 1914: Beitrag zur Kenntnis der Tertiär-Flora aus dem Gebiet des Vierwaldstätter Sees. *Mém. Soc. Paléont. Suisse* 40, 1–81.
- BOLLIGER, T. 1998: Fussspuren von Wirbeltieren (?Amphocyonidae, Mammalia) aus der basalen Süswassermolasse (OSM) des Kantons Luzern. *Eclogae geol. Helv.* 91, 541–547.
- BOLLIGER, T. 1999: Trace fossils and trackways in the Upper Freshwater Molasse of central and eastern Switzerland. *N. Jb. Geol. Paläont. Abh.* 214, 3, 515–536.
- BOLLIGER, T. & GUBLER, T. 1997: Arthropodenlaufspuren von Hochdorf (LU) und weitere Arthropodennachweise aus der Oberen Süswassermolasse der Schweiz. *Eclogae geol. Helv.* 90, 3, 617–627.
- BOY, J. A. 1976: Überblick über die Fauna des saarpfälzischen Rotliegenden (Unterperm). *Mainzer geowiss. Mitt.* 41, 13–35.
- BOYD, A. 1993: Paleodepositional setting of the Late Cretaceous Pautut flora from West Greenland as determined by sedimentological and plant taphonomical data. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 103, 251–280.
- BRÄM, H. 1954: Fährten von Wirbeltieren aus der subalpinen Molasse des Bergsturzgebietes von Goldau. *Eclogae geol. Helv.* 47(2), 406–417.
- BRAND, L.R. 1996: Variations in salamander trackways resulting from substrate differences. *J. Paleont.* 70, 1004–1010.
- BRUSTUR, T. 1996: Ephemeral traces of animal activity on the beach sand from Mamaia. *Geo-Eco-marina* 1, 75–91.
- BRUSTUR, T. & ALEXANDRESCU, G. 1993: Paleoichnological potential of the Lower Miocene molasse from Vrancea (East Carpathians). *Rev. roumaine Géol., Géophys. Géogr.* 37, 77–94.
- BUATOIS, L. A. & MÁNGANO, G. M. 1993: The ichnotaxonomic status of *Plangtichnus* and *Treptichnus*. *Ichnos* 2, 217–224.
- BUATOIS, L. A. & MÁNGANO, M. G. 1995: The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos* 4, 151–161.
- BUATOIS, L. A. & MÁNGANO, G. M. 1998: Trace fossil analysis of lacustrine facies and basins. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 140, 367–382.
- BUATOIS, L.A. & MÁNGANO, G.M. 2002. Trace fossils from Carboniferous floodplain deposits in western Argentina: complications for ichnofacies models of continental environments. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 183, 71–86.
- BUATOIS, L. A., JALFIN, G. & ACEÑOLAZA, F. G. 1997: Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina, ichnologic signatures of substrate consolidation and colonization sequences. *J. Paleont.* 71(2), 324–336.
- BUATOIS, L.A., MANGANO, M.G., GENISE, J.F. & TAYLOR, T. 1998: The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. *Palaios* 13, 217–240.
- CHAMBERLAIN, C.K. 1975: Recent *Lebensspuren* in non-marine environments. In: *The Study of Trace Fossils* (Ed. by FREY, R.W.). Springer Verlag, New York. 431–458.
- CLERCO, S.W.G., DE & HOLST, H.K.H. 1971: Footprints of birds and sedimentary structures from the subalpine molasse near Flühli (Canton of Luzern). *Eclogae geol. Helv.* 64 (1), 63–69.
- COHEN, A., LOCKLEY, M., HALFPENNY, J. & MICHEL, A.E. 1991: Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *Palaios* 6, 371–389.
- D'ALESSANDRO, A. & BROMLEY, R. G. 1987: Meniscate trace fossils and the *Muensteria-Taenidium* problem. *Palaeontology* 30(4), 743–763.
- DONOVAN, S.K. 1994: Insect and other trace-makers in non-marine environments and palaeoenvironments. In: *The Palaeobiology of Trace Fossils* (Ed. by DONOVAN, S.K.), 200–220, John Wiley & Sons, Chichester.
- EMMONS, E. 1844: The taconic system based on observations in New-York, Massachusetts, Maine, Vermont, and Rhode-Island. 63 p., Albany (Carroll and Cook).
- FIEGE, K. 1949: Sediment und Lebensspuren einer Regenpfanne im Mittleren Keuper Südhannovers. *Z. dtsh. geol. Ges.* 99, 132–138.
- FIEGE, K. 1961: Beobachtungen an rezenten Insekten-Fährten und ihre palichnologische Bedeutung. *Meyniana* 11, 1–7.
- FILLION, D. & PICKERILL, R. K. 1990: Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada. *Palaeontographica canad.* 7, 1–119.
- FITCH, A. 1850: A historical, topographical and agricultural survey of the County of Washington. Part 2–5. *Trans. New York agric. Soc.* 9, 753–944.
- FORDYCE, R.E. 1980: Trace fossils from Ohika Formation (Pororari Group, Lower Cretaceous), lower Buller Gorge, Buller, New Zealand. *New Zealand J. Geol. Geophys.* 23, 121–124.
- FREGENAL MARTÍNEZ, M. A., BUATOIS, L. A. & MANGANO, M. G. 1995: Invertebrate trace fossils from Las Hoayas fossil site (Serraní de Cuenca, Spain). *Paleoenvironmental interpretations. In: II International Symposium on Lithographic Limestones, Lleida-Cuenca (Spain), 9th–16th July 1995. Extended Abstracts. Universidad Autónoma de Madrid* 67–70.
- GENISE, J.F., BUATOIS, L., MANGANO, M.G., LAZA, J.H. & VERDE, M. 2000: Insect trace fossil associations in paleosols: the *Coprinisphaera* Ichnofacies. *Palaios* 15(1), 49–64.
- GIBBARD, P.L. 1977: Fossil tracks from varved sediments near Lammi, South Finland. *Bull. geol. Soc. Finland* 49, 53–57.
- GIBBARD, P.L. & DREIMANIS, A. 1978: Trace fossils from late Pleistocene glacial lake sediments in southwestern Ontario, Canada. *Canadian J. Earth Sci.* 15, 1967–1976.
- GIBBARD, P.L. & STUART, A.J. 1974: Trace fossils from proglacial lake sediments. *Boreas* 3, 69–74.
- GIBERT, J. M. DE, FREGENAL MARTÍNEZ, M. A., BUATOIS, L. A. & MÁNGANO, M. G. 2000. Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 156(1–2), 89–101.

- GOLDRING, R. & SEILACHER, A. 1971: Limulid undertracks and their sedimentological implications. *N. Jb. Geol. Paläont., Abh.* 137, 422–442.
- GLUSZEK, A. 1995: Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geol. Pol.* 108, 171–202.
- HASIOTIS, S. T. 2002: Continental trace fossils. *SEPM Short Course Notes* 51, 1–132.
- HASIOTIS, S.T. & BOWN, T.M. 1992: Invertebrate trace fossils: the backbone of continental ichnology. In: *Trace Fossils* (Ed. by MAPLES, C.G. & WEST, R.R.). *Paleont. Soc. Short Course in Paleontology* 5, 64–104.
- HITCHCOCK, E. 1858: *Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks.* W. White, Boston, 220.
- HEER, O. 1855: *Flora Tertiaria Helvetiae*, B.I. Winterthur, 117.
- 1856: *Flora Tertiaria Helvetiae*, B.II. Winterthur, 110.
- HOFMANN, H. J. 1990: Computer simulation of trace fossils with random patterns, and the use of goniograms. *Ichnos* 1, 15–22.
- HOFMANN, H. J. & PATEL, I. M. 1989: Trace fossils from the type “Etchemian Series” (Lower Cambrian Ratcliffe Brook Formation), Saint John area, New Brunswick, *Canad. Geol. Mag.* 126, 139–157.
- JENSEN, S., GEHLING, J. G., DROSER, M. L. & GRANT, S. W. F. 2002: A scratch circle origin for the medusoid fossil *Kullingia*. *Lethaia* 35, 291–299.
- KEIGHLEY, D. G. & PICKERILL, R. K. 1995: The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. *Ichnos* 3, 301–309.
- KELLER, B. 1982: Fossile Vogelfährten aus der Luzerner Molasse. *Mitt. natf. Ges. Luzern* 17, 99–109.
- MÁNGANO, M. G., BUATOIS, L. A. & CLAPS, G. L. 1996: Grazing trails formed by soldier fly larvae (Diptera: Stratiomyidae) and their paleoenvironmental and paleoecological implications for the fossil record. *Ichnos* 4, 163–167.
- MERTA, T. 1980: Arthropod and mollusc traces in the varved clays of Central Poland. *Acta geol. pol.* 30(2), 165–173.
- MEZ, R. 1987a: Sinusoidal trail formed by a recent biting midge (family Ceratopogonidae): trace fossil implications. *J. Paleont.* 61, 312–314.
- 1987b: Insect traces from nonmarine ephemeral puddles. *Boreas* 16, 189–195.
- 1989: Desiccation cracks initiated by recent nonmarine biogenic sedimentary structures. *Bull. New Jersey Acad. Sci.* 34, 15–19.
- 1990: Tunnels formed by mole cricket (Orthoptera: Gryllotalpidae): paleoecological implications. *Ichnos* 1, 139–141.
- 1991: Scratch circles from the Towaco Formation (Lower Jurassic), Riker Hill, Roseland, New Jersey. *Ichnos* 1(3), 233–235.
- 1995: Ichnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southeastern Pennsylvania. *Ichnos* 4, 43–51.
- 1996: Nonmarine trace fossils from the Late Triassic and Early Jurassic of New Jersey. *Bull. New Jersey Acad. Sci.* 41(2), 1–5.
- 1998: Nematode trails from the Late Triassic of Pennsylvania. *Ichnos* 5(4), 303–308.
- MICHEALIS, P. 1972: *Belorhapha kochi* (Ludwig 1969), eine Wurmspur im europäischen Karbon. *Geol. Jb.* 71, 299–330.
- MILLER, S. A. 1889: *North American Geology and Paleontology for the use of Amateurs, Students and Scientists.* Western Methodist Book Concern, Cincinnati, Ohio, 664.
- MOUSSA, M.T. 1970: Nematode fossil trails from the Green River Formation (Eocene) in the Uinta Basin, Utah. *J. Paleont.* 44, 304–307.
- NARBONNE, G. M. & AITKEN, J. D. 1990: Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. *Palaeontology* 33, 945–980.
- OCHSNER, 1975: *Geologischer Atlas der Schweiz*, Blatt 1133 Linthebene. Erläuterungen. Schweiz. Geol. Komm., Kiemmerly & Frei AG Bern, 9.
- PEMBERTON, G. S. & FREY, R. W. 1982: Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *J. Paleont.* 56, 843–881.
- PRATS, M. & LÓPEZ, G. 1995: Síntesi de la icnofauna del Sinclinal d’Agramunt, entre el Meridà d’Argamut i el riu Segre (Prov. de Lleida). *Paleontologia i Evolució* 28–29, 247–267.
- RATCLIFFE, B.C. & FAGERSTROM, J.A. 1980: Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. *J. Paleont.* 54(3), 614–630.
- RINDSBERG, A. K. 1994: Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous Formations. *Geol. Surv. Alabama, Bull.* 158, 1–107.
- RODE, H. & STAAR, G. 1961: Die photographische Darstellung der Kriechspuren (Ichnogramme) von Nematoden und ihre Bedeutung. *Nematologica* 6, 266–271.
- SANDSTEDT, R., SULLIVAN, T. & SCHUSTER, M.L. 1961: Nematode tracks in the study of movement of *Meloidogyne incognita incognita*. *Nematologica* 6, 261–265.
- SEILACHER, A. 1967: Bathymetry of trace fossils. *Marine Geol.* 5, 413–428;
- SCHMIDT, H. 1926: Merkwürdige Regenwurmspuren. *Natur und Volk* 56(1), 97–101.
- SCHWARZBACH, M. 1940: Das diluviale Klima während des Höchststandes einer Vereisung. *Z. dtsh. geol. Ges.* 92, 565–583.
- SCRIVNER, P.J. & BOTTJER, D.J. 1986: Neogene avian and mammalian tracks from Death Valley National Monument, California: their context, classification and preservation. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 57, 285–331.
- SMITH, R.M.H., MASON, T.R. & WARD, J.D. 1993: Flash-flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia. *Sediment. Geol.* 85, 579–599.
- SPECK, J. 1945: Fährtenfunde aus dem subalpinen Burdigalien und ihre Bedeutung für Fazies und Paläogeographie der oberen Meeresmolasse. *Eclogae geol. Helv.* 38, 411–416.
- STANLEY, D. C. A. & PICKERILL, R. K. 1998: Systematic ichnology of the Late Ordovician Georgian Bay Formation of southern Ontario. *R. Ontario Mus., Life Sci. Contr.* 162, 1–56.
- TARR, W.A. 1935: Concretions in the Champlain Formation of the Connecticut River Valley. *Bull. geol. Soc. Amer.* 46, 1493–1534.
- TEVESZ, M.J.S. & MCCALL, P.L. 1982: Geological significance of aquatic non-marine trace fossils. In: *Animal-Sediment Relations: The Biogenic Alteration of Sediments* (Ed. by MCCALL, P.L. and TEVESZ, M.J.S.). Plenum Press, New York and London 257–285.
- TOULA, F. 1908: Kriechspuren von *Pisidium amnicum* Müller. Beobachtungen auf einer Donauschlickbarre bei Kahlenbergerdorf-Wien. *Verh. k.k. geol. Bundesanst.* 11, 239–244.
- UCHMAN, A. & ÁLVARO, J.J. 2000: Non-marine invertebrate trace fossils from the Tertiary Calatayud-Teruel Basin, NE Spain. *Rev. españ. Paleontol.* 15(2), 203–218.
- VIALOV, O.S. 1965: *Stratigraphia Neogenovih Molass Predkarpatskoho Progi-ba.* Naukova Dumka, Kiev 192.
- WALTER, H. & SUHR, P. 1998: Lebensspuren aus kaltzeitlichen Bändersedimenten des Quartärs. *Abh. staat. Mus. Miner. Geol. Dresden* 43/44, 311–328.
- WEIDMANN, M. & REICHEL, M. 1979: Traces de pattes d’oiseaux dans la Molasse suisse. *Eclogae geol. Helv.* 72(3), 953–971.
- WHITAKER, J.H.McD. 1979: A new trace fossil from the Ringerike Group, Southern Norway. *Proc. Geologists’ Assoc.* 91: 85–89.
- WU, X. 1985: Trace fossils and their significance in non-marine turbidite deposits of Mesozoic coal and oil bearing sequences from Yima-Jiyuan basin, western Henan, China. *Acta sedimentol. sinica* 3, 23–31.
- YANG, S. & SHEN, Y. 1999: Early Tertiary trace fossils from King George Island, West Antarctica. *Acta palaeontol. sinica* 38(20), 203–217.

Manuscript received June 23, 2003
Revision accepted January 26, 2004