Trepostomids (Bryozoa) from the Devonian of Salair, Kuznetsky Basin, Gorny and Rudny Altai, Russia

OLGA P. MESENTSEVA

Trepostomid bryozoa from the Devonian of the Salair-Altai region (SAR) have been investigated. Analysis of collected data has allowed the late Silurian-Devonian-Tournaisian interval to be divided into 16 stages, each represented by a specific association of trepostomids. Cyclic changes in trepostomid species composition are marked by alternations of low diversity. Four cycles can be recognized, beginning with an interval of high species diversity and ending with an interval of low species diversity. Synchronicity between cycles of species diversity and recognized transgressive-regressive cycles is evident in the SAR. Diversity peaks correspond to transgressions, whereas minimum diversity to regressions. Local cyclicity of the trepostomid diversity in the SAR does not coincide with a global bryozoan cyclicity. Species duration of Devonian trepostomids is assessed and their potential for biostratigraphical correlation within the SAR proven. • Key words: bryozoans, trepostomids, species association, diversity changes, Devonian, Salair-Altai region.

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The territories of the Salair, Gorny and Rudny Altai Mountains in central Asia are now regarded as the Salair-Altai region (SAR). Until the end of the 20th century Devonian bryozoans from the SAR, including trepostomids, were rarely investigated. Late Givetian and Frasnian examples were described in detail by Nekhoroshev (1948), Morozova (1961) and Volkova (1974), whereas Lochkovian-Pragian (Astrova & Yaroshinskaya 1968) and Frasnian (Morozova, 1961) trepostomids were poorly investigated and Emsian–Early Givetian trepostomids were completely unstudied. Therefore it was impossible to trace changes in trepostomid specific composition during the Devonian in the region. Also, trepostomids as well as other bryozoans were not used as paleontological evidence during the construction of the stratigraphic charts for the SAR.

Within the last 20 years most part of these gaps have been filled. Yaroshinskaya studied Přídolian-early Lochkovian trepostomids (Pushkin *et al.* 1990, Yaroshinskaya 1997) and Mesentseva and Udodov have described more than 60 species of Emsian-Eifelian-Early Givetian trepostomids, including 42 new species (Mesentseva 1997, 2000; Mesentseva & Udodov 2003). The distributions of these species in several dozen sections in the SAR have been investigated. New data on Famennian trepostomids within the vicinity of the Kuznetsk Basin of Russia have also been obtained (Tolokonnikova 2006). In total, more than 150 species of Devonian trepostomids are now known from numerous localities more or less regularly distributed across the SAR territory (Fig. 1).

Special attention has been given to Devonian reference sections from the Altai-Sayan Folded Area (ASFA), exposed on the eastern slope of the Salair Ridge (near Gur'evsk town) and in the northwestern margin of the Kuznetsk Basin. The Devonian stratigraphic charts for the ASFA and the SAR were created mainly on the basis of detailed studies of these sections. In the modern version of this chart (Yolkin *et al.* 2005), 16 horizons (regional stages) are recognized in the Devonian (Fig. 2).

The Tom'-Chumysh, Salairka and Shanda horizons are subdivided into beds with characteristic faunas (formations, subhorizons). Based on the detailed subdivision of Devonian strata in the reference sections, trepostomid species can be placed reliably into a biostratigraphic framework. The majority of strata recognized in Salair have also been traced into Altai where they have local names. Trepostomids are very rare in Lochkovian of Salair (Tom'-Chumysh and Petz horizons) as well as in Pragian (Krekov and Maly Bachat horizons). In Salair, the early Lochkovian strata of the Tom'-Chumysh Horizon, divided into the Sukhoi and Tomskiy Zavod formations (beds with fauna), contain very few trepostomids. Therefore, the present paper deals with trepostomids from the stratigraphic

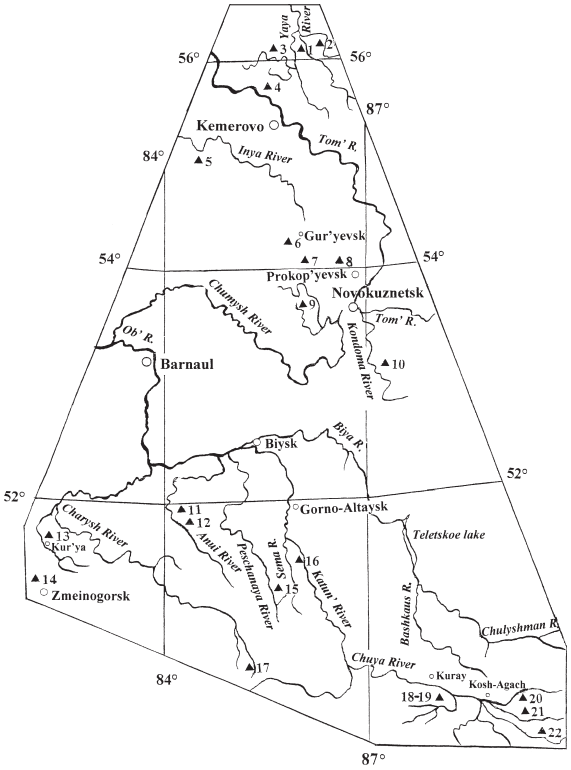


Figure 1. Map showing localities with Devonian trepostomids in the Salair-Altai region, Russia. 1 – Yaya; Upper Devonian (Rzonsnitskaya 1968, sine 1992). 2 – Alchedat; Middle Devonian, Upper Givetian (Rzonsnitskaya 1968; sine 1992). 3 – Mazalovsky Kitat; Middle Devonian, Upper Givetian (Rzonsnitskaya 1968; sine 1992). 4 – Kemerovo; Upper Devonian (Bakharev *et al.* 2004). 5 – Vassino; Upper Devonian (Rzonsnitskaya 1968; sine 1992). 6 – Gur'evsk; Lower Devonian–Middle Devonian, Eifelian (Yolkin *et al.* 1986, 1987; Bakharev *et al.* 2004). 7 – Stary Bachat; Middle Devonian, Lower Givetian (Mesentseva *et al.* 2007). 8 – Prokop'evsk-Kiselevsk; Middle Devonian, Lower Givetian (Mesentseva *et al.* 2007). 9 – Kara-Chumysh; Lower Devonian, Emsian–Middle Devonian, Eifelian (Mesentseva & Udodov 2000). 10 – Osman; Upper Devonian (Rzonsnitskaja 1968, Udodov *et al.* 1987). 11 – Ganin Creek; Lower Devonian (Yolkin 1968). 12 – Sibiryachikha; Lower Devonian (Stepanov *et al.* 1972, Mesentseva & Udodov 2007). 13 – Kur'ya; Lower Devonian (Bakharev *et al.* 2004). 14 – Zmeinogorsk; Lower Devonian, Emsian–Middle Devonian (Bakharev *et al.* 2004). 15 – Kuvash; Lower Devonian, Emsian (Yolkin 1968, Mesentseva & Udodov 2007). 16 – Sema; Lower Devonian, Emsian (Mesentseva & Udodov 2007). 17 – Mendursakon; Lower Devonian, Emsian–Middle Devonian (Mesentseva & Udodov 2007). 18 – Daya; Lower Devonian, Emsian (Volkova 1974). 19 – Chagan-Uzun; Middle Devonian, Upper Givetian–Upper Devonian (Volkova 1974). 20 – Tabachek; Middle Devonian, Upper Givetian–Upper Devonian (Volkova 1974). 21 – Kyzyl-Shin; Middle Devonian, Upper Givetian–Upper Devonian (Volkova 1974, Gutak 2006). 22 – Bar-Burgazy; Upper Devonian, Frasnian (Volkova 1974).

equivalents of these strata, namely the Sibirka, Remnyov and Yakushin beds from Altai.

Materials and methods

Bryozoan collections from the type sections of the Přídolian (upper Silurian), Devonian and Tournaisian (Lower Carboniferous) of the SAR have been accumulated by the author over 25 years. Using standard techniques, the bryozoans were studied in thin section under a binocular microscope. Special attention was paid to intraspecific variability, and therefore, 10 or more colonies of each species were studied. The studied collections are stored in the Paleontological Museum of the Kuzbass State Education Academy, where. In addition, previously published results of the following researchers were used: Nekhoroshev (1948, 1956), Trizna (1958), Morozova (1961), Yaroshinskaya (*in* Astrova & Yaroshinskaya 1968; Pushkin *et al.* 1990), Volkova (1974), Udodov (2004), and Tolokonnikova (2006).

Trepostomid distribution in Devonian of Salair, Kuznetsk Basin, Gorny and Rudny Altai

The distribution of Devonian trepostomids from the SAR is summarized in below. In most cases, a rather specific trepostomid association characterizes each horizon of the regional stratigraphic chart. Major changes in trepostomid species usually coincide with boundaries between strata. Whereas such faunal changes usually correlate with facies changes, the fact that the material used for this study came from many distant sections means that changes in trepostomids were caused more by extinction and origination than by simple facies changes. Thus, in most cases the duration of formation for each horizon can be regarded as a stage in trepostomid evolution. In some cases major changes in trepostomid fauna coincide not with bed rather than horizon boundaries. As a result, the boundaries of the trepostomid stages (biozones) do not always coincide with the boundaries of horizons. Within the Přídolí–Early Tournaisian interval 16 stages those boundaries are interpreted as innovation boundaries. The brief characteristics of each stage are given below.

Ludlow

Trepostomid species present: *Lioclema varium* Astrova, 1959, *Eridotrypa alternans* Astrova, 1965, *Amplexopora subseptosa* Modzalevskaya, 1979, *Discotrypa podolica* (Astrova, 1965).

Přídolí

Přídolian stage. – Age: Přídolian (upper part of Kuimov and Cherny Anui formations). Trepostomid species present:

System	Series	Stage	Conodont Zone	Age	Lithostratigraphy Salair and Kuznetsk Basin	
Carbon.	Lower	Tour.			Taydon	Lower
Devonian			praesulcata	359	Abyshevo	
	Upper	Famennian	expansa		Podonino	
			postera	374		
			trachitera			
			marginifera		Peshcherka	
			rhomboidea			
			crepida			
			triangularis			
		Frasnian	linguiformis	385	Solomino	
			rhenana			
			jamieae		Vassino	
			hassi			
			punctata			
			transitans			
			falsiovalis			
	Middle	Givetian		391		
			disparilis		Mazalovsky Kitat	
			hermanni.			
			varcus		Safonovo	
				397	Kerlegesh	
			hemiansatus		Mamontovo	
		Eifelian	kockelianus			
			australis			
			costatus			
			partitus		Shanda	Upper
	Lower	Emsian	patulus			
			serotinus			Middle
			inversus			
			nothoperbons	407		Lower
			excavatus		Belovo	
			kitabicus		Salairka	Upper
						Middle
				411		Lower
		Pragian	pireneae		Maly Bachat	
			kindlei			
			sulcatus			
		Lochkovian	pesavis		Krekov	
			delta			
			eurekaensis		Peetz	
			postwoschmidti-woschmidti		Tom'-Chumysh	Upper Remnevo
				416		Sibirca
Silurian		Přídolian				

Figure 2. Regional stratigraphic chart for the Devonian of the Salair region (modified from Yolkin *et al.* 1997).

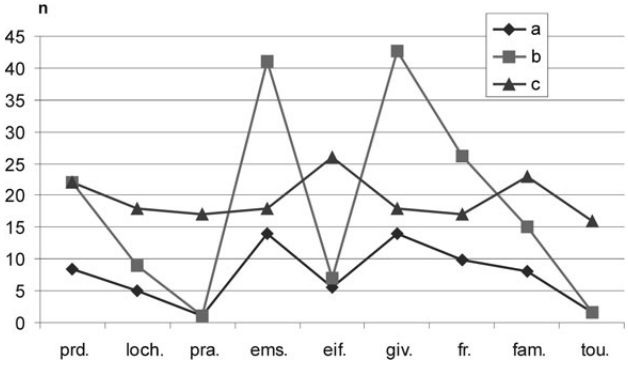


Figure 3. Dynamics of trepostomid specific and generic diversity during Přídolian-Devonian-Early Carboniferous. a, b – trepostomid diversity from the Salair-Altai region: a – species, b – genera, c – global generic trepostomid diversity (after Gorynova *et al*. 2004); n – number of species (genera).

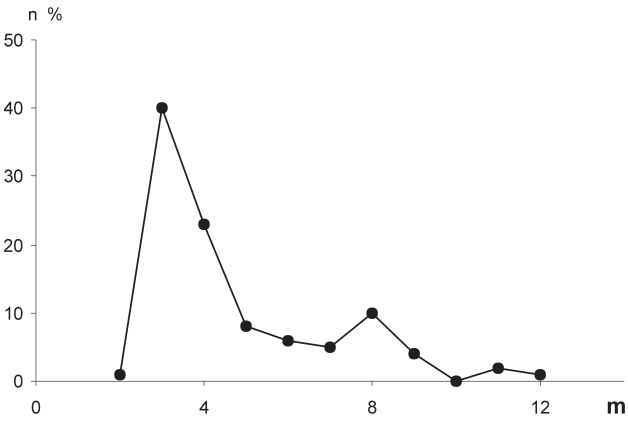


Figure 4. Ranges of Přídolian-Devonian-Early Carboniferous trepostomids (Bryozoa) from the Salair, vicinity of the Kuznetsk Basin, Gorny and Rudny Altai. Trepostomid species lifespan was estimated on the basis of investigation of their ranges in the Altai-Sayan Folded Area sections and duration of the Silurian, Devonian and Carboniferous stages (Gradstein *et al.* 2004). n – species number (%) from the total number (151 species); m – ranges of existence (Ma).

Lioclema varium Astrova, 1959, *Eridotrypa alternans* Astrova, 1965, *Amplexopora subseptosa* Modzalevskaya, 1979, *Discotrypa podolica* (Astrova, 1965), *Eridotrypa callosa* Morozova, 1961, *Eridotrypa acifera* Modzalevskaya, 1978, *Eridotrypa angusta* Yaroshinskaya, 1990, *Hemieridotrypa altaica* Kopaevich, 1968, *Hemieridotrypa insolens* Kopaevich, 1968, *Hemieridotrypa tscherkesovae* Astrova, 1965, *Lioclema morozovae* Yaroshinskaya, 1990, *Lioclema altaica* Yaroshinskaya, 1997, *Lioclema praepassitabulatum* Yaroshinskaya, 1990, *Discotrypa infans* Yaroshinskaya, 1997, *Heterotrypa enormis* Astrova, 1959, *Lioclema gloria* Astrova, 1964, *Atactotoechus verus* Yaroshinskaya, 1990, *Eridotrypella ampla* Yaroshinskaya, 1990, *Lioclema modzalevskaja* Yaroshinskaya, 1990, *Lioclema angulatum* Yaroshinskaya, 1990, *Amplexopora ramosa* Yaroshinskaya, 1990.

Lochkovian

Sibirca stage. – Age: early Lochkovian (Sibirka Formation). Trepostomid species present: *Atactotoechus verus* Yaroshinskaya, 1990, *Eridotrypella ampla* Yaroshinskaya, 1990, *Lioclema modzalevskaja* Yaroshinskaya, 1990, *Lioclema angulatum* Yaroshinskaya, 1990, *Amplexopora ramosa* Yaroshinskaya, 1990.

Remnyov stage. – Age: late Lochkovian (Remnyov Formation). Trepostomid species present: *Lioclema multiacanthoporum* Astrova, 1968, *Lioclema netshlavense* Astrova, 1964, *Cyphotrypa variabile* Mesentseva, 2008, *Atactotoechus simplex* L. Nekhoroshev, 1968.

Pragian

Pragian stage. – Age: Pragian (Yakushinkin Formation). Trepostomid species present: *Lioclema subramosum* Ulrich & Bassler, 1913.

Emsian

Early-Middle Salairka stage. – Age: early Emsian (lower and middle Salairka Formation). Trepostomid species present: *Neotrematopora multi* Mesentseva, 2000, *Eridotrypa neocallosa* Mesentseva, 2000, *Eridotrypa grandialveolatum* Mesentseva, 2000, *Chondraulus salairicus* Mesentseva, 2000, *Cyphotrypa minor* Mesentseva, 2000, *Eostenopora notabilisica* Mesentseva, 2003, *Kysylschinipora* sp. 1, *Lioclema florea* Modzalevskaya, 1965, *Lioclema polymorpha* Mesentseva, 1997, *Neotrematopora spinula* Mesentseva, 2000.

Late Salairka-Middle Shanda stage. – Age: middle Emsian (upper Salairka, Belovo, lower and middle Shanda formations). Trepostomid species present: *Lioclema polymorpha* Mesentseva, 1997, *Lioclema lucida* Mesentseva, 2000, *Lioclema parvum* Yaroshinskaya, 1974, *Lioclema pseudobugusunica* Mesentseva, 2000, *Lioclema pseudogloria* Mesentseva, 2000, *Lioclema akarachica* J. Udodov, 2004, *Lioclema schandiensis* Mesentseva, 2000, *Paralioclema protea* Mesentseva, 1997, *Paralioclema magnumformis* Mesentseva, 2000, *Paralioclema volkovae* Mesentseva, 1997, *Neotrematopora spinula* Mesentseva, 2000, *Neotrematopora leptoclada* Mesentseva, 2000, *Neotrematopora salairiensis* (Morozova, 1961), *Neotrematopora crassiramosa* Mesentseva, 2000, *Neotrematopora celebrata* (Yaroshinskaya, 1968), *Neotrematopora vulgaris* Mesentseva, 2000, *Neotrematopora yolkini* Mesentseva, 2000, *Neotrematopora rudnoaltaica* Mesentseva, 2000, *Neotrematopora schebalinoensis* Mesentseva, 2000, *Eridotrypa kuzbassica* Mesentseva, 2000, *Eridotrypa nekhoroshevi* Yaroshinskaya, 1968, *Eridotrypa beloviense* Mesentseva, 2000, *Atactotoechus basarginensis* Mesentseva, 2000, *Anomalotoechus bublitschenkoi* (Nekhoroshev, 1948), *Leptotrypella gurievensis* Astrova, 1968, *Eostenopora tenuitubulosum* Mesentseva, 2000, *Eridotrypella pluristratosa* J. Udodov, 2003.

Late Shanda stage. – Age: late Emsian (upper Shanda Formation). Trepostomid species present: *Lioclema salairiense* Morozova, 1961, *Lioclema florea ampla* Mesentseva, 1997, *Paralioclema volkovae* Mesentseva, 1997, *Neotrematopora schebalinoensis* Mesentseva, 2000, *Neotrematopora pesterevensis* J. Udodov, 2004, *Neotrematopora pulchra* J. Udodov, 2007, *Minussina udodovi* Mesentseva, 2000, *Leptotrypa prima* (Duncan, 1939).

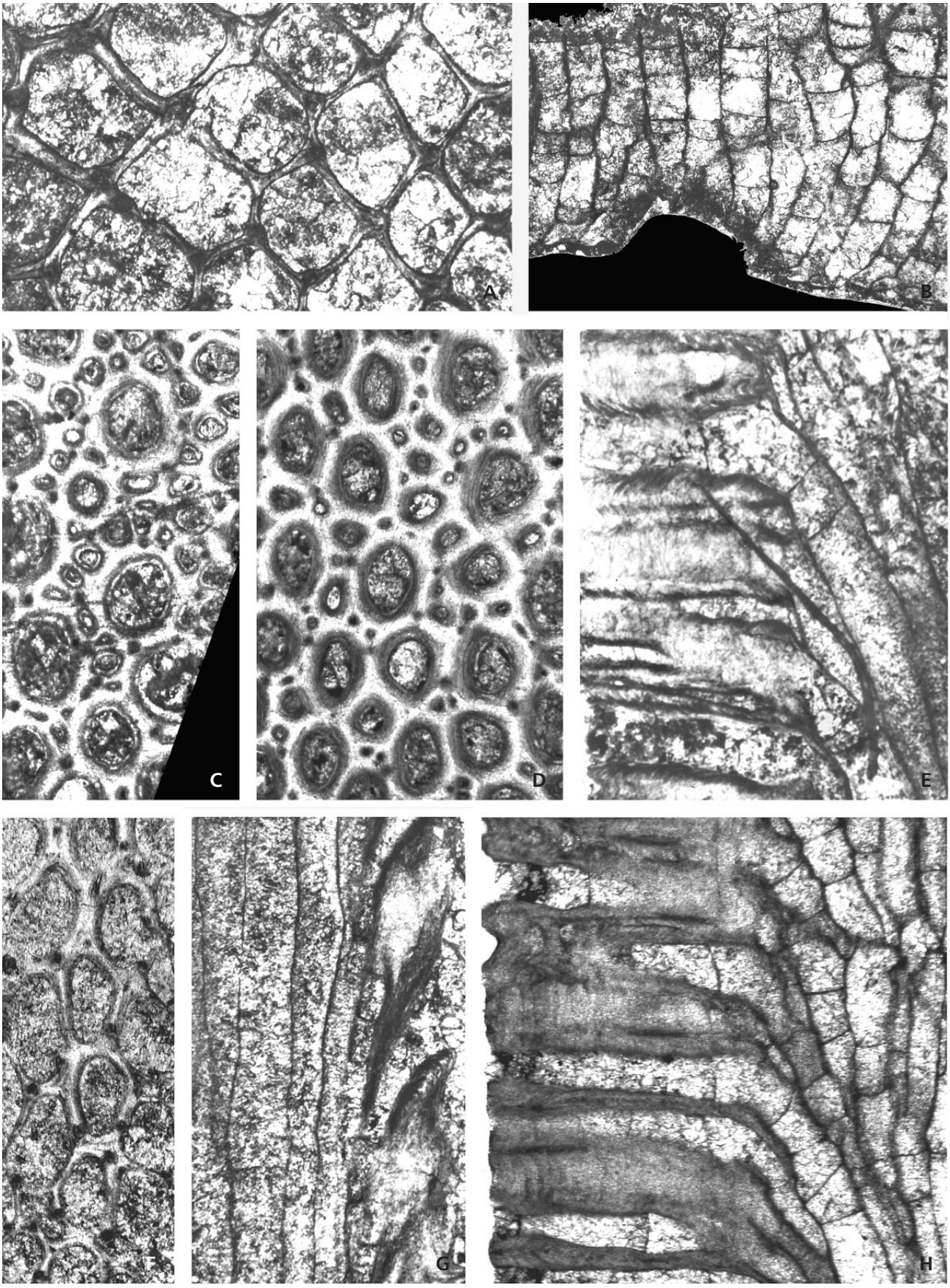
Eifelian

Mamontovo stage. – Age: Eifelian (Mamontovo Formation). Trepostomid species present: *Lioclema florea ampla* Mesentseva, 1997, *Neotrematopora pulchra* J. Udodov, 2007, *Neotrematopora eifeliensis* J. Udodov, 2004, *Raissiella fragilis* J. Udodov, 2007, *Eridotrypella distributa* J. Udodov, 2003, *Kysylschinipora* sp. 2, *Anomalotoechus typicus* Duncan, 1939.

Givetian

Kerlegesh-Safonovo stage. – Age: early Givetian (Kerlegesh and Safonovo Formations). Trepostomid species present: *Neotrematopora pulchra* J. Udodov, 2007, *Kysylschinipora* sp. 3, *Lioclema bascuscanensis* J. Udodov, 2007, *Lioclema rara* J. Udodov, 2007, *Leptotrypa spinosa* J. Udodov, 2007, *Eridotrypella bachatensis* J. Udodov, 2007, *Kysylschinipora* sp. 4.

Figure 5. Emsian trepostomid bryozoans from the Salair (Gur'evsk town vicinity). • A, B – *Cyphotrypa minor* Mesentseva, 2000, sample B-829-12/6, holotype; A – tangential section, × 58, B – longitudinal section, × 23; Salairka Horizon, Emsian, Lower Devonian. • C–E – *Leptotrypella gurievensis* Astrova, 1968, sample B-829-16-/18; C – tangential section of macula, × 58, D – tangential section, × 58, E – longitudinal section, × 64; Belovo Horizon, Emsian, Lower Devonian. • F, G – *Eridotrypa neocallosa* Mesentseva, 2000, sample B-829-11c/13, holotype; F – tangential section, × 76, G – longitudinal section, × 60; Salairka Horizon, Emsian, Lower Devonian. • H – *Neotrematopora salairiensis* (Morozova, 1961), sample B-829-15/51, longitudinal section, × 62; Salairka Horizon, Emsian, Lower Devonian.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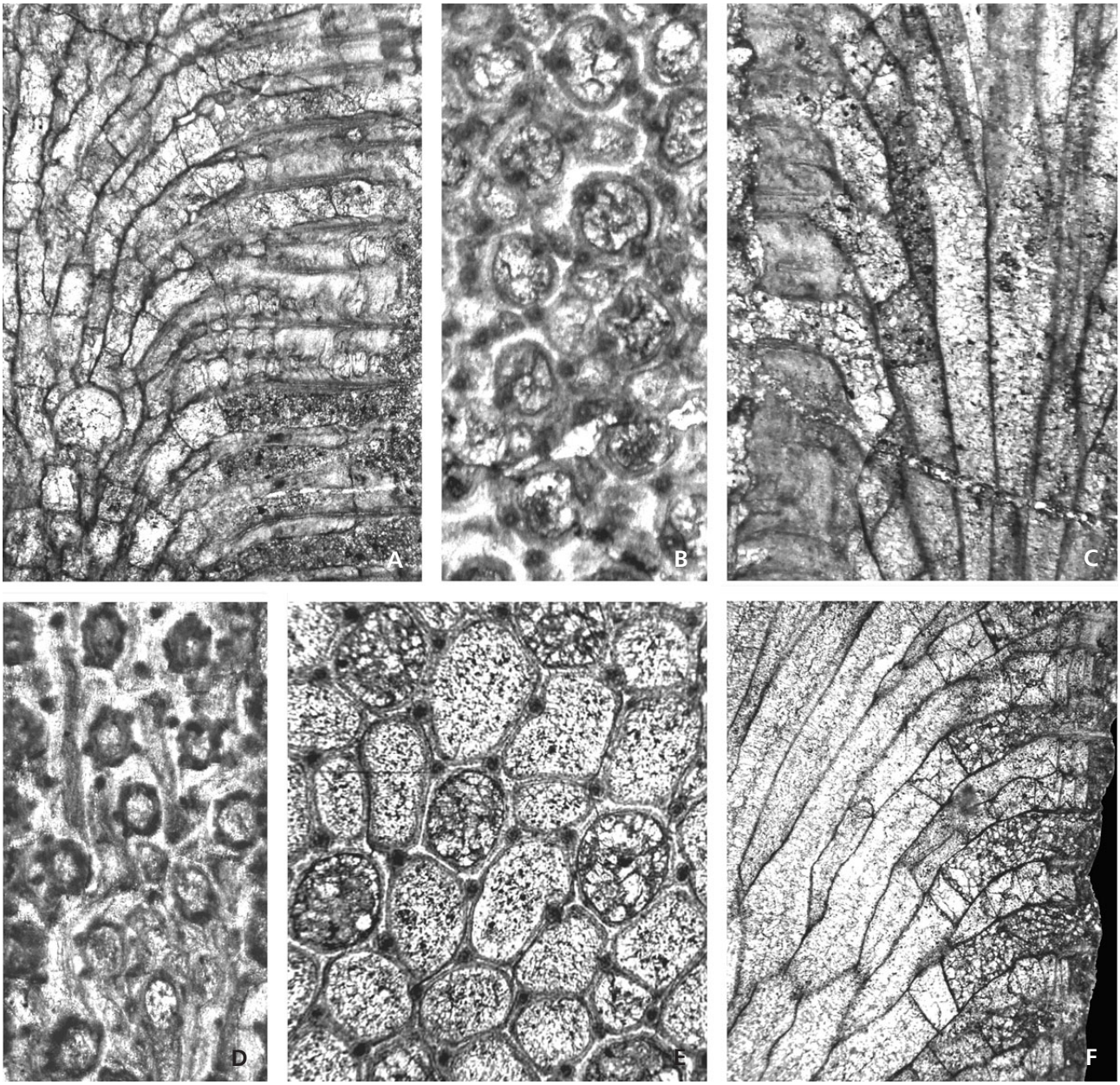


Figure 6. Emsian and Eifelian trepostomids from the Salair (Gur'evsk town vicinity). • A, B – *Neotrematopora multi* Mesentseva, 2000, sample Yo-837-1/1, holotype; A – longitudinal section, × 38, B – tangential section, × 60; Salairka Horizon, Emsian, Lower Devonian. • C, D – *Raissiella fragilis* J. Udodov, 2007, sample 29033/110, holotype; C – longitudinal section, × 70; D – tangential section, × 70; Mamontovo Horizon, Eifelian, Middle Devonian. • E, F – *Lioclema schandiensis* Mesentseva, 2000, sample Yo-828-1/2-2, holotype; E – tangential section, × 76, F – longitudinal section, × 32; Shanda Horizon, Emsian, Lower Devonian.

Mazalovskiy Kitat stage. – Age: late Givetian (Alchedat and Izyly formations). Trepostomid species present: *Lioclema bugusunicum* Nekhoroshev, 1948, *Lioclema polenovi* Nekhoroshev, 1948, *Lioclema mirum* Morozova, 1961, *Lioclema multum* Volkova, 1974, *Lioclema celebratum* Morozova, 1961, *Lioclema maculatum* Nekhoroshev, 1948, *Lioclema occidens* (Hall & Whitfield, 1873), *Paralioclema vulgatum* Morozova, 1961, *Monotrypa usitata* Volkova, 1974, *Neotrematopora typica* Morozova, 1961, *Neotrematopora tschuensis* (Nekhoroshev, 1948), *Neotrematopora plena* Volkova, 1974, *Neotrematopora koksairiensis* Volkova, 1974, *Neotrematopora vasilievskiji* (Schoenmann, 1926), *Minussina kitatensis* Morozova, 1961, *Cyphotrypa minuscula* Volkova, 1974, *Atactotoechus solidus* Volkova, 1974, *Anomalotoechus crassimuralis* (Volkova, 1974), *Anomalotoechus corrugatus* (Nekhoroshev, 1948), *Anomalotoechus kisilschinicus* (Nekhoroshev, 1948), *Leptotrypella tenuis* Volkova, 1974,

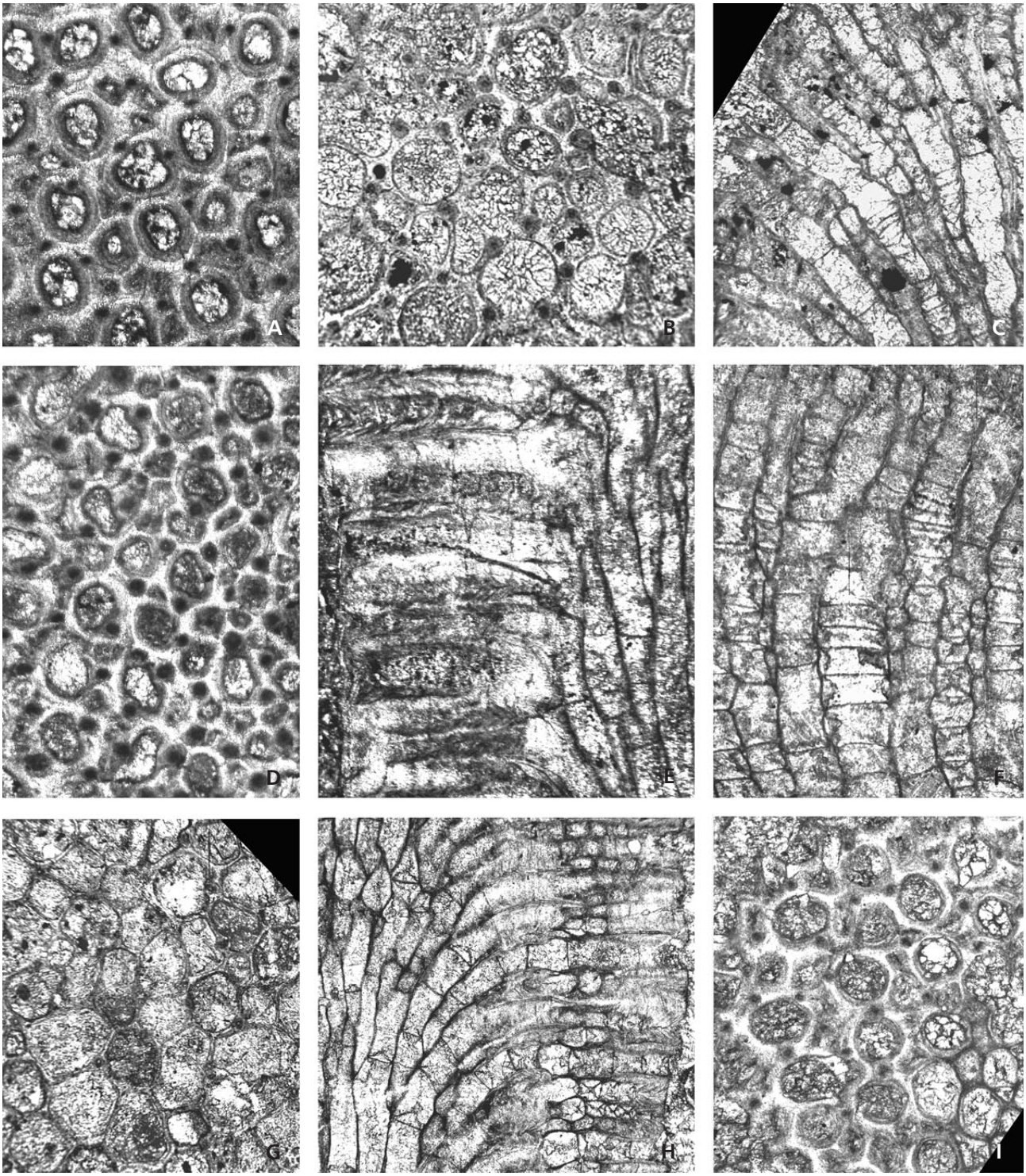


Figure 7. Emsian trepostomids from the Salair (Gur'evsk town vicinity, Novo-Pesteryovo Village, right bank of Kara-Chumysh River). • A – *Neotrematopora salairiensis* (Morozova, 1961), sample B-829-15/51, tangential section, × 58; Salairka Horizon, Emsian, Lower Devonian. • B, C – *Paralioclema magnumformis* Mesentseva, 2000, sample Ya-854-3/10, holotype; B – tangential section, × 54, C – longitudinal section, × 30; Shanda Horizon, Emsian, Lower Devonian. • D, E – *Neotrematopora yolkini* Mesentseva, 2000, sample Yo-828-1/1-199, holotype; D – tangential section, × 46; E – longitudinal section, × 57; Shanda Horizon, Emsian, Lower Devonian. • F, G – *Lioclema salairiense* Morozova, 1961, sample 25030/1; F – longitudinal section, × 38; G – tangential section, × 50; Shanda Horizon, Emsian, Lower Devonian. • H, I – *Neotrematopora pesterevensis* J. Udodov, 2004, sample B-8323-3/6, holotype; H – longitudinal section, × 36, I – tangential section, × 52; Shanda Horizon, Emsian, Lower Devonian.

Leptotrypella protea Volkova, 1974, *Dyscritella devonica* Volkova, 1968, *Petalotrypa perforata* Nekhoroshev, 1948, *Eridotrypella grandis* (Volkova, 1974), *Eridotrypella devonica* (Nekhoroshev, 1948), *Eridotrypella valentinae* Morozova, 1961, *Eridotrypella angusta* Volkova, 1974, *Eridotrypella perrara* Volkova, 1974, *Eridotrypella rara* Volkova, 1974, *Eridotrypella instabilis* Volkova, 1974, *Kysylschinipora orbis* Volkova, 1974, *Kysylschinipora nekhoroschevi* Volkova, 1974, *Anomalotoechus ramosus* (Morozova, 1959), *Lioclema yakovlevi* (Schoenmann, 1926), *Lioclema heitaiense* Yang, 1956.

Frasnian

Vassino stage. – Age: early Frasnian (Vassino Formation). Trepostomid species present: *Lioclema yakovlevi* (Schoenmann, 1926), *Lioclema heitaiense* Yang, 1956, *Lioclema vassinense* Morozova, 1961, *Lioclema tschuyaense* Volkova, 1969, *Lioclema plicatile* Volkova, 1969, *Lioclema incrustans* Nekhoroshev, 1948, *Lioclema editum* Morozova, 1961, *Paralioclema ninae* Morozova, 1961, *Paralioclema multiforme* Volkova, 1974, *Minussina atypica* Volkova, 1974, *Minussina grandis* Morozova, 1961, *Anomalotoechus ramosus* (Morozova, 1959), *Cyphotrypa definita* Morozova, 1961, *Leptotrypa rhombocella* Morozova, 1961, *Anomalotoechus yayaensis* Morozova, 1957, *Anomalotoechus insuetus* (Morozova, 1959), *Atactotoechus belskayae* Morozova, 1957, *Leptotrypella aperta* Morozova, 1958, *L. inaudita* Morozova, 1961, *Eridotrypella conspersa* (Volkova, 1974).

Solomino stage. – Age: late Frasnian (Solomino Formation). Trepostomid species present: *Lioclema editum* Morozova, 1961, *Minussina akkayensis* Volkova, 1974, *Anomalotoechus bifoliatus* (Morozova, 1959), *Eridotrypella ornamentata* (Morozova, 1958), *Eridotrypella justa* Morozova, 1961, *Eridotrypella granulosa* (Morozova, 1955), *Schulgina nesterenkoae* Morozova, 1957.

Famenian

Peshcherka stage. – Age: early Famennian (Peshcherka Formation). Trepostomid species present: *Lioclema ivanovae* Morozova, 1961, *Lioclema numerosum* Morozova, 1961, *Neotrematopora majuscula* (Volkova, 1974), *Minussina akkayensis* Volkova, 1974, *Anomalotoechus laminaris* Tolokonnikova, 2006, *Microcampylus daedaleus* Tolokonnikova, 2006, *Crustopora devonica* Tolokonnikova, 2006.

Podonino stage. – Age: middle Famennian (Podonino Formation). Trepostomid species present: *Minussina akkayensis* Volkova, 1974, *Lioclema ramosum* Nekhoroshev, 1948, *Anomalotoechus proprius* Tolokonnikova, 2006, *Eridocampylus striatum* Tolokonnikova, 2006, *Eridocampylus rotundatum* Tolokonnikova, 2006.

Abyshevo stage. – Age: late Famennian (Abyshevo Formation). Trepostomid species present: *Lioclema podunskense* Trizna, 1958, *Lioclema textilum* Trizna, 1958, *Tabuliporella vesca* Trizna, 1958, *Tabuliporella risilla* Trizna, 1958.

Carboniferous, Tournaisian

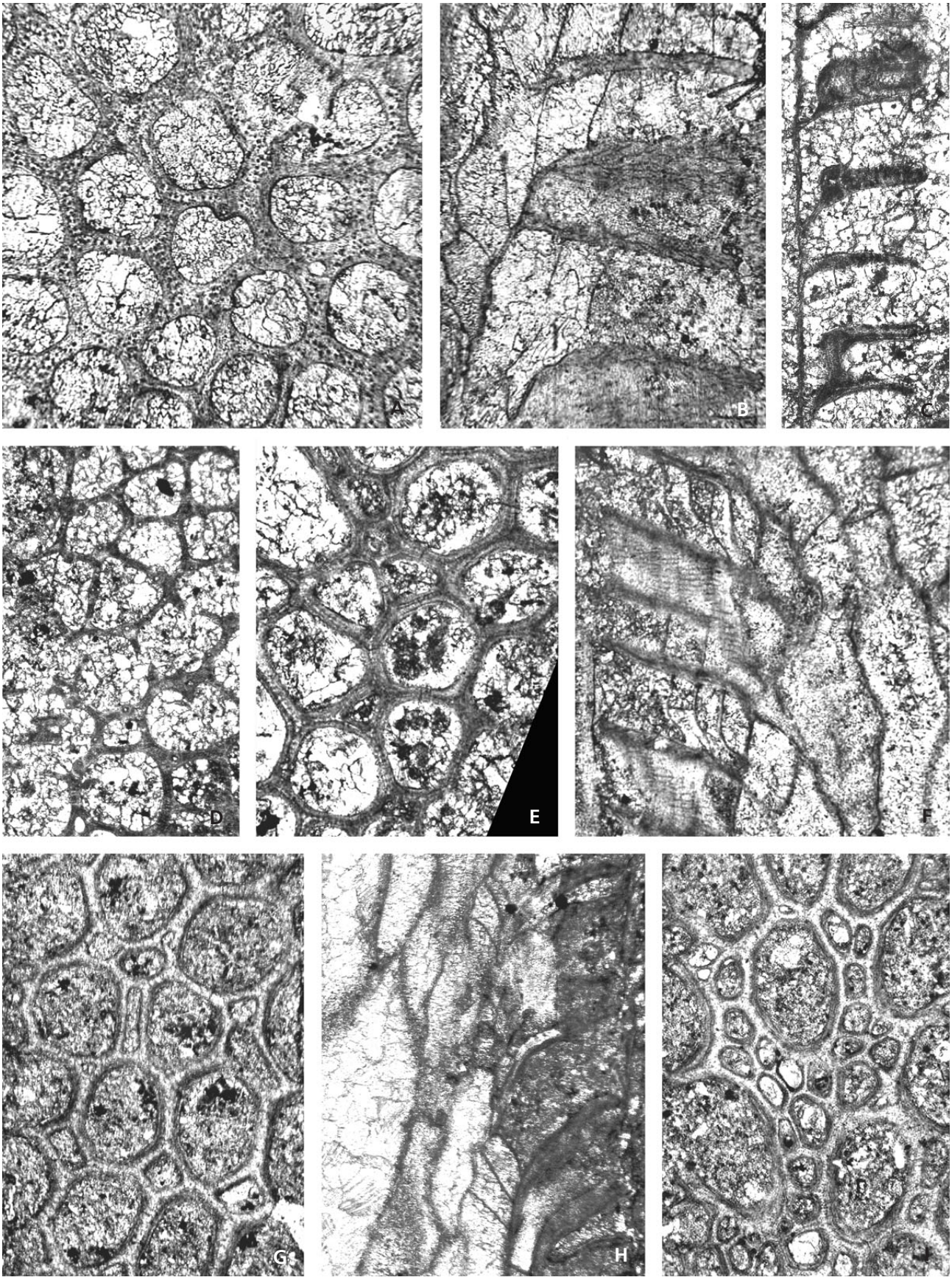
Early Tournaisian stage. – Age: early Carboniferous (Taydon Formation). Trepostomid species present: *Tabuliporella mosjuchensis* Trizna, 1958, *Petalotrypa kossmati* Nikiforova, 1933.

Results

Boundaries of the trepostomid biozones are considered as times of evolutionary innovations. The number of trepostomid species that pass through such boundaries usually does not exceed two or three, except for four, the Ludlow-Přídolian, Přídolí-early Lochkovian, Middle-Late Shanda, Late Taydon-Fominskoe, where it is four to six species. The comparatively large number of species passing through the Přídolian-early Lochkovian boundary, apparently reflects insufficient study of this interval, which has meant that the boundary has previously been placed at different stratigraphical levels.

The results obtained allow the use of Devonian trepostomids from the SAR for the correlation of horizons. In some cases more detailed correlations are also possible. In particular, trepostomids now allow correlation of the Upper Shanda Subhorizon sequences within the SAR. The

Figure 8. Eifelian and Early Givetian trepostomids from the Salair (Gur'evsk and Prokop'evsk towns vicinity). • A, B – *Eridotrypella distributa* J. Udodov, 2003, sample 29033/30, holotype; A – tangential section, × 66, B – longitudinal section, × 67; Mamontovo Horizon, Eifelian, Middle Devonian. • C, D – *Leptotrypa spinosa* J. Udodov, 2007, sample M-01-50/37, holotype; C – longitudinal section, × 56, D – tangential section, × 52; Safonovo Horizon, lower part of Givetian, Middle Devonian. • E, F – *Kysylschinipora* sp. 2, sample 29030/28, holotype; E – tangential section, × 56, F – longitudinal section, × 52; Mamontovo Horizon, Eifelian, Middle Devonian. • G–I – *Kysylschinipora* sp. 3., sample 29008/2, holotype; G – tangential section, × 66, H – longitudinal section, × 56, I – tangential section of macula, × 52; Safonovo Horizon, lower part of Givetian, Middle Devonian.


A
B
C
D
E
F
G
H

species composition of the Lower and Upper Salairka trepostomid faunas are useful for correlation. Along with other marine faunal groups the trepostomids have been included in a new version of the regional stratigraphic chart for the Devonian of the ASFA that is under preparation.

Diverse Devonian trepostomid species have been obtained from the SAR (Fig. 3). The late Lochkovian-Pragian (Peetz-Maly Bachat age), early Givetian (Kerlegesh-Safonovo age) and late Famennian-Early Tournaisian (Abyshevo-Taydon age) intervals are characterized by the lowest species diversities (1–8 species). Maximum species diversities (19–36 species) were observed in the Přídolian, Middle Emsian (Late Salairka-Middle Shanda age), late Givetian (Mazalovsky Kitat age), Early Frasnian (Vassino age) and late Tournaisian (Fominskoe age). Thus, during the late Silurian-Tournaisian, alternations of times of the low and high trepostomid species diversity occurred, producing a cyclicity. Three cycles can be recognized: Přídolian-Pragian, Emsian-early Givetian and late Givetian-early Tournaisian with durations of 16, 19 and 30 million years, respectively. In the second half of the Tournaisian a fourth Early-mid-Carboniferous cycle began. The start of each cycle is characterized by high species diversity, the end by low diversity. Three of the cycles (Emsian-early Givetian, late Givetian-early Tournaisian and early-middle Carboniferous) coincide with cycles of transgression-regression such that phases of maximum diversity correspond to phases of transgression (middle Emsian, late Givetian, late Tournaisian), and those of minimum diversity to epochs of regression (early Givetian, late Famennian, late Viséan). The only exception is the late Lochkovian-Pragian, which coincided with a transgression, but is characterized by low species diversity. The reasons for this anomaly remain unclear. However, the prevailing facies during the late Lochkovian-Pragian transgression provide a possible explanation. During this time coral reefs were formed within the Salair paleobasin with rare trepostomids. Back reef facies often possessed abundant trepostomids, but their species diversity was low. Lagoons occurring in the Altai are characterized by the broadest distribution but of only one species. In particular, the Pragian sequences in the vicinity of Kur'ya Village contain only *Lioclema subramosum* Ulrich & Bassler, 1913.

Discussion & Conclusions

The dynamics of trepostomid species diversity in the SAR can be compared with data on the global diversity of this group at generic level for the Devonian published by Goryunova *et al.* (2004). To make this comparison the diagram for trepostomid genera was made for the SAR (Fig. 3, curve a, b).

The patterns for the SAR are very similar at species and genus levels. However, they contrast with Goryunova *et al.*'s (2004) global pattern (Fig. 3, curve c), which is interpreted as caused by the fact that the dynamics at regional and global levels were controlled by different factors. The global pattern probably reflects the transgression-regression cycles driven by global eustatic sea-level fluctuations. The diversity dynamics of the trepostomids in the SAR reflects the transgression-regression at a regional level. During the Devonian the territory of the SAR experienced high levels of tectonic activity. Transgression-regression cycles in this region were driven mostly by tectonic movement and only by global eustatic sea-level fluctuations to a small degree.

The stratigraphic range of trepostomid species has been determined on the basis of modern data on the duration of geological epochs from the International Geochronological Scale (Gradstein *et al.* 2004) and new data on trepostomid distribution in upper Silurian-Tournaisian sections in the SAR (Fig. 2). In total, ranges of 151 species have been established (Fig. 4).

Time ranges of 40% of trepostomid species do not exceed 3 million years; over 60% of species existed for less than 4 million years; over 70% of species for less than 6 million years; about 25% of species are characterized by significantly longer time ranges (6–10 million years). These latter ranges are similar to brachiopods and corals, supporting significantly longer time ranges (6–10 million years). This similarity to brachiopods and corals supports the significant biostratigraphical value of trepostomids.

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