

# Benthic ostracods from the Early–Middle Frasnian transition in the north-western East European Platform, Russia

IRINA O. EVDOKIMOVA



Evdokimova, I.O. 2006. Benthic ostracods from the Early–Middle Frasnian transition in the north-western East European Platform, Russia. *Acta Palaeontologica Polonica* 51 (4): 773–788.

Pronounced changes in benthic ostracod associations in the north-west part of the East European Platform, across the Early–Middle Frasnian (Devonian) transition, track a marine transgression event. More than 80 ostracod species belonging to the Eifelian Mega-Assemblage were recorded. Cavellinidae and Acratiidae generally dominate the Early Frasnian Sargaevo Horizon. Middle Frasnian ostracod associations of the Semiluki Horizon are more diverse and are characterised by different dominant both geographically and stratigraphically, resulting from significant palaeo-basin bottom relief and benthic biotope differentiation. The ostracod associations are indicative of very shallow, well oxygenated semi-restricted epeiric environment, with occasional marine influence, alternating with short periods of open shelf conditions. The relative abundance of ostracod species in the different associations, and faunal diversity indices, show considerable variations throughout the Early–Middle Frasnian, and suggest a less restricted position within an intra-platform setting in the Middle Frasnian, relative to a more restricted ostracod habitat in the Early Frasnian. The succession of Early–Middle Frasnian micro-benthic associations within the Main Devonian Field seems to be of a regional scale, and resulted from a marine regression-transgression couplet, corresponding to eustatic cycles I1b–I1c. This was paired with synsedimentary tectonic subsidence in adjacent areas of the north-east East European Platform, progressively improving marine water circulation in the extremely shallow-water shelf seas.

Key words: Ostracoda, palaeoecology, Frasnian, Main Devonian Field, East European Platform, Russia.

Irina O. Evdokimova [Irina\_Evdokimova@vsegei.ru], All-Russian Geological Research Institute (VSEGEI), 74 Srednii Pr., 199026 St. Petersburg, Russia.

## Introduction

In the East European Platform, the recently proposed Early–Middle Frasnian boundary (= beginning of the *Palmatolepis punctata* Zone; Ziegler and Sandberg 2001) is best exposed in the north-eastern part of the region, the Timan-Pechora Province, where it coincides with a conformable transition from pelagic carbonates (with the goniatite *Komioceras*) of the top-most Ust'yarega Formation to argillaceous and siliceous beds of the basal part of the Domanik Formation (Yudina and Moskalenko 1997; Belyaeva and Ivanov 2000; House et al. 2000; Becker et al. 2001). The pronounced facies change is caused by an important regional marine deepening event, which is correlated with the transgressive black-shale Middlesex Event (Becker et al. 1993, 2001; House et al. 2000), and with the base of depopphase I1c of Johnson et al. (1985).

In more shallow-water palaeo-settings this interval is known in the north-west part of the East European Platform (the Main Devonian Field, MDF) and in the central parts of the Platform (the Central Devonian Field, CDF), where it corresponds to the boundary between the Sargaevo and the Semiluki horizons (Rodionova et al. 1995; Ziegler et al. 2000; Ovnatanova and Kononova 2001). In the MDF significant variation in sediments and palaeo-habitats within an

extremely shallow-water epeiric environment are observed (Hecker 1954, 1983; Sorokin 1978; Tikhomirov 1995). According to Zhuravlev et al. (2006), positive and negative  $\delta^{13}\text{C}$  excursions from 2.6‰ to –0.9‰ registered in the early Middle Frasnian in the MDF can be correlated with large-scale biogeochemical perturbations in global carbon cycling (Yans et al. in press). The positive  $\delta^{13}\text{C}$  excursion in the Svinord Beds can be related to the positive anomaly detected in the early *Pa. punctata* Zone in other Laurussian and Chinese shelves (Zhuravlev et al. 2006; Yans et al. in press). The purpose of this study is: (1) to illustrate changes in the benthic ostracod association and to evaluate ostracod faunal diversity across the Early–Middle Frasnian boundary interval in the MDF; and (2) to compare these changes with those in other parts of the epicontinental marine basin spanning the East European Platform at that time.

*Institutional abbreviation.*—PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; all the illustrated specimens under collection No 5128.

*Other abbreviations.*—CDF, Central Devonian Field; EEP, East European Platform; E–MF, Early–Middle Frasnian; MDF, Main Devonian Field; TPP, Timan-Pechora Province.

## Terminology

**Geography.**—The Main Devonian Field (MDF) is a historical name for a large area in the north-west part of the EEP, where the Devonian deposits are exposed. An area with the main natural exposures in the central parts of the EEP along the rivers Don and Oka and their tributaries is historically called as the Central Devonian Field (CDF).

**Stratigraphy.**—According to official definition in the Stratigraphic Code of Russia (Zhamoïda 2006), the horizon is a basic working unit of a regional stratigraphic scale that includes all rocks formed during a definitive time of the geological history of a region (palaeobasin). It is distinguished by its lithostratigraphic and/or biostratigraphic peculiarities. According to the Code, horizon is a chronostratigraphic unit of a regional scale. It serves as a tool for the correlation of the local lithostratigraphic units (formations) within the region and assigning these strata to the standard global units. In the literature, the term “Regional Stage” is often used for “Horizon” (see House et al. 2000; Ziegler et al. 2000; Ovnatanova and Kononova 2001 and others).

The “Beds with geographical names” is a unit ranking below a horizon or subhorizon and distinguishing by its lithostratigraphic and/or biostratigraphic features.

## Material and methods

This study is based on the ostracod material from seven sections and boreholes in the MDF (Fig. 1) collected by the author in 1999–2005. Comparative material comes from the Middle Frasnian strata of the CDF (Semiluki section and Il'men borehole). About 5,500 carapaces and valves were extracted and identified. Ostracod-bearing clay samples have been washed with water, decanted and sieved. Limestone samples were crushed and treated with glacial acetic acid (99–100%, see Coen 1985, and Lethiers and Crasquin-Soleau 1988). After decanting the acid, samples were neutralised with ammonia, then gently washed in running water and sieved. The state of preservation of calcareous specimens varied depending on the extent of matrix recrystallisation.

## Geological setting

The MDF is situated in the north-western part of the EEP within the Latvian Uplift, the Luga and Ladoga Monoclines, and the north-western part of the Moscow Syncline (Fig. 1; see also Zhuravlev et al. 2006). In this palaeo-shelf region, the E–MF strata are represented by an alternation of carbonate and terrigenous sediments containing numerous well preserved brachiopods, ostracods, conodonts, bivalves, echinoderms, and vertebrates (Ivanov et al. 2005; Zhuravlev et al. 2006).

The E–MF stratigraphy of the MDF was constructed during the 1930s by Obruchev (1930) and Hecker (1933). Later

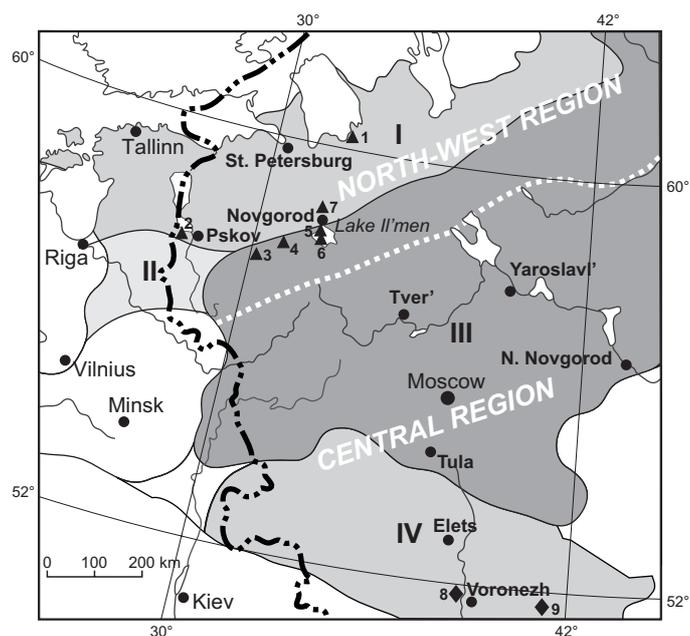


Fig. 1. Overview map of the region: I, Luga and Ladoga monoclines; II, Latvian Uplift; III, Moscow Syncline; IV, Voronezh Antecline; 1, Early Frasnian section in the Syas' River; 2, Early Frasnian section in the vicinity of the town Stary Izborsk; 3, Early–Middle Frasnian section in the town of Porkhov; 4, Early–Middle Frasnian section in the town of Soltsy; 5–7, Early–Middle Frasnian boreholes in the Lake Il'men area; 8, Middle Frasnian section in the town of Semiluki; 9, Early–Middle Frasnian Il'men borehole.

studies added more stratigraphical detail (Hecker 1941, 1954, 1983; Sorokin 1978; Zhuravlev et al. 1997). The E–MF deposits were subdivided into a set of sub-regional units (Beds) based on the lithological features and the distribution of brachiopod- and, partly, vertebrate-associations (Snetnaya Gora, Pskov, Chudovo, Shelon', Svinord, Il'men, Buregi, and Snezha beds). Later the Shelon' Beds representing the E–MF transition strata were subdivided into two units—the Porkhov and the Dubnik beds—separated by a regional unconformity (Hecker 1964). The lower boundary of the Porkhov Beds, corresponding to the base of the Semiluki Horizon, approximates to the proposed substage boundary between the Lower and Middle Frasnian (Ivanov et al. 2005; see also Ziegler et al. 2000). This level is characterised by significant facies and biotic changes as a result of an extensive marine deepening. Lithologically, the sharpest changes are recorded in the central part of the MDF where carbonate deposits of the Porkhov Beds follow terrigenous, often gypsiferous, sediments of the Dubnik Beds. In other parts of the MDF, facies changes are less remarkable and the boundary can be distinguished by faunal changes only (Ivanov et al. 2005; Zhuravlev et al. 2006).

## Previous ostracod studies

Ostracods were first mentioned from the MDF in the 1930–40s. Rare finds of ostracod material were described by Öpik

(1935), Hecker (1939), and Batalina (1941). In the 1950s Devonian ostracod studies in Northwestern Russia were intensified as a result of mapping projects and stratigraphical studies. Polenova (1953), Egorov (1950, 1953, 1954), and Zaspelova (1952, 1959) in their monographic works greatly increased knowledge of ostracod taxonomy and biostratigraphy. However, the stratigraphic chart used at that time for the E–M F transition interval referred only to undivided Shelon' Beds, leading to a lack of knowledge about the exact position of ostracod samples within the sections, and precluding a detailed understanding of the precise stratigraphical distribution of ostracods. Since 1959 no purposeful taxonomical investigations have been performed. In the late 1990s, medium scale mapping in the region promoted the restudy of the main key sections. A large number of new samples were obtained and processed for ostracods, but the results have not yet been published except for some biostratigraphical data and palaeoecological remarks (Zhuravlev et al. 1997; Sokiran et al. 1999; Zhuravlev et al. 1999; Evdokimova 2002). The new material permits a more precise stratigraphical understanding of ostracod taxa, as well as enabling the characterisation of ostracod associations in the E–M F transition (Evdokimova 2002; Ivanov et al. 2005; Zhuravlev et al. 2006).

## Ostracod data and palaeoecological implications

In the Early and Middle Frasnian strata of the MDF ostracods occur almost ubiquitously; however, the state of their preservation and abundance vary considerably (only 58 of 129 samples yielded identifiable ostracods consisting of a minimum of 5 and a maximum of 1130 specimens per sample). The stratigraphical distribution of the 85 identified taxa is shown in Figs. 2–4 and some of them are illustrated (see Figs. 5 and 7–10).

In biostratigraphical context, the E–MF ostracod succession can be subdivided into four faunal intervals (see Zhuravlev et al. 2006). Only two of them, the *Cavellina batalinae* and the *Neodrepanella tricornis* intervals, corresponding to the E–MF transition, are examined in this study.

Generally, the Early and Middle Frasnian ostracod associations under study belong to the Eifelian Ecotype of Becker (in Bandel and Becker 1975; Becker 2000), or using the terminology of Casier (in Casier et al. 2004, 2005), to the Eifelian Mega-Assemblage. They may also be considered as particular cases of the Assemblage I and to a lesser degree the Assemblage II proposed by Casier (1987a; also Casier and Pr at 2003), which are indicative respectively of semi-restricted water conditions and well-oxygenated marine environment above fair-weather wave base. In the Middle Frasnian, the Bairdioidean and Paraparchitoidean ecozone established by Crasquin (1984) can also be recognised.

**Early Frasnian associations.**—In general, ostracods from the Early Frasnian (Snetnaya Gora–Chudovo Beds) are repre-

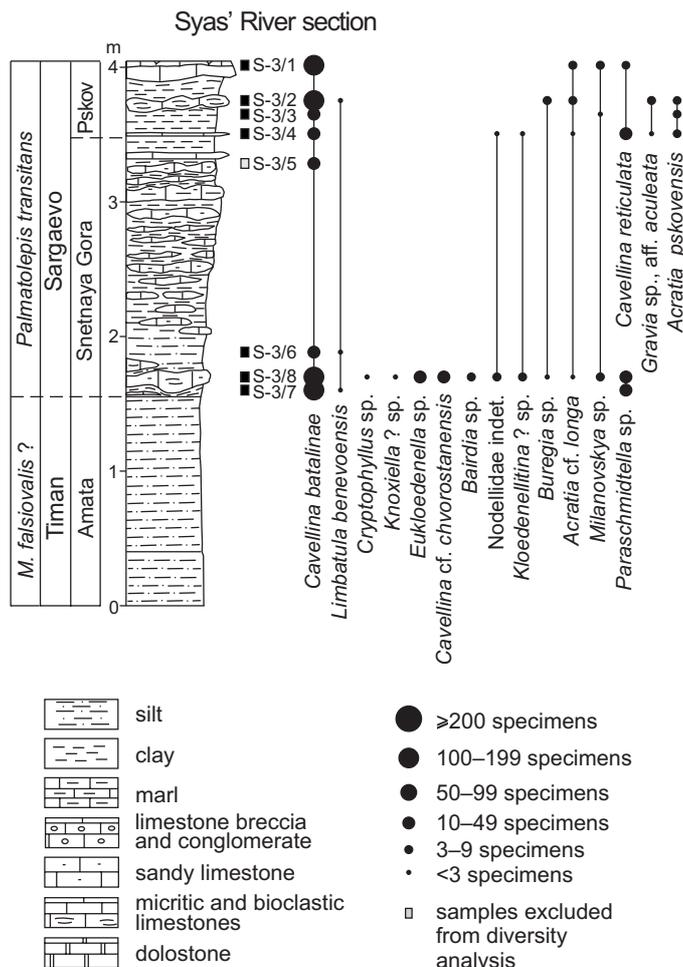


Fig. 2. Stratigraphical distribution of ostracods in the Syas' River section (after Zhuravlev et al. 2005 with additions). Abbreviation: *M.*, *Mesotaxis*.

sented mostly by platycopids, podocopids and less common palaeocopids (Fig. 5). These associations are usually of high abundance and low diversity, and are strongly dominated by *Cavellina batalinae* Zaspelova, 1959, making up 73 to 95% of the relative abundance. They include also *Acratia*, which are dominant in terms of numbers of species. Some palaeocopids (*Amphissites*, *Gravia*, *Limbatula*, *Neodrepanella*) occur sporadically in very small numbers, whilst *Paraschmidtella* and *Buregia* make up to 26% (Syas' River section, Snetnaya Gora Beds; Fig. 2) and 42% of relative abundances (Izborsk Quarry section, Chudovo Beds; Fig. 3) respectively. A reduction in the relative abundance of *Cavellina batalinae* in the last two cases resulted in a higher diversity and seems to indicate a subtle seaward facies shift.

A specific association is found in clays in the lowermost part of the Dubnik Beds (Izborsk Quarry section, Fig. 3). Showing the highest species richness (20), it is dominated by very small-sized thin-shelled palaeocopids *Nodella* aff. *dobroljubovi* Shishkinskaja, 1968 and *Pseudonodella nodosa* Zaspelova, 1952 each with 22% of relative abundance. In somewhat smaller percentages, the platycopids *Cavellina batalinae* (17%), *Knoxiella* "aff. *dubia*" Polenova, 1952 (15%)

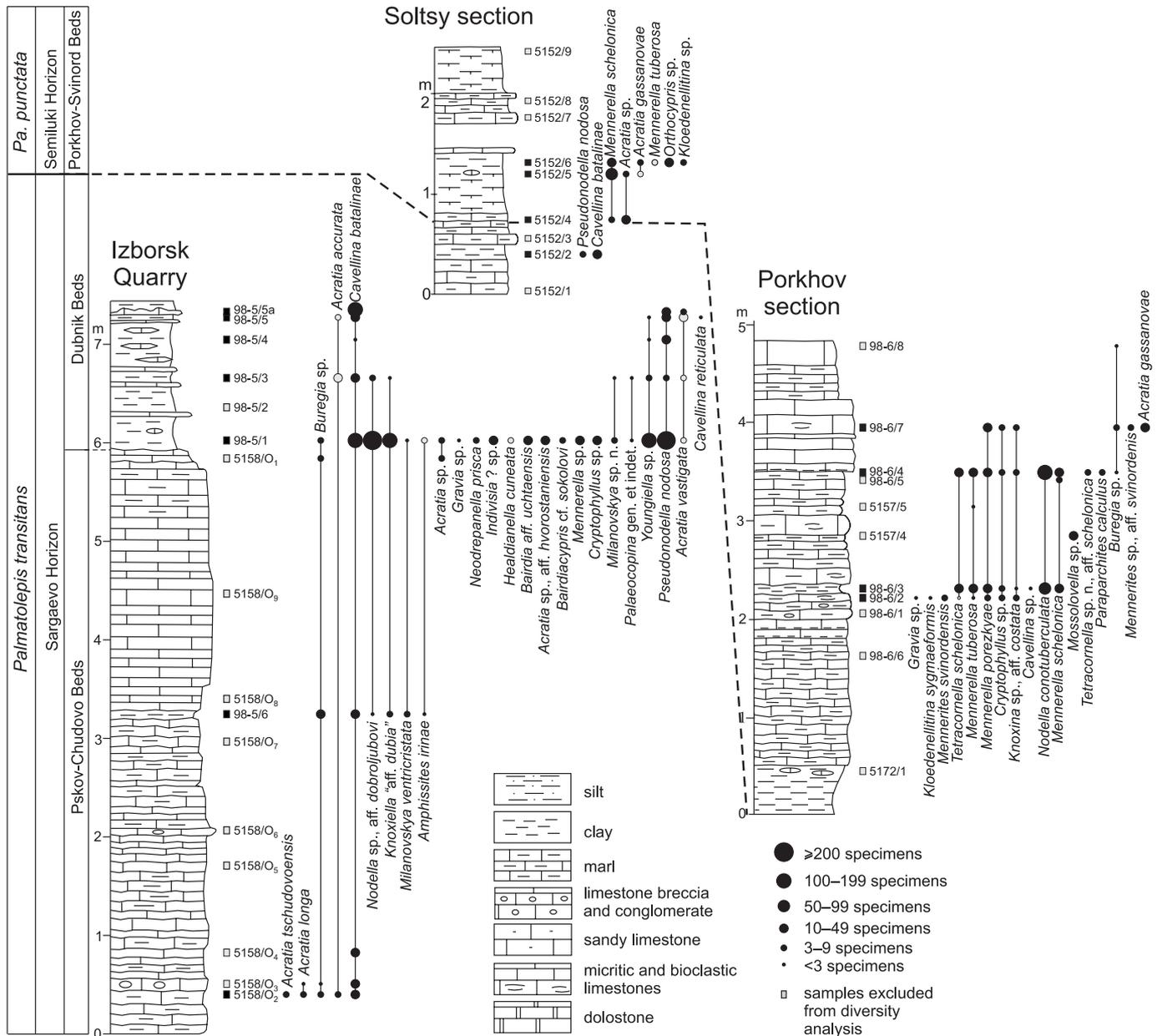


Fig. 3. Stratigraphical distribution of ostracods in the Izborsk Quarry, Soltsy, and Porkhov sections (partly after Ivanov et al. 2005 with additions).

and palaeocopids *Youngiella* sp. (13%) are present. This rather diverse ostracod association suggests a low-energy semi-restricted shelf environment, however, the presence of rare podocopids *Healdianella* cf. *cuneata* Rozhdestvenskaja, 1972, *Bairdiacypris* cf. *sokolovi* (Egorov, 1953), and *Bairdia* aff. *uchtaensis* Egorov, 1953 may indicate the influence of more off-shore marine conditions.

**Middle Frasnian associations.**—The Dubnik-Porkhov boundary is marked by an abundant and diverse Middle Frasnian ostracod association having no species in common with the Early Frasnian one (Figs. 2, 3). This coincides with the onset of a transgressive phase of cycle IIc (see Zhuravlev et al. 2006). The ostracod associations of this interval vary lat-

erally and stratigraphically, resulting from significant biotope differentiation (see Fig. 5).

In clay-rich deposits of low-energy environments the thin-shelled nodellid *Nodella conotuberculata* Zaspelova, 1952 constitutes some 50–60% of relative abundance (Porkhov section, Fig. 3). Other important species in this association are *Tetracornella schelonica* Zaspelova, 1952, species belonging to the genus *Mennerella*, *Knoxina* aff. *costata* (Zaspelova, 1959), and *Mennerites svinordensis* Egorov, 1950. The podocopids *Acrotia gassanovae* Egorov, 1953 occur in small numbers.

One more palaeocopid-dominated association contains *Paraparchites calculus* Zaspelova, comprising up to 30% of relative abundance. Many other species are present, including

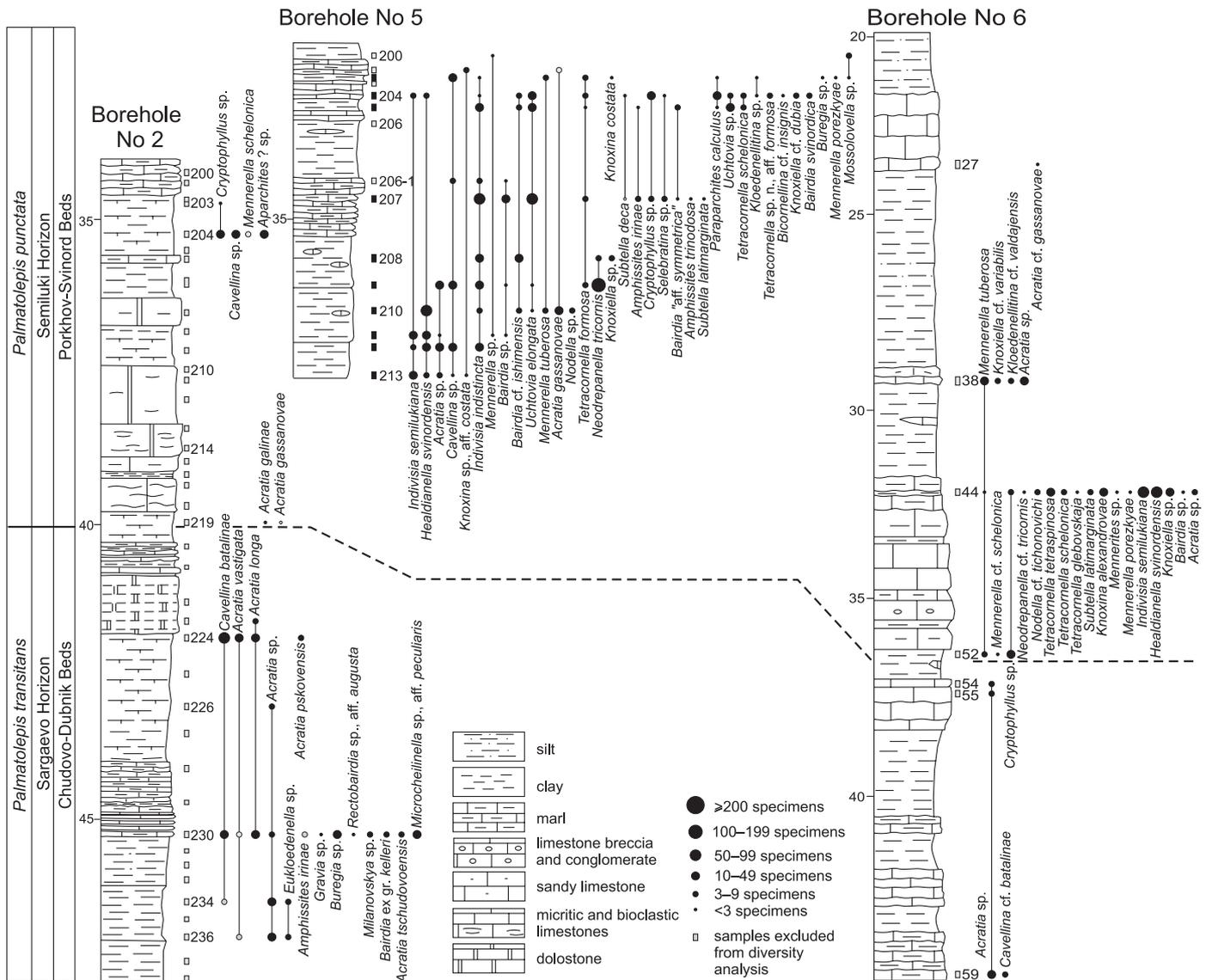


Fig. 4. Stratigraphical distribution of ostracods in boreholes located in the Lake Il'men area (see Zhuravlev et al. 2006).

in order of abundance the platycopids *Uchtovia*, *Indivisia*, *Knoxiiella* as well as the rare palaeocopids *Tetracornella*, *Bicornellina*, and *Subtella*. Infrequent occurrence of podocopids of the genera *Healdianella* and *Bairdia* signifies some influence of more off-shore marine conditions.

In more agitated-water habitats, both podocopids (*Healdianella svinordensis* Zaspelova, 1959) and platycopids (*Indivisia indistincta* Zaspelova in Egorov, 1954, *Indivisia semilukiana* Egorov, 1954, *Uchtovia elongata* Glebovskaja and Zaspelova in Egorov, 1950) are abundant and locally become dominant elements of the associations (Figs. 3, 5). Other genera (*Neodrepanella*, *Nodella*, *Tetracornella*, *Subtella*, *Kloedennellitina*, *Mennerites*, *Mennerella*, *Mossolovella*, *Acratia*, and *Bairdia*) are less common (Zaspelova 1952, 1959; Egorov 1950, 1953, 1954; Evdokimova 2002).

**Diversity indices.**—Biodiversity is commonly measured by a species richness (S), an equitability index (J'), as well as by a

proportional statistics that accounts for the richness and the percent of each species in a biodiversity sample (e.g., Shannon-Wiener index, H') (Stirling and Wilsey 2001). Species richness (S), or the number of species, is the most widely used diversity measure, but it does not take in account the proportion and distribution of each species in a community. Relative species abundance is measured with an equitability or evenness index (J'). Values of this index range from near 0, which indicates low equitability or high single-species dominance, to 1, which indicates equal abundance of all species or maximum equitability. Typically, a community is thought to be more diverse as its equitability score approaches 1. Finally, proportional abundance indices such as the Shannon-Wiener index (H') sum species weighted by their relative abundance. The absolute magnitude of Shannon's diversity index is not particularly meaningful; therefore, it is used as a relative index for comparing different communities. Proportional diversity (H')

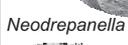
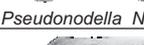
		Ostracod Intervals	DOMINANT GENERA IN OSTRACOD ASSOCIATIONS				
			Izborsk Quarry	Soltsy section	Porkhov section	Lake Ilmen area	Syas' River section
<i>Palmatolepis punctata</i>	Semiluki Horizon	 <i>Neodrepanella tricornis</i>			   <i>Mennerella</i>	     <i>Paraparchites</i> <i>Neodrepanella</i> <i>Uchtovia</i> <i>Healdianella</i> <i>Indivisia</i>	
	Porkhov-Svinord Beds			 <i>Mennerella</i>			
<i>Palmatolepis transitans</i>	Dubnik Beds	 <i>Cavellina batalinae</i>	 <i>Cavellina</i>	 <i>Cavellina Pseudonodella</i>			
	Sargaevo Horizon		  <i>Pseudonodella</i> <i>Nodella</i>			 <i>Acratia</i>	
	Snetnaya Gora-Chudovo Beds		  <i>Buregia</i> <i>Cavellina</i>			 <i>Cavellina</i>	
						 <i>Cavellina</i>	

Fig. 5. Dominant genera in ostracod associations in the Early–Middle Frasnian transition interval in the north-western East European Platform.

is sensitive to both species richness and equitability and is a measure of their joint influence (Stirling and Wilsey 2001). This index is not strongly affected by rare species and is relatively independent of the sample size (see Ishizaki et al. 1993; Stirling and Wilsey 2001).

**Diversity dynamics of the ostracod associations.**—The taxonomical structure of associations and diversity indices show considerable variation throughout the E–MF (Fig. 6). Species richness is highest (16–20 species) in semi-restricted shelf deposits with a low energy regime and presumably normal salinity, as well as in the agitated-water more open-marine bioclastic bar or shoal deposits (Facies B and C, respectively, *sensu* Zhuravlev et al. 2006).

Diversity analysis comparing only the number of ostracod species (S) indicates that in nearly all cases, when micro-benthic associations were similar in terms of species richness, the disproportionate representation of a single species in an association apparently resulted in relatively low equitability (minimum 0.052 for 95% relative abundance as opposed to maximum 0.597 for less than 35% relative abundance of a single species) and, therefore, generally low or moderate diversity

indices (0.163–2.549) for the E–MF ostracod associations in the north-western EEP.

In the Early Frasnian the diversity index varies considerably from low to moderate (Fig. 6). The highest value 1.995 is coupled with a very low equitability (0.284) and occurs in the lowermost Dubnik Beds (Fig. 6). On the whole, the Early Frasnian ostracod associations show low equitability possibly resulting from unstable environmental conditions and fluctuating salinity. This may be responsible for some impoverishment of the ostracod associations.

In the Middle Frasnian the ostracod associations appear to be a little more uniform in composition (Fig. 6) showing a slightly higher equitability upwards through the sequence, which may reflect a gradual stabilisation of the shelf ecosystem and an improved water circulation in the extremely shallow-water basin, due to a progressive deepening trend in the early Middle Frasnian (Zhuravlev et al. 2006). The relatively higher species diversity in the Middle Frasnian is thought to indicate a greater degree of environmental heterogeneity and, consequently, a greater number of micro-benthic niches at that time.

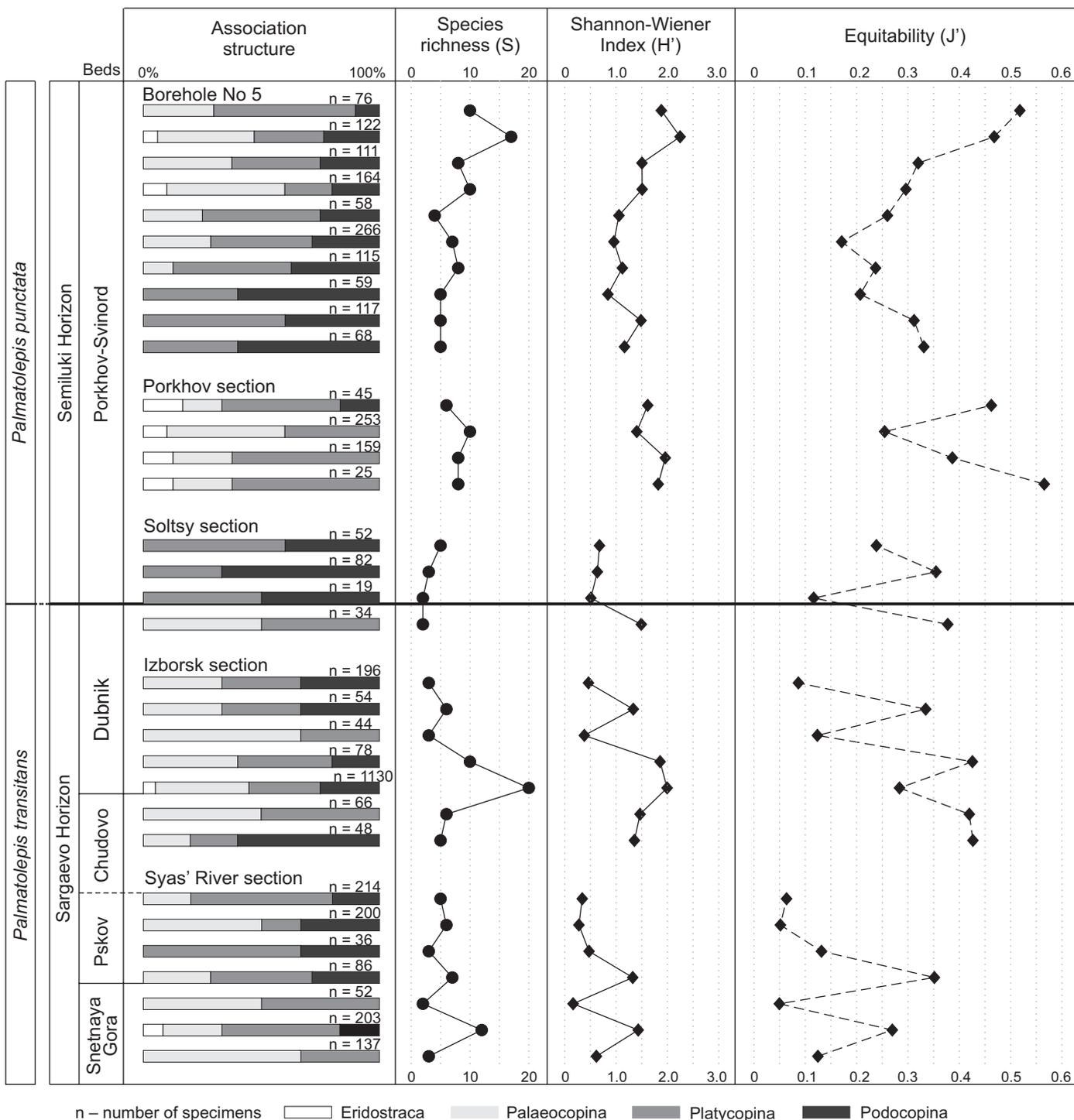


Fig. 6. Structure, species richness, diversity and equitability of the Early–Middle Frasnian ostracod associations.

## Comparison with other East European ostracod associations

**Timan-Pechora Province (TPP).**—In the TPP, the proposed E–MF boundary coincides with the lithological boundary between the Ust’yarega and Domanik Formations. The Ust’yarega Formation of the southern Timan-Pechora

area represents a transgressive system tract terminated by calcarenites above the *Komioceras* Beds, indicating a brief marine shallowing event (House et al. 2000). Locally, in depressions within the carbonate shelf, thin bituminous deep-water deposits of the so-called “domanikoid” facies type occurred. A significant marine deepening event is represented by the commencement of the Domanik Formation deposition, and this correlates approximately with the Middlesex

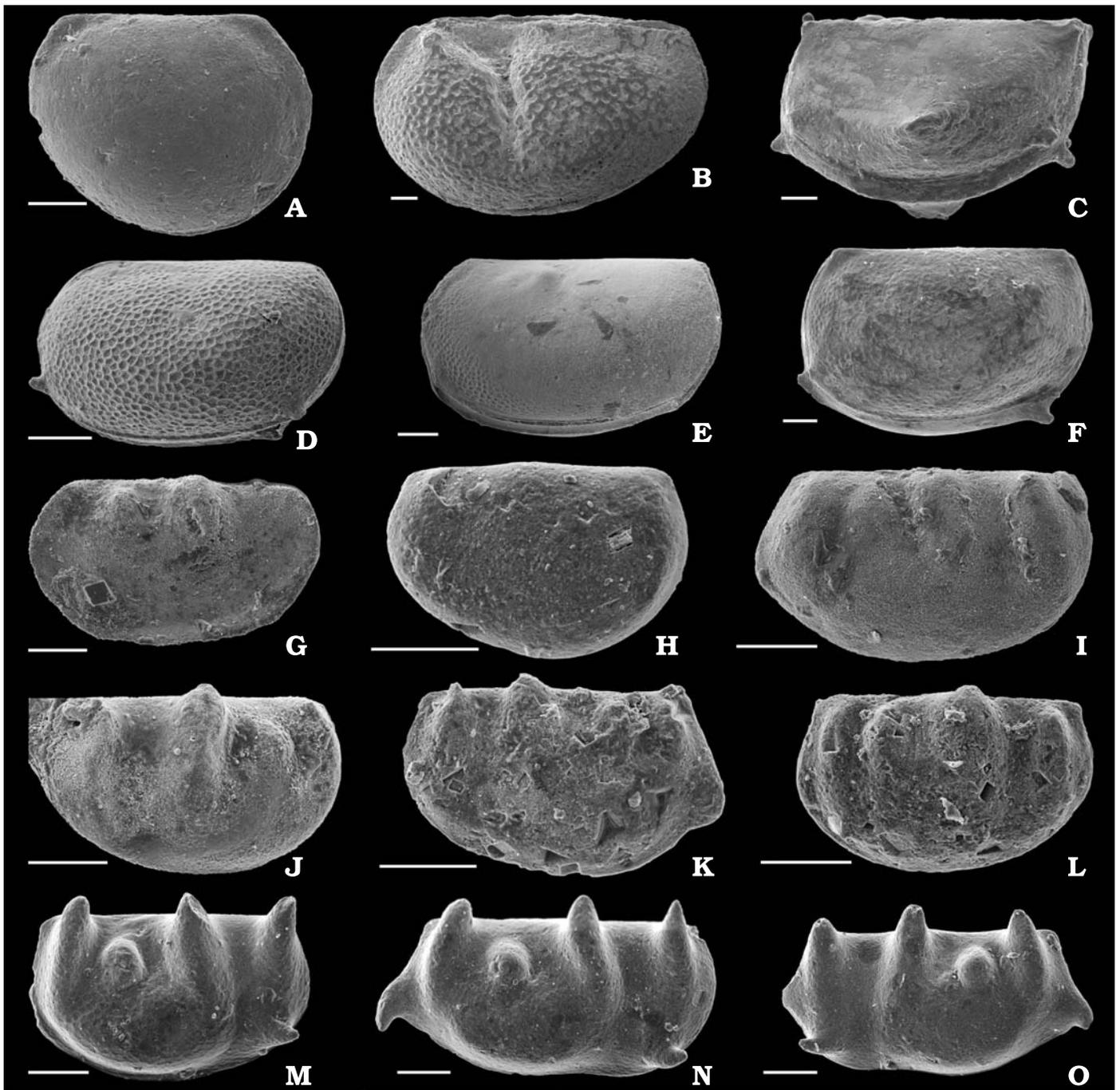


Fig. 7. **A.** *Paraparchites calculus* (Glebovskaja and Zaspelova in Zaspelova, 1959). Tecnomorph right valve PIN 5128/1; MDF, Porkhov section, sample 6/4; Porkhov Beds, *Palmatolepis punctata* Zone. **B.** Palaeocopina gen. et sp. indet. Carapace PIN 5128/2 in left lateral view; MDF, Izborsk Quarry section, sample 5/3; Dubnik Beds, *Pa. transitans* Zone. **C.** *Gravia?* sp. nov. aff. *schallreuteri* Becker, 1970. Carapace PIN 5128/3 in left lateral view; CDF-9/9; Semiluki Horizon, *Pa. punctata* Zone. **D.** *Buregia* sp. Carapace PIN 5128/4 in left lateral view; CDF, Il'men borehole, sample 830; Semiluki Horizon, *Pa. punctata* Zone. **E.** *Buregia* aff. *depressa* Polenova, 1953. Carapace PIN 5128/5 in left lateral view; MDF, Izborsk Quarry section, sample 5158-O2; Chudovo Beds, *Pa. transitans* Zone. **F.** *Buregia* sp. nov. Carapace PIN 5128/6 in left lateral view; CDF, Il'men borehole, sample 849; Semiluki Horizon, *Pa. punctata* Zone. **G.** *Subtella* cf. *deca* Zaspelova 1952. Left valve PIN 5128/7; MDF, borehole No 5, sample i5/207; *Pa. punctata* Zone. **H.** *Pseudonodella* cf. *nodosa* Zaspelova 1952. Right valve PIN 5128/8; MDF, Izborsk Quarry section, sample 5/4; Dubnik Beds, Early Frasnian. **I.** *Nodella* aff. *tichonovichi* Zaspelova, 1952. Male? left valve PIN 5128/9; MDF, borehole No 6, sample 6/44; Porkhov Beds, *Pa. punctata* Zone. **J–L.** *Nodella* aff. *dobroljubovi* Schishkinskaja, 1968. **J.** Right female valve PIN 5128/10; CDF, Il'men borehole, sample 58; Sargaevo Horizon, *Pa. transitans* Zone. **K.** Male right valve PIN 5128/11; MDF, Izborsk Quarry section, sample 5/1; Dubnik Beds, *Pa. transitans* Zone. **L.** Female left valve PIN 5128/12; MDF, Izborsk Quarry section, sample 5/1; Dubnik Beds, *Pa. transitans* Zone. **M–O.** *Nodella conotuberculata* Zaspelova, 1952. **M.** Female left valve PIN 5128/13. **N.** Male left valve PIN 5128/14. **O.** Male right valve PIN 5128/15. MDF, Porkhov section, sample 5157/2; Porkhov Beds, *Pa. punctata* Zone. Scale bars 0.1 mm, except B for which is 0.2 mm.

black shale of New York (House et al. 2000), and the base of the Middle Frasnian (Becker et al. 2001). The development of specific domanikoid facies is related to the existence of rather deep, mostly starved basin settings (House et al. 2000) marked by a strong differentiation of the basin bottom relief (Menner 1989; Kuzmin et al. 1997; House et al. 2000).

In the Ust'yarega Formation, rich associations comprising up to 50 species occur (Yudina and Moskalenko 1997; Kuzmin et al. 1997; Belyaeva and Ivanov 2000). In the lower part of the formation the ostracod fauna is dominated by podocopids and platycopids, and palaeocopids are rare. Upwards through the sequence entomozoids indicative of hypoxic water conditions appear and are dominant in the upper part of the formation (Yudina and Moskalenko 1997).

In the most complete sections, the Domanik Formation is subdivided into three parts. The lower part is characterised by an intercalation of siliceous limestone, bituminous shales, siliceous shales and cherts. There is a complete absence of ostracods, owing to the marked development of anoxic and hypoxic conditions (Belyaeva and Ivanov 2000; House et al. 2000).

In the middle part of the formation there are limestone lenses and entomozoid ostracods such as *Richteria distincta* Polenova, 1955. Higher in the succession, ostracods become more diverse and species belonging to the genera *Nehdentomis*, *Rabienites*, and *Franklinella* occur (Yudina and Moskalenko 1997; Belyaeva and Ivanov 2000).

**Volga-Urals region, Bashkortostan.**—The boundary level coincides with a lithological change between dark bituminous limestones of the Sargaevo Horizon, and alternating bituminous limestones, siliceous shales and cherts of the Domanik Horizon. The Early Frasnian ostracod fauna is diverse and consists of palaeocopids, platycopids, podocopids, and entomozoids with podocopids dominant in terms of species richness (Rozhdestvenskaja 1972: 122, 126, tables 3, 4 therein). The Middle Frasnian fauna is characterised by a new benthic ostracod association and an increase of entomozoid species richness due to the incoming of new taxa. Podocopids are second in terms of diversity. Only two entomozoid species, *Franklinella (F.) jaregae* (Martinova, 1955) and *Richteria scabrosa* Polenova, 1955, crossed the E–MF boundary (Rozhdestvenskaja 1972: 128, table 5 therein).

**Central regions of the EEP.**—In the central parts of the EEP, the E–MF boundary corresponds to that between the Sargaevo Horizon, composed of limestones and dolomites, and the Semiluki Horizon represented mainly by carbonate-clay deposits. The Semiluki Horizon is characterised by greater facies variability (Rodionova et al. 1995; Ziegler et al. 2000).

According to Polenova (1953), the Early Frasnian ostracod associations are of a moderate diversity (9 species) and are dominated by the platycopid *Cavellina* and the podocopid *Acratia*. Rare palaeocopids (*Neodrepanella prisca* Zaspelova, 1952) occur. The Middle Frasnian association is more diversified and characterised by a new composition with the dominance of platycopids and palaeocopids, and subordinate numbers of podocopids (Polenova 1953).

## Review of some ostracod taxa

Some 85 species assigned to 37 genera (see Figs. 5 and 7–10) have been identified. About 30 of these species are endemic to the MDF and CDF, while the remainder are known from other regions of the EEP. This section provides a taxonomic review of the more poorly-known and probably new ostracod species identified. The genera are successively presented in alphabetic order.

***Bairdia* aff. *symmetrica* Egorov, 1953** (Fig. 10N).—This species occurs rarely in the Semiluki Horizon (*Palmatolepis punctata* Zone) in the MDF and CDF. It differs from *Bairdia symmetrica* in having a shorter and higher carapace with a higher anterior end.

***Buregia* sp. A** (Fig. 7D).—This species occurs in the Semiluki Horizon (*Pa. punctata* Zone) in the MDF and CDF. It is distinguished by a distinct adductorial scar, narrow marginal ridges, well-defined antero- and posteroventral spines on the left valve, while the right valve bears only a less pronounced posteroventral spine and no anteroventral one. The position of the two posteroventral spines is at a lower level than the anteroventral spine.

***Buregia* aff. *depressa* Polenova, 1953** (Fig. 7E).—This species is common in the Chudovo-Dubnik beds (*Pa. transitans* Zone). It is most similar to *Buregia depressa* Polenova, 1953 from the *Pa. punctata* Zone (Semiluki Horizon) of the CDF in having a poorly defined adductorial sulcus ( $S_2$ ), distinct marginal ridges and four small spines located nearly symmetrically in pairs, but differs from it in having a more gently curved anteroventral border.

***Buregia* sp. nov. A** (Fig. 7F).—It occurs in the Semiluki Horizon (*Pa. punctata* Zone) in the central regions of the EEP. It differs from other species of *Buregia* in having prominent valve overlap and in bearing a stout posteroventral spine only on the right valve and at a much lower level than the anteroventral spines.

***Cavellina batalinae* Zaspelova, 1959** (Fig. 10H).—This species is abundant in the Sargaevo Horizon (*Pa. transitans* Zone) in the MDF and occurs occasionally in the CDF and TPP. In spite of an unusual for the Cytherelloidea left/right overlap of the valves, this species is assigned to this superfamily and to the genus *Cavellina*. Such the features as an oval lateral carapace outline, the lack of any sulci and ornaments, holosolenic contact of valves, and a key feature—the presence of a limen, separated brood chamber in heteromorphs—are well observable on the mould specimen illustrated in Fig. 10I.

***Cavellina* cf. *chvorostanensis* Polenova, 1953** (Fig. 10G).—This species is common in the Sargaevo Horizon (*Pa. transitans* Zone) in the EEP. This clearly dimorphic species with the left/right overlap of the valves is assigned to the genus *Cavellina* too.

**Gravia? sp. nov. A aff. schallreuteri Becker, 1970** (Fig. 7C).—It occurs in the Semiluki Horizon (*Palmatolepis punctata* Zone) in small numbers. The carapace is large, up to 0.79 mm in length, slightly preplete, with a much larger right valve. A long straight dorsal margin is terminated by a thick spine at the posterior end and by a less distinct spine at the anterior end of both valves, whereas in the type species of *Gravia* (*G. aculeata* Polenova, 1953) dorsal spines occur only on the right valve. Valves are provided with an adventral spur situated midventrally like that in *Gravia schallreuteri* Becker, 1970. Heteromorphs have not been found. This species is distinguished from others assigned to *Gravia* in having antero- and posteroventral spines on each valve like those in the species of *Buregia*. The presence of ventral spines may be a character diagnostic of a new genus. This form cannot be properly defined until heteromorphs are available.

**Knoxiella? dubia Polenova, 1953** (Fig. 9J).—This species is common in the Semiluki Horizon (*Pa. punctata* Zone) in the CDF. The species shows a considerable degree of variability and the specimen figured somewhat differs from those illustrated by Polenova (1953) in having a preplete outline of carapace.

**Knoxina aff. costata (Zaspelova, 1959)** (Fig. 9G).—This species occurs in the Porkhov Beds (*Pa. punctata* Zone) in the MDF. The species differs from *Knoxina costata* (Zaspelova, 1959) in its amplete outline and in having an anterior lobe bearing a straight long ridge that extended down to the anteroventral margin, rather than curved parallel to it.

**Mennerites aff. svinordensis Egorov, 1950** (Fig. 9I).—This species occurs in small numbers in the Porkhov Beds (*Pa. punctata* Zone) in the MDF. Although Egorov (1950) stated a considerable degree of variability in *Mennerites svinordensis*, this species is distinguished from the latter in having an inequivalved carapace with a rather greatly curved ventral margin of the both valves, a posterior lobe bearing a thin straight ridge parallel to the dorsal margin and terminated by a tiny spine, and in lacking anterodorsal spines. Moreover, the ventral ridge is distinct, straight, long and not terminated by a spine.

**Neodrepanella aff. parva Zaspelova, 1952** (Fig. 8S).—It occurs in the Semiluki Horizon (*Pa. punctata* Zone) in the CDF. It differs from *N. parva* Zaspelova, 1952 in its elongate outline.

**Nodella aff. tichonovichi Zaspelova, 1952** (Fig. 7I).—This species occurs in the Porkhov Beds (*Pa. punctata* Zone) of the MDF in small numbers. It differs from *Nodella tichonovichi* Zaspelova, 1952 in having more diffuse lobes.

**Nodella aff. dobroljubovi Schishkinskaja, 1968**.—This species occurs in the *Pa. transitans* Zone of both the MDF and CDF (Fig. 7J–L). This tiny species (less than 0.4 mm) is similar to *Nodella dobroljubovi* Schishkinskaja, 1968 from the *Pa. transitans* Zone of the CDF in its L/H ratio and by lacking a carinate ridge and a spine on posterior lobe ( $L_4$ ). It differs from *N. dobroljubovi* in having a somewhat more distinct anterior ( $L_1$ ) and preadductorial ( $L_2$ ) lobes.

**Nodella conotuberculata Zaspelova, 1952** (Fig. 7M–O).—This species is very abundant in the Porkhov Beds (*Pa. punctata* Zone) of the MDF. Described originally as subspecies, *Nodella conotuberculata* and *N. conotuberculata* “var. *ansula*” are considered to be dimorphs with a peculiar “nodellid” dimorphism (see Becker 1968a, 1968b, 1998; herein Fig. 7M, N). Noteworthy is the specimen illustrated in Fig. 7O. Being an exact double of *N. conotuberculata* (Fig. 7N), it demonstrates a marginal process at the posterior end of the carapace in addition to the hamus situated anteriorly.

**Palaeocopina gen. et sp. indet.** (Fig. 7B).—It occurs in small numbers only in the Dubnik Beds (*Pa. transitans* Zone) in the Stary Izborsk Quarry. The carapace is very large, up to 2.95 mm in length and 1.75 mm in height, preplete, slightly pinched dorsally, with a long straight dorsal margin. The right valve is slightly larger than the left one. A very long and deep adductorial sulcus extends almost down to the ventral margin. A preadductorial lobe ( $L_2$ ) is not developed. A thick spine occurs on each valve anterodorsally. The surface is reticulated. The morphology of the figured, presumably male, specimen may be compared with that described for the genus *Pseudoleperditia* Schneider, 1956 in its preplete outline, large carapace,

Fig. 8. A–C. *Tetracornella tetraspinosa* Zaspelova, 1952. A. Male left valve PIN 5128/16; sample 6/4; Porkhov Beds, *Palmatolepis punctata* Zone. B. Male left valve PIN 5128/17; borehole No 5, sample i5/202; Porkhov Beds, *Pa. punctata* Zone. C. Female right valve PIN 5128/18; Svinord Beds, *Pa. punctata* Zone. D, E. *Tetracornella?* sp. nov. A. Female carapaces PIN 5128/19 and PIN 5128/20 in left and right lateral views; CDF, Il'men borehole, sample 67; Semiluki Horizon, *Pa. punctata* Zone. F. *Tetracornella formosa* Zaspelova, 1952. Female left valve PIN 5128/21; MDF, borehole No 5, sample i5/205; *Pa. punctata* Zone. G, H. *Tetracornella* cf. *glebovskaja* Zaspelova, 1952. G. Female left valve PIN 5128/22; MDF, Porkhov section, sample 98-6/3; Porkhov Beds, *Pa. punctata* Zone. H. Male left valve PIN 5128/23; MDF, Porkhov section, sample 98-6/4; Porkhov Beds, *Pa. punctata* Zone. I, L. *Tetracornella schelonica* Zaspelova, 1952. I. Female right valve PIN 5128/24; MDF, Porkhov section, sample 98-6/4; Porkhov Beds, *Pa. punctata* Zone. L. Female left valve PIN 5128/25; MDF, borehole No 6, sample i6/44; *Pa. punctata* Zone. J, K. *Tetracornella* sp. nov. B aff. *schelonica* Zaspelova, 1952. J. Female right valve PIN 5128/26; MDF, borehole No 6, sample i6/44; *Pa. punctata* Zone. K. Female right valve PIN 5128/27; MDF, Porkhov section, sample 98-6/3; Porkhov Beds, *Pa. punctata* Zone. M–O. *Neodrepanella tricornis* (Batalina, 1941). M. Carapace PIN 5128/28 in left lateral view; MDF, borehole No 5, sample i5/209; Porkhov Beds, *Pa. punctata* Zone. N, O. Right valves PIN 5128/29 and PIN 5128/30; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. P. *Neodrepanella gnedensis* Zaspelova, 1952. Right valve PIN 5128/31; MDF, Porkhov section, sample 98-6/4; Porkhov Beds, *Pa. punctata* Zone. Q, R. *Neodrepanella tichomirovi* Zaspelova, 1952. Right and left valves PIN 5128/32 and PIN 5128/33; CDF, sample CDF-9/9; Semiluki Horizon, *Pa. punctata* Zone. S. *Neodrepanella* aff. *parva* Zaspelova, 1952. Carapace PIN 5128/34 in left lateral view; CDF, Il'men borehole, sample 49; Semiluki Horizon, *Pa. punctata* Zone. T. *Neodrepanella* cf. *prisca* Zaspelova, 1952. Left valve PIN 5128/35; MDF, Izborsk Quarry section, sample 5/1; Dubnik Beds, *Pa. transitans* Zone. U. *Neodrepanella* sp. Right valve PIN 5128/36; MDF, Koloshka River, Svinord Beds, *Pa. punctata* Zone. Scale bars 0.1 mm. →

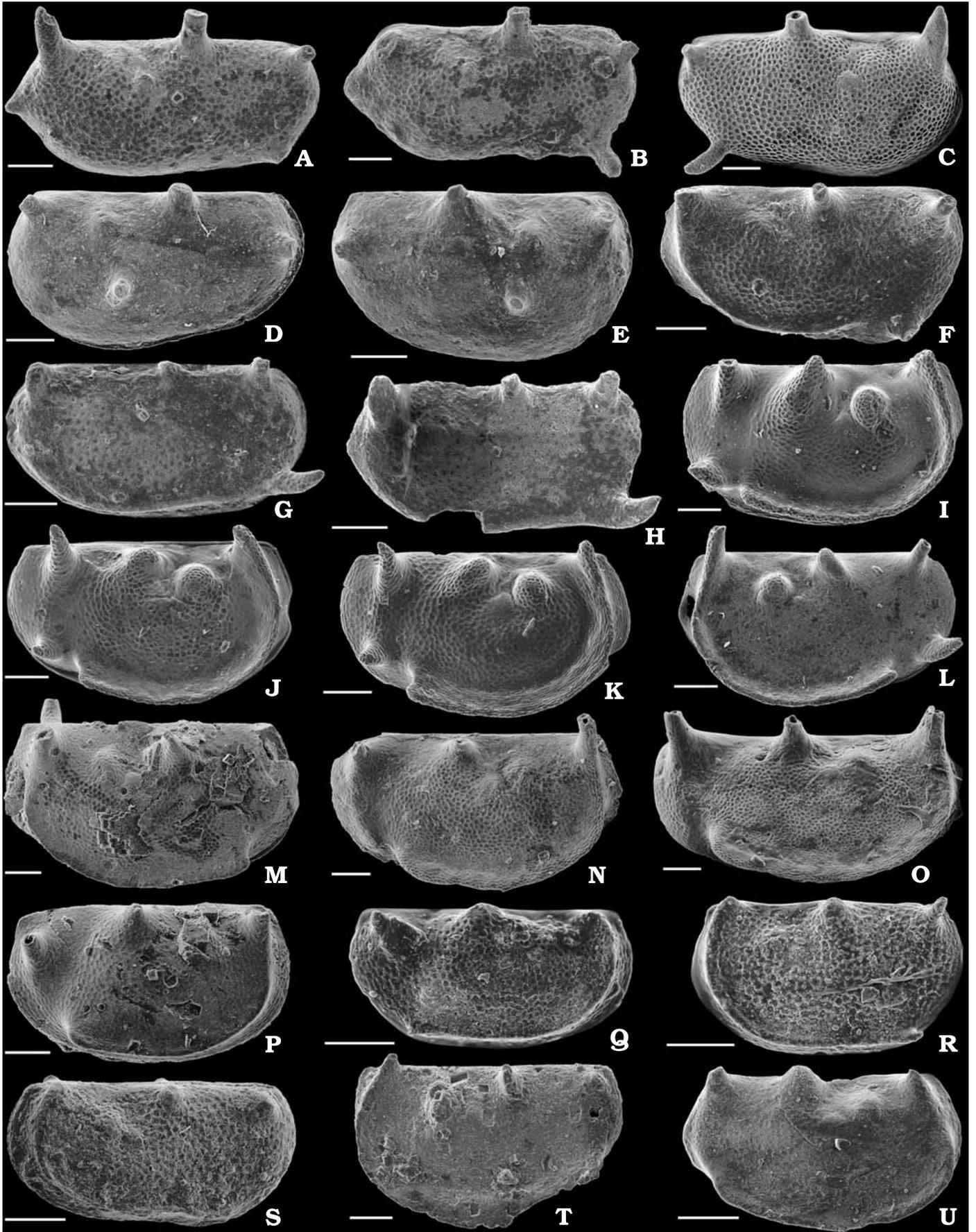




Fig. 9. **A.** *Eukloedenella* sp. Tecnomorph carapace PIN 5128/37 in left lateral view; MDF, Syas' River, sample S-3/8; Snetnaya Gora Beds, *Palmatolepis transitans*? Zone. **B.** *Milanovskya* cf. *ventricristata* Zaspelova, 1959. Tecnomorph carapace PIN 5128/38 in left lateral view; MDF, Syas' River, sample S-3/8; Snetnaya Gora Beds, *Pa. transitans*? Zone. **C.** *Milanovskya bicornis* Glebovskaja and Zaspelova in Egorov, 1950. Tecnomorph carapace PIN 5128/39 in left lateral view; CDF, sample CDF-9/9; Semiluki Horizon, *Pa. punctata* Zone. **D.** *Indivisia semilukiana* Egorov, 1954. Heteromorph carapace PIN 5128/40 in right lateral view; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. **E.** **F.** *Knoxina* cf. *alexandrovae* (Egorov, 1950). **E.** Tecnomorph left valve PIN 5128/41; MDF, borehole No 6, sample i6/44; *Pa. punctata* Zone. **F.** Tecnomorph right valve PIN 5128/42; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. **G.** *Knoxina* aff. *costata* (Zaspelova, 1959). Tecnomorph carapace PIN 5128/43 in left lateral view; MDF, borehole No 5, sample i5/201; Porkhov Beds, *Pa. punctata* Zone. **H.** *Mennerites svinordensis* Egorov, 1950. Tecnomorph left valve PIN 5128/44; MDF, Koloshka River, Svinord Beds, *Pa. punctata* Zone. **I.** *Mennerites* aff. *svinordensis* Egorov, 1950. Tecnomorph carapace PIN 5128/45 in left lateral view; MDF, Porkhov section, sample 98-6/2; Porkhov Beds, *Pa. punctata* Zone. **J.** *Knoxella?* *dubia* Polenova, 1953. Tecnomorph right valve PIN 5128/46; CDF-9/9; Semiluki Horizon, *Pa. punctata* Zone. →

and the long adductorial sulcus. It is distinguished, however, by lacking the preadductorial lobe and in having a spine anterodorsally rather than posterodorsally. Moreover, the absence of dimorphic specimens discounts a more exact placement of this species within the Palaeocopina.

***Paraparchites calculus* (Glebovskaja and Zaspelova, 1959)** (Fig. 7A).—This species was established by Glebovskaja and later described by Zaspelova (1959). It is abundant in the Porkhov Beds (*Palmatolepis punctata* Zone) of the MDF. Previously described as *Aparchites calculus*, this species appeared to have been dimorphic. Females bear a diffuse crumina located midventrally.

***Sulcella (Postsulcella) sp. A*** (Fig. 10C).—It occurs in the Semiluki Horizon (*Pa. punctata* Zone) in the CDF. Having general carapace morphology similar to that of *Sulcella (Sulcella) zaspelovae* (Egorov, 1950), this species lacks an adductorial pit, which is regarded to be a characteristic feature of the subgenus *Sulcella (Sulcella)* (Adamczak 2003). It should be noted that Egorov (1950) described that species as a type of the genus *Semilukiella*. He noted a considerable degree of variability in *S. zaspelovae* and regarded specimens both with a pit and without it as *S. zaspelovae*. Now *Semilukiella* is considered to be a younger synonym of *Sulcella (Sulcella)* Coryell and Sample, 1932 (Adamczak 2003). So the precise specific assignment of our specimens requires further revision of *S. zaspelovae* sensu Egorov 1950.

***Sulcella (Postsulcella) sp. B*** (Fig. 10D).—It occurs in the Semiluki Horizon (*Pa. punctata* Zone) in the CDF. Like the above species, its morphology resembles that of *Sulcella (S.) arcuata* (Egorov, 1950) but an adductorial pit is not developed. Revision of *S. arcuata* sensu Egorov 1950 is also needed.

***Tetracornella? sp. nov. A*** (Fig. 8D, E).—It occurs in the *Pa. punctata* Zone in the CDF (Semiluki Horizon, Il'men borehole). It is distinguished from other species of *Tetracornella* in having a posterodorsal spine in a very low position, as well as in having the fourth spine located beneath the preadductorial lobe adventrally.

***Tetracornella formosa* Zaspelova, 1952** (Fig. 8F).—This species occurs in the *Pa. punctata* Zone (Porkhov-Svinird beds) in the MDF. It was previously described by Zaspelova (1952) as *Tetracornella ornata* var. *formosa*, but it differs from *T. ornata* Zaspelova, 1952 in having long tubiform rather than cone-like posterior lobes ( $L_3$  and  $L_4$ ), and a stout posteroventral spine. These features are supposed to be of a species level significance.

***Tetracornella sp. nov. B aff. schelonica* Zaspelova, 1952** (Fig. 8J, K).—It occurs in the Porkhov Beds (*Pa. punctata* Zone) in the MDF. It is very similar to *Tetracornella schelo-*

*nica*, but differs in having a bulbous posterior lobe  $L_3$ . Dimorphs have not been found.

***Timanella sp. A*** (Fig. 10E).—This species occurs in small numbers in the Semiluki Horizon (*Pa. punctata* Zone) in the CDF and MDF. It differs from *Timanella typica* Egorov, 1950 in the amplete outline of the left valve.

***Timanella sp. B*** (Fig. 10F).—It occurs in the Svinord Beds (*Pa. punctata* Zone) in the MDF. It differs from *Timanella typica* Egorov, 1950 in its amplete subrectangular outline of the left valve as well as in having the right valve more sharply curved dorsally and ventrally.

***Uchtovia aff. elongata* Glebovskaja and Zaspelova in Egorov, 1950** (Fig. 10B).—The specimens from the Semiluki Horizon of the CDF differ from *Uchtovia elongata* in having a longer and lower carapace with a less curved dorsal part of the left valve.

## Conclusions

The Early and Middle Frasnian ostracod associations of the MDF belong to the Eifelian Ecotype of Becker (in Bandel and Becker 1975; Becker 2000), or using the terminology of Casier (2004, 2005), to the Eifelian Mega-Assemblage. The associations are indicative of a very shallow, well oxygenated semi-restricted epeiric environment, sometimes with open marine influence, alternating with short periods of open shelf conditions. The assemblages, characterised by entomozoids indicative of anoxic condition, and leperditicopids typical of true lagoon environment, have not been recorded.

Early Frasnian ostracod associations exhibit unstable and mainly low equitability, probably resulting from environmental stress/unstable ecological conditions producing impoverished ostracod associations.

Middle Frasnian ostracod associations show a slightly higher equitability upwards through the sequence, which may reflect environmental stabilization and improving water circulation due to deepening marine pulses in the early Middle Frasnian. The relatively higher species diversity in the Middle Frasnian seems to indicate a larger environmental heterogeneity and, consequently, a greater number of ecological niches at that time. The ostracod associations suggest a more open marine position during the Middle Frasnian, in an intra-shelf setting, rather than the intra-shelf habitats of the Early Frasnian.

Generally speaking, the most remarkable changes in the benthic ostracod associations across the E–MF transition can be observed in very shallow shelf deposits in the MDF and CDF Basins primarily due to prominent facies changes (see also Zhuravlev et al. 2006). In open marine settings—bioherm and laterally adjacent facies of the Ardennes (Becker 1971;

**K, L.** *Kloedenellitina pseudosygymaeformis* Egorov, 1950. Female left PIN 5128/47 and right PIN 5128/48 valves; MDF, Koloshka River; Svinord Beds, *Palmatolepis punctata* Zone. **M, N.** *Mennerella tuberosa* Glebovskaja and Zaspelova in Egorov, 1950. Small tecnomorph and male carapaces PIN 5128/49 and PIN 5128/50 in left lateral view; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. **O.** *Mennerella porezkyae* Egorov, 1950. Tecnomorph carapace PIN 5128/51 in left lateral view; MDF, Porkhov Section, sample 98-6/2; Porkhov Beds, *Pa. punctata* Zone. Scale bars 0.1 mm.

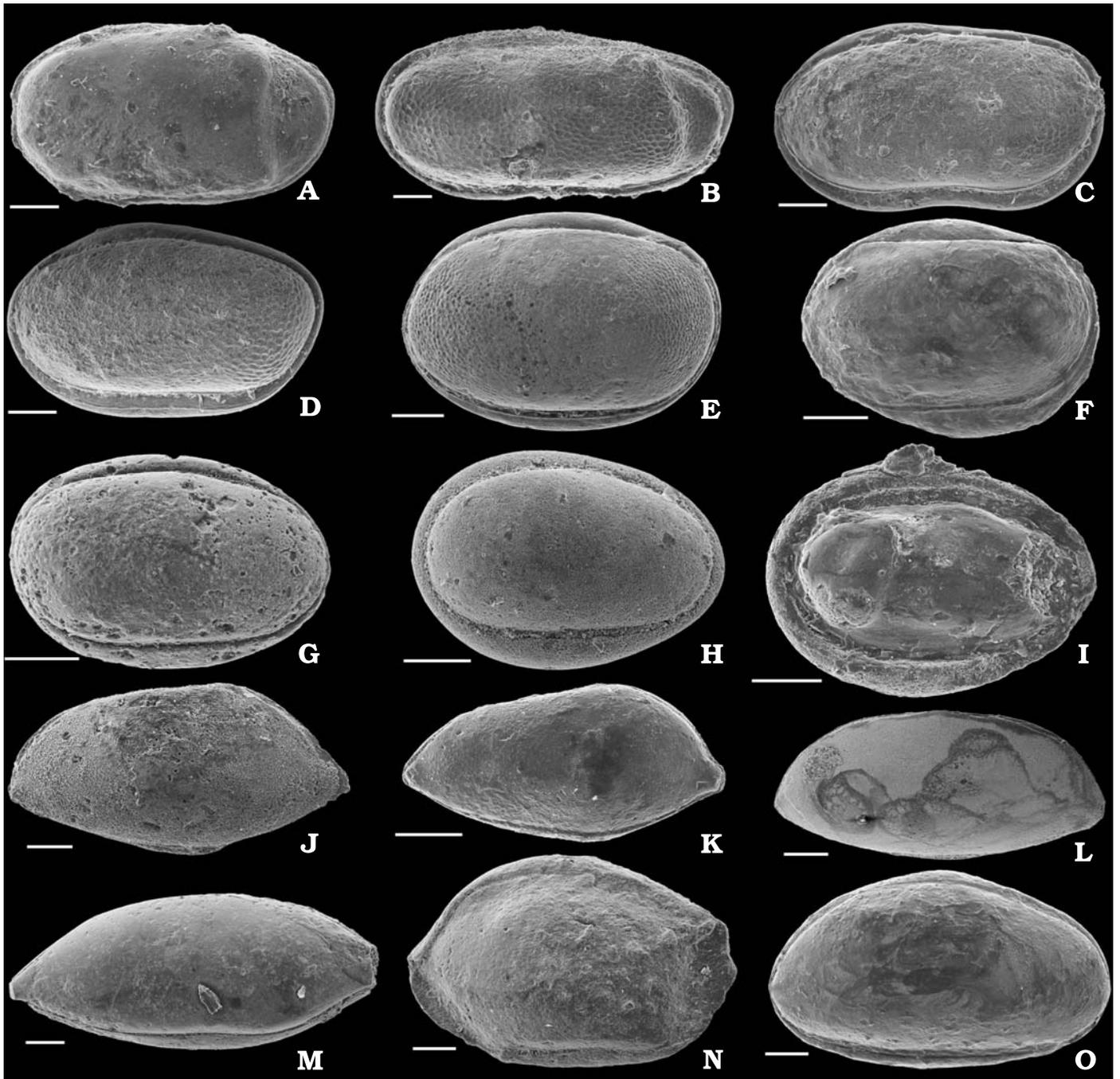


Fig. 10. **A.** *Uchtovia elongata* Glebovskaja and Zaspelova in Egorov, 1950. Tectonormorph carapace PIN 5128/52 in left lateral view; MDF, borehole No 5, sample i5/207; *Palmatolepis punctata* Zone. **B.** *Uchtovia* aff. *elongata* Glebovskaja and Zaspelova in Egorov, 1950. Tectonormorph carapace PIN 5128/53 in left lateral view; CDF-9/9, Semiluki Horizon, *Pa. punctata* Zone. **C.** *Sulcella* (*Postsulcella*) sp. A. Female carapace PIN 5128/54 in left lateral view; CDF-9/9, Semiluki Horizon, *Pa. punctata* Zone. **D.** *Sulcella* (*Postsulcella*) sp. B. Female carapace PIN 5128/55 in left lateral view; CDF-9/9, Semiluki Horizon, *Pa. punctata* Zone. **E.** *Timanella* sp. A. Tectonormorph carapace PIN 5128/56 in left lateral view; CDF, Il'men borehole, sample 68; Semiluki Horizon, *Pa. punctata* Zone. **F.** *Timanella* sp. B. Tectonormorph carapace PIN 5128/57 in left lateral view; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. **G.** *Cavellina* cf. *chvorostanensis* Polenova, 1953. Female carapace PIN 5128/58 in right lateral view; MDF, Pskov Beds, *Pa. transitans* Zone. **H, I.** *Cavellina batalinae* Zaspelova, 1959. Female carapaces PIN 5128/59 and PIN 5128/60 in right lateral views; MDF, Syas' River, sample S-3/1; Pskov Beds, *Pa. transitans* Zone. **J.** *Acrattia* cf. *pskovensis* Egorov, 1953. Carapace PIN 5128/61 in right lateral view; MDF, Izborsk section, sample 5158/O2; Chudovo Beds, *Pa. transitans* Zone. **K.** *Acrattia* cf. *tschudovoensis* Zaspelova, 1959. Carapace PIN 5128/62 in right lateral view; MDF, Izborsk section, sample 5158/O2; Chudovo Beds, *Pa. transitans* Zone. **L.** *Acrattia* cf. *longa* Zaspelova in Polenova, 1955. Carapace PIN 5128/63 in right lateral view; MDF, Syas' River, sample S-3/1; Pskov Beds, *Pa. transitans* Zone. **M.** *Acrattia* cf. *schelonica* Egorov, 1950. Carapace PIN 5128/64 in right latero-ventral view; CDF, Il'men borehole, sample 48; Semiluki Horizon, *Pa. punctata* Zone. **N.** *Bairdia* aff. *symmetrica* Egorov, 1953. Carapace PIN 5128/65 in right lateral view. CDF, Il'men borehole, sample 53; Semiluki Horizon, *Pa. punctata* Zone. **O.** *Heladianella* cf. *svinordensis* Glebovskaja and Zaspelova, 1959. Carapace PIN 5128/66 in right lateral view; MDF, Koloshka River; Svinord Beds, *Pa. punctata* Zone. Scale bars 0.1 mm.

Casier 1987b; Casier et al. 2006) and Poland (Olempska 1979; Żbikowska 1983; Malec and Racki 1993) no significant changes in the E–MF ostracod succession can be recognised. In the deep-water domanikoid facies of the TPP, the absence of ostracods in the earliest Middle Frasnian is considered to be due to the marked development of anoxic and hypoxic conditions (House et al. 2000). This appears to be an ostracod “expression” of the regional “Domanik crisis”, which was caused by a significant marine deepening event and reinforced with tectonic subsidence of the area (Kuzmin et al. 1997). Consequently, the significant changes in ostracod associations marked by changes of dominant taxa, disappearance and appearance of some taxa in the E–MF transition seems to be of a regional scale.

According to Zhuravlev et al. (2006), the positive  $\delta^{13}\text{C}$  excursion recorded upward the sequence in the Svinord Beds can be correlated with the positive anomaly detected in the early *Pa. punctata* Zone in other Laurussian and Chinese shelves (Yans et al. in press). The ostracod records in the shallow-water environment of the MDF Basin do not show any proved mass ostracod extinction associated with this large-scale positive carbon isotopic excursion, although there is a significant biotic turnover (see discussion in Zhuravlev et al. 2006). In open marine settings there is no large scale faunal changes at that time recognised either with main exception of some reef biota (see Pisarzowska et al. 2006; Yans et al. in press).

## Acknowledgements

I would like to express my sincere gratitude to Grzegorz Racki (Institute of Paleobiology of the Polish Academy of Science, Warsaw and University of Silesia, Sosnowiec, Poland) and the two reviewers Mark Williams (University of Leicester, Leicester, UK) and Jean-Georges Casier (Belgian Royal Institute of Natural Sciences, Brussels, Belgium) for their careful reviews, linguistic corrections and suggestion of many useful improvements to the original manuscript. Sincere thanks to Ivan Ofman (VNIGNI, Moscow, Russia) for providing the ostracod collection from the Il'men borehole (CDF). SEM photographs were made at the Palaeontological Institute RAS, Moscow with the help of Lev T. Protasevich and Alexandr V. Kravtsev. This study is a contribution to IGCP 499 Project “Devonian land-sea interaction: Evolution of ecosystems and climate” (DEVEC). It was also supported by RFBR grant N 04-05-65208-a.

## References

- Adamczak, F.J. 2003. The Platycopine Dynasty 2. Family Cavellinidae Egorov, 1950. Authentic platycopines. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 229: 375–391.
- Bandel, K. and Becker, G. 1975. Ostracoden aus paläozoischen pelagischen Kalken der Karnischen Alpen (Silurium bis Unterkarbon). *Senckenbergiana lethaea* 56: 1–83.
- Batalina, M.A. 1941. Ostracods of the Main Devonian Field [in Russian]. In: R.F. Hecker [Gekker, R.F.] (ed.), *Fauna Glavnogo devonskogo polâ 1*, 285–314. Izdatel'stvo Akademii Nauk SSSR, Moskva.
- Becker, G. 1968a. Geschlechtsdimorphismus bei Ostracoden. 2. *Natur und Museum* 98: 119–172.
- Becker, G. 1968b. Ostracoda aus den Refrath-Schichten (Oberdevon) der Paffrather Mulde (Bergisches Land). 2: Zur Morphologie und Systematik der Palaeocopida-Gattungen *Nodella* Zaspelova und *Aechminella* Harlton. *Senckenbergiana lethaea* 49: 547–563.
- Becker, G. 1970. Primitiopsacea (Ostracoda, Palaeocopida) aus dem Rheinischen Devon. *Senckenbergiana lethaea* 51: 49–65.
- Becker, G. 1971. Ostracoda aus dem Mittel-Frasnium (Oberdevon) der Mulde von Dinant. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 47 (34): 1–82.
- Becker, G. 1998. The Superfamily Nodellacea Becker, 1968. Family Nodellidae Zaspelova, 1952. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210: 289–304.
- Becker, G. 2000. Progress in mid Palaeozoic palaeoceanographical studies from Ostracoda—from local to global importance (a review). *Senckenbergiana lethaea* 80: 555–566.
- Becker, R.T., House, M.R., and Kirchgasser, W.T. 1993. Devonian goniatite biostratigraphy and timing of facies movements in the Frasnian of the Canning Basin, Western Australia. In: E.A. Hailwood and R.B. Kidd (eds.), *High Resolution Stratigraphy. Geological Society Special Publication* 70: 293–321.
- Becker, R.T., Menner, V.V., Ovnatanova, N.S., Kuzmin, A., and House, M.R. 2001. A potential Middle Frasnian stratotype section at Chut River (Southern Timan, Russia)—a preliminary account. *SDS Newsletter* 18: 45–51. <http://sds.uta.edu/sds18/page0045.htm>.
- Belyaeva, N.V. and Ivanov, A.O. (eds.) 2000. Pan-Arctic Palaeozoic Tectonics, Evolution of Basins and Faunas, South Timan Field Trip Guidebook. *Ichthyolith Issues* (Supplement to Special Publication 6): 1–84.
- Casier, J.-G. 1987a. Étude biostratigraphique et paléocéologique des ostracodes du récif de marbre rouge du Hautmont à Vodelée (partie supérieure du Frasnien, Bassin de Dinant, Belgique). *Revue de Paléobiologie* 6: 193–204.
- Casier, J.-G. 1987b. Étude biostratigraphique et paléocéologique des ostracodes du Sommet du Givetien et de la base du Frasnien à Ave-et-Auffe (bord sud du bassin de Dinant, Belgique). *Bulletin de la Société belge de Géologie* 96: 23–34.
- Casier, J.-G. 2004. The mode of life of Devonian entomozocean ostracods and the Myodocopid Mega-Assemblage proxy for hypoxic events. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 74 (Supplement): 73–80.
- Casier, J.-G. and Préat, A. 2003. Ostracods and lithofacies of the Devonian–Carboniferous boundary beds in the Avesnois, North of France. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 73: 83–107.
- Casier, J.-G., Berra, I., Olempska, E., Sandberg, C., and Préat, A. 2006. Ostracods and facies of the Early and Middle Frasnian at Devils Gate in Nevada: Relationship to the Alamo Event. *Acta Palaeontologica Polonica* 51: 813–828.
- Casier, J.-G., Lebon, A., Mamet, B., and Préat, A. 2005. Ostracods and lithofacies close to the Devonian–Carboniferous boundary in the Chanxhe and Rivage sections, northeastern part of Dinant Basin, Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 75: 95–126.
- Coen, M. 1985. Ostracodes givétiens d'Ardenne. *Mémoires de Institut Géologique de Université de Louvain* 32: 1–48.
- Crasquin, S. 1984. L'Écozone à Bairdiacea et Paraparchitacea (Ostracoda) au Dinantien. *Géobios* 17: 341–348.
- Egorov, V.G. 1950. *Ostrakody franskogo ârusa Russkoj platformy – 1: Kloedenellidae*. 175 pp. Gostoptehizdat, Moskva.
- Egorov, V.G. 1953. *Ostrakody franskogo ârusa Russkoj platformy – 2: Bairdiidae, Holliniidae, Kirkbyidae*. 133 pp. Gostoptehizdat, Moskva.
- Egorov, V.G. 1954. Indivisiinae—a new subfamily of Kloedenellidae from the Frasnian Stage of the Russian Platform [in Russian]. *Paleontologičeskij sbornik* 1: 5–21.
- Evdokimova, I. 2002. Changes in benthic ostracode associations across the Sargaev-Semiluki boundary beds (Frasnian) in the Main Devonian Field, Russia. In: J. Satkūnas and J. Lazauskienė (eds.), *The Fifth Baltic Stratigraphical Conference “Basin Stratigraphy—Modern Methods and Problems”, September 22–27, 2002, Vilnius, Lithuania: Extended Abstracts*, 35–37. Vilnius.
- Hecker, R.F. [Gekker, R.F.] 1933. Carbonate rocks of Devonian deposits [in Russian]. In: E.P. Bruns and S.G. Višňakov (eds.), *Karbonatnye porody*

- Leningradskoj oblasti, Severnogo kraâ i Karel'skoj ASSR, Vypusk 2*, 16–43. Gosudarstvennoe naučno-tehničeskoe gorno-geologo-neftânoe izdatel'stvo, Leningrad.
- Hecker, R.F. [Gekker, R.F.] 1939. A *Leperditia* from the Middle Devonian of the Leningrad region [in Russian]. *Izvestiâ Akademii Nauk SSSR, otdelenie biologičeskikh nauk* 1939: 232–240.
- Hecker, R.F. [Gekker, R.F.] 1941. The deposits, fauna, and flora of the Main Devonian Field [in Russian]. In: R.F. Hecker (ed.), *Fauna Glavnogo devonskogo polâ 1*, 17–84. Izdatel'stvo Akademii Nauk SSSR, Moskva.
- Hecker, R.F. [Gekker, R.F.] 1954. Comparison of sections of eastern and western parts of the Main Devonian Field and main features of ecology of its fauna and flora [in Russian]. *Izvestiâ Akademii Nauk SSSR. Seriiâ Geologičeskââ 4*: 75–100.
- Hecker, R.F. [Gekker, R.F.] 1964. The “Shelon’ problem” and its general methodic meaning [in Russian]. In: V. Karatajute-Talimaa and V. Narbutas (eds.), *Voprosy stratigrafii i paleogeografii devona Pribaltiki*, 104–112. Vilnius.
- Hecker, R.F. [Gekker, R.F.] 1983. Taphonomic and ecological features of the fauna and flora of the Main Devonian Field [in Russian]. *Trudy Paleontologičeskogo Instituta* 190: 1–144.
- House, M.R., Menner, V.V., Becker, R.T., Klapper, G., Ovnatanova, N.S., and Kuz'min, A.V. 2000. Reef episodes, anoxia and sea-level changes in the Frasnian of the southern Timan (NE Russian Platform). In: E. Insalaco, P.W. Skelton, and T.J. Palmer (eds.), *Carbonate Platform Systems: Components and Interactions. Geological Society, London, Special Publications* 178: 147–176.
- Ishizaki, K., Irizuki, T., and Sasaki, O. 1993. Cobb Mountain spike of the Kuroshio Current detected by Ostracoda in the lower Omma Formation (Early Pleistocene), Kanazawa City, central Japan: analysis of depositional environments. In: K.G. McKenzie and P.J. Jones (eds.), *Ostracoda in the Earth and Life Sciences*. Proceedings of the 11<sup>th</sup> International Symposium on Ostracoda, 315–334. A.A. Balkema Publishers, Rotterdam.
- Ivanov, A., Zhuravlev, A., Stinkulis, G., Evdokimova, I., Dronov, A., Sokiran, E., Shishlov, S., Broushkin, A., and Myshkina, N. 2005. *Devonian sections of North-West of East European Platform*. Guidebook. 66 pp. St. Petersburg University Press, St. Petersburg.
- Johnson, J.G., Klapper, G., and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euroamerica. *Geological Society of America Bulletin* 96: 567–587.
- Kuzmin, A.V., Yatskov, S.V., Orlov, A.N., and Ivanov, A.O. 1997. “Domanic Crisis” in the evolution of fauna of the Frasnian marine basin in the South Timan. *Paleontological Journal* 31: 251–258.
- Lethiers, F. and Crasquin-Soleau, S. 1988. Comment extraire les microfossiles à tests calcitiques des roches calcaires dures. *Revue de Micropaléontologie* 31: 56–61.
- Malec, J. and Racki, G. 1993. Givetian and Frasnian ostracod associations from the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37: 359–384.
- Menner, V.V. 1989. *Litologičeskije kriterii neftegazonosnosti paleozojskikh tolš severo-vostoka Russkoj platformy*. 156 pp. Nauka, Moskva.
- Obruchev, D.V. [Obruchev, D.V.] 1930. Importance of the ichtyofauna for the stratigraphy of the northwestern Devonian [in Russian]. *Trudy Glavnogo geologo-razvedočnogo upravleniâ* 49: 1138–1145.
- Olempska, E. 1979. Middle to Upper Devonian Ostracoda from the southern Holy Cross Mountains, Poland. *Palaeontologia Polonica* 40: 57–162.
- Õpik, A.A. 1935. Ostracoda from the Old Red sandstone of Tartu, Estonia. *Tartu Uelikooli Geologia-Instituudi Toimetused* 45: 1–10.
- Ovnatanova N.S. and Kononova, L.I. 2001. Conodonts and Upper Devonian (Frasnian) Biostratigraphy of Central Regions of Russian Platform. *Courier Forschungsinstitut Senckenberg* 233: 1–115.
- Pisarszowska, A., Sobstel, M., and Racki, G. 2006. Conodont-based event stratigraphy of the Early–Middle Frasnian transition on the South Polish carbonate shelf. *Acta Palaeontologica Polonica* 51: 609–646.
- Polenova, E.N. 1953. Ostracoda from the Devonian deposits of the Central Devonian Field and the Middle Volga area [in Russian]. *Trudy Vsesoûznogo nefitânogo naučno-issledovatel'skogo geologo-razvedočnogo instituta (VNIGRI), Novaâ seriâ* 68: 1–157.
- Polenova, E.N. 1955. Devonian Ostracoda of the Volga-Ural area [in Russian]. *Trudy Vsesoûznogo nefitânogo naučno-issledovatel'skogo geologo-razvedočnogo instituta (VNIGRI), Novaâ seriâ* 87: 191–287.
- Rodionova, G.D., Umnova, V.T., Kononova, L.I., Ovnatanova, N.S., Rzhonsnitskaya, M.A. [Ržonsnickââ, M.A.], and Fedorova, T.I. 1995. *Devon Voronežskoj anteklizi i Moskovskoj sineklizi*. 265 pp. Rosgeolfond, Moskva.
- Rozhdestvenskaja, A.A. [Rožděstvenskââ, A.A.] 1972. *Ostrakody verhnego devona Baškirii*. 192 pp. Nauka, Moskva.
- Shishkinskaja, A.F. [Šiškinskââ, A.F.] 1968. New Devonian ostracodes of the Family Drepanellidae from the Volgograd district [in Russian]. *Paleontologičeskij žurnal* 1: 39–45.
- Sokiran, E.V., Evdokimova, I.O., and Zhuravlev, A.V. [Žuravlev, A.V.] 1999. Correlation of the Middle Frasnian deposits of the Main Devonian Field and South Timan based on microfauna and brachiopods [in Russian]. In: N.P. Ūškin (ed.), *Geologiâ i mineral'nye resursy evropejskogo severo-vostoka Rossii: novye rezul'taty i novye perspektivy*. Materialy XIII Geologičeskogo s'ezda Respubliki Komi 2, 231–233. Geoprint, Syktyvkar.
- Sorokin, V.S. 1978. *Etapy razvitiâ severo-zapada Russkoj platformy vo franskom veke*. 268 pp. Zinatne, Riga.
- Stirling, G. and Wilsey, B. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist* 158: 286–299.
- Tikhomirov, S.V. [Tihomirov S.V.] 1995. *Etapy osadkonakopleniâ devona Russkoj platformy i obšie voprosy razvitiâ i stroeniâ stratisfery*. 445 pp. Nedra, Moskva.
- Yans, J., Corfield, R.M., Racki, G., and Prêat A. (in press). Evidence for a major perturbation of the carbon cycle in the middle Frasnian *punctata* conodont Zone. *Geological Magazine*.
- Yudina, Yu.A. [Ūdina, Ū.A.] and Moskalenko, M.N. 1997. *Opornye razrezy franskogo ârusa ūžnogo Timana*. 80 pp. TPO VNIGRI, Ukhta.
- Zaspelova, V.S. 1952. Ostracoda of the family Drepanellidae from the Upper Devonian deposits of the Russian Platform [in Russian]. *Trudy Vsesoûznogo nefitânogo naučno-issledovatel'skogo geologo-razvedočnogo instituta (VNIGRI), Novaâ seriâ* 60 (Mikrofauna SSSR 5): 157–216.
- Zaspelova, V.S. 1959. Ostracoda and their value for the stratigraphy of the Devonian of the north-western regions of the Russian Platform [in Russian]. *Trudy Vsesoûznogo nefitânogo naučno-issledovatel'skogo geologo-razvedočnogo instituta (VNIGRI), Novaâ seriâ* 136 (Mikrofauna SSSR 10): 5–131.
- Zhamoida, A.I. [Žamojda, A.I.] (ed.) 2006. *Stratigrafičeskij kodeks Rossii*. Third edition. 96 pp. Mežvedomstvennyj stratigrafičeskij komitet Rossii, VSEGEI Press, Sankt-Peterburg.
- Zhuravlev, A.V., Evdokimova, I.O., and Sokiran, E.V. 1997. New data on conodonts, brachiopods and ostracodes from the stratotypes of the Ilmen and Buregi beds (Frasnian, Main Devonian Field). *Proceedings of the Estonian Academy of Sciences, Geology* 46 (4): 169–186.
- Zhuravlev, A.V., Evdokimova, I. O., and Sokiran, E. V. 1999. Lower–Middle Frasnian biostratigraphy of middle part of Main Devonian Field. In: E. Lukševičs, G. Stinkulis, and L. Kalniņa (eds.), *The 4<sup>th</sup> Baltic Stratigraphical Conference. Problems and Methods of Modern Regional Stratigraphy. Abstracts*, 113–114. Riga.
- Zhuravlev, A.V., Evdokimova, I. O., and Sokiran, E.V. 2005. Sedimentary environments and fossils of the Syas Formation (Upper Devonian, East of the Main Devonian Field, East European Platform). In: E.A. Yolkin, N.G. Izokh, O.T. Obut, and T.P. Kipriyanova (eds.), *Devonian Terrestrial and Marine Environments: From Continent to Shelf* (IGCP 499 Project/SDS joint field meeting: Contributions of International Conference, 149–150. Publishing House of SB RAS, “Geo” Branch, Novosibirsk.
- Zhuravlev, A.V., Sokiran, E.V., Evdokimova, I.O., Dorofeeva, L.A., Rusetskaya, G.A., and Małkowski, K. 2006. Faunal and facies changes at the Early–Middle Frasnian boundary in the North-West of the East European Platform. *Acta Palaeontologica Polonica* 51: 747–758.
- Ziegler, W., Ovnatanova, N., and Kononova, L. 2000. Devonian polygnathids from the Frasnian of the Rheinisches Schiefergebirge, Germany, and the Russian Platform. *Senckenbergiana lethaea* 80: 593–645.
- Ziegler, W. and Sandberg, C.A. 2001. Utility of palmatolepids and icriodontids in recognizing Upper Devonian series, stage, and possible substage boundaries. *Courier Forschungsinstitut Senckenberg* 225: 335–347.
- Żbikowska, B. 1983. Middle to Upper Devonian ostracods from north-western Poland and their stratigraphic significance. *Palaeontologia Polonica* 44: 3–108.