Taxonomic diversity of foraminifers of the Devonian-Carboniferous boundary interval in the South Urals

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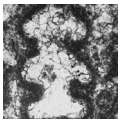

The taxonomic diversity of foraminifers from the Devonian-Carboniferous boundary beds was studied in the key sections on the western slope of the South Urals in Russia and from Mugodzhary in Kazakhstan. These sections are mainly composed of marine carbonates, apparently deposited in a shallow-water environment. The boundary interval contains 111 species belonging to 30 genera within the foraminiferal zones *Quasiendothyra communis, Q. kobeitusana, Tournayellina beata pseudobeata, Earlandia minima,* and *Chernyshinella disputabilis* of the Russian General Stratigraphic Scale. Maximum diversification is recorded in the *Q. kobeitusana* Zone, and minimum species diversity is observed in the *Earlandia minima* Zone. • Key words: foraminifers, Devonian, Late Famennian, Tournaisian, Early Carboniferous, South Urals, biodiversity.

KULAGINA, E.I. 2013. Taxonomic diversity of foraminifers of the Devonian-Carboniferous boundary interval in the South Urals. *Bulletin of Geosciences 88(2)*, 265–282 (8 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received February 17, 2012; accepted in revised form May 17, 2012; published online January 9, 2013; issued June 7, 2013.

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The systematic description of foraminifers from the Devonian-Carboniferous boundary deposits of the South Urals within Russia and Kazakhstan is presented in many publications (Chernysheva 1952; Lipina 1955, 1960, 1965; Reitlinger 1961; Chuvashov 1965; Grozdilova 1973). The sequence of foraminiferal assemblages in the key sections of the western slope of the South Urals (Zilim-Zigan region) was first established in 1960–1970 (Lipina 1960, Kononova & Lipina 1971, Grozdilova 1973, Sinitsyna 1975).

As part of a program to locate a Devonian-Carboniferous boundary GSSP, Russian task groups studied a number of sections on the western slope of the South Urals (Zilim-Zigan region), and subdivided them into chronozones, regional zones, and local beds based on foraminifers, conodonts, ostracods, and miospores (Sinitsyna *et al.* 1984; Kochetkova *et al.* 1985, 1986, 1988). Reitlinger & Sinitsyna documented the foraminifers in each section (Kochetkova *et al.* 1985). However, only the Berchogur assemblage at Mugodzhary at the southern end of the Urals has been described, illustrated, and compared to the assemblages of the eastern slope of the South Urals, Russian Platform, and Western Europe (Kochetkova *et al.* 1987). Since then, numerous studies (Sinitsyna *et al.* 1995; Kulagina & Sinitsyna 2000; Pazukhin *et al.* 2004, 2009; Pazukhin 2008, 2009; Artyushkova *et al.* 2011) have added new information on the faunal composition of the Devonian-Carboniferous boundary beds. The purpose of the present paper is to describe the foraminiferal sequence across the boundary in the South Ural reference sections and analyze the changes in taxonomic diversity.

Material

Samples used in this study come from the author's collections at Sikaza, Usuili, and Muradymovo in Russia and Berchogur in Kazakhstan. They are supplemented by materials collected jointly by E.A. Reitlinger, N.M. Kochetkova, and V.N. Pazukhin in 1976–1978 and from Pazukhin's other collections.

Biostratigraphy

The Devonian-Carboniferous beds in the South Urals were studied in the West-Uralian (Zilim-Zigan region), Central-Uralian (Zilair Megasynclinorium) and Berchogur zones (Fig. 1).

In the Zilim-Zigan region the deposits are represented by three lithofacies: clayey carbonate (Sikaza, Zigan),

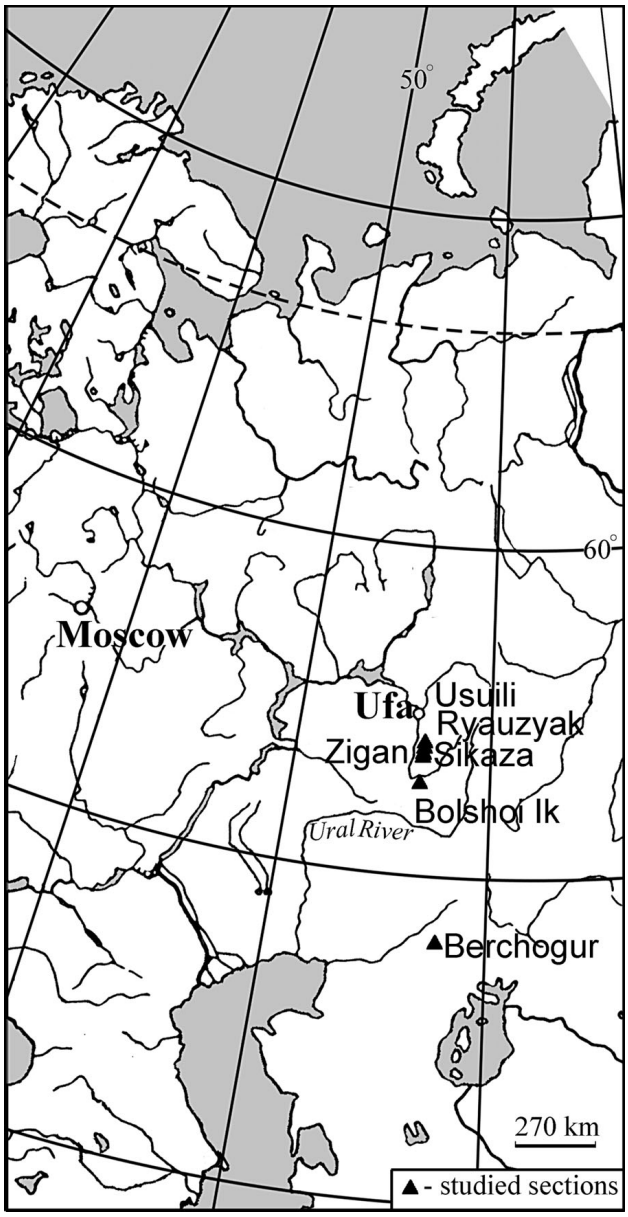


Figure 1. Location of studied sections.

carbonate (Usuili, Ryauzyak), and cherty carbonate (Bolshaya Kushelga). The first two correspond to open, shallow shelf environments with abundant foraminiferal faunas, and the third to a shelf depression. Deposits of Zilair Megasynclinorium in the Central-Uralian zone are slope facies, consisting of tectonically altered carbonate-terrigenous rocks. The Berchogur sections in Kazakhstan contain rich, shallow-water, algal beds deposited within a semi-isolated marine basin.

The Devonian-Carboniferous boundary interval spans the upper Famennian and lower Tournaisian substages that include the regional units of the Urals – Murzakaevian, Kushelgian, Lytvian, and lower Gumerovian horizons in the Upper Famennian, and upper Gumerovian, Malevkian, and Upian horizons in the Lower Tournaisian (Fig. 2). The boundary is placed at the first appearance of the conodont *Siphonodella sulcata* (Huddle) within the Gumerovian (Pazukhin 2008, 2009; Pazukhin *et al.* 2009). The Gumerovian stratotype is the Zigan section (Fig. 3; right bank of the Zigan River near the village of Gumerovo), and the parastratotype is the Sikaza section (Kochetkova *et al.* 1986, 1988). The boundary beds contain foraminiferal assemblages belonging to the *Quasiendothyra communis, Q. kobeitusana, Tournayellina beata pseudobeata, Earlandia minima,* and *Chernyshinella disputabilis* zones of the Russian General Stratigraphic Scale (Kulagina *et al.* 2003).

The Murzakaevian and Kushelgian horizons are defined by conodonts (Artyushkova *et al.* 2011) and contain foraminifers of the *Q. communis* Zone. In the Zilim-Zigan region the irregularly dolomitized limestones of the Murzakaevian range from 6.3 m thick in the Ryauzyak section to 18 m in the Zigan section (Kochetkova *et al.* 1985). The Kushelgian Horizon in the Zigan section is 21.7 m thick and consists of bedded limestones with a brachiopod coquina at the base. In the Zilair Megasynclinorium (Bolshoi Ik section) the Kushelgian contains shale, argillaceous limestone, and limy chert, and is 20–40 m thick (Pazukhin *et al.* 2004). At Mugodzhary (Berchogur) the Murzakaevian–Kushelgian interval is represented by bioclastic packstones and lithoclastic grainstones of the lower Dzhangana Formation with a thickness of about 90 m.

The Lytvian Horizon is divided into the Abiyuskan and Zigan beds in the West Uralian Fold Zone (Stratigraphic schemes 1993), and is characterized by foraminifers of the *Q. kobeitusana* Zone. The thickness of the Lytvian is up to 19.5 m. The Abiyuskan beds consist mostly of bioclastic packstones and finely brecciated limestone, with layers of partly dolomitized, litho-bioclastic grainstones. The Zigan beds, belonging to the *Siphonodella praesulcata* conodont Zone (Pazukhin 2009), contain bioclastic packstones, intraclastic biosparites, algal nodules of *Garwoodia gregaria* Nicholson, ostracods, crinoids, bryozoans, and brachiopods. In the type Zigan section, foraminifers are not found in these beds. The thickness of the deposits range from 0.3 m at Sikaza to 2.5–2.8 m at Zigan (Kochetkova *et al.* 1988). In the Zilair Megasynclinorium the Lytvian is represented by intercalations of argillaceous limestone, cherty shale, and cherty limestone with a thickness of 40–60 m. In the Berchogur sections the same age deposits are represented by fossiliferous limestones of the Dzhangana Formation (foraminiferal-algal wackestone and packstone), with a thickness exceeding 100 m.

The Gumerovian Horizon is a transitional interval in which essential changes took place in the evolution of many faunal and floral groups, connected with the Hangenberg event (Walliser 1984, Kalvoda 2002). In the South Urals changes are recorded in foraminifers, ostracods,

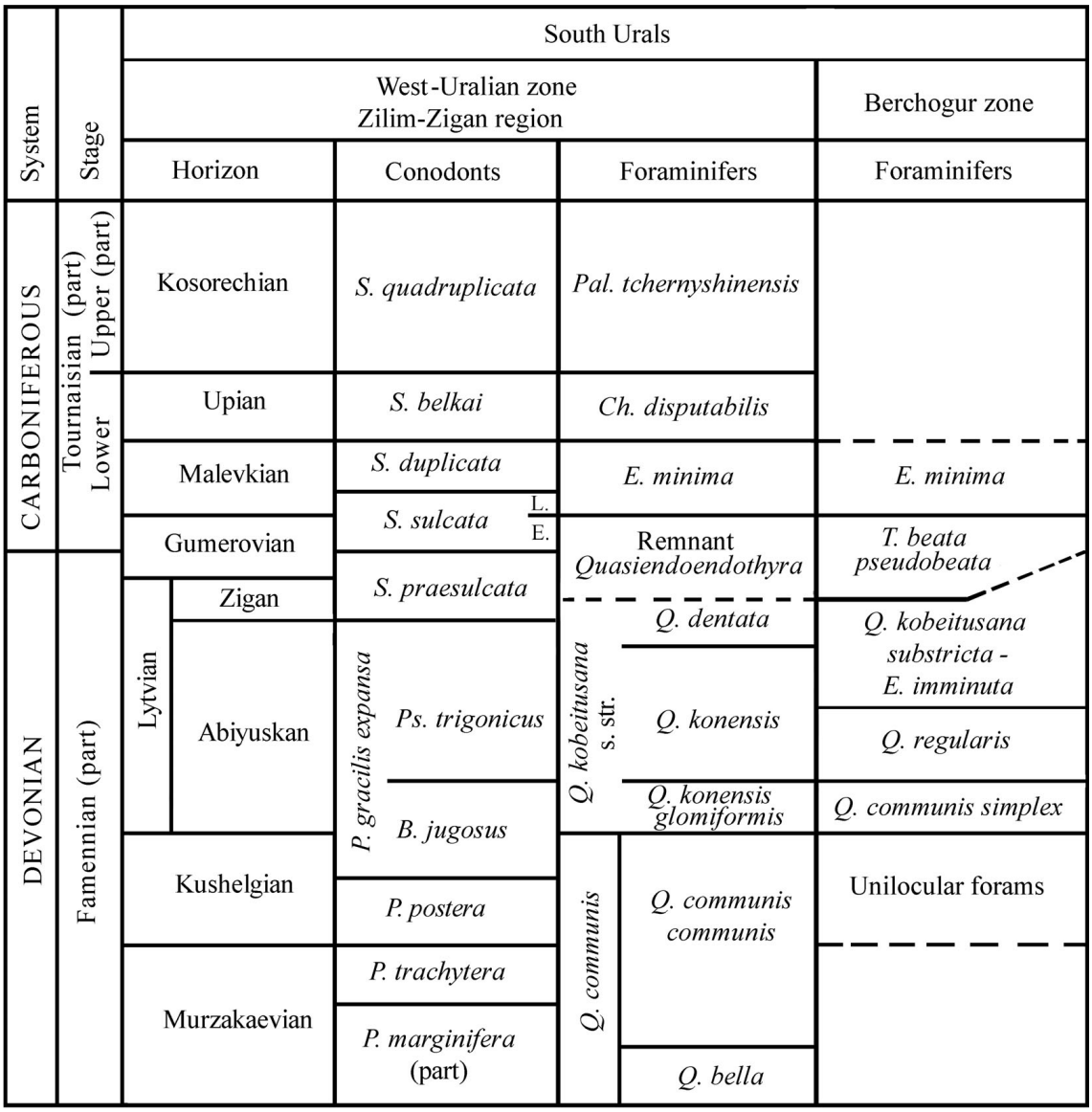


Figure 2. Stratigraphic units of the Famennian–Tournaisian of the Western subregion of the South Urals (Stratigraphic schemes 1993, Artyushkova *et al.* 2011) and foramifiral zones of the Berchogur Zone of the East subregion (Kochetkova *et al*. 1987).

ammonoids, conodonts, and miospores (Kochetkova *et al.* 1988, Barskov *et al.* 1988).

The lower boundary of the Gumerovian is defined by the base of the *Pseudoleperditia tuberculifera-Coryellina alba-Cribroconcha primaris* ostracod Zone (Kochetkova *et al.* 1986, 1988), followed by the appearance of the conodont *Siphonodella sulcata* at the Devonian-Carboniferous boundary in the middle Gumerovian near the base of the PLE (*pusillites-lepidophyta-explanata*) palynozone (Pazukhin 2008). In all of the Zilim-Zigan sections (except Usuili) the lowermost part of the Gumerovian is a thin-bedded and dolomitized, friable argillaceous limestone rich in brachiopods, ostracods, and trilobites that is overlain by medium-bedded wackestones and packstones. This part of the Gumerovian probably coincides with the Hangenberg event in the La Serre section (Kaiser 2009). The thickness of the Gumerovian changes from 1.3 m at Sikaza to 1.9 m at Zigan. In the Usuili section the Gumerovian consists of massive wackestones and algal pelmicrites more than 3 m thick. But the Gumerovian is virtually absent at the Ryauzyak section (Fig. 4) where the unit is probably represented by a paleokarst surface. Equivalents of the Gumerovian at Berchogur (Burtybai section, Fig. 5) correspond to the upper member of the Dzhangana Formation (*Acutimitoceras* Beds) that includes micrites and pelmicrites with bioclasts and nodules of *Garwoodia gregaria*.

The Malevkian Horizon contains conodonts of the Late *Siphonodella sulcata* Subzone and *S. duplicata* Zone

(Pazukhin 2009). Thicknesses at the Sikaza, Zigan and Usuili sections vary from 2.9–6 m. In the Ryauzyak section the thickness is about 0.5 m. Lithologies include slightly dolomitized pelsparites in the lower part changing upward to brecciated bioclastic limestones with silica lenses (Sikaza) and oncoids (Zigan), the latter often composed of *Garwoodia gregaria* and *Solenopora* algae. Massive calcisphaerid wackestones occur at Usuili. In the Zilair Megasynclinorium the Malevkian consists of 30–60 m of terrigenous mudstone interlayed with sandstone and siltstone.

The Upian Horizon is characterized by conodonts of the *S. belkai* Zone and foraminifers of the *Ch. disputabilis* Zone. In the Zilim-Zigan region the thickness is 7.0–17.5 m with lithologies consisting of partly dolomitized pelsparites and dolomites at Sikaza, and fossiliferous wackestones and packstones at Zigan, Usuili, and Ryauzyak; 20–30 m of bio-lithoclastic packstones and grainstones occur at the Zilair Megasynclinorium section. The Upian is overlain by massive fossiliferous limestones of the lower Kosorechian Horizon, which contains foraminifers of the *Chernyshinella glomiformis-Palaeospiroplectammina tchernyshinensis* Zone at the Sikaza and Usuili sections (Sinitsyna 1975, Kulagina & Sinitsyna 2000).

Foraminiferal zonal sequence

The *Quasiendothyra communis* Zone corresponds to the Murzakaevian and Kushelgian horizons and to the beds with unilocular foraminifers in the Bolshoi Ik and Berchogur sections. The *Quasiendothyra bella* Subzone occurs in the lower part of the zone in the Zigan section (beds 1–3, lower part of bed 4) and Sikaza section (bed 1, Kochetkova *et al.* 1985, Artyushkova *et al.* 2011). It contains an impoverished foraminiferal assemblage of *Archaesphaera minima* Suleimanov*, Eovolutina elementa* Antropov, *Bisphaera* spp., *Quasiendothyra bella* (N. Chernysheva), *Q. communis simplex* Brazhnikova, and rare *Septaglomospiranella* sp.

The most upper part of the *Quasiendothyra communis* Zone covers the uppermost part of Murzakaevian and the lowermost part of the Kushelgian (Zigan, beds 4 (upper)–13; Sikaza, beds 2, 3; Ryauzyak, beds 3–15). Characteristic for this subzone is the occurrence and wide development of *Quasiendothyra bella* (Fig. 6K, L), *Q. communis* (Rauser-Chernousova) with its subspecies, and also the symmetrical form *Q. regularis* (Lipina) (Fig. 6M–R). In the Sikaza section there is a considerable variety of parathuramminids and tournayellids (Fig. 8K, N, R).

Large quasiendothyrins of the *Q. communis* group (Fig. 6Y, Z) appear in the top of the *Q. communis* Zone in some sections (Zigan, bed 13; Ryauzyak, beds 11–15) along with the first small *Q.* ex gr. *radiata* Reitlinger (Kochetkova *et al.* 1985).

The *Quasiendothyra kobeitusana* Zone (*s.s.*) corresponds to the Lytvian Horizon. In the Zigan, Ryauzyak and Sikaza sections this zone is subdivided locally into the following subzones: *Q. konensis glomiformis, Q. konensis-Q. kobeitusana, Q. dentata* (Kochetkova *et al.* 1985).

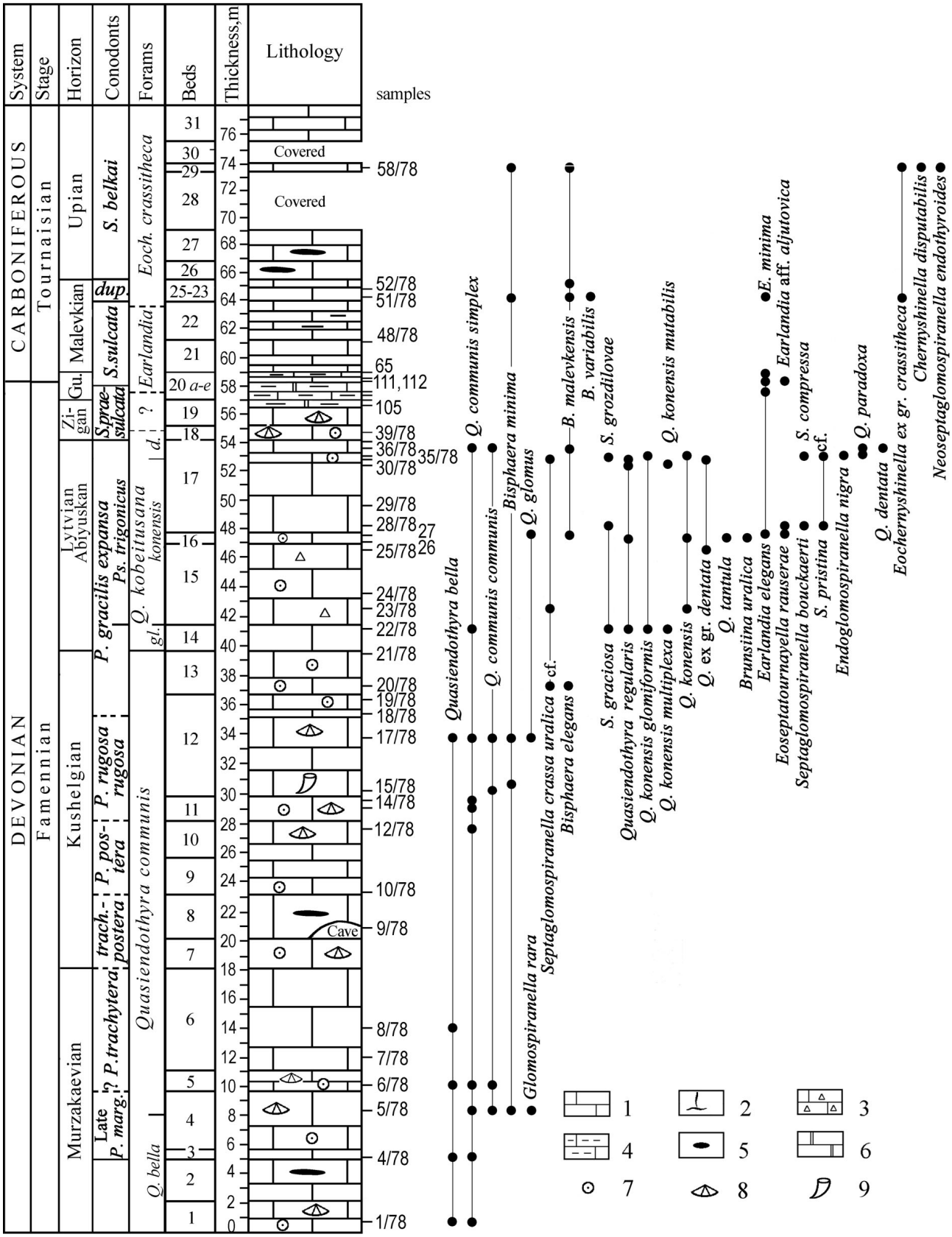
The lower boundary of the *Q. kobeitusana* Zone is defined by the appearance of quasiendothyrins with well-developed radial wall layers such as *Q. konensis glomiformis* Reitlinger (Fig. 7Q, R), *Q. konensis multiplexa* Grozdilova (Fig. 7P), rare *Q. konensis* (Lebedeva)*, Q. kobeitusana* (Rauser-Chernousova)*,* and *Q. mirabilis* (N. Chernysheva). Taxa from the preceding zone, including *Bisphaera* spp., *Septaglomospiranella* spp., and the *Q. communis* group (Fig. 7K) are still present. *Quasiendothyra konensis* and *Q. kobeitusana* Subzone (Zigan, beds 15, 16, and lower most part of 17; Sikaza, beds 5, 6; Ryauzyak, beds 18–23) show an increase in the diversity and number of advanced quasiendothyras and of the *Q. regularis* group (Fig. 7T, U). *Endoglomospiranella imminuta* (Conil & Lys) (Fig. 8O, P, V), *Septaglomospiranella crassa uralica* Lipina (Fig. 8AF) also appear in those beds. The last *Quasiendothyra* ex gr. *konensis* occur in the Sikaza section in bed 6a (Fig. 7J).

Q. dentata Subzone is recorded in the Zigan (upper 0.6 m of bed 17) and Ryauzyak (bed 24) sections, and is defined by the occurrence of *Q. dentata* (Fig. 7V) and *Q. paradoxa. Endoglomospiranella nigra* (Conil & Lys) and *E. alta* (Conil & Lys) (Fig. 7S) occurs here too.

The local zonal sequence corresponding to the *Quasiendothyra kobeitusana* Zone was established at Berchogur (Kochetkova *et al.* 1987): *Q. communis simplex*, *Q. regularis*, and *Q. kobeitusana substricta-Endoglomospiranella imminuta*.

The *Tournayellina beata pseudobeata* Zone was first described in the Berchogur sections (Burtybai, member IX, 4.5 m thick) as the *Tournayellina* Beds based on the occurrences of numerous *Tournayellina beata pseudobeata* Reitlinger & Kulagina (Kochetkova *et al.* 1987). However, their earlier appearance is known. A solitary specimen of this species (as reported by Reitlinger) was found in Borehole BCC-1 in the Berchogur Syncline in *Q. substricta-E. imminuta* Zone (Kochetkova *et al.* 1987, Table 3, spl. 36). In this borehole the D-C boundary is not exposed,

Figure 3. Ranges of endothyrids, tournayellids and some representatives of other groups of foraminifers in the Zigan section (modified from Kochetkova *et al.* 1985, 1988 and Pazukhin *et al.* 2009). Conodont zones after Pazukhin (2008, 2009). 1 – bedded limestone, 2 – massive limestone, 3 – lithoclastic, brecciated limestones, 4 – clayey limestone, 5 – chert, 6 – dolomites, 7 – crinoids, brachiopods, corals.


System
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Horizon
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Thickness,m
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CARBONIFEROUS
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Murzakaevian
Kushelgian
Lytvian
Abiyuskan
Upian
Malevkian
Gu.
Zi-gan
Late
P. marg.
? P. trachytera
trach.-postera
P. pos-tera
P. rugosa
rugosa
P. gracilis expansa
Ps. trigonicus
S. belkai
dup.
S.sulcata
S.prae-sulcata
Eoch. crassitheca
Earlandia
Q. kobeitusana
konensis
gl.
d.
Q. bella
Quasiendothyra communis
Covered
Cave
Quasiendothyra bella
Q. communis simplex
Q. communis communis
Bisphaera minima
Q. glomus
Glomospiranella rara
Septaglomospiranella crassa uralica
cf.
Bisphaera elegans
B. malevkensis
B. variabilis
S. graciosa
S. grozdilovae
Quasiendothyra regularis
Q. konensis glomiformis
Q. konensis multiplexa
Q. konensis mutabilis
Q. konensis
Q. ex gr. dentata
Q. tantula
Brunsiina uralica
Earlandia elegans
E. minima
Eoseptatournayella rauserae
Earlandia aff. aljutovica
Septaglomospiranella bouckaerti
S. compressa
S. pristina
cf.
Endoglomospiranella nigra
Q. paradoxa
Q. dentata
Eochernyshinella ex gr. crassitheca
Chernyshinella disputabilis
Neoseptaglomospiranella endothyroides
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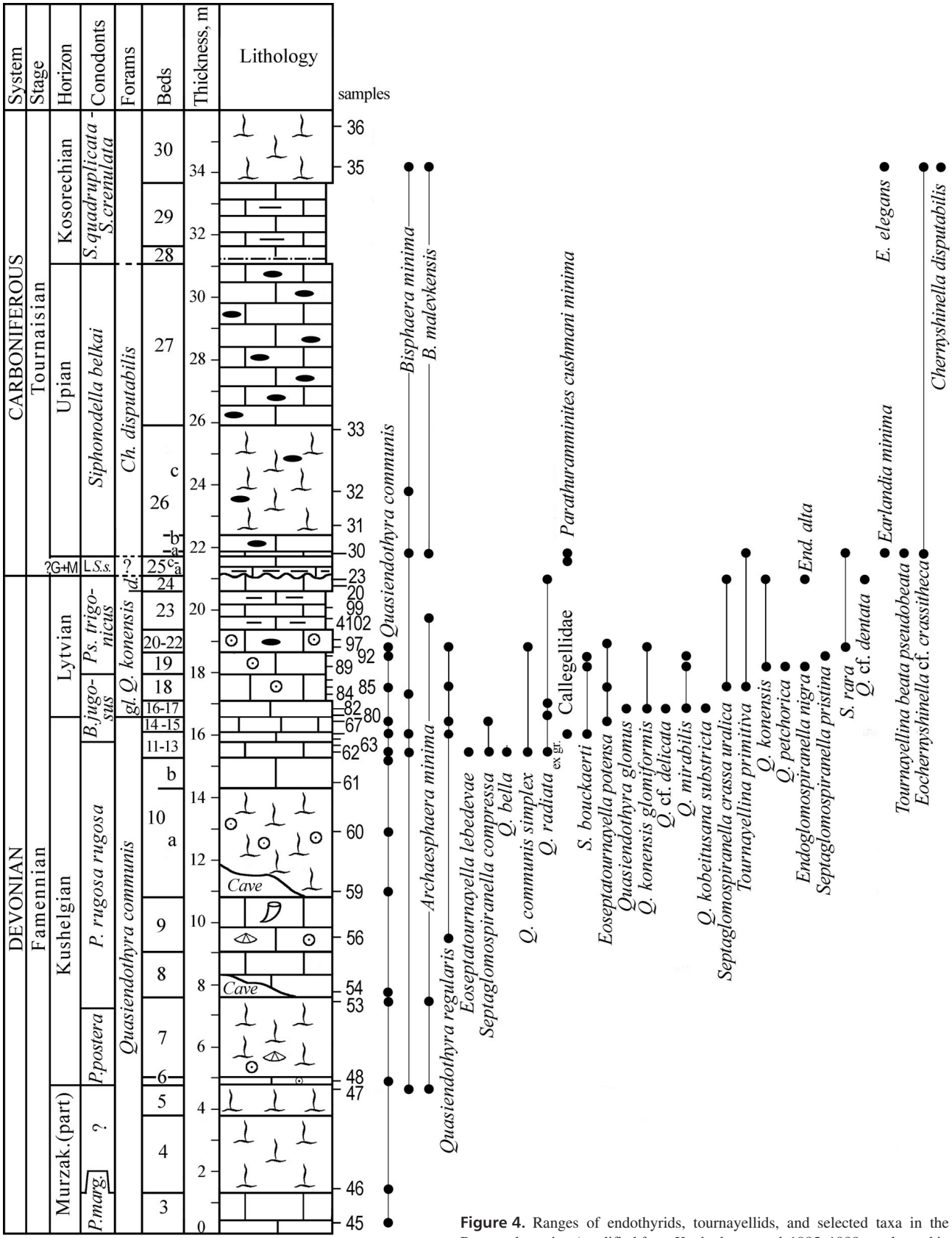


Figure 4. Ranges of endothyrids, tournayellids, and selected taxa in the Ryauzyak section (modified from Kochetkova *et al.* 1985, 1988; see legend in Fig. 3).

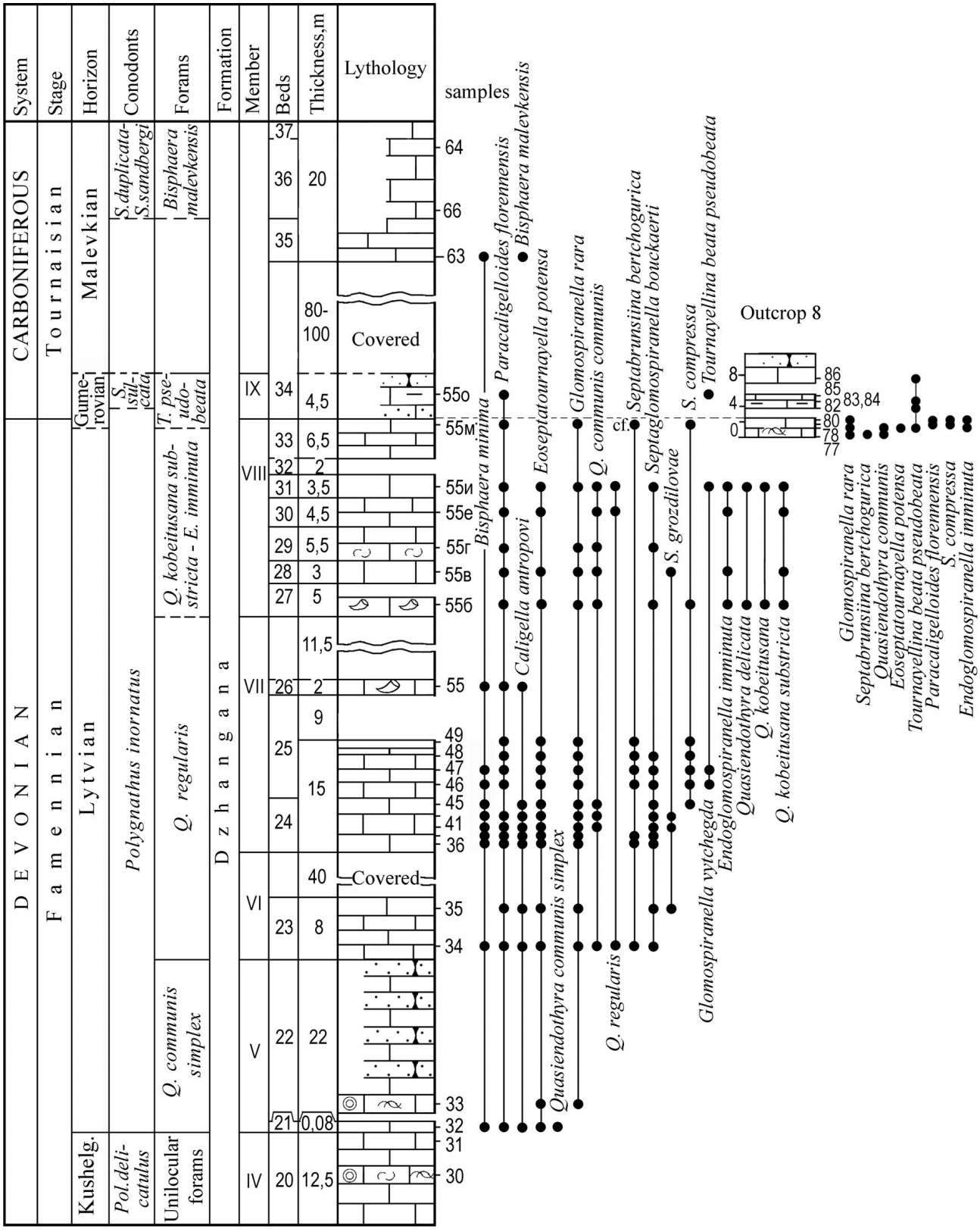


Figure 5. Ranges of selected taxa of foraminifers in the Burtybai and Outcrop 8 sections in Mugodzhary (modified from Kochetkova *et al.* 1987; see legend in Fig. 3).

but based on correlation, the appearance of *T. beata pseudobeata* is fixed about 4.5 m below the D-C boundary. The first rare *T. beata pseudobeata* occurs in Outcrop 8 (spl. 78) in the algal limestone along with *Septabrunsiina bertchogurica* Reitlinger & Kulagina, *Paracaligelloides florennensis* (Conil & Lys), and algae *Girvanella* spp. Therefore, the lower boundary of the zone should be presumed lower in the section. Thus, the lower part of the zone contains the first, rare *T. beata pseudobeata* and corresponds to the upper part of the *Polygnathus inornatus* conodont zone. *T. beata pseudobeata* becomes abundant in the upper part of zone (Fig. 8I, J) that correspond to the ammonoid *Acutimitoceras* Beds, conodonts *S. sulcata* Zone (Barskov *et al.* 1988), and the upper part of the Gumerovian, while *Quasiendothyra* is not found.

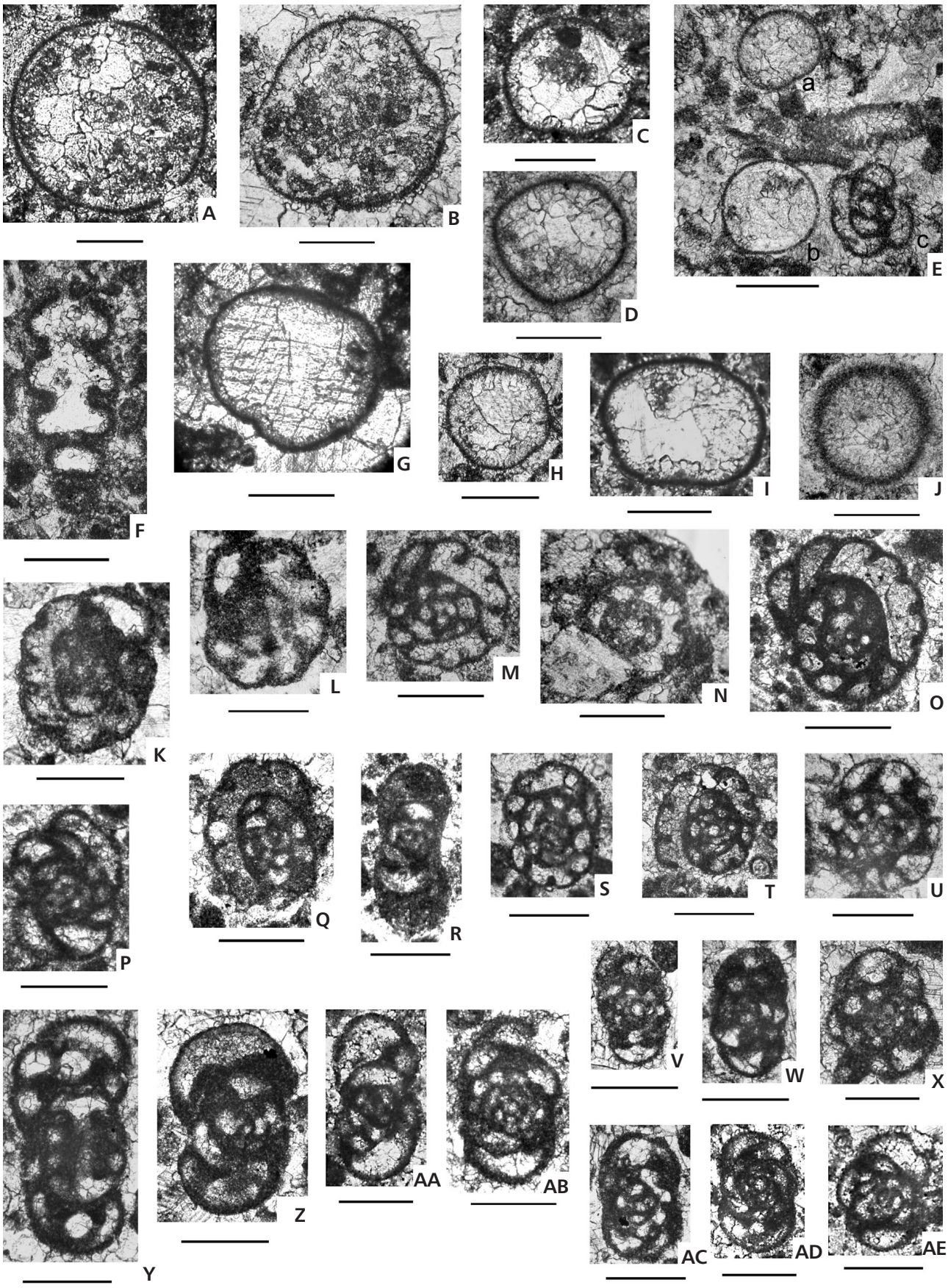
The correlation of *T. pseudobeata* Zone with sections of the Zilim-Zigan region of the western slope of the South Urals is difficult because no *Tournayellina* were found in that region in the Lytvian and Gumerovian. In the Zilim-Zigan region the last *Quasiendothyra* of the *Q. konensis* group are found in the Zigan beds in association with the conodonts *S. praesulcata* (Sikaza and Usuili sections). However, in some regions, *Quasiendothyra konensis* and *Q. kobeitusana* continue to the lower part of the Tournaisian, *e.g*., in Moravia (Kalvoda 1990, 2002) and in the Polar Urals (Chermnykh *et al.* 1988). In the Zigan section the lowermost horizons of *S. praesulcata* Zone correspond to the uppermost *Q. dentata* Zone, whereas its upper, larger part corresponds to a barren interval with no foraminifers. The *S. sulcata* Zone corresponds to the interval of the section containing solely members of *Earlandia* in this section. In the Ryauzyak section, the Gumerovian Horizon is apparently eroded, as beds with the conodonts of *Ps. trigonicus* Zone are overlain by beds with conodonts of the Late *S. sulcata* Zone, which corresponds to the Malevkian. In the Usuili section, the *S. praesulcata* zone correlates with the upper part of the *Q. dentata* Zone and lower part of beds with remnant *Quasiendothyra* sp. The *S. sulcata* Zone correlates with the beds with unilocular foraminifers (Parathuramminidae). The foraminiferal assemblage in the Sikaza section met with first conodonts of *Siphonodella sulcata* Zone contains *Glomospiranella rara* Lipina (Fig. 8Y), *Eoseptatournayella* sp. (Fig. 8L), *Septaglomospiranella grozdilovae* Pojarkov, *S. primaeva* (Rauser-Chernousova) (Fig. 8AC, AH), *Endoseptaglomospiranella nigra* (Fig. 8U), and *Quasiendothyra communis* (Fig. 7N, O).

Therefore the correlation of the sections of the Zilim-Zigan area of the South Urals and those in the Berchogur Syncline is to some extent provisional. Based on conodonts, it is possible to assume that the upper part of the Gumerovian, which in Sikaza contains remnant species of *Quasiendothyra*, corresponds to beds with abundant *T. beata pseudobeata* in Berchogur.

Apparently, the *Tournayellina beata pseudobeata* Zone of Berchogur corresponds to beds with remnant *Quasiendothyra*, upper part of the *S. praesulcata* and Early *S. sulcata* in the Zilim-Zigan region on the western slope of the South Urals that are equivalent to the Gumerovian. The *T. beata pseudobeata* Zone and corresponding to it beds has have transitional characteristic features and can be considered as part of either the *Quasiendothyra* or to *Chernyshinella* genozones (Reitlinger & Durkina 1988).

The *Earlandia minima* Zone corresponds to the Malevkian and mostly contains unilocular foraminifers (Zigan, beds 21, 22; Sikaza, beds 7, 8; Ryauzyak, bed 25b, v). Quasiendothyrins and many tournayellids disappear. A monotonous assemblage of simple morphology forms predominate, consisting of *Earlandia minima* (Birina), *Bisphaera malevkensis* Birina, *B. variabilis* Conil & Lys., *Eotuberitina reitlingerae* M.-Maklai, and *Vicinesphaera angulata* Antropov. Only *Parathurammina* spp. occurs in the Usuili section (Kulagina & Sinitsyna 2000), whereas

Figure 6. A–D, G–I – *Bisphaera malevkensis* Birina, 1948 (= *B. irregularis* Birina, 1948); A – No. 123/233, Sikaza, Spl. 6g/4 (2), B – No. 123/334, Sikaza, Spl. 1/1 (2), Murzakaevian; C – No. 123/335, Sikaza, Spl. 3/2 (1); D – No. 123/336, Zigan, Spl. 40 (1); G – No. 123/337, Sikaza, Spl. 6g/4 (4), Gumerovian; H – No. 123/338, Sikaza, Spl. 6g/4(2), Gumerovian; I – Zigan, No. 123/339, Spl. 27 (1), Lytvian. • E – foraminiferal packstone with *Bisphaera minima* Lipina, 1955 (a), *Eotuberitina reitlingerae* M.-Maklai, 1958, and *Septaglomospiranella bouckaerti* Conil & Lys, 1970, No. 123/340, Sikaza, Spl. 6g/3 (2), Gumerovian. • F – *Rectoseptaglomospiranella* sp. Fragment of shell. Sikaza, No. 123/341, Spl. 3/2 (2), Kushelgian. • J – *Bisphaera elegans* Vissarionova, 1950, Sikaza, No. 123/342, Spl. 3/1 (2), Kushelgian. • K, L – *Quasiendothyra bella* (N. Chernysheva, 1952), K – No. 123/343, L – No. 123/344, both from Sikaza, Spl. 2/2 (2), Murzakaevian. • M, O, P, Q, AA – *Quasiendothyra communis* (Rauser-Chernousova, 1948); M – No. 123/345, Sikaza, Spl. 3/2 (2), Kushelgian; O – No. 123/346, Sikaza, Spl. 3/2 (2), Kushelgian; P – No. 123/347, Zigan, Spl. 17 (1), Kushelgian; Q – No. 123/348, Sikaza, Spl. 3/1 (1), Kushelgian; AA – No. 123/349, Zigan, Spl. 40 (1), Lytvian. • N, R – *Quasiendothyra regularis eoregularis* Durkina, 1984; N – No. 123/350, Sikaza, Spl. 2/2 (1), Murzakaevian; R – No. 123/351, Sikaza, Spl. 3/2 (1), Kushelgian. • S, AD – *Quasiendothyra communis simplex* Brazhnikova, 1962; S – No. 123/352, Sikaza, Spl. 3/1 (1), Kushelgian; AD – No. 123/353, Zigan, Spl. 40 (1), Lytvian. • T, V, W – *Quasiendothyra baidjansaica* (Bogush & Yuferev, 1960); T – No. 123/354, Sikaza, Spl. 2/7 (1), Kushelgian; V – No. 123/355, Sikaza, Spl. 3/7 (1), Kushelgian; W – No. 123/356, Sikaza, Spl. 3/1 (3), Kushelgian. • U, X, AG – *Quasiendothyra baidjansaica globosa* Durkina, 1984; U – No. 123/357, Sikaza, Spl. 3/7 (1), Kushelgian; X – No. 123/358, Sikaza, Spl. 3/7 (2), Kushelgian; AG – No. 123/359, Sikaza, Spl. 3/2 (2), Kushelgian. • Y – *Quasiendothyra regularis* (Lipina, 1955), No. 123/360, oblique section, Sikaza, Spl. 3/7 (1), Kushelgian. • Z – *Quasiendothyra glomus* Grozdilova, 1973, No. 123/361, Sikaza, Spl. 3/7 (1), Kushelgian. • AB, AC – *Quasiendothyra communaeformis* Grozdilova, 1973, axial section; AB – No. 123/362, Sikaza, Spl. 3/1 (3), Kushelgian; AC – No. 123/363, Zigan, Spl. 17, Kushelgian. Scale bar is 0.2 mm.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Eochernyshinella ex gr. *crassitheca* Lipina was recorded from the top of the Malevkian in the Zigan section (spl. 52).

The *Chernyshinella disputabilis* Zone corresponds to the Upian and possibly to the upper part of the Malevkian. The zonal name bearer and *Eochernyshinella crassitheca* appear at the base of the zone at Sikaza (Kulagina *et al.* 2003). In other sections (Zigan, top of bed 22; Ryauzyak, beds 26, 27) only *E. crassitheca* (Fig. 8A, B) is common in the basal beds (Kochetkova *et al.* 1985). The zone contains *Tournayellina beata pseudobeata* (Fig. 8G, H) in the Ryauzyak section, and parathuramminids, rare *Tournayellina* sp. and common *Septaglomospiranella* spp. at Usuili.

Taxonomic diversity

More than 111 species and intraspecific taxa of 30 genera are identified in the Devonian-Carboniferous boundary deposits in the South Urals, belonging to the orders Parathuramminida, Earlandiida, Tournayellida, Endothyrida, and *incertae sedis*. The Parathuramminida is represented by the families Parathuramminidae, Archaesphaeridae, Bisphaeridae, Rauserinidae, and Cribrosphaeroididae (Vdovenko *et al.* 1993). Of the 31 taxa of parathuramminids and *incertae sedis* (Table 1, 1–31), two – *Rauserina notata* (Rauserinidae) and *Eovolutina elementa* – are bilocular; the remainder unilocular.

The Earlandiida is represented by the Caligellidae and Earlandiidae (Table 1, 32–37). The first family has a two-chambered test, sometimes with a slightly isolated proloculus and a tubular chamber divided by irregular wall constrictions. The Earlandiidae include forms with a proloculus and an elongate, subcylindrical chamber.

Multilocular foraminifers belong to the Tournayellida and Endothyrida (Rauser-Chernousova *et al.* 1996). Families included with the first order are Tournayellidae (Table 1, 38–46), Lituotubellidae (Table 1, 47–72), and Chernyshinellidae (Table 1, 73–82). The Tournayellidae is represented by *Eoseptatournayella* and *Conilites*; the Lituotubellidae by *Septabrunsiina, Brunsiina, Glomospiranella*, *Rectoseptaglomospiranella,* and *Neoseptaglomospiranella* of the Septabrunsininae and *Septaglomospiranella* and *Endoglomospiranella* of the Septaglomospiranellinae; and the Chernyshinellidae by *Tournayellina* and *Eochernyshinella* of the Tournayellininae and *Chernyshinella* of the Chernyshinellinae.

The Endothyrida is represented by *Quasiendothyra* and *Klubovella* of the Quasiendothyrinae and by the Loeblichiidae, with the most abundant taxa belonging to the three *Quasiendothyra* subgenera (Rauser-Chernousova *et al.* 1996; Table 1, 83–111). It is noteworthy that some authors consider *Quasiendothyra* subgenera as genera in their own right (Gibshman & Nikolaeva 2011, Hance *et al.* 2011 and others). Indeed, *Quasiendothyra (Eoquasiendothyra) – Q. (Eoendothyra) – Q. (Quasiendothyra)* represent an evolutionary trend, which is instrumental in the stratigraphy and correlation of the Famennian-Tournaisian boundary beds, although the subgenera have many intermediate stages between them. Originally *Eoendothyra* M.-Maklai, 1960 was established as genera, but *Quasiendothyra* (*Eoquasiendothyra*) Durkina, 1963 in Decision 1963, as subgenera (Durkina 1984). The *Q. communis* Zone contains 47 species and subspecies of 19 genera distributed among the Parathuramminida (9 genera), Earlandiida (3 genera), Tournayellida (6 genera), and Endothyrida (1 genus).

The number of foraminiferal species in the lower part of the *Q. kobeitusana* Zone remains almost constant, but increases to 75 in the upper of the zone within the *Q. konensis-Q. kobeitusana* and *Q. dentata* subzones in the Zilim-Zigan region of the South Urals and the *Q. substricta-E. imminuta* Zone in Berchogur. Here the Quasiendothyrinae reach maximum diversity with 26 species and subspecies recorded from the *Q. kobeitusana* Zone.

Figure 7. A–C – *Paracaligelloides florennensis* (Conil & Lys, 1964); A – fragment of the longitudinal section, B, C – transversal sections. A – No. 123/364, Zigan, Spl. 22 (1), Lytvian; B – longitudinal section, No. 123/365, Zigan, Spl. 35 (1), Lytvian; C – No. 123/366, Sikaza, Spl. 6g/4 (2), Gumerovian. • D – *Earlandia* aff. *aljutovica* (Reitlinger, 1950), longitudinal section, No. 123/231, Zigan, Spl. 111 (3), Gumerovian. • E – bioclastic wackestone with longitudinal and transversal sections of *Earlandia elegans* (Rauser-Chernousova & Reitlinger, 1940), Zigan, No. 123/406, Spl. 111 (2), Gumerovian. • F, G, I – *Earlandia elegans* (Rauser-Chernousova & Reitlinger, 1940), longitudinal section; F – No. 123/367, Zigan, Spl. 27, Lytvian; G – No. 123/227, Spl. 65 (2), Gumerovian; I – No. 123/333, Spl. 112 (1), Gumerovian. • H – *Earlandia minima* (Birina, 1948), transversal section, No. 123/368, Zigan, Spl. 51, Malevkian. • J – *Quasiendothyra* ex gr. *konensis* (Lebedeva, 1956), oblique section, No. 123/369, Sikaza, Spl. 6a (1), Lytvian, Zigan Beds. • K – *Quasiendothyra communis kamenkaensis* (Durkina, 1959), sagittal section, No. 123/370, Ryauzyak, Spl. 23, Lytvian. • L – *Quasiendothyra turbida* (Durkina, 1959), axial section, No. 123/371, Zigan, Spl. 35, Lytvian. • M–O – *Quasiendothyra communis* (Rauser-Chernousova, 1948), axial sections; M – No. 123/372, Zigan, spl. 30, Lytvian; N – No. 123/238, Sikaza, 6g/4 (3), O – No. 123/237, Sikaza, Spl. 6g/4 (5), Gumerovian. • P – *Quasiendothyra konensis multiplexa* Grozdilova, 1973, sagittal section, No. 123/373, Zigan, Spl. 22, Lytvian. • Q, R – *Quasiendothyra konensis glomiformis* Reitlinger, 1961; Q – sagittal section, No. 123/407, Zigan, Spl. 22, Lytvian; R – No. 123/380, near axial section, Zigan, Spl. 27, Lytvian. • S–U – *Quasiendothyra regularis* (Lipina, 1955); S, U – sagittal section, S – No. 123/374, Zigan, Spl. 36; U – No. 123/375, Zigan, Spl. 30; T – axial section, No. 123/376, Zigan, Spl. 27. All from Lytvian. • V – *Quasiendothyra dentata* (Durkina, 1959), axial section, No. 123/377, Zigan, Spl. 36, Lytvian. • W – *Quasiendothyra kobeitusana* (Rauser-Chernousova, 1948), sagittal section, No. 123/378, Muradymovo, Spl. 18b (1). • X – *Baituganella* ex gr. *chernyshinensis* Lipina, 1955, No. 123/379, Zigan, Spl. 27, Lytvian. A, B, G, H, L, M, P–V, X – from Reitlinger collection (GIN RAS). Scale bar is 0.2 mm.

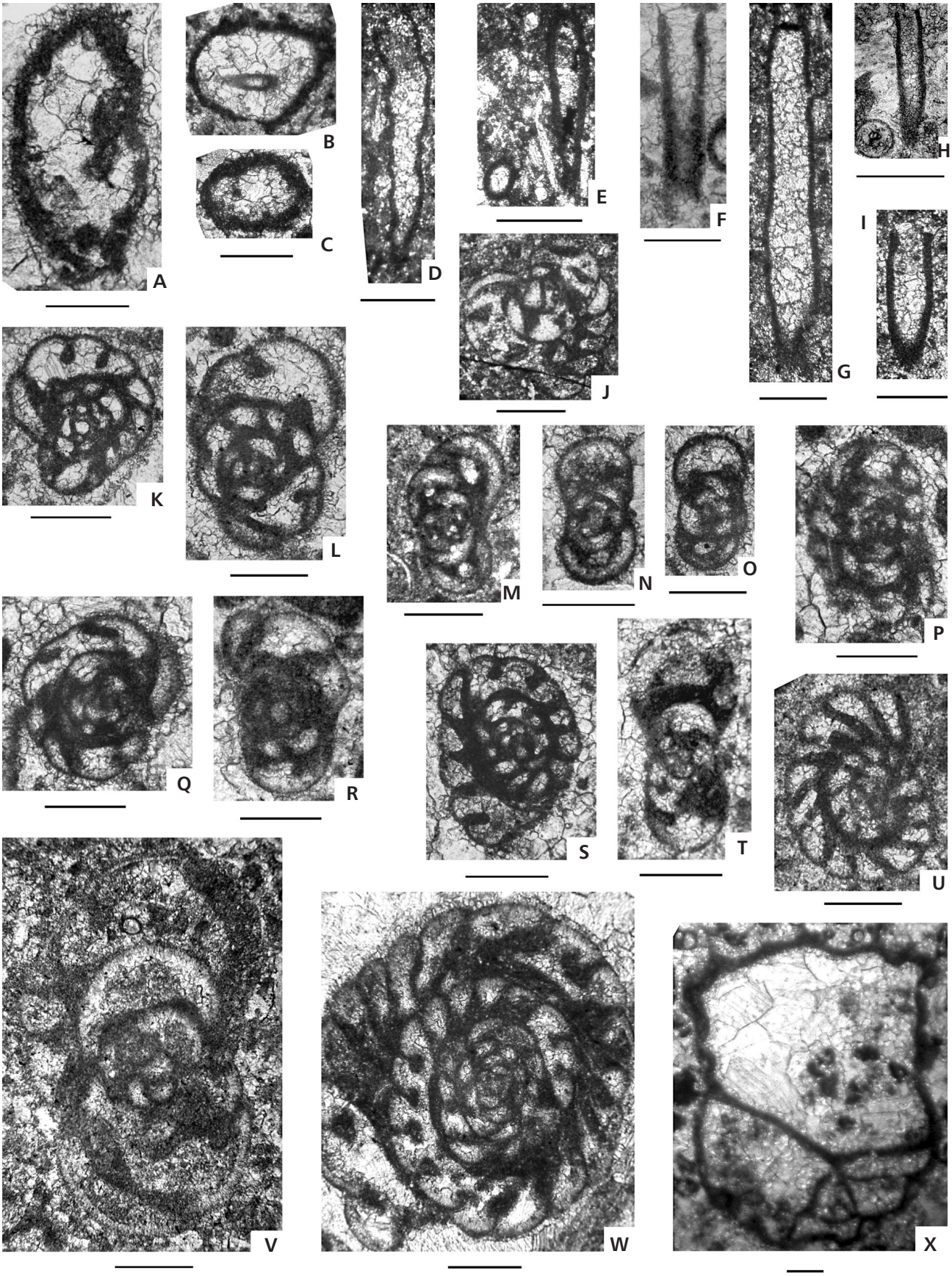
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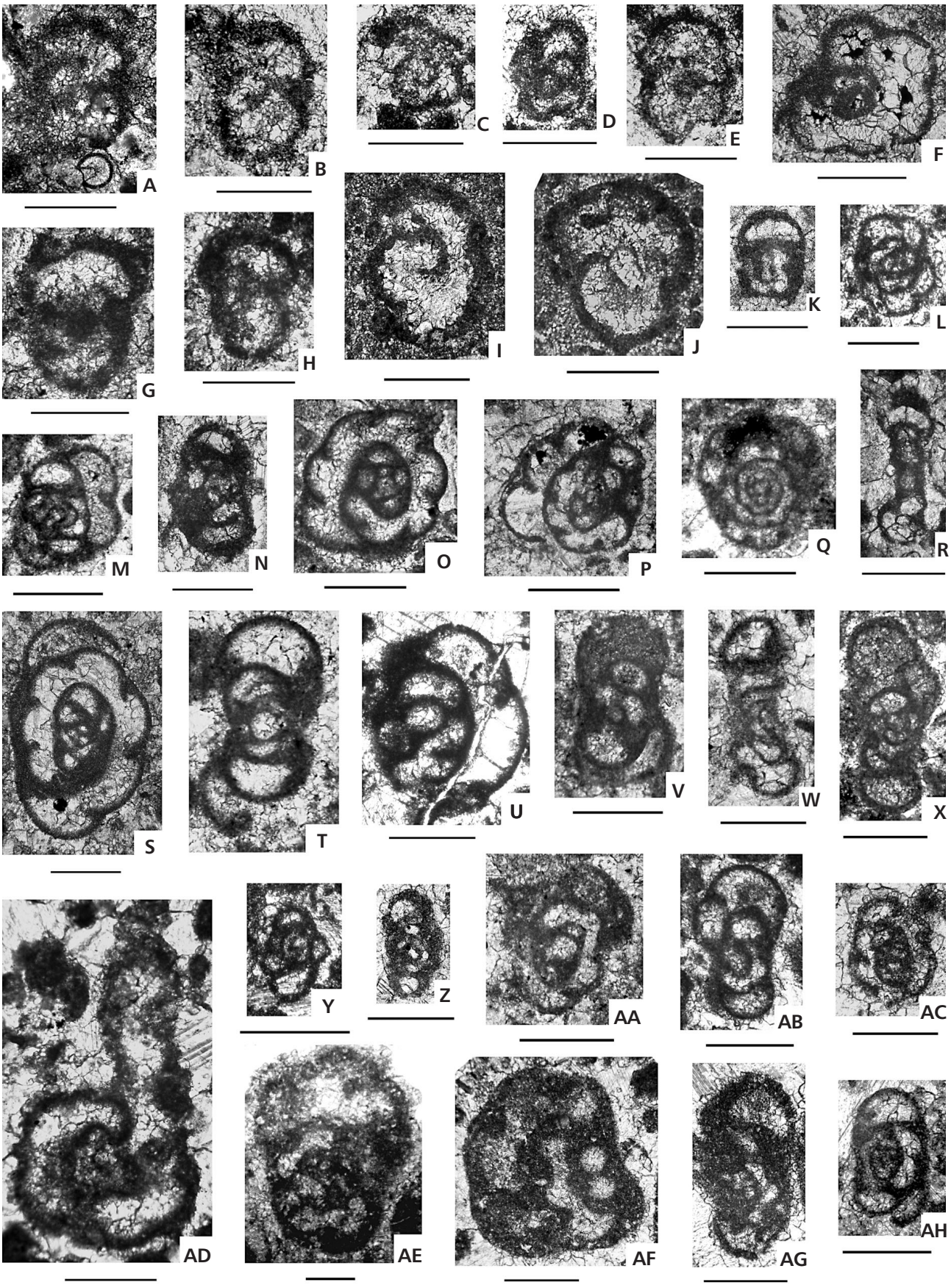
Table 1. Ranges of foraminifers in the Devonian-Carboniferous boundary beds in the South Urals and Mugodzhary (used Grozdilova 1973; Sinitsyna 1975; Kochetkova *et al.* 1985, 1988; Sinitsyna *et al.* 1995; Kulagina & Sinitsyna 2000; Pazukhin *et al.* 2009). Abbreviations: Murzak. – Murzakaevian; Kush. – Kushelgian; Q. com. – *Q. communis* Zone; Q. kob. – *Q. kobeitusana* Zone; 1 – *Q. konensis glomiformis* Subzone; 2 – *Q. konensis-Q. kobeitusana* and *Q. dentata* subzones; r. Q. – T. ps. – remnant *Quasiendothyra* Beds – *Tournayellina beata pseudobeata* Zone; Ch. dis. – *Chernyshinella disputabilis* Zone; Pal. tchern. – *Palaeospiroplectammina tchernyshinensis* Zone. Scale bar is 0.2 mm.

No.	Foraminifers	Stage	Famennian				Tournaisian			
		Series	Upper				Lower		Upper (part)	
		Substage	Murzak Kush.	Lytvian		Gumerovian	Malevkian	Upian	Kosorechian	
		Zones	Q. com.	Q. kob.		r. Q. – T. ps.	E. min.	Ch. dis.	Pal. tchern.	
				1	2					
1	2		3	4	5	6	7	8	9	10
1	*Parathurammina suleimanovi* Lipina, 1949		+		+	+	+	+	+	+
2	*P. stellata* Lipina, 1950		+		+		+	+	+	+
3	*P. spinosa* Lipina, 1949		+			+	+	+	+	+
4	*P. radiata* Antropov, 1950				+				+	
5	*P. tuberculata* Lipina, 1949				+		+			
6	*P. oldae* Suleimanov, 1948					+	+	+	+	
7	*P. gekkeri* Antropov, 1950				+		+	+		
8	*Parathuramminites cushmani* (Suleimanov, 1945)		+			+	+		+	+
9	*P. cushmani minima* (Antropov, 1950)				+		+		+	
10	*Archaesphaera minima* Suleimanov, 1945		+	+	+	+	+	+	+	
11	*A. crassa* Lipina, 1950				+		+	+		+
12	*A. grandis* Lipina, 1950		+		+		+	+	+	
13	*A. gigantea* Malakhova, 1959				+		+	+	+	+
14	*Vicinesphaera squalida* Antropov, 1950		+	+	+	+	+	+	+	+
15	*V. minima* Lipina, 1950			+	+					
16	*V. angulata* Antropov, 1950		+	+	+	+	+	+	+	+
17	*V. parva* Reitlinger, 1954					+	+			
18	*Bisphaera minima* Lipina, 1955		+	+	+	+	+	+	+	+
19	*B. elegans* Vissarionova, 1950		+	+	+	+	+		+	
20	*B. grandis* Lipina, 1955		+	+	+	+			+	+
21	*B. malevkensis* Birina, 1948		+	+	+	+	+	+	+	+
22	*B. elongata* Pojarkov, 1961			+						
23	*B. variabilis* Conil & Lys, 1964						+			
24	*Rauserina notata* Antropov, 1950		+		+	+	+	+	+	+
25	*Baituganella vulgaris* Lipina, 1955			+	+	+				+
26	*B. chernyshinensis* Lipina, 1955				+					
27	*Cribrosphaeroides simplex* Reitlinger, 1954				+	+			+	
28	*C. simplex donica* Brazhnikova & Rostovzeva, 1966		+							
29	*Diplosphaerina anaequalis* (Derville, 1931)		+							
30	*Eotuberitina reitlingerae* M.-Maklai, 1958			+	+	+	+	+	+	+
31	*Eovolutina elementa* Antropov, 1950		+		+				+	
32	*Paracaligelloides florennensis* (Conil & Lys, 1964)		+	+	+	+				
33	*P. muricatiformis* (Tchuvashov, 1965)			+						
34	*Caligella antropovi* (Lipina, 1955)		+	+	+	+	+	+	+	
35	*Earlandia minima* (Birina, 1948)		+	+	+	+	+	+	+	+
36	*E. elegans* (Rauser-Chernousova & Reitlinger, 1940)				+			+	+	+
37	*E.* aff. *aljutovica* (Reitlinger, 1950)					+				+
38	*Eoseptatournayella rauserae* (Lipina, 1955)		+	+	+					

1	2	3	4	5	6	7	8	9	10
39	*E. rauserae recta* (Lipina, 1965)	+							
40	*E. potensa* (Durkina, 1959)	+		+	+				
41	*E. potensa variabilis* (Reitlinger & Kulagina, 1987)			+					
42	*E. lebedevae* (Pojarkov, 1961)	+	+	+					
43	*E. lata* (Reitlinger & Kulagina,1987)		+						
44	*E. praesegmentata* (Bogush & Juferev, 1960)			+					
45	*Tournayella mica* Skvortzov, 1969			+					
46	*Conilites* sp.			+					
47	*Septabrunsiina* ex gr. *kingirica* Reitlinger, 1961	+	+	+					
48	*S. kingirica* Reitlinger, 1961			+					
49	S. *bertchogurica* Reitlinger & Kulagina, 1987		+	+					
50	*S. umboplicata* (Pojarkov, 1969)			+					
51	*Brunsiina uralica* Lipina, 1955			+				+	+
52	*Glomospiranella rara* Lipina, 1955	+		+	+	+	+		
53	*G. vytchegda* (Durkina, 1959)		+	+					
54	*Neoseptaglomospiranella endothyroides* (Dain, 1953)				+				
55	*Rectoseptaglomospiranella* sp.	+							
56	*R. kynensis* Grozdilova, 1973						+		
57	*Brunsia obtusa* Durkina, 1959	+							
58	*B. ezhwadorica* Durkina, 1959	+							
59	*Septaglomospiranella primaeva* (Rauser-Chernousova, 1948)	+	+	+	+				
60	*S. primaeva kazakhstanica* Reitlinger, 1961	+	+	+					
61	*S. crassa* Reitlinger, 1961	+		+					
62	*S. crassa uralica* Lipina, 1965	+		+					
63	*S. compressa* Lipina, 1965	+	+	+					
64	*S. bouckaerti* Conil & Lys, 1970	+	+	+	+				
65	*S. grozdilovae* Pojarkov, 1981	+		+	+			+	
66	*S. chernyshinelliformis* Durkina, 1984	+		+					
67	*S. pristina* Grozdilova, 1973			+					
68	*S. graciosa* Reitlinger, 1961			+					
69	*S. nana* Reitlinger, 1961						+		cf.
70	*Endoglomospiranella nigra* (Conil & Lys, 1964)			+	+				
71	*E. alta* (Conil & Lys, 1970)			+					
72	*E. imminuta* (Conil & Lys, 1964)			+	+				
73	*Tournayellina vulgaris* Lipina, 1955		+						
74	*T. primitiva* Lipina, 1965			+			+		+
75	*T. beata pseudobeata* Reitlinger & Kulagina, 1987			+		+			
76	*Eochernyshinella* ex gr. *crassitheca* Lipina, 1955				+				
77	*E. crassitheca* Lipina, 1955						+		
78	*Chernyshinella (Prochernyshinella) disputabilis* Lipina, 1955						+	+	
79	*Ch. (P.) oldae* (Grozdilova & Lebedeva, 1954)					+	+		
80	*Ch. (Chernyshinella) paucicamerata* Lipina, 1965					+	+	+	
81	*Ch. (Ch.) gelida plicata* Durkina, 1997						+	+	
82	*Ch. (Ch.) subrotunda* Malakhova, 1956						+		
83	*Quasiendothyra (Eoqusiendothyra) bella* (N. Chernysheva, 1952)	+	+	+					
84	*Q. (Eoq.) baidjansaica* (Bogush & Juferev, 1960)	+	+	+					
85	*Q. (Eoq.) baidjansaica globosa* Durkina, 1984	+							

1	2	3	4	5	6	7	8	9	10
86	*Q. (Eoq.) tantula* (Durkina, 1959)			+					
87	*Quasiendothyra (Eoendothyra) communis communis* (Rauser-Chernousova, 1948)	+	+	+	+				
88	*Q. (E.) communis simplex* Brazhnikova, 1962	+	+						
89	*Q. (E.) communis evoluta* Durkina, 1959		+						
90	*Q. (E.) communis kamenkaensis* Durkina, 1959		+						
91	*Q. (E.) communaeformis* Grozdilova, 1973	+	+						
92	*Q. (E.) delicata* Durkina, 1959	+	+	+	+				
93	*Q. (E.) regularis* (Lipina, 1955)	+	+	+					
94	*Q. (E.) regularis eoregularis* Durkina, 1984	+							
95	*Q. (E.) regularis conferta* (Durkina, 1959)	+							
96	*Q. (E.) glomus* Grozdilova, 1973	+	+						
97	*Q. (E.) absoluta* (Durkina, 1959)		+	+					
98	*Q. (E.) turbida* (Durkina, 1959)		+	+					
99	*Q. (E.) petchorica* (Durkina, 1959)		+	+					
100	*Q. (E.) umbilicata* (Lebedeva, 1956)			+					
101	*Q. (Quasiendothyra) radiata* (Reitlinger, 1961)	+	+						
102	*Q. (Q.) konensis multiplexa* Grozdilova, 1973		+						
103	*Q. (Q.) konensis glomiformis* Reitlinger, 1961		+	+					
104	*Q. (Quasiendothyra) kobeitusana* (Rauser-Chernousova, 1948)			+					
105	*Q. (Q.) kobeitusana substricta* Conil & Lys, 1964		+	+					
106	*Q. (Q.) mirabilis* (N. Chernysheva, 1952)			+					
107	*Q. (Q.) konensis* (Lebedeva, 1956)			+					
108	*Q. (Q.) konensis mutabilis* Reitlinger, 1961			+					
109	*Q. (Q.) dentata* (Durkina, 1959)			+					
110	*Q. (Q.) paradoxa* (Durkina, 1959)			+					
111	*Klubovella markovskyi* (N. Chernysheva, 1952)			+					

Figure 8. A, B – *Eochernyshinella crassitheca* (Lipina, 1965); A – axial sections, No. 123/381; B – oblique sagittal section, No. 123/382, both from Ryauzyak, Spl. 30 (2), Upian. • C, D – *Eochernyshinella* sp., axial sections; C – No. 123/383, Ryauzyak, Spl. 30 (4); D – No. 123/384 Ryauzyak, Spl. 30 (6), Upian. • E, F – *Tournayellina primitiva* Lipina, 1965; E – axial sections, No. 123/384, Ryauzyak, Spl. 30, Upian; F – sagittal section, No. 123/385, Ryauzyak, Spl. 4102, Lytvian. • G–J – *Tournayellina beata pseudobeata* Reitlinger & Kulagina, 1987; G – axial section, No. 123/386, H – oblique section, No. 123/387, both from Ryauzyak, Upian, G – Spl. 30 (6), H – Spl. 30 (6); I, J – axial sections, I – No. 123/409, J – No. 123/410, Mugodzhary, Dzhangansai, Spl. 681i, Dzhangana Formation, *Acutimitoceras* Beds. • K – *Septaglomospiranella* sp., near axial section, No. 123/388, Sikaza, Spl. 2/1 (1), Murzakaevian. • L – *Eoseptatournayella* sp. No. 123/240, Sikaza, Spl. 6g/4 (2), Gumerovian. • M, N – *Septaglomospiranella pristina* Grozdilova, 1973; M – close to axial section, No. 123/389, Zigan, Spl. 28, Lytvian; N – No. 123/390, Sikaza, Spl. 2/7 (2), Kushelgian. • O, P, V – *Endoglomospiranella imminuta* (Conil & Lys, 1964); O, P – sagittal sections, V – axial section. O – No. 123/391, P – No. 123/392, V – No. 123/393; O, V – Zigan, Spl. 28, Lytvian; P – Ryauzyak, Spl. 4102, Lytvian. • Q, R – *Eoseptatournayella potensa* (Durkina, 1959); Q – sagittal section, No. 123/394, Zigan, Spl. 28, Lytvian; R – axial section, No. 123/395, Sikaza, Spl. 3/1 (3), Kushelgian. • S – *Endoglomospiranella alta* (Conil & Lys, 1964), sagittal section, No. 123/395, Ryauzyak, Spl. 23, Lytvian. • T–U – *Endoglomospiranella nigra* (Conil & Lys, 1964); T – axial section, No. 123/396, Zigan, Spl. 35, Lytvian; U – sagittal oblique section, No. 123/244, Sikaza, Spl. 6g/4 (1), Gumerovian. • W, X – *Septabrunsiina bertchogurica* Reitlinger & Kulagina, 1987, nearly axial sections; W – No. 123/397, Zigan, Spl. 27; X – No. 123/398, Zigan, Spl. 28. • Y, Z – *Glomospiranella rara* Lipina, 1955, axial sections; Y – No. 123/245, Sikaza, Spl. 6g/4 (1), Gumerovian; Z – No. 123/399, Sikaza, Spl. 3/7 (2), Kushelgian. • AA, AB – *Septaglomospiranella chernyshinelliformis* Durkina, 1984; AA – sagittal section, No. 123/400, AB – axial section, No. 123/401, both from Zigan, Spl. 35, Lytvian. • AC, AH – *Septaglomospiranella primaeva* (Rauser-Chernousova, 1948); AC – sagittal section, No. 123/400, AH – axial sections, No. 123/239, both – Sikaza, Spl. 6g/4 (5), Gumerovian. • AD – *Conilites* sp., sagittal section, No. 123/402, Zigan, Spl. 26, Lytvian. • AE, AF – *Septaglomospiranella crassa uralica* Lipina, 1965, oblique sections; AE – No. 123/403, Zigan, Spl. 33, Lytvian; AF – No. 123/404, Ryauzyak, Spl. 23, Lytvian. • AG – *Septaglomospiranella* ex gr. *kingirica* Reitlinger, 1961, near axial sections, Sikaza, Spl. 1/1 (1), Murzakaevian. A–J, M–Q, T, V–X, AA–AB, AD–AF – from Reitlinger collection (GIN RAS).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Quasiendothyra kobeitusana is found in the Sikaza, Usuili, and Bolshoi Ik sections (Fig. 7W), although *Quasiendothyra konensis* is more common, and in Mugodzhary the smaller subspecies *Q. kobeitusana substricta* dominates. The increase in species numbers within the zone also reflects an increase in genera. Overall the *Q. kobeitusana* Zone contains 83 species and subspecies and 24 genera.

This maximum diversification reflects the rapid and successive evolution of Late Devonian endothyrids culminating in a radiating "explosion" near the end of the Late Famennian (Reitlinger 1979). Thereafter, evolutionary rates declined, followed by extinction, connected with the Hangenberg event (Walliser 1984). The taxonomic diversity decreased in the *Tournayellina beata pseudobeata* Zone and in the beds with remnant *Quasiendothyra*. At that time species numbers were reduced to 30 and genera to 18, more than half of these represented by unilocular forms. The remaining multilocular foraminifers include *Glomospiranella*, *Septaglomospiranella*, *Endoglomospiranella*, and rare *Q. communis.*

The lowest species diversity is observed in the *Earlandia minima* Zone with only 24 taxa divided among 19 unilocular taxa (*Archaesphaera* – 3 species, *Vicinesphaera* – 3, *Parathurammina* – 5, *Parathuramminites* – 3, *Bisphaera* – 4, *Eotuberitina* – 1), three bilocular forms (*Rauserina notata*, *Earlandia minima, Caligella antropovi*) and two multilocular foraminifers (*Glomospiranella rara* and *Eochernyshinella* ex gr. *crassitheca*). Species diversity begins to increase in the *Ch. disputabilis* Zone and reaches 60 species and 30 genera in the overlying *Palaeospiroplectammina tchernyshinensis* Zone, due to radiation within the subfamily Chernyshinellinae.

Conclusions

The foraminiferal fauna in the South Urals in the Devonian-Carboniferous boundary interval includes four orders, 12 families, 29 genera, and more than 101 specific and intraspecific taxa, although more than one third of the latter belong to long-ranging, unilocular and bilocular forms. Changes in taxonomic composition are related mostly to evolution within the Endothyrida and Tournayellida that began at the beginning of the Murzakaevian Horizon in the late Famennian, specifically the rapid development of the Quasiendothyrinae and Lituotubellidae.

The beginning of the Murzakaevian is marked by the occurrence of *Quasiendothyra bella* and *Q. communis*; the end is marked by increasing intraspecific variation among these first quasiendothyrins. Evolution accelerated during the Lytvian, leading to an "explosion" of new forms at about the time of the appearance of *Q. dentata* within the Endothyrida and *Tournayellina* within chernyshinellids. This interval of peak diversity at the end of the late Famennian was followed at the beginning of the Tournaisian (Zigan-Gumerovian time) by a steep drop in evolutionary rates and extinction of many endothyrids. Diversity reached a minimum in the Malevkian as communities reorganized and calcareous microbiotas were dominated by euryfacial unilocular forms.

Acknowledgements

The author is grateful to P.L. Brenckle for editing of the manuscript and for valuable remarks and to the reviewers N.B. Gibshman and J. Kalvoda, whose important suggestions considerably improved the paper. The study was supported by the Russian Foundation for Basic Research, grant No. 10-05-01076. This paper is a contribution to the IGCP 596 project.

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