Early Devonian trace fossils in marine to non-marine redbeds in Podolia, Ukraine: palaeoenvironmental implications

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Abstract

Lochkovian redbeds in the Dnester formation in Podolia, Ukraine, record an upward transition from marginal-marine to fluvial conditions. A 60-m-thick section through transitional strata reveals a regressive stack of three facies associations laid down in: offshore lagoon, inshore lagoon or bay, and a fluvial-estuarine plain. The offshore lagoonal association shows green to variegated alternation of fossiliferous, bioturbated limestones, quartz arenites and shales. Numerous coquinas contain schizohaline ostracods, vermiform gastropods, Lingula, charophyte gyrogonites, all mixed with fragments of marine forms such as articulate brachiopods, tabulates, goniatites and leiospheres. Trace fossil assemblages contain abundant *Skolithos*, *Spirophyton*, *Teichichnus* and simple tubular forms. The inshore lagoon or bay association is a largely non-fossiliferous, locally bioturbated, red succession of interbedded mudstones and sandstones, which are arranged in coarsening-up units capped by thin, channelized sandstones. The presence of *Lockeia*, *Monomorphichnus*, *Rusophycus* and *Skolithos* suggests that the coarsening-up units could have originated as small bayhead deltas and washover fan-channel complexes. A new ichnospecies, *Monomorphichnus podolicus*, described here, occurs also in these deposits. In the overlying fluvial-estuarine association, the only trace fossil recorded is *Skolithos*, which occurs in dense clusters along upper levels of cross-bedded ribbon-shaped channel fills. Until now, piperock has been considered as an ichnofabric of the *Skolithos* ichnofacies that is typical of sandy beaches, bars and spits, whereas the findings presented here expand landwards the environmental range of *Skolithos* piperocks into more intracoastal marine-influenced settings.
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Keywords: Trace fossils; Bay; Estuary-lagoon shoreline; Redbeds; Devonian; Ukraine

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1. Introduction

It is commonly difficult to interpret palaeoenvironments based exclusively on sedimentological research. In many examples, ichnological data contributes to understanding the sediments, and vice versa, sedimentology assists to refine ichnological interpretations. Redbeds comprise a group of facies where such feedback is needed, especially in marine/continental transitions, where saline or brackish waters intrude into various marginal environments and extensive oxidation tends to remove much of the skeletal biotic record. Problems of this type have been encountered in lower Devonian redbeds in Podolia, Ukraine, where a 60-m-thick section was studied in natural outcrops near Ustechko (Fig. 1). Lower Devonian trace fossils of the region are poorly known. Narbutas (1984) listed some trace fossils from the studied unit and compared them to *Dimorphichnus* or *Diplichnites*, *Cruziana* or *Rusophycus*, *Chomatichnus* and *Helminthopsis*. The aim of the present paper is to provide the sedimentological and ichnological interpretation of the Ustechko section. The illustrated trace fossil specimens are housed in the Kraków Research Centre of the Institute of Geological Sciences, Polish Academy of Sciences (collection abbreviated as ZNG PAN A-I-129).

2. Geological setting

The lower Devonian redbeds of Podolia form part of a westward-dipping, non- to weakly deformed monocline made of Palaeozoic epicratonic sediments. These belong to the Volyn'-Podolia Monocline that flanks the metamorphic core of the Ukrainian Shield on the west (Fig. 1). In the Dnester River Basin, Lower Devonian redbeds strata are up to 1800 m thick and range from Lochkovian to Eifelian in age (Narbutas, 1984; Drygant, 2000a,b). Together with the underlying marine Silurian, they form an internally conformable, regressive unit that is capped along a regional, erosional hiatus by middle and upper Devonian transgressive carbonates (Drygant, 2000a,b, 2001). The Lower Devonian succession fills a wide (80–150 km) halfgraben that is bounded to the west by the NW-trending Teisseyre-Tornquist Fault Zone now concealed under the Carpathian Foreland Basin. The strata thicken towards (and locally overstep) the Teisseyre-Tornquist line that was apparently responsible for the observed thickening trend. Late Silurian subsidence that affected the southwestern margin of the East European Platform farther to the north has been interpreted in terms of flexural bending due to Caledonian thrust loading (Poprawa and Pacześna, 2002; Narkiewicz, 2002). The early Devonian subsidence pulse in Podolia appears to have been aided, by a dextral transtension along the Teisseyre-Tornquist Fault Zone.

The Lower Devonian succession in the Dnester River Basin of Podolia is informally divided into three formations (Fig. 2) (Dickenstein, 1957; Narbutas, 1984; Drygant, 2000a,b). The Lochkovian–lowest Pragian Ikva formation comprises red-coloured, continental to marine sandstones and shales that are
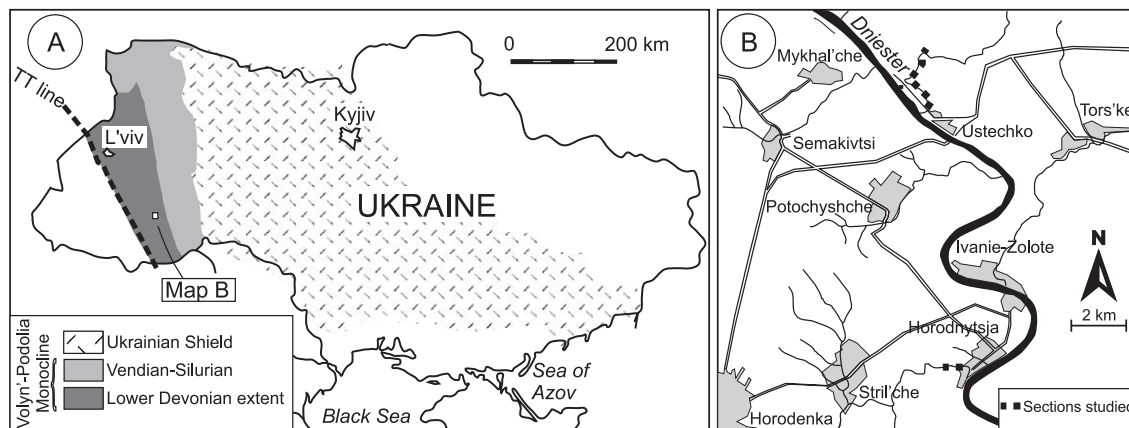

Fig. 1. (A) Location of study area in the Ukraine. (B) Detailed map of study area, showing locations of outcrop sections.
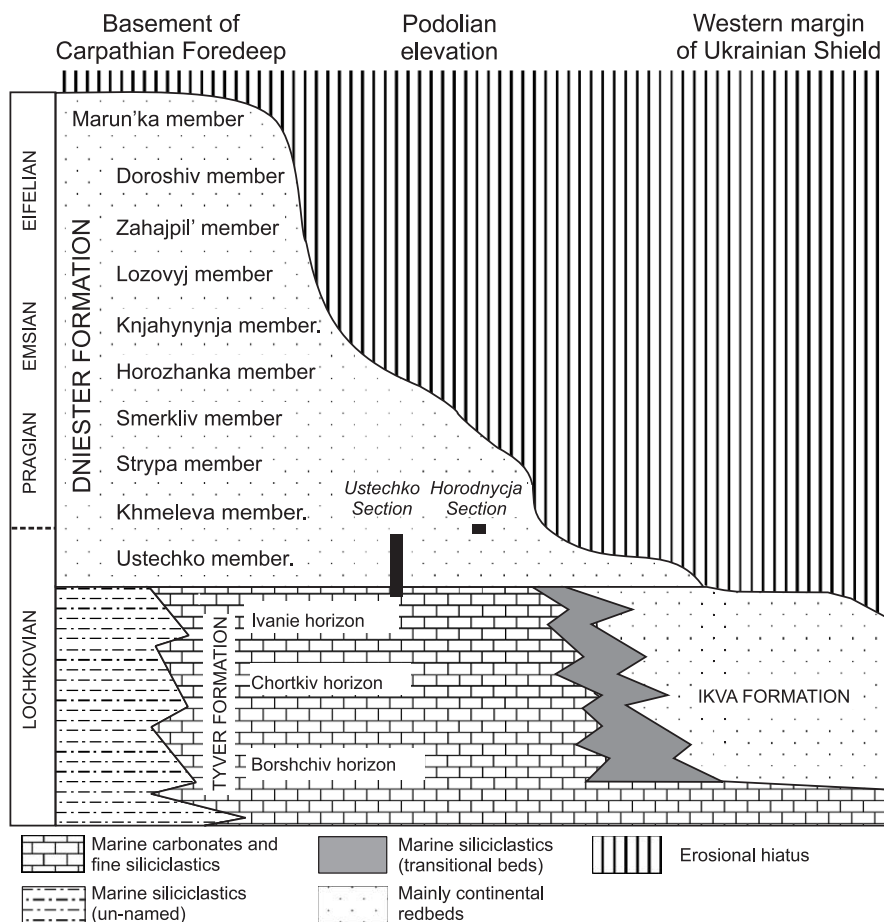
Fig. 2. Stratigraphic scheme of Lower Devonian strata in Podolia, Ukraine (Drygant, 2000a,b).

restricted to the eastern basin margin. They pass westwards into marine shales (Pomyanovskaya, 1974; Drygant, 2000a,b), which interfinger farther to the west with the fossiliferous, biohermal carbonates and argillaceous sediments of the Tyver formation. The latter represents an uninterrupted continuation of Silurian marine deposition into the Lochkovian (Nikiforova et al., 1972). The main body of the Old Red Sandstone facies represents the Dnester formation that consists of mudstones and siltstones with variable admixture of quartz arenites. These deposits contain abundant fish remains along numerous horizons (Zych, 1927).

The Lower Devonian in Podolia records transitions from restricted marine and deltaic to terrestrial depositional systems (Kozłowski, 1929; Brovkov, 1954). The Dnester formation is thought to have been deposited within a vast alluvial plain constructed by mixed-load streams and periodically occupied by shallow lakes (Narbutas, 1984).

3. Study area and age

The studied trace fossils come from the Ustechko member of the Dnester formation exposed in the Dzhurin stream at the Ustechko village and from the basal part of the overlying Khmeleva member at Horodnycja (Fig. 1; Narbutas, 1984, localities 9 and 29, respectively). Spore assemblages (Shepeleva, 1963; Arkhangelskaya, 1980), brachiopods and fish remains (Blieck and Cloutier, 2000 and literature therein), point to the Lochkovian (early Devonian) age of these members. Two samples (U1 and U2),
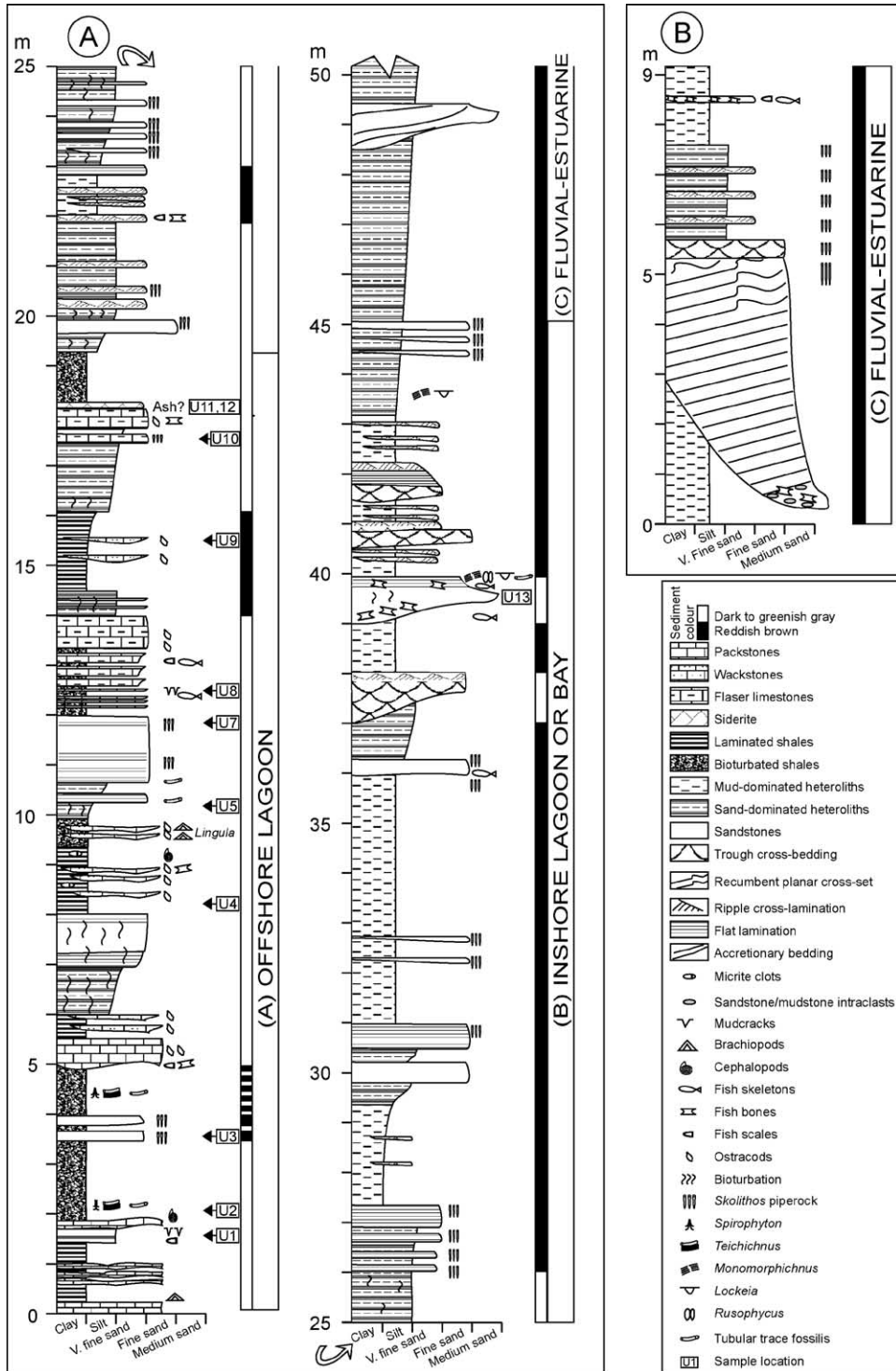
Fig. 3. Sedimentological logs of the ichnofossiliferous outcrops. (A) Ustechko section and (B) Horodnycja section.

taken near the base of the Ustechko section (Fig. 3A), yielded an impoverished miospore assemblage that includes *Ambitisporites dilutus* Richardson et Lister, *Archaeozonotriletes chulus* Cramer var. *nanus* Richardson et Lister, *Laevolancis divellomedium* (Tchibrikova) Burgess et Richardson, *Emphanisporites micrornatus* Richardson et Lister, *Chelinospora retorrida* Turnau, *Apiculiretusispora plicata* Allen, *Retusotriletes* sp., *Cymbosporites* sp. These taxa appear in the newportensis-micrornatus miospore zone of the Lochkovian (Richardson and McGregor, 1986). *Chelinospora retorrida*, known from SE Poland, does not extend above the Lochkovian (Turnau, 1986). Thin sections from the above two samples revealed the presence of rhambdosom fragments of the graptolite *Linograptus posthumus* (R. Richter) (Fig. 4B,C), whose stratigraphic range spans the middle Ludlov to Lochkovian (kozlowskii biozone to hercynicus biozone—Urbanek, 1997). In the Radom–Lublin area of SE Poland, this species does not extend beyond the uniformis zone (Porębska, 2003); hence, it is probably not younger than the early Lochkovian.

4. Sedimentological background

The Ustechko member is 55–60 m thick (Dickenstein, 1957; Drygant, 2000a,b). In the studied sections, this member, together with the underlying upper part of the Ivanie horizon of the Tyver formation and the overlying basal part of the Khmeleva member, is subdivided into three, stacked facies associations. These are, in ascending order: (A) mixed carbonate/siliciclastic deposits, (B) thin-bedded heteroliths intercalated with coarsening-up units and (C) thin-bedded heteroliths alternating with channelized sandstones.

### 4.1. Facies association A: offshore lagoon

The basal 18 m of the Ustechko section (upper part of Ivanie horizon) is a fossiliferous, dark grey and dark green succession of interbedded sandy limestones and siliciclastic mudrocks, with rare and thin intercalations of quartz arenites. Carbonate beds are 1–70 cm thick, and tend to reveal graded bedding and plane, parallel lamination near the top. Petrographi-

cally, the carbonates include whole-fossil packstones, sandy to dolomitic biopelsparites and sandy wackestones. The packstones are mostly bivalve-ostracod coquinas that are dominated by the schizohaline ostracods *Leperditia tyraica* Sch., *Welleriella prostrata* Abush., *W. reticularis* Abush., *W. centrireticularis* Abush., *Kloedenella pennsylvanica* Jones, *Dizygopleura oleskoiensis* Neck., *Zygobeyrichia dubia* Abush., *Cornikloedenia carina* Abush. and *C. alata* Abush. (Nikiforova et al., 1972) (Fig. 4D). The subordinate bioclasts include vermiform gastropods, both redeposited and in situ encrusters on micritized bivalve shells, fish scales and skeleton fragments, brachiopod Lingula shells and gyrogonites of charophytes (Fig. 4A,D–G). Shelter cavities, dolomitized marly matrix and radial-fibrous calcite cements, are common. A similar bioclast spectrum is also present in biopelsparites and wackestones, although rare remains of fully marine forms were also encountered, such as articulated brachiopods and fragments of tabulate corals, goniatites and orthoceratiids.

The interbedded mudrocks consist of marly greenish grey to dark grey, finely laminated to completely bioturbated shales and mudstones. These are rich in amorphous organic matter, spores, land plant tissues, fish bones and scales, and micrite clots. They also contain microphytoplankton represented by small numbers of *Leiosphaeridia* and *Lophosphaeridium*. Unidentifiable shell fragments also were encountered. Trace fossil assemblage includes *Spirophyton*, *Teichichnus* and simple tubular forms.

Sandstones are very fine to fine-grained, well-sorted quartz arenites and wackes, and are commonly cemented with calcite. Fossils include fish teeth and finely comminute bone detritus, rare abraded shells of vermiform gastropods and micritized remnants of calcareous algae or calcified charophyte stems. Sandstone facies comprise (a) centimetre-thick graded to laminated beds showing densely crowded *Skolithos* and (b) coarsening-upwards, bioturbated, muddy sandstone units. The graded beds show sharp bases and diffuse, burrowed tops; flat lamination is locally discernible between *Skolithos* tubes. Beds are 1–10 cm thick, and occur together with thin sandy wackestone lenses and layers within metre-tick layers of an entirely bioturbated mudstone.

The coarsening-up units are 0.5–1.5 m thick and display bioturbated (mottled) fabrics with *Planolites*
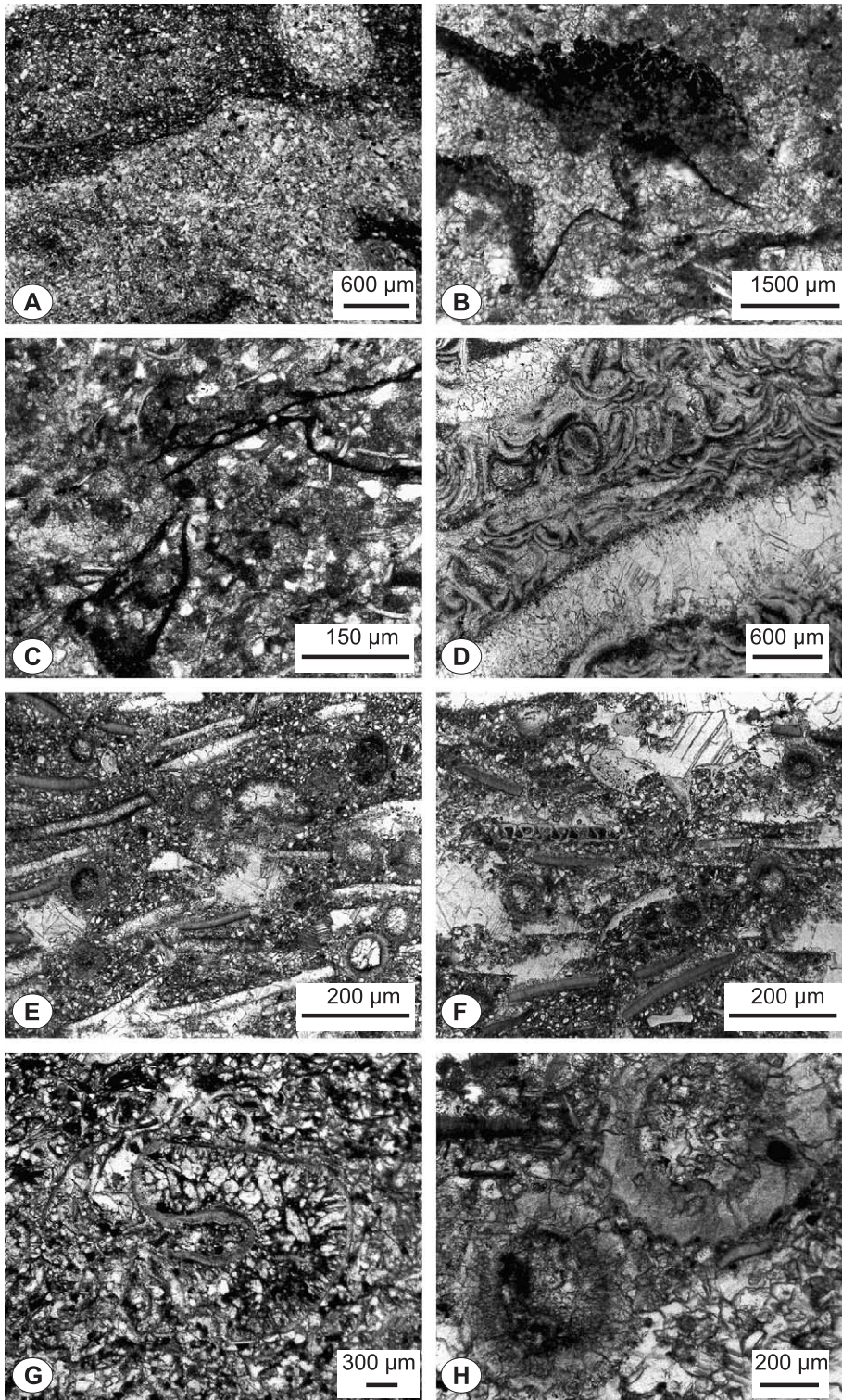
occasionally present along lower, more heterolithic segments of the units. Thin, parallel to low-angle inclined laminasets become well pronounced towards bed tops and they tend to be penetrated by abundant *Skolithos*. Mud-cracked levels are common along both sandstone tops and internal sand–mud interfaces. The coarsening-up units appear to form siliciclastic caps to thicker, upward-shallowing lithosomes that are rich in carbonate beds in their lower parts.

4.1.1. Interpretation

The features of facies association A point to deposition within a marginal-marine environments that was barred from the open sea by a zone of mixed carbonate/siliciclastic shoals or an emerged barrier, and was subjected to intermittent changes in salinity and water depth, common in brackish lagoons and central estuarine basins (e.g. Dalrymple et al., 1992). The association of *Lingula*, vermiform gastropods, monospecific ostracod coquinas and charophytes, is a particularly good indicator of a schizohaline environment (Burchette and Riding, 1977; Malec et al., 1987). The dark to green grey, laminated shales and mudstones alternating with bioturbated horizons reflect a mass input of organic matter and its decay in conditions of strongly fluctuating redox conditions within the sediment (Savrda et al., 1991). The ostracod–charophyte assemblage represents indigenous biotas that were affected in most cases by storm events to form parautochthonous coquinas (e.g. Kidwell, 1986). The thin, graded-laminated sandstones with *Skolithos* reflect suspension plus fallout deposition probably from storm surges (e.g. Hayes, 1967). The burrowed to laminated, coarsening-up, muddy sandstone units possibly represent mainly storm washover fans and sheets (e.g. Andrews, 1970), although some also may correspond to the distal reaches of small bayhead deltas (Dalrymple et al., 1992). The mud-cracked horizons may reflect periods of desiccation of the entire lagoon.

4.2. Facies association B: inshore lagoon or bay

In the uppermost Ivanie horizon, carbonates and invertebrate macrofauna disappear, except for sporadic occurrences of the ostracods *Leperditia tyraica* Sch., and unidentified pelecypods, whereas pelitic intervals become thicker (>5 m) and siltier and the sediment acquires a dark-reddish brown colour (19–45 m in Fig. 3A). Pelitic rocks range from massive to crudely laminated, silty shales, sandy mudstones to thin-bedded sand/mud heteroliths. These rocks are unfossiliferous except for rare, thin, fish bone beds and bioturbated levels.

Sandstones occur as coarsening-up units and thin, broadly channelised bodies. The latter may form either erosional cappings to the coarsening-up units, or solitary bodies encased within the pelitic host. The coarsening-up units are up to 9 m thick and reveal ripple cross-laminated bedsets separated along diffuse to bioturbated boundaries by more massive, muddier intervals. The trace fossils *Lockeia* and *Monomorphichnus* are locally present in these heterolithic facies. Upwards, parallel-laminated to heavily *Skolithos*-burrowed beds become predominant. The channelised bodies vary in thickness between 0.5 and 1.1 m, and tend to show laterally lensing and swelling geometries. Internally, these bodies exhibit grossly upward-fining patterns from fine to very fine sand and are associated with a simple internal structuring. Typically, a channel fill begins with fish-bone lag that is overlain by trough cross-bedded fine-grained sandstone. This passes upwards directly, or through a flat-laminated interval, into cross-laminated, very fine sandstone. The trace fossil *Monomorphichnus podolicus* comes from such a flat-laminated interval (Fig.

Fig. 4. Microfacies details from lagoonal facies association seen in thin sections under parallel nicols, scale bars in micrometers. (A) Bivalve shells, fish remains and ostracodes in heavily bioturbated silty, calcareous, fine-grained, grey sandstone. (B, C) Rhabdosome fragments of *Linograptus posthummus* visible as black, organic-walled structures. (D) Sandy ostracod-bivalve coquina composed of monotaxial accumulation of leperditicopid carpaces accompanied by coiled, attached vermiform gastropod incrustations with micrite protoconch (arrow). Completely recrystallized and micritized fragment of bivalve shell is present at the lower part of picture. (E) Fish scales and bones in a calcareous sandstone. (F) Micritized bivalve shells and calcified charophyte stems, charophyte oogonia and leperditicopid ostracod carpaces. (G) Section parallel to coil axial plane through vermiform gastropod tubular shell "floating" in calcareous sandstone matrix. (H) Section trough calcified charophyte oogonia, showing surficial ribs and funnel-shaped foramen.

3B), where it is associated with *Rusophycus*, *Lockeia* and simple tubular forms (Fig. 3A).

4.2.1. Interpretation

The thick, red mudrocks showing bioturbated intervals reflect deposition in a well-oxygenated water body, such as an upper estuary or intracoastal, semi-enclosed bay, which was subjected at least periodically to an inflow of marine waters. The absence of carbonate skeletal detritus and marine plankton suggests a relatively distant location this environment with respect to a contemporaneous marine shoreline, and possibly an increased siliciclastic influx. The ripple cross-laminated, coarsening-up units are mostly progradational bodies, probably mouth bars of small bayhead deltas and washover fan-channel complexes. The plane-laminated *Skolithos* piperocks represent storm event beds, but some could have resulted from post-storm swash imposed on the mouth bars. The cross-bedded channelized sandstones may represent the traces of minor distributary channels; however, those scoured directly in mudstones and showing graded-bioturbated fills appear more compatible with washover channels associated with storm erosion and deposition.

4.3. Facies association C: fluvial-estuarine

The section of the Khmeleva member at Horodnycja (Fig. 3B) either overlies the Ustechko member, or else forms a lateral equivalent to its uppermost part. This section reveals dark-reddish brown mudrocks that are interbedded with thick, upward-fining, channelized sandstones. The latter are fine to medium grained and occur as 2–7 m thick, ribbons and sheets that vary in the lateral extent between a few tens and several hundreds of metres. A deeply incised channel floor tends to be covered with a lag of mudstone intraclasts, fish bones and quartz granules. This is overlain by a single, high-angle planar cross-set, up to 5 m thick, which reveals signs of water escape in the form of recumbent-folded to convoluted upper foreset reaches. This is overlain by 0.5–2 m thick cosets of trough cross-stratification that passes upwards either into a heterolithic interval, or is sharply overlain by a mudstone. A dense network of very long *Skolithos* (up to 1 m long) commonly spreads from the top of the channel fill downwards (Figs. 3C and 7). The overlying sand-dominated heterolithics tend to be poorly structured internally, except for thin

intervals of ripple cross-lamination, occasionally with wave-modified ripple forms preserved, and they reveal *Skolithos* piperock fabrics. The latter disappear upwards within mudstones and mud-dominated heterolithic beds that are unbioturbated and locally intercalated with discontinuous, centimeter-thick, lag-type accumulations of fish bones. No clear evidence of tidal couplets was found in these heterolithic facies.

4.3.1. Interpretation

Except for the trace fossil *Skolithos*, the facies spectrum in association C is consistent with deposition on a mud-dominated floodplain crossed by low-mobility, sinuous fluvial channels. However, the ubiquitous presence of these burrows within the upper channel fills strongly suggests that these channels were at least occasionally affected by incursions of seawaters.

5. Systematic description of trace fossils

5.1. Lockeia *(James, 1879)*

Description: Bilaterally symmetrical, elongated, commonly almond-shaped, rarely triangular or heart-shaped outline with smooth margin, preserved commonly as hypichnial mounds, commonly with a distinct median crest. A vertical spreite can be present (Rindsberg, 1994; Schlirf et al., 2001).
Remarks: *Lockeia* is interpreted most commonly as a bivalve resting trace (Seilacher and Seilacher, 1994) occurring in marine and non-marine environments since the Late? Cambrian (Fillion and Pickerill, 1990). Small crustaceans also can be potential producers (Bromley and Asgaard, 1979; Pollard, 1981).

5.2. Lockeia siliquaria *(James, 1879)*

Description: *Lockeia siliquaria* is diagnosed as thin, elongate, to stout, generally high-standing, almond-shaped, smooth hypichnial ridges, with strongly arcuate to almost obtuse terminations; occasionally showing a vertical spreite (Schlirf et al., 2001). In the studied material, it occurs as smooth, hypichnial, straight to slightly curved, single, carinate-shaped elongate mound with pointed terminations. The vertical axis of the mound can be inclined. The mound is up to 5

mm wide and up to 25 mm long (Figs. 5B–D and 6A).
Remarks: Taxonomy of *Lockeia* was discussed by
Schlirf et al. (2001) and Mangáno et al. (2001). *Lockeia*
is a common shallow marine trace fossil, occurring for
instance in the Devonian Taunusquartzit of Germany
(Schlirf et al., 2002).

5.3. Monomorphichnus (Crimes, 1970)

Description: In concave epirelief or convex hypore-
lief, a series of straight to slightly wavy, parallel to
intersecting striae is visible. Groups of sets of striae
may be repeated in series, or obliquely, or parallel to
each other (after Fillion and Pickerill, 1990).
Remarks: Taxonomic problems of *Monomorphichnus*
have been discussed by Fillion and Pickerill (1990) and
Keighley and Pickerill (1998). Originally, *Monomor-
phichnus* was interpreted as a trace of trilobites, which
raked sea-floor as they were driven by currents (Crimes,
1970), or which lashed out of control due to currents, or
which grazed the sediment surface without any
significant current action (Fillion and Pickerill, 1990).
As an exception, Keighley and Pickerill (1998)
described *M.* cf. *lineatus* from Carboniferous non-
marine deposits of eastern Canada, and they interpreted
it as a trace of non-marine crustaceans. Moreover, *M.
semilineatus* from the Cambrian of Czech Republic is
interpreted as a trace of an endemic arthropod *Kody-
mirus* (Mikuláš, 1995). *Monomorphichnus* occurs
mainly from the base of the Cambrian (*Phycodes
pedum* zone) (Narbonne and Myrow, 1988), but Crimes
(1994) indicated that it occurs since the Ediacarian.

5.4. Monomorphichnus podolicus isp. nov.

Material: Two slabs and more material in the field
(Fig. 5).
Holotype: ZNG PAN A-I-129/1.
Type horizon: Ustechko member (lower Devonian),
Podolia, Ukraine.
Derivation of name: From the Podolia region of
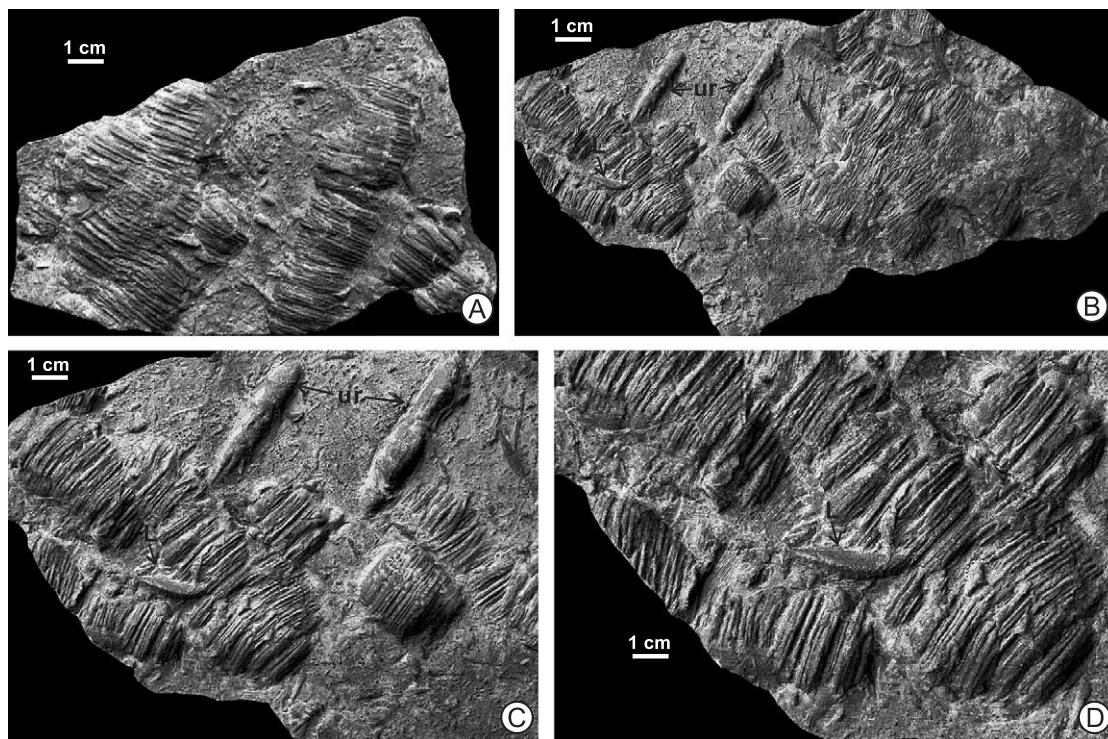Ukraine, where the studied section is located.

Fig. 5. *Monomorphichnus podolicus* from the lower Devonian (Lochkovian) redbeds at Ustechko, fine-gained sandtones, hypichnial convex reliefs: (A) holotype, ZNG PAN A-I-129/2; (B–D) specimen ZNG PAN A-I-129/1, general view (A) and details (C, D), L—*Lockeia siliquaria*, ur—hypichnial undulating ridges. Scale bars=1 cm.
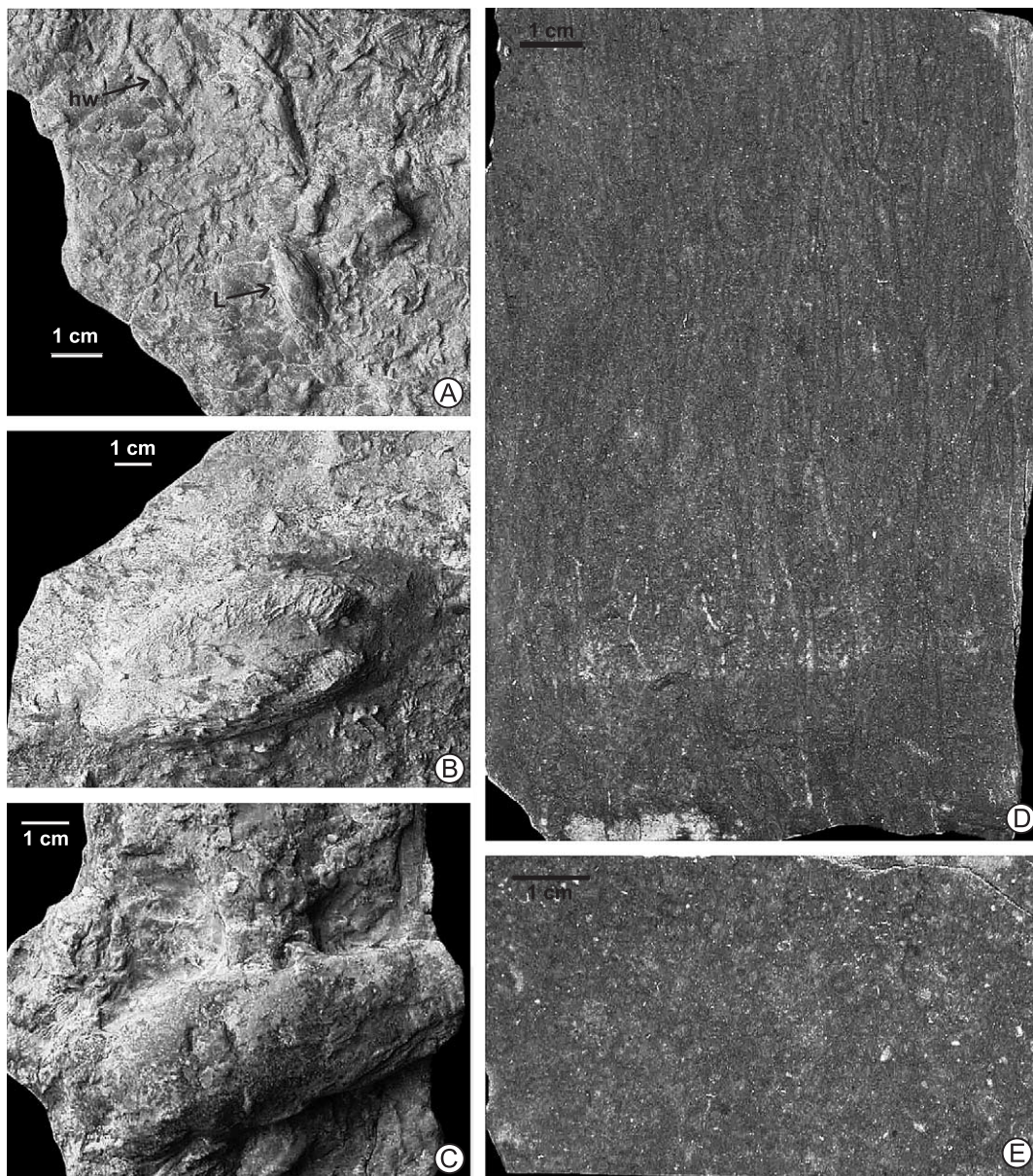
Fig. 6. Other trace fossils from the lower Devonian redbeds at Ustechko, fine-grained sandstones: (A) *Lockeia siliquaria* (L) and hypichnial horizontal, winding semicircular ridges (hw), hypichnial convex reliefs, ZNG PAN A-I-129/4; (B) *Rusophycus* isp., hypichnial convex relief; ZNG PAN A-I-129/3; (C) hypichnial horizontal tunnel, convex relief, ZNG PAN A-I-129/6; (D) *Skolithos linearis* in a pipe rock, vertical cross-section, polished slab, ZNG PAN A-I-129/13; (E) *Skolithos linearis* in a pipe rock, horizontal cross-section, polished slab, ZNG PAN A-I-129/14. Scale bars=1 cm.

Diagnosis: *Monomorophichnus* with densely packed striae arranged in bundles (4–6 striae/bundle). The bundles form parallel to subparallel ridges, whose axis is elevated and perpendicular to the bundles.

Description: Hypichnial, parallel or subparallel, rarely crossing, densely packed thin ridges (striae), 1–2 mm wide, 20–35 mm long, preserved in semi-reliefs. The distance between the striae is smaller than the width of

the ridges. Most of the striae touch the adjacent ones. The striae are arranged in distinct to indistinct bundles, with 4–6 striae/bundle. The central striae in bundle are more elevated above the sole than the others. The striae plunge in the bed and their centre is gently elevated. Therefore, they form a main ridge, whose axis is straight to slightly curved and perpendicular to the bundles. The examined slabs contain several main ridges, which are parallel to subparallel, and locally overlapping. Edges of the ridges are uneven, because the striae plunge in the bed not exactly along the same line.

Remarks: *Monomorphichnus podolicus* is the transitional form between *Monomorphichnus* Crimes and *Cruziana* d'Orbigny. The similarity to *Cruziana* is manifested by arrangement of the striae in locally bilobate ridges. However, it is impossible to distinguish a clear pair of the ridges which could be individualised in the *Cruziana* pattern. *Monomorphichnus podolicus* instead resembles an overlapped *Cruziana*. Similar features are visible in *Rusophycus hanynagensis* Yang et al. (1987), but this trace fossil is at least two to three times smaller, shorter and it lacks bundles of striae.

Monomorphichnus podolicus is distinctly different from the other *Monomorphichnus* ichnospecies by its densely packed striae arranged in bundles (more than 4 striae/bundle) and large size. These features do not occur in most Cambrian ichnospecies, such as *M. bilinearis* Crimes (1970), *M. lineatus* Crimes et al. (1977), *M. monolinearis* Shah and Sudan (1983), *M. semilineatus* Mikuláš (1995), *M. biserialis* Mikuláš (1995) and *M. henanensis* Yang and Wang (1991). *M. devonicus* Yang et Hu (Yang et al., 1987) from the Devonian of China is characterised by more sparse striae, which are not arranged in bundles. In *M. intersectus* Fillion and Pickerill (1990) striae cross each other. *M. multilineatus* Alpert (1976) displays shorter bundles, with five to six sets of striae that are deeper in the bundle centre. *M. pectenensis* Legg (1985) contains 8–9 striae/bundle. *M. cretacea* Badve and Ghare (1980) is interpreted by Fillion and Pickerill (1990) as a physical structure. Most probably, the same interpretation applies to *Monomorphichnus gaopoensis* (Yang et al., 1982).

Monomorphichnus podolicus, similarly to forms described by Fillion and Pickerill (1990), can be interpreted as a grazing trace. Dense packing of the striae suggests large number of grazing appendages of the trace maker. Its large size and similarity to *Cruziana* point to trilobites as the most probable trace makers. The non-marine or non-trilobite forms (see discussion of the ichnogenus) display much sparser striae.

5.5. Rusophycus (Hall, 1852)

Description: Short, bilobate, rarely multilobate traces. Lobes are symmetrical or cleft. Convex forms with a distinct median furrow in hypichnia; concave forms with median ridge when epichnial. Outline is ovate to coffee-bean shaped; sculptured with oblique to transverse striae in various arrangements or almost smooth (after Schlirf et al., 2001).

Remarks: Apart from obvious *Rusophycus*, there are transitional forms to *Cruziana*, which show a length/width ratio of about 2:1, which is recommended by Keighley and Pickerill (1996) as the diagnostic criterion for distinction between *Cruziana* and *Rusophycus*. However, the transitional forms do not display evidences of the distinct downward directed digging (Seilacher, 1970) typical of *Rusophycus*, which should be considered as one of the most important diagnostic features of *Rusophycus*, expressed in the coffee-been shape. For a taxonomic discussion, see Fillion and Pickerill (1990). Palaeozoic *Rusophycus* is thought to be produced predominantly by trilobites (Osgood, 1970; Rindsberg, 1994).

5.6. Rusophycus isp.

Description: Elliptical, bilobate, almost symmetrical mound, maximum 40 mm wide and 72 mm long, separated by shallow median, slightly cleft furrow. One side is covered with short, thin ridges (striae), which are <1 mm wide and 7 mm long (Fig. 6B).

Remarks: The overall shape of the described trace fossil is not similar to any known *Rusophycus* species, but details of its sculpture are poorly preserved, and therefore more detailed determination is impossible.

5.7. Skolithos (Haldeman, 1840)

Description: Cylindrical or subcylindrical, perfectly straight and vertical to slightly curved or inclined

burrows. Burrows wall distinct to indistinct may be annulated (Schlirf, 2000).

Remarks: *Skolithos* occurs mostly in various shallow-marine environments from the Late Precambrian to the Recent (see Fillion and Pickerill, 1990 for review) and was produced probably by annelids or phoronids (Alpert, 1974). In non-marine environments, *Skolithos* can be produced by insects (e.g. Ratcliffe and Fagerstrom, 1980).

5.8. Skolithos linearis (Haldeman, 1840)

Description: *Skolithos linearis* is diagnosed as cylindrical to subcylindrical, perfectly straight and vertical to slightly curved or inclined burrows. Burrow wall distinct to indistinct, may be annulated (Schlirf, 2000). In the studied material, it occurs as vertical, straight, tubular, densely packed cylinders with a wall, 1.0–2.2 mm in diameter and at least 25 cm long. The wall contains more clay minerals than the filling and the surrounding rock. It is 0.1–0.2 mm thick (Figs. 6D–E and 7).

Remarks: Dense occurrences of *Skolithos linearis* commonly are called piperocks, which are typical ichnofabrics of the *Skolithos* ichnofacies in the lower Palaeozoic, especially in the Cambrian (Droser, 1991).

Fig. 7. Population of dense *Skolithos linearis* (piperock) cutting across a trough cross-bed located near the top of major channel fill (Fig. 3B). Scale (enriched) is 8 cm long. (For colour see online version).

5.9. Spirophyton (Hall, 1863)

Description: Spirally coiled circularly outlined spreite whorls arranged around a central axis. Radius of the whorls gradually diminishes towards the top. The whorls are concave-up, commonly with distinctly wrapped up edges.

Remarks: Differences between *Spirophyton* and *Zoophycos* were discussed by Miller (1991). *Spirophyton* is a characteristic fodinichnion for nearshore Devonian fine-grained facies in many continents. As reviewed by Goldring and Langenstrassen (1979), it occurs in estuarine, interdistributary bay or restricted bay-lagoonal lower and middle Devonian mudstones and siltstones of the Rhenische Schiefergebirge. In the middle–upper Devonian Catskill shoreline deposits from the New York State, *Spirophyton* occurs mostly in siltstones to very fine sandstones deposited in brackish estuarine settings and floodplain ephemeral ponds, where its producer colonized freshly deposited sediments (Miller and Johnson, 1981; Miller, 1991; Miller and Woodrow, 1991). In the Devonian of Antarctica, *Spirophyton* has been noted in coarse to very-coarse, trough cross-bedded sandstones interpreted as the deposits of nearshore sand bars dissected by a tidal delta (Bradshaw et al., 2002).

5.10. Spirophyton isp.

Description: *Spirophyton* isp. has been observed in vertical cross-section of a green mudstone bed. A vertical to slightly oblique axial tunnel, 1.5–3.0 mm wide, at least 50 mm long, with bilateral spreite structures that are visible in cross section as slightly oblique and arcuate, concave-up uneven stripes, 1–2 mm wide, up to 22 mm long and up to 5 mm apart. The axial tunnel is filled with coarser sediment (Fig. 8).

Remarks: Limited observations in cross-sections do not allow for species determination. The coarser filling of the axial tunnel and the uneven spreiten were noted in *Spirophyton eifeliense* by Antun (1950), which are more regular in outline than in the described material.

5.11. Teichichnus (Seilacher, 1955)

Description: Long, wall-like burrows formed by vertical displacement of horizontal and oblique tubes (Fürsich, 1974).
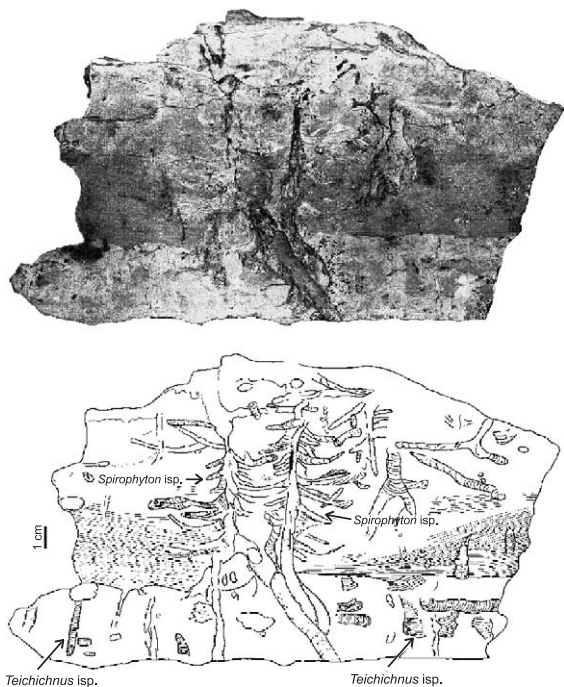
Fig. 8. *Spirophyton* isp. *Teichichnus* isp. from the lower Devonian redbeds at Ustechko (facies association A, green marly mudstone–siltstone). Vertical cross-section, polished slab. ZNG PAN A-I-129/15. Scale bar=1 cm.

Remarks: *Teichichnus* is a deposit-feeding structure ranging from the lower Cambrian to the Recent. It may be produced by various invertebrates, among which annelids and arthropods are most likely (see Fillion and Pickerill, 1990, for review). It is considered as a fully marine, commonly deeper-water form. However, it also occurs in brackish lower Jurassic deltaic facies (Vossmerbäumer, 1970), and in lagoonal settings of late Jurassic (Fürsich, 1981) and early Cretaceous age (Nielsen et al., 1989). According to Pemberton et al. (2001, p. 324), *Teichichnus* is common in lower shoreface to offshore, but prevalent in brackish-water lagoon/bay environments.

5.12. Teichichnus isp.

Description: *Teichichnus* isp. has been observed in vertical cross-section of a green mudstone bed. It is visible as a vertically stacked series of fine, retrusive spreite structures. This trace fossil is 15 mm high and

about 2 mm wide perpendicularly to the axis (Fig. 8). *Remarks*: The described *Teichichnus* occurs in totally bioturbated shales.

5.13. Unidentified trace fossils

(1) A hypichnial horizontal tunnel, 26 mm wide, at least 70 mm long, ellipsoidal in cross section, plunging in the bed at one termination. The tunnel is filled with the same sandstone as in the bed (Fig. 6C). This is a burrow of unknown origin.

(2) Hypichnial undulating ridges, plunging in the bed, up to 10 mm wide preserved in semi-relief. They display short protruding perpendicular and longitudinal irregularities (Fig. 5B–C). Slightly carinate cross-section suggests a bivalve loco-motion trace fossil.

(3) Hypichnial horizontal, winding semicircular ridges, about 1.5 mm wide, up to 20 mm long (Fig. 6A). This trace fossil can be ascribed to *Planolites* or *Palaeophycus*, but details of the burrow margin and sediment fill are too poorly preserved for a taxonomic decision.

6. Discussion

The distribution of the most common trace fossils recognized in the field is shown in Fig. 3. For the lower part of the section (facies association A), the distribution agrees with both the palaeoenvironmental interpretation of particular ichnotaxa and the sedimentological interpretation of the host rock. The shales of facies association A are bioturbated and contain *Spirophyton* and *Teichichnus*. These ichnogenera occur most commonly in the lagoonal-brackish facies (Goldring and Langenstrassen, 1979; Pemberton et al., 2001), including the central estuarine basin of incised-valley estuaries (Porębski, 1995). The offshore lagoonal origin of association A is consistent with the presence of limestone coquinas containing both schizohaline and euryhaline biotas.

If *Monomorphichnus podolicus* and/or *Rusophycus* isp. were indeed produced by trilobites, as suggested here, they would indicate marine influences

in the upper middle part of the section (facies association B). Trilobites were generally fully marine organisms, but the trace fossil *Cruziana* produced by them is common in Palaeozoic tidal flat deposits (Mángano et al., 2002). However, there are other potential trace makers. For example, large *Cruziana*, produced probably by stomatopod or decapod crustaceans, has been found in the Triassic (Zonneveld et al., 2002). *Monomorphichnus podolicus* and *Rusophycus* occur in the upper part of a small channel fill (Fig. 3A, 40–41 m). This channel may have been a small deltaic distributary or, more likely, a washover channel. In both instances, marine producers of these two trace fossils are most probable.

The most problematic is *Skolithos linearis* that forms piperocks throughout the entire section. Generally, piperocks are considered to be shallow marine (Droser, 1991), but their Permian occurrences in Antarctica were interpreted as fluvial in origin (Fitzgerald and Barret, 1986). Similarly, Woolfe (1990) interpreted piperocks in the Devonian Taylor Group from Antarctica as fluvial and belonging to the *Scoyenia* ichnofacies. However, these deposits that contain also *Cruziana*, *Diplichnites*, *Rusophycus* and *Skolithos* were interpreted earlier as marine (Bradshaw, 1981). Also detailed studies of the Emsian part of the Battery Point Formation, Quebec, Canada, show that piperock occurs in brackish to marine bay (washover sands?) (Hotton et al., 2001). Piperock sandstones from Middle–Upper Devonian of New York and Pennsylvania, USA, were considered as crevasse splays or minor deltas that prograded into floodplain marshes and lakes or brackish interdistributary bays–lagoons (Bridge, 2000).

In the present case, *Skolithos* does not change in terms of size, shape, density and abundance throughout the studied section. The lagoonal environment for facies association A, where the piperocks also occur, is well documented. Therefore, it is concluded that the piperocks were formed in comparable settings with respect to energy and salinity levels, and the burrows were produced by the same trace makers. These settings included washover fans and shoals in the lagoon (facies association A), mouth bars and storm-washover channels in the inshore part of the lagoon or bay (facies association B), and major fluvial channels that turned into estuaries during storm peak discharges or base-level rises (facies association C). It is difficult to find a domichnia-producing animal that crosses the salinity barrier.

Piperock typically has been considered as a characteristic ichnofabric of the *Skolithos* ichnofacies that is characteristic of foreshore and shoreface sandy beaches, bars and spits (Pemberton et al., 2001, p. 91), i.e., open shoreline environments. The findings presented here expand landwards the environmental range of *Skolithos* piperocks into more intracoastal, but still marine-influenced settings.

It is worth pointing out that the *Cruziana* ichnofacies, represented here by *Monomorphichnus*, *Rusophycus*, *Lockeia* and the horizontal tubular burrows, can occur in even shallower-water environments than the *Skolithos* ichnofacies, in tidal flats and lagoons (e.g. Mángano and Buatois, 1999). Trace fossils in the investigated lagoonal muds (*Spirophyton* and *Teichichnus*) are similar to those that characterize the *Zoophycos* ichnofacies, which is typical for deeper water.

7. Conclusions

(1) Lochkovian (lower Devonian) redbeds in the Dnester formation in Podolia, Ukraine, record an upward transition from marginal-marine to fluvial deposits.

(2) *Monomorphichnus podolicus* isp. nov. and *Rusophycus* isp. probably were produced by trilobites. The occurrence of these trace fossils is taken as strong evidence of marine influences in the upper part of the studied section, where sedimentological features are not diagnostic.

(3) The piperock ichnofabric (*Skolithos* ichnofacies) can be present in the sand-rich sub-environment of a lagoon or bay, such as washover channels and fans, mouth bars of bayhead deltas and fluvial channels that turned into estuaries during storm floods or base-level rises.

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