Frasnian–Famennian extinction and recovery of rhynchonellid brachiopods from the East European Platform

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In contrast to dramatic losses of the Atrypida and Pentamerida at the Frasnian–Famennian boundary, the Rhynchonellida demonstrated relatively high rate of survival, and recolonized vacated benthic ecospace after the F–F extinction events. The Late Devonian evolution of rhynchonellid faunas from the East European Platform shows three distinctive periods of their mass appearance. High abundance of rhynchonellids is characteristic for early–middle Frasnian (*Palmatolepis transitans–Pa. punctata* zones) and early Famennian (*Pa. crepida* Zone). Invasion of taxonomically diverse and rich rhynchonellid faunas usually corresponds to the major transgressive episodes, whereas decline coincides with regressive conditions of the basin. Rhynchonellid assemblages were replaced in the late Frasnian (Late *Pa. hassi–Pa. linguiformis* zones) by theodossiid- and cyrtospiriferid- dominated assemblages, which occupied habitats in newly expanding marine environments. The extinction of theodossiids at the end of the Frasnian and the next transgressive episode possibly stimulated an expansion of rhynchonellids. The early Frasnian species *Ripidiorhynchus livonicus* (Buch, 1834), and the early Famennian *R. huotinus* (Verneuil, 1845) and *R. griasicus* (Nalivkin, 1934) are revised. Early Famennian species *Paromoeopygma koscharica* (Nalivkin, 1934) from the central region is redescribed. *Ripidiorhynchus chencinensis* sp. nov. from the latest Givetian of Poland, as well as *Globulirhynchia minima* sp. nov. from the late Frasnian of the central region of the Russia, are described.

Key words: Brachiopoda, Rhynchonellida, sea-level changes, extinction, Frasnian, Famennian, East European Platform, Russia.

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Introduction

The Rhynchonellida were an abundant shelly benthic group during the Late Devonian, but like other brachiopods, they were affected by the Frasnian–Famennian (F–F) mass extinctions (McGhee 1996). These brachiopods were richly represented in the Frasnian deeper water, hypoxic habitats (see Racki et al. 1993a; Sartenaer et al. 1998), and this biofacies was the least affected during the F–F biotic crisis than were reef-dwelling brachiopods (e.g., Racki 1998).

The aim of this paper is a revision of Frasnian to early Famennian Trigonirhynchiidae and Pugnacidae from the central and northwestern parts of the East European Platform. These brachiopods were pioneer colonizers of inner shelf environments (Sorokin 1978) that survived the F–F bio-crises. In addition, a late Givetian trigonirhynchiid species from the Holy Cross Mountains (Central Poland) are described. The regional diversity dynamics of rhynchonellids are reviewed in the context of sea-level fluctuations.

Institutional abbreviations.—CNIGR, Chernyshev's Museum in St. Petersburg, Russia; GIUS, Department of Earth Sciences, Silesian University in Sosnowiec, Poland.

Other abbreviations.—EEP, East European Platform; T–R, transgressive (T)–regressive (R) cycle.

Regional history of rhynchonellid dynamics

The Frasnian–early Famennian history of Rhynchonellida on the East European Platform reveals three distinct periods of mass appearance and diversification: in the early Frasnian, middle Frasnian and early Famennian. These periods coincide with the major transgressive episodes (see Alekseev et al. 1996), and disappearance of rhynchonellid communities was forced by reduction of basin area with normal marine salinity (Tikhomirov 1967; Rodionova et al. 1995). Thus, it is evident that a correlation exists between the sea-level fluctuations and rhynchonellid diversity (Fig. 1).

During the early and middle Frasnian rhynchonellids are common in the northwestern and central regions of the platform. They are represented by Trigonirhynchiidae (*Cupularostrum*, *Ripidiorhynchus*), Hypothyridinidae (*Hypothyridina, Uchtella*), Ladogiidae (*Comiotoechia*, *Ladogia*), Leio-

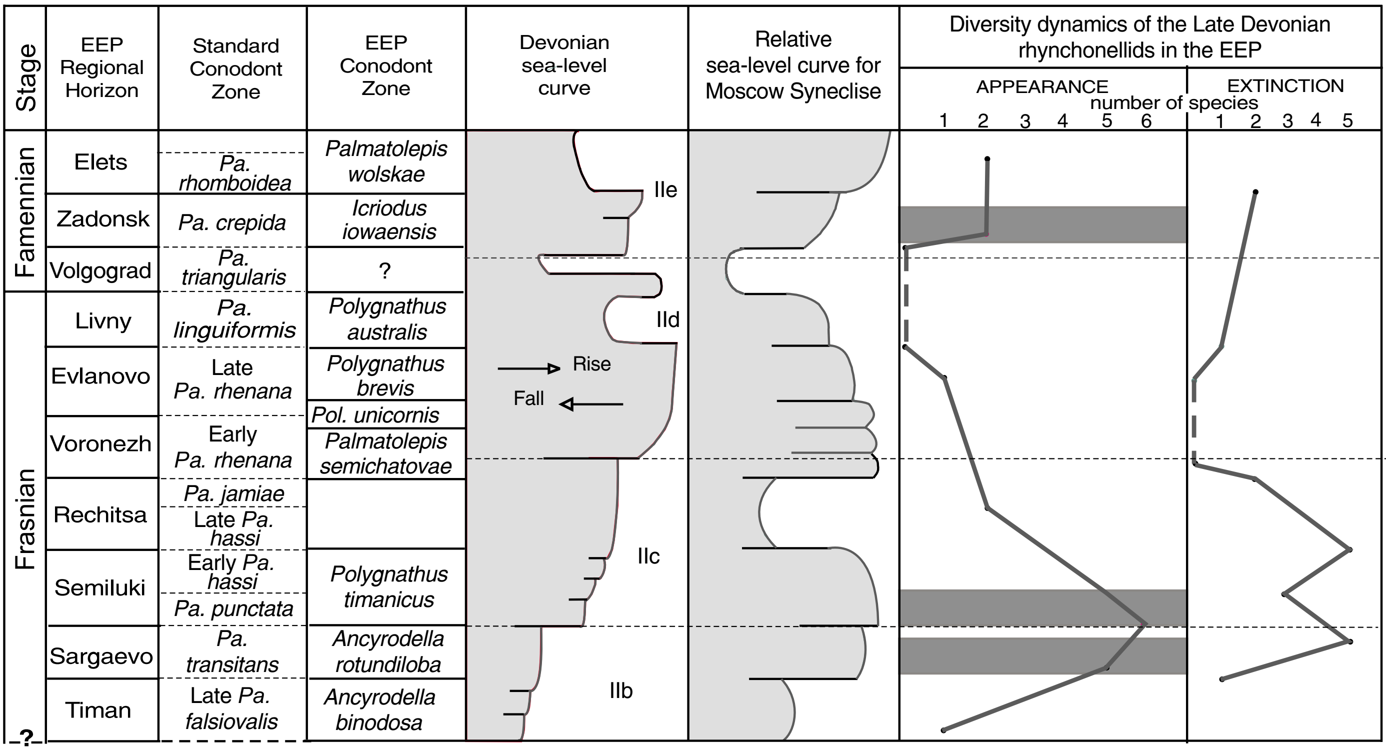

Fig. 1. Diversity dynamics of the Late Devonian rhynchonellids in the East European Platform (EEP). Three radiation levels of the Late Devonian rhynchonellids are marked as dotted areas. Devonian sea-level curve (after Johnson et al. 1985) and curve of relative Devonian sea-level changes in Moscow Syneclise (after Alekseev et al. 1996). The Standard Conodont Zonation by Klapper and Ziegler 1979, Ziegler and Sandberg 1990 and Conodont Zonation for Devonian of the East European Platform (EEP) proposed by Aristov 1988.

rhynchidae ("*Leiorhynchus*", *Canavirila*, *Stenometoporhynchus*, *Tomestenoporhynchus*), and Pugnacidae ("*Pugnax*") (Fig. 2).

Wide dispersal of rhynchonellids at that time coincided with two Late Devonian marine transgressions and expanded carbonate sedimentation. Facies changes can be correlated with transgressive (T)–regressive (R) cycles IIb–IIc of Johnson et al. (1985). The early Frasnian (*Palmatolepis transitans* Zone) immigration of *Ripidiorhynchus* in northwestern region of the platform coincides with a transgressive episode correlated with T–R cycle IIb (see Alekseev et al. 1996; II b/c subcycle of Racki 1993a: 157). Normal salinity dominated almost the entire platform, inducing mixed carbonate-clastic deposition and rich and diverse benthic life.

A second rhynchonellid diversification in central regions of the shelf took place during the middle Frasnian (*Pa. punctata* Zone). Abundant *Stenometoporhynchus* and *Tomestenoporhynchus* are characteristic of the Semiluki Horizon (Fig. 2). This interval corresponds to the next marine flooding event correlated with the onset T–R cycle IIc *sensu* Johnson et al. (1985). However, a short-term regression at beginning of the late Frasnian (Late *Pa. hassi*–*Pa. jamiae* zonal interval) was probably the main reason for significant ecosystem change.

After the regressive event, there is evidence of uplift of the Voronezh Anteclise (central region of the East European Platform; Alekseev et al. 1996). Consequently most rhynchonellids disappeared, and only rare pugnacids are known from the central region (Ljashenko 1959). However, the Leiorhynchidae (*Calvinaria*, *Caryorhynchus*) and coral-brachiopod limestone facies (Samsonovo and Alatyr suites) with *Hypothyridina* characterize the late Frasnian open marine facies in the eastern region (Rzhonsnitskaya 1988). Three transgressive pulses are recorded in the Early *Pa. rhenana* Zone (Alekseev et al. 1996). This interval is characterized in the central region by beginning of theodossiid expansion which together with cyrtospiriferids were dominant elements of late Frasnian shallow-water brachiopod communities on the East European shelf. Conversely, rhynchonellid faunas collapsed. Only rare representatives of "*Pugnax*" and *Globulirhynchia* are known from this interval. It is possible that *Globulirhynchia* occurred also in the Volga Ural area at the same time ("*Pugnax*" *lummatoniensis* sensu Novozhilova 1955). Shallow and coastal marine, mostly terrigenous sedimentary regimes developed over most of the platform whereas reefs were limited to the eastern periphery (Rzhonsnitskaya 1988).

The Frasnian–Famennian transition is characterized by a regression and platform emergence, causing common hiatus (Alekseev et al. 1996). At this time great turnovers took place among almost all fossil groups. Atrypids, pentamerids, spiriferids such as *Theodossia,* and many other brachiopod genera completely disappeared, and a great majority of corals and tentaculitids became extinct (Rzhonsnitskaya 1988; Rzhonsnitskaya et al. 1998). The lower boundary of the Famennian

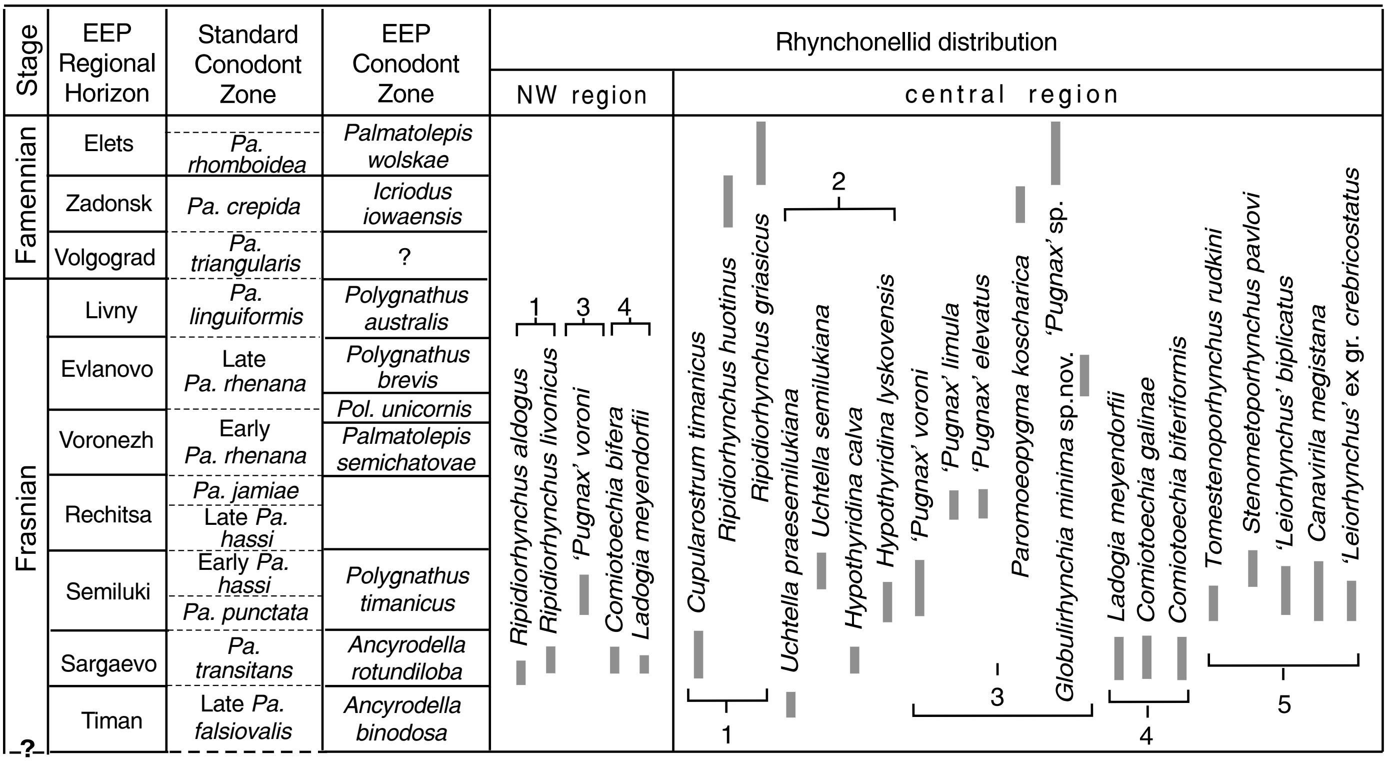

Fig. 2. Rhynchonellid distribution in Frasnian–lower Famennian of the central and northwestern region of the East European Platform. 1, Trigonirhynchiidae; 2, Hypothyridinidae; 3, Pugnacidae; 4, Ladogiidae; 5, Leiorhynchidae.

on the East European Platform is drawn at the base of the Volgograd Horizon stage (*Pa. triangularis* Zone), but in the central region a hiatus coincides with the F–F passage (Alekseev et al. 1996). Shallow-marine normal salinity basin was re-established in late early Famennian times, simultaneously with a transgression culminating during the *Pa. rhomboidea* Zone (Elets Horizon, Alekseev et al. 1996). In the central region of the platform, *Ripidiorhynchus* again became the most abundant brachiopod in a community including many cyrtospiriferids, athyridids, and rare pugnacids, such as *Paromoeopygma*.

Low diversity, but abundant rhynchonellid faunas occur in succeeding levels, correlated with the *Pa. crepida* (Zadonsk Horizon) and *Pa. rhomboidea* zones (Elets Horizon). In the Zadonsk Horizon rhynchonellids were mainly represented by numerous *Ripidiorhynchus huotinus* (Verneuil, 1845), which formed dense clusters with cyrtospiriferids, productids, and occasionally pugnacids such as *Paromoeopygma koscharica* (Nalivkin, 1934). During the Elets time *Ripidiorhynchus griasicus* (Nalivkin, 1934) is a widespread with cyrtospirferids, athyrids and rare pugnacids formed dense clusters. On the East European Platform, the early Famennian is almost everywhere represented by shallow marine carbonate facies, especially in the central and western regions, whereas deeper marly facies are restricted to the Volga–Ural area (Rzhonsnitskaya 1988).

Changes in the composition of rhynchonellid communities during the Late Devonian on the East European Platform is perhaps best explained by eustatic factors, which controlled the diversity and abundance of benthos. However, the decrease of rhynchonellids during the late Frasnian coincides with the environmental expansion of theodossiids and cyrtospiriferids, which became the main colonizers of the shallow water environments. The theodossiid extinction at the end of the Frasnian, and subsequent resumption of platform deposition associated a major early Famennian marine transgression of T–R cycle IIe, possibly provided new impulses for rediversification of rhynchonellid faunas. These environmental trends are quite different from the patterns reported by McGhee (1992) from the New York area, where sea-level rises were tied to expansion of anoxia and destruction of benthic life. It is clear that anoxic Kellwasser facies are not evidenced in the shallow water deposits of the central regions of the East European Platform.

Terminology

According to the official definition in the Russian Stratigraphic Code (Zhamoida 1992: 32), horizons, local zones and beds with geographic names are taxonomical units of regional stratigraphic subdivision. Horizon is a main unit at the regional scale, and according to the Code this is a chronostratigraphic unit with isochronous boundaries corresponding to a single or several biostratigraphic zones. Beds with geographic names

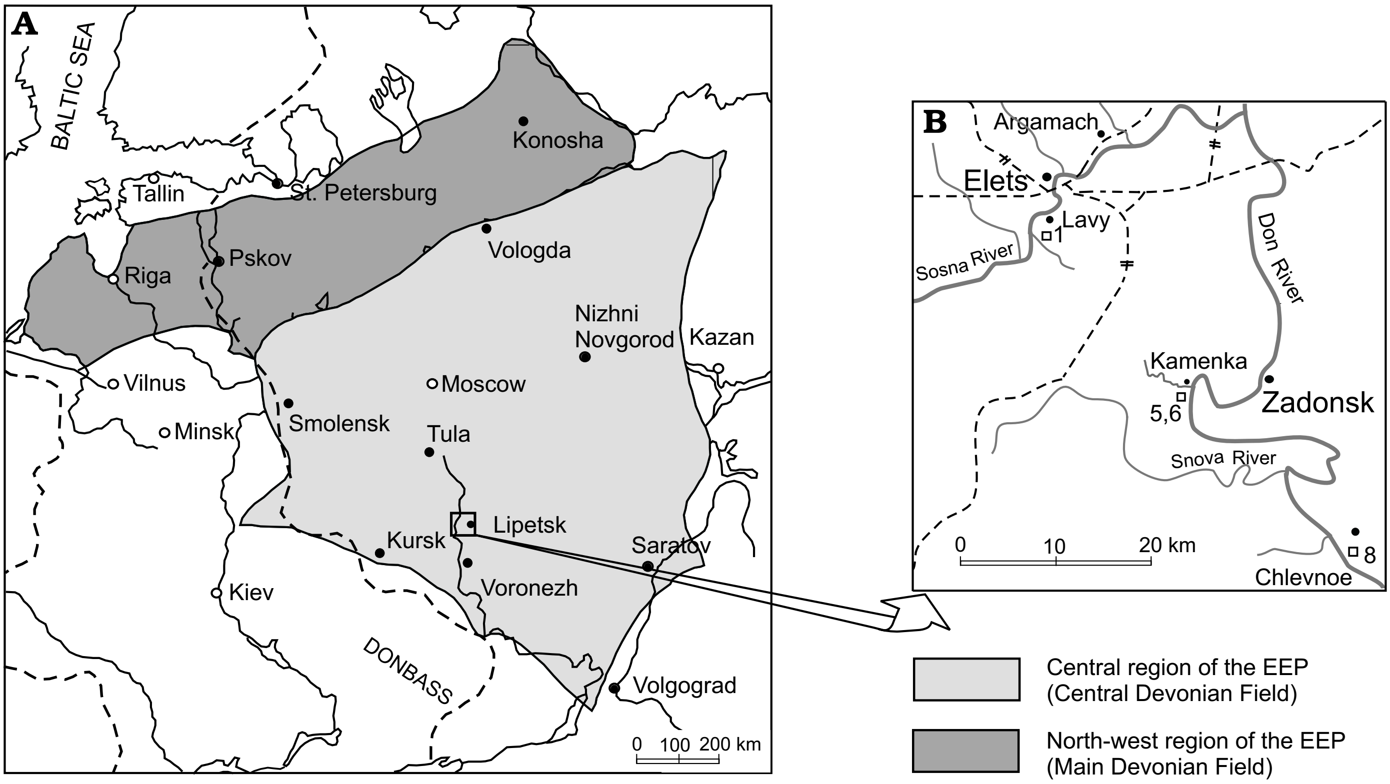

Fig. 3. Location of the regions and sections studied.

are lithostratigraphic or biostratigraphic units of lower rank than horizon or subhorizon.

Stratigraphic setting of rhynchonellid-bearing sequences of the East European Platform

North-western region (Main Devonian Field) (Fig. 3A).—Frasnian shallow-water sequences in this part of the platform are characterized by a mixture of carbonate and terrigenous sediments that contain abundant but taxonomically sparse benthic faunas (brachiopods, bivalves, gastropods, corals, and stromatoporoids).

The lower Frasnian deposits are represented by Snetogorsk, Pskov, Chudovo, and Dubnik Beds (Bekker 1924; Hecker 1933; Obrutchev 1933) that are correlated with Sargaevo Horizon (Fig. 4). These strata are correlated with the *Pa. transitans* Zone (= Lower *Polygnathus asymmetricus* Subzone; Rzhonsnitskaya 1988; Ovnatanova and Kononova 1999; Ziegler, Ovnatanova and Kononova 2000). Among rhynchonellids, representatives of *Ripidiorhynchus*, i.e. *R. aldogus* (Nalivkin, 1941) and *R. livonicus* (Buch, 1834), occur in the Pskov, Chudovo, and Dubnik Beds. *Ladogia meyendorfii* Verneuil, 1845, occurs only in the Pskov Beds, and *Comiotoechia bifera* (Phillips, 1841) is limited to the Chudovo Beds. Species of *Ripidiorhynchus* occur in dolomitized limestones, limestones and mainly marly limestones (Fig. 4). The overall thickness of these beds varies from 16 to 69 m (Sorokin 1978).

Pugnacids ("*Pugnax*" *voroni* Nalivkin, 1930) first appear, in deposits of the Semiluki Horizon, corresponding to the *Pa. punctata*–Early *Pa. hassi* (= Middle–Upper *Polygnathus asymmetricus* subzones, Ovnatanova and Kononova 1999) zonal interval. These deposits were distinguished by Hecker (1933, 1964) and Obrutchev (1933) as the Porchov, Svinord, Ilmen, and Buregi beds, and include shallow-water carbonate and terrigenous sediments with numerous brachiopods (mostly cyrtospiriferids), gastropods and stromatoporoids. "*Pugnax*" *voroni* is a comparatively rare rhynchonellid species of the Main Devonian Field, which sporadically occurs in the Svinord Beds. The thickness of these deposits varies from 5 to 58 m (Sorokin 1978).

In late Frasnian and early Famennian strata brachiopods are rare and rhynchonellids are absent in the regions.

Central regions (Central Devonian Field) (Fig. 3A).—The early Frasnian–early Famennian shallow-water sequences of the central region include open-marine carbonate and terrigenous sediments. The early Frasnian Sargaevo Horizon is known mainly from boreholes and characterized by fossiliferous limestones, dolomitized limestones, calcareous shales, and clays. The limestones contain bivalves, gastropods, ostracods, corals, and crinoids (Rodionova et al. 1995).

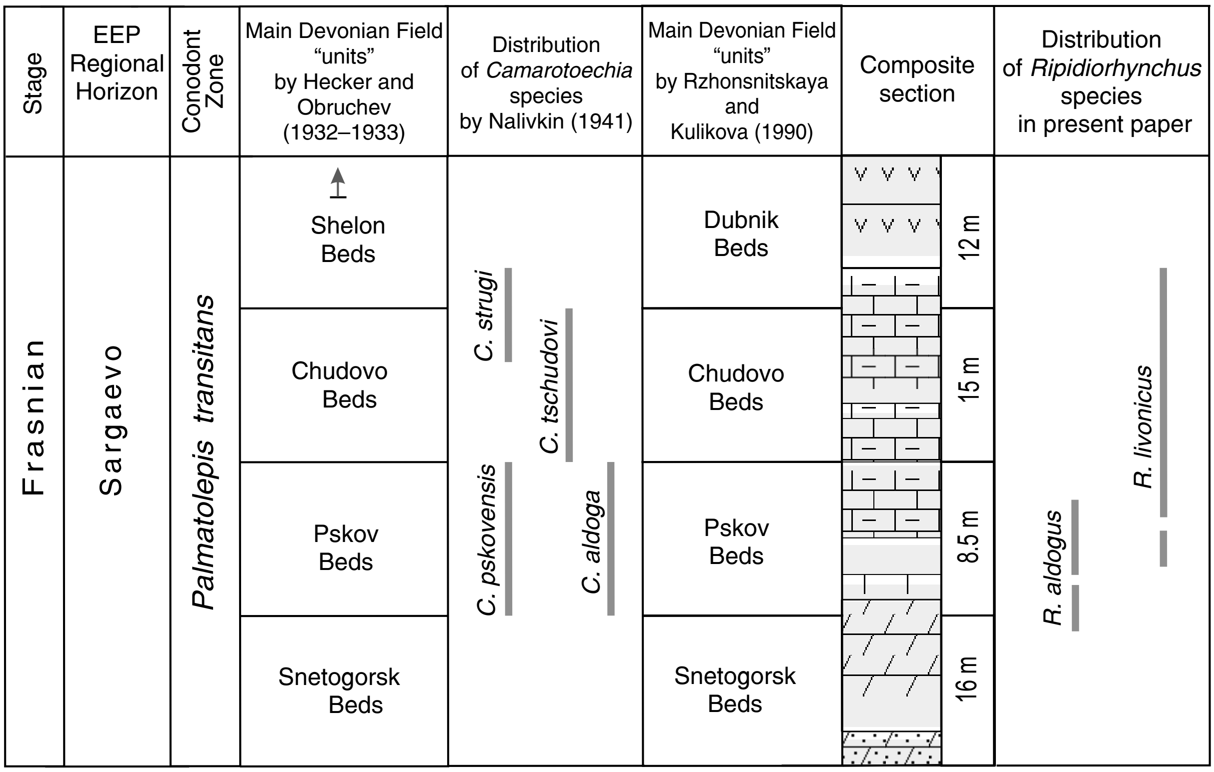

Fig. 4. Distribution of *Ripidiorhynchus* in the early Frasnian of the Main Devonian Field (northwestern region) (Nalivkin's species of *Camarotoechia*). For the legend see Fig. 5.

Rhynchonellid species such as *Ladogia meyendorfii*, *Cupularostrum timanicus,* and *Comiotoechia galinae* are abundant and associated with atrypids (*Pseudoatrypa velikaja, Iowatrypa timanica*) and spiriferids (*Eleutherokomma novosibirica*, *Elita fimbriata*). Strata of the middle Frasnian Semiluki Horizon (*Pa. punctata* Zone) are up to 60 m thick (Rodionova et al. 1995), and overlay deposits of the Sargaevo Horizon. Deposits of the Semiluki Horizon are composed mainly of limestones and marly limestones with brachiopods, bivalves, gastropods, and crinoids. At the same time, on the eastern periphery of the platform the so-called "Domanik" facies developed, characterised by deep-water bituminous–siliceous deposits. The lower part of the Semiluki Horizon is rich in *Tomestenoporhynchus rudkini* (Ljaschenko, 1959) whereas in the upper part *Stenometoporhynchus pavlovi* (Nalivkin, 1930) with "*Pugnax*" *voroni* Nalivkin, 1930 are most characteristic. According to Ljaschenko (1959), pugnacids also occur in the Rechitsa Horizon (Late *Pa. hassi–Pa. jamiae* conodont zones), e.g., "*Pugnax*" *elevatus* Ljashenko, 1959 and "*Pugnax*" *limula* Ljashenko, 1959. The Rechitsa Horizon attains 40 m (Rodionova et al. 1995), and is marked by sandstones and claystones, replaced to the north by carbonates. This unit is most completely represented in Volga–Urals area, where it includes open marine deposits with goniatites (Rzhonsnitskaya 1988).

The late Frasnian Evlanovo and Livny Horizons are composed of shallow water calcareous deposits. Rhynchonellids are represented there only by *Globulirhynchia minima*, restricted to the Evlanovo Horizon (Fig. 5A). According to Aristov (1988), unit contain *Polygnathus australis* (*sensu* Aristov 1988), correlated with the Late *Pa. rhenana* Zone. The Evlanovo Horizon is 80 m thick (Rodionova et al. 1995), and is represented by alternating limestones, marly limestones, claystones and marls. Fossils include diverse brachiopods (mainly *Theodossia* and *Cyrtospirifer*), gastropods, corals, bryozoans, and algae. In the overlying Livny Horizon, rhynchonellids are unknown, where numerous *Theodossia* and *Cyrtospirifer* dominate (Fig. 5B). Early Famennian strata are represented by open marine, carbonate–terrigeneous deposits with many brachiopods, bivalves, gastropods, and crinoids. The earliest Famennian sediments of Volgograd Horizon are absent in the central region. The lower part of the early Famennian (Zadonsk Horizon), up to 25 m thick (Rodionova et al. 1995), is very rich in *Ripidiorhynchus* and *Cyrtospirifer* (Fig. 5C), associated with the pugnacid *Paromoeopygma koscharica* (Nalivkin, 1934). The horizon corresponds to the beds with *Icriodus iowaensis* (*sensu* Aristov 1988), that is correlated with the *Pa. crepida* Zone. The overlying Elets Horizon, up to 105 m thick (Rodionova et al. 1995), is represented mainly by limestones and dolomitized limestones. It is conformable with the Zadonsk Horizon. Brachiopods, ostracods, crinoids algae, and cephalopods are commonly present. This interval is distinguished by the mass appearance of athyrids (Fig. 5D) with *Ripidiorhynchus griasicus* and rare "*Pugnax*" sp.

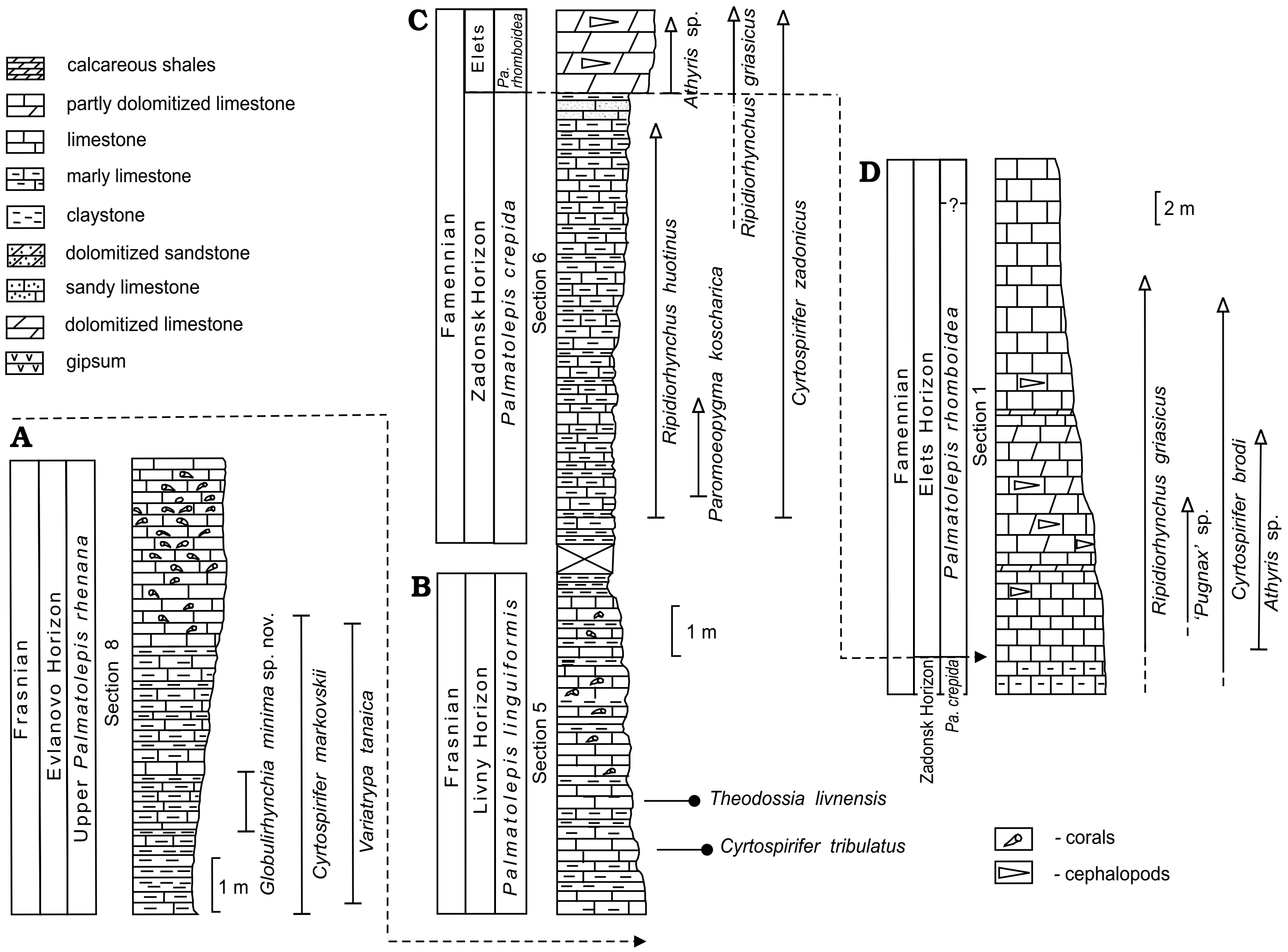

Fig. 5. **A**. Stratigraphic column of section 8 (see Fig. 3B); distribution of *Globulirhynchia minima* sp. nov. and other co-occurring brachiopods within the Evlanovo Horizon. **B**. Stratigraphical column of section 5 (see Fig. 3B); the uppermost part of the Frasnian, Livny Horizon. **C**. Stratigraphical column of section 6 (see Fig. 3B); appearance and distribution of *Ripidiorhynchus huotinus* (Verneuil, 1845) in Zadonsk Horizon. **D**. Stratigraphical column of section 1 (see Fig. 3B); distribution of *Ripidiorhynchus griasicus* (Nalivkin, 1934) in Elets horizon.

Systematic paleontology

Family Trigonirhynchiidae Schmidt, 1965
Subfamily Ripidiorhynchinae Savage, 1996
Genus *Ripidiorhynchus* Sartenaer, 1966
Ripidiorhynchus chencinensis sp. nov.

Figs. 6A–H, 7.

Rhynchonella letiensis Gosselet; Sobolev 1909: 508, pl. 6: 25a, b.
Rhynchonella aff. *R. ferquensis* Gosselet; Sobolev 1909: 508–509, pl. 6: 24a, b.
Ripidiorhynchus aff. *R. pskovensis* Nalivkin; Racki 1993b: 302, pl. 3: A–C, E, J, K.

Holotype: GIUS 4-216/R-10; complete, well preserved shell, illustrated in Fig. 6A–D.

Type locality: Abandoned western quarry, Góra Zamkowa, Chęciny, Holly Cross Mountains, Poland.

Type horizon: Jaźwica Member (set A2; Racki 1993b: 96), late Givetian.

Derivation of the name: From the village of Chęciny, near the type locality.

Diagnosis.—Close to *R. livonicus* but differs in having median rib in sulcus stronger and thinner dental plates internally.

Material.—Six complete and ten damaged shells, and eight incomplete valves.

Description.—Shell medium sized, up to 19 mm long and 21 mm wide, usually wider than long, dorsibiconvex, transversally elliptical in outline; cardinal margin curved, lateral margins rounded; anterior commissure uniplicate.

Ventral valve moderately convex, beak small, slightly incurved, sulcus well marked begins at posterior one-third of the valve length, anteriorly forming long trapezoidal tongue.

Dorsal valve deeper than ventral valve, with well-developed fold that begins at posterior one-third of the valve length.

Shell surface covered by simple ribs beginning from the

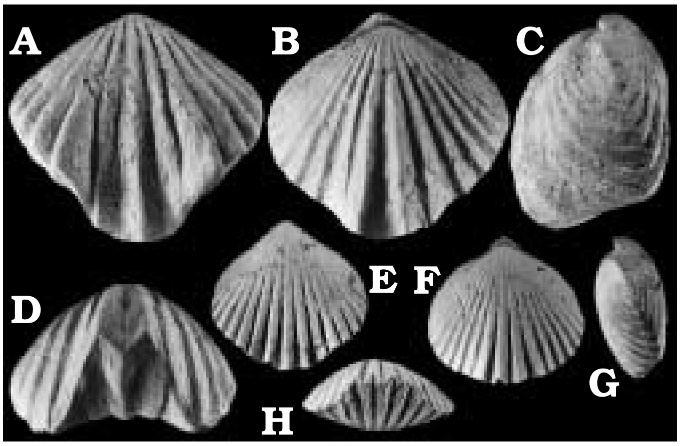

Fig. 6. *Ripidiorhynchus chencinensis* sp. nov. from the late Givetian of Poland. **A**–**D**. Holotype, GIUS 4-216/R-10 in ventral, dorsal, lateral, and anterior views, × 1.5. **E**–**H**. Juvenile shell GIUS 4-216/R-10-1 in ventral, dorsal, lateral, and anterior views, × 1.5. Jaźwica Mbr., Góra Zamkowa.

beaks; 3 ribs on sulcus, with one median rib usually stronger, and 4 ribs on fold, with the medial rib usually stronger; up to 8–9 lateral ribs on each valve flank. Most with smooth fold and sulcus slopes; occasionally, rare parietal rib present.

Ventral interior as for the genus (Fig. 7).

Remarks.—Racki (1993b: 302) described specimens from Góra Zamkowa and Stokówka as *R.* aff. *R. pskovensis* and noted that they are most similar to *R. pskovensis* from the early Frasnian of the Main Devonian Field. He suggested that the rhynchonellid from Poland might represent a new species that is described here. Although *R. chencinensis* sp. nov. proposed here is very close externally to *R. livonicus* (including *R. pskovensis* after revision) it differs from the latter in the usual absence of parietal ribs and development of a strong median rib in the sulcus opposed by two strong ribs on fold; *R. livonicus* has 2–5 equally developed median ribs and 2–3 parietal ribs.

Occurrence.—Latest Givetian (*Pa. falsiovalis* Zone) of the Holy Cross Mountains, Poland: Jaźwica Member at Góra Zamkowa and Stokówka.

Ripidiorhynchus livonicus (Buch, 1834)

Figs. 8 E–P, 9.

Terebratula livonica; Buch 1834: 136, pl. 14: 5.
Camarotoechia pskovensis sp. n.; Nalivkin 1941: 158, pl. 3: 1–4.
Camarotoechia tschudovi sp. n.; Nalivkin 1941: 161, pl. 3: 5–6.
Camarotoechia strugi sp. n.; Nalivkin 1941: 160, pl. 3: 7–10.
Ripidiorhynchus livonicus; Sartenaer 1966: 7, pl. 1: 1–7.

Emended diagnosis.—*R. livonicus* is characterized by highly variable shell morphology expressed in different height and width of tongue, number of radial ribs, internally by varying deflection of crura. From similar *R. huotinus* differs by less convex ventral and dorsal valve, depper sulcus, which begins in the first half of the ventral valve and more long septum, while *R. huotinus* has shallower sulcus beginning in the second half of the ventral valve and short septum. Adult individuals of *R. livonicus* have a well defined and acute tongue, while adult individuals of *R. huotinus* have obtuse tongue and top of the fold near the anterior commisure, curved toward the ventral valve.

Material.— More than 80 specimens.

Remarks.—*Terebratula livonica* was described by Buch (1834) from the early Frasnian of the Main Devonian Field. Until 1960, however type material of the species was lost. In the 1930s, Hecker (1933) and Obruchev (1933) lithostratigraphically subdivided the Frasnian strata of the Main Devonian Field. A few years later Nalivkin (1941) described four new species of *Camarotoechia* from Hecker's and Obruchev's units: *C. aldoga, C. pskovensis, C. tschudovi*, and *C. strugi* (Fig. 4). He included these species in the *livonica* group, and consequently *C. livonica* sensu stricto was abandoned. In 1960 Sartenaer, however, found the type material of *T. livonica* in the Institut für Paläontologie und Museum der math.-

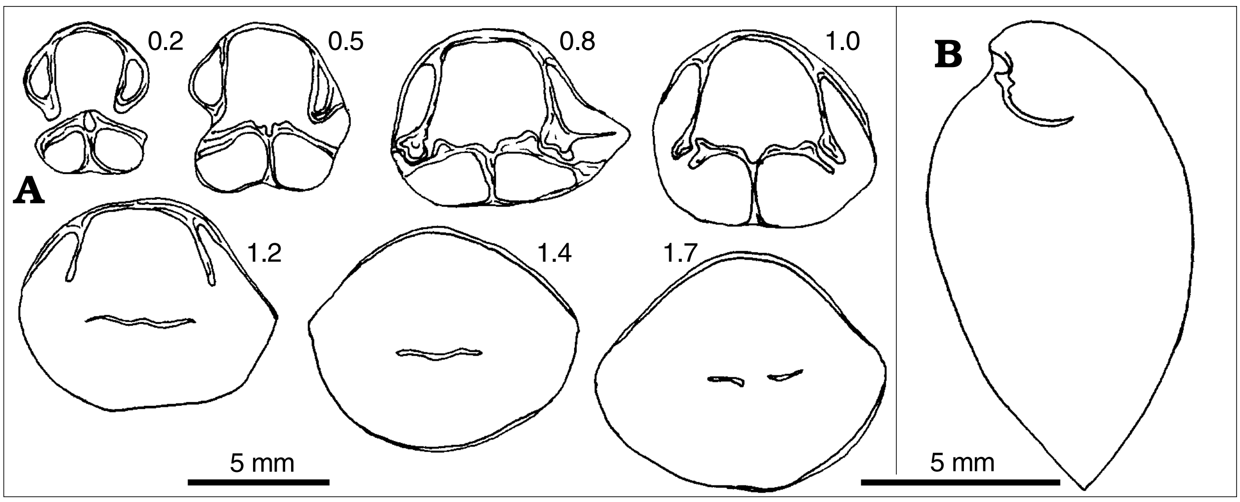

Fig. 7. Transverse serial sections of *Ripidiorhynchus chencinensis* sp. nov. from the Givetian, Jaźwica Mbr., Góra Zamkowa, Poland. Numbers refer to distances in mm from the top of the ventral umbo. **A**. GIUS 4-216/R-10-2. **B**. Longitudinal section of GIUS 4-216/R-10-3.

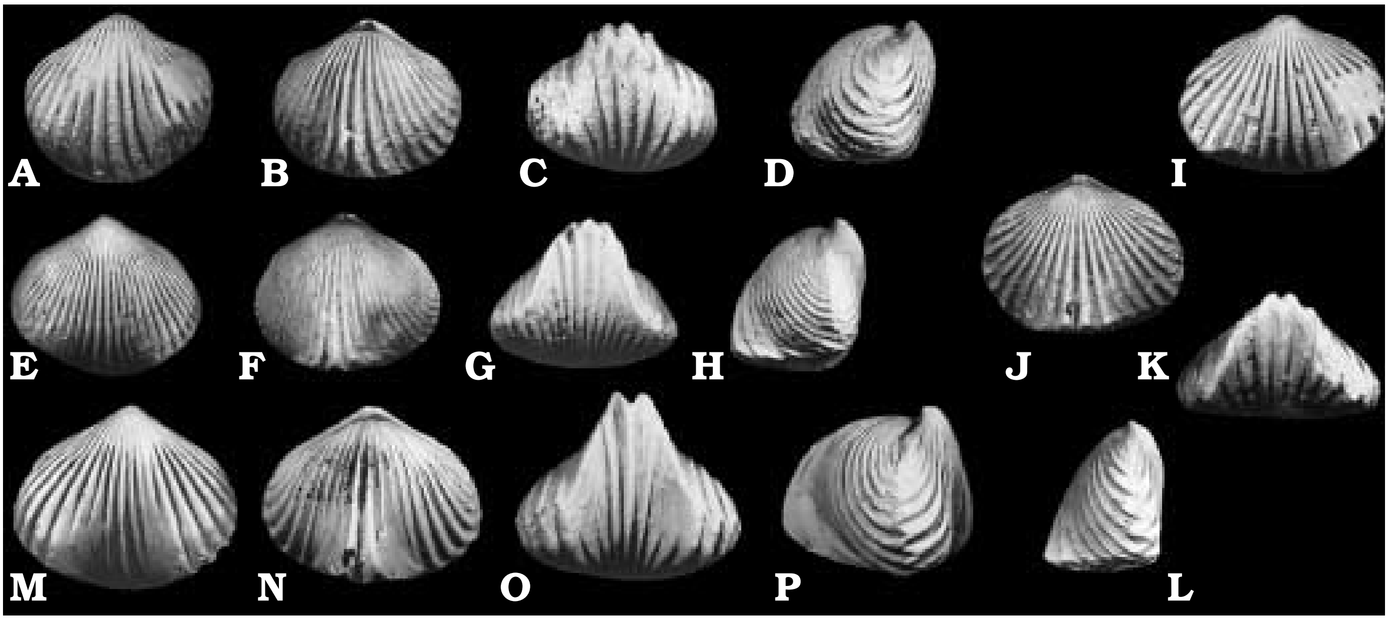

Fig. 8. Early Frasnian (*Pa. transitans Zone) Ripidiorhynchus* from Main Devonian Field, northwestwern Russia. **A**–**D**. *Ripidiorhynchus aldogus* (Nalivkin, 1941), CNIGR 40/6993, ventral, dorsal, anterior, and lateral views. Pskov beds, Sjas River, Konopljankina village. **E**–**P**. *Ripidiorhynchus livonicus* (Buch, 1834). **E**–**H**. CNIGR 45/6993, ventral, dorsal, anterior, and lateral views. Chudovo beds, Velikaya River, Vybuty rapids. **I**–**L**. CNIGR 47/6993, ventral, dorsal, anterior, and lateral views. Chudovo beds, Kerest River, Luki village. **M**–**P**. CNIGR 37/6993, in ventral, dorsal, anterior, and lateral views. Pskov beds, Velikaya River. All × 1.5

naturwissenschaftlichen Fakultät der Humboldt Universität in Berlin (see Sartenaer 1966, 1997) and erected the genus *Ripidiorhynchus*, with *Terebratula livonica* as type species. In addition, he included all of Nalivkin's *Camarotoechia* species from the Main Devonian Field in *Ripidiorhynchus* (Sartenaer, 1966). Furthermore, he assumed that *Ripidiorhynchus pskovensis* was a junior synonim of *R. livonicus*, because they share a high tongue, high and acute median costae strongly indenting the upper part of the tongue, and similar numbers of costae (Sartenaer 1997). Indeed, the lectotype of *Ripidiorhynchus livonicus* (see Sartenaer 1966: pl. 1: 1a–e) is very similar to *R. pskovensis.*

Ripidiorhynchus from the Main Devonian Field shows highly variable features, such as the number of ribs, height and width of tongue, features considered by Nalivkin as diagnostic for his species. For *R. pskovensis*, Nalivkin (1941) noted that this species had 16–22 ribs on the surface of shell. However, the illustrated paratype of *R. pskovensis* (Nalivkin 1941: pl. 3: 1a–d) bears about 40 ribs. The number of ribs on the tongue of *R. pskovensis* is 2–3, as many as in *R. strugi*, illustrated by Nalivkin (1941: pl. 3: 7–10). The representatives of *Ripidiorhynchus* are especially numerous in the upper part of the Chudovo Beds and lower part of the Dubnik Beds in the Izborsk region, but identification of Nalivkin's species is here practically impossible due to the highly variable morphotypes in sampled populations, expressed in the shape of the tongue and the character of shell ribbing. Biometric investigation of more than 60 complete specimens of *Ripidiorhynchus* from the lower part of Dubnik Beds of Izborsk locality showed that they have 16 to 45 ribs per 5 mm from the beak, a tongue height from 5.9 to 14.1 mm, and the number of ribs on the tongue varies from 2 to 5. In fact, the specimens could be interpreted as a co-occurence of *R. strugi*, *R. pskovensis* and *R. tschudovi*.

Sartenaer (1997) noted that the type material of *R. livonicus* originated from four different localities: Gauena on the Gauja River (Central Latvia), Izborsk, Pskov and Chudovo districts (NW Russia). Specimens from these localities are from different levels within the Sargaevo regional stage (i.e., from the Pskov Beds to the Dubnik Beds). The type material of *Ripidiorhynchus livonicus,* illustrated by Sartenaer (1966: pl. 1), is also derived from different stratigraphic levels. Thus, it is here considered that *R. pskovensis*, *R. tschudovi* and *R. strugi* are synonyms of the long-ranging form *R. livonicus* (see Fig. 4).

The oldest representatives of *Ripidiorhynchus* are known from the Main Devonian Field of the upper part of the Snetogorsk Beds (Sorokin 1978) and are assigned to *R. aldogus* (Nalivkin, 1941). *Ripidiorhynchus aldogus* differs from *R. livonicus* by its more convex shell, obtuse shell margin, low tongue and weakly developed fold. The various species of "*Camarotoechia*" described by Nalivkin (1941) are reillustrated here in Fig. 8.

Occurrence.—Early Frasnian, *Pa. transitans* Zone, Sargaevo Horizon, northwestern Russia, Latvia, and Lithuania.

Ripidiorhynchus huotinus (Verneuil, 1845)

Figs. 10A–I, 11, 12.

Terebratula huotina; Verneuil 1845: 81, pl. 10: 4.

Rhynchonella livonica; Venyukov 1886: 534, pl. 5: 2, 3, 7.

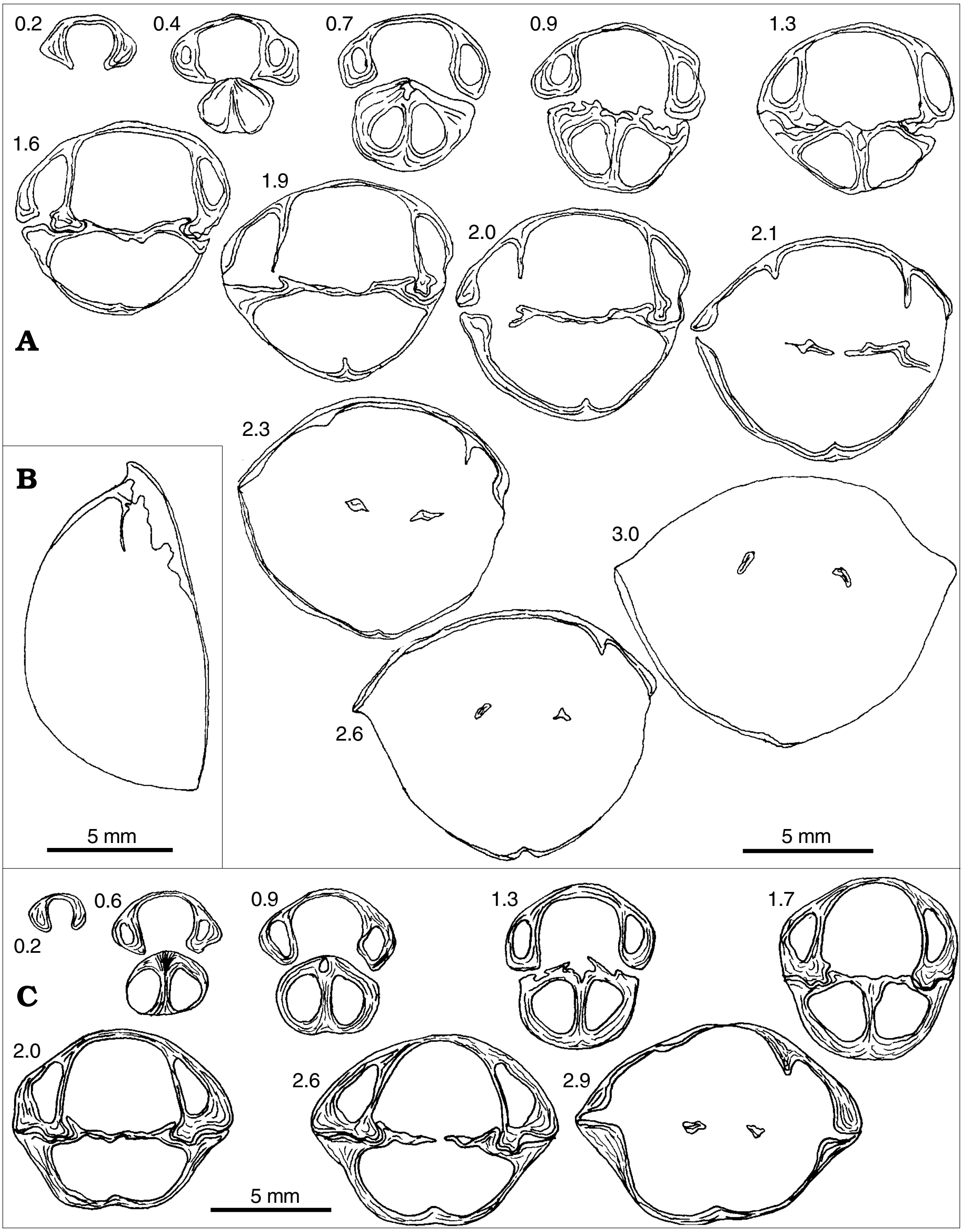

Fig. 9. Transverse serial sections of *Ripidiorhynchus livonicus* (Buch, 1834) from the early Frasnian of the Main Devonian Field, northwestern Russia. Numbers refer to distances in mm from the top of the ventral umbo. **A**. CNIGR 1/13076. **B**. Longitudinal section. CNIGR 2/13076, Chudovo beds, Vybuty rapids, Velikaya River, Pskov region. **C**. CNIGR 3/13076, Dubnik beds, quarry near town Stary Izborsk, Pechory district.

Camarotoechia huotina; Nalivkin 1934: 22, pl. 2: 4–6.
Camarotoechia zadonica n. sp.; Nalivkin 1934: 23, pl. 3: 1–8.
Camarotoechia zadonica; Sarycheva and Sokolskaya 1952: 163, pl. 46: 246.
Camarotoechia huotina; Ljashenko 1959: 205, pl. 76: 1, 2.
Camarotoechia zadonica; Ljashenko 1959: 205, pl. 76: 3–5.

Emended diagnosis.—Internally *R. huotinus* have short septum and lenticular crura, which are strongly curved ventrally. Closely related *R. griasicus* differs mainly by smaller sizes, shallow and wide sulcus, combined with the greatest width of shell situated nears the anterior margin.

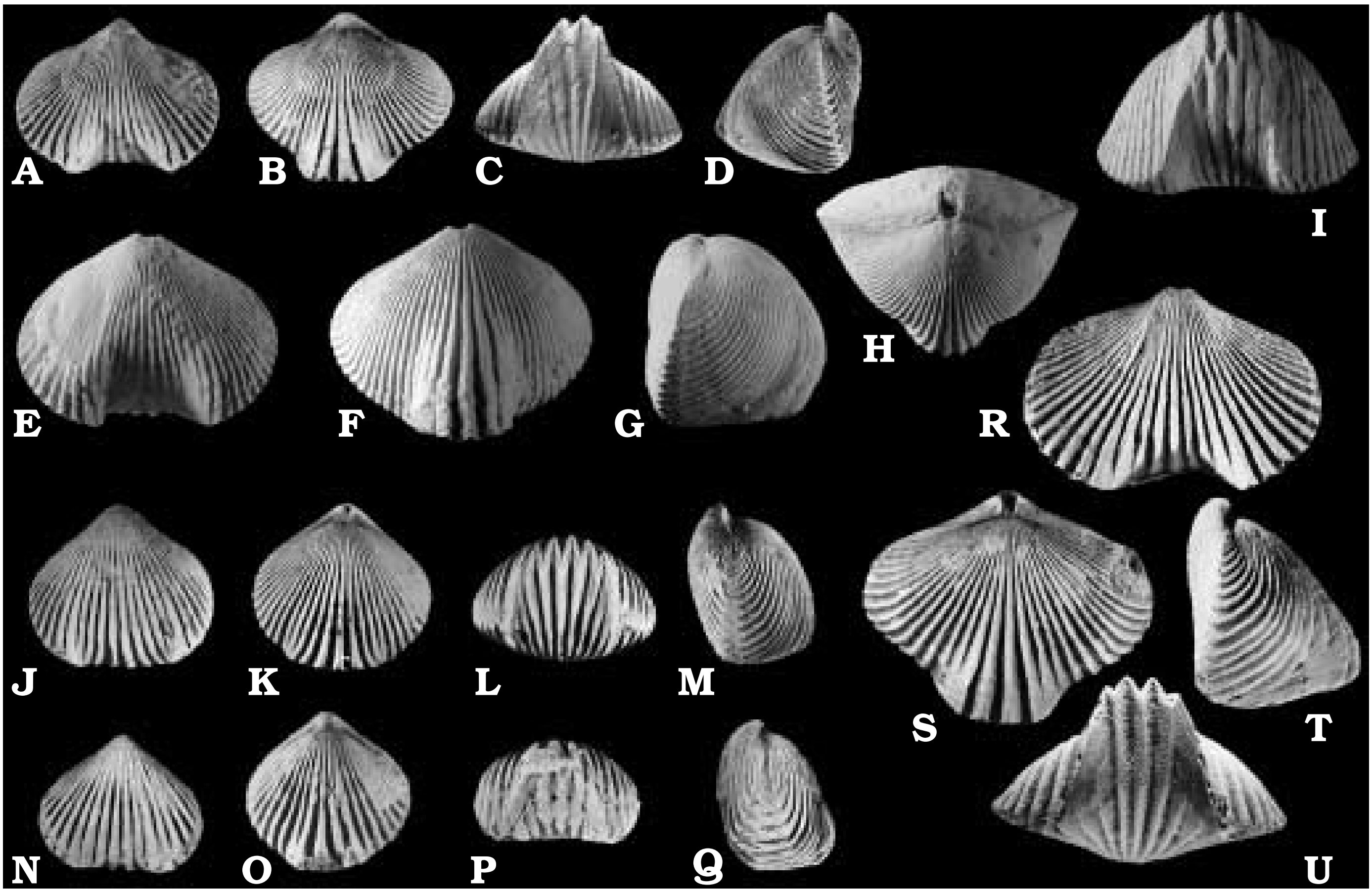

Fig. 10. **A**–**I**. *Ripidiorhynchus huotinus* (Verneuil, 1845). **A**–**D**. CNIGR 763/4572 from the early Famennian, Zadonsk Horizon, central regions of Russia, in ventral, dorsal, anterior, and lateral views. Sosna River basin. **E**–**I**.CNIGR 4/13076, ventral, dorsal, lateral, posterior, and anterior views. Kamenka village. **J**–**Q**. *Ripidiorhynchus griasicus* (Nalivkin, 1934), from early Famennian, Elets Horizon, Sosna River basin. **J**–**M**. Neotype. CNIGR 266/4572, ventral, dorsal, anterior, and lateral views. **N**–**Q**. CNIGR1046/4572, ventral, lateral, dorsal, and anterior views. **R**–**U**. *Ripidiorhynchus cernosemicus* (Nalivkin, 1934) CNIGR 862/4572, ventral, dorsal, anterior, and lateral views. Early Famennian, Zadonsk Horizon, Sosna River basin. All × 1.5.

Material.— More than 50 specimens.

Remarks.— Sartenaer (1966) included in the genus *Ripidiorhynchus* five early Famennian species from central regions: *Terebratula huotina* Verneuil, 1845, *Camarotoechia cernosemica* Nalivkin, 1934, *C. zadonica* Nalivkin, 1934, *C. brodica* Nalivkin, 1934, and *C. griasica* Nalivkin, 1934. Originally, *Terebratula huotina* was described by Verneuil (1845) from Zadonsk region of the central Russia, i.e. from the Zadonsk Horizon. Verneuil (1845) noted that this species occurs in the Orel district and in the Chudovo district to the northwest. Thus, he apparently combined the early Famennian (*Pa. crepida* Zone) *R. huotinus* with the early Frasnian *R. livonicus.* Nalivkin (1934) described *Camarotoechia zadonica* from the Zadonsk Horizon of the Elets and Russkii Brod districts. According to Nalivkin (1934), the main difference between this species and *C. huotina*, concerns a narrower fold, higher triangular tongue and more numerous ribs in *C. zadonica*. He also noted that *C. zadonica* has 12–15 ribs on each side of the shell, 2–4 in sulcus, and 2–3 parietal ribs. On the other hand *C. huotina* shows 15–18 ribs on each flank of the valve, 2–4 in sulcus, and 2–3 parietal ribs. Nalivkin (1934: 22–23) wrote that *C. huotina* is a variety of *C. zadonica*, because they are similar and occur together, but the latter species has a wider distribution. The development of dorsal fold curvature near the anterior margin, as the diagnostic feature of *huotina*, depends on the age of the shell (Fig. 11). Thus, *Ripidiorhynchus zadonicus* should be regarded as a junior synonym of *Ripidiorhynchus huotinus*.

Nalivkin (1934) described *C. cernosemica* (Fig. 10Q–T) from the Zadonsk Horizon. This species co-occurs with *C. zadonica* and *C. huotina*, and, according to Nalivkin, is distinguished by its flat umbonal region of the dorsal valve, wide beak and transversally elliptical shell outline.

Occurrence.—Early Famennian, *Pa. crepida* Zone, Zadonsk Horizon, central Russia.

Ripidiorhynchus griasicus (Nalivkin, 1934)

Figs. 10J–Q, 13.

Rhynchonella livonica; Venjukov 1886: pl. 5: 6.
Camarotoechia griasica; Nalivkin 1934: 23, pl. 3: 1–6.
Camarotoechia brodica; Nalivkin 1934: 24, pl. 3: 9–14.
Camarotoechia griasica; Nalivkin 1947: 37, pl. 19: 8.
Camarotoechia brodica; Ljashenko 1959: 212, pl. 81: 4, 5.

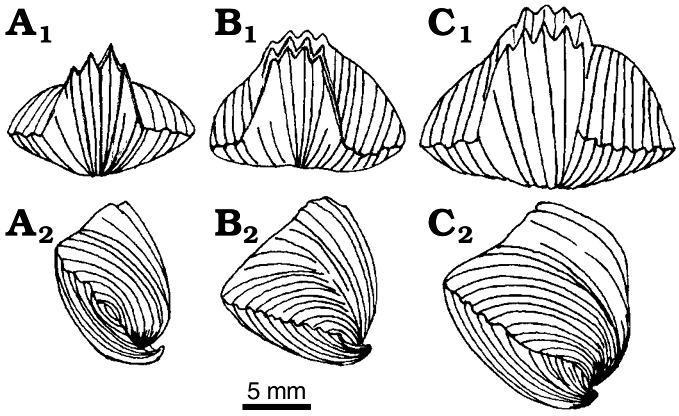

Fig. 11. Growth changes of shell of the *Ripidiorhynchus huotinus* (Verneuil, 1845) from the early Famennian, Zadonsk Horizon, Kamenka village, showing different fold deflection of the dorsal valve. **A**. CNIGR 5/13076. **B**. CNIGR 6/13076. **C**. CNIGR 4/13076.

Camarotoechia griasica; Ljashenko 1959: 212, pl. 81: 6, 7.

Neotype.—Complete shell from the Nalivkin collection (1934), CNIGR 266/4572, Fig. 10I–L.

Emended diagnosis.—Small Ripidiorhynchinae externally closely related to *Hunanotoechia tieni* described by Ma (1993) from the late Frasnian of the central Hunan, but latter have a broader septalium without connectivum.

Material.— Above 40 specimens.

Remarks.—Camarotoechia griasica was described by Nalivkin (1934) from the Elets Horizon of the central regions of the Russia (Griasi, Lipetsk, Elets, and Russkii Brod districts). Nalivkin (1934) also described *C. brodica*, as that rare form co-occurs with the former species in the Elets Horizon of Russkii Brod district. According to Nalivkin (1934: 24) the diagnostic characters of *C. brodica* are its flattened lateral flanks and a more convex dorsal valve. He noted that *C. griasica* has 8–12 lateral ribs, 4–5 ribs in sulcus, and 1–2 parietal ribs, whilst *C. brodica* bears 8–12 lateral ribs, 4 ribs in the sulcus and 1–2 parietal ribs. However, the greater convexity of the dorsal valve of *C. brodica* (see Nalivkin 1934: pl. 4: 11I–L) is a variable feature. External and internal shell morphology of these co-occuring species is very similar; consequently, *C. brodica* is considered here as a junior synonym of *C. griasica*.

Nalivkin originally has not chosen holotypes for *C. griasica* and *C. brodica,* therefore, a neotype of *Ripidiorhynchus griasicus* is selected here.

Occurrence.—Early Famennian, *Pa. crepida–Pa. rhomboidea* zones, Elets Horizon, central Russia.

Family Pugnacidae Rzhonsnitskaya, 1956
Genus *Globulirhynchia* Brice, 1981
Globulirhynchia minima sp. nov.

Figs. 14A–E, 15.

Pugnax lummatoniensis (Davidson, 1864); Sarycheva and Sokolskaya 1952: 167, pl. 47: 256.

Pugnax lummatoniensis; Ljashenko 1959: 197, pl. 70: 8, 9.

Holotype: Complete shell CNIGR 13/13076, illustrated in Fig. 14A–D.

Type locality: Zadonsk area, Don River basin, central Russia.

Type horizon: Evlanovo Horizon, Late *Pa. rhenana* Zone.

Derivation of the name: From small size of shell.

Diagnosis.—This small, smooth pugnacid is closely related to *Globulirhynchia lemesli* Brice, 1981, but differs from the latter by a smaller sizes and less convex shell. Internally *G. minima* has shorter dental plates whilst *G. lemesli* exhibits longer dental plates.

Material.—50 complete shells.

Description.—Shell small size, up to 8 mm long and 9 mm wide, usually wider than long; biconvex to dorsibiconvex; subpentagonal in outline; cardinal margin short and slightly curved; lateral and anterior margins rounded; anterior commissure uniplicate.

Ventral valve with well-defined and convex umbo; beak small, slightly incurved; mesothyrid foramen with open delthyrium; wide sulcus starting in anterior half of the valve; tongue high and trapezoidal.

Dorsal valve sometimes slightly more convex than ventral valve; low fold starting in anterior part of valve. Umbonal part smooth; low, rounded and infrequent ribs begin near to the anterior margin of shell; two low ribs are on flanks; 2–3 on fold and 1–2 on sulcus. Shell surface smooth, with concentric growth lines rarely preserved.

Ventral interior with short dental plates that are divergent in apical part, and parallel anteriorly. Crural bases directed dorso-laterally.

Remarks.—The *G. minima* was previously (Sarycheva and Sokolskaya 1952; Ljashenko 1959) described as *Pugnax lummatoniensis* (Davidson 1864). The investigation of recently collected material showed that this form is indeed related to *Globulirhynchia lemesli* from the early Frasnian of Ferques (Biozone 2 in Brice et al. 1976, *Po. asymmetricus* Zone: see Brice 1981). It is possible, that "*Pugnax*" *limula* Ljashenko, 1959 and "*Pugnax*" *elevatus* Ljashenko, 1959, from the Rechitsa Horizon (Late *Pa. hassi–Pa. jamiae* conodont zones) of the central Russia could be referred to *Globulirhynchia* after their restudy.

Occurrence.—Late Frasnian, Evlanovo Horizon, Late *Pa. rhenana* Zone, central Russia.

Genus *Paromoeopygma* Sartenaer, 1968
Paromoeopygma koscharica (Nalivkin, 1934)

Figs. 14F–M, 16.

Pugnax koscharica n. sp.; Nalivkin 1934: 24, pl. 2: 1–3.
Pugnax koscharica Nalivkin; Ljashenko 1959: 205, pl. 75: 7.
Paromoeopygma koscharica Nalivkin; Pushkin 1986: 73–74, pl. 1: 6.

Emended diagnosis.—*P. koscharica* differs from type species of genus *P. bellicastellana* Sartenaer, 1968, mainly by its parallel or slightly divergent dental plates and laterally directed crura, while *P. bellicastellana* is characterized by divergent dental plates and dorso-laterally directed crus.

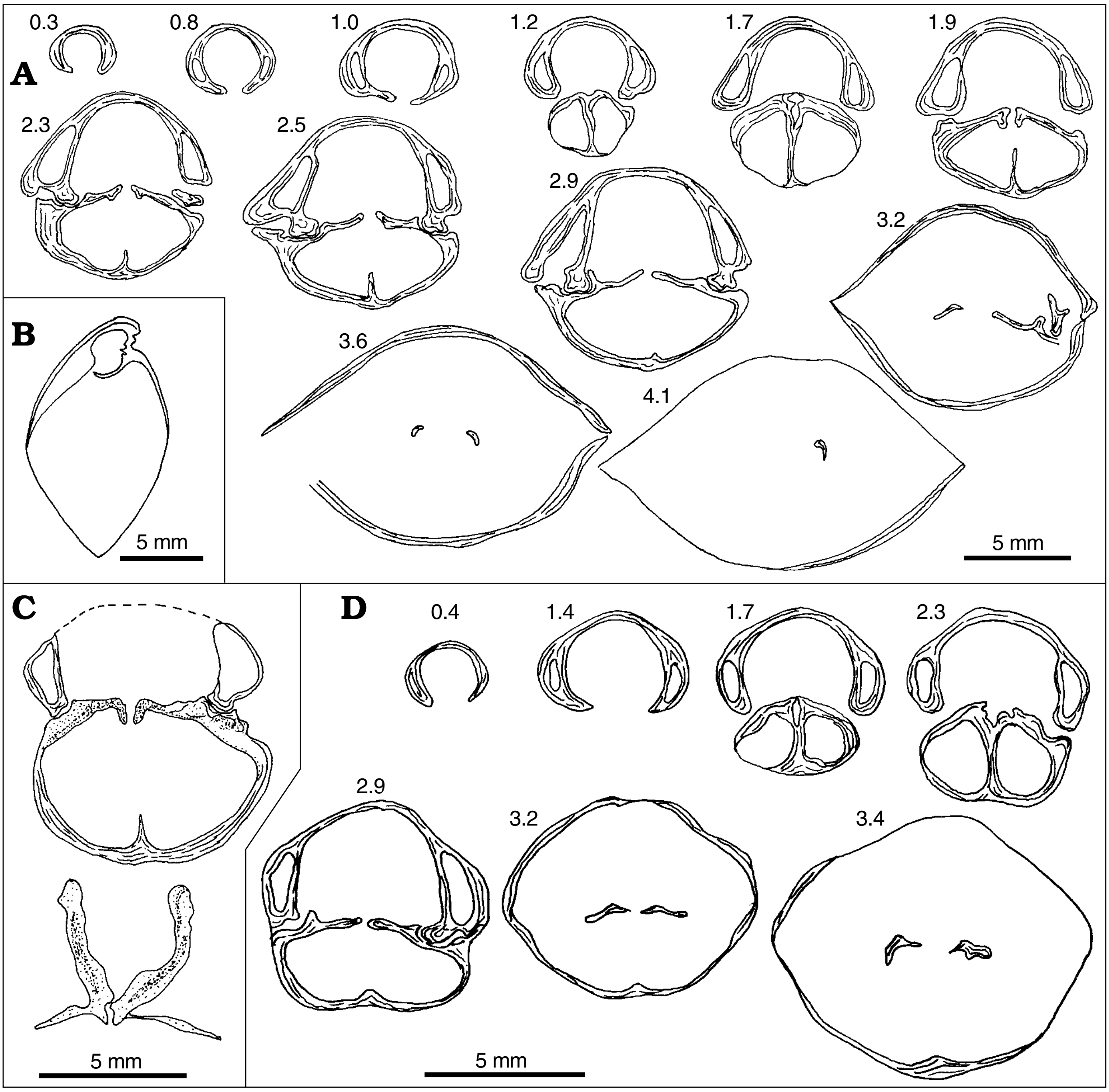

Fig. 12. **A**. Transverse serial section of *Ripidiorhynchus huotinus* (Verneuil, 1845). Numbers refer to distances in mm from the top of the ventral umbo, CNIGR 7/13076. **B**. Longitudinal section. CNIGR 8/13076. **C**. Reconstruction of the crural plates, CNIGR 9/13076. Early Frasnian, Zadonsk Horizon, Kamenka village, Elets region. **D**. CNIGR 10/13076 Zadonsk Horizon, Zadonsk region.

Neotype.—Complete shell from the Nalivkin collection CNIGR 1085/4572, Fig. 14F–I.

Material.—Five well preserved shells (including three specimens from Nalivkin's collection).

Description.—Shell medium-sized, dorsibiconvex, subelliptic to suboval in outline; short curved hinge line, lateral and anterior margins rounded; anterior commissure uniplicate.

Ventral valve moderately convex, beak small, slightly incurved, wide and shallow sulcus starts at anterior part of the valve, tongue high and rounded. Dorsal valve deeper than ventral valve; weakly defined fold begins at anterior part of the valve.

Shell smooth with exception of coarse, rounded ribs developed near the anterior margin only. Microornamentation of radial striae (8 per 1mm); growth lines rarely preserved. Internally with nearly parallel dental plates; median septum absent. Crural bases directed laterally.

Remarks.—Originally this species was referred by Nalivkin (1934) to *Pugnax,* but he noted, that fine radial striae on the surface of the shell of *P. koscharica* distinguish it from other species of *Pugnax.* Furthermore he noted, that presence of striae is a very important feature and possibly this species should be assigned to a new genus (Nalivkin 1934; Pushkin 1986). On the base of microornamentation Pushkin (1986)

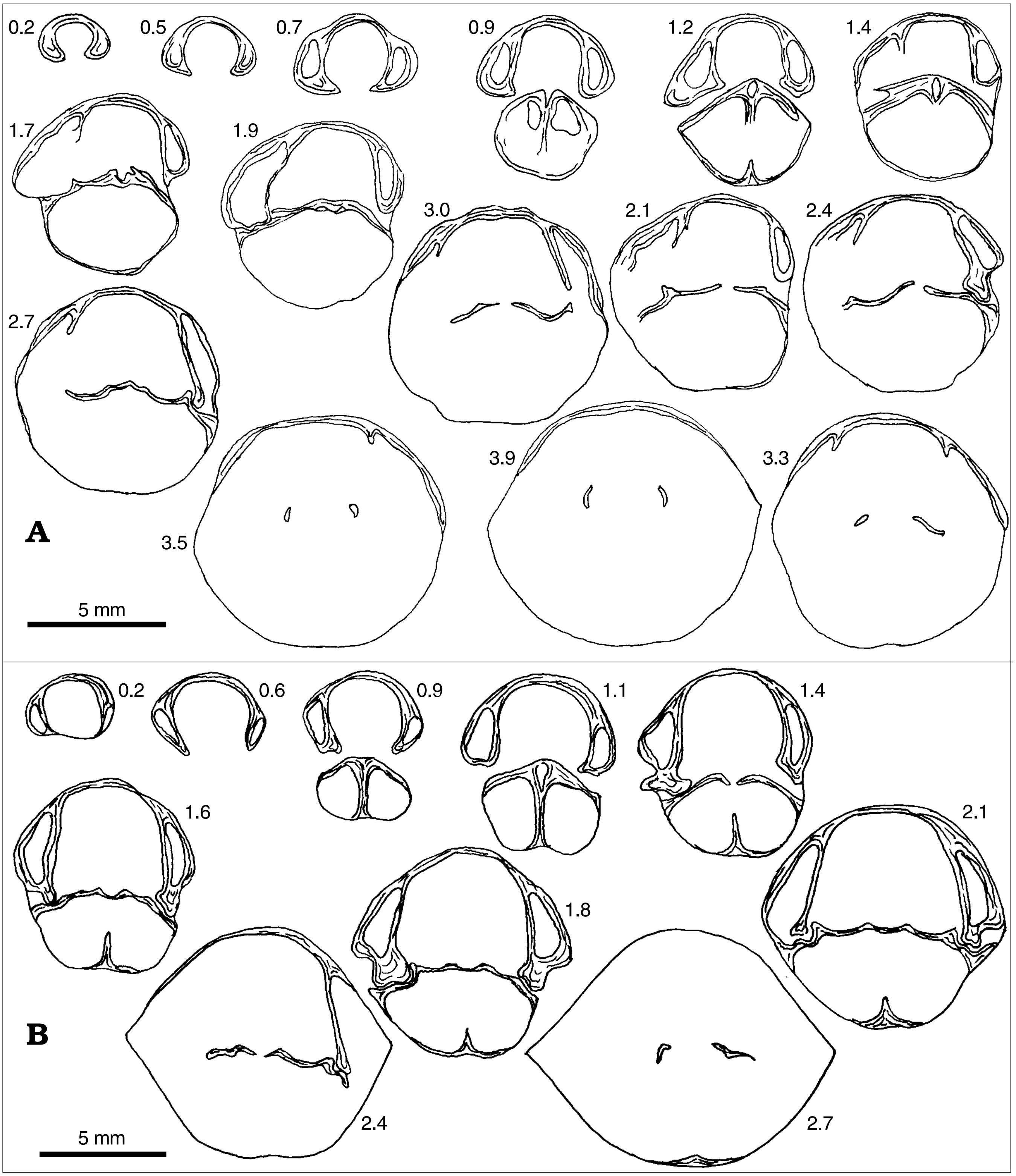

Fig. 13. Transverse serial sections of *Ripidiorhynchus griasicus* (Nalivkin, 1934) from the early Famennian, Elets Horizon. Numbers refer to distances in mm from the top of the ventral umbo. **A**. CNIGR 11/13076. Argamach quarry, Elets region, **B**. CNIGR 12/13076. Lavy quarry, Elets region.

transferred *Pugnax koscharica* to *Paromoeopygma*. Furthermore, he assigned to this genus some early Famennian species from Byelorussia: *P. janischevskii*, *P. sergei*. It should be noted, that *P. komarovichensis,* which he included in *Paromoeopygma* (see Pushkin 1986: 73), is the type species of his genus *Striatorhynchus* (see Pushkin 1986: 91); it fol-

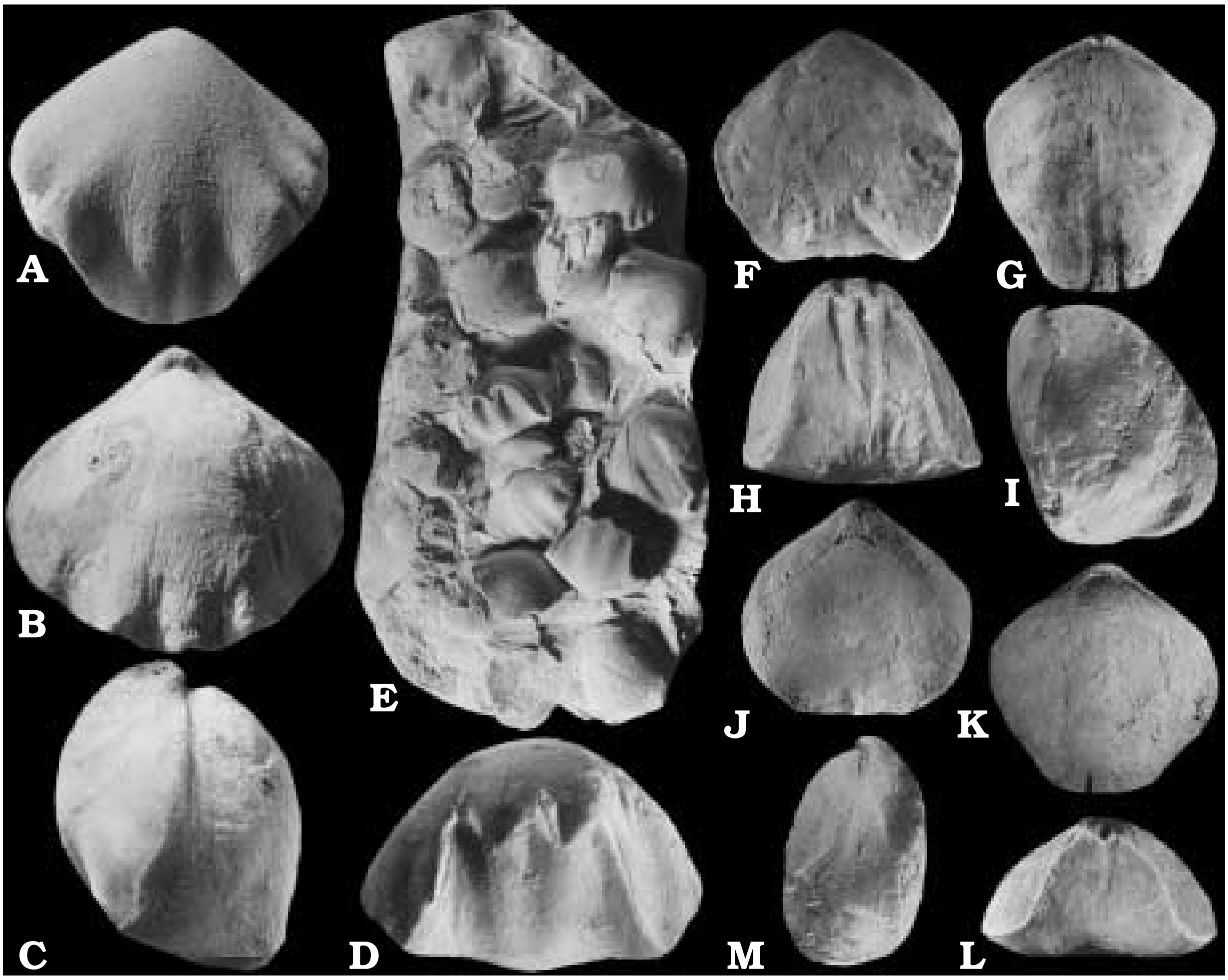

Fig. 14. **A**–**E**. *Globulirhynchia minima* sp. nov. from late Frasnian, Evlanovo Horizon, Chlevnoe village, Don River Basin. **A**–**D**. Holotype, CNIGR 13/13076, ventral, dorsal, lateral, and anterior views, × 5. **E**. CNIGR 14/13076, × 2. **F**–**M**. *Paromoeopygma koscharica* (Nalivkin, 1934) from early Famennian, Zadonsk Horizon, Koschary village, Zadonsk region. **F**–**I**. Neotype, CNIGR 1085/4572 ventral, dorsal, anterior, and lateral views, × 1.5. **J**–**M**. CNIGR 1083/4572, × 1.5.

lows that probably his attribution to *Paromoeopygma* was a mistake. All these species are characterized externally by presence of fine striae, internally by parallel dental plates and absence of dorsal septum, except *Striatorhynchus komarovichensis* that has a dorsal septum. Although these species have similar internal and external morphology to *Paromoeopygma*, they differ from *P. koscharicus* generally by their shorter dental plates.

Occurrence.—Early Famennian, *Pa. crepida*–*Pa. rhomboidea* zones, Elets Horizon, central Russia; Byelorussia.

Discussion

It is remarkable, that only representatives of Trigonirhynchiidae and Pugnacidae crossed the Frasnian–Famennian boundary, in the central regions of the East European Platform. These families had a world-wide distribution in shallow shelf environments during early Frasnian–early Famennian interval. When comparing development of the rhynchonellid groups from the East European shelf, pugnacids were present continuously during the whole Late Devonian, whilst trigonirynchiids occurred sporadically. The pugnacids appeared during the Early Devonian, and became most diverse in the Famennian (12 genera, see Savage 1996). On the northwestern and central region of the platform this is a low diversity brachiopod group during the mid-Frasnian to early Famennian interval (Fig. 2), but in contrast to Trigonirhynchiidae the pugnacids occur also in late Frasnian (“*Pugnax*”, *Globulirhynchia*). During early Famennian, pugnacids were represented by genus *Paromoeopygma*, which participated in the medium diversity rhynchonellid–cyrtospiriferid brachiopod assemblages.

The first Trigonirhynchiidae are known from middle Ordovician, but they were most diverse during Early–Middle Devonian. According to Savage (1996), 26 genera were present in this interval. During Late Devonian, however, they were taxonomically impoverished (15 genera by Savage 1996), and during Early Carboniferous they totally disappeared.

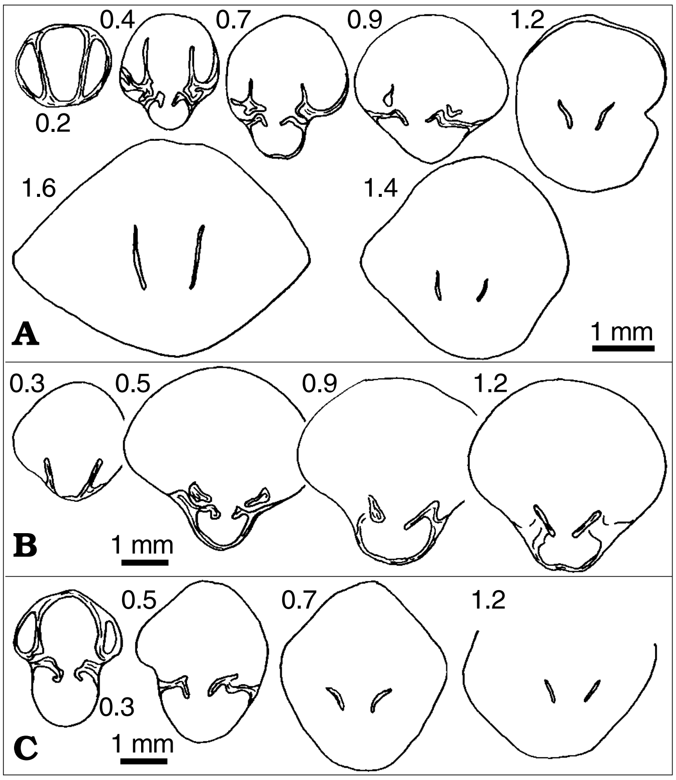

Fig. 15. Transverse serial sections of *Globulirhynchia minima* sp. nov. from the early Famennian, Evlanovo Horizon, Don River basin, Zadonsk region, central Russia.Numbers refer to distances in mm from the top of the ventral umbo. **A**. CNIGR 15/13076. **B**. CNIGR 16/13076. **C**. CNIGR 17/13076.

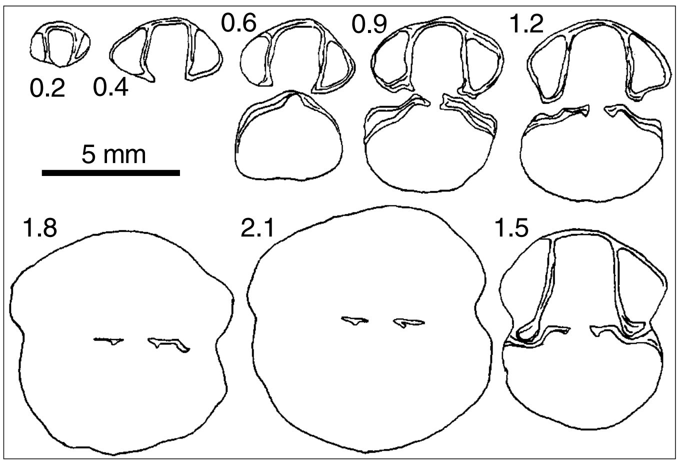

Fig. 16. Transverse serial sections of *Paromoeopygma koscharica* (Nalivkin, 1934) from the early Famennian, Zadonsk Horizon, Don River Basin, Zadonsk region. Numbers refer to distances in mm from the top of the ventral umbo, CNIGR 18/13076.

The Trigonirhynchiidae from the northwestern region of the EEP include only *Ripidiorhynchus,* while Late Devonian Trigonirhynchidae from the central Russia include five genera: *Cupularostrum*, *Ripidiorhynchus*, *Sinotectirostrum*, *Macropotamorhynchus* and *Centrorhynchus* (Rodionova et al. 1995). The early Frasnian genus *Comiotoechia* was removed from Trigonirhynchiidae by Savage (1996) and assigned to Ladogiidae.

Ripidiorhynchus was a common component of the shallow marine benthic communities of Laurussia and Gondwana during the Frasnian and early Famennian times. Sartenaer (1985) discussed the stratigraphic significance of this genus. This author noted that the presence of an early representative of the genus in the late Givetian of Poland (Racki 1993b) cannot be rejected. Therefore, initial expansion of *Ripidiorhynchus* to northwestern region of platform and to the Ardenne shelf possibly began from the Polish region during the early Frasnian transgression. It is noteworthy, that *Ripidiorhynchus* was one of the first brachiopods, which appeared in platform habitats during the Frasnian. *Ripidiorhynchus* is not known from the late Frasnian of the East European Platform, but it reappeared unexpectedly in mass occurrences in early Famennian of the central region, Volga-Ural and possibly South Timan (Yudina 1999), where it occurs in high density assemblages with cyrtospiriferids. Representatives of *Ripidiorhynchus* are common pioneer species that rapidly recolonized vacated ecospace after the F–F extinction event. In addition, Lazarus effect can be considered for *Ripidiorhynchus* from East European Platform, because the genus reappeared suddenly during and after the flood of ecological generalists in the early Famennian (see Harris et al. 1996).

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References

Alekseev, A.S, Kononova, L.I., and Nikishin, A.M. 1996. The Devonian and Carboniferous of the Moscow Syneclise (Russian Platform): stratigraphy and sea-level changes. *Tectonophysics* 268: 149–168.

Aristov, V.A. 1988. *Devonskie konodonty Central'nogo Devonskogo Polâ*. 120 pp. Nauka, Moskva.

Bekker, H. 1924. The Devonian rocks of the Irboska district (S.E. Estonia) with the description of a new cemented brachiopod. *Archiv Naturkunde Estlands, I Ser.*, Bd. 10, T. 1: 1–55.

Brice, D. 1981. Nouvelles observations sur les Orthida et les Rhynchonellida (Brachiopodes) du Frasnian de Ferques (Boulonnais). *Annales de la Societé Geologique du Nord C (1980, 3e trimestre):* 139–153.

Brice, D., Bultynck, P., Colbeaux, J.P., Lethiers, F., Mistiaen, B., Rohart, J.Cl., and Bigey, F. 1976. Une novelle coupe dans le Devonien de Ferques. *Annales de la Societé Geologique du Nord* 46: 135–155.

Buch, L. 1834. Über Terebrateln, mit einem Versuch, sie, zu classificiren und zu beschreiben. *Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin*, 21–144.

Davidson, T. 1864. A monograph of the British Devonian Brachiopoda. *Paleontographical Society I* 3: 1–131.

Harries, P.J., Kauffman, E.G., and Hansen, T.A. 1996. Models for biotic survival following mass extinction. *In*: M.B. Hart (ed.), Biotic Recovery from Mass Extinction Events. *Geological Society Special Publication* 102: 41–60.

Hecker, R.F. 1933. Carbonate rocks of Devonian deposits [in Russian]. *In*: E.P. Bruns and S.G. Višnâkov (eds.), *Karbonatnye porody Leningradskoj oblasti, Severnogo kraâ i Karel'skoj ASSR*, Vypusk 2, 16–43. Gosudarstvennoe naučno-techničeskoe gorno-geologo-neftânoe izdatel'stvo, Leningrad.

Hecker, R.F. 1964. "Schelonian problem" and its general methodic significant [in Russian]. *In*: V. Karatajüte-Talimaa and V. Narbutas (eds.), *Voprosy stratigrafii i paleogeografii devona Pribaltiki*, 104–112. Mintis, Vilnus.

Johnson , J.G., Klapper, G., and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin* 96: 567–587.

Lyashenko, A.I. [Lâšenko, A.I.] 1959. *Atlas brahiopod i stratigrafiâ devonskih otloženij central'nyh oblastej Russkoj Platformy.* 451 pp. Gostoptehizdat, Moskva.

Ma, X.P. 1993. *Hunanotoechia*: A new Late Devonian Rhynchonellid brachiopod from Xikuangshan, Hunan, China. *Acta Palaeontologica Sinica* 32: 716–724.

Markovskii, B.P. [Markovskij, B.P] and Nalivkin, D.V. 1934. The Zadonsk and the Elets beds [in Russian]. *Trudy Glavnogo Geologo-Gidrogeodezičeskogo Upravleniâ* 313: 1–38.

McGhee, G.R. 1992. Evolutionary biology of the Devonian brachiopoda of New York State: No correlation with rate of change of sea-level? *Lethaia* 25: 165–172.

McGhee, G.R. 1996*. The Late Devonian Mass Extinction. The Frasnian–Famennian Crisis*. 303 pp. Columbia University Press, New York.

Nalivkin, D.V. 1930. The Semiluki and the Voroneje Beds of the Upper Devonian of Voroneje region [in Russian]. *Izvestiâ Geologorazvedočnogo Upravleniâ* 49: 53–93.

Nalivkin, D.V. 1934. Description of faunan [in Russian]. *In*: B.P Markovskii and D.V. Nalivkin (eds.), Zadonskie i Eleckie sloi. *Trudy Glavnogo geologo-razvedočnogo Upravleniâ* 313: 17–55.

Nalivkin, D.V. 1941. Brachiopods of the Main Devonian Field [in Russian]. *In*: A.A. Borisâk and R.F. Hecker (eds.), *Fauna Glovnogo devonskogo polâ, 1*, 139–221. Paleontologičeskij Institut AN SSSR, Moskva.

Nalivkin, D.V. 1947. Brachiopods [in Russian]. *In:* D.V. Nalivkin (ed.), *Atlas rukovodâŝih form iskopaemyh faun SSSR*, III, 63–134. Geologoizdat, Leningrad.

Novozhilova, S.I. [Novožilova, S.I.] 1955. Devonian brachiopods of Kuibyshev and Chkalov districts [in Russian]. *Trudy Vsesoûznogo Neftânnogo Naučno-Issledovatel'skogo Geologorazvedočnogo Instituta, Novaâ Seriâ* 88: 61–106.

Obrutchev, D.V. [Obručev, D.V.] 1933. Note on stratigraphy of Middle Devonian of the Leningrad district [in Russian]. *Zapiski Mineralogičeskogo Obŝestva, Seriâ 2*, Vypusk 2: 405–420.

Ovnatanova, N.S. and Kononova, L.I. 1999. Shallow-water Frasnian conodont assemblages from Central part of Russian Platform [in Russian]. *Bûletin Moskovskogo Obŝestva Ispytatelej Prirody, Otdel Geologičeskij* 74 (1): 56–68.

Pushkin, V.I. [Puškin, V.I.] 1986. Famennian rhynchonellids (Brachiopoda) of Byelorussia [in Russian]. *In*: P.A. Gareckii, S.F. Zubovič, and V.I. Puškin (eds.), *Novye i maloizvestnye vidy životnyh i rastenii Belorussii*, 63–96. Nauka i tehnika, Minsk.

Racki, G. 1993a. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37: 87–182.

Racki, G. 1993b. Brachiopod assemblages in the Devonian Kowala Formation of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37: 297–357.

Racki, G. 1998. The Frasnian–Famennian brachiopod extinction events: A preliminary review. *Acta Palaeontologica Polonica* 43: 395–411.

Rodionova, G.D., Umnova, V.T., Kononova, L.I., Ovnatanova, N.S., Rzhonsnitskaya, M.A. [Ržonsnickaâ, M.A], and Fedorova, T.I. 1995. *Devon Voronežskoj anteklizy i Moskovskoj sineklizy.* 265 pp. Rosgeolfond, Moskva.

Rzhonsnitskaya, M.A. 1988. Biostratigraphic scheme of Devonian of the Russian Platform. *Canadian Society of Petroleum Geologists, Memoir* 14: 691–702.

Rzhonsnitskaya, M.A. [Ržonsnickaâ, M.A] and Kulikova, V.F. (eds.) 1990. *Rešenie Mežvedomstvennogo regional'nogo stratigrafičeskogo soveŝaniâ po srednemu i verhnemu paleozoû Russkoj platformy s regional'nymi stratigrafičeskimi shemami*. 60 pp. All–Russian Geological Research Institute (VSEGEI), Leningrad.

Rzhonsnitskaya, M.A., Markovskii, B.P., Yudina, Y.A., and Sokiran, E.V. 1998. Late Frasnian Atrypida (Brachiopoda) from the South Urals, South Timan and Kuznetsk Basin (Russia). *Acta Palaeontologica Polonica* 43: 305–344.

Sartenaer, P. 1966. *Ripidiorhynchus*, nouveau genre de Brachiopode Rhynchonellide du Frasnien. *Bulletin de l'Instut royal des Sciences naturelles de Belgique* 42 (30): 1–15.

Sartenaer, P. 1977. Un nouveau genre de Rhynchonellide de la fin du Frasnien. *Annales de la Société geologique du Nord* 97: 67–76.

Sartenaer, P. 1985. The biostratigraphical significance of rhynchonellid genera at the Givetian–Frasnian boundary. *Courier Forschungsinstitut Senckenberg* 75: 311–318.

Sartenaer, P. 1997. Are all species of the Main Devonian Field assigned to the genus *Ripidiorhynchus* Sartenaer, P., 1966 valid? *Proceedings of the Estonian Academy of Sciences* 46 (3): 146–149.

Sarycheva, T.G. [Saryčeva, T.G.] and Sokolskaya, A.N. [Sokolskaâ, A.N.] 1952. Key to Palaeozoic brachiopods of Sub-Moscow region [in Russian]. *Trudy Paleontologičeskogo Instituta AN SSSR* 38: 1–307.

Savage, N.M. 1996. Classification of Palaeozoic rhynchonellid brachiopods. *In*: P. Copper and J. Jin (eds.), *Brachiopods*, 249–260. Balkema, Rotterdam.

Schmidt, H. 1965. Neue Befunde an paläozoischen Rhynchonellacea (Brachiopoda). *Senckenbergiana Lethaea* 46: 1–25.

Sobolev, D. 1909. Middle Devonian of Kielce–Sandomierz chain. *Materialy po Geologii Rossii* 24: 41–536.

Sorokin, V.S. 1978. *Etapy razvitiâ severo-zapada Russkoj platformy vo franskom veke*. 282 pp. Zinatne, Riga.

Tikhomirov, S.V. [Tihomirov, S.V.] 1967. *Etapy osadkonakopleniâ devona Russkoj platform*y. 268 pp. Nedra, Moskva.

Venyukov, P.N. [Venûkov, P.N.] 1886. *Fauna devonskoj sistemy severozapadnoj i centralnoj evropejskoj Rossii*. 129 pp. Tipografiâ V. Demakova, Sankt-Petersburg.

Verneuil, E. 1845. *Geologie de la Russie d'Europe et des Montagnes de l'Oural*. Paleontologie 2: 1–512. Paris.

Yudina, Yu.A. 1999. A new rhynchonellid brachiopod species *Ptychomaletoechia izhmaensis* from the Famennian of South Timan. *Paleontological Journal* 33 (2): 15–17.

Zhamoida, A. I. [Žamojda, A.I.] (ed.) 1992. *Stratigrafičeskij kodeks* (2nd edition) (supplemented). 120 pp. Meževedomstvennyj stratigrafičeskij komitet, VSEGEI, Sankt-Petersburg.

Ziegler, W., Ovnatanova, N., and Kononova, L. 2000. Devonian Polygnathids from the Frasnian of the Rheinischen Schiefergebirge, Germany, and the Russian Platform. *Courier Forschungsinstitut Senckenberg* 80: 593–645.