Late Frasnian Atrypida (Brachiopoda) from the South Urals, South Timan and Kuznetsk Basin (Russia)

MARIA A. RZHONSNITSKAYA, BORIS P. MARKOVSKII †, YULIA A. YUDINA, and ELENA V. SOKIRAN

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Late Frasnian Atrypida (Brachiopoda) from the South Urals, South Timan and Kuznetsk Basin in Russia (east Laurussian and south Siberian shelf domains in Devonian time) reveal significant generic and specific diversity in the broadly defined Frasnian-Famennian (F-F) bio-crisis time. Eighteen species of atrypid brachiopods have been recorded, representing 4 subfamilies and 10 genera. The new genus *Gibberosatrypa* Markovskii & Rzhonsnitskaya, and the new subgenus *Spinatrypa (Plicspinatrypa)* Rzhonsnitskaya are proposed. Four new species *Spinatrypina (Spinatrypina) sosnovkiensis* Yudina, *Spinatrypa (Plicspinatrypa) rossica* Rzhonsnitskaya, *Iowatrypa nalivkini* Rzhonsnitskaya & Sokiran, and *Carinatina*(?) *biohermica* Yudina are described. The representatives of the Variatrypinae (including especially common *Desquamatia (Desquamatia) alticoliformis*), Spinatrypinae (*Spinatrypina*) and Atrypinae (*Pseudoatrypa*, ?*Costatrypa*) are widely distributed in the studied regions. The Pseudogruenewaldtiinae are represented by *Iowatrypa* and *Pseudogruenewaldtia*, of which the first is distributed worldwide, whereas the only undoubted species of the second is restricted to South Timan, and probably represents a localized latest Frasnian descendant of *Iowatrypa*. The decline phase of atrypid development was controlled by a variety of environmental factors tied to the global Kellwasser events, although it was not directly triggered by anoxic conditions. The investigated atrypid brachiopods, which were all confined to lower latitudes, disappeared during the F-F mass extinction, independently of their environmental and biogeographic settings.

Key words: Brachiopoda, Atrypida, biostratigraphy, taxonomy, mass-extinction, Kellwasser Crisis, Frasnian, Famennian, Devonian, Russia.

Maria A. Rzhonsnitskaya, Boris P. Markovskii [deceased 4th July, 1966], and Elena V. Sokiran [stratigr@mail.wplus.net], All-Russian Geological Research Institute (VSEGEI), 74 Srednii Pr., 199026 St. Petersburg, Russia.
Yulia A. Yudina [tpsrc@veer.komi.ru], Timan-Pechora Scientific Research Centre, Ukhta, 2 Pushkin St. 169400 Komi, Russia.

Introduction

The representatives of the order Atrypida (Brachiopoda) are particularly significant in the context of the Frasnian-Famennian (F-F) mass extinction, marked by the demise of this previously abundant shelly benthic group, confined to the tropical latitudes in the Devonian (e.g., Copper 1966a, 1986). This group of Devonian brachiopods is common in many regions of Russia. Detailed investigation of the faunas from the western slope

of the South Urals began in the 1930s by Nalivkin (1931, 1947, 1951) and Markovskii (1948b). They collected a rich material, but Markovskii's manuscript (1948a) was not published. It was only in 1989 when some new species of the Frasnian atrypids were re-described and prepared for posthumous publication by K. I. Adrianova (Markovskii 1989). The Frasnian atrypids from the Timan Ridge were more extensively studied earlier by Lyashenko (1959, 1973), while those from the Kuznetsk Basin were documented by Alekseeva (1962) and Rzhonsnitskaya (1964, 1975).

The paper contains a comprehensive systematic description of atrypid brachiopods from the late Frasnian of the three principal Devonian regions of Russia, belonging to different east Laurussian and Siberian domains (Fig. 1). The shelly faunas were extensively collected at several stratigraphic levels on the west slope of the South Urals, in South Timan, and in the Kuznetsk Basin. The main basis to this study is the large collection made by B.P. Markovskii from the South Urals (deposited in CNIGR Museum, St Petersburg, Russia). Only a few taxa, notably spinatrypinids, are omitted due to their poor representation in the material and/or bad preservation. Special emphasis is paid to the recently established subfamily Pseudogruenewaldtiinae (Rzhonsnitskaya *et al.* 1997), as well as to documentation of internal characters, which were not adequately studied in the most atrypid species from Russia until now. The stratigraphic distribution of late Frasnian atrypid species is discussed in detail in order to identify possible atrypid occurrences in the survival (earliest Famennian) phase of this bio-crisis. The atrypid-bearing strata span the Late *Palmatolepis rhenana* to *Palmatolepis linguiformis* zones in the standard conodont biozonation scale of Ziegler & Sandberg (1989).

The authorship is indicated in parentheses in the description of particular regions and taxa.

Institutional abbreviations: CNIGR – Chernyshev's Museum in St. Petersburg; TPNITch – Timan-Petchora Research Geological Exploration at Ukhta.

Stratigraphic setting of atrypid-bearing sequences

West slope of South Urals (M.A. Rzhonsnitskaya & B.P. Markovskii). — The Frasnian stratigraphy and faunas of the SW Urals were elaborated by Chernyshev (1885) and Nalivkin (1930, 1947) and, in more details, by Markovskii (1948a, b); supplementary data were supplied, among others, by Domratchev *et al.* (1948) and Tiazheva (1961, 1973). The conodont zonation of the Frasnian strata was recently given by Abramova (1992).

Late Frasnian sequences in this part of the Urals comprise open marine, relatively deep-water deposits (see Fig. 26), mostly of condensed thicknesses, belonging to goniatite and brachiopod facies. The strata are subdivided into: (1) Mendym horizon (dated as Early *P. rhenana* Zone), followed by (2) Askyn horizon (corresponding to undivided Late *P. rhenana* and *P. linguiformis* zones), correlated with the *Manticoceras intumescens* and *Crickites expectatus* regional goniatite zones, respectively (Domrachev *et al.* 1948; Tiazheva 1973).

The Mendym horizon overlies the siliceous-shaly Domanik suite. The lower part of the Mendym horizon is developed in goniatite facies, composed of grey, partly dolomitized limestones (2–20 m thick), rich in goniatites, brachiopods, the bivalve *Buchiola*, crinoids and, locally, corals; atrypids are absent. The goniatite facies is succeeded by brachiopod facies in the upper part of the Mendym horizon (= 'lower *Cuboides* beds' of Markovskii 1948a, b; Samsonovo suite of Domrachev *et al.* 1948). The deposits of the brachiopod facies, 20 to 100–140 m thick, are massive light and reddish-grey limestones, and locally dolomites. The Askyn horizon overlies the Mendym horizon without a break, and light and grey fossiliferous limestones (= 'upper *Cuboides* beds' of Markovskii

Fig. 1. Location of regions studied against the palaeogeography of the Devonian world (modified from Streel 1986: fig. 4); 1 – Timan, 2 – South Urals, 3 – Kuznetsk Basin.

1948a, b) are the most characteristic lithology. Bioclastic intercalations, composed mostly of diverse brachiopods, crinoids, corals and bryozoans, are common. In some regions, the massive limestones are laterally replaced by units of darker, bituminous and locally dolomitized brachiopod-bearing limestones, up to 140 m thick.

The overlying Barma formation, 4 to 25 m in thickness, is composed of similar light-grey massive limestones with common brachiopod shell beds. The Frasnian versus Famennian age of the Barma succession was discussed by Nalivkin (1931), Markovskii (1948a, b) and Tiazheva (1961, 1973), but conodont faunas argued for an earliest Famennian assignment (*Palmatolepis triangularis* Zone; see Abramova 1992).

South Timan (Y.A. Yudina). — The stratigraphy and brachiopod faunas of South Timan were investigated by Lyashenko (1959, 1973), Rzhonsnitskaya (1960), Yudina (1994, 1996), Yudina & Lyashenko (1997) and Yudina & Moskalenko (1997).

The lower part of the upper Frasnian substage (Vetlasyan suite) is developed in so-called 'Ukhta' facies type, characterized by a sequence of marls and argillaceous limestones (see Fig. 27), representing an infill phase of the basin in the Early *P. rhenana* Zone. The stratigraphically slightly younger lower Sirachoy suite is a shallow shelf facies with rich and diverse faunas, mainly brachiopods, corals, stromatoporoids, and with oncolites. The upper Sirachoy suite (dated still as Early *P. rhenana* Zone) is dominated by fossiliferous reef carbonates with many stromatoporoids, corals, stromatolites and brachiopods.

The lower Liyayel suite, dated as earliest *P. rhenana* Zone, represents a marly facies deposited on the slope below the Sirachoy reefs. Higher in the sequence, in the Sedyu basin, clays with marly intercalations have yielded numerous well-preserved brachiopods. The associated biota includes stromatoporoids, gastropods and ostracods; oncolites are also present. The stratigraphically younger Vezhavozh and Sedyu reefal limestones, within the large Bolshoi Keran biohermal unit, have also yielded numerous brachiopods from small coquinoid lenses, distributed within the stromatoporoid-algal limestones and secondary dolomites.

The overlaying evaporite-carbonate deposits of the topmost Frasnian in South Timan are without brachiopod faunas, and the F-F transition is poorly documented in these fossil-impoverished sequences.

Kuznetsk Basin (M.A. Rzhonsnitskaya). — Several facies developed in the late Frasnian and early Famennian of the Kuznetsk Basin area (see Fig 28): (1) shallow open-marine (NW and W borders), passing westward into a deep marine basin; (2) nearshore-marine (NE border), within a small, restricted basin; and (3) red-coloured, continental (E and S borders). Deposits of this age are lacking along the NW slope of the Salair domain (see Rzhonsnitskaya 1968). The F-F passage is traced in the first two settings (Rzhonsnitskaya *et al.* 1992). The nearshore-marine facies contains low diversity endemic faunas (with the brachiopod *Anathyrella*). The shallow open-marine shelf sequences of the Kolyvan'-Tomsk geosynclinal zone are developed as the thick (up to 1200 m) sandy-shaly and carbonate deposits with common bioherms, and abundant brachiopods and corals.

The late Frasnian succession of the Kuznetsk Basin is subdivided into four horizons, which are only partly correlated with conodont zones (Rzhonsnitskaya 1968). The Teryokhino horizon (correlated with *Manticoceras–'Leiorhynchus' depressus* Zone) is in sedimentary continuity with the early Frasnian succession. Fossils are rare in these largely terrigenous deposits, 250 m thick, and only rhynchonellids have been found. The stratigraphically younger Kurlyak horizon (correlated with the *Anathyrella tyzhnovi* Zone) is composed of more fossiliferous, marly detrital limestones with common brachiopod lumachelles (350 m thick). The latter are composed mainly of atrypids and *Anathyrella*.

Higher in the succession, the Glubokaya horizon (correlated with the *Hypothyridina cuboides westsibirica* Zone), up to 400 m thick, is composed of various limestones. These are mostly massive reefoidal stromatoporoid-coral and algal (with '*Girvanella*' and '*Solenopora*') limestones. Bioclastic crinoid-brachiopod and darker micrite varieties also occur. In addition to the main Glubokaya reef builders, brachiopods are widely distributed and diverse, dominated by gypidulids, rhynchonellids, atrypids and cyrtospiriferids. Conodonts, such as *Ancyrodella nodosa* Ulrich & Bassler, 1926 and *Palmatolepis subrecta* Miller & Youngquist, 1947, refer the Glubokaya massive limestones to the *P. rhenana* Zone. The topmost Frasnian (*P. linguiformis* Zone) strata are represented by the Solomino horizon (correlated with *Anathyrella ussovi* Zone), 150–200 m thick. Nodular, sandy-bioclastic limestones, calcareous mudstones and sandstones are the principal lithologies. Brachiopods (mostly the genus *Anathyrella*) are the most frequent fossils in the Solomino horizon and are associated with bryozoans, corals and crinoid remains.

The Famennian stage in the Kuznetsk Basin is subdivided into three regional substages, of which the lower (Pestchorka), and upper (Abyshevo), correspond mostly to marine facies, and the middle (Podonino), to continental settings. The boundary between the Solomino and Pestchorka sequences, approximating to the F-F boundary, is marked by a gradual shift to more shallow water facies. This boundary is emphasised by abrupt faunal turnover, especially among the brachiopods, corals and bryozoans. The Pestchorka horizon (correlated with the *Cyrtospirifer tschernyschewi* Zone), up to 175 m thick, is developed mostly as carbonates, shales and sandstones. The earliest Famennian deposits are predominatly thin- to medium-bedded, dark-grey and black algal limestones (Kosoy-Utes beds; 25 m thick).

The F-F transition in the Kuznetsk Basin is evidenced by the occurrence of *Icriodus iowanensis* Youngquist & Peterson, 1947, and, in the upper part of the Kosoy-Utes beds, by the occurrence of *Palmatolepis minuta* Branson & Mehl, 1934. The latter points already to the early Famennian Late *P. triangularis* Zone (see Fig. 28; Rzhonsnitskaya *et al.* 1992). The numerous brachiopods in the Kosoy-Utes beds are associated with calcareous algae ('*Girvanella*', '*Solenopora*'), solitary corals, bryozoans, gastropods, bivalves and fish remains.

Systematic Palaeontology

Description of the Uralian atrypids is based on the collection of B.P. Markovskii, stored in the Chernyshev's Museum in St. Petersburg (Cataloque Number CNIGR 6755). This fauna was described in an unpublished monograph (Markovskii 1948a). The description of several new taxa was published in a posthumous paper (Markovskii 1989). The descriptions presented below are based on the original diagnoses by Markovskii, but revised (mostly in terms of generic assignments) by

Rzhonsnitskaya & Sokiran. Collections from South Timan were made and investigated by Yudina, and are stored in Timan-Petchora Research Geological Exploration at Ukhta (Cataloque Number TPNITch 7–8). Late Frasnian atrypid materials from the Kuznetsk Basin, stored in the Chernyshev's Museum in St. Petersburg (Cataloque Number CNIGR 7859), were described in Rzhonsnitskaya (1975), but are here revised; several holotypes and lectotypes are thus re-illustrated. Shell morphology is described in terms of Copper (1967c).

Abbreviations: L – length of the pedicle valve; W – width of shell; T – thickness of shell; R – total number of ribs; R-5, R-10, R-15 – number of ribs per 5 mm in distance 5, 10 and 15 mm from the shell apex, respectively; Ra – number of ribs per 5 mm at (near) the anterior margin; C – number of growth lamellae per 5 mm.

Order Atrypida Rzhonsnitskaya, 1960
Family Atrypidae Gill, 1871
Subfamily Atrypinae Gill, 1871
Genus *Pseudoatrypa* Copper, 1973

Remarks. — Due to lack of illustrations of the type species, *P. devoniana* Webster, 1921, in the original description, the common understanding of this species based on Fenton & Fenton (1924: p. 134, pl. 26: 16–24). According to those authors, the distinctive crest-like dorsal fold and sinus-like ventral sulcus belong to the most characteristic features of *Atrypa* (= *Pseudoatrypa*) *hackberryensis* Fenton & Fenton, 1924, which is probably conspecific with *P. devoniana*. However, Copper (1973) selected as lectotype a specimen from Webster's original collection that is quite different from the specimens figured by Fenton & Fenton (1924) as well as clearly seen in the sulcus-fold development. The similar sulcus-fold development is in the Uralian specimens, but limited material precludes the possibility of describing a new species and of emending the diagnosis of *Pseudoatrypa*.

Pseudoatrypa ex gr. *devoniana* (Webster, 1921)

Fig. 2.

Material. — The collection of Markovskii, comprising about 100 specimens of this taxon, described as *Atrypa devoniana* Webster in an unpublished study (Markovskii 1948a), has been lost, with the exception of one mature specimen.

Description. — Shell large-sized (W = 38.8 mm), significantly inflated (T = 22.7 mm) and dorsibiconvex, transversely-oval in outline (W/L = 1.24). Hinge line weakly curved.

The ventral valve is more convex near the umbo, lateral parts flattened, wing-shaped. Beak minute, incurved, foramen and deltidial plates invisible. The interarea low, short, almost invisible. A broad, deepening sulcus with flat bottom developed in the anterior half, but accentuated apically. The width of sulcus bottom is almost constant anteriorly, changing from 11 mm in mid-valve to 13 mm at the anterior commissure; the tongue is high and arched.

Dorsal valve deeply convex, with low beak covered by the ventral apex. Fold starting from the umbonal part, poorly defined in the posterior third, but rapidly widened anteriorly, distinct in the median part, and strongly elevated near the anterior periphery. The fold of constant width and arch-shaped transversally, corresponding to tongue development. Ribs fine, bifurcating and intercalating; R-10 = 14. Growth lamellae indistinct, frill-like, crowded anteriorly, but spaced 2–3 mm in remaining parts of the shell.

Remarks. — This taxon probably represents a new species, closely resembling *P. devoniana* (Webster, 1921) *sensu* Fenton & Fenton (1924) in the tendency to develop a distinctive dorsal fold. However, the Uralian species differs from the latter by showing deep median sulcus in the ventral valve, an elongated, crest-like dorsal fold, and subdued growth lamellae. From the lectotype of *P. devoniana*, selected by Copper (1973: p. 492, pl. 1: 3–6) among Webster's originals, the Uralian species differs additionally in having a stronger fold and sulcus.

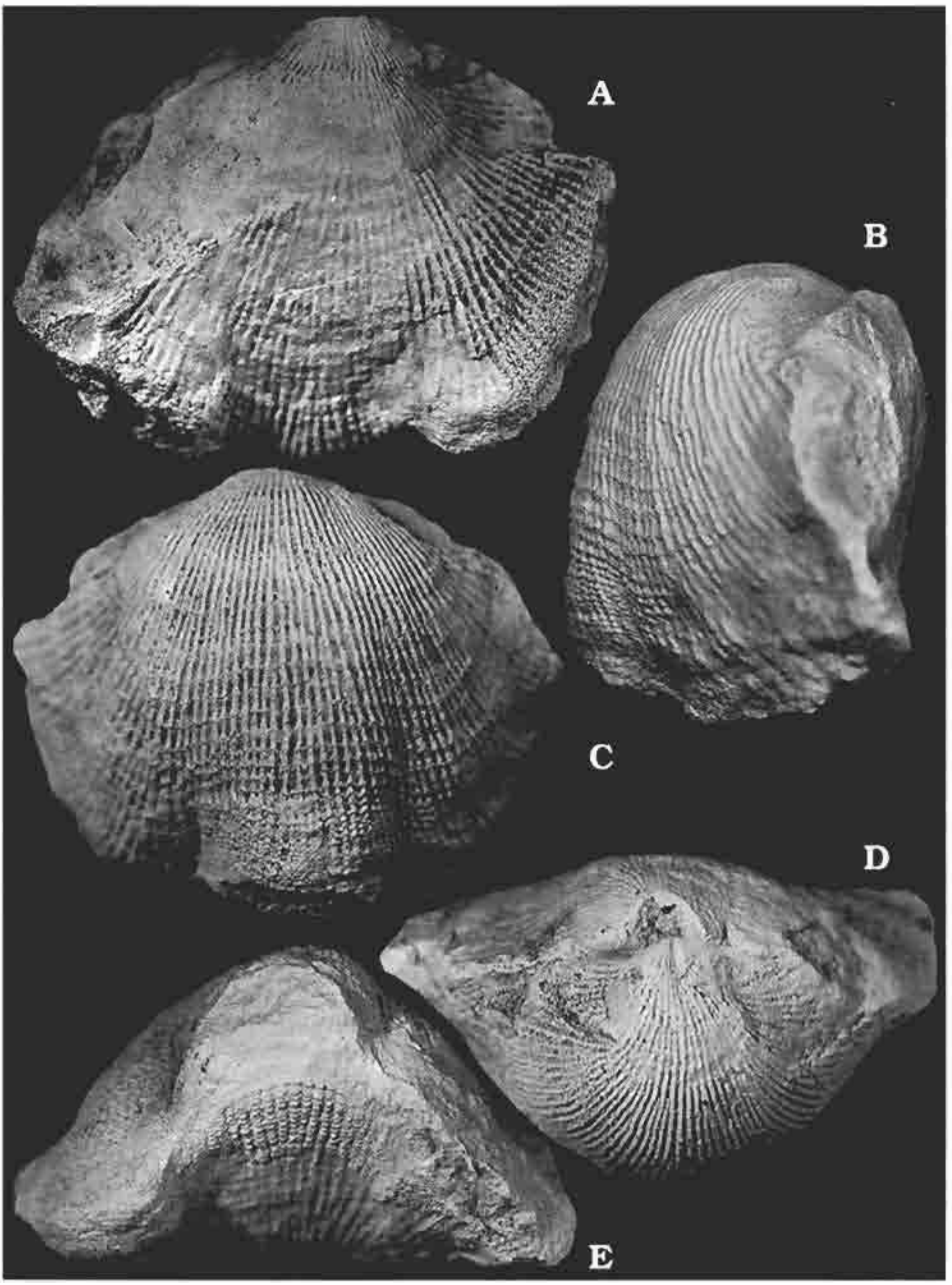


Fig. 2. *Pseudoatrypa* ex gr. *devoniana* (Webster, 1921) from the late Frasnian Askyn horizon, river Zilim (opposite the Kuk-tash rock), SW Urals, Russia. **A–D**. Gerontic shell CNIGR 6755/147 in ventral, lateral, dorsal, posterior, and anterior views; × 2.

Distribution. — Late Frasnian, Early *P. rhenana–P. linguiformis* zones, Mendym and Askyn horizons; W slope of the South Urals (exposures along the river Zilim; Bolshaya Kinderli and Kuk-tasch rocks), Middle Urals (near the river Tshusovaya).

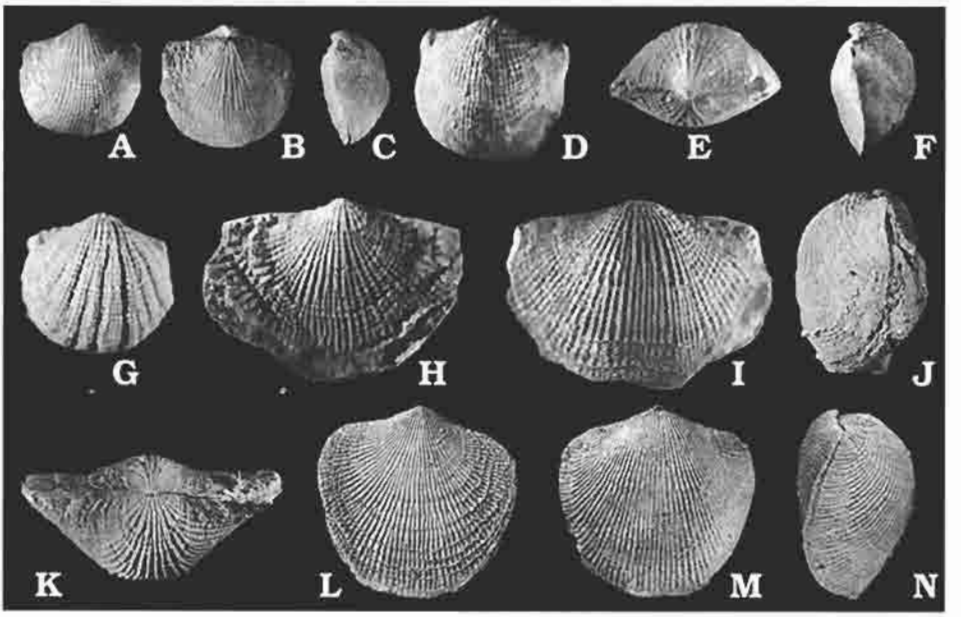


Fig. 3. Late Frasnian atrypids from South Timan, Russia. **A–G**. *Iowatrypa* sp., Liyayel suite, Vezhavozh river. **A–C**. Holotype TPNITch 8/50 in ventral, dorsal, and lateral views. **D–F**. Shell TPNITch 8/74 in ventral, posterior, and lateral views, × 2. **G**. Shell TPNITch 8/49 in ventral view; note additional folds; × 1.8. **H–K**. *'Atryparia' vetlasjanica* Lyashenko & Yudina, 1997; shell TPNITch 7/150 in ventral, dorsal, lateral, and posterior views; Vetlasyan suite, river Ukhta. **L–N**. *Pseudoatrypa symmetrica* (Lyashenko, 1959); shell TPNITch 7/51 in ventral, dorsal and lateral views; Sirachoi suite, river Ukhta; natural size.

Pseudoatrypa symmetrica (Lyashenko, 1959)

Figs 3L–N, 4.

Atrypa symmetrica sp. n.; Lyashenko 1959: p. 186, pl. 61: 1–5.

Diagnosis. — Medium-sized (L up to 32 mm), subcircular to oval (W/L = 1.03–1.21) and weakly uniplicate species of *Pseudoatrypa* that differs from *P.*(?) *posturalica* (Markovskii, 1955 in Mikriukov 1955) by finer ribs (R-10 = 8–9).

Material. — Thirty well and moderately well preserved shells.

Internal characters. — Inside ventral valve (Fig. 4) thin deltidial plates, subdivided teeth with distinct main lobe and lateral lobes directed laterally and dorso-laterally; lateral cavities of medium size. In dorsal valve, thin hinge plates and internal socket plate developed; crura fibrous.

Variability. — Only anterior concavity on ventral valve shows some variation, being well expressed as a weak sinus in gerontic shells only; this also concerns the corresponding dorsal fold.

Occurrence. — Late Frasnian, Early *P. rhenana* Zone; Alatyr horizon, central parts of the East European Platform (see Lyashenko 1959); Sirachoy suite, Timan-Petchora area; Russia.

Genus *Atryparia* Copper, 1966

'Atryparia' vetlasjanica Lyashenko & Yudina, 1997

Fig. 3H–K.

Atryparia vetlasjanica Lyashenko & Yudina sp. n.; Yudina 1997a: p. 65, pl. 5: 3–4, fig. 2.

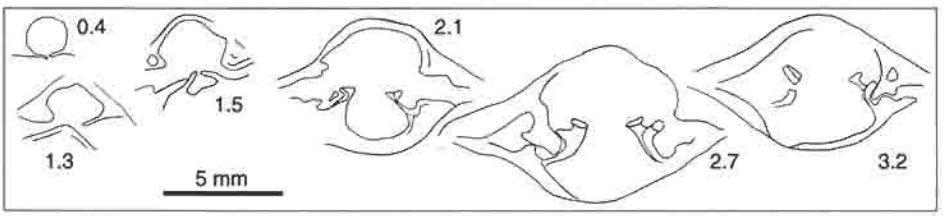


Fig. 4. Transverse serial sections of *Pseudoatrypa symmetrica* (Lyashenko, 1959); specimen TPNITch 7/106 from the late Frasnian Sirachoi suite, river Ukhta, South Timan. Numbers refer to distances in mm from the top of the ventral umbo.

Diagnosis. — This questionable species of *Atryparia* distinguished by large (W up to 32 mm), strongly dorsibiconvex (T up to 15 mm) and transversely extended, trapezoidal shell (W/L = 1.19–1.39), with coarse ribs (R-10 = 4–5) and frequent growth lamellae, continued as large frills. From *Atryparia rubra* Cooper & Dutro, 1982 from the late Givetian of New Mexico it differs by larger shell size and coarser ribs.

Material. — Thirty complete and 19 damaged shells and 21 fragments.

Description and remarks. — See Yudina (1997a). P. Copper (personal communication 1997) suggests that this species belongs to the allied genus *Costatrypa* Copper, 1973.

Occurrence. — Late Frasnian, Early *P. rhenana* Zone; Vetlasyan suite, South Timan, Russia (see Yudina 1997a).

Genus *Costatrypa* Copper, 1973

Costatrypa(?) *posturalica* (Markovskii, 1955 in Mikryukov 1955)

Figs 5, 6.

Atrypa reticularis L.; Chernyshev 1884: p. 18, pl. 3: 3.

Atrypa posturalica Markovskii (*in coll.*); Mikryukov 1955: p. 239, pl. 4: 5; Petreneva 1955: p. 285, pl. 3: 1; Adrianova 1955: p. 370: pl. 7: 1–2.

Atrypa posturalica Markovskii; Rzhonsnitskaya 1975: p. 89, pl. 19: 4–9, fig. 26; Markovskii 1989: p. 89, pl. 1: 1–3.

Diagnosis. — Questionable species of *Costatrypa* which differs from all other species of the genus [e.g., *Costatrypa variabilis* (Godefroid, 1970)] by combination of medium shell size (W up to 32 mm), moderate biconvexity (T up to 16 mm), roundish to oval outline (W/L = 0.9–1.32), weak sinus and fold developed only near the anterior margin, moderately thick ribs (R-10 = 5–6), paired with subdued growth lamellae.

Material. — About 140 shells gathered from Uralian outcrops (coll. Markovskii), and 320 complete to nearly complete shells and 33 isolated valves from Kuzbass.

Internal characters (Fig. 6). — Large teeth with additional lobes (denticulae), directly fixed to lateral valve walls; dental cavities undeveloped. Hinge plates massive, separated by rather broad cavity, dental sockets deep with supplementary cavities for denticulae; crural bases small, spiralia consist of 7 whorls.

Variability. — The following characters are variable: (1) shell outline (ranging from roundish and weakly transversely extended to elongated); (2) sinus and fold (from weakly to strongly developed at anterior margin; extreme specimens are with fairly high tongue); and (3) number of ribs and growth lamellae.

Remarks. — The lack of any dental nucleus and the rather shallow, non-tubular wavy ribs are major features suggesting the affinity of *Atrypa posturalica* with *Costatrypa*, although there is a general similarity to some species of *Pseudoatrypa*, such as *P. symmetrica* (Lyashenko, 1959).

The specimens from Kuzbass are almost identical with those from the Urals. They differ from the holotype only in having less numerous ribs at the anterior margin (50–60 and 68, respectively).

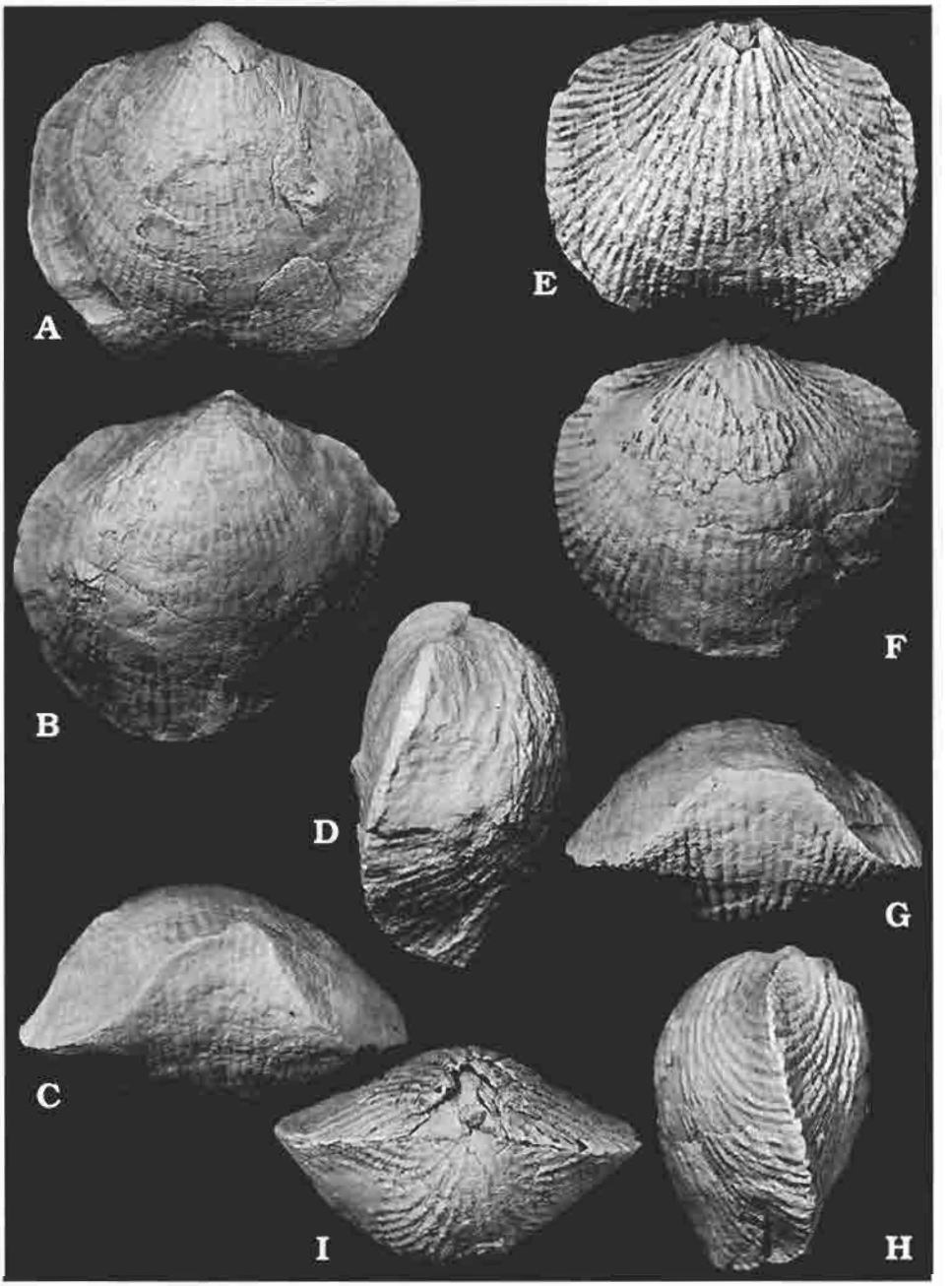


Fig. 5. *Costatrypa*(?) *posturalica* (Markovskii in Mikryukov 1955) from the late Frasnian Glubokaya horizon, river Strelnaya, NW border of Kuznetsk Basin (**A–D**), and Askyn horizon, river Sargai, SW Urals (**E–H**), Russia. **A–D**. Shell CNIGR 7859/146 in ventral, dorsal, lateral and posterior views. **E–H**. Holotype CNIGR 6755/155 in ventral, dorsal, lateral and posterior views. All × 2.

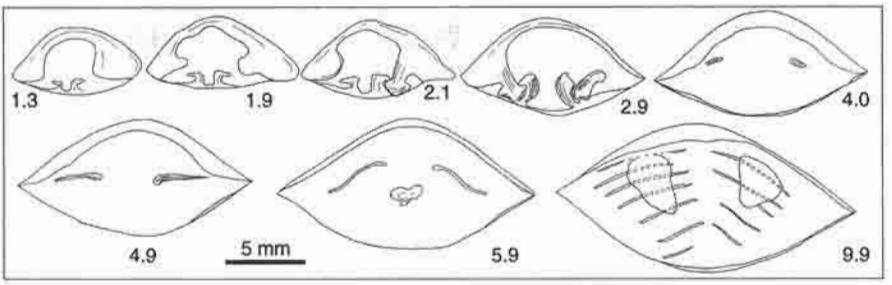


Fig. 6. Transverse serial sections of *Costatrypa*(?) *posturalica* (Markovskii in Mikryukov 1955); specimen CNIGR 7859/349 from the late Frasnian Glubokaya horizon, NW border of Kuznetsk Basin. Numbers refer to distances in mm from the top of the ventral umbo.

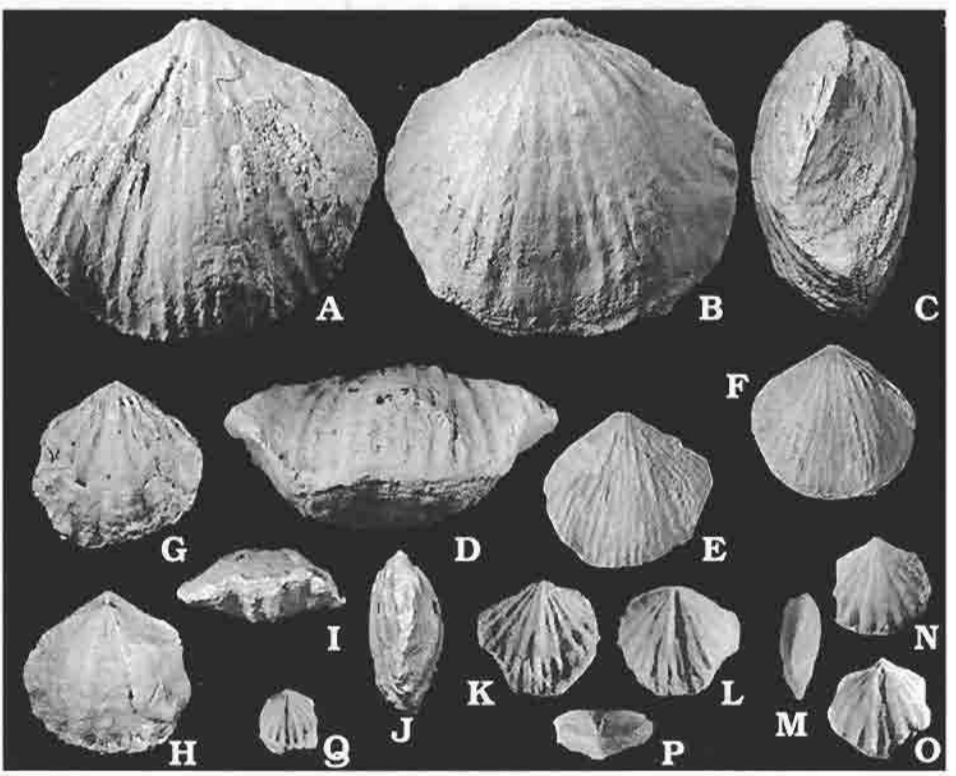


Fig. 7. Late Frasnian atrypids from SW Urals (**A–J**) and South Timan (**K–W**), Russia. **A–J**. *Gibberosatrypa gibberosa* (Markovskii, 1989). Askyn horizon, river Zilim (Suvaltash Rock). **A–F**. Holotype CNIGR 6755/161 in ventral (**A**, **E**), dorsal (**B**, **F**), lateral (**C**) and anterior (**D**) views; natural size (**E–F**) and ×2 (**A–D**). **G–J**. Juvenile shell CNIGR 6755/163 in ventral, dorsal, anterior, and lateral views; ×2. **K–Q**. *Carinatina*(?) *biohermica* Yudina sp. n., Bolshoi Keran biohermal suite, river Vezhavozh. **K–M**. Holotype TPNITch 7/501 in ventral, dorsal, and lateral views; ×2. **N–Q**. Shell TPNITch 7/489 in ventral, dorsal, and posterior views; natural size (**Q**) and ×2 (**N–P**).

The species described is clearly distinguished from the stratigraphically older *Costatrypa*(?) *uralica* (Nalivkin 1930: p. 74, pl. 6: 10) from the Semiluki horizon of the East European Platform by the more deeply convex ventral valve, subdued growth lamellae and coarser ribbing.

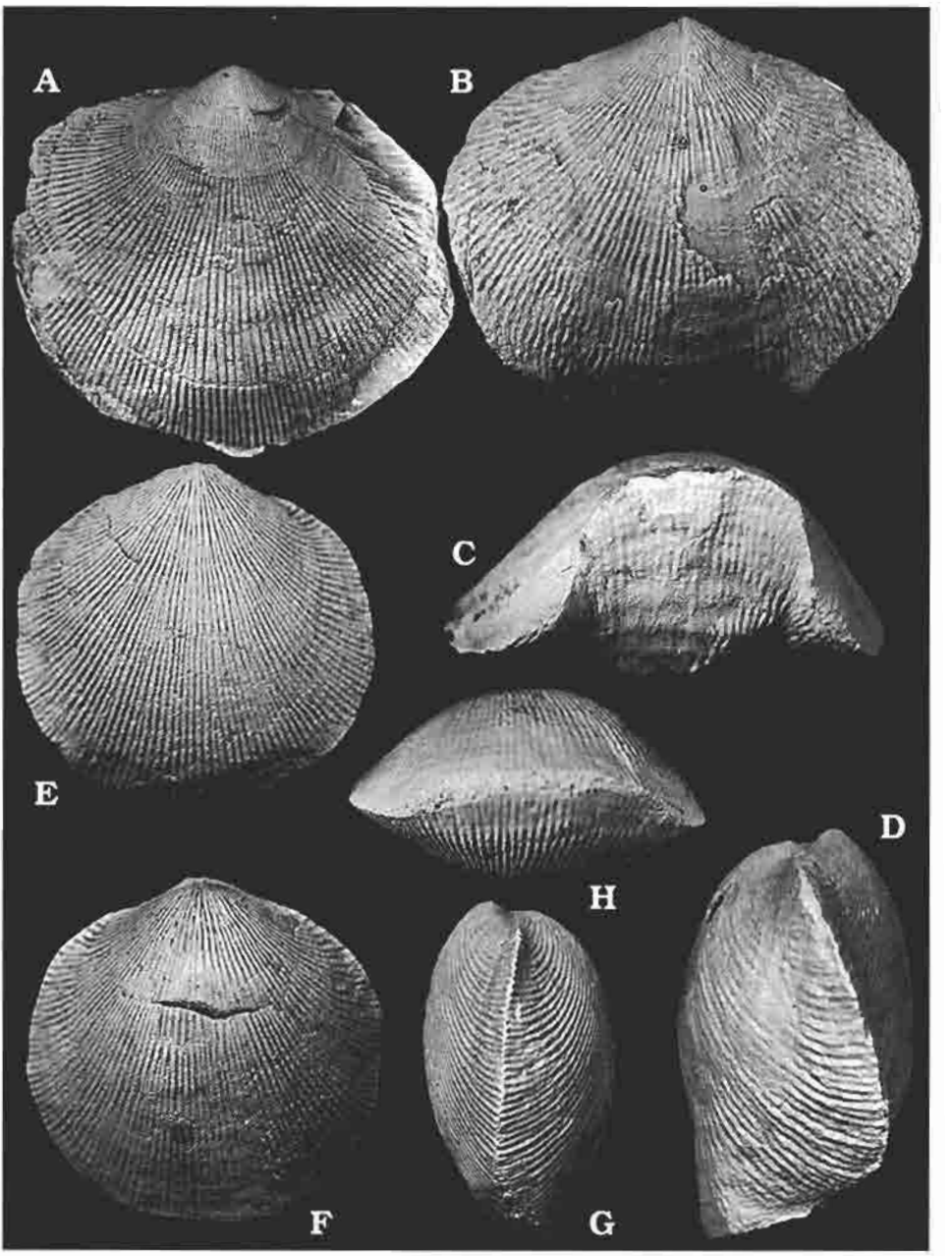


Fig. 8. *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975 from the late Frasnian Kurlyak horizon, river Izyly, NW Kuzbass (**A**), and Askyn horizon, river Zilim (Aktash Rock), SW Urals (**B–H**); Russia. **A**. Holotype CNIGR 7859/230, dorsal view. **B–D**. Shell CNIGR 6755/319 in ventral, anterior, and lateral views. **E–H**. Shell CNIGR 6755/320 in ventral, dorsal, lateral, and anterior views. All × 2.

Occurrence. — Late Frasnian (*P. rhenana–P. linguiformis* zones); Askyn horizon, W slope of South Urals (localities along the rivers Sikaza, Sargay, Zilim, Bolshaya Kyndyrli, Malyi Askyn) and Middle

Urals (near the river Tshusovaya); Kurlyak and Glubokaya horizons, NW periphery of the Kuznetsk Basin (along the rivers Glubokaya, Bolshaya Strelnaya, Tom, Inya, Bolshoy Kurlyak, Kluchevaya and Berezovka), Russia. C.(?) *posturalica* was reported also from Askyn horizon of Volga-Ural area (Baschkiria, Udmutrya; see Adrianova 1955, Mikryukov 1955, Petreneva 1955).

Genus *Gibberosatrypa* Markovskii & Rzhonsnitskaya gen. n.

Type species: *'Atrypa' gibberosa* Markovskii 1989; Askyn horizon, outcrops near river Zilim, western slope of the South Urals.

Derivation of the name: From *gibberosa* – the type species.

Diagnosis. — Medium-sized coarsely ribbed atrypids differing from other genera by subquadrate-subcircular shell, combined with median rounded wide ridge in sinus in ventral valve, and sinus-like longitudinal shallow depression in fold in dorsal valve.

Remarks. — The genus *Gibberosatrypa* is similar (also internally) to *Mogoliella* Ischnasarov, 1972 known from the Givetian of the Chatkal Mountains, Uzbekistan (Ischnasarov 1972: pp. 68–72; pl. 33, 34: 1–7), but *Gibberosatrypa* is distinguished by having coarse rounded ribs and a short hinge line.

Occurrence. — Western slope of the South Urals (late Frasnian), possibly also Main Devonian Field of the East European Platform (early Frasnian), Russia.

Species assigned. — In addition to the type species, to the new genus may belong also *Anatrypa heckeri*, described from the early Frasnian Chudovo beds of Main Devonian Field (Nalivkin 1941: p. 173: pl. 8: 1–5). This is especially suggested by the development of a median keel-like ridge (carina) along the dorsal valve. *Carinatina*(?) *biohermica* Yudina, sp. n., described from the late Frasnian of South Timan in the present paper, is also assignable to this poorly-known species group, possibly related to the Middle Devonian carinatinids (see also Copper 1978: p. 304).

Gibberosatrypa gibberosa (Markovskii, 1989)

Fig. 7A–J.

'Atrypa' gibberosa sp. n.; Markovskii 1989: p. 90, pl. 1: 4–6.

Diagnosis. — Medium-sized (W up to 24 mm), moderately biconvex (T up to 10.5 mm) atrypids conspicuous due to subquadrate-subcircular outline (W/L = 1.0–1.1), straight hinge line, suberect ventral beak, and coarse rounded ribs (R = ca. 30) bifurcating from the apex, paired with flattened growth lamellae, forming papillae-like thickenings on rib crests. *G. gibberosa* can be distinguished from *Anatrypa heckeri* Nalivkin, 1941 by the less transverse shell, less angular ribs and shorter hinge line.

Material. — Forty three complete shells.

Internal characters. — Still poorly known due to strong interior recrystallization, but the presence of small dental cavities and a dorsal median ridge is established.

Growth changes. — Immature specimens have a fold encompassing the mid-ribs, and the sinus appears as a flattened furrow between the two central ribs, starting from the umbo. In the ventral depression of more mature shells is a median rib, and development of the sulcus and fold led to a low trapezoidal tongue interrupted by medial deflection.

Occurrence. — Late Frasnian, *P. rhenana–P. linguiformis* zones; Askyn horizon, SW Urals, localities along the rivers Zilim (Suval-tash, Ak-kyr, Kuk-tash rocks) and Malyi Askyn (left bank opposite the rocky hill Sussak-tash), Russia.

Subfamily Variatrypinae Copper, 1978

Genus *Desquamatia* Alekseeva, 1960

Subgenus *Desquamatia (Desquamatia)* Alekseeva, 1960

Desquamatia (Desquamatia) alticoliformis Rzhonsnitskaya, 1975

Figs 8–10, 11A–F.

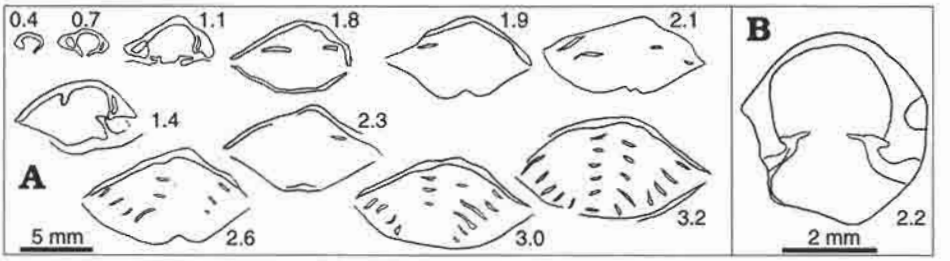


Fig. 9. Transverse serial sections of *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975; specimen CNIGR 7859/B3/14 from the late Frasnian Kurlyak horizon, river Izyly (**A**); specimen TPNITch 7/7 from the late Frasnian Bolshoi Keran biohermal suite, river Bolshoi Keran (**B**). Numbers refer to distances in mm from the top of the ventral umbo.

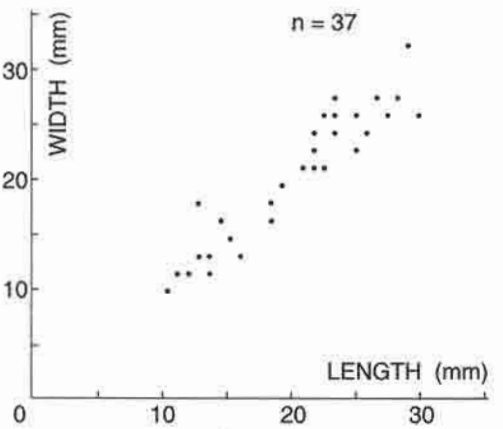


Fig. 10. *Desquamatia (Desquamatia) alticoliformis* (Rzhonsnitskaya, 1975) from the late Frasnian Askyn horizon, river Zilim, SW Urals. Scatter diagrams plotting shell width (W) to shell length (L).

Atrypa alticola Frech; Nalivkin 1930: p. 99, pl. 7: 2, 5; Nalivkin 1947: p. 100, pl. 22: 14–15; Nalivkin 1951: p. 17, pl. 4: 1; Mikriukov 1955: p. 240, pl. 5: 4; Adrianova 1955: p. 368, pl. 7: 1.
Atrypa desquamata Sow.; Kraevskaya 1936: p. 62, pl. 4: 1, 3.
Atrypa desquamata var. *alticola* Frech; Kraevskaya 1936: p. 63, pl. 4: 5.
Atrypa desquamata var. *globus*; Kraevskaya 1936: p. 62, pl. 4: 2, 4.
Desquamatia (Desquamatia) alticoliformis sp. n.; Rzhonsnitskaya 1975: p. 131, pl. 28: 10–13, fig. 41.

Diagnosis. — Medium-sized to large (W up to 31.5 mm), moderately dorsibiconvex (T up to 17.5 mm), mostly roundish (W/L = 0.87–1.12), and finely ribbed (R-10 = 10–12) species of *Desquamatia*, with anterior commissure uniplicate and arched to trapezoidal tongue; dorsal fold weakly expressed.

Material. — The type material from Kuzbass (Rzhonsnitskaya's collection) includes 40 loose valves, and 6 complete immature shells. Collection from the South Urals comprises 625 complete, but recrystallized shells; 32 specimens come from South Timan.

Internal characters. — As seen in immature specimens from Kuznetsk Basin (Fig. 9), dental cavities rather small; teeth relatively massive, interlocked with rather deep cardinal sockets. Hinge plates relatively thin, dorsal septal ridge not very well developed to totally absent.

Variability. — Usually circular and wide shells, but some elongated (see Fig. 10). Ribbing variable, and R-10 ranged from 9–10 (coarse-ribbed shells) to 17–18 (finely-ribbed shells).

Occurrence. — Late Frasnian; Kuznetsk Basin (SW border), Kurlyak and Glubokaya horizons (along the rivers Izyly, Ilnya, Mitichia); South Urals, Askyn horizon, western slope (near the rivers

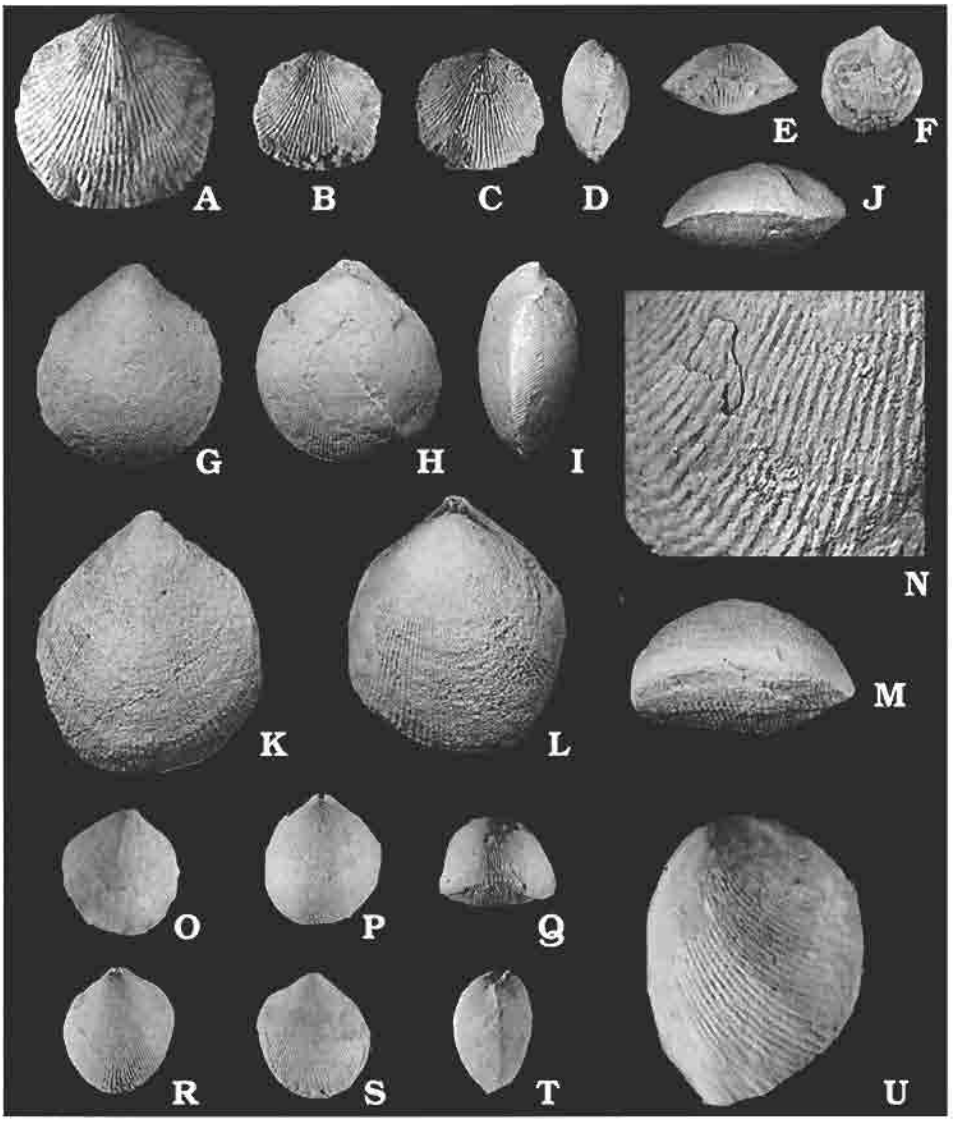


Fig. 11. Late Frasnian atrypids from South Timan (**A–F**; **O–U**), SW Urals (**G–J**) and SE Urals (**K–M**), Russia. **A–F**. *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975. Bolshoi Keran biohermal suite, river Vezhavozh. **A–E**. Shell TPNITch 7/145 in ventral, dorsal, lateral, and anterior views; natural size (**B–E**) and × 2.5 (**A**). **F**. Dorsal valve TPNITch 7/294; natural size. **G–U**. *Radiatrypa magnitica* (Nalivkin, 1947). **G–J**. Shell CNIGR 6755/308 in ventral, dorsal, lateral, and anterior views. Koltuban limestones, lake Koltuban. **K–M**. Lectotype CNIGR 5057/33 in ventral, dorsal, and anterior views. Askyn horizon, river Zilim. **N**. Shell CNIGR 5057/34, details of ornamentation; × 2 except **N** taken × 5. Sedyu suite, river Sedyu. **O–Q**. Shell TPNITch 7/282 in ventral, dorsal, and anterior views. **R–U**. Shell TPNITch 7/285 in dorsal, ventral, and lateral views (**R–T**), ornamentation (**U**); natural size (**R–S**), × 2 (**O–Q**) and × 2.5 (**U**).

Malyi Askyn, Aichay, Zilim, Bolshoj Kyndyrli, Usuli, Sargai, Sikaza); Middle Urals, Askyn horizon (river Tchusovaya, 0.5 km downstream from the village of Tchizmy); South Timan (biohermal

massive, river Sedyu). In addition, the species was quoted from Novosibirsk area, the eastern slope of the Urals and Western Fergana (Kraevskaya 1936; Adrianova 1955; Mikriukov 1955), as well as from Central and Western Europe (Godefroid & Helsen 1998; Racki & Baliński 1998).

Genus *Radiatrypa* Copper, 1978

Radiatrypa magnitica (Nalivkin, 1947)

Figs 11G–U, 12.

Atrypa magnitica; Nalivkin 1947: p. 100, pl. 22: 18–19; Nalivkin 1951: p. 18, pl. 4: 4–5; Adrianova 1955: pl. 7: 3.

Lectotype: Complete shell CNIGR 5057/33, illustrated in Nalivkin (1951: pl. 4: 4), re-illustrated in Fig. 11K–M. Other type material (including one syntype) stored in the Chernyshev's Museum in St. Petersburg.

Diagnosis. — Small (W below 18 mm), inflated (T up to 12.4 mm), elongated-oval (W/L = 0.87–0.97) species of *Radiatrypa* which differs from all other species of the genus by very fine ribs (R-15 = 16–20), dorsi-biconvexity, strongly curved hinge line and gently arched (slightly convex) tongue. *R. magnitica* differs from early Frasnian biconvex *Radiatrypa tenuisulcata* (Venjukov, 1886) by total absence of growth lamellae (see Copper 1978).

Material. — Two type specimens from SE Urals, more than 50 well-preserved shells from South Timan and five shells from the SW Urals.

Internal characters. — Shell interior recrystallized, but in the specimens from Timan it is possible to recognize a thin pedicle layer, wand-shaped teeth, reduced dental cavities, slender hinge plates and minute crura (Fig. 12).

Variability. — Transition from elongated to transversely outlined shells occurs in the Uralian material.

Occurrence. — Late Frasnian, Askyn horizon; South Urals, E slope (lake Koltuban) and west slope (along the rivers Zilim, Sargai, Sikaza); Middle Urals (near the river Tchusovaja); South Timan, Vezhavozh bioherm, along the river Vezhavozh.

Subfamily Spinatrypinae Copper, 1978

Genus *Spinatrypina* Rzhonsnitskaya, 1964

Subgenus *Spinatrypina (Spinatrypina)* Rzhonsnitskaya, 1964

Spinatrypina (Spinatrypina) sosnovkensis Yudina sp. n.

Figs 13A–E, 14.

Holotype: Complete shell TPNITch 7/178, Fig. 13A–D.

Type locality: Exposure near the village of Sosnovka, river Ukhta (left bank), South Timan.

Type horizon: Ukhta suite, late Frasnian.

Derivation of the name: From the village of Sosnovka.

Diagnosis. — Small (W below 16 mm), oval spinatrypinids with moderately biconvex shell, without sinus and fold, ornamented with frequent deflected growth lamellae. The species can be distinguished from *S. nana* (Khalfin, 1937) by less coarse ribs (R-10 = 5–6) and shorter hinge line (see Alekseeva 1962).

Material. — Twenty seven moderately well preserved specimens.

Dimensions (in mm):

Cat. No.	L	W	T	W/L
TPNITch 7/178 (holotype)	14.4	14.7	8.6	1.02
TPNITch 7/202	14.2	16.0	7.1	1.12
TPNITch 7/204	13.3	12.2	5.9	0.91

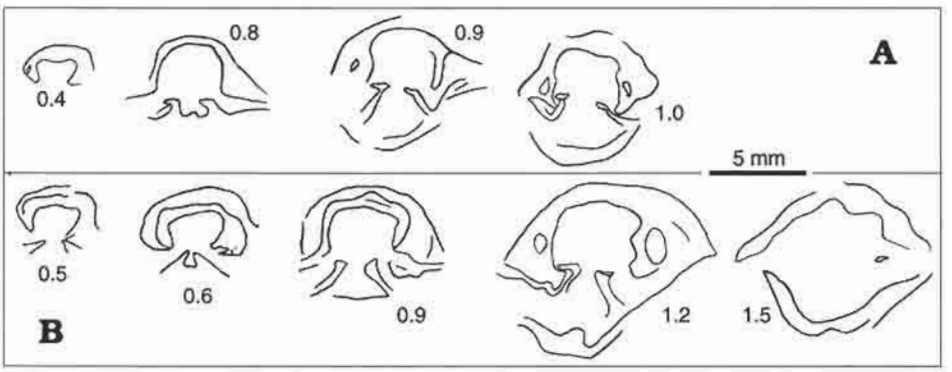


Fig. 12. Transverse serial sections of *Radiatrypa magnitica* (Nalivkin, 1947); specimen TPNITch 7/16 (**A**) and TPNITch 7/17 (**B**) from the late Frasnian Vezhavozh suite, South Timan. Numbers refer to distances in mm from the top of the ventral umbo.

Description. — Shell small, oval in outline, usually transversely elongated, biconvex to slightly ventribiconvex. Hinge line gently curved or straight, equals or little more than half of shell width, located mid-valve or posteriorly. Hinge angles rounded. Anterior commissure straight, but gently arched in gerontic specimens.

Ventral valve moderately convex with indistinct keel in umbonal area. Beak orthocline, with apical foramen; area distinctive, not very large. Sinus undeveloped, only rarely observed as a flattening near anterior margin.

Dorsal valve moderately and uniformly convex. No fold, but anterior margin is gently curved in some mature shells.

Sculpture tubular-imbricated (R-10 = 5–6; C = 7–8 mid-valve).

Internally with small deltidial plates and pedicle layer (Fig. 14). Teeth massive, with poorly differentiated lateral lobes; lateral cavities of moderate size. Hinge plates strong, rather thick. Septal ridge low. Crural bases directed ventrally, crura flame-shaped at beginning, grade into fibrous.

Variability. — Most shells are biconvex, with rectimarginate anterior commissure. Gerontic specimens typified by ventribiconvex and initially uniplicate shells.

Remarks. — Similar spinatrypinids were previously assigned (see e.g., Nalivkin 1947; Lyashenko 1959) to *Spinatrypina* ex gr. *tubaecostata* (Paeckelmann, 1913). However, *S. (S.) sosnovkensis* sp. n. differs from the typical *Spinatrypina (Exatrypa) tubaecostata* in the less inflated shell and underdevelopment of the sinus (see Copper 1967a).

Occurrence. — Late Frasnian, Ukhta suite, South Timan, Russia.

Subgenus *Spinatrypina (Exatrypa)* Copper, 1967
Spinatrypina (Exatrypa?) bifurcata (Markovskii, 1989)

Fig. 15F–M, S.

'Atrypa' bifurcata sp. n.; Markovskii 1989: p. 92, pl. 1: 7–11.

Diagnosis. — Small-sized (W below 15 mm), weakly dorsibiconvex spinatrypinids (T up to 5.5 mm), subcircular to transverse-oval (W/L = 1.07–1.15) ornamented by bifurcating ribs (R = 16–20); distinctive growth lamellae, 1.5–2 mm spaced; rib bifurcation is markedly expressed on ventral valve, starting near umbo, irregularly recurring anteriorly.

Material. — Fifty five shells of variable preservation, usually strongly recrystallized.

Internal characters. — Almost unknown due to interior recrystallization: dental cavities undeveloped, hinge plates thickened, coalesced with bases.

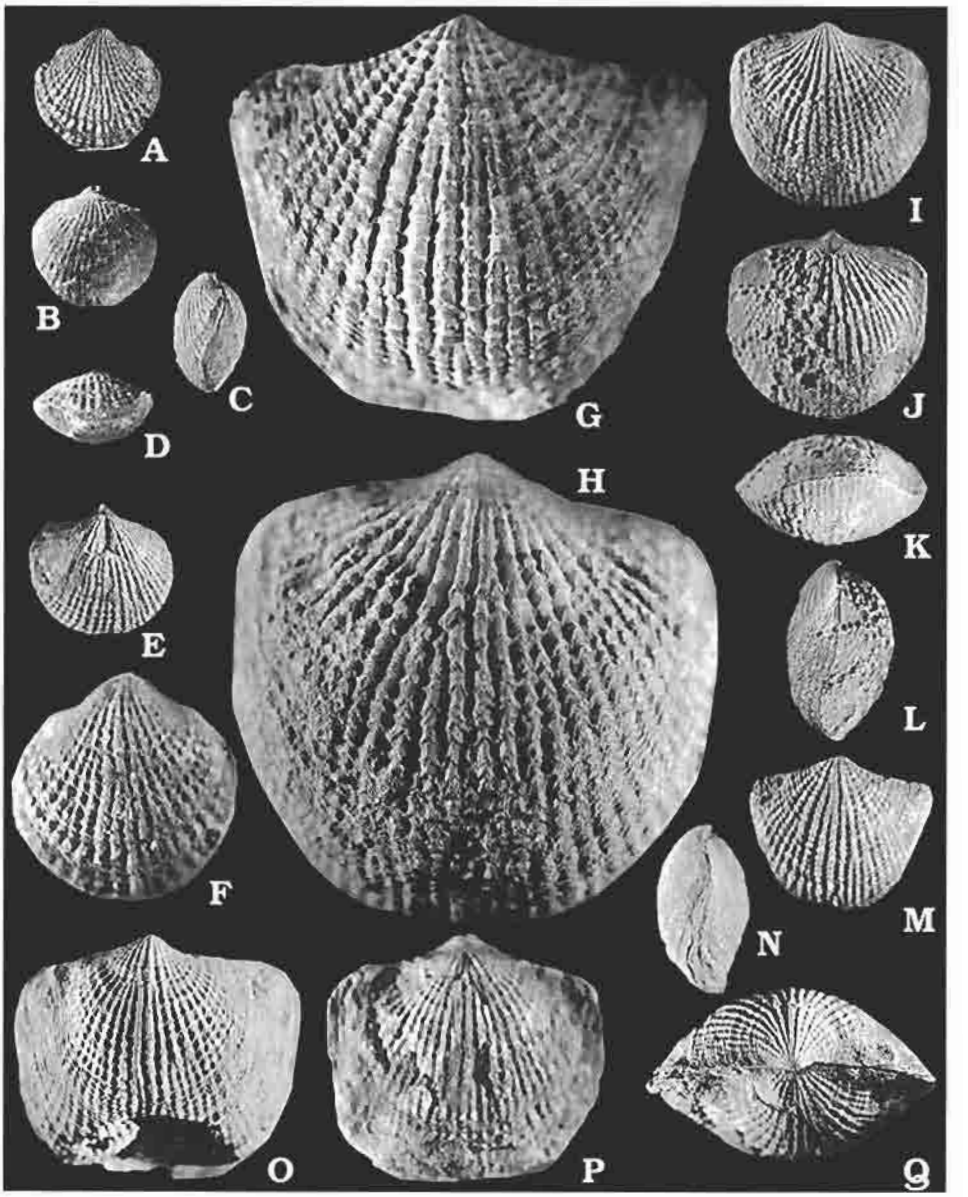


Fig. 13. Late Frasnian atrypids from South Timan, Russia. **A–E**. *Spinatrypina (Spinatrypina) sosnovkensis* Yudina sp. n. Ukhta suite, river Ukhta. **A–D**. Holotype TPNITch 7/178 in ventral, dorsal, lateral, and anterior views. **E**. Shell TPNITch 7/202 in dorsal view; × 2. **F–Q**. *Iowatrypa*(?) *nebulosa* Yudina, 1997. Sedyu suite, river Sedyu. **F**. Shell TPNITch 7/174 in ventral view, × 3. **G, M, N**. Shell TPNITch 7/272 in ventral and lateral views, × 5 (**G**), and natural size (**M, N**). **H–L**. Holotype TPNITch 7/270 ventral, dorsal, anterior, and lateral views, natural size (**I–L**) and × 5 (**H**). **O–Q**. Shell TPNITch 7/275 in ventral, dorsal and posterior views; × 2.

Remarks. — In shell size, shape, and ornamentation *S. (E.?) bifurcata* is close to some specimens of *S. (E.) tubaecostata* (Paeckelmann, 1913: p. 281, pl. 6: 6, 7), especially to those illustrated by

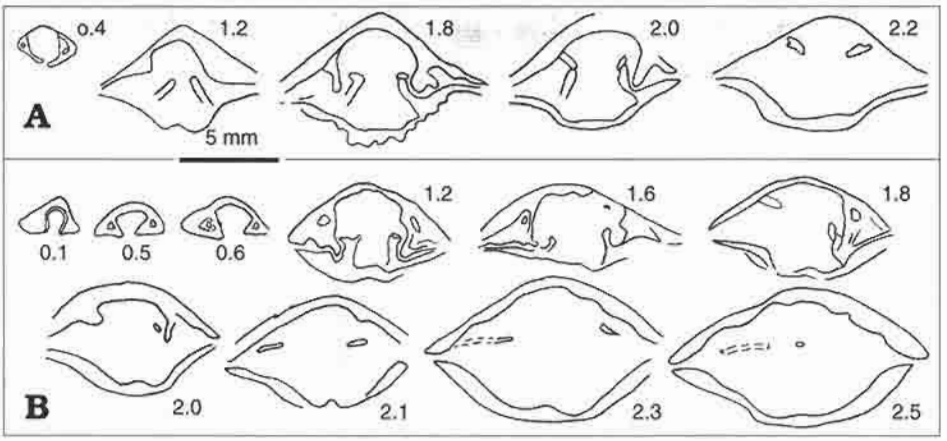


Fig. 14. Transverse serial sections of *Spinatrypina (Spinatrypina) sosnovkensis* Yudina sp. n.; specimen TPNITch 7/197 (**A**) and TPNITch 7/21 (**B**) from the late Frasnian Ukhta suite, river Ukhta, South Timan. Numbers refer to distances in mm from the top of the ventral umbo.

Copper (1967a: p. 123, pl. 19: 1–5). The species from the Urals differs in overall small shell size, less transverse outline and conspicuously less frequent and thicker ribs; its (sub)generic designation is somewhat unclear.

Occurrence. — Late Frasnian, Late *P. rhenana–P. linguiformis* Zone, Askyn horizon; SW Urals (exposures near the rivers Zilim, Malyi Askyn, Alankush, Mendym, Sargai, Sikaza); Russia.

Genus *Spinatrypa* Stainbrook, 1951

Subgenus *Spinatrypa (Plicspinatrypa)* Rzhonsnitskaya subgen. n.

Type species: *Spinatrypina* (*Spinatrypina*?) *plicata* Rzhonsnitskaya, 1964; Late Devonian (latest Frasnian), Kuznetsk Basin, Russia.

Derivation of the name: From the specific name *plicata*.

Diagnosis. — *Spinatrypa (Plicspinatrypa)* is distinguished among spinatrypinids by combination of coarse, *Spinatrypa*-type ribbing with distinctive dental plates (like in *Spinatrypina*). The new subgenus is distinguished from *Spinatrypa (Spinatrypa)* Stainbrook, 1951 by presence of well developed dental plates.

Occurrence. — Late Frasnian of the Kuznetsk Basin and the Urals, Russia; ?USA.

Species assigned. — *Spinatrypa (Plicspinatrypa) plicata* (Rzhonsnitskaya, 1975); *Spinatrypa (Plicspinatrypa) rossica* Rzhonsnitskaya sp. n.; perhaps also some species placed in *Spinatrypa* from North America, such as *Spinatrypa trulla decorticata* Cooper & Dutro, 1982.

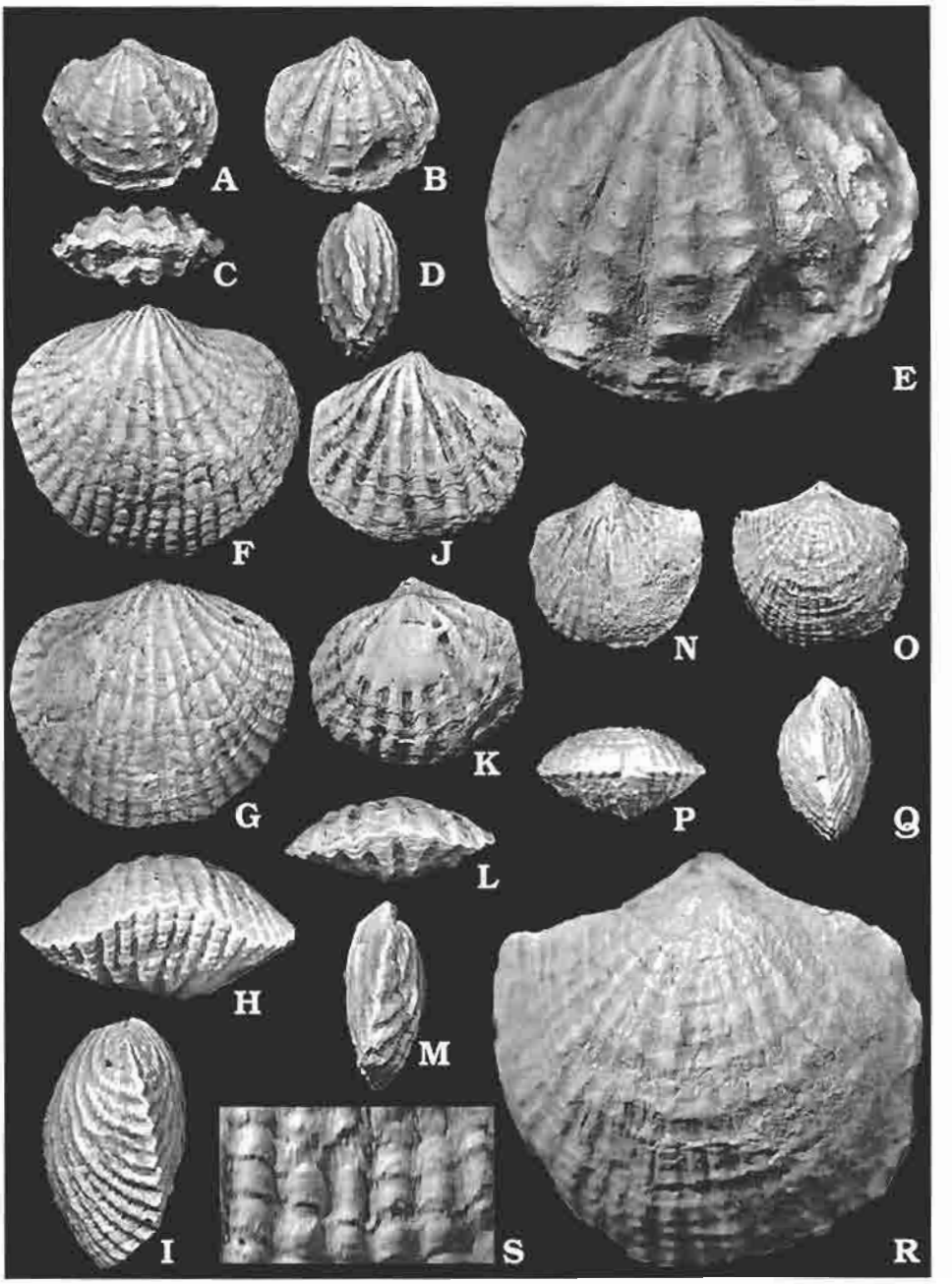
Spinatrypa (Plicspinatrypa) plicata (Rzhonsnitskaya, 1964)

Figs 15A–E, 16.

Spinatrypina plicata sp. n.; Rzhonsnitskaya 1964: p. 101; fig. 17A–E.
Spinatrypina (*Spinatrypina*?) *plicata;* Rzhonsnitskaya 1975: p. 124, fig. 37, pl. 25: 15.

Diagnosis. — Small-sized (W below 13 mm), subcircular (W/L = 1.1) species of *Spinatrypa (Plicspinatrypa)* marked by coarse, simple and widely separated ribs (R = 7–8), combined with frequent, 1.5–3 mm spaced growth lamellae.

Fig. 15. Late Frasnian atrypids from NW Kuznetsk Basin (**A–E, N–R**) and SW Urals (**F–M, S**), Russia. **A–E**. *Spinatrypa (Plicspinatrypa) plicata* (Rzhonsnitskaya, 1975). Holotype CNIGR 7859/202 in dorsal, ventral, anterior, and lateral views (**A–D**), and ornamentation of ventral valve (**E**), Solomino horizon, Golyi



Mys Rock. **F–M, S.** *Spinatrypina (Exatrypa?) bifurcata* (Markovskii, 1989). Askyn horizon, river Zilim. **F–I.** Holotype CNIGR 6755/168 in ventral, dorsal, anterior, and lateral views. **J–M, S.** Juvenile shell CNIGR 6755/169 in ventral, dorsal, anterior, and lateral views, and details of ornamentation (**S**). **N–R.** *Iowatrypa(?) kadzielnioides* (Rzhonsnitskaya, 1975). Kurlyak horizon, river Bolshaya Strelnaya (village of Solomino). Holotype CNIGR 7859/221 in ventral, dorsal, anterior, and lateral views (**N–Q**), and ornamentation of ventral valve (**R**). All × 2 except for **E**, **R** and **S** taken × 5.

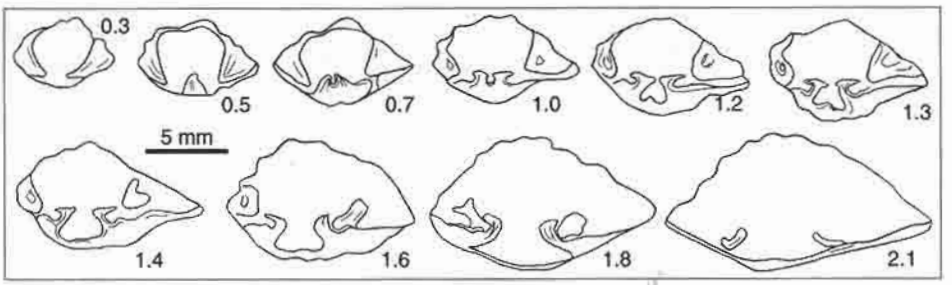


Fig. 16. Transverse serial sections of *Spinatrypa (Plicspinatrypa) plicata* (Rzhonsnitskaya, 1975); specimen CNIGR 7859/656 from Solomino horizon, Golyi Mys rock, Kuznetsk Basin. Numbers refer to distances in mm from the top of the ventral umbo.

Material. — Thirty specimens.

Internal characters (Fig. 16). — Deltidial cavity broad; dental cavities small. Hinge plates rather thin, with widely separated bases; spiralia not observed.

Occurrence. — Late Frasnian, *P. linguiformis* Zone; Solomino horizon (S slope of Golyi Mys Rock, 3 km W of village of Abyshevo) and Kurlyak horizon, *P. rhenana* Zone (Bolshaya Strelnaya near village of Tshelkino); W border of the Kuznetsk Basin, Russia.

Spinatrypa (Plicspinatrypa) rossica Rzhonsnitskaya sp. n.

Figs 17, 18A–D.

Holotype: Complete shell CNIGR 6755/316; Fig. 17A–E.

Type locality: Exposure near the river Zilim, opposite of the Kuk-tash Rock, SW Urals. Russia.

Type horizon: Askyn horizon, late Frasnian, Late *P. rhenana* Zone.

Derivation of the name: From Russia.

Diagnosis. — Medium-sized (W up to 21 mm), widened (W/L = 0.97–1.39) dorsibiconvex and variably uniplicate species of *Spinatrypa (Plicspinatrypa)* marked by very coarse (undulose-interrupted) and rarely subdivided ribs (R = 10–14). It differs from species described as *Spinatrypa trulla decorticata* Cooper & Dutro, 1982 in distinctive ribs, in contrast to weak, laterally disappearing sculpture in the late Frasnian species from New Mexico; internal characters of this American species remain vague, however.

Material. — One hundred eighty five shells of different maturity and preservation, mainly strongly recrystallized.

Dimensions (in mm):

Cat. No.	L	W	T	W/L
CNIGR 6755/316 (holotype)	15.0	20.9	7.0	1.39
CNIGR 6755/318	17.3	19.4	11.9	1.12
CNIGR 6755/317	20.7	20.1	14.0	0.97

Description. — Shell medium-sized, circular to transversely oval, moderately dorsibiconvex and uniplicate. Hinge line gently curved, narrower than the largest width, which is close to the mid-valve.

Ventral valve weakly convex, maximally inflated at central part. Area not very large, triangular; delthyrium covered by deltidial plates; foramen circular, apical. Sinus developed in anterior half, tongue fairly arch-like to high, strongly incurved dorsally (see Fig. 17D).

Dorsal valve usually more convex, with rounded fold well expressed near anterior commissure.

Ribs very coarse, R = 10–14, mostly undivided, but rarely dichotomizing. Growth lamellae strongly developed, projected on rib crests (?incipiently spinose). Internal characters marked by well developed dental cavities, and wand-shaped teeth of moderate size. Hinge plates with distinctive

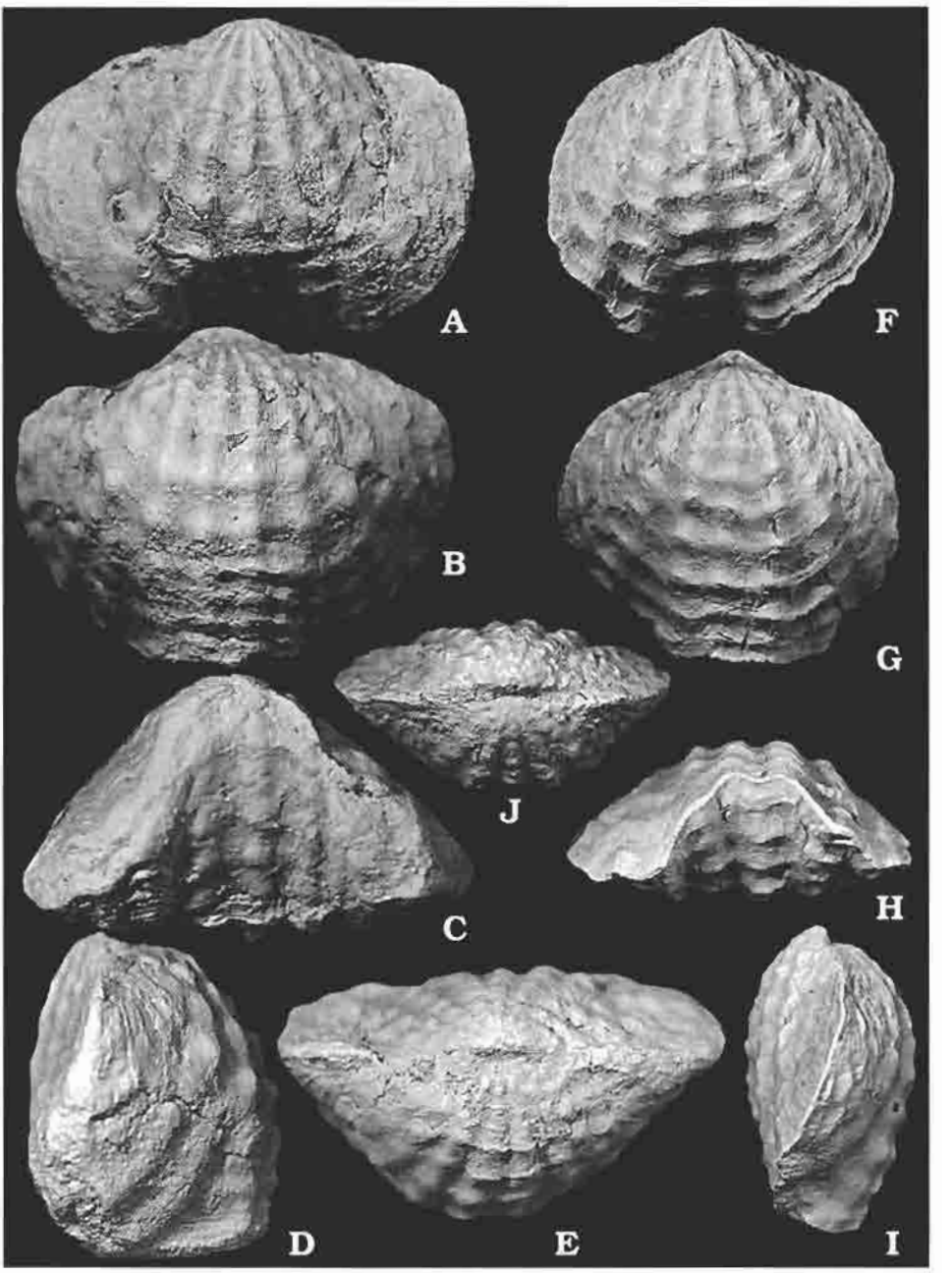


Fig. 17. *Spinatrypa (Plicspinatrypa) rossica* Rzhonsnitskaya sp. n. from the late Frasnian Askyn horizon, river Zilim (Kuk-tash rock), SW Urals; Russia. **A–E**. Holotype CNIGR 6755/316 in ventral, dorsal, anterior, lateral, and posterior views. **F–J**. Shell CNIGR 6755/317 in ventral, dorsal, anterior, lateral, and posterior views. All × 2.

external and internal ribs; crura bases directed laterally; rather massive septum or septal ridge. Spiralia not seen.

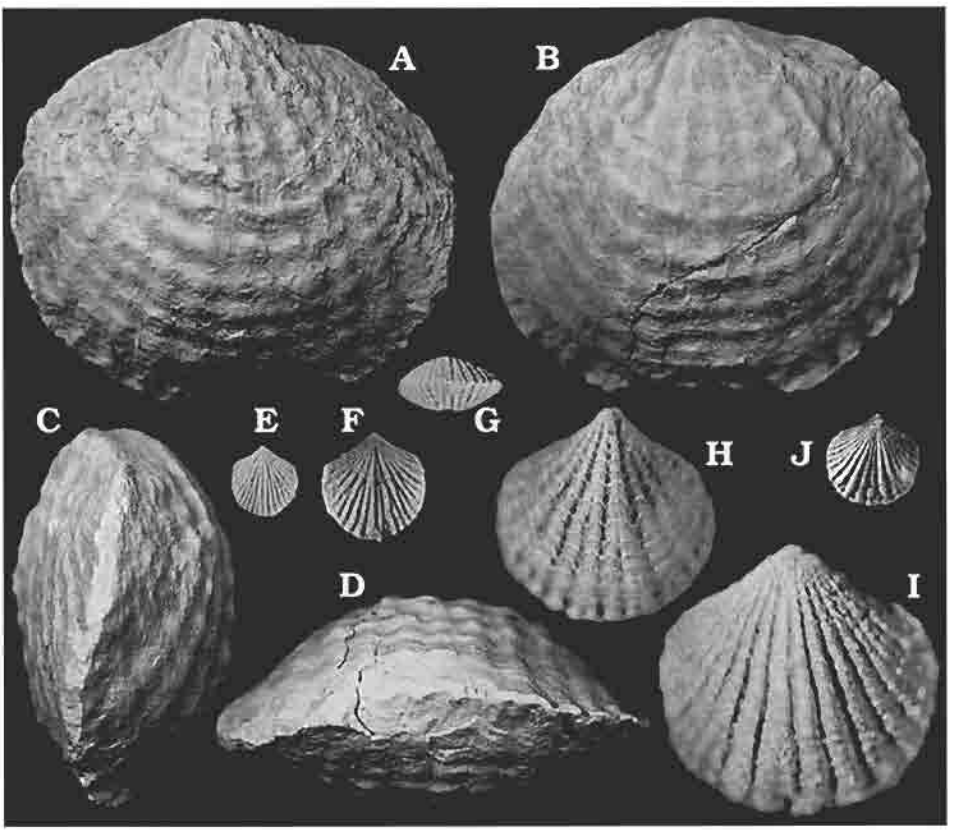


Fig. 18. Late Frasnian atrypids from SW Urals (**A–D**) and South Timan (**E–J**), Russia. **A–D.** *Spinatrypa (Plicspinatrypa) rossica* Rzhonsnitskaya sp. n.; Askyn horizon, river Zilim (Kuk-tash Rock), shell CNIGR 6755/318 in ventral, dorsal, lateral and posterior views; × 2. **E–J.** *Waiotrypa*(?) sp. A. Sedyu suite, river Sedyu. **E–G.** Shell TPNITch 7/380 in ventral, dorsal and anterior views. **H, J.** Shell TPNITch 7/12 in ventral and dorsal views. **I.** Shell TPNITch 7/317 in dorsal views. All × 2 except for **E** (natural size), **H** and **I** (× 5).

Variability. — The species is variable in shell shape, sinus-fold development and ribbing. Typical specimens are subcircular-quadrate, distinctly uniplicate, with 2–3 ribs in the sinus. In addition, there is a variety with indistinct sinus, typified by convex bottom and manifested only as a weak curvature of anterior margin; number of ribs in the sinus increases to 4 and more (see Fig. 17A–D).

Remarks. — In an unpublished study, Markovskii (1948a) identified the Uralian species as *Atrypa planosulcata* Webster, 1888, originally described from the Frasnian of North America, which indeed exhibits a similarity in general shell shape (see e.g., Fenton & Fenton 1924: p. 130, pl. 27: 13–16). However, the Russian *Spinatrypa (Plicspinatrypa) rossica* sp. n. is clearly distinguishable from the latter in having coarser ribbing.

Ornamentation and internal features (well developed dental cavities, almost horizontal, laterally directed crural bases) reveal an affinity with the diminutive type species of the subgenus, *S. (P.) plicata* from the Frasnian of the Kuznetsk Basin.

Occurrence. — Late Frasnian, Late *P. rhenana–P. linguiformis* zones, Askyn horizon; SW Urals (exposures near the rivers Zilim, Malyi Askyn, Usuili), Russia.

Genus *Waiotrypa* Baliński, 1997

Waiotrypa(?) sp. A

Fig. 18E–J.

Material. — More than 100 specimens.

Remarks. — The Timan specimens are small (W below 8.5 mm), gently biconvex (T up to 4.1 mm) subcircular (W/L = 0.94–1.06), without sinus and fold, ornamented with rather coarse ribs (R = 18–22) and frequent growth lamellae. This atrypid seems to be closely related to the stratigraphically older and poorly known species *'Atrypa' aschensis* Markovskii, 1989 (see Markovskii 1989: p. 94, pl. 2: 1), described from the late Frasnian Mendym horizon of the SW Urals (see Fig. 22A–E), but is distinguishable by thicker ribs, higher ventral area and unfolded anterior margin. Affinities of the minute atrypids from Timan with the Polish type species of *Waiotrypa*, *Waiotrypa sulcicarina* Baliński, 1997, are remarkable, especially due to the presence of a distinctive elongated furrow on the dorsal valve, and they are tentatively assigned to this genus. This possibly also concerns a few similar specimens from the Askyn horizon, SW Urals (outcrops near the river Zilim), co-occurring with *Iowatrypa nalivkini* sp. n. (see below).

Occurrence. — Late Frasnian; Sedyu suite, along the rivers Liyayel and Bolshoi Keran, South Timan, Russia.

Subfamily Pseudogruenewaldtiinae Rzhonsnitskaya, Yudina & Sokiran, 1997 (= Pseudogruenewaldtinae [sic] Rzhonsnitskaya, Yudina & Sokiran, 1997)

Diagnosis. — Variously sized atrypids markedly distinguished by strongly ventribiconvex *Gruenewaldtia*-like shell with weakly convex or almost flat dorsal valve, fine tubular-imbricate ribs (with scale-like deflected concentric lamellae), undeveloped dental cavities, and with elevated muscle platform and pedicle layer.

Genera included. — *Pseudogruenewaldtia* Rzhonsnitskaya, 1960; *Iowatrypa* Copper, 1973.

Remarks. — Copper & Chen (1995) described a new subfamily Invertininae based on a re-investigation of the Middle Devonian *Atrypa aspera* var. *sinensis* Kayser (1883: p. 83, pl. 9: 3a–g) from China. They considered that *Pseudogruenewaldtia* and *Iowatrypa* belonged to this new subfamily. We assign these genera to the subfamily Pseudogruenewaldtiinae, because the representatives of these genera differ from the nominative spinatrypinid-like species of the subfamily Invertininae, *Invertina sinensis* (Kayser, 1883), in the shield-shaped shell outline, finer imbricated ornamentation, thinner and distinct deltidial plates, and development of muscle platform and pedicle layer in umbonal part of pedicle valve.

Both these closely allied genera are highly characteristic of the Frasnian age (see discussion in Copper 1973: p. 495). *Pseudogruenewaldtia* is described so far only from the late Frasnian of South Timan, but its occurrence is supposed also for Central Europe by Copper (1973: p. 491). *P. elongata* Alekseeva, 1996 from NE Siberia (see Alekseeva *et al.* 1996: p. 136, pl. 15: 3–4, figs 74, 75) differs from the type species, *P. tschernyschewi* Rzhonsnitskaya, 1960, in the subdued (?maybe lacking) growth lamellae and the larger number of whorls in the spiralia (up to 12), and it possibly represents a separate genus.

Occurrence. — Late Devonian, Frasnian, Eurasia, North America.

Genus *Pseudogruenewaldtia* Rzhonsnitskaya, 1960

Diagnosis. — Genus of Pseudogruenewaldtiinae that differs from *Iowatrypa* in having a large shell, usually shorter and nearly curved hinge line, and internally in total absence of raised ventral muscle platform and pedicle collar, and reduced number of whorls in spiralia (below 5 in *Pseudogruenewaldtia*, and up to 8–9 in *Iowatrypa*; see Copper 1973, Godefroid 1994).

Remarks. — The genus belongs to one of the last atrypids but externally mimic the Middle Devonian *Gruenewaldtia* Chernyshev, 1885; the main differences include the tightly imbricated rib structure,

and the absence of the pedicle collar and muscle platforms with septa in the ventral and dorsal valves.

Occurrence. — Late Frasnian, Late *P. rhenana* Zone, South Timan, Urals, possibly North-East Russia, as well as Poland and Germany (Copper 1973; personal communication 1997).

Pseudogruenewaldtia tschernyschewi Rzhonsnitskaya, 1960

Figs 19, 20.

Gruenewaldtia latilinguis Chernyshev, 1885; Lyashenko 1959: p. 175, pl. 51: 5–7.

Pseudogruenewaldtia tschernyschewi sp. n.; Rzhonsnitskaya 1960: p. 49, pl. 1: 7, pl. 2: 4; Rzhonsnitskaya 1964: p. 107, figs 4, 5, pl. 2: 6.

Rugosatrypa enchorica sp. n.; Yudina 1997a: p. 65, pl. 6: 1, 2, fig. 3.

Diagnosis. — Large (W above 30 mm), strongly ventribiconvex, subcircular-subpentagonal to ovate, and weakly uniplicate shells, with short, hinge line and fine, closely imbricated ribbing; internally marked by spiralia with few whorls.

Material. — More than 100 shells of fair to good preservation (collected by Y.A. Yudina) and 156 shells of good preservation (collected by M.A. Rzhonsnitskaya).

Revised description. — Large (W up to 31 mm), strongly ventribiconvex (T up to 25 mm), subcircular-subpentagonal to ovate (W/L = 0.57–1.11), and weakly uniplicate shells with gently curved hinge line, corresponding to 1/2 to 2/3 of the maximal shell width, located at mid-valve.

Ventral valve varies in outline from subtriangular to subpentagonal, and its convexity is twice as great as that of dorsal valve. Beak hypercline, adpressed in mature specimens; foramen small, apical. Sinus flat, developed only in anterior part, widened anteriorly. Anterior commissure deflected in broad arch.

Dorsal valve ovate, moderately and uniformly convex, fold absent.

Ribs fine (R-15 = 8–9), dichotomizing and of equal width over all the length. Concentric sculpture is represented by thin, distinctly, and imbricated roller-like lamellose valve.

Inside very thickened ventral valve (Figs 20, 21), deltidial plates thin, pedicle collar absent, teeth laterally directed, with narrowed long main lobe and a broad lateral lobe, dental cavities minute. Hinge plates thin, crural bases oriented ventrally and toward mid-valve, crura feather-like, jugal plates thick, jugum disjunct, spiralia with few (up to 4?) whorls.

Growth changes. — Juveniles characterized by reduced shell convexity, and orthocline ventral beak that progressively incurves in ontogeny. Sinus is sometimes almost totally undeveloped even in mature individuals.

Occurrence. — Late Frasnian, Late *P. rhenana–P. linguiformis* zones; Sedyu suite, limestone massifs near the rivers Sedyu and Bolshoi Keran, South Timan, Russia.

Genus *Iowatrypa* Copper, 1973 emend. Copper & Chen 1994

Diagnosis. — The genus is distinguished from *Pseudogruenewaldtia* in its smaller size, mainly shield-like outlines and relatively long and straight hinge line, and internally in raised muscle platform in thick ventral valve, spiralia with increased number of whorls, and pedicle collar absent or variously developed.

Remarks. — Russian species of ventribiconvex ('reversed') atrypids were previously considered (e.g., Nalivkin 1947, 1951; Lyashenko 1959; Markovskii 1989; see also Baliński 1979) as members of *Anatrypa* Nalivkin, 1941. As established by Copper (1973: p. 495; 1978: p. 294, fig. 1) and Rzhonsnitskaya (1975: p. 128, fig. 38) in the type species *A. micans* (Buch, 1840), the true *Anatrypa* is marked by tubular ribs and thin, sharply outlined dental plates. Thus, *Anatrypa* is restricted to the early Frasnian of the Main Devonian Field, whilst several other coeval Russian species, typified by imbricated ribs and minute dental cavities obviously represent *Iowatrypa*.

It is possible to distinguish two late Frasnian species groups in *Iowatrypa* on the basis of external and internal structure: type *Iowatrypa owenensis*-group, differing from the *I. nalivkini*-group (see below) by more elongated shell and thinner ribs toward the anterior commissure. In addition, the

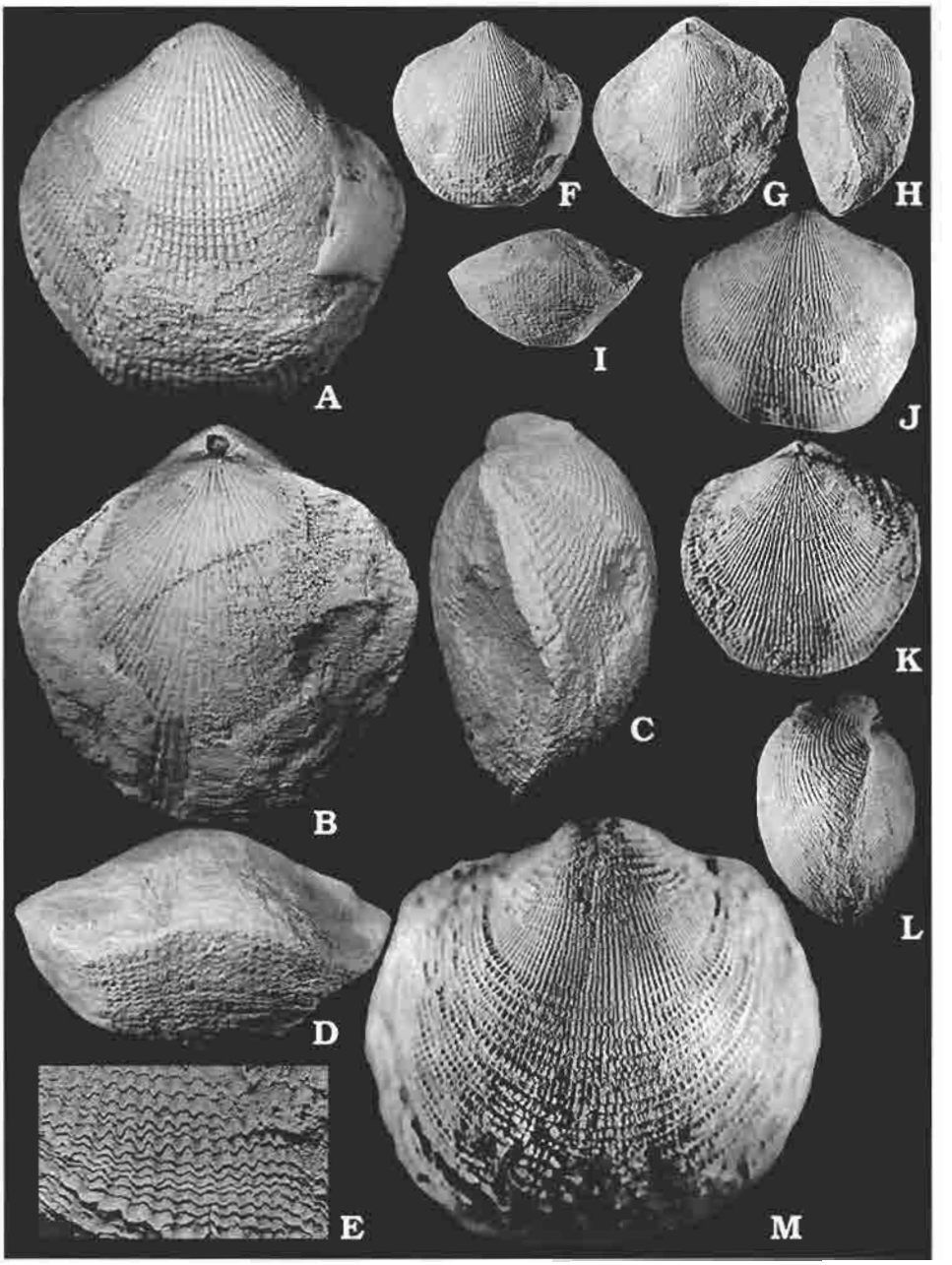


Fig. 19. *Pseudogruenewaldtia tschernyschewi* Rzhonsnitskaya, 1960 from the late Frasnian Sudyu suite, river Bolshoi Keran, bioherm (**A–I**) and river Sedyu (**J–L**), South Timan, Russia. **A–I**. Holotype CNIGR 475/1684 in ventral, dorsal, lateral, and anterior views (**A–D**, **F–I**), and details of ornamentation (**E**). **J–K**. Shell TPNITch 7/41 in ventral and dorsal views. **L**. Shell TPNITch 7/43 in lateral view. **M**. Shell TPNITch 7/47 in ventral view. All × 2 except for **F–L** (natural size) and **E** (× 5).

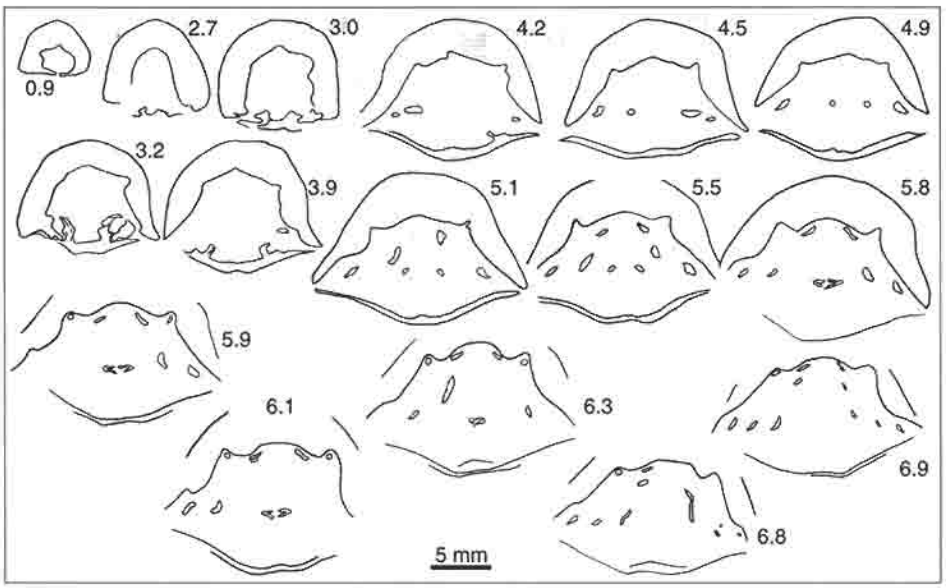


Fig. 20. Transverse serial sections of *Pseudogruenewaldtia tschernyschewi* Rzhonsnitskaya, 1960; specimen TPNITch 7/130 from the late Frasnian Sudyu suite, river Sedyu South Timan. Numbers refer to distances in mm from the top of the ventral umbo; × 3.

early Frasnian *timanica*-group is marked by a larger-sized shell, subcircular-subquadrate outline with long and straight hinge line, median depression on its dorsal valve, and internally by raised muscle platform and pedicle layer in ventral valve, and totally absent pedicle collar (e.g., *Iowatrypa timanica* Markovskii, 1955 *in* Mikriukov 1955; see Figs 21F–J and 22).

Iowatrypa nalivkini Rzhonsnitskaya & Sokiran sp. n.

Fig. 23A–T.

Anatrypa sigasa sp. n.; Nalivkin 1941: p. 174, pl. 8: 6 [pro parte].

Anatrypa sikasa [sic!] Nalivkin (in coll.); Adrianova 1955: p. 371, pl. 7: 4.

Holotype: Complete shell CNIGR 6755/177; Fig. 23A–F.

Type locality: River Zilim, Suvaltash Rock, SW Urals, Russia.

Type horizon: Askyn horizon, late Frasnian.

Derivation of name: In honour of Academician Dmitrii V. Nalivkin.

Diagnosis. — Medium-sized species (W up to 18 mm) of *Iowatrypa*, with subquadrate to shield-like outline, keel in umbonal part of ventral valve and dichotomizing, mostly thin ribs, thicker posteriorly, tightly imbricated anteriorly. *I. nalivkini* sp. n. differs from *I. rotundicollis* Godefroid, 1994 in its coarser ribs.

Material. — Two hundred eighty well preserved but strongly recrystallized shells from Markovskii's collection.

Dimensions (in mm):

Cat. No.	L	W	T	W/L
CNIGR 6755/177 holotype	15.5	15.1	10.3	0.97
CNIGR 6755/309	16.1	17.4	8.3	1.18
CNIGR 6755/312	14.9	14.4	7.9	0.96

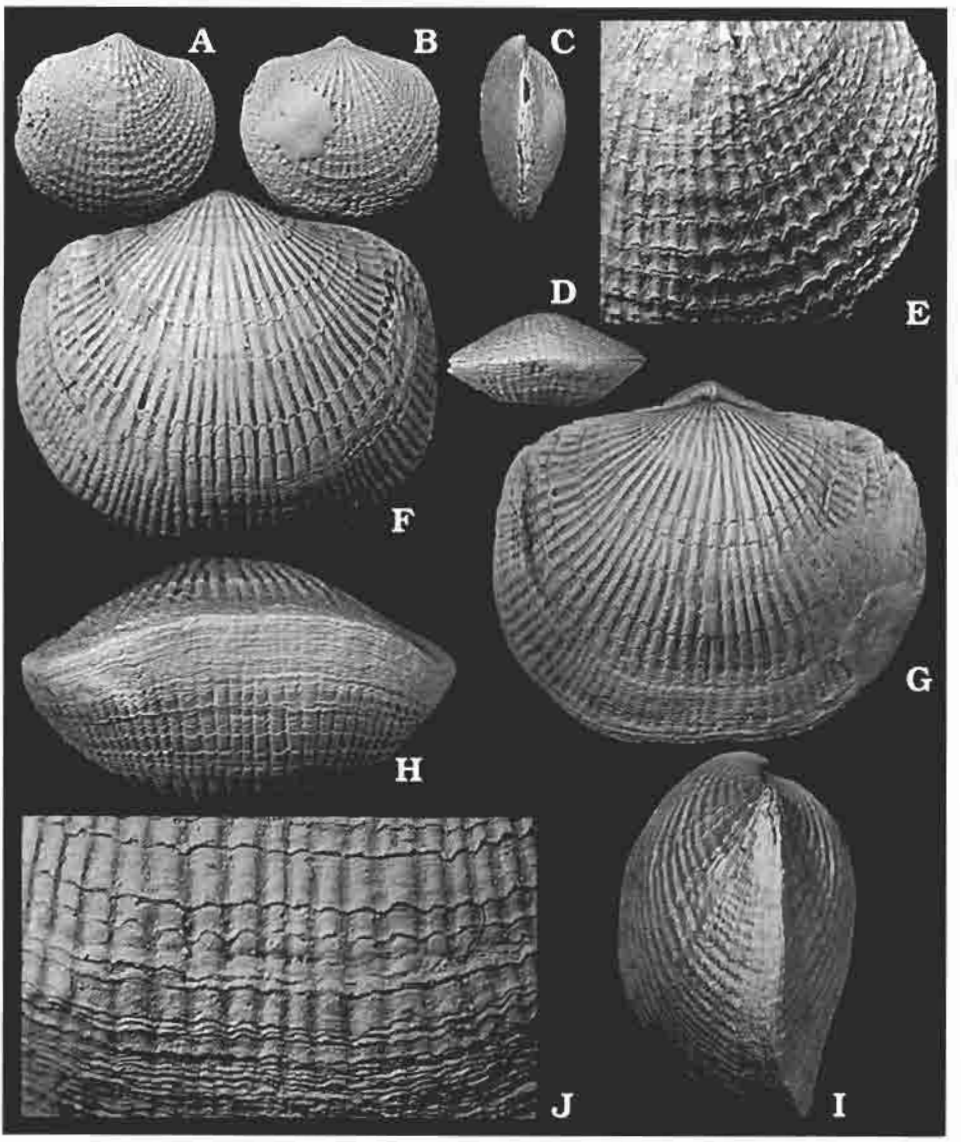


Fig. 21. Frasnian atrypids from SW Urals, Russia. **A–E**. *Spinatrypina*(?) *aschensis* (Markovskii, 1989). Late Frasnian, Mendym horizon, Bolshaya Asha (stream Tochilnyi). Holotype CNIGR 6755/175 in ventral, dorsal, lateral and anterior views (**A–D**), and details of ornamentation (**E**). **F–J**. *Iowatrypa timanica* (Markovskii in Mikryukov, 1955). Early Frasnian, Sargaievo horizon, river Sikaza. Shell CNIGR 6755/181 in ventral, dorsal, anterior and lateral views (**E–I**), and details of ornamentation (**J**). All × 2 except for **E** and **J** that are taken × 5.

Description. — Medium-sized, ventribiconvex, subquadrate to shield-like shells, with straight hinge line shorter than or equal to maximal shell width. Hinge angles rounded, ears small and not always distinguishable. Anterior commissure weakly uniplicate.

Ventral valve maximally convex in umbonal part, where it has rounded keel-like elevation. Beak minute, typically hypercline; area minute; delthyrium covered with deltidial plates; foramen apical.

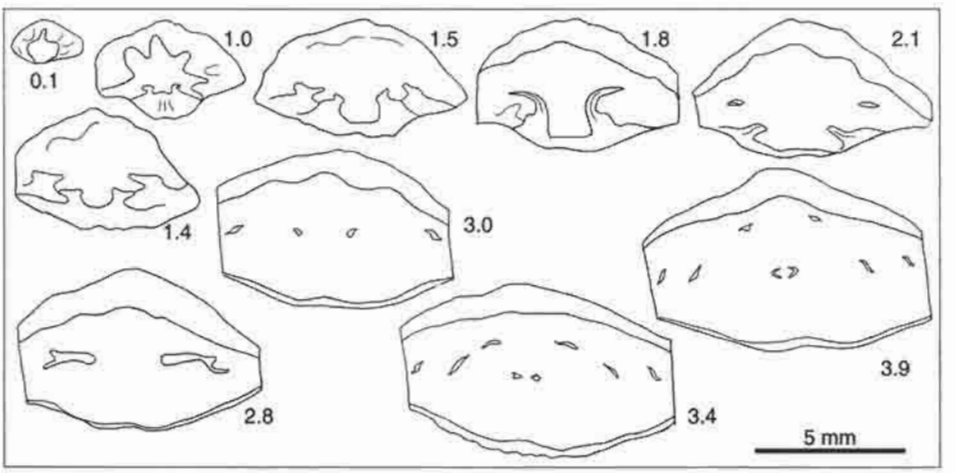


Fig. 22. Transverse serial sections of *Iowatrypa timanica* (Markovskii in Mikryukov 1955); specimen CNIGR 6755/181a from early Frasnian, Sargaievo horizon, river Ust-Yarega. Numbers refer to distances in mm from the top of the ventral umbo.

Indistinct and narrow sinus-like depression, slightly widened anteriorly, occurs in anterior part of some specimens only.

Dorsal valve gently convex, inflated in umbonal part, flattened to slightly concave laterally. Small, narrowed furrow developed only in the posteriormost part.

Ribs fine and tubular, coarser and widely spaced in posterior part; occur up to 11 ribs near beak. Dichotomy and intercalation common, and the latter prevails on dorsal valve. Newly appearing ribs distinctly thinner than primary ones, and in consequence, the ribs become thinner anteriorly (R-10 = 6–8, Ra = 7–9; R approaches 60). Growth lamellae lamellose, widely spaced anteriorly, and more distinct and crowded anteriorly (C = 3 posteriorly, C = about 12 close to anterior margin).

Walls of ventral valve thickened due to pedicle layer (Fig. 22); dental plates absent, teeth massive with obscured additional denticulae, merged with valve walls. Hinge plates of moderately thickness; low septal ridge present; crural bases directed ventrally, jugum and spiralia not recognized.

Growth changes and variability. — Juvenile shells have an almost flat dorsal valve with central sinus-like furrow and convex ventral valve with keel; ribs are widely spaced.

The most variable features include the sinus-like depression in dorsal valve (up to its total absence), ears and beak curvature. A *Waiotrypa*-like biconvex variety with orthocline beak persisting in mature specimens, is distinguishable, as well as a diminutive thin-ribbed morphotype.

Remarks. — Nalivkin first identified this species in 1934 as *Anatrypa sigasa* in the late Frasnian collection from Urals, but without description and figures. Then the name *Anatrypa sikasa* [sic!], was used by some authors (Markovskii 1948a, unpublished; Adrianova 1955). However, Nalivkin described *Anatrypa sigasa* in 1941 on the base of disarticulated poorly-preserved valves (Fig. 23U) from the early Frasnian (Ilmen beds) of the Main Devonian Field (Nalivkin 1941). He considered this species as conspecific with the late Frasnian species from Urals. However, the holotype does not correspond to the species from Urals, being more elongated and having distinctly separated umbo and oval, weakly-convex ventral valve; the last two characters are not characteristic for *Iowatrypa* (see Fig. 23U). Thus, the new species *Iowatrypa nalivkini* is established herein on the basis of the rich Markovskii collection from the Urals, which earlier was considered as *Anatrypa sikasa* by Markovskii (1948a) and Adrianova (1955).

Occurrence. — Late Frasnian, Late *P. rhenana–P. linguiformis* zones, Askyn horizon; SW Urals (outcrops near the rivers Sikaza, Zilim, Usui-li, Bolshaya Kyngyrli, Mendym, Sargai), N Urals; Russia.

Iowatrypa sp.

Fig. 3A–G.

Iowatrypa keranica (Ljasch.) MS; Yudina & Moskalenko 1997: p. 55 [nomen dubium].

Diagnosis. — A species of *Iowatrypa* distinguished by combination of small shell size (W up to 12 mm), shield-like outline (W/L = 0.9–1.1), well developed ears, lacking sinus and fold, and thin ribs (R-5 = 12–14). From *I. nalivkini* sp. n. differs in having developed pedicle collar, finer ribbing, and presence of concentric growth lines on whole shell.

Material. — More than 100 well preserved shells.

Description and remarks. — See Yudina (in press).

Variability. — Ventral beak usually moderately curved, but may be also strongly incurved and adpressed on gerontic shells. Distinctive ears are replaced in some specimens by flat hinge extremities. Furthermore, few largest shells are marked by additional folds (see Fig. 3G).

Occurrence. — Late Frasnian, Early *P. rhenana* Zone, Liyayel suite; Timan-Petchora region, Russia.

Iowatrypa(?) *nebulosa* Yudina, 1997

Fig. 13F–Q.

Spinatrypa(?) *nebulosa* sp. n.; Yudina 1997a: p. 66, pl. 6: 3, 4, fig. 4.

Diagnosis. — A questionable species of *Iowatrypa* which differs from all other species of the genus by combination of medium size (W up to 16 mm), biconvexity to dorsibiconvexity (T up to 9 mm), subrectangular outline (W/L = 0.9–1,2), lacking sinus and fold, and moderate coarse, imbricated ribs (R-5 = 5), as well as internally by developed pedicle collar.

Material. — More than 50 shells of fair and good preservation.

Description. — See Yudina (1997a).

Remarks. — The species is re-assigned herein with question to the genus *Iowatrypa*, but compared with that genus it has a relatively less convex ventral valve. It can be distinguished from *Spinatrypa* by the subrectangular outline and moderately coarse, imbricated ribs, as well as internally by the developed pedicle collar.

Occurrence. — Late Frasnian, Late *P. rhenana–P. linguiformis* Zone; Sedyu suite; outcrops near the river Sedyu; South Timan, Russia.

Iowatrypa(?) *kadzielnioides* (Rzhonsnitskaya, 1975)

Figs 15N–R, 24.

Spinatrypa tubaecostata (Paeckelmann); Alekseeva 1962: p. 141, pl. 2: 8, fig. 66.
'Anatrypa' kadzielnioides sp. n.; Rzhonsnitskaya 1975: p. 126, pl. 28: 1–4, fig. 38.

Diagnosis. — A species of *Iowatrypa*(?) marked by small-sized (W mostly below 15 mm) subcircular to transversely-ovate shell (W/L = 1.05–1.45), combined with moderate equi- to weak dorsibiconvexity (T up to 7 mm), by orthocline to slightly anacline beak, by delthyrium with exposed deltidial plates, and by thin dichotomizing ribs (R = 25–26).

Material. — Thirty four mostly poorly preserved shells.

Internal characters. — Partly recognized (Fig. 24): dental cavities undeveloped, crural bases directed ventrally.

Growth changes. – Juvenile shells are more extended transversely, with gently convex ventral valve bearing small keel on umbo, and flattened dorsal valve with corresponding median furrow. With growth, the shell outline grades into subcircular, the convexity increases (particularly of dorsal valve), paired with curving of beak and uniplication of anterior commissure.

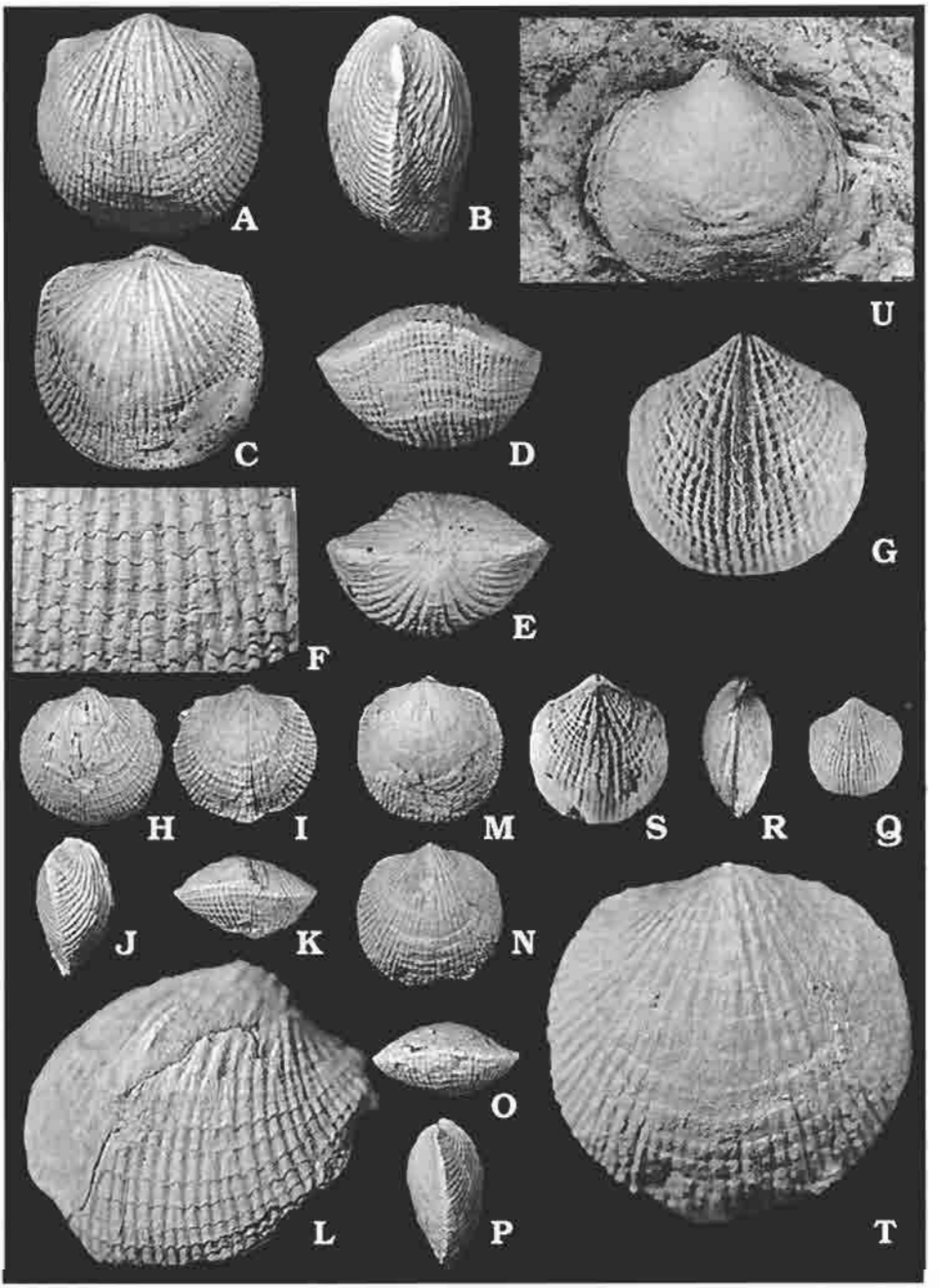


Fig. 23. **A–T.** *Iowatrypa nalivkini* Rzhonsnitskaya & Sokiran sp. n. from the late Frasnian of SW Urals (**A–F**) and South Timan (**G–U**), Russia. **A–F.** Holotype CNIGR 6755/177 in ventral, lateral, dorsal, anterior, and posterior views (**A–E**), and details of ornamentation in anterior part (**F**); Sudyu suite, river Sedyu. **G, Q–S.** Shell TPNITch 7/174 in ventral (**G, Q**), lateral, and dorsal views. **H–L.** Shell CNIGR 6755/322 in ventral, dorsal, lateral and anterior views (**H–K**), and ornamentation (**L**). **M–T.** Shell CNIGR

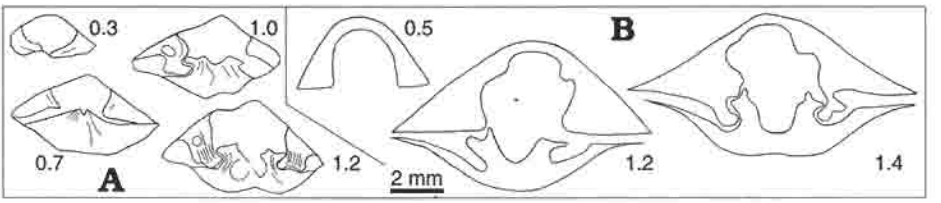


Fig. 24. Transverse serial sections of *Iowatrypa*(?) *kadzielnioides* (Rzhonsnitskaya, 1975); specimen CNIGR 7859/222d (**A**) and CNIGR 7859/223d (**B**) from the late Frasnian Kurlyak horizon, rivers Bolshaya Strelnaya (**A**) and Inya (**B**), Kuznetsk Basin. Numbers refer to distances in mm from the top of the ventral umbo.

Remarks. — Similar shells were previously compared by Nalivkin (1947, 1951) and Alekseeva (1962) with a poorly-known Polish species, *Atrypa kadzielniae* Gürich, 1896, which, according to Racki (1993: p. 308), belongs to the Variatrypinae.

The species is referred tentatively to *Iowatrypa* on the basis of shell outline (especially straight hinge line) and rib structure. The nearly equal valve convexity, orthocline beak and exposed deltidial plates suggest connection with *Waiotrypa* Baliński, 1997, but the specimens from Kuzbass are distinguished by an overall lack of carination, and presumably represent a separate genus (see also *Waiotrypa*? *pluvia* Godefroid & Helsen, 1998).

Occurrence. — Late Frasnian, *P. rhenana Zone*, Kurlyak horizon, exposures near the rivers Inya (village of Izylinskaya) and Bolshaya Strel'naya (village of Solomino); NW border of Kuznetsk Basin, Russia.

Family Davidsoniidae King, 1950

Subfamily Carinatininae Rzhonsnitskaya, 1960

Genus *Carinatina* Nalivkin, 1930

Carinatina(?) *biohermica* Yudina sp. n.

Figs 7K–Q, 25.

Holotype: Complete shell TPNITch 7/501; Fig. 7K–M.

Type locality: Exposure near the river Vezhavozh (middle part), South Timan, Russia.

Type horizon: Biohermal Vezhavozh unit, late Frasnian.

Derivation of the name: From bioherm, to emphasize a limited facies distribution of the species.

Diagnosis. — A problematic carinatininid species marked by diminutive (W up to 10.5 mm), subcircular, flattened shell, paired with coarse ribs (R up to 17) and sharp keel on ventral valve.

Material. — Fifteen shells of fair and good preservation.

Dimensions (in mm):

Cat. No.	L	W	T	W/L
TPNITch 7/501 (holotype)	6.9	7.3	2.3	1.06
TPNITch 7/497	9.1	10.3	3.9	1.13
TPNITch 7/489	6.9	7.3	3.3	1.06

6755/323 in dorsal, ventral, anterior, and lateral views (**M–P**), and enlarged view of dorsal view (**T**).U. *I*(?). *sigasa* (Nalivkin, 1941), middle Frasnian, Ilmen beds, river Koloshka, and Main Devonian Field, East European Platform, Russia. Holotype CNIGR 107/101, ventral valve. All × 2 except for **F**, **G**, **L** and **U** that are taken × 5.

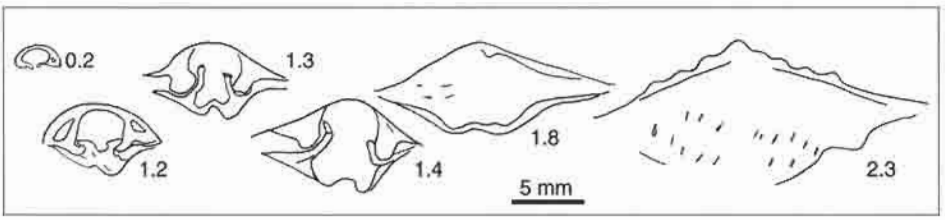


Fig. 25. Transverse serial sections of *Carinatina*(?) *biohermica* Yudina, sp. n.; specimen TPNITch 7/350 from the late Frasnian Sedyu biohermal unit, river Sedyu. Numbers refer to distances in mm from the top of the ventral umbo.

Description. — Small, ovate and circular shells, with largely somewhat transversely outline, and weakly biconvex. Hinge line long and straight, slightly shorter than maximal width. Hinge angles gently rounded. Anterior commissure rectimarginate to weakly uniplicate.

Ventral valve feebly convex, almost flat laterally; in central part occurs sharply developed keel, expanded anteriorly as a result of the mid-rib dichotomy, and somewhat reduced in height. Beak orthocline, with large subapical foramen; area triangular, high.

Dorsal valve uniformly and gently inflated. Narrow, deep furrow developed in middle part.

Ribs tubular, coarse, dichotomizing, 6 on each lateral half of ventral valve; mid-rib of the keel on umbonal part divided anteriorly into 3 or even 5 ribs. In the median furrow of dorsal valve occurs a single rib, supplemented by 7 ribs on each lateral part. Micrornamentation consists of delicate, concentric ridges.

Internally (Fig. 25), well developed deltidial plates and pedicle layer; teeth massive, weakly subdivided, with prominent lateral cavities; socket plates tiny, crural bases large, directed laterally, crura flame-shaped; spiralia comprise 4–5 whorls.

Remarks. — The new species assigned with question to the davidsoniid genus *Carinatina* (but see also remarks under *Gibberosatrypa* gen. n), possibly being the only known Late Devonian representative of *Carinatina*.

Occurrence. — Late Frasnian, Late *P. rhenana* Zone; Vezhavozh and Sedyu biohermal units, outcrops near the rivers Vezhavozh and Sedyu; South Timan, Russia.

Brachiopod assemblages and distribution of atrypids

West slope of South Urals (M.A. Rzhonsnitskaya & B.P. Markovskii). — Brachiopods are abundant and diverse in the late Frasnian succession of the west slope of the South Urals. Atrypids and rhynchonellids dominate the coquinoid accumulations, especially in the Zilim river section (Fig. 26).

Most of the brachiopods of the Mendym horizon occur in sporadic 'nests', composed of schizophoriids, gypidulids, productellids, rhynchonellids and spiriferids (Markovskii 1948a). Atrypids are represented only by *Desquamatia (D.) alticoliformis*, *Pseudoatrypa* ex gr. *devoniana*, and *Spinatrypina*(?) *aschensis*.

Higher in the sequence, in coquinas of the Askyn limestones, Markovskii (1948a) recorded 18 brachiopod species, including, in addition to abundant atrypids, also schizophoriids, gypidulids, productellids, terebratulids, diverse rhynchonellids (pugnacids, *Hypothyridina*, *'Calvinaria'*, etc.) and spiriferids (*Adolfia*, *Warrenella*, *Cyrtospirifer*, *Thomasaria*). Six atrypid species are determined: *D. (D.) alticoliformis*, *Costatrypa*(?) *posturalica*, *Gibberosatrypa gibberosa*, *Spinatrypina* (*Exatrypa*?) *bifurcata*, *Spinatrypa (Plicspinatrypa) rossica* sp. n., and *Iowatrypa nalivkini* sp. n. The

dolomitized facies equivalents of the Askyn limestones usually contain only the spiriferid *Theodossia*. The exception is the lower interval, which locally contains a more diverse faunal assemblage (*Amphipora*, rugosans, brachiopods dominated by spiriferids); atrypids are limited to unidentified species of *Spinatrypa*.

A minute rhynchonellid *'Pugnoides triaequalis'* (Gosselet, 1877) *sensu* Markovskii (1948a) and *Athyris globosa* (Roemer, 1860) are the most common brachiopod species of the overlying Fammenian Barma Formation, with associated species of *Mesoplica*, *Cyrtospirifer* and *'Camarotoechia'*. According to Markovskii (1948a), some Frasnian genera persisted in the bottom part of this unit, as exemplified by *Hypothyridina*, *Theodossia*, and at least two atrypid species: *D. (D.) alticoliformis* and *I. nalivkini* sp. n. The occurrence of Frasnian taxa was not confirmed by Yudina (1997b). The Barma Formation is succeeded by the Makarovo Formation, containing typical Famennian brachiopods (*Zilimia*, *Mesoplica*, *Cyrtiopsis*) and the goniatite *Cheiloceras*.

Atrypid distribution in the late Frasnian section along the river Zilim (Fig. 26) reveals that their acme took place within Askyn reef facies. The diverse brachiopod fauna is called the *Hypothyridina* ex gr. *cuboides–Desquamatia (D.) alticoliformis* Assemblage. The atrypids disappeared in the dark amphiporid-*Theodossia* calcareous facies. It is noteworthy that their extinction level is situated in the Uralian domain within a uniform carbonate depositional regime near the F-F transition.

South Timan (Y.A. Yudina). — Atrypids are one of the most important brachiopod groups in the Frasnian of South Timan (Yudina 1996). *Pseudoatrypa* and *Iowatrypa* are the most typical of the early Frasnian (*Palmatolepis transitans* Zone). *Desquamatia*, *Spinatrypina* and *Spinatrypa* lived in the region throughout this age, but their role in the brachiopod biotas was mostly minor. In the late Frasnian interval, encompassing the *P. rhenana–P. linguiformis* zones, *Spinatrypina* was abundant, and *Radiatrypa*, *'Rugosatrypa'*, *Pseudogruenewaldtia* and *Carinatina*(?) appeared.

The lower part of the upper Frasnian substage (Vetlasyan suite) is developed in the so-called Ukhta facies type (Fig. 27A). This interval is marked by a proliferation of the *'Atryparia' vetlasjanica* Assemblage, concomitant with the shallowing of the sea in the Early *P. rhenana* Zone. The stratigraphically slightly younger *Adolfia sarotschoica* Assemblage has been encountered in the lower Sirachoy suite. The most common atrypid there is *Pseudoatrypa symmetrica*, but rare specimens of *Spinatrypa* ex gr. *semilukiana* Lyashenko, 1959 have also been found. In the upper Sirachoy suite the *Theodossia uchtensis* Assemblage appears, and *Spinatrypa* aff. *planosulcata* has been collected.

A rhynchonellid-dominated *Calvinaria elegans* Assemblage, without atrypids, flourished in the coeval lower Liyayel suite (Fig. 27B), which represents marly slope facies. The upper Liyayel suite has also yielded brachiopod-dominated assemblages. One of these, the *Iowatrypa* sp.–*Caryorhynchus rossicus* Assemblage, contains the index atrypid species in abundance. Higher, in the Sedyu shales, there occurs a rich *Biernatella timanica* Assemblage with numerous and well-preserved atrypid shells, associated with the double-spired athyridid *Biernatella*, *Cyrtospirifer* and gypidulids. The diverse atrypids from Sedyu shales are represented by six species, of which *Pseudogruenewaldtia tschernyschewi* is endemic. The shell sizes are notably variable,

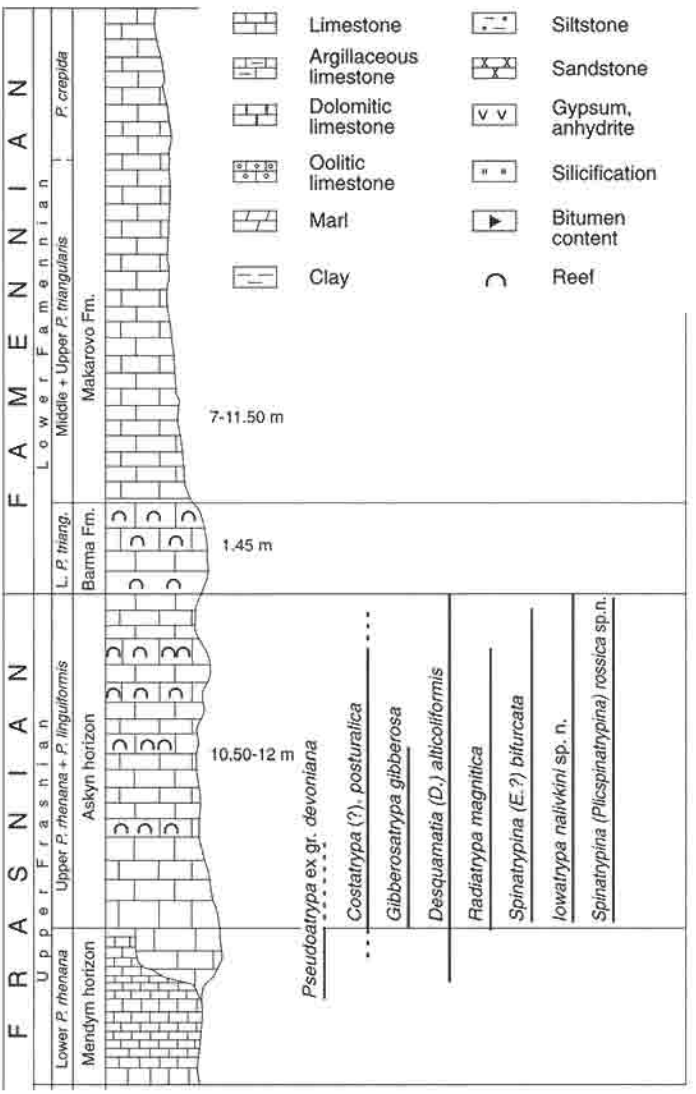


Fig. 26. Distribution of the late Frasnian atrypids in the Zilim river section, west slope of South Urals.

ranging from large *Pseudogruenewaldtia* to minute *Waiotrypa*(?) sp. A, with the shell of the former serving as a substrate for many algal epibionts.

The *Hypothyridina cuboides–'Gypidula' biplicataeformis* Assemblage occurs in small coquinoid lenses within the late Frasnian reefs. Here, atrypids are of minor significance, but three small-sized species are identified. The endemic diminutive species *Carinatina*(?) *biohermica* sp. n. is very rare, whilst the widely geographically distributed *D. (D.) alticoliformis* and *Radiatrypa magnitica* characterize the Sedyu and Vezhavozh bioherms, respectively.

In summary, the stratigraphically youngest atrypid-bearing interval in South Timan is exceptional in comparison to that of other regions in that it reveals a maximal

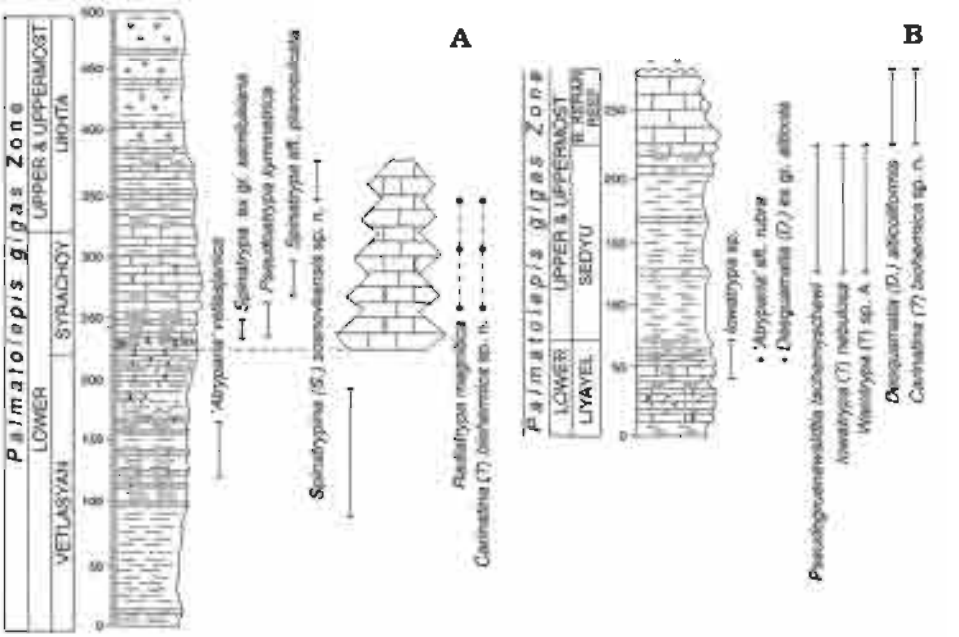


Fig. 27. Distribution of the late Frasnian atrypids in the Uklita type (**A**) and Liyayel (**B**) sequences of South Timan. Key to lithological symbols in Fig. 26.

diversification of the brachiopods, which is referred to have been partly caused by strong facies differentiation within a gradually shallowing basin.

Kuznetsk Basin (M.A. Rzhonsnitskaya). — Although atrypids are one of the most common brachiopod groups in the Frasnian chiefly offshore carbonate facies of the Kuznetsk Basin (Fig. 28), they were less diverse than in the Early and Middle Devonian (see Rzhonsnitskaya 1975). In addition, early and late Frasnian atrypid associations were quite different, the former being dominated by mass-occurring large-sized species of *Sibiratrypa*.

The late Frasnian atrypid association includes largely small- and medium-sized species, which participated in three broadly-defined brachiopod assemblages. Of them, the *Anathyrella tyzhnovi* Assemblage is known from shelly accumulations in marly limestones of the Kurlyak Horizon. This assemblage is rich in atrypids. *Costatrypa*(?) *posturalica* and *D. (D.) alticoliformis* are the most abundant, occurring together with rarer *Iowatrypa*(?) *kadzielnioides* and sporadic *Spinatrypa* cf. *planosulcata*. The fauna is characterized by the endemic plicathyrid *Anathyrella tyzhnovi* Khalfin, 1933, and a variety of typical late Frasnian schizophoriids, gypidulids, pugnacids, the spiriferid *Adolfia*, athyridids, and infrequent productellids and cyrtinids.

The *Hypothyridina cuboides* Assemblage is linked mainly to crinoidal varieties of the Glubokaya limestones. *C.*(?) *posturalica*, *D. (D.) alticoliformis* and *S.* (*E.*?) cf. *bifurcata* co-occur with schizophoriids, gypidulids, rhynchonellids (*Hypothyridina*, *'Isopoma'*, pugnacids), various spiriferids (*Adolfia*, *Cyrtospirifer*, *Theodossia*) and athyridids (*Athyris*, *Anathyris*). Brachiopods are poorly represented in reefal, stroma-

toporoid-coral facies, where only *Adolfia*, *C.*(?) *posturalica* and rare gypidulids have been encountered.

The brachiopod fauna of the latest Frasnian (*P. linguiformis* Zone) is typified by an acme of *Anathyrella*. Two facies-related assemblages are distinguishable (see Belskaya 1960). In the offshore succession (Fig. 28, left), the most abundant species is *A. ussovi* (Khalfin, 1933), which is supplemented by *Spinatrypa (Plicspinatrypa) plicata, S.* (*E*?). cf. *bifurcata*, and other poorly preserved atrypids, probably *C.*(?) *posturalica*. These are associated with orthids (*Aulacella*), gypidulids, rhynchonellids (*'Isopoma'*, pugnacids), and spiriferids, especially several species of *Adolfia*, and rarer *Cyrtospirifer*. A coeval less diverse *Anathyrella monstrum–Cyrtospirifer ussovi* Assemblage occasionally flourished in a shallow, restricted basin, developed over the N and NW Kuznetsk domain (Fig. 28, right). In addition to the large-shelled index species, rare stropheodontids, productellids, spiriferids and athyridids have also been recovered; the coquinoid intercalations in the uppermost Kelbes suite contain only rare minute undeterminable atrypids.

In general, the late Frasnian faunas include the endemic species of the Altai-Sayan Province, but further west, in a more open-shelf domain, significant biogeographic affinity with the Urals and Western Europe is apparent. The link between both of the Kuznetsk areas is supported by westward migration of *Anathyrella*, the typical Altai-Sayan brachiopod (see also Rzhonsnitskaya & Modzalevskaya 1996). The F-F boundary is marked by the regional extinction of atrypids. Expansion of previously unknown productellids from the *Mesoplica meisteri–M. praelonga* group, cyrtospiriferids (*Cyrtospirifer tschernyschewi–C. asiaticus* group) and athyridids [*Athyris globularis* (Phillips, 1841), *Athyris angelica* Hall, 1867] was a significant brachiopod event in the early Famennian recovery interval. This fauna exhibits similarities with coeval assemblages from Kazakhstan (*Meisteri* Beds), but is less diverse. However, there is a notable component participation of Uralian forms, such as *C. tschernyschewi* Khalfin, 1933.

Concluding remarks

Taxonomic analysis of the late Frasnian atrypids from the Urals, Timan and the Kuznetsk Basin reveals their significant generic and specific diversity in the broadly defined crisis interval. This is well established within the subfamilies Atrypinae, Variatrypinae, Spinatrypinae and Pseudogruenewaldtiinae. The latter subfamily encompasses two genera, *Pseudogruenewaldtia* and *Iowatrypa*. In contrast to the cosmopolitan genus *Iowatrypa* (e.g., Copper 1973; Godefroid 1994), the undoubted *Pseudogruenewaldtia* is restricted in occurrence to South Timan (possibly also in Central Europe; see Copper 1973), and possibly represents a localized latest Frasnian descendant of *Iowatrypa* (cf. Yudina 1996).

Representatives of the subfamily Atrypinae appear to be quite numerous, with abundant *Costatrypa*(?) in carbonate habitats known being from SW Siberian to East European domains, whilst *Atryparia*(?) colonized the semi-isolated Timan sea. Variatrypinids, represented by *Desquamatia* and *Radiatrypa*, were more common, mainly due to mass occurrences of *D. (D.) alticoliformis* in the Uralian and Kuznetsk sections. Spinatrypinids are similarly abundantly represented in the late Frasnian faunas under

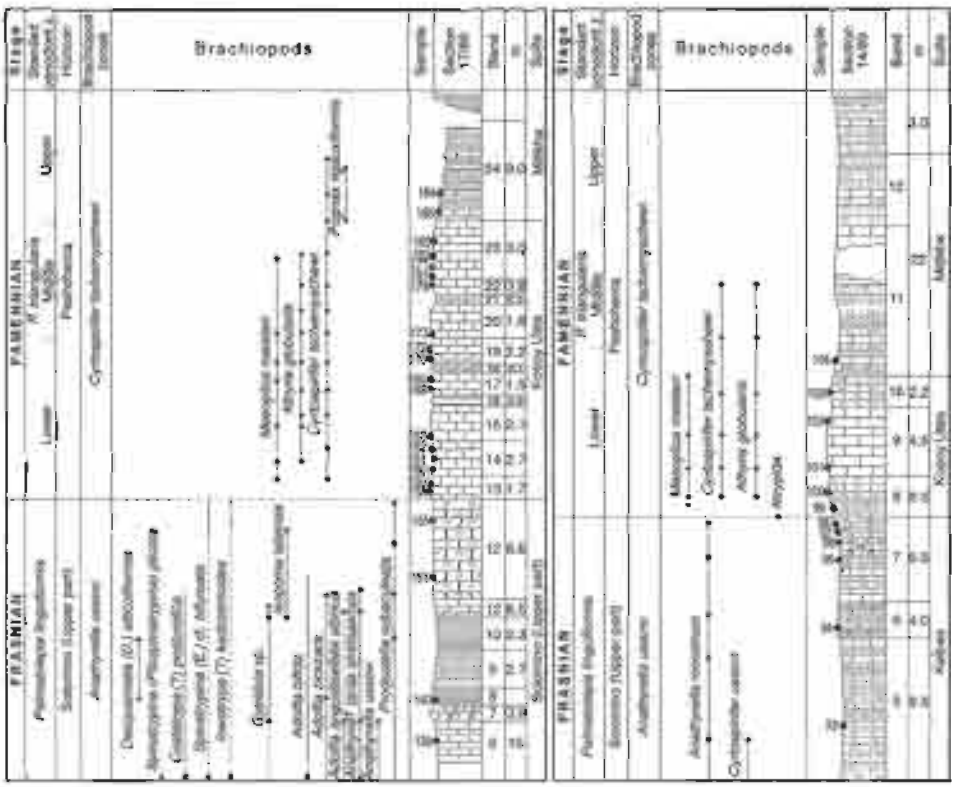


Fig. 28. Distribution of brachiopods and conodonts in the late Frasnian to early Famennian offshore carbonate sequence in the Tom river section (Kosoy Utes Rock; A), and nearshore terrigenous-carbonate sequence in the Yaya river section (left shore in W part of the Yaya-Petropavlovsky meander; B), north-western periphery of Kuznetsk Basin. Note a single atrypid occurrence in the topmost Kelbes suite. Key to lithological symbols in Fig. 26.

study, especially some species of *Spinatrypina*. However, this generic set still needs further taxonomic refinement, as exemplified by the Timan spinatrypinids. Among the others, *Spinatrypa trulla*–*'Spinatrypa' planosulcata* group, comprising North American species described by Fenton & Fenton (1924), Stainbrook (1945) and Cooper & Dutro (1982), may be allied with the new subgenus *Spinatrypa* (*Plicspinatrypa*). Several other species, e.g., *Spinatrypina*(?) *aschensis*, *Spinatrypina* (*Exatrypa*?) *bifurcata*, *Waiotrypa*(?) sp. A, *Iowatrypa*(?) *nebulosa*, and *I.*(?) *kadzielnioides* are still of questionable taxonomic position. Severe ambiguity concerns also Late Devonian carinatininids firstly reported in this paper.

In general, the decline phase of atrypid development was strongly influenced by a variety of environmental factors related to the global late Frasnian Kellwasser (KW) Crisis (see summary in Walliser 1996), associated primarily with major sea-level changes, in particular abrupt eustatic fall near the F-F boundary, and volcano-tectonic activity in the Eurasian regions (Veimarn *et al.* 1996). Notably, however, anoxic KW-type facies is absent in the sequences under study. The end-Frasnian atrypid demise was clearly independent of varying environmental and biogeographic settings

in the east Laurussian and Siberian domains. This stepdown brachiopod extinction is evidenced in the Russian successions not only among atrypids and gypidulids, but also in spiriferids and plicathyridines (e.g., Lyashenko 1959; Rzhonsnitskaya 1988; Rzhonsnitskaya & Modzalevskaya 1996).

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