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Citation style: Filipiak Paweł, Zatoń Michał, Szaniawski Hubert, Wrona Ryszard, Racki Grzegorz. (2012). Palynology and microfacies of Lower Devonian mixed carbonatesiliciclastic deposits in Podolia, Ukraine. "Acta Palaeontologica Polonica" (2012, vol. 57, no. 4, s. 863-877), doi 10.4202/app.2011.0184

Palynology and microfacies of Lower Devonian mixed carbonate-siliciclastic deposits in Podolia, Ukraine

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Filipiak, P., Zatoń, M., Szaniawski, H., Wrona, R., and Racki, G. 2012. Palynology and microfacies of Lower Devonian mixed carbonate-siliciclastic deposits in Podolia, Ukraine. *Acta Palaeontologica Polonica* 57 (4): 863–877.

Investigation of mixed carbonate-siliciclastic Lower Devonian deposits have been carried out in the Ivanye Zolote and Ustechko sections in Podolia, Ukraine. Based on palynomorph evidence, the age of the samples studied is late Lochkovian, not older than the NM Oppel Miospore Zone, specifically the Si Lineage Zone. The presence of acritarchs and chitinozoans points to dominantly marine depositional conditions. However, a regressive environmental change toward more brackish conditions is indicated by a decrease in the taxonomic diversity of acritarchs in the topmost samples, the simultaneous disappearance of chitinozoans, and an increase in leiosphaerid frequency. Furthermore, evolution of limestone microfacies demonstrates a progressive transition from a shrinking marine basin toward a brackish, storm-affected muddy lagoon, manifested by recurrent profusion of impoverished, mostly opportunistic and euryhaline shelly benthos (nuculanid bivalves, leperditicopids and other ostracods, terebratulid brachiopods), chaetetid demosponges and diverse ichthyofauna. The association of plant (mainly nematophytes and some tracheids) and animal (eurypterid, ?scorpion, and possibly other arthropod) remains points to the presence of nearby Early Devonian wetland vegetation, providing food and shelter for various semi-aquatic and other terrestrial arthropods.

Key words: Eurypterids, palynostratigraphy, palynofacies, carbonate microfacies, cuticles, Lower Devonian, Podolia.

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Received 29 November 2011, accepted 10 August 2012, available online 13 August 2012.

Introduction

Upper Silurian and Lower Devonian deposits occur as many natural exposures in the Podolia region of Ukraine (Fig. 1). However, biostratigraphic subdivision of the sedimentary successions remains unsatisfactory, especially of those strata deposited during the late Lochkovian, when conditions changed from marginal marine to alluvial (Uchman et al. 2004; Małkowski et al. 2009; Drygant 2010; Voichyshyn 2011). Palynological studies have proven useful for subdividing and correlating various sedimentary facies, as well as can also assist in interpreting changes in sedimentary environments (e.g., Tyson 1993; Batten 1996; Wicander and Wood 1997; Filipiak 2002; Filipiak and Zatoń 2011). In Podolia, such integrative palynological analyses are especially needed (Le Hérissé et al. 1997) to decipher the evolution of sedimentary conditions during this regressive Early Devonian interval, supplementing the sedimentological-ecological data provided by Uchman et al. (2004).

Kirjanov (1978) presented comprehensive data concerning phytoplankton (mainly acritarch) distribution in the Silurian of the Volyno-Podolia region. He described over 70 species, some of which were recognized during the current study. Arkhangelskaya (1980) identified such miospores as *Emphanisporites* cf. *micrornatus* and *Streelispora* sp. from the Ivanye Horizon, indicative of the middle and upper parts of the *Emphanisporites micrornatus–Streelispora newportensis* Spore Zone of Richardson and McGregor (1986). Based on the presence of *Emphanisporites micrornatus*, Richardson et al. (1981) and Richardson and McGregor (1986) assigned the Ivanye Horizon to the NM Miospore Zone. Paris and Grahn (1996) studied chitinozoans of Přidoli and Lochkovian beds of Podolia and tentatively dated their youngest low-diversity *Ancyrochitina*-dominated assemblage, from the Ivanye Horizon, as Lochkovian. Palynostratigraphic data from two samples from the Ustechko section were presented by Turnau in Uchman et al. (2004). Based on the presence of miospore taxa, Turnau recognized the Lochkovian *Emphanisporites micro-*

http://dx.doi.org/10.4202/app.2011.0184

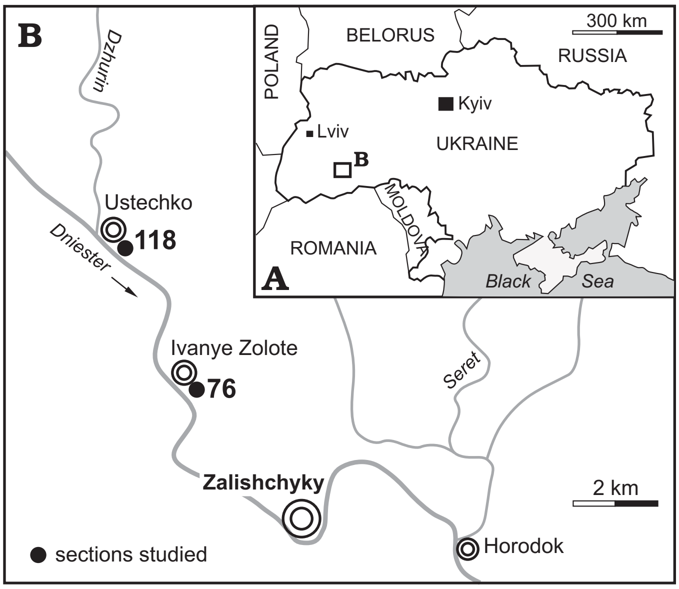


Fig. 1. **A**. Location of study area in Ukraine. **B**. Detailed map of study area in Podolia, showing locations of outcrop sections. Numbers of sections after Nikiforova et al. (1972).

rnatus–Streelispora newportensis Miospore Zone. In the phytoplankton assemblage she only noticed the occurrence of *Leiosphaeridia* and *Lophosphaeridium*. The presence of amorphous organic matter and plant tissues was mentioned by Uchman et al. (2004).

The aim of the present paper is to establish a palynostratigraphic framework and to characterize, in the paleoenvironmental context, the palynofacies and carbonate microfacies in the upper part of the Lochkovian deposits of Podolia. In particular, analysis of associations of marine and land-derived palynoflora, as well as plant and animal cuticle remains, refines interpretation of the development of marginal-marine facies in the section under study.

Institutional abbreviations.—GIUS, Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland.

Other abbreviations.—AOM, amorphic organic matter; CH., chitinozoa; IZ, Ivanye Zolote; LEIO., leiospheres.

Geological setting

Lower Devonian deposits of the Dniester Basin are located on the southwestern margin of the East European Platform (Fig. 1; Nikiforova et al. 1972; Małkowski et al. 2009; Drygant 2010). Their lower part, about 530 m thick, comprises an open marine sedimentary sequence, the Tyver Series (Fig. 2A). This unit is composed mainly of shale and siltstone beds with irregular limestone interbeds and passes upwards into terrigenous, marginal-marine and fluvial facies of the Old Red Sandstone-type referred to as the Dniester Series (Nikiforova et al. 1972; Abushik et al. 1985; Małkowski et al. 2009; Drygant 2010;

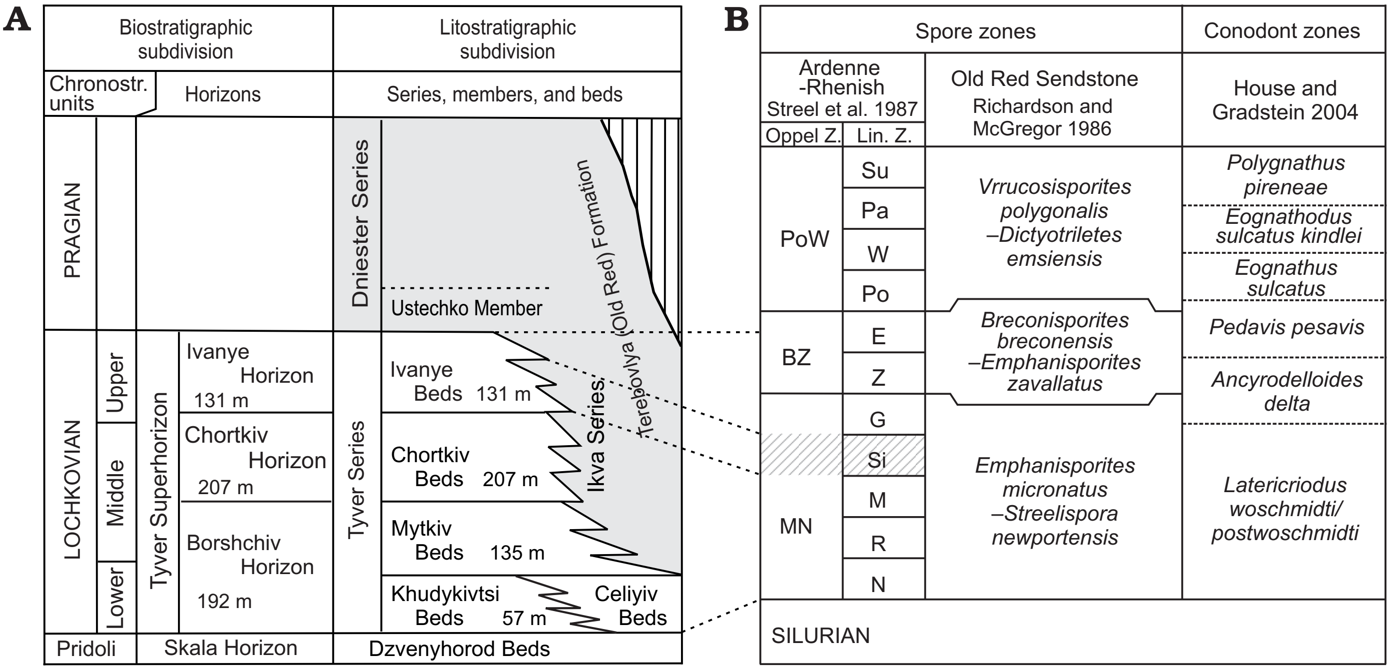


Fig. 2. **A**. Stratigraphical subdivision of the Lower Devonian in Podolia, Ukraine (Drygant 2010). **B**. Correlation of miospore and conodont zonal schemes (see the updated biostratigraphy in Becker et al. 2012). Dashed area on B presents palynostratigraphy; dotted lines—approximate correlation. Abbreviations: BZ, *Breconisporites breconenesis–Emphanisporites zavallatus*; E, *Dictyotriletes emsiensis*; G, *Emphanisporites zavallatus* var. *gedinniensis*; M, *Emphanisporites micrornatus* var. *micrornatus*; MN, *Emphanisporites micrornatus–Streelispora newportensis*; N, *Streelispora newportensis*; Pa, *Camarozonotriletes parvus*; Po, *Verrucosisporites polygonalis*; PoW, *Verrucosisporites polygonalis–Dibolisporites wetteldorfensis*; R, *Chelinospora retorrida*; Si, *Emphanisporites micrornatus* var. *sinuosus*; Su, *Dictyotriletes subgranifer*; W, *Dibolispories wetteldorfensis*; Z, *Emphanisporites zavallatus*; Lin., Lineage; Z., Zone.

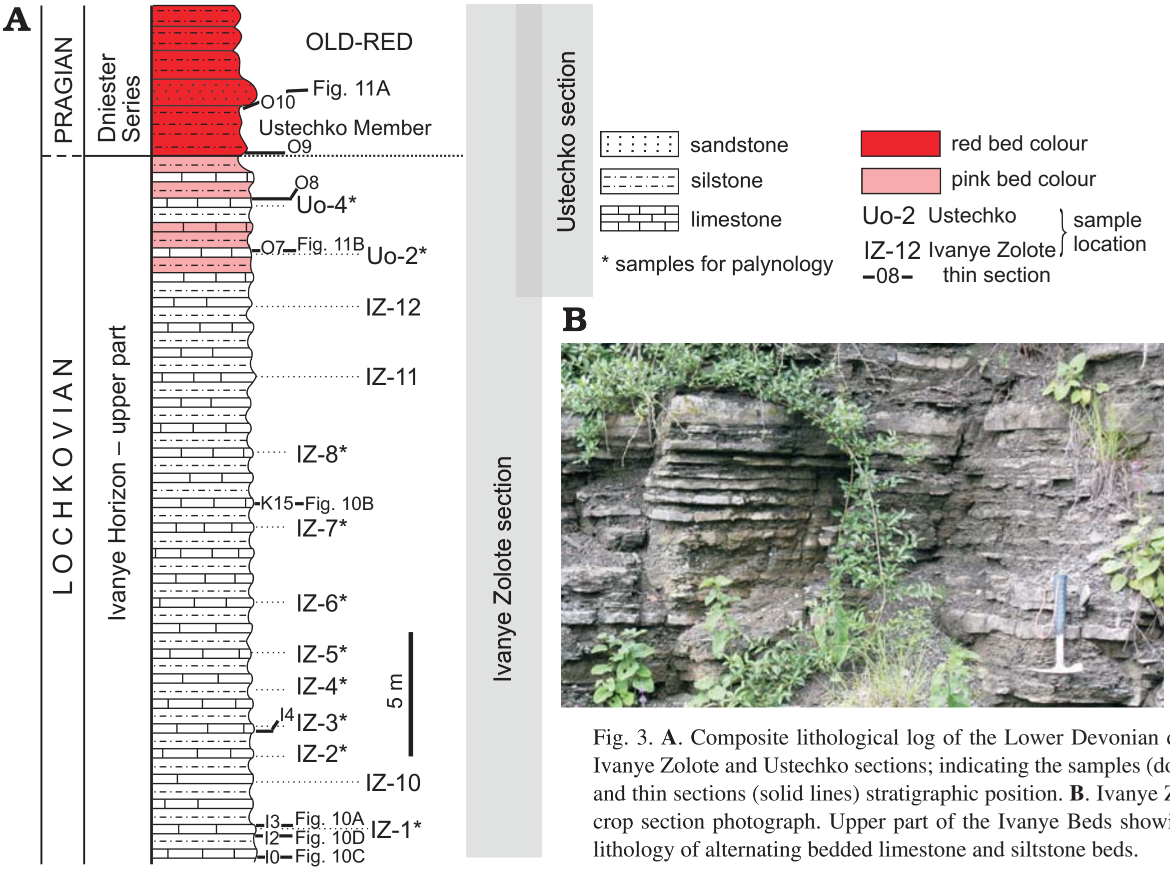


Fig. 3. **A**. Composite lithological log of the Lower Devonian deposits in Ivanye Zolote and Ustechko sections; indicating the samples (dotted lines) and thin sections (solid lines) stratigraphic position. **B**. Ivanye Zolote outcrop section photograph. Upper part of the Ivanye Beds showing typical lithology of alternating bedded limestone and siltstone beds.

Voichyshyn 2011). All the deposits are well exposed at many localities along the Dniester River valley and its tributaries. Their stratigraphy has been based on abundant and diverse invertebrate fossils, abundant fish remains and microfossils, which have been extensively studied since the 19th century (see Kozłowski 1929; Nikiforova et al. 1972; Drygant 2010; Voychyshyn 2011; Olempska 2012; Olempska et al. 2012). The open marine sediments are most probably of Lochkovian age. However, the precise stratigraphic position of their boundary with the overlying red beds of the Dniester Series is still under discussion (Drygant and Szaniawski 2012). The problem is complicated by diachronism caused by gradual shrinking of the marine basin and its shifting toward the west. The Tyver Series is biostratigraphically and lithostratigraphically subdivided into three units: in ascending order, the Borshchiv, Chortkiv and Ivanye horizons and beds (Fig. 2A). Only the uppermost part of the Ivanye Horizon/Beds (ca. 30 m thick) has been sampled for the palynofacies analysis. The youngest marine deposits, passing gradually into the Old Red facies, are well exposed near the village of Ivanye Zolote, and in part also near Ustechko (Fig. 1), at the locality studied by Uchman et al. (2004). The Ivanye Zolote section is ca. 25 m thick, whereas near Ustechko only the uppermost 5 m were available for sampling (Fig. 3). The argillaceous content gradually increases upwards in both of the outcrops. The “calcareous interbeddings” within the uppermost part in fact contain only a small admixture of calcium carbonate. As shown by geochemical analyses (7 samples) of the coeval facies transition at nearby Zalishchyky locality (Fig. 1B; section 58 in Małkowski et al. 2009; Voichyshyn 2011), the $CaCO_3$ content drops upwards from ca. 80% to less than 2%, whilst quartz (SiO_2) and aluminosilicate (Al_2O_3) levels increase simultaneously from ca. 10% and 2% to above 50% and 15%, respectively; total organic carbon (TOC) content for 3 samples is between 0.17 and 0.22% (see details in Racki et al. 2012: SOM 3 and 4).

The diversity and number of macrofossils mostly bivalves, brachiopods, and nautiloids, gradually decrease up the section (Nikiforova et al. 1972; see below). However, most of the microfossils (ostracods, conodonts, scolecodonts, chitinozoans, nematophytes, and prasinophytes) are still abundant, even in the uppermost “calcareous layers” (Fig. 3). Phosphatic fish scales and spines are very abundant, and in some layers fragments of acanthodian jaws are comparatively well preserved (Voichyshyn 2011; Voichyshyn and Szaniawski 2012). The uppermost gray-coloured and marine in origin beds of the Tyver Series can easily be distinguished from the overlying pink or red “Old Red” rocks.

Material and methods

In total, twenty three samples were collected from the two localities. Ten of them were taken mainly from marly limestone layers for the palynological investigation—eight from the

~25 m thick interval of the Ivanye Zolote (IZ) section and two from the ~5 m thick Ustechko section (Fig. 3). An additional ten samples from the Ivanye Zolote section were studied in large-sized (4.5 × 6.5 cm) thin sections. Eight of them represent calcareous layers and two of them represent the Old Red facies (Fig 3). Three additional samples (IZ10–IZ12) have been studied with respect to chitinozoans exclusively.

Standard laboratory procedures for palynological samples containing mineral matter were employed (Wood et al. 1996). Samples were treated using palynological HCl-HF-HCl acid maceration techniques. The organic residue obtained was finally sieved using an 18 μm mesh nylon sieve. At least four slides were prepared from each residue. The preservation of palynomorphs from Ivanye Zolote varies in quality. Some samples are completely weathered (IZ-3), some are partly weathered (IZ-6) but generally the state of preservation of organics in the rest of the samples analysed is good, especially those from the lower part of the section. Generally, microflora derived from the Ivanye Zolote is moderately rich in taxonomically differentiated assemblages of miospores and phytoplankton taxa. Some plant tracheids, scolecodonts, chitinozoans, and arthropod remains were noticed, as well. The worst preserved and less taxonomically differentiated material have been derived from the Ustechko outcrop. Phytoplankton is better represented here but miospores are rare and possess less stratigraphic value. Therefore, those two samples were excluded from further quantitative analyses.

For quantitative palynofacies analyses, each countable kerogen component from the samples from the IZ section was counted for up to 100 specimens. The relative frequency of cryptospores, miospores, acritarchs, chitinozoans, and leiospheres was noted. The remaining slides were examined for the presence of other components that had not been identified in the previously examined portions. Furthermore, occurrences of amorphous organic matter (AOM), miospore tetrads and arthropod remains were noted, as well.

The palynological slides and residues are housed at GIUS. Examination and documentation was done using the Nikon Eclipse 50i transmitted light microscope. The stratigraphically important miospores and phytoplankton taxa are illustrated on Figs. 4, 7; other plant, animal remains, and some chitinozoans are showed on Figs. 5, 8, 9.

Palynostratigraphy

The presence of several characteristic and eponymous species for the Lower Devonian (Table 1) permits to assign the miospore assemblages to the assemblage zones of Richardson and McGregor (1986), and the Oppel and interval/lineage zones of Steemans (1989; Streel et al. 1987; Fig. 2B). The latter division is more detailed and useful for the finer biostratigraphy and therefore will be employed in this paper.

Ivanye Zolote.—Based on the presence of eponymous and characteristic miospore species, the Lochkovian MN Oppel Zone that corresponds to the *Emphanisporites micrornatus*–*Streelispora newportensis* Assemblage Zone has been recognized (Fig. 2B). *Emphanisporites micrornatus* var. *micrornatus* the index species of the NM Oppel Zone is present in the lowermost analysed sample but *Streelispora newportensis* has not been detected in the material analysed. The presence of *Amicosporites jonkeri* in the lowermost sample is also important. According to Steemans (1989), its first appearance marks the base of the Si Lineage Zone (Fig. 2B), attributed to upper Lochkovian, which tentatively corresponds to the *Latericriodus woschmidti/postwoschmidti*–*Ancyrodelloides delta* conodont zones (House and Gradstein 2004); however, Drygant and Szaniawski (2012) dated the upper part of IZ Horizon, according to present zonation, as the *Pedavis gilberti*–*Caudicrodus steinachensis* Conodont Zone (guided by uncommon species *Pandorinellina praeoptima*, *Zieglerodina serrula*, and *Caudicriodus serus*). Microspore species defining the base of the next succeeding palynological zone (BZ Oppel Zone) were not encountered.

The assemblage is moderately taxonomically diverse. Cryptospores are not diverse and represented by ca. 20–40% of all kerogen components. Among miospores the most com-

Table 1. Distribution of some frequent and important spore and phytoplankton taxa in the sections investigated.

SECTIONS		Ivanye Zolote							Ustechko	
PALYNOLOGICAL SAMPLES		1	2	4	5	6	7	8	2	4
SPORES	*Ambitisporites* sp.	●		●					●	
	Amicosporites jonkeri	●		●						
	Apiculiretusispora plicata	●		●	●	●	●			
	Archaeozonotriletes chulus	●	●	●	●		●		●	●
	Artemopyra recticosta	●		●						
	Chelinohilates glabrimarginatus		●	●			●	●		
	Chelinospora retorrida	●		●						
	Cymbohilates pusillius	●								
	Cymbosporites sp.	●		●		●	●			
	Emphanisporites micrornatus var. *micrornatus*	●	●	●				●		
	Emphanisporites neglectus	●		●		●				
	Emphanisporites sp.	●		●		●	●	●	●	●
	Gneudnaspora divellomedia	●	●	●	●	●	●	●	●	●
	Gneudnaspora plicata		●	●		●	●			
	Leonispora argovejae	●								
	Retusotriletes dubiosus	●	●	●	●	●	●	●	●	●
	Retusotriletes triangulatus	●		●	●			●		
PHYTOPLANKTON	*Ammonidium* cf. *A. garrasinoi*	●		●						
	Baltisphaeridium scabrosum		●				●	●		
	Dictyotidium eurydictyotum		●					●		●
	Elektoriskos sp.	●		●	●	●			●	
	Geron gracilis			●	●					
	Geron guerillerus			●						
	Helosphaeridium guttatum	●	●	●	●		●	●	●	●
	Helosphaeridium microclavatum	●	●		●			●	●	
	Leiosphaeridia spp.	●	●	●	●	●	●	●	●	●
	Multiplicisphaeridium cf. *raspa*	●	●	●	●				●	
	Oppilatala cf. *O. vulgaris*	●		●			●			
	Tyligmasoma alargadum		●	●	●				●	●
	Veryhachium trispinosum	●	●	●	●	●		●	●	

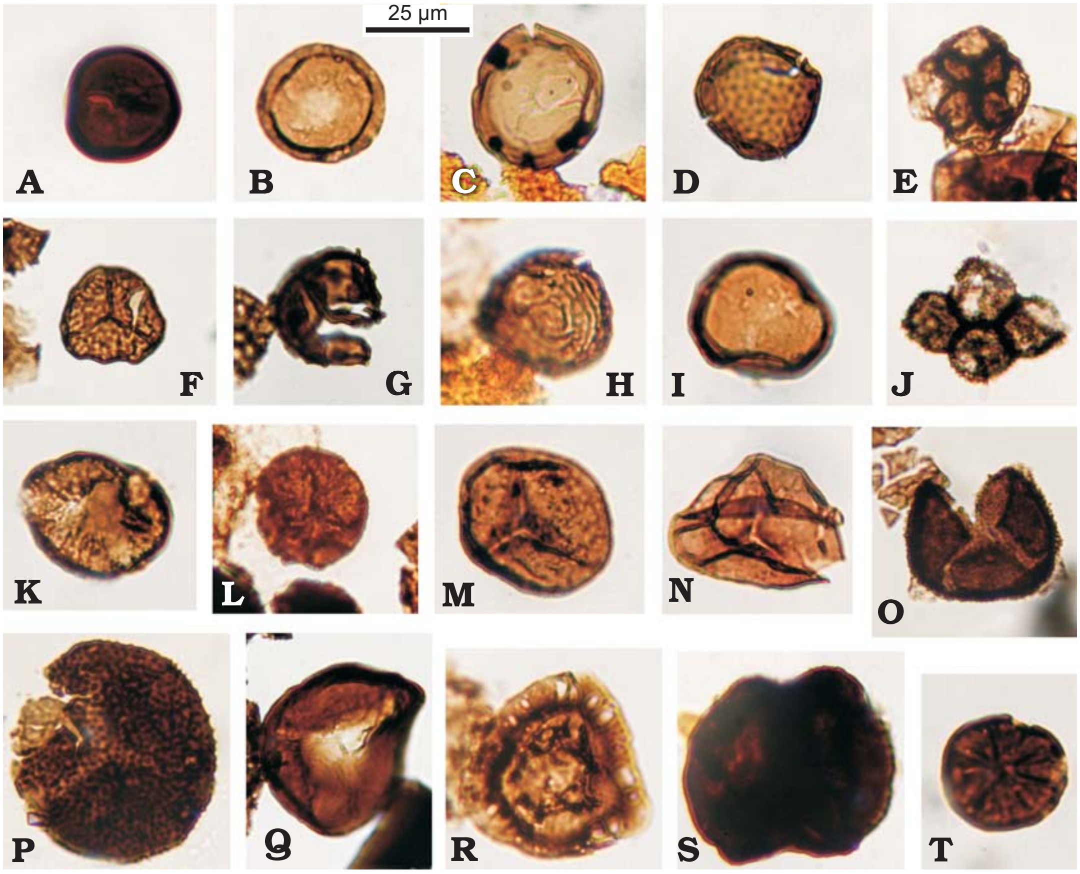


Fig. 4. Miospores from the Ivanye Zolote section. GIUS 4-3592. **A**. *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988; IZ-1 sample. **B**. *Gneudnaspora plicata* (Burgess and Richardson) Breuerr, Al-Ghazi, Al-Ruwaili, Higgs, Steemans, and Wellman, 2007; IZ-4 sample. **C**. *Gneudnaspora plicata* (Burgess and Richardson) BreuerAl-Ghazi, Al-Ruwaili, Higgs, Steemans, and Wellman, 2007; IZ-2 sample. **D**. *Chelinohilates glabrimarginatus* (Turnau and Jakubowska) Turnau, 2003; IZ-7 sample. **E**. *Tetrahedraletes medinensis* (Strother and Traverse) Wellman and Richardson,1993; IZ-4 sample. **F**. *Chelinospora retorrida* Turnau, 1986; IZ-1 sample. **G**. *Leonispora argovejae* Cramer and Diez, 1975; IZ-1 sample. **H**. Unidentified; IZ-8 sample. **I**. *Archaeozonotriletes chulus* (Cramer) Richardson and Lister, 1969; IZ-1 sample. **J**. *Quadrisporites* sp.; IZ-1 sample. **K**. *Emphanisporites* cf. *rotatus* (McGregor) McGregor, 1973; IZ-4 sample. **L**. *Emphanisporites* var. *micrornatus* Steemans and Gerrienne, 1984; IZ-1 sample. **M**. *Retusotriletes triangulatus* (Streel) Streel, 1967; IZ-1 sample. **N**. *Calamospora atava* McGregor, 1973; IZ-1 sample. **O**. *Apiculiretusispora plicata* Allen, 1965; IZ-6 sample. **P**. *Apiculiretusispora spicula* Richardson and Lister, 1969; IZ-4 sample. **Q**. *Amicosporites jonkeri* (Riegel) Steemans, 1989; IZ-1 sample. **R**. *Camptozonotriletes* sp.; IZ-4 sample. **S**. Diad; IZ-4 sample. **T**. *Emphanisporites epicautus* Richardson and Lister, 1969; IZ-4 sample.

monly occurring taxa are *Archaeozonotriletes chulus*, *Cymbosporites* sp., *Retusotriletes dubiosus*, and *R. triangulatus*. Less common are *Apiculiretusispora plicata*, *Chelinospora retorrida*, *Cymbohilates pusillius*, *Emphanisporites neglectus*, and *Leonispora argovejae* (Fig. 4; Table 1). According to Richardson and McGregor (1986), *Apiculiretusispora plicata* is an important miospore for the *E. micrornatus–S. newportensis,* the stratigraphical equivalent for the NM Zone (Fig. 2); moreover, according to Turnau (1986) also important is the presence of *Chelinospora retorrida* which does not extend above the Lochkovian. The stratigraphical range of these taxa is well known from SE Poland (Turnau 1986). Among cryptospores, frequent were: *Artemopyra recticosta*, *Chelinohilates glabrimarginatus*, *Gneudnaspora divellomedia*, and *Gneudnaspora plicata* (Fig. 4). *Quadrisporites,* previously treated as miospore but recently classified as nonmarine or brackish acritarch or algal fossils by Le Hérissé et al. (2009), were noticed as well.

Four of seven samples prepared from the Ivanye section contain a moderately well preserved chitinozoan assemblage comprising *Calpichitina* sp. cf. *C. velata*; *Angochitina filosa*; *Sphaerochitina* sp. aff. *S. densibaculata* (Fig. 5). This poorly diversified assemblage, however, represents species occurring in the upper Lochkovian up to the lowermost Pragian (Paris et al. 2000). Chitinozoan vesicles are compressed, deformed, often with partly destroyed ornamentation and broken spines. The abundance in the studied samples ranges from a several dozens of specimens in the lowermost sample (IZ-1) and decreases up to a few specimens in the upper-lying sample (IZ-5) in the section. Three uppermost samples (IZ-6, IZ-7, IZ-8) were barren of Chitinozoa. The observed pattern of the chitinozoan distribution is also consistent with a frequency pattern in adjacent contemporaneous Early Devonian sequences in Poland (Wrona 1980), Barrandian region (Paris et al. 1981; Chlupač et al. 1985; Chlupač and Hladil 2000), and many other different areas (Paris et al. 2000).

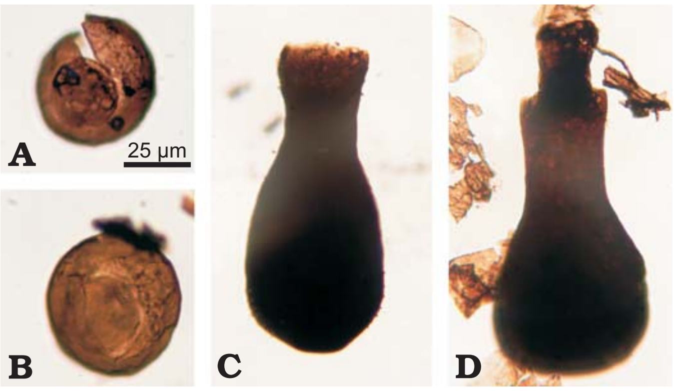


Fig. 5. Chitinozoans from the Ivanye Zolote section, GIUS 4-3592. **A**, **B**. *Calpichitina* sp. cf. *C. velata* (Wrona, 1980); IZ-1 sample. **C**. *Angochitina filosa* Eisenack, 1955; IZ-4 sample. **D**. *Sphaerochitina* sp. aff. *S. densibaculata* Volkheimer, Melendi, and Salas, 1986; IZ-4 sample.

Ustechko.—The land-derived microflora is poorly represented only in the two uppermost samples analysed (Uo-2 and Uo-4; Fig. 3, Table 1). Any important miospores for strict microfloristic horizons were not recognized. The assemblage consists of miospores and cryptospores with broad stratigraphical ranges. Among them such species were recognized as: *Ambitisporites* sp., *Archaeozonotriletes chulus*, *Emphanisporites* sp., *Gneudnaspora divellomedia*, and *Retusotriletes dubiosus* (Fig. 4, Table 1). The lack of eponymous and characteristic taxa precludes assignment to a biozone; the presence of the species mentioned above is rather characteristic for the broad Upper Silurian–Lower Devonian interval (Richardson and McGregor 1986; Rubinstein and Steemans 2002).

Palynofacies from the Ivanye Zolote section

Organic matter preserved in the samples comprises two components: (i) autochthonous, represented by acritarchs, leiospheres, chitinozoans, and scolecodonts, and (ii) allochthonous, represented by miospores and land plant cuticles and tracheids. Animal remains probably belonging to semi-aquatic creatures like eurypterids form the third category. All those particles are mixed and appear in different relative frequency. The proportions of miospores, acritarchs, leiospheres, and chitinozoans are shown in Fig. 6.

Miospores are represented by spores and cryptospores. Their relative proportion ranges from ca. 40% to 80% of all countable components. Cryptospores appear slightly more frequently than spores. The most frequently appearing and important taxa are mentioned in the palynostratigraphic chapter.

Taxonomically differentiated acritarchs are represented by ca. 5% in the IZ-4 sample to over 50% of all countable components in the IZ-2 sample. The assemblage is more differentiated in bottom samples (IZ-1–5; Table 1). Frequently appear acritarchs like: *Baltisphaeridium scabrosum*, *Dictyotidium eurydictyotum*, *Elektoriskos* sp., *Geron gracilis*, *G. guerillerus*, *Helosphaeridium guttatum*, *H. microclavatum*, *Multiplicisphaeridium* cf. *raspa*, *Oppilatala* cf. *Oppilatala vulgaris*, *Riculasphaera fissa*, *Tyligmasoma alargadum*, and *Veryhachium trispinosum* "complex" (see Fig. 7; Table 1). Small acritarchs with short spines (*Helosphaeridium* type) are more frequent in samples from the top of the section (IZ-8).

Prasinophyta are represented by *Leiosphaeridia* spp. Their relative frequency constantly increases, reaching ca. 8% in the upper part of the section. They are more frequently represented in the upper part of the section as compared to its lower part. Chitinozoans, on the other hand, are more frequent in the lower part and nearly absent in the upper part of the section investigated. Their maximum frequency was no-

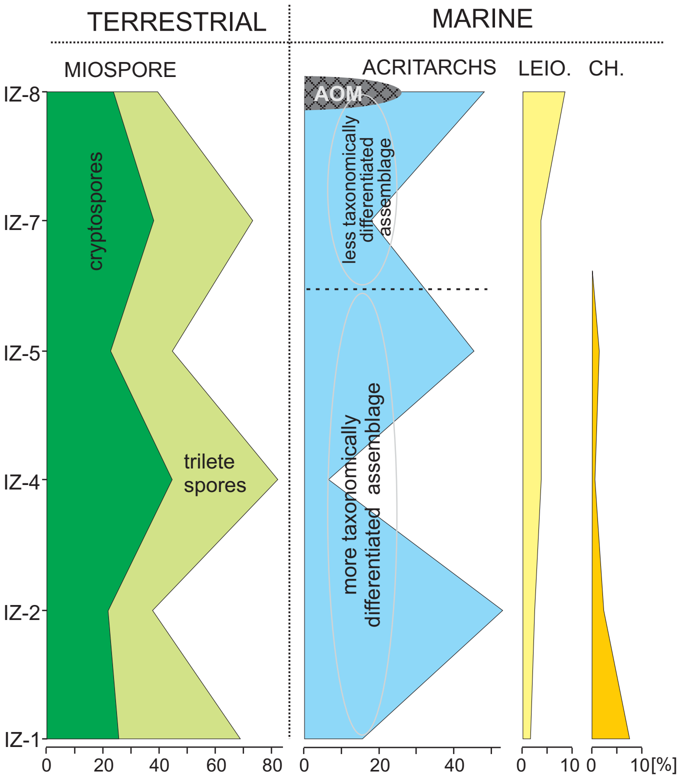
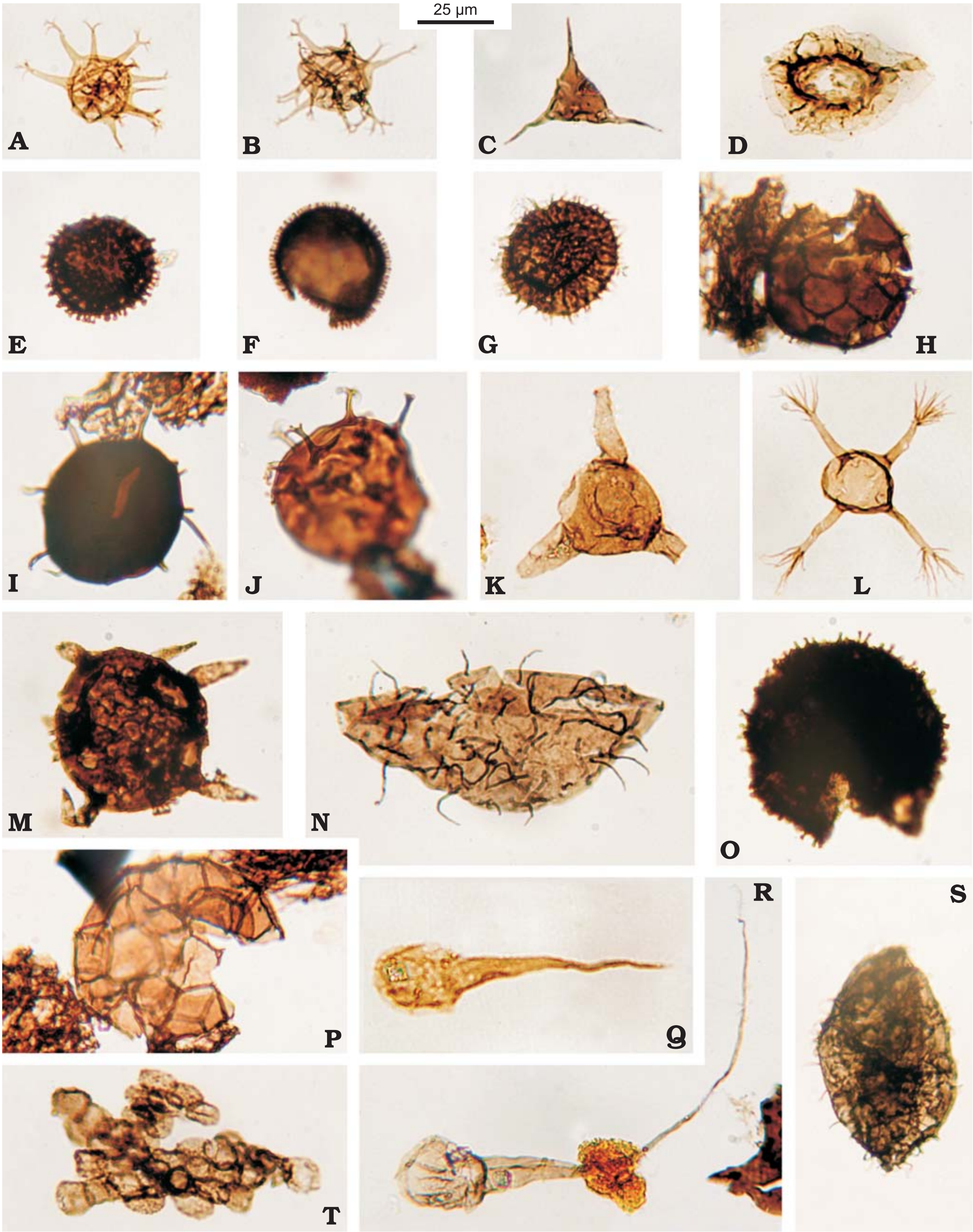


Fig. 6. Percentages of kerogen components in the Ivanye Zolote section. Abbreviations: AOM, amorphous organic matter; LEIO., leiospheres; CH., chitinozoa.

Fig. 7. Phytoplankton from the Ivanye Zolote section. GIUS 4-3592. **A**. *Multiplicisphaeridium* cf. *M. raspa* (Cramer) Wicander, 1986; IZ-4 sample. **B**. *Multiplicisphaeridium* cf. *M. raspa* (Cramer) Wicander, 1986; IZ-4 sample. **C**. *Veryhachium trispinosum* (Eisenack) Deunff, 1954; IZ-4 sample. **D**. *Riculasphaera fissa* Loeblich and Drugg, 1968; IZ-5 sample. **E**. *Helosphaeridium* cf. *guttatum* Playford, 1981; IZ-4 sample. **F**. *Helosphaeridium microclavatum* Playford, 1981; IZ-1 sample. **G**. *Elektoriskos* sp.; IZ-4 sample. **H**. *Dictyotidium eurydictyotum* Kirjanov, 1978; IZ-8 sample. **I**. *Baltisphaeridium scabrosum* Kirjanov, 1978; IZ-8 sample. **J**. *Ammonidium* cf. *A. garrasinoi* Ottone, 1996; IZ-1 sample. **K**. *Tyligmasoma alargadum* (Cramer) →



Playford, 1977; IZ-4 sample. **L**. *Oppilatala* cf. *O. vulgaris* Loeblich and Wicander, 1970; IZ-4 sample. **M**. *Baltisphaeridium* sp.; IZ-1 sample. **N**. *Elektoriskos* sp; IZ-1 sample. **O**. *Helosphaeridium* sp.; IZ-1 sample. **P**. *Dictyotidium eurydictyotum* Kirjanov, 1978; IZ-8 sample. **Q**. *Geron guerillerus* Cramer, 1966 ex Cramer, 1969; IZ-4 sample. **R**. *Geron gracilis* Cramer, 1969; IZ-4 sample. **S**. *Elektoriskos* cf. *E. brevispinosum* Vanguestaine, 1979; IZ-5 sample. **T**. *Synsphaeridium* sp.; IZ-1 sample.

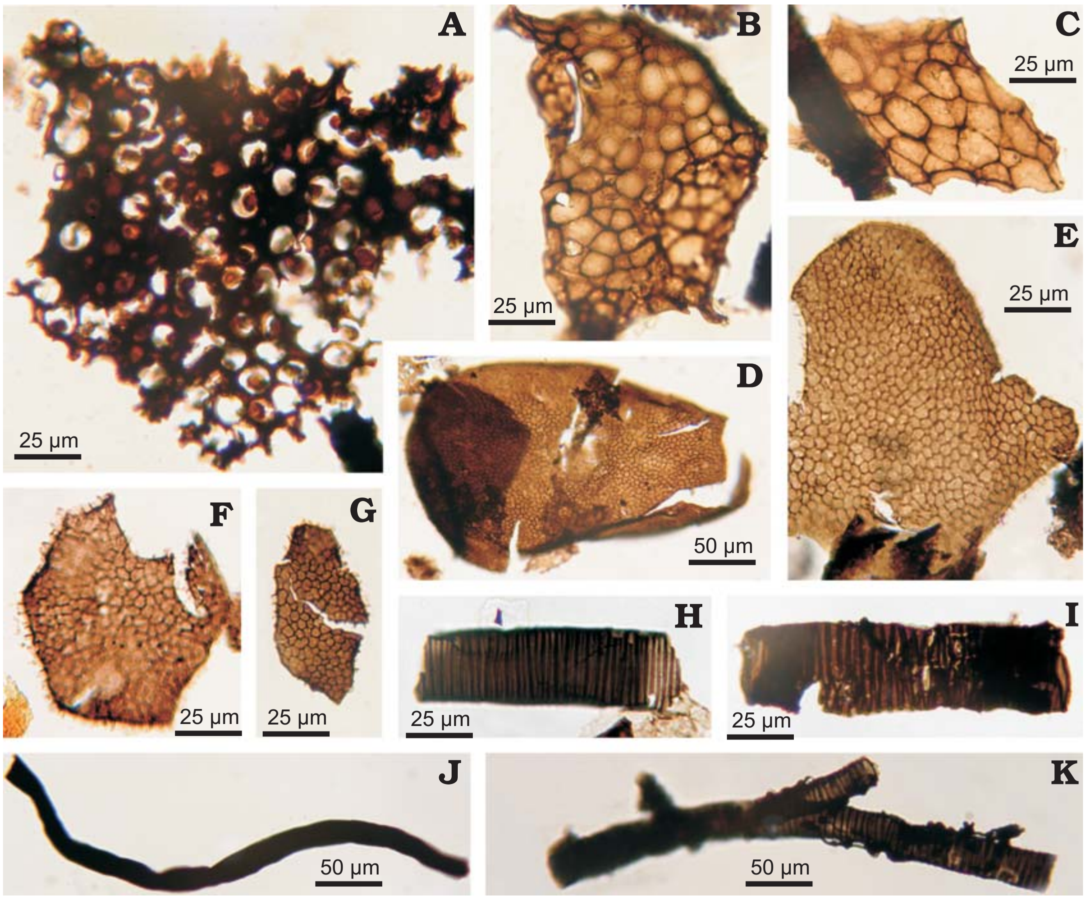


Fig. 8. Plant cuticles and tracheids from the Ivanye Zolote section. GIUS 4-3592. **A**. *Cosmochlaina verrucosa* Edwards, 1986; IZ-7 sample. **B**. *Nematothallus* sp.; IZ-7 sample. **C**. *Nematothallus* sp.; IZ-1 sample. **D**–**G**. *Nematothallus*? like structures. **D**, **E**. IZ-6 sample. **F**, **G**. IZ-1 sample. **H**–**I**. *Porcatitubulus annulatus* Burges and Edwards, 1991. **H**. IZ-5 sample. **I**. IZ-4 sample. **J**. *Laevitubulus* sp.; IZ-1 sample. **K**. *Porcatitubulus annulatus* Burges and Edwards, 1991; IZ-5 sample.

ticed in the IZ-1 sample, reaching ca. 8%. Also scolecodonts, and other animal cuticles, including the parts of eurypterid respiratory organs, accompanied by land-derived plant debris were noticed in the kerogen. The presence of AOM was noticed only in the topmost IZ-8 sample (Fig. 6).

Among plant particles, sheets of enigmatic *Nematothallus* sp. were more frequently noticed than those of *Cosmochlaina* sp. (Fig. 8A–C). Plant tubes and filaments were mainly represented by *Laevitubulus* spp., *Porcatitubulus spiralis*, and *P. annulatus* tissue (Fig. 8H, I, K). Paris and Grahn (1996: pl. 2: 7–9) also documented the presence of *Porcatitubulus* taxa from the Ivanye Beds. Some cuticles were encountered, but none had stomata like those of higher plants. Similar cuticles of enigmatic taxa were recently noticed in the marginal-marine/alluvial clastic Pragian–Emsian deposits from southern Poland (Filipiak 2011; Filipiak and Zatoń 2011).

Animal cuticle remains

The most numerous animal cuticle remains are of arthropod origin well known from the Podolian Upper Silurian to Lower Devonian localities (e.g,. Krzemiński et al. 2010). They are often characteristically folded, possess irregularly distributed pores, setae, and spines, or may be stiffened. In that manner they differ from the associated plant cuticles (e.g., Gensel et al. 1990; see also Filipiak and Zatoń 2011). None of the animal cuticles are found to be associated with any larger diagnostic part of arthropod exoskeleton, so many of them are difficult to be unequivocally assigned to a particular group of arthropod animal. Only some characteristic respiratory organs allow identification as belonging to eurypterids that are known to occur in the strata studied (see Voichyshyn 2011). In transmitted light, the cuticles are translucent yellowish-brown in appearance.

Eurypterid respiratory organs.—These are the most characteristic animal structures present in the material investigated (Fig. 9B–D). They are represented by conical structures (spinules) that usually occur as single individuals (Fig. 9B, C) and very rarely as grouped structures (Fig. 9D). Usually, they are preserved as fragments. The best preserved (?complete) spinule is ca. 175 µm in length and ca. 100 µm in width. Two morphological varieties of spinules are present: (i) conical, with a wide base and narrow top ended with a dis-

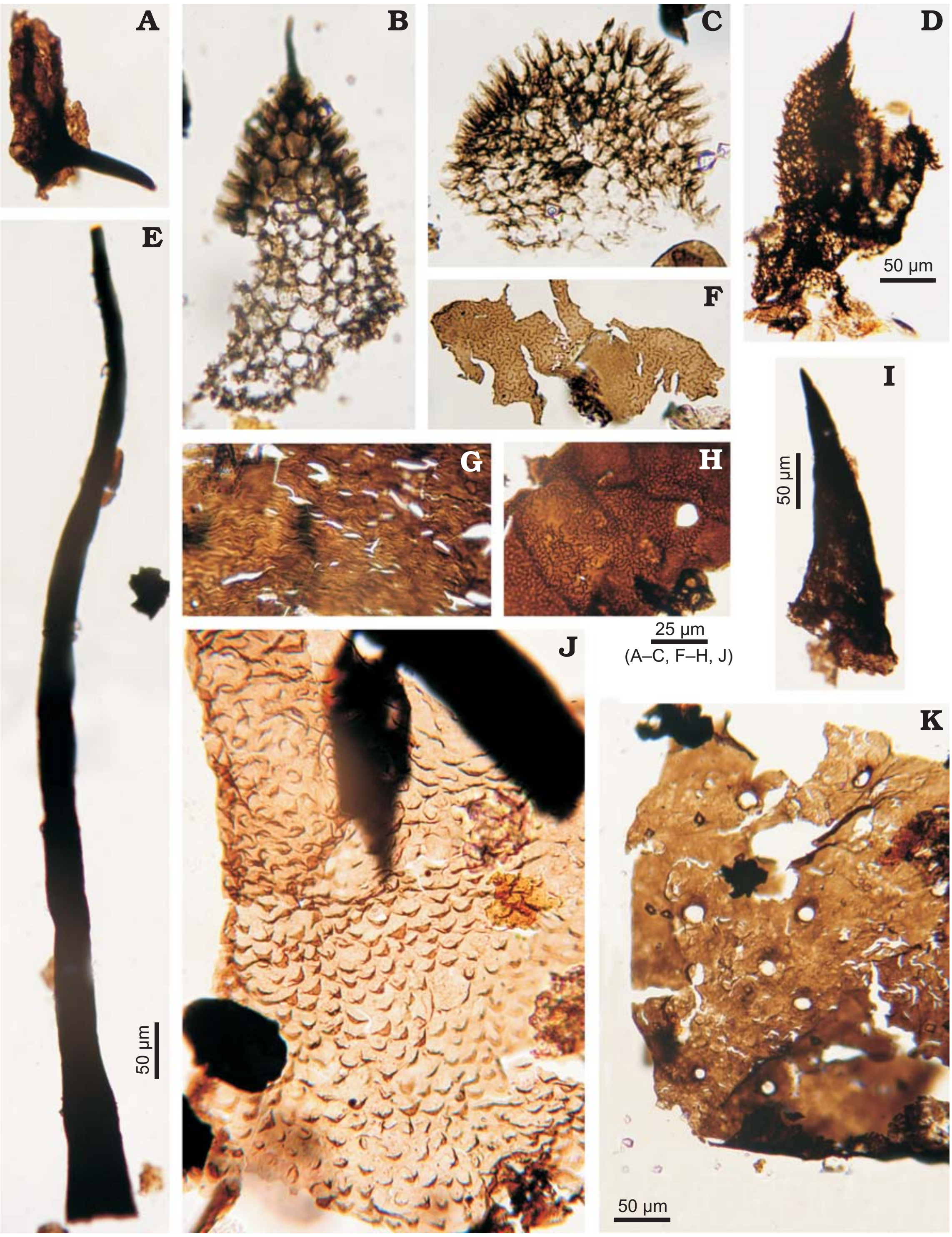


Fig. 9. Animal cuticles, spines and respiratory organs from the Ivanye Zolote section; GIUS 4-3592. **A**. Stiff conical structure of uncertain affinity; IZ-1 sample. **B**–**D**. Eurypterid respiratory organs. **B**. IZ-7 sample. **C**. IZ-4 sample. **D**. IZ-5 sample. **E**. Setae of uncertain affinity detached from cuticle surface; IZ-7 sample. **F**, **H**. Cuticles with meandering structures of possible eurypterid affinity; IZ-5 sample. **G**. Folded cuticle fragment with wrinkles of uncertain affinity; IZ-5 sample. **I**. Structure similar to scorpion claw; IZ-4 sample. **J**. Eurypterid cuticle fragment with crescent-shaped lunules; IZ-5 sample. **K**. Eurypterid cuticle fragment with raised, elliptical openings; IZ-4 sample.

tinct spine (Fig. 9B), and (ii) oval in outline, with well-rounded top devoid of a spine, slowly widening toward its base (Fig. 9C). The entire surface of spinules is covered by thin microscopic cuticular projections, ca. 10 μm in length and ca. 10 μm in width (Fig. 9B, C). The projections are distinctly arranged in groups of six, forming a hexagon that is internally empty (Fig. 9B) (see also Manning and Dunlop 1995; Filipiak and Zatoń 2011).

Our spinules are very similar to those described from Upper Silurian and Lower Devonian by Manning and Dunlop (1995) and Filipiak and Zatoń (2011), and interpreted as eurypterid accessory air-breathing respiratory organs (*Kiemenplatten* or "gill tracts", see Manning and Dunlop 1995 and references cited therein). Those spinules possessing a spine at their top are especially similar to those from the Upper Silurian (Manning and Dunlop 1995). The latter may only differ in having somewhat more robust spines. Those that are spine-less and have rounded top, on the other hand, are most similar to those described recently by Filipiak and Zatoń (2011) from the Lower Devonian of Poland. Although morphologically different, it is not excluded that the both forms of spinules described here may have belonged to the same eurypterid species, as such grouped spinules consisting of both spiny and spine-less forms are known from the Emsian–Eifelian of Saudi Arabia (Breuer 2007).

Eurypterid and ?scorpion cuticles.—The dispersed arthropod cuticle fragments studied have more or less folded surface showing pores, spines and tooth-like projections. However, as all of them are dissociated from the larger diagnostic parts of the exoskeleton and as their ornamentation may differ between different exoskeletal parts (e.g., Wills 1959; Tollerton 1989; Jeram 1994), their unequivocal determination to a specific arthropod group is difficult.

Some of the cuticle remains, however, possess features identical or very similar to other cuticle remains previously illustrated in the literature. Thus, at least some of them may be classified with a greater confidence.

The cuticles having characteristic crescent-shaped foldings (lunules) on the surface (Fig. 9J) can be found in eurypterid (e.g., *Eurypterus*, *Pterygotus*) cuticles illustrated by Clarke and Ruedemann (1912) from the Silurian of the New York State. They were also described and illustrated by Taugourdeau (1967) from Silurian–Devonian of Africa, as belonging to eurypterids. The same concerns the cuticle fragments with distinct raised, elliptical openings (Fig. 9K) presented by Taugourdeau (1967) as true eurypterid cuticles. Structures similar to the latter were also found in the Lower Devonian of Scotland. They were figured, but not discussed further (Wellman 1995). Such structures were also recently described and illustrated by Filipiak and Zatoń (2011) from the Lower Devonian of Poland. The cuticles showing characteristic meandering structures on the surface (Fig. 9F, H) somewhat resemble the cuticle ornamentation present in the eurypterid *Tylopterus* (see Clarke and Ruedemann 1912: 217, fig. 42).

The rest of the cuticles and cuticular structures associated with the eurypterid remains, are equivocal and difficult for confident assignment. They may well belong either to eurypterids, scorpions or even other arthropod groups. They consist of different, more or less folded cuticle remains with or without openings and characteristic wrinkles (Fig. 9G), and setae detached from the cuticle surface (Fig. 9E), as well as long, stiff conical structures pointed distally (Fig. 9A). Such setae and conical structures have already been described and illustrated by Taugourdeau (1967) and recently by Filipiak and Zatoń (2011). These structures could well be either of eurypterid, scorpion or even different arthropod origin. The stiff spiny structure with sharply pointed tip and wide base (Fig. 9I), for example, is somewhat similar to some scorpion claws (e.g., Bartram et al. 1987), but again, a larger diagnostic cuticle fragment attached would be better for more certain assignment.

Cuticles of uncertain affinity

Some of our cuticles are characterised by reticulate, polygonal-like pattern and smooth surface lacking stomata (Fig. 8D–G). In this respect, they are very similar to the plant cuticles classified as *Nematothallus* (Pratt et al. 1978; Edwards 1982; see also Filipiak and Zatoń 2011). It is possible, that the *Nematothallus* cuticles could represent the remains of early liverworts (Graham et al. 2004). However, the similarity of the cuticles investigated here to *Nematothallus* seems to be superficial. The cuticles discussed are stiffer, and have much smaller polygonal, cell-like fields and tiny flanges, well-visible on the cuticle margins (Fig. 8F, G). In most cases, they are delicate, from 2 to 2.5 μm high but sometimes they are completely reduced forming only the flat pattern on the surface. However, the thickness and projection of flanges are uniform in each individual sheet. A regular reticulum with more or less isodiametric, angular units are 3 × 4.5 μm in size, so they are twice as small as in typical *Nematothallus* taxa sensu Edwards (1982; see Fig. 8B, C). Therefore, the systematic position of these cuticle remains is uncertain.

Microfacies of calcareous layers

In the Ivanye Horizon to Ustechko Member transition at Ivanye Zolote, calcareous interbeddings within the mixed carbonate-siliciclastic succession embrace two distinct microfacies types, extremely differing in fossil frequency. The most characteristic are thin (mostly less than 10 cm) coquinas, corresponding to bivalve-ostracod packstone to grainstone (Fig. 10). The frequently sorted shell accumulations show typically a densely-packed biofabric, in places clustered (nesting to stacking sensu Kidwell et al. 1986) or chaotic. These skeletal concentrations rarely display an erosional contact with underlying mudrocks and graded beddingin, and comprise mostly concordantly oriented, convex-upward millimetre-sized disarticulated shells and fragmented, non-micritized valves; larger fossils (above 1 cm) occur only in some debris layers. Silty/sandy and/or peloidal partings are common, paired with plane parallel (rarely, oblique and/or graded) laminations in some layers. Among other skeletal constituents, diverse ichthyolites are most numerous, accompanied by orthocone nautiloids and brachio-

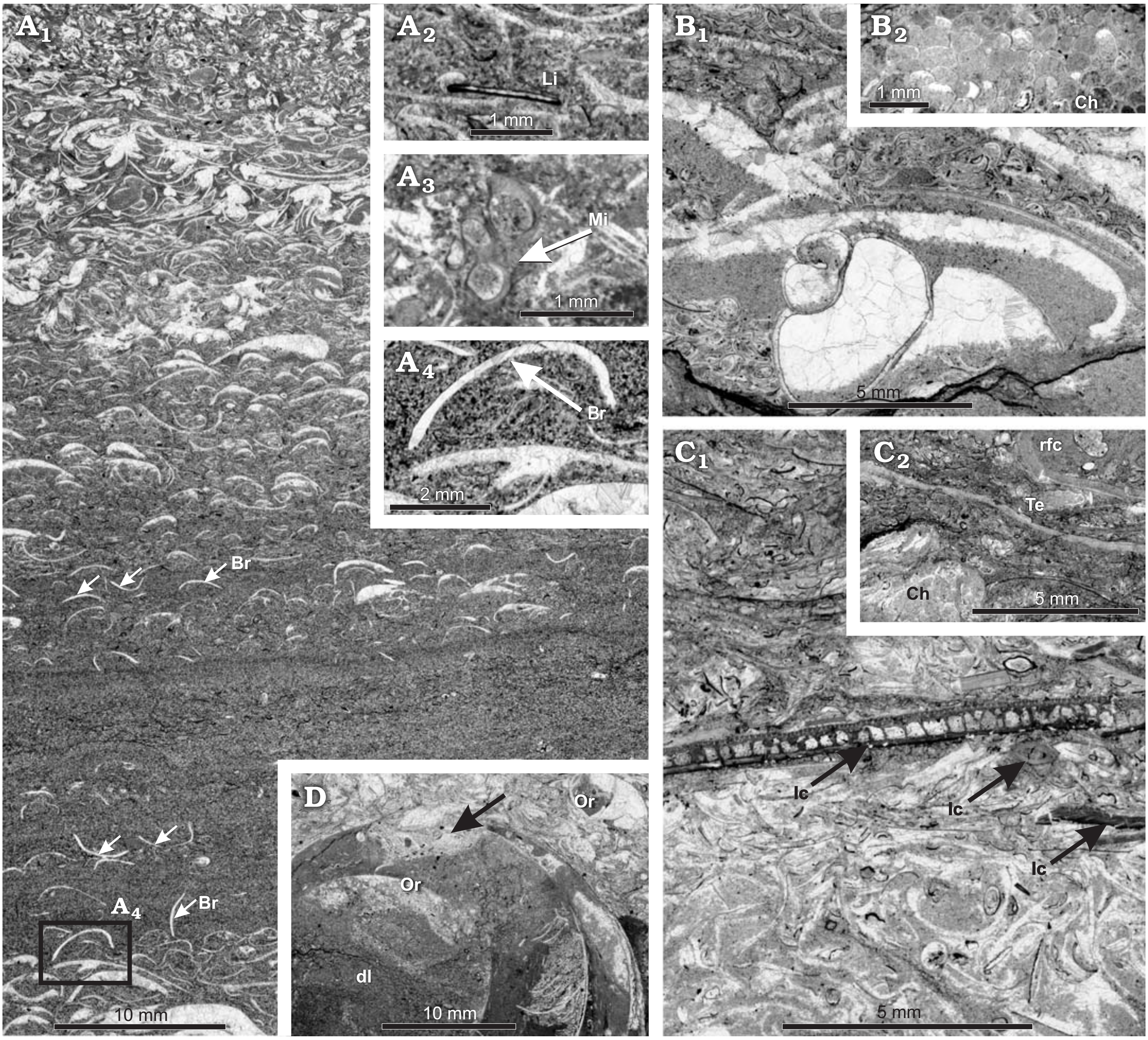


Fig. 10. Lower Devonian bivalve-ostracod bioclastic limestone microfacies of the uppermost Ivanye Horizon, Ivanye Zolote locality (see Fig. 3 for the sample location; compare coeval microfacies details from Ustechko in Uchman et al. 2004: fig. 4). Variable but mostly micrite-dominated peloidal-sandy matrix, and variously packed (stacking in some places) skeletal concentrations of originally aragonitic bivalve valves (as moulds) and largely disarticulated calcitic ostracod shells are most numerous. Note a distinctive graded bedding (normal in the lower part and reversed in the upper half) and plane lamination (**A**, sample I3; close-ups of coquina partings in A_2–A_4), frequent shelter cavities and geopetal infillings (within gastropod shell, **B**; sample K15), as well as iron oxide impregnation of the shelly material (largely ostracods) and ferruginized pressure-solution seam (**B**), and dolomitized internal sediment (dl in **D**; sample I2). Associated skeletal components include diverse ichthyoliths (Ic, arrowed in **C**; sample I0), locally abundant small-sized and smooth articulate brachiopods (Br, arrowed in **A**, note different preservation of brachiopod and bivalve shells in A_4) and orthocone nautiloids (Or, note a broken wall chamber, arrowed in **D**), as well as chaetetid demosponge colonies (cf. Gritsenko et al. 1999; Ch in B_2 and C_2, rfc, radial-fibrous cement), "vermiform" microconchids (Mi in A_3), phosphatic lingulid shells (Li in A_2), and conical ribbed tentaculitids (Te in C_2).

pods (articulates and lingulids), as well as subordinate gastropods, tentaculitids (including putative "vermiform" microconchids), chaetetid sponges and fragmented probable graptolites. In addition, nautiloids and in situ lingulids are abundant e.g., in time-equivalent beds at Zalishchyky.

Calcareous-sandy layers, characterized by variable thicknesses (up to 15 cm), occur in the topmost Ivanye Horizon, and a discontinuous level is found also in the bottom part of red clayey Ustechko Member. Mostly extremely impoverished fossil remains, limited to ichthyolites and poorly-preserved shelly, largely ostracod faunas, occur in the micrite- or sparry-sandy, frequently laminated matrix (Fig. 11).

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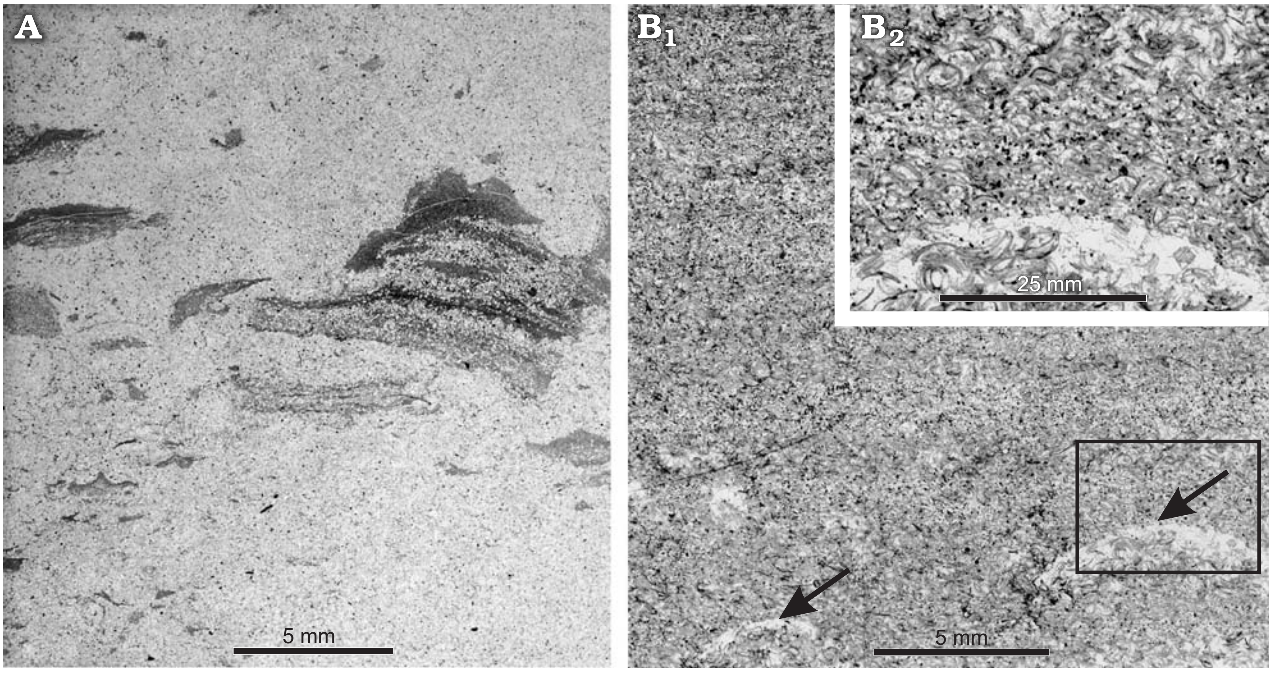

Fig. 11. Lower Devonian sparry-sandy, locally ferruginous microfacies of the topmost Ivanye Horizon (**B**; sample O7) and basal Ustechko Member (**A**; sample O1), Ivanye Zolote locality (see Fig. 3). Note scattered inter-laminated pelitic-sandy intraclasts (**A**), and a single recrystalized pelecypod valves (arrowed) in the faintly laminated packed ostracod microcoquina (B_1; rectangular magnified in B_2).

Palaeoenvironment and paleoecology

Investigated samples from Ivanye Zolote and Ustechko were taken from the Early Devonian marginal marine sequences consisting of carbonates intercalated with siliciclastics. Inorganic geochemical proxies from the correlative uppermost Ivanye Beds at adjacent Zalishchyky section (see above) reveal an overall environmental characteristics close to the regional background (Racki et al. 2012: fig. 8), and suggest mostly progressively clay-dominated, lower-productivity, and well-oxygenated sedimentary conditions up the succession. In addition, a distinctive enrichment trend in light carbon and oxygen isotopes in this locality is explained by a hydrochemical peculiarity and/or early meteoritic diagenetic overprint in an episodically restricted epeiric sea (Małkowski et al. 2009).

The highest calcareous layers in the Podolian succession well illustrate a consequent paleoenvironmental shallowing-upward evolution of the shrinking marine basin, forced by an eustatic sea-level fall (e.g., Walliser 1996: fig. 3), manifested in a recurrent blooming of low-diversity opportunistic shelly benthos only. Progressive fluctuating brackish or even freshwater conditions, suitable for the fish fauna thriving (all major agnathan and gnathostome groups; Voichyshyn 2011: table 1; Voichyshyn and Szaniawski 2012) may be assumed (see summary in Flügel 2004: 618–619), as well as their link with gradual development of the Old Red-type, coastal lagoon to fluvial-estuarine habitats (Uchman et al. 2004). The rock-forming assemblage includes the nuculanid bivalve *Palaeoneilo tschortkovensis* and more diverse ostracods (*Leperditia tyraica* and several species of *Welleriella*, among others; see full faunal lists in Nikiforova et al. 1972: 247–250). In fact, remarkable leperditicopid microcoquinas probably record large populations of detritus-feeding euryhaline arthropods on microbial and/or algal mats developed in tidal mudflats and supratidal marshes, within semi-restricted lagoons, bays or estuarian complexes (Vannier et al. 2001).

Such noteworthy sessile benthic species as the terebratulid brachiopod *Mutationella podolica* (also athyridid *Protathyris*) and chaetetid demosponge *Tiverina vermiculata*, as well actinocerid nautiloid *Ormoceras dobrovljanensis*, and *Tentaculites ornatus* were listed by Nikiforova et al. (1972) and Gritsenko et al. (1999; their *M. podolica* and *T. vermiculata* communities, as updated by Mike Foote in the Paleobiology Database). The most common bivalve *Palaeoneilo* represents mobile infaunal deposit feeders (see Gritsenko et al. 1999), whilst *M. podolica* is well known in the low-diversity, high-dominance suspension-feeder biotas in extremely shallow-shelf habitats ("intertidal" Benthic Assemblages, BA 1–2 of Boucot 1975; compare Kozłowski 1929: 11–14). This endemic species was probably also successful in unstable salinity conditions (as several other Middle Paleozoic "schizohaline" terebratulids; Racki 1988) because it is reported even from the highest calcareous layers in the succession as the only macrofaunal element (Nikiforowa et al. 1972; see the Rhenish biofacies pattern in Boucot 1975: 215–216). In addition, also *Tiverina vermiculata* is seen as a unique colonizer of Siberian hypersaline basins (Dubatolov and Krasnov 1997), and similar euryhaline preferences are postulated for tentaculitoid microconchids (= "vermiform gastropods" of Uchman et al. 2004; see Zatoń and Vinn 2011). Gritsenko et al. (1999: 481) suggest "transition from BA 2, for medium diversity community, through BA 1 for the monospecific unit, to the nonmarine or estuarine vertebrate community".

Nautiloids exemplified the most frequent open marine mobile macrofaunal dwellers, but probably redeposited into the nearshore muddy lagoon due to episodic, both simple and complex storm actions. The recurrent well-agitated conditions are mostly extensively recorded in the bioclast reworking of bivalve shelly banks near carbonate/siliciclastic shoals and barriers, whereas bioturbation was generally minor. Similar upward shift from marginal-marine to fluvial facies was described from the Ustechko succession by Uchman et al. (2004).

Generally, amongst the palynofloral remains, those of land-origin predominate. Spore assemblages are taxonomically moderately diverse comprising ca. 40%–80% of the relative abundance. The other component, phytoplankton, comprises the remaining ca. 20% but sometimes reaches 60% (Fig. 6). Besides palynomorphs, large-sized cuticles and plant tracheids together with organic sheets of *Nematothallus* and *Cosmochlaina* are present, as well. Moreover, some arthropod remains are also present in the material investigated.

The constant presence of acritarchs in the all samples investigated points to marine conditions during sedimentation (e.g., Batten 1996). It is worth to notice the decreasing tendency in taxonomic diversity of acritarchs in the topmost samples what is characteristic for nearshore environments (Dorning 1981). Also interesting is the proportion between the microflora of land-origin (spores and cryptospores) versus phytoplankton (represented mainly by acritarchs), which shows distinct fluctuations (Fig. 6). It can be explained as a result of the sea level changes and/or the presence of some factors influencing macroflora development on a nearby land. Three periods of domination of the land-derived particles (IZ-1, IZ-4, and IZ-7), separated by three periods with phytoplankton increase (IZ-2, IZ-5, and IZ-8) can be distinguished. Interesting is also the constant chitinozoan decrease with simultaneous leiosphaeres increase (Fig. 6). The presence of leiosphaeres is explained as a result of brackish surface water conditions (Tyson 1993). Thus, changes of marine chemistry to more brackish, as noted above, could also be responsible for the decrease of a relative abundance of chitinozoans (Wrona 2009) and an impoverishment of acritarch assemblage at the same time. Symptomatic is also a small dominance of cryptospores over trilete spore taxa (Fig. 6). According to Steemans et al. (2007) crytospores were environmentally more restricted to damp land habitats comparing to trilete spores (see also Wellman et al. 2000).

Generally, the palynofacies described above is characteristic of nearshore environments. In such sedimentary conditions the land-derived organic particles are deposited frequently (e.g., Batten 1996). The presence of large-sized plant tracheids (*Laevitubulus* and *Porcatitubulus*), cuticles of enigmatic *Nematothallus* and *Cosmochlaina*, and abundant miospores and arthropod remains confirm such an interpretation (e.g., Tyson 1993; Batten 1996).

Moreover, large number of phytoclasts (e.g., *Nematothallus*, *Cosmochlaina*, and banded tubes) may suggest the presence of sufficient vegetation on the Early Devonian Ukrainian land, which was a source of perspective food and a temporary shelter for the semi-aquatic eurypterids and maybe even other terrestrial arthropods (see also discussion in Filipiak and Zatoń 2011). It is also obvious, that the Early Devonian macroflora were, to a great extent, spore-producing plants, strongly restricted to moist environments.

Palynological results from the Podolian sections are also consistent with sedimentological factors and comparable with those observed in the neighbouring Silurian–Devonian boundary section in the Barrandian area, Czech Republic (Fatka et al. 2003; Brocke et al. 2006). Moreover, Podolian occurrence of the eurypterid fauna is in accordance with similar purely marine eurypterid faunas known from Scotland, America, Africa, and Europe, where they occur together with other marine biota and well document their marine environmental conditions (e.g., Kjellesvig-Waering 1961; Caster and Kjellesvig-Waering 1964; Kříž et al. 1986).

Conclusions

Palynological investigation indicates the existence of abundant, well-preserved microflora assemblages in the mixed carbonate-siliciclastic Lower Devonian deposits from Podolia, consisting mainly of miospore and phytoplankton taxa. Based on the appearance of characteristic miospores, this assemblage is not older than the NM Oppel Miospore Zone, strictly the Si Lineage Zone (upper Lochkovian) and tentatively corresponds to the *Latericriodus woschmidti/L. postwoschmidti–Ancyrodelloides delta* conodont zones.

The constant presence of acritarch taxa in all samples investigated indicates marine conditions during sedimentation. However, the decreasing tendency in taxonomic diversity of acritarchs in the topmost samples, together with simultaneous disappearance of chitinozoans and increase in leiosphere frequency may indicate a change of environmental conditions from marine toward more brackish ones at the top of IZ section.

Microfacies evolution of stratigraphically highest calcareous layers also well demonstrates progressive shallowing-upward transition from the marginal marine basin to brackish habitats, manifested in recurrent thriving of impoverished, mostly opportunistic and euryhaline benthos and diverse ichthyofauna only. Effective storm and current reworking of bivalve-dominated shelly banks is well recorded in the bioclastic accumulations, widely distributed in the shallowing mud-rich lagoonal environments (compare Uchman et al. 2004).

The association of plant and arthropod cuticles point to the presence of sufficient vegetation on the nearby land, where semi-aquatic eurypterids and other terrestrial arthropods could have found food and temporary shelter in that moist environment.

Acknowledgements

Geoffrey Playford (University of Queensland, Brisbane, Australia), Reed Wicander (Central Michigan University, Mount Pleasant, USA), and Philippe Steemans (University of Liège, Belgium) are thanked for the taxonomic consultation concerning microflora taxa. We are deeply grateful to Elżbieta Turnau (Polish Academy of Science, Cracow, Poland) for her valuable insight into the first version of this manuscript. We warmly thank Daniel Drygant (State Museum of Natural History, L'viv, Ukraine) for introducing us into the field at Podolia. Geoffrey Playford, Claudia Rubinstein (Unidad de Paleopalinología, CONICET IANIGLA, Mendoza, Argentina) and an anonymous referee are acknowledged for valuable remarks and constructive comments. Kyle Freeman (Institute of Paleobiology, Warsaw, Poland) is acknowledged for linguistic improvement of the final version of the text. The research was supported by a grant (No. N N307 057834) from the Ministry of Science and Higher Education to Hubert Szaniawski (Institute of Paleobiology, Warsaw, Poland). This is a contribution related with the UNESCO/IGCP projects no 596 on "Climate change and biodiversity patterns inMid Paleozoic (Early Devonian to Early Carboniferous)" and no 591 on "The Early to Middle Paleozoic Revolution".

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http://dx.doi.org/10.4202/app.2011.0184