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FRASNIAN (UPPER DEVONIAN) BRACHIOPODS FROM ARMENIA: BIOSTRATIGRAPHIC AND PALAEOBIOGEOGRAPHIC IMPLICATIONS

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Abstract. An assemblage of seven brachiopod species belonging to the orders Rhynchonellida, Atrypida and Spiriferida are studied from three localities (Ertych, Djravank and Noravank) of Central Armenia. The examined material is recovered from shallow water nodular limestones and provides insights into the diversity of Frasnian brachiopods on that part of the northern margin of Gondwana preserved within the South Armenian Block. The revision of *Atrypa* (*Planatrypa*) *ertichensis*, a biostratigraphically significant species for the Frasnian of the Lesser Caucasus (Armenia and Nakhichevan), revealed the presence of frills, an ornamental feature rarely observed in *Atrypa* (*Planatrypa*) representatives and considered as unknown in this species. Taxonomic discussion also involves the selection of neotypes for *Ripidiorhynchus gnishikensis* and *A.* (*P.*) *ertichensis*. The newly described taxon, *Angustisulcispirifer arakelyani* n. gen., n. sp., appears to be one of the most biostratigraphically important species for the Frasnian of Armenia. The size variability of *Cyphoterorhynchus koraghensis* and *Desquamatia* (*Seratrypa*) *abramianae* is documented quantitatively for the first time and it shows a continuous and progressive growth without any distinct groupings; the former is a palaeobiogeographically important species for the Frasnian strata of the northern Gondwana margin. Pending the revision of the Pakistani and Iranian material ascribed to *C. koraghensis*, that may include several subspecies, a plaster cast of its lectotype from the Frasnian of Kuragh in Chitral (northwest Pakistan) and the holotype as well as one of the paratypes of *Cyphoterorhynchus koraghensis interpositus* from the Frasnian Bahram Formation of the Ozbak-Kuh region in eastern Iran are illustrated herein. Finally, a new Frasnian brachiopod zone, namely the *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* assemblage Zone is here introduced for the studied sections. Although its base and top cannot be identified, it is constrained to the Frasnian based on conodonts identified in the Djravank section. It may be considered as a partly lateral equivalent of the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone established in Nakhichevan.

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Introduction

During the Devonian, brachiopods were the most abundant and diverse group of filter-feeding organisms, thriving in shallow-water tropical and subtropical marine environments (Ma & Day 1999; Curry & Brunton 2007; Alroy 2010). However, they were severely affected in the course of the Late Devonian due to different events associated with major sea-level changes and marine anoxia, especially during the Frasnian–Famennian (F–F) biotic crisis (McGhee 1996; Racki 1998; Racki & House 2002; Huang et al. 2018). Regional taxonomic and biostratigraphic studies of these calcite shelled marine invertebrates are important to better understand the regional impact of Late Devonian crisis events to their diversity, evolution and palaeobiogeographic distribution.

The Upper Devonian sequences of the Lesser Caucasus (Armenia and Nakhichevan; Fig. 1) are represented by shallow water, mixed carbonate-siliciclastic deposits. They constitute the South Armenian Block, which was then part of the northern margin of Gondwana (Sosson et al. 2010). More particularly, during the Late Devonian, this realm was part of a considerable carbonate platform that was positioned within the tropical zone of the southern hemisphere (Brock & Yazdi 2000; Scotese 2014; Golonka 2020). The Upper Devonian sequences in Armenia are highly fossiliferous and contain a diverse and well-preserved brachiopod fauna. Thus, their fossil record may provide valuable insights to the brachiopod diversity of the northern margin of Gondwana.

The Devonian outcrops in the area were first studied by the famous German geologist Hermann Abich in 1858, who also described several new brachiopod species from them, notably the cyrtospiriferid *Spirifer orbelianus* Abich, 1858, which was recently revised and reassigned to the newly erected genus *Aramazdospirifer* Serobyan et al. (2022a). Few other papers dealt with Devonian brachiopods in the first part of the 20th century (e.g., Frech & Arthaber 1900; Bonnet 1947). Following World War II, Upper Devonian–Carboniferous brachiopods and their biostratigraphy were studied systematically by Abrahamyan during the years 1949 to 1974. In her groundbreaking monography, Abrahamyan (1957) described and illustrated 36 brachiopod species from the Famennian–Tournaisian interval. Later, Abrahamyan (1959) wrote an article mainly devoted to the Frasnian species, where she described some rhynchonellides and atrypides, which were partly revised by her afterwards (Abrahamyan 1974), in addition to newly studied Frasnian species. However, as shown by some recent papers dealing with the Devonian brachiopods of the Lesser Caucasus (Alekseeva et al. 2018a, b; Serobyan et al. 2019, 2021, 2022a, b), in contrast to the Famennian brachiopods, the Frasnian ones have received relatively little attention and remain largely undocumented from a taxonomic point of view, not to mention their palaeoecological, palaeobiogeographic, or evolutionary understandings.

Consequently, the main objective of this paper is to revise and update the systematic classification of the Frasnian brachiopods from Armenia. This revision is mainly based on newly collected material from three distinct localities in Central Armenia (Ertych, Djravank and Noravank; Fig. 1), and is supplemented by brachiopod specimens stored in the collections assembled by Abrahamyan and Arakelyan, between 1940 and 1980. Furthermore, the biostratigraphy of the Frasnian–lower Famennian brachiopods from the Lesser Caucasus is also discussed. Since it was not possible to recognise the previously established biozones in the studied sections, we introduce a new local brachiopod assemblage zone for the Frasnian sequences of Armenia, which is constrained by conodonts to the Frasnian and correlated with likely lateral equivalents in Nakhichevan. We finally discuss the palaeobiogeographic affinities of the studied Frasnian brachiopods.

Stratigraphic setting

An over 1500 m-thick pile of Middle Devonian–lower Carboniferous deposits is present in the Lesser Caucasus (Fig. 1). The Middle Devonian part has a restricted distribution in Armenia and crops out only along the border with Nakhichevan, whereas the Upper Devonian part has a relatively wider distribution, but correlating the different sections still remains complicated due to biostratigraphic uncertainties. The Upper Devonian sequences consist essentially of marly and sandy biogenic limestones, rich in brachiopods, with intercalations of arenitic and fine-grained

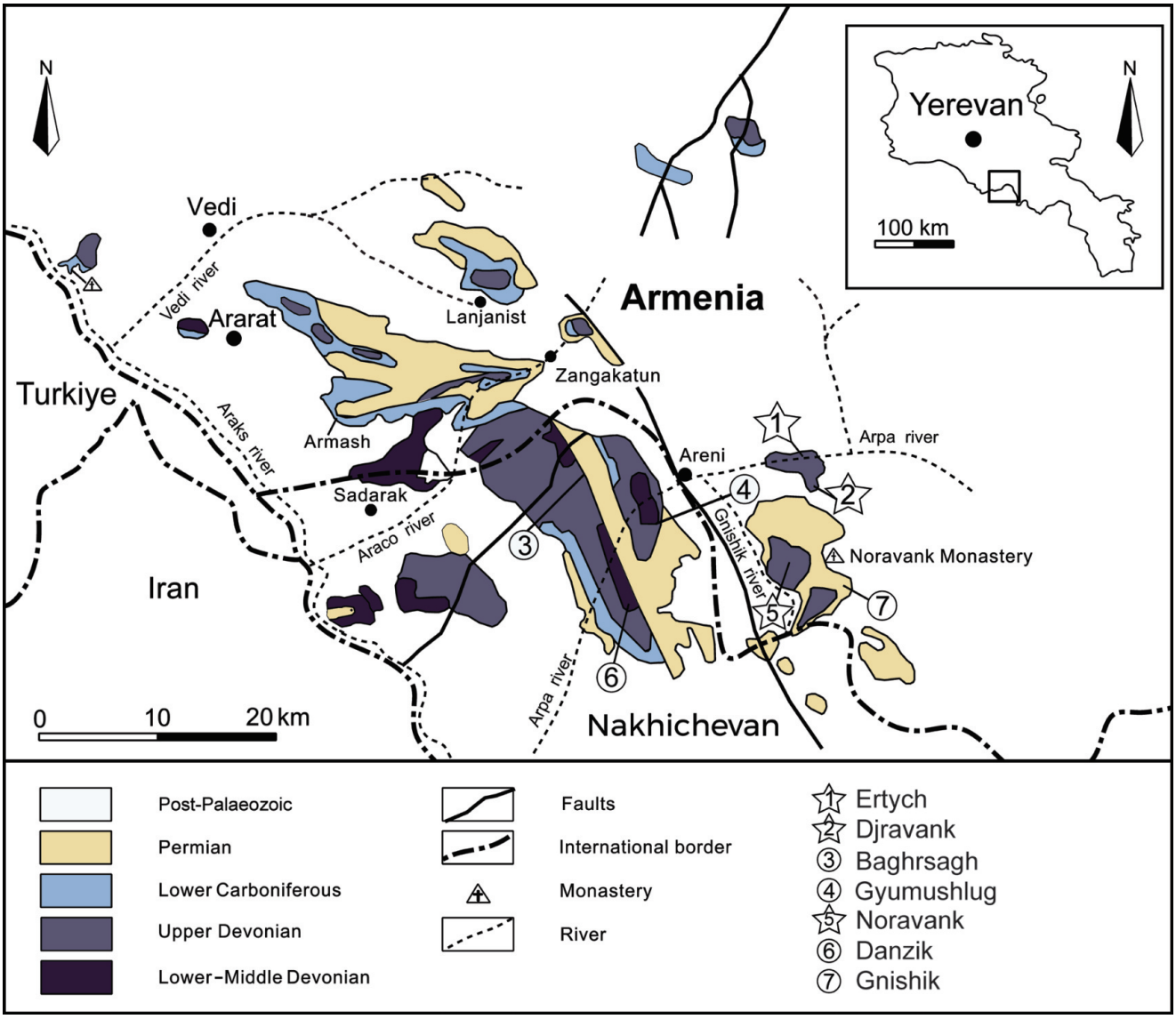

Fig. 1 - Schematic geological map and distribution of the Upper Palaeozoic sequences in the Lesser Caucasus (Central Armenia and Nakhichevan), including the location of the three studied sections (modified from Serobyan et al. 2019).

sandstones and shales. Only a few sections exposing the Frasnian–lower Famennian shallow-water facies are known in Armenia and further research is necessary. The sections covering this particular stratigraphic interval, which were studied in the last decades, provide valuable information on different fossil groups, such as corals (Sytova et al. 1974), chondrichthyan microremains (Ginter et al. 2011), conodonts (Grigoryan et al. 2019), and trilobites (Crônier et al. 2021), but limited information is available on lithostratigraphy. The F–F sequences are exposed mainly below the monastery of Noravank and around the locality Ertych (Fig. 1). The latter consist chiefly of two distinct nodular limestone intervals, one of which crops out at the base, whereas the second one at the top of the sections. The lower limestone interval is overlain by an interval of black shales, which, in turn, is overlain by well-sorted sandstones (Fig. 2). The brachiopods of the upper limestone interval were recently revised and documented by Serobyan et al. (2021, 2022a, b) and Serobyan and Mottequin (2022). The brachiopod assemblage of the lower limestone interval is the subject of this paper.

Material and methods

The examined material was collected during several field seasons organised during 2018–2022 from three sections (Fig. 2) cropping out in the Vayots Dzor Province of Southwest Central Ar-

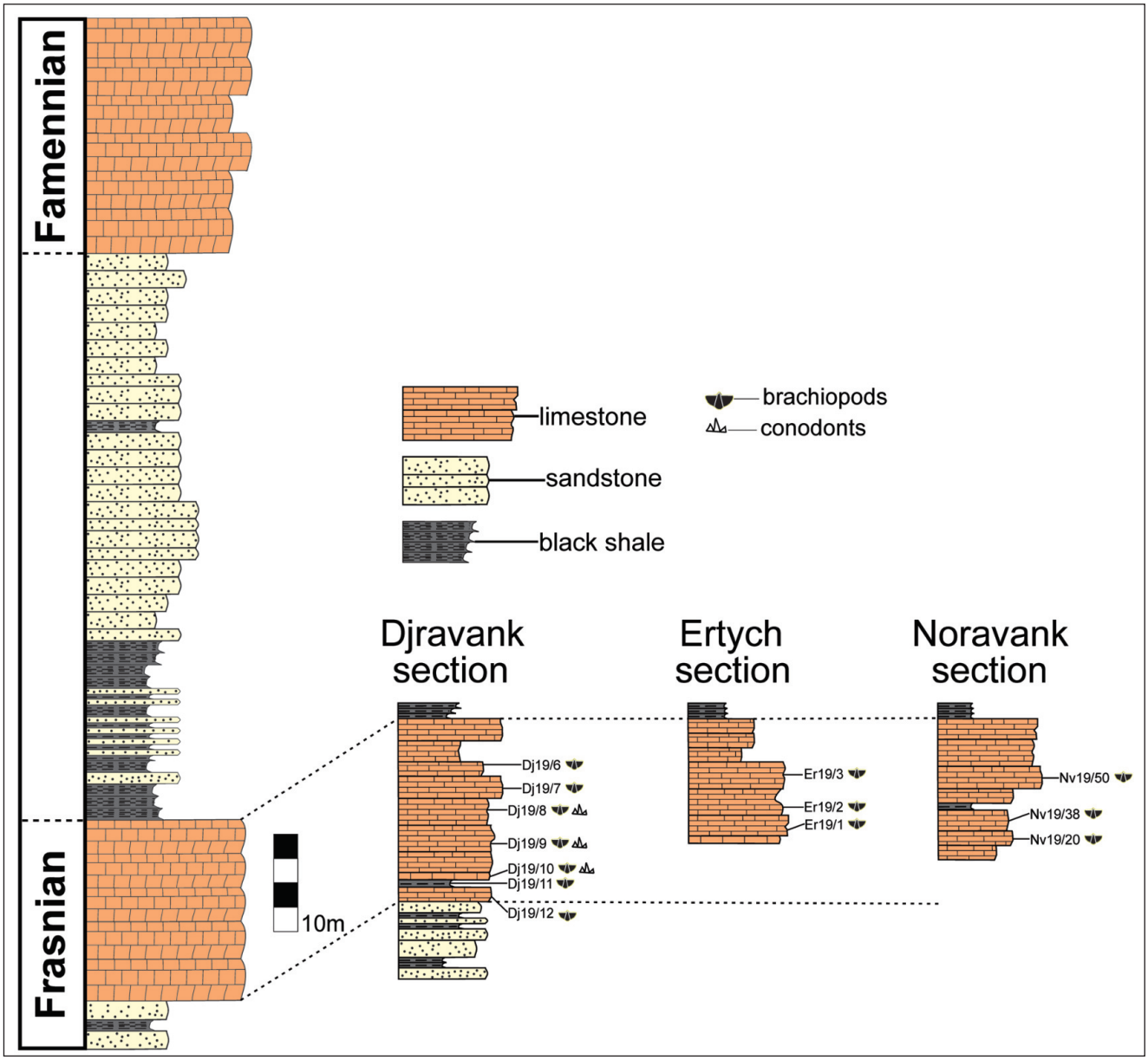

Fig. 2 - Schematic lithostratigraphy of the Frasnian–lower Famennian succession in Armenia and detailed lithostratigraphy, as well as sampled beds of the lower limestone interval in the three studied sections (Djravank, Ertych and Noravank).

menia. Two of them, Ertych and Noravank sections, were already studied by Arakelyan (1964) and Ginter et al. (2011), respectively, while the Djravank section was only briefly presented in Grigoryan et al. (2019). The latter is situated ca. 9 km east of the little town of Areni (39°43.670' N, 45°16.145' E). The studied section crops out along a mountainous path leading to a small abandoned church. Here the lower limestone interval is observed with its entire thickness of 22 m, intercalated between sandstones and shales at the base and shales at the top. The Ertych section is situated on the southern bank of the Arpa River (ca., 8.5 km east of Areni), in an abandoned quarry (39°43.850' N, 45°16.300' E). Here, only the upper 10 m of limestones are observed, overlain stratigraphically by a thick sequence of blackish shales. Finally, in the Noravank section, situated just below the famous monastery (39°41.110' N 45°13.730' E) only the upper 12 m of the limestone interval could be observed, overlain in their turn by shales. Most of the specimens illustrated and investigated herein are deposited at the Geological Museum of the Institute of Geological Sciences of the National Academy of Sciences of Armenia, Yerevan (prefixed IGSNASRAGM/PS). The prefix PS indicates the laboratory of Pale-

	Ertych section			Djravank section							Noravank section		
	Er 19/3	Er 19/2	Er 19/1	Dj 19/6	Dj 19/7	Dj 19/8	Dj 19/9	Dj 19/10	Dj 19/11	Dj 19/12	Nv 19/50	Nv 19/38	Nv 19/20
Ripidiorhynchus gnishikensis	X	X	X			X	X	X	X	X	X	X	
Cyphoterorhynchus koraghensis	X	X	X	X	X	X					X	X	
Atrypa (Planatrypa) ertichensis			X										
Spinatrypa sp.			X										
Desquamatia (Seratrypa) abramianae	X	X	X			X			X	X		X	X
Angustisulcispirifer arakelyani	X	X	X			X	X	X	X		X	X	
Cyrtospiriferinae gen. indet.		X						X					

Tab. 1 - Occurrence table of brachiopods identified in the three studied sections.

ontology and Stratigraphy. A few specimens are housed at the public palaeontological collection of the Lille University, France. Additional illustrated specimens are curated at the Royal Belgian Institute of Natural Sciences in Brussels (prefixed RBINS), notably one plaster cast of a sample curated at the Geological Survey of India (Kolkata) (prefixed GSI). The internal morphology of the specimens was investigated by using the standard technique of serial sections and acetate peels. In order to capture the fine details related to the development of internal features, the serially sectioned specimens were photographed directly under a Canon EOS 700D camera that was attached to a Zeiss SteREO Discovery V20 Microscope. Specimens deposited at the IGSNASRAGM were coated with magnesium oxide before being photographed by a Canon EOS 700D camera, equipped with the Canon EFS 60 mm macro lens. RBINS material was photographed using an Olympus OM-D E-M10 Mark II digital camera, equipped with the Olympus M.Zuiko Digital ED 60 mm macro lens, and coated with ammonium chloride.

Conodonts were obtained from three samples of the lower limestone interval of the Djravank section (Fig. 2) after processing with formic acid at the Institute of Geological Sciences (Yerevan). Several tens of conodont elements were recovered and picked up in Yerevan. Some of them were mounted on SEM stubs and gold coated for ca. 2 minutes. They were photographed by a ZEISS EVO 10 Scanning Electron Microscope hosted with the Palaeontology team of Lille University (UMR 8198 Evo-Eco-Paleo).

Systematic palaeontology

The beds from which brachiopods were collected are indicated in Figure 2. Table 1 provides the occurrence of the identified brachiopod species in the three studied sections. The supraspecific classification used herein follows Savage (2002, 2007) for the Order Rhynchonellida instead of the one adopted by Sartenaer (2001, 2003), wherein the Subfamily Ripidiorhynchinae Savage, 1996 is elevated to the family level with *Ripidiorhynchus* Sartenaer, 1966a as its only representative. Likewise, the supraspecific classification follows Copper (2002) for the order Atrypida, except otherwise stated, and Carter et al. (1994) and Johnson (2006) for the Order Spiriferida.

Order **Rhynchonellida** Kuhn, 1949
Superfamily Rhynchotrematoidea Schuchert, 1913
Family Trigonirhynchiidae Schmidt, 1965
Subfamily Ripidiorhynchinae Savage, 1996
Genus *Ripidiorhynchus* Sartenaer, 1966a

Type species: *Terebratula livonica* von Buch, 1834, from the Sargaevo Regional Stage, lower Frasnian, Central Latvia and northwestern Russia.

Ripidiorhynchus gnishikensis (Abrahamyan, 1959)

Fig. 3–4; Tab. 2

1959 *Camarotoechia strugi* Nal. subsp. *gnishikensis* Abrahamyan, p. 6, pl. 2, fig. 5–7.
1964 *Camarotoechia strugi* Nal. subsp. *gnishikensis* Abrahamyan, 1959 - Arakelyan, pp. 67, 70, 74, 92, 93.
1975 *Ripidiorhynchus* (*Camarotoechia*) *strugi* var. *gnishikensis* (Abr.) - Arakelyan et al., p. 22.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	9	9	9	9	9	9	9
Mean value	16.52	14.13	12.26	8.59	0.86	0.74	0.52
Standard deviation	0.98	1.2932	1.1349	0.5326	0.0549	0.0299	0.0335
Standard error±	±0.3274	±0.431	±0.3783	±0.1775	±0.0183	±0.0099	±0.0112
Min	15.1	13	11	7.9	0.78	0.7	0.49
Max	17.9	16.2	13.7	9.3	0.93	0.77	0.58

Tab. 2 - Measurements in mm and ratios of *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

2018a *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) - Pakhnevich in Alekseeva et al., pp. 852, 905, pl. 6, fig. 6a–d; pl. 14, fig. 6 and 18; text-fig. 50.

2019 *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) - Serobyan et al., p. 7.

Neotype: Although Abrahamyan (1959: pl. 2, fig. 5–7) designated a holotype among the three specimens she illustrated, neither the holotype nor other specimens examined in her publication were traced within Abrahamyan's brachiopod collections stored at the IGSNASRAGM and are therefore considered as lost. Consequently, the single specimen figured in Figure 3 is hereby designated as the neotype (IGSNASRAGM 3927/PS 3033).

Type horizon: Bed Dj19/10 (Fig. 2), Frasnian nodular limestones.

Type locality: Djravank section (ca. 9 km east of Areni, Vayots Dzor Province, Southwest Central Armenia) (Fig. 1, 2).

Material: Nine articulated specimens and four ventral valves from the Ertych (Er19/1 - IGSNASRAGM 3926/PS 3032, IGSNASRAGM 3926/PS 3032.1; Er19/2 - IGSNASRAGM 3926/PS 3032.2; Er19/3 - IGSNASRAGM 3926/PS 3032.3), Djravank (Dj19/8 - IGSNASRAGM 3926/PS 3032.4; Dj19/9 - IGSNASRAGM 3926/PS 3032.5; Dj19/10 - IGSNASRAGM 3927/PS 3033 (neotype), IGSNASRAGM 3926/PS 3032.6; Dj19/11 - IGSNASRAGM 3926/PS 3032.7; Dj19/12 - IGSNASRAGM 3926/PS 3032.8, IGSNASRAGM 3926/PS 3032.9) and Noravank (Nv19/20 - IGSNASRAGM 3926/PS 3032.10; Nv19/50 - IGSNASRAGM 3926/PS 3032.11) sections.

Description. Shell small-sized (up to 17.9 mm in width, 16.2 mm in length, 13.7 mm in thickness) (Tab. 2), slightly wider than long, rounded subtriangular in outline, sharply dorsibiconvex; widest at about 2/3 of the shell length, highest near umbones; anterior margin slightly rounded to emarginate; anterior commissure uniplicate, serrate.

Ventral valve gently inflated in both lateral and posterior profiles with flanks sloping gently towards lateral commissures; highest near umbo then, decreasing progressively towards anterior margin; umbo prominent, inflated; beak long, straight; foramen unobserved; sulcus wide, shallow to moderately deep, imperceptibly originating in the umbonal area, flat- to slightly round bottomed at front; tongue high and wide, with sharp borders, subtrapezoidal in outline, perpendicular to commissural plane or slightly bent dorsally.

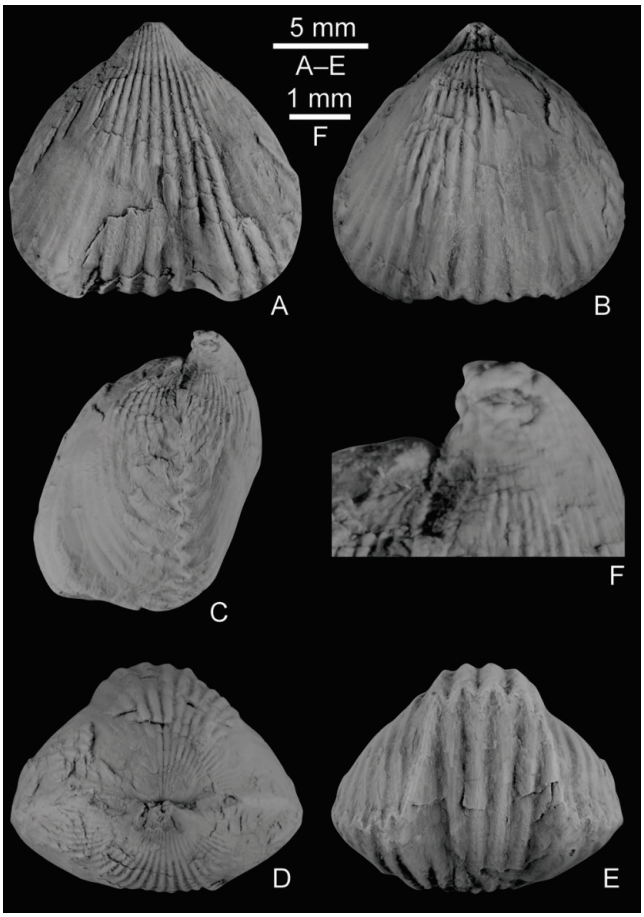

Fig. 3 - *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). A–F) IGSNASRAGM 3927/PS 3033 (neotype, Djravank), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (A–E), and close-up of the long and straight beak (F).

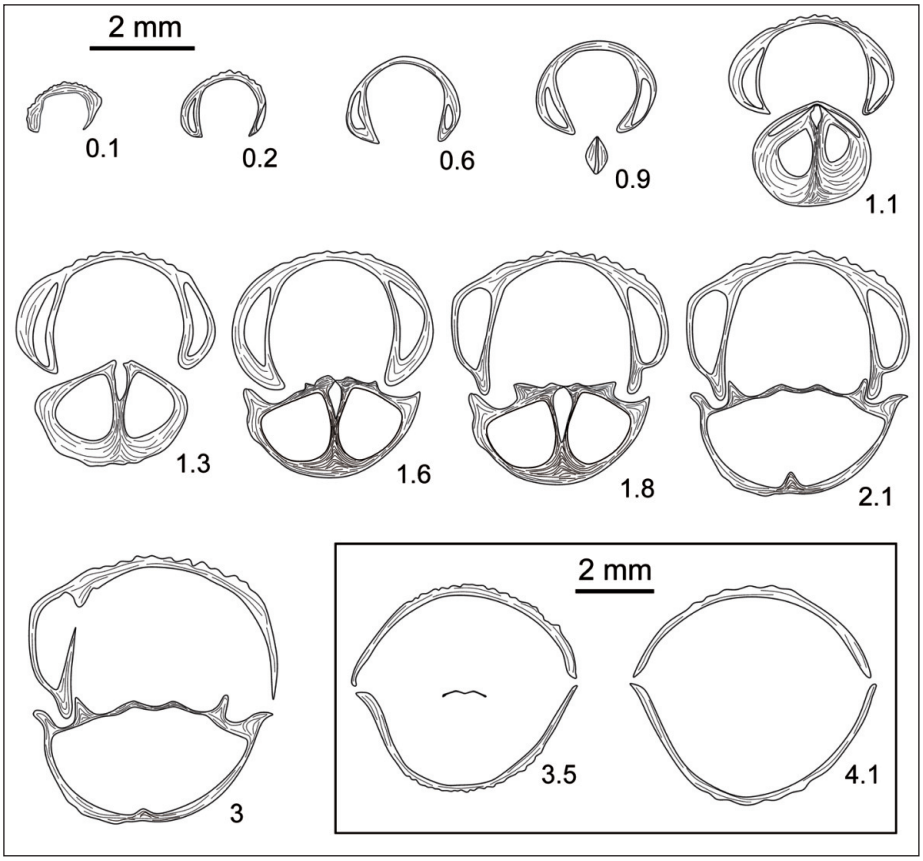

Fig. 4 - Transverse serial sections of *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) (IGSNASRAGM 3926/PS 3032) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Djravank, Central Armenia). Numbers refer to distances in mm from the tip of the ventral umbo.

Dorsal valve inflated, regularly curved in posterior and lateral profile views with convex flanks sloping moderately to strongly towards lateral commissures; highest in the anterior third of the valve margin, progressively decreasing towards posterior margin; fold low to moderately high, starting more posteriorly to midlength, more developed anteriorly, flat-topped at front.

Ornamentation of low, angular costae, originating at beaks and thickened anteriorly; costae in sulcus and on fold larger than those present on flanks; 10–13 costae on flanks, 4–5 costae in sulcus, 5–6 costae on fold, one pair of faint costae developed on the flanks of the fold and on the margins of the sulcus; costae wider than interspaces.

Ventral valve interior (Fig. 4) with thin, long dental plates converging ventrally; teeth massive, subrectangular in outline; central apical cavity wide.

Dorsal valve interior (Fig. 4) with low and very short septum; septalium deep, Y-shaped and covered anteriorly; hinge plate united.

Remarks. *Ripidiorhynchus gnishikensis* was described initially by Abrahamyan (1959) as a subspecies of *Camarotoechia strugi* Nalivkin, 1941, based on some external characters observed on her Armenian brachiopod material, such as the finer costae and a lower trapezoidal tongue. Note that Nalivkin's (1941) species was considered by Sokiran (2002) as a synonym of *R. livonicus* (von Buch, 1834). Based on the detailed study of material from Nakhichevan, Pakhnevich (in Alekseeva et al. 2018a) raised the subspecies *gnishikensis* to the species level and transferred it to the genus *Ripidiorhynchus*; this assignment was based on the general shape and outline of the shell, the well-developed sulcus and fold beginning at some distance from the beaks, the ventrally convergent dental plates as well as the presence of a low septum and a covered septalium. The material described in Armenia appears to be conspecific with the specimens recovered in the sections of Nakhichevan.

Occurrence. *Ripidiorhynchus gnishikensis* was first described in Armenia by Abrahamyan (1959), in the Frasnian sequences of the Gnishik section (Fig. 1). Later it was reported by Arakelyan (1964) in the Frasnian sequences of the Baghrsagh and Danzik sections (Fig. 1) as well as in the lower Famennian of the Noravank, Ertych and Gyumushlug sections (Fig. 1) within a brachiopod assemblage including Frasnian spiriferides. Presumably Arakelyan (1964) confused *R. gnishikensis* with a lower Famennian representative of that genus as Abrahamyan's

species occurred only in the Frasnian. Unfortunately, the specimens identified as *R. gnishikensis* by Arakelyan cannot be traced within his collections and are considered as lost, which excludes any possibility of re-examination. However, Arakelyan et al. (1975) mentioned *R. gnishikensis* amongst the biostratigraphically significant species characterising the Frasnian in Armenia. Afterwards, Pakhnevich in Alekseeva et al. (2018a) examined numerous specimens from several localities in Nakhichevan and specified that it actually occurs within the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov (2000) (coeval with the *falsiovalis–punctata* conodont zones), confirming the viewpoint of Arakelyan et al. (1975) that *R. gnishikensis* is restricted to the Frasnian strata. Additionally, it is judicious to remind here that recent sampling also revealed the presence of this species only in the Frasnian strata.

Genus *Cyphoterorhynchus* Sartenaer, 1964

Type species: *Uncinulus* (*Uncinulina*) *koraghensis* Reed, 1922, from the middle and upper Frasnian of northwestern Pakistan.

Remarks. Sartenaer's paper was issued as a separate in 1964, whereas the Scientific reports of the Italian expeditions to the Karakorum (K2) and Hindu Kush was released in 1965. Following the article 21.8 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature (ICZN), 1999), the former is the only valid date.

Cyphoterorhynchus koraghensis (Reed, 1922)

Fig. 5–7, 8A–E; Tab. 3

1922 *Uncinulus* (*Uncinulina*) *koraghensis* Reed, p. 40, 120, 123–125, pl. 7, fig. 10–13 (see also for synonymy before 1922).
?1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *pentagonalis* Reed, p. 42, 120, 123, 125, pl. 7, fig. 14–17.
?1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *transiens* Reed, p. 43, 120, 123, 125, pl. 7, fig. 18–20.
?1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *ponderosa* Reed, p. 44, 120, 123, 125, pl. 7, fig. 21–22a; pl. 8, fig. 1, 1a.
1952 *Uncinulus* (*Uncinulus*) *koraghensis* Reed - Arakelyan, p. 36.
1964 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Sartenaer, p. 51, pls. 4–5.
1966b *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Sartenaer, p. 28–29, 34–37 (see also for synonymy of Iranian material).
1971 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Brice, p. 47, 309–315, 318, 323, 336, pl. 3, fig. 1a–d, 6a–d; text-fig. 13A; tab. 5.
1975 *Cam.* [*Camarotoechia*] *karaghensis* [*sic*] *koraghensis* Reed - Arakelyan et al., p. 24.
2000 *Cyphoterorhynchus koraghensis* Reed, 1922 - Rzhonsnitskaya & Mamedov, p. 330.
2002 *Cyphoterorhynchus koraghensis* (Reed, 1922) - Savage, p. 1076, fig. 728, 1 a–n (copy of Sartenaer, 1964, pl. 4, fig. 4 a–b, d–e).
2010 *Cyphoterorhynchus koraghensis* Reed - Mirieva, p. 74, 75, tab. 1.

Lectotype: As Reed (1922) did not designate any holotype amongst the specimens he illustrated, Sartenaer (1964) designated the specimen (GSI 12115) figured by Reed (1922: pl. 7, fig. 10–10a) as the lectotype of this species (see also Sartenaer, 1966b). The plaster cast of the lectotype, sent by B.C. Roy to P. Sartenaer in 1965, is illustrated herein (Fig. 8A–E).

Type locality. Upper Devonian, Kuragh Ridge in Chitral, NE of Reshun (northwestern Pakistan) (see Hayden 1916; Reed 1922; Sartenaer 1964).

Material examined: Twenty-five articulated specimens and four ventral valves from the Ertych (Er19/1 - IGSNASRAGM 3933/PS 3039, IGSNASRAGM 3935/PS 3041.1, IGSNASRAGM 3935/PS 3041.2, IGSNASRAGM 3935/PS 3041.3, IGSNASRAGM 3935/PS 3041.4, IGSNASRAGM 3935/PS 3041.5, IGSNASRAGM 3935/PS 3041.6, IGSNASRAGM 3935/PS 3041.7, IGSNASRAGM 3935/PS 3041.8, IGSNASRAGM 3935/PS 3041.9; Er19/2 - IGSNASRAGM 3935/PS 3041.10, IGSNASRAGM 3935/PS 3041.11, IGSNASRAGM 3935/PS 3041.12, IGSNASRAGM 3935/PS 3041.13, IGSNASRAGM 3935/PS 3041.14, IGSNASRAGM 3935/PS 3041.15, IGSNASRAGM 3935/PS 3041.16, IGSNASRAGM 3935/PS 3041.17; Er19/3 - IGSNASRAGM 3935/PS 3041.18, IGSNASRAGM 3935/PS 3041.19), Djravank (Dj19/6 - IGSNASRAGM 3932/PS 3038, IGSNASRAGM 3934/PS 3040; Dj19/7 - IGSNASRAGM 3935/PS 3041; Dj19/8 - IGSNASRAGM 3935/PS 3041.20, IGSNASRAGM 3935/PS 3041.21) and Noravank (Nv19/38 - IGSNASRAGM 3935/PS 3041.22, IGSNASRAGM 3935/PS 3041.23, IGSNASRAGM 3935/PS 3041.24; Nv19/50 IGSNASRAGM 3935/PS 3041.25) sections.

Description. Shell medium-sized, attaining up to 27 mm in width, 24.3 mm in length and18.5 mm in thickness (Tab. 3), transversally ovate in outline, wider than long, widest and highest at about midlength, strongly dorsibiconvex, anterior margin emarginate; anterior commissure uniplicate and serrate.

Ventral valve slightly inflated with flanks sloping gently towards lateral commissures; beak suberect; foramen minute, permesothyrid; sulcus wide, shallow to moderately deep, generally well-defined by sulcus bounding costae, imperceptibly starting from midlength or more anteriorly, deepening gradually towards anterior margin, flat- to round-bottomed at

Fig. 5 - *Cyphoterorhynchus koraghensis* (Reed, 1922) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). A–E) IGSNASRAGM 3933/PS 3039 (Ertych), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. F–J) IGSNASRAGM 3934/PS 3040 (Djravank), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. K–O) IGSNASRAGM 3935/PS 3041 (Djravank), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views.

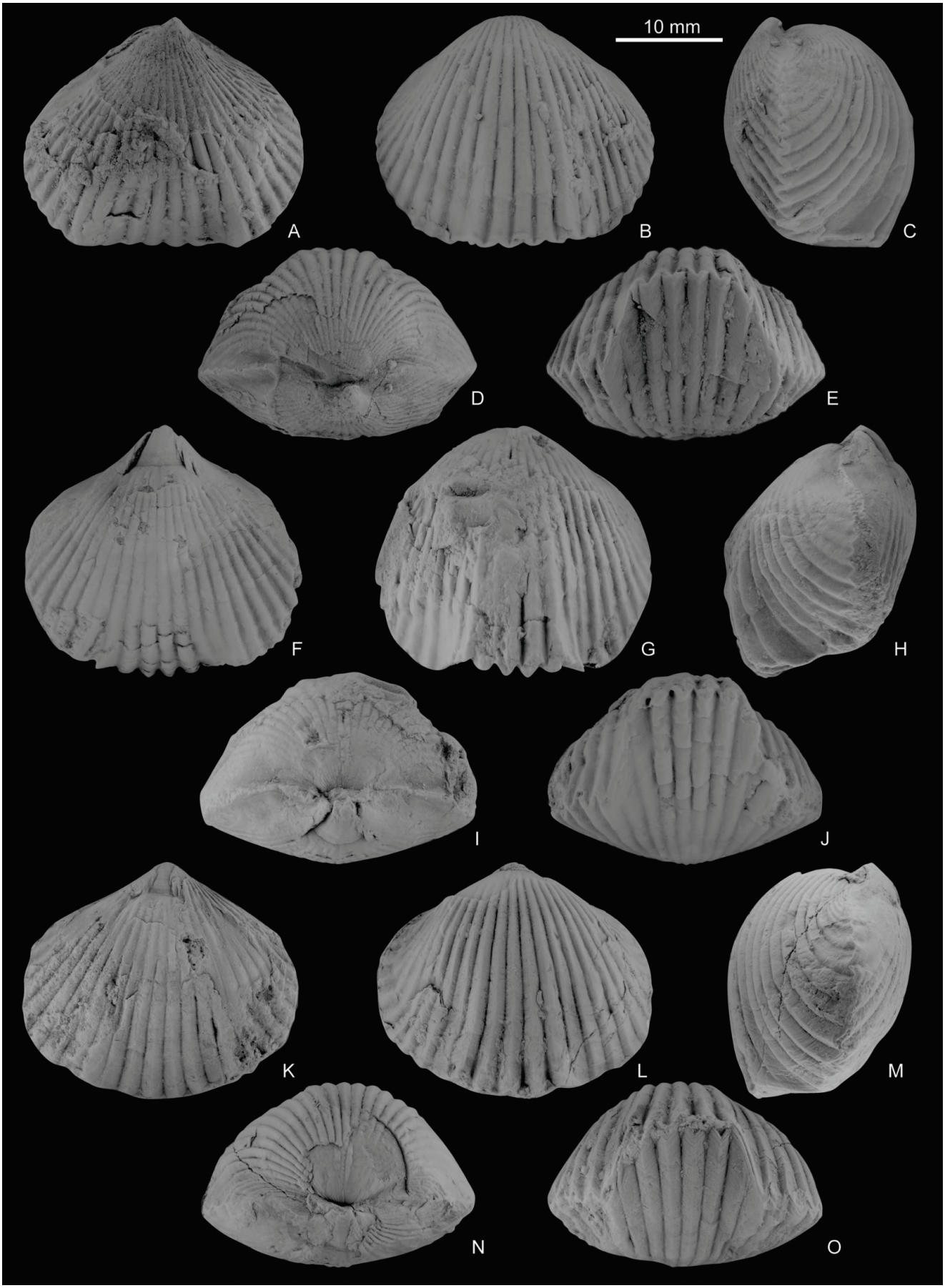

FIGURE 5

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	25	25	25	25	25	25	25
Mean value	25.93	21.8	17.88	12.94	0.84	0.69	0.5
Standard deviation	0.7482	1.3312	0.5711	1.0448	0.0361	0.0266	0.0321
Standard error±	±0.1496	±0.2662	±0.1142	±0.209	±0.0072	±0.052	±0.0064
Min	24	19.7	15.7	10.4	0.79	0.64	0.42
Max	27	24.3	18.5	13.9	0.92	0.72	0.53

Tab. 3 - Measurements in mm and ratios of *Cyphoterorhynchus koraghensis* (Reed, 1922). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

front; tongue high, perpendicular to commissural plane, subtrapezoidal in outline.

Dorsal valve strongly inflated, regularly and strongly curved in posterior and lateral profile views with flanks sloping strongly towards lateral commissures, highest at about midlength, then decreasing progressively towards anterior margin; umbo inflated, prominent, protruding beyond posterior margin; beak covering the delthyrium; fold low, more defined anteriorly, wide, inconspicuously originating from midlength or slightly posteriorly to it, flat-topped at front.

Ornamentation of coarse angular costae originating from beaks; costae in sulcus and on fold larger than those present on flanks; 10–13 costae on flanks becoming fainter towards posterolateral margins, 4–6 costae in sulcus, 5–7 costae on fold; one pair (occasionally two) of costae generally developed on the flanks of the fold and sulcus; costae wider than interspaces; growth lines numerous.

Ventral valve interior (Fig. 6) with short, stout and subparallel dental plates situated close to the walls; teeth massive, subrectangular in outline;

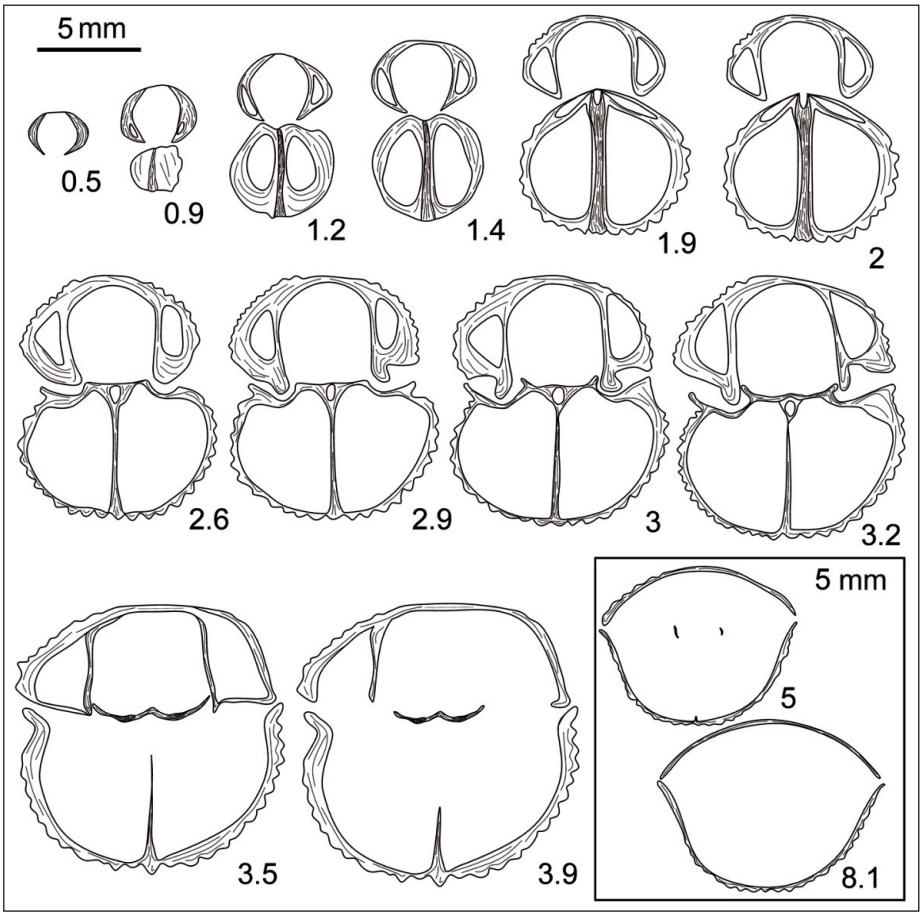

Fig. 6 - Transverse serial sections of *Cyphoterorhynchus koraghensis* (Reed, 1922) (IGSNASRAGM 3932/PS 3038) from the Frasnian *Ripidiorhynchus gnishikensis– Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Djravank, Central Armenia). Numbers refer to distances in mm from the tip of the ventral umbo.

central apical cavity wide; lateral apical cavities poorly infilled by callosity.

Dorsal valve interior (Fig. 6) with high and long septum; septalium V-shaped, not deep, relatively narrow and covered anteriorly; hinge plates united anteriorly to septalium; crural bases stout, diverging dorsally.

Shell ontogeny. The size distributions of *C. koraghensis* during growth, as represented by the width/length, the width/thickness and the width/width of sulcus plots, show a continuous and progressive growth with no distinct grouping (Fig. 7). The relative proportions of *C. koraghensis* represented by sufficient material remain constant (linear regression: y = ax+b; significant probability value: $p < 0.001$***) whatever the degree of development of individuals (Fig. 7). Moreover, the correlation is positive with width varying proportionally with length, thickness and width of sulcus. To complete the scatter plots, the measurements of numerous individuals of *C. koraghensis* are also presented in Tab. 3.

Remarks. According to the article 45.6.4 of the International Code of Zoological Nomenclature (ICZN 1999), the epithets, which were used for the varieties of *Uncinulus* (*Uncinulina*) *koraghensis* introduced by Reed (1922) (see synonymy list), must be considered as of subspecific rank in his publication. In erecting the genus *Cyphoterorhynchus*, Sartenaer (1964) estimated that these varieties (sic) could fall within the limits of the variability of the species and stressed that further specimens from a tighter sampling were needed to decide on this matter. Sartenaer (1966b), after having examined the plaster casts of Reed's (1922) illustrated specimens, definitely considered that the varieties (sic) enter in the limits of the variability of the species. Nevertheless, Sartenaer (1966b) complicated the situation in erecting *Cyphoterorhynchus koraghensis interpositus* from the Frasnian (Bahram Formation) of the Ozbak-Kuh region in eastern Iran, of which the holotype (Fig. 8F–K) and one of the paratypes (Fig. 8L–P) are illustrated here. Indeed, he considered that some of the specimens from the type locality of *C. koraghensis*, including some paralectotypes, may belong to his new subspecies and thus ignored the names introduced by Reed (1922). Moreover, he indicated that the two *C. koraghensis* subspecies and *C. arpaensis* (Abrahamyan, 1957) occur in the same beds within the Iranian sections, which is puzzling biologically speaking as the subspecies must be geographically or stratigraphically separated from each other. Pakhnevich in Alekseeva et al. (2018a) recently placed Sartenaer's (1966b) subspecies in synonymy with *C. arpaensis*. We do not comment further on the validity of the subspecies *interpositus*, leaving

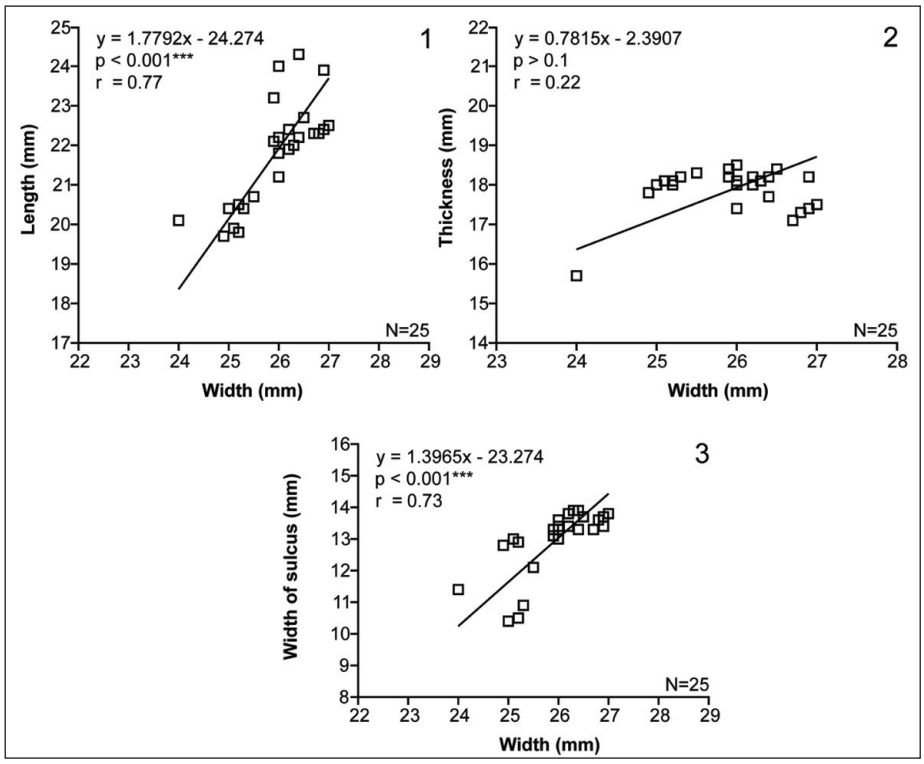

Fig. 7 - Scatter diagrams of *Cyphoterorhynchus koraghensis* (Reed, 1922). 1) Relation between shell width and length. 2) Relation between shell width and thickness. 3) Relation between shell width and width of sulcus. Abbreviations: *n*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

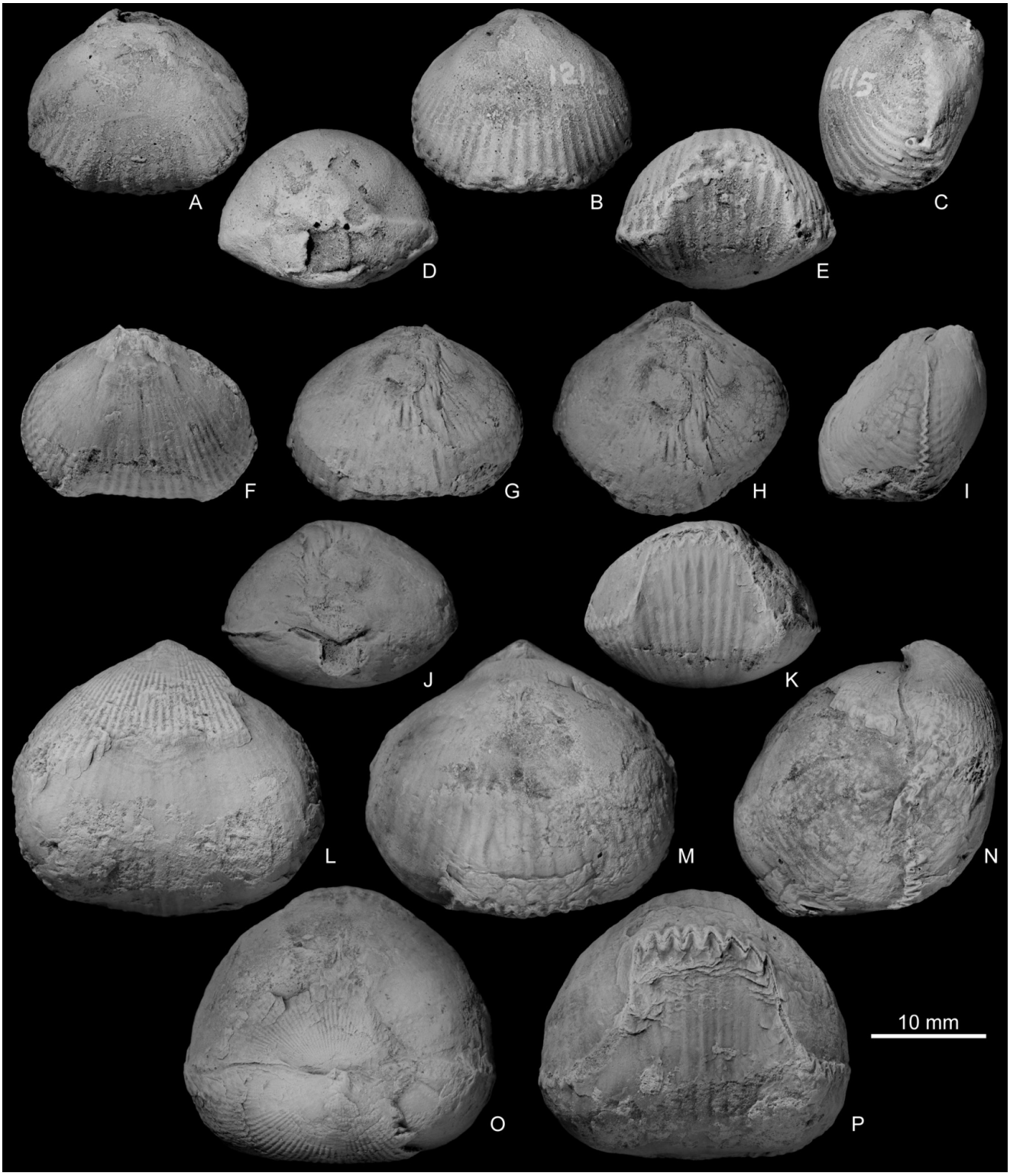

Fig. 8 - A–E) *Cyphoterorhynchus koraghensis* (Reed, 1922) from the Frasnian of Kuragh in Chitral (northwest Pakistan). Plaster cast (deposited at the RBINS) of the articulated specimen GSI 12115 (lectotype) in ventral, dorsal, lateral, posterior and anterior views. F–P) *Cyphoterorhynchus koraghensis interpositus* Sartenaer, 1966b from the Frasnian (Bahram Formation) of the eastern flank of Kuh-e-Gushkamar, section of Gor-e-Sorch-e-Niur–Kuh-e-Gushkamar (Iran, Ozbak-Kuh region). F–K) RBINS a11338 (holotype), articulated specimen in ventral, dorsal, inclined dorsal, lateral, posterior and anterior views; locality F-3 (see Sartenaer 1966). L–P) RBINS a11339 (paratype), articulated specimen in ventral, dorsal, lateral, posterior and anterior views; locality F-4 (see Sartenaer 1966b).

it temporarily aside from the nominal subspecies, as only the study of large collections of *Cyphoterorhynchus* specimens from the Kuragh Ridge and the revision of the Pakistani material investigated by Reed (1922), which is curated at the GSI, will shed new light on the taxonomical issues related to *C. kora-*

ghensis. This is the reason for which we have placed Reed's (1922) varieties (= subspecies) into doubtful synonymy, pending their revision, but these could simply be morphotypes or even ecotypes of the same species.

The material investigated herein fits well with Sartenaer's (1964) description of *C. koraghensis* although the teeth and dental sockets of the studied specimens lack the crenulations observed in the Chitral specimens. This species, which has already been recognised within the Frasnian of Central Armenia (Arakelyan 1952; Arakelyan et al. 1975) and Nakhichevan (Mirieva 2010; Rzhonsnitskaya & Mamedov 2000), is also known from the middle and upper Frasnian of northwestern Pakistan (Chitral; Reed 1922), Afghanistan (Brice 1971; Kuhn, 1977) and Iran (Sartenaer 1966b), thus from Gondwanan terranes. Furthermore, Gourvennec (2006) illustrated a single specimen from the Upper Devonian (probably from the lower Frasnian) of Eastern Taurus (Turkey) and identified it as *C. koraghensis*. Although he did not examine its internal structure, this assignment seems to be the most satisfactory as it does not differ externally from Reed's species. Moreover, his assignment can be further supported by the resemblance of Devonian brachiopod assemblage recovered by him from the Eastern Taurus (Turkey) with those described in Afghanistan, Iran, Pakistan and the Lesser Caucasus.

C. koraghensis displays strong similarities with *C. arpaensis* (Abrahamyan, 1957); however, the latter differs by its subcircular tongue and having fainter and fewer costae on flanks and in sulcus and on fold. *C. arpaensis* is one of the most biostratigraphically valuable species in the Lesser Caucasus and used for the definition of a Frasnian brachiopod zone, namely the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya & Mamedov (2000). However, our recent sampling did not reveal the presence of this species in the Frasnian of our studied sections. Although Abrahamyan (1957) did not designate a type specimen among the two she illustrated, Pakhnevich in Alekseeva et al. (2018a) considered the only photographed specimen (Abrahamyan 1957: pl. 5, fig. 6) as the holotype. According to the Article 73 of the International Code of Zoological Nomenclature (ICZN 1999), the holotype of a new species can only be fixed in the original publication and by the original author, and thus Abrahamyan's specimen selected by Pakhnevich cannot be considered as the valid holotype. Moreover, the specimen chosen by Pakhnevich from Abrahamyan (1957)'s publication is lost. Therefore, a neotype must be designated among the specimens of Abrahamyan (1957)'s collection, which is currently stored at the IGSNASRAGM.

Contrary to Pakhnevich's statement (in Alekseeva et al. 2018a: 910), *Cyphoterorhynchus arpaensis* does not occur in the Frasnian of Belgium, where the genus has never been recovered. Furthermore, *Cyphoterorhynchus* seems to be a Gondwana-restricted genus as, besides the aforementioned areas, it is also known from Australia (e.g. Sartenaer 1964; Roberts et al. 1972; Dring 1980), Libya (Mergl & Massa 1992, 2000) and southern Spain (Pardo & García-Alcalde 1984) (see Brock & Yazdi 2000: fig. 5).

Occurrence. In Armenia, recent samplings revealed the presence of this species only in the Frasnian interval. Previous reports of it by Arakelyan (1952) and Arakelyan et al. (1975) from the lower Famennian strata of the Gyumushlug section (Fig. 1) need to be considered as dubious, as the position of the Frasnian–Famennian boundary is not known yet due to the absence of the diagnostic conodont species. Moreover, Reed's (1922) species was reported only in the Frasnian of Nakhichevan by Rzhonsnitskaya & Mamedov (2000) and Mirieva (2010).

Order **Atrypida** Rzhonsnitskaya, 1960
Suborder **Atrypidina** Moore, 1952
Superfamily Atrypoidea Gill, 1871
Family Atrypidae Gill, 1871
Subfamily Atrypinae Gill, 1871
Genus *Atrypa* Dalman, 1828
Subgenus *Atrypa* (*Planatrypa*) Struve, 1966

Type species: *Atrypa* (*Planatrypa*) *collega* Struve, 1966, from the Junkerberg beds, middle Eifelian, Eifel (Germany).

Atrypa (*Planatrypa*) *ertichensis* (Abrahamyan, 1959)

Fig. 9A–F

1959 *Atrypa tubaecostata* Paeck. var. *ertichensis* Abrahamyan, p. 7, pl. 1, fig. 1–3.
1974 *Spinatrypa ertichensis* - Abrahamyan, p. 57, pl. 17, fig. 4.
1985 *Spinatrypina ertichensis* - Mamedov & Rzhonsnitskaya, p. 148.
1997 *Atrypa* (*Planatrypa*) *ertichensis* - Komarov, p. 87, pl. 1, fig. 5.
2018a *Atrypa* (*Planatrypa*) *ertichensis* - Grechishnikova in Alekseeva et al., p. 24, 26.

Type material: Abrahamyan (1959: p. 7, pl. 1, fig. 1a–d) selected the articulated specimen (IGSNASRAGM 270/3–54) from the Frasnian of Ertych section (Armenia) as the holotype. Although Abrahamyan's collection is stored at the Geological Museum in Yerevan, many of her specimens were lost in 2010 (when the entire museum with its collections was moved to another building), as was the holotype of *Atrypa* (*Planatrypa*) *ertichensis*. Currently, the type material stored at the museum consists of three specimens, of which one (IGSNASRAGM 3936/AB205/4–54), illustrated by Abrahamyan (1959: p. 8, table 1, fig. 2a–d) is designated here as the neotype. In addition, here we illustrate for the first time one of the paratypes (IGSNASRAGM 3936/AB270/82/3–54) (Fig. 9.A–F).

Additional material: Two partly exfoliated articulated specimens from the Ertych section (Er19/1 - IGSNASRAGM 3936/PS 3936.1, IGSNASRAGM 3936/PS 3936.2).

Description. Shell medium-sized (up to 30.1 mm in width, 29.7 mm in length and 16.9 mm in thickness), strongly dorsibiconvex, shield-shaped to semi-elliptic in outline; hinge line shorter than the maximum width; widest slightly posteriorly to midlength; anterior margin rounded to straight; anterior commissure undulose to slightly uniplicate.

Ventral valve slightly convex in posterior view, with anterolateral parts inclined to become flat; shoulder lines indented by umbo; beak small, erect to incurved; foramen unobserved; sulcus wide, poorly-defined, very shallow, perceptible only at front, flat-bottomed at front; tongue low, wide, semi-rounded to semi-elliptic in outline, not perpendicular to commissural plane.

Dorsal valve sharply inflated with convex flanks sloping steeply towards the lateral commissures; highest at about midlength or more posteriorly to it, then decreasing progressively towards the anterior margin; fold absent.

Ornamentation of tubular-imbricate, coarse costae originating at beaks and becoming fainter towards lateral cardinal extremities; costae increasing principally by bifurcation on ventral valve and by intercalation on dorsal valve; 65–72 costae on the entire shell; generally 5–6 costae per 5 mm at anterior margin; growth lamellae more crowded near the anterior and lateral margins, extending into frills (Fig. 9A).

Internal morphology not observed.

Remarks. Initially described by Abrahamyan (1959), this species was mistakenly considered as a variety of *Atrypa tubaecostata* Paeckelmann, 1913, a late Givetian species assigned to *Exatrypa* by Copper (1967a), based on some external differences observed in the Armenian material such as a larger size, a more inflated dorsal valve and the presence of sulcus. However, Abrahamyan (1974) transferred it to *Spinatrypa* Stainbrook, 1951 and raised it at the species level, whereas Mamedov & Rzhonsnitskaya (1985) attributed it to *Spinatrypina* Rzhonsnitskaya, 1964. Afterwards, Komarov (1997) re-assigned it to *Atrypa* (*Planatrypa*) Struve, 1966 owing to the general shell shape, external ornamentation and absence of dental plates. Although Komarov (1997) did not insist on the absence of dental nuclei, his illustrations of internal features clearly demonstrate that these structures are not developed and support this subgeneric assignment (see Copper 2002). However, the examination of Abrahamyan's species revealed the presence of frills, an ornamental feature that was considered unknown in Struve's (1966) subgenus by Copper (2002), but their presence in this subgenus was challenged notably by Komarov (1997), Halamski & Baliński (2013) and Halamski et al. (2022). As Baliński & Halamski (2023) noted the existence of species presenting intermediate characters that cannot be assigned definitely to one of the subgenera previously recognised within *Atrypa* (see Copper 2002) or to *Kyrtatrypa* Struve, 1966, we presently follow Komarov's (1997) subgeneric assignment, pending a reassessment of some features used in (sub) generic distinctions among atrypides, which is well beyond the scope of this work.

Occurrence. Although Abrahamyan (1959) initially described this species from Frasnian strata of Armenia, Komarov (1997) specified that it mainly occurs in the upper Givetian *Adolfia zickzack* brachiopod Zone of Rzhonsnitskaya & Mamedov (2000) and occasionally in the lower part of the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of the same authors, which is likely of lower–middle Frasnian in age (Serobyan et al. 2022b). Thus, it appears that *Atrypa* (*Planatrypa*) *ertichensis* ranges through the upper Givetian to the lower–middle Frasnian sequences of the Lesser Caucasus.

Subfamily Spinatrypinae Copper, 1978
Genus *Spinatrypa* Stainbrook, 1951

Type species: *Atrypa hystrix* var. *occidentalis* Hall, 1858 from the Cedar Valley limestone, upper Givetian, Iowa, USA.

Spinatrypa sp.
Fig. 9G–L

Material: Two partly exfoliated articulated specimens from the Ertych section (Er19/1 - IGSNASRAGM 3937/PS 3043, IGSNASRAGM 3937/PS 3043.1).

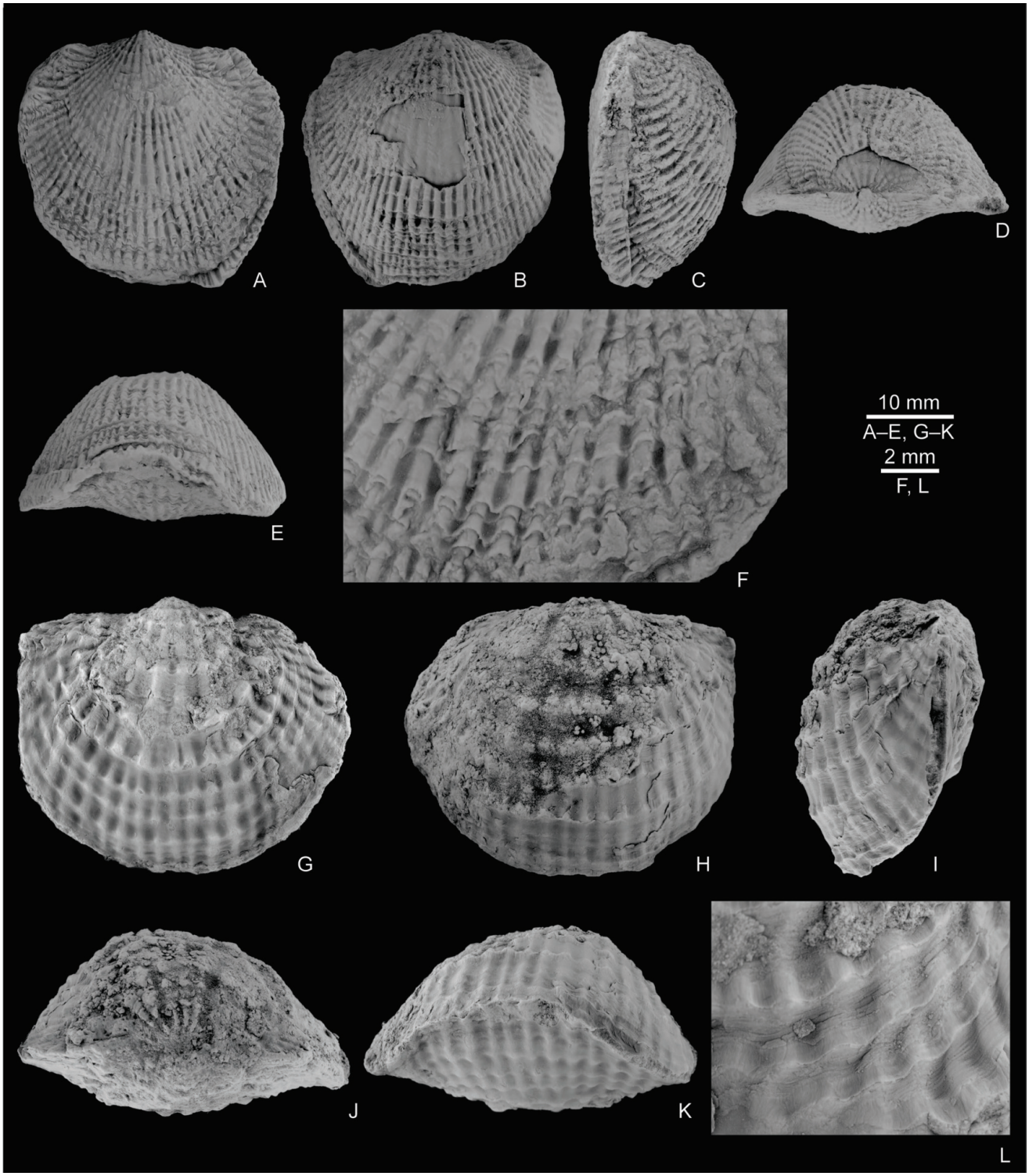

Fig. 9 - A–F) *Atrypa* (*Planatrypa*) *ertichensis* (Abrahamyan, 1959) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Ertych, Central Armenia). IGSNASRAGM 3936/AB270/82/3–54 (paratype), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (A–E), close-up of ornament showing the bifurcation of on the ventral valve (F). G–L) *Spinatrypa* sp. from the Frasnian *R. gnishikensis–A. arakelyani* brachiopod assemblage Zone (Ertych, Central Armenia). IGSNASRAGM 3937/PS 3043, almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (G–K), and close-up to the micro-ornament displaying the undulose growth lamellae covered by microlines (L).

Description. Shell medium-sized (ca. 37.1 mm in width, 32 mm in length and 19 mm in thickness), sharply dorsibiconvex, wider than long, semi-elliptic in outline; cardinal extremities appear to be rounded (although they are incomplete); anterior margin flat; anterior commissure uniplicate.

Ventral valve slightly convex in posterior and lateral profile views with maximum convexity in the umbonal area; anterolateral parts inclined to become flat; umbo inflated, prominent; beak incurved; foramen unobserved due to deficient preservation; sulcus wide but extremely shallow; tongue low, wide, largely rounded in outline, not perpendicular to commissural plane.

Dorsal valve inflated, regularly curved in posterior and lateral profile views, with convex flanks sloping steeply towards the lateral commissures; posterolateral areas inclined; highest at about midlength or slightly anteriorly to it, then progressively decreasing towards the anterior margin; fold absent.

Ornamentation of up to 30 undulose, coarse costae increasing generally by bifurcations on both valves; generally 3–4 costae per 5 mm at anterior margin; growth lamellae covered by microlines (6–8 per mm) and more closely spaced near the commissure, sometimes thickened as growth varices.

Internal morphology unknown.

Remarks. Based on its large size, strongly dorsibiconvex profile and coarse as well as undulose ornamentation, our material is ascribed to *Spinatrypa,* but complementary specimens are needed for a specific assignment. Additionally, it is also pertinent to stress that this is the first record of the genus in the Frasnian of the Lesser Caucasus, since representatives of this genus, known from the study of Komarov (1997), were described only in the Middle Devonian (Eifelian–Givetian) of Nakhichevan.

Subfamily Variatrypinae Copper, 1978
Genus *Desquamatia* Alekseeva, 1960
Subgenus *Desquamatia* (*Seratrypa*) Copper, 1967a

Type species: *Desquamatia* (*Seratrypa*) *pectinata* Copper, 1967a, from the lower Frasnian of Germany (Bergisches Land).

Desquamatia (*Seratrypa*) *abramianae* Komarov, 1992

Fig. 10–12; Tab. 4

1992 *Desquamatia* (*Seratrypa*) *abramianae* Komarov, p. 99, pl. 1, fig. 3–4.

1997 *Desquamatia* (*Seratrypa*) *abramianae* - Komarov, p. 151, pl. 4, fig. 5–8; pl. 5, fig. 1–6.

2018a *Desquamatia* (*Seratrypa*) *abramianae* - Alekseeva et al., pp. 852–853.

Holotype: The holotype (Komarov 1992: pl. 1, fig. 3) is from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov (2000) of the Danzik section, left bank of the Arpa River, Nakhichevan. It is currently housed at the Vernadsky State Geological Museum (Moscow), under the registration no. VI-223/3a.

Material: Twenty-three articulated specimens and four ventral valves from the Ertych (Er19/1 - IGSNASRAGM 3941/PS 3047.1, IGSNASRAGM 3941/PS 3047.2, IGSNASRAGM 3941/PS 3047.3, IGSNASRAGM 3941/PS 3047.4, IGSNASRAGM 3941/PS 3047.5, IGSNASRAGM 3941/PS 3047.6, IGSNASRAGM 3941/PS 3047.7, IGSNASRAGM 3941/PS 3047.8; Er19/2 - IGSNASRAGM 3941/PS 3047.9, IGSNASRAGM 3941/PS 3047.10, IGSNASRAGM 3941/PS 3047.11, IGSNASRAGM 3941/PS 3047.12, IGSNASRAGM 3941/PS 3047.13; Er19/3 - IGSNASRAGM 3941/PS 3047.14), Djravank (Dj19/8 - IGSNASRAGM 3938/PS 3044, IGSNASRAGM 3940/PS 3046, IGSNASRAGM 3941/PS 3047, IGSNASRAGM 3941/PS 3047.15, IGSNASRAGM 3941/PS 3047.16, IGSNASRAGM, 3941/PS 3047.17, IGSNASRAGM 3941/PS 3047.18; Dj19/11 - IGSNASRAGM 3941/PS 3047.19, IGSNASRAGM 3941/PS 3047.20, IGSNASRAGM 3941/PS 3047.21; Dj19/12 - IGSNASRAGM 3941/PS 3047.22) and Noravank (Nv19/20 - IGSNASRAGM 3939/PS 3045; Nv19/38 - IGSNASRAGM 3941/PS 3047.23) sections.

Description. Shell medium-sized (up to 39.6 mm in width, 37.7 mm in length and 27.9 mm in thickness) (Tab. 4), wider than long to longer than wide, sharply dorsibiconvex, relatively equidimensional, widest at about mid-length or more posteriorly to it, semi-elliptic to semi-rounded in outline; hinge line shorter than greatest width; anterior margin slightly rounded to straigth; anterior commissure undulose to slightly uniplicate.

Ventral valve inflated posteriorly with flanks sloping moderately towards the lateral commissures; highest in the posterior third of the valve, then de-

	W	L	T	L/W	T/W
Number of individuals	23	23	23	23	23
Mean value	25.5	25.7	16.02	1.01	0.64
Standard deviation	6.42	5.9774	4.2855	0.05	0.1496
Standard error±	±1.3388	±1.2464	±0.8936	±0.0104	±0.011
Min	12.5	14	7	0.95	0.39
Max	39.6	37.7	24.6	1.12	1.16

Tab. 4 - Measurements in mm and ratios of *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell.

Fig. 10 - *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992 from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). A–E) IGSNASRAGM 3939/PS 3045 (Noravank), partly corroded juvenile specimen in ventral, dorsal, lateral, posterior and anterior views. F–J) IGSNASRAGM 3940/PS 3046 (Djravank), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. K–P) IGSNASRAGM 3941/PS 3047 (Djravank), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (K–O), and close-up of tubular costae increasing by bifurcation and intercalation on the ventral valve (P).

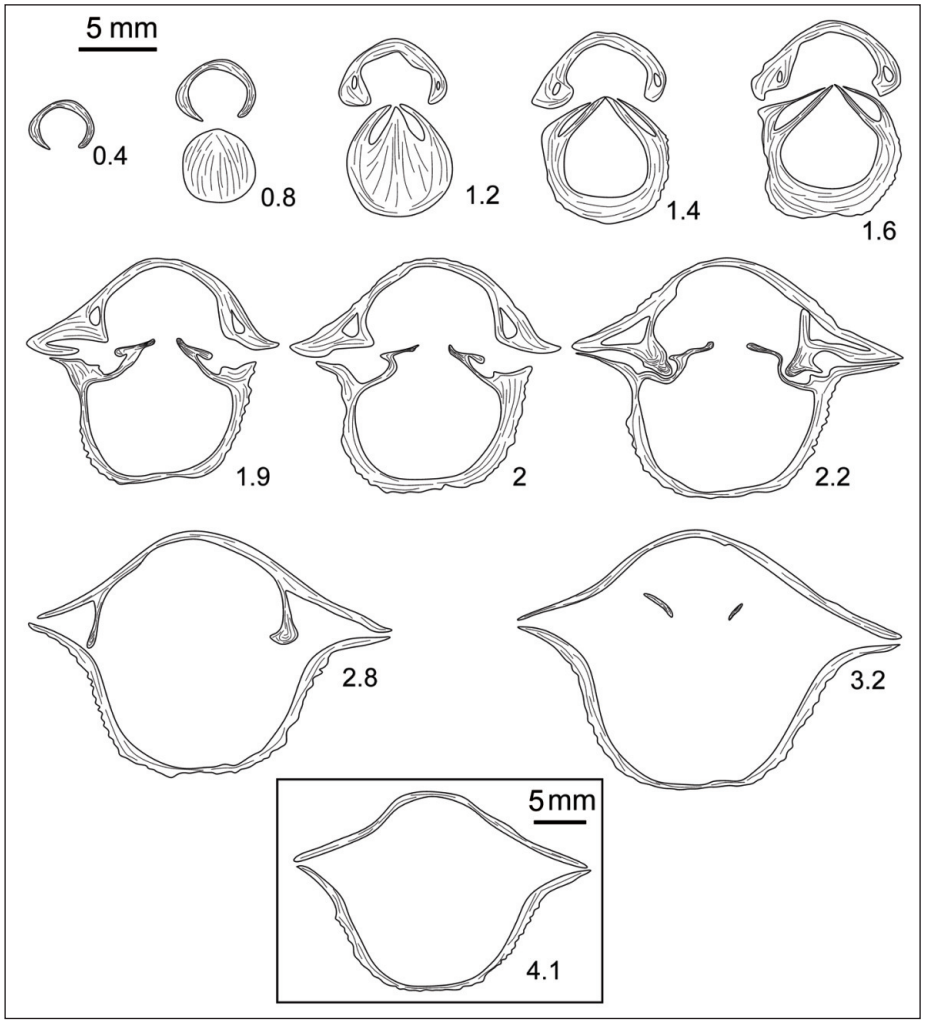

Fig. 11 - Transverse serial sections of *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992 (IGSNASRAGM 3938/PS 3044) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Djravank, Central Armenia). Numbers refer to distances in mm from the tip of the ventral umbo.

creasing progressively towards the anterior margin; umbo inflated, prominent; beak acute, incurved; interarea very small, concave, hypercline; foramen and deltidial plates unobserved due to deficient preservation; sulcus very shallow and only perceptible at front, flat- to slightly round-bottomed at front; tongue low, wider than high, semi-rounded to semi-elliptic, not perpendicular to commissural plane.

Dorsal valve sharply inflated with convex flanks sloping steeply towards the lateral commissures; highest at about midlength or more posteriorly to it, then decreasing progressively towards the posterior margin; umbo inflated; fold not developed.

Ornamentation of fine, tubular costae increasing by bifurcation and intercalation on both valves; generally 125–140 costae on the entire shell, 7–8 costae per 5 mm at anterior margin; growth lamellae more crowded near the lateral and anterior margins.

Ventral valve interior (Fig. 11) with stout but short dental plates; dental nuclei relatively large, well-marked; teeth massive, simple; central apical cavity not filled in by callosities.

Dorsal valve interior (Fig. 11) with a weak cardinal process in form of a pad, enclosed within the cardinal pit; dental sockets not deep, divided by a median crest; crural bases stout; crura ventrally directed; jugal processes and spiral cones not observed.

Shell ontogeny. Juveniles display a thinner shell with rectimarginate anterior commissure and semi-elliptic as well as very low tongue. Although not developed in juveniles, a sulcus occurs in older shells. Beak inclination angle does not change with age because juveniles also have an incurved beak. The size distributions of *Desquamatia* (*Seratrypa*) *abramianae* during growth, as represented by the scatter plots of the widht/length, the width/thickness and the width/width of sulcus, show a continuous and progressive growth with no distinct grouping (Fig. 12). The relative proportions of *D.* (*S.*) *abramianae* represented by sufficient material remain constant (linear regression: $y = ax+b$; significant probability value: $p < 0.001$*** whatever the degree of development of individuals

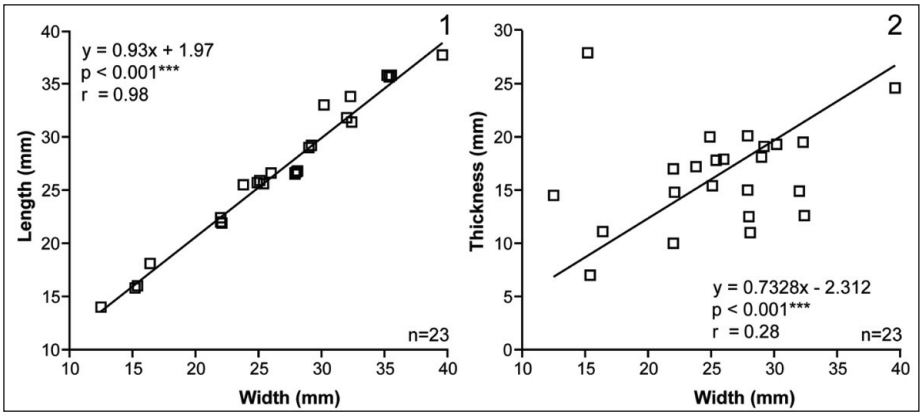

Fig. 12 - Scatter diagrams of *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992. 1) Relation between shell width and length. 2) Relation between shell width and thickness. Abbreviations: *n*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

(Fig. 12). Moreover, the correlation is positive with width varying proportionally with length, thickness and width of sulcus. To complete the scatter plots, the measurements of numerous individuals of *D.* (*S.*) *abramianae* are also presented in Tab. 4.

Remarks. Although Komarov (1992, 1997) examined numerous specimens from Nakhichevan identified as *Desquamatia* (*Seratrypa*) *abramianae*, this species was previously known only from illustrations of a few partially exfoliated samples of which only the ventral internal features were documented. Our better-preserved material has allowed a complete redescription of this taxon.

Copper (1967a) identified two morphotypes in *D.* (*S.*) *pectinata*: coarsely ribbed and finely ribbed. *D.* (*S.*) *abramianae* appears to be closely related to the latter; however Komarov's species differs by its finer costae (7–8 costae per 5 mm at the anterior margin near sulcus and fold vs. 4–5 costae in *D.* (*S.*) *pectinata*), incurved ventral beak and lower tongue. *D.* (*S.*) *abramianae* is distinguished externally from *D.* (*S.*) *frasniensis* Godefroid, 1970, known from the lower–middle Frasnian of Belgium, by its more inflated shell, lower tongue and incurved ventral beak. Externally *D.* (*S.*) *abramianae* is close to *D.* (*S.*) *refrathensis* Ma and Ebbighausen in Ma et al. (2008), which is known from the topmost lower to lower part of middle Frasnian of the Bergisch Gladbach area (Rhenish Massif, Germany); however the former lacks a furrowed median ridge, parallel grooves and ridges in the posterior part of the muscle field that is observed in the latter. Moreover, *D.* (*S.*) *abramianae* has 14–16 spiralial whorls (Komarov 1997: p. 152), whereas *D.* (*S.*) *refrathensis* displays spiral cones with at least 20 whorls per cone. *D.* (*S.*) *abramianae* differs from *D.* (*S.*) *orbiculata* Godefroid and Jacobs, 1986, known from the upper Givetian–lower Frasnian of Belgium, by its larger size, less circular shell and slightly finer ribs. *D.* (*S.*) *abramianae* is distinguished from *D.* (*S.*) *globosa* (Gurich, 1896) as revised by Racki & Baliński (1981), known from the upper Givetian–lower Frasnian of the Holy Cross Mountains (Poland), by its less inflated shall, incurved ventral beak, low tongue and by the absence of a weakly developed dorsal fold.

Occurrence. This species was originally reported from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov (2000) in Nakhichevan (Komarov 1992, 1997). It is recorded herein for the first time from the Frasnian strata of the Ertych, Djravank and Noravank sections (Fig. 1).

Order **Spiriferida** Waagen, 1883
Suborder **Spiriferidina** Waagen, 1883
Superfamily Cyrtospiriferoidea Termier & Termier, 1949
Family Cyrtospiriferidae Termier & Termier, 1949
Subfamily Cyrtospiriferinae Termier & Termier, 1949
Genus *Angustisulcispirifer* n. gen.

Type species: *Angustisulcispirifer arakelyani* n. gen., n. sp., from the Frasnian of Central Armenia.

Derivation of the name: *Angustus, a, um* (Latin): narrow; *sulcus, i* (Latin): furrow; *spirifer* is the usual ending for spiriferide genera. The name draws attention to the narrow sulcus of the genus.

Diagnosis: Shell medium- to large-sized, ventribiconvex, subpentagonal in outline; cardinal extremities mucronate; ventral interarea moderately high, triangular, apsacline; delthyrium wide; fold low; sulcus narrow; costae numerous, low, rounded; increasing by bifurcation in sulcus and on fold; micro-ornament of closely spaced growth lines, sometimes thickened as growth varices; dental plates robust, extrasinal posteriorly then becoming subsinal or intrasinal anteriorly; delthyrial plate short; ctenophoridium composed of numerous vertical lamellae and supported by a strong callosity.

Comparision with related genera. *Angustisulcispirifer* n. gen. is included in the Superfamily Cyrtospiriferoidea on account of its dental plates, delthyrial plate and ctenophoridium. *Angustisulcispirifer* n. gen. is assigned to the Family Cyrtospiriferidae, as

defined by Johnson (2006), based on costate sulcus and fold. It is further placed within the Subfamily Cyrtospiriferinae as defined by Johnson in Carter et al. (1994) and Johnson (2006) due to its wide hinge line and its slightly mucronate cardinal extremities.

The new genus is distinguished externally from *Cyrtospirifer* Nalivkin in Fredericks, 1924, as revised by Ma & Day (2003), by its more globular, longitudinally elongated and ventrally inflated shell as well as poorly developed fold and sulcus. Internally, *Angustisulcispirifer* n. gen. differs by its short delthyrial plate and robust dental plates.

Angustisulcispirifer n. gen. resembles to some extent to the genus *Uchtospirifer* Ljashenko, 1957 as revised by Sokiran (2006), known notably from the upper Givetian?–lower Frasnian of Russia as well as from the same interval in Poland (Racki & Baliński 1981) and probably Belgium (Sartenaer 1974; Mottequin 2019), based on its strongly ventribiconvex profile, subpentagonal shell with flanks closely ornamented by low, flattened costae and high ventral interarea, but the former displays a wide hinge line (*vs*. short hinge line for *Uchtospirifer*), mucronate cardinal extremities (*vs*. rounded ones for *Uchtospirifer*), narrow sulcus and fold (*vs*. moderately wide ones for *Uchtospirifer*), and low tongue. Additionally, the new genus has costae in sulcus and on fold that are not transformed into capillae, flattening or disappearing as it is observed in *Uchtospirifer* representatives. Internally, *Angustisulcispirifer* n. gen. differs by its supported ctenophoridium.

The new genus differs externally from the upper–uppermost Famennian genus *Dichospirifer* Brice, 1971, as revised by Mottequin & Brice (2019), by its larger size, shell shape, wide hinge line and narrow but conspicuous sulcus and fold. Moreover, the former bear simple and flattened costae on flanks, while the latter has bifurcating costae, exceptionally trifurcating or increasing by intercalation on flanks (Mottequin & Brice 2019). Additionally, *Angustisulcispirifer* n. gen. differs by its supported ctenophoridium, whereas *Dichospirifer* representatives possess an unsupported ctenophoridium bilobed posteriorly.

Angustisulcispirifer n. gen. is separable from *Plicapustula* Ma & Day, 2007, known from the lower Famennian of South China and North America, by its more rounded and longitudinally elongated shell outline, low fold, narrow sulcus and very low tongue. Furthermore, *Angustisulcispirifer* n. gen. differs by its more robust dental plates, rudimentary delthyrial plate and supported ctenophoridium.

Angustisulcispirifer n. gen. resembles some representatives of *Wenjukovispirifer* Oleneva, 2016 in terms of size, general shape and outline, but the new genus differs externally by its larger size as well as poorly developed fold and sulcus. It is worth noting that only little is known about the internal morphology of *Wenjukovispirifer*, but Oleneva (2016) mentioned the presence of a ventral septum (=myophragm?), a character which is absent in *Angustisulcispirifer* n. gen.

Occurrence. Frasnian of Armenia, Nakhichevan and possibly Famennian of Kazakhstan.

Other included species. As the morphological characters of *Cyrtospirifer* (*C.*) *kursaensis* Sidjachenko, 1962 and *C.* (*C.*) *limatus* Solkina in Sidjachenko (1962) from the Famennian of Central Kara-Tau (Kazakhstan) fit well with the diagnosis of the new genus, the latter may be tentatively assigned to it, though the type of pseudodeltidium as well as the micro-ornament of both species are undocumented. *Uchtospirifer subarchiaci* (Martelli, 1902) sensu Afanasjeva in Alekseeva et al. (2018b) (not *Plicapustula subarchiaci* (Martelli, 1902), see Ma & Day 2007) is also included in the new genus. Moreover, it most likely belongs to the same phylogenetic lineage as *A. arakelyani* n. gen., n. sp. because both species display strong similarities.

Angustisulcispirifer arakelyani n. gen., n. sp.

Fig. 13–16; Tab. 5

1952 *Cyrtospirifer subarchiachi* [*sic*] Martelli - Arakelyan, p. 31, 36.
1957 *Cyrtospirifer subarchiaci* (Martelli) - Abrahamyan, p. 9.
1964 *Cyrtospirifer subarchiaci* (Martelli) - Arakelyan, p. 67, 70, 74, 92.
1973 *Cyrtospirifer subarchiaci* (Martelli) - Abrahamyan et al., p. 217.
1975 *Cyrtospirifer subarchiaci* (Martelli) - Arakelyan et al., p. 22.

Fig. 13 - *Angustisulcispirifer arakelyani* n. gen., n. sp. from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). The arrows indicate the anterior margin. A–F) IGSNASRAGM 3970/PS 3076 (Djravank), partly exfoliated juvenile specimen in ventral, oblique ventral, dorsal, lateral, posterior and anterior views. G–L) IGSNASRAGM 3971/PS 3077 (holotype, Noravank), almost complete specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. M–R) IGSNASRAGM 3972/AR 3078 (Ertych), partly exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. S–AA) IGSNASRAGM 3973/PS 3079, (Noravank section), almost complete specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views (S–W), and close-up of the ventral interarea showing the remnants of a delthyrial cover of unknown origin (Y–Z). AA) IGSNASRAGM 3974/PS 3080 (Ertych), incomplete specimen, close-up of the ventral interarea clearly displaying the delthyrial plate, though it is partly concealed by sediment.

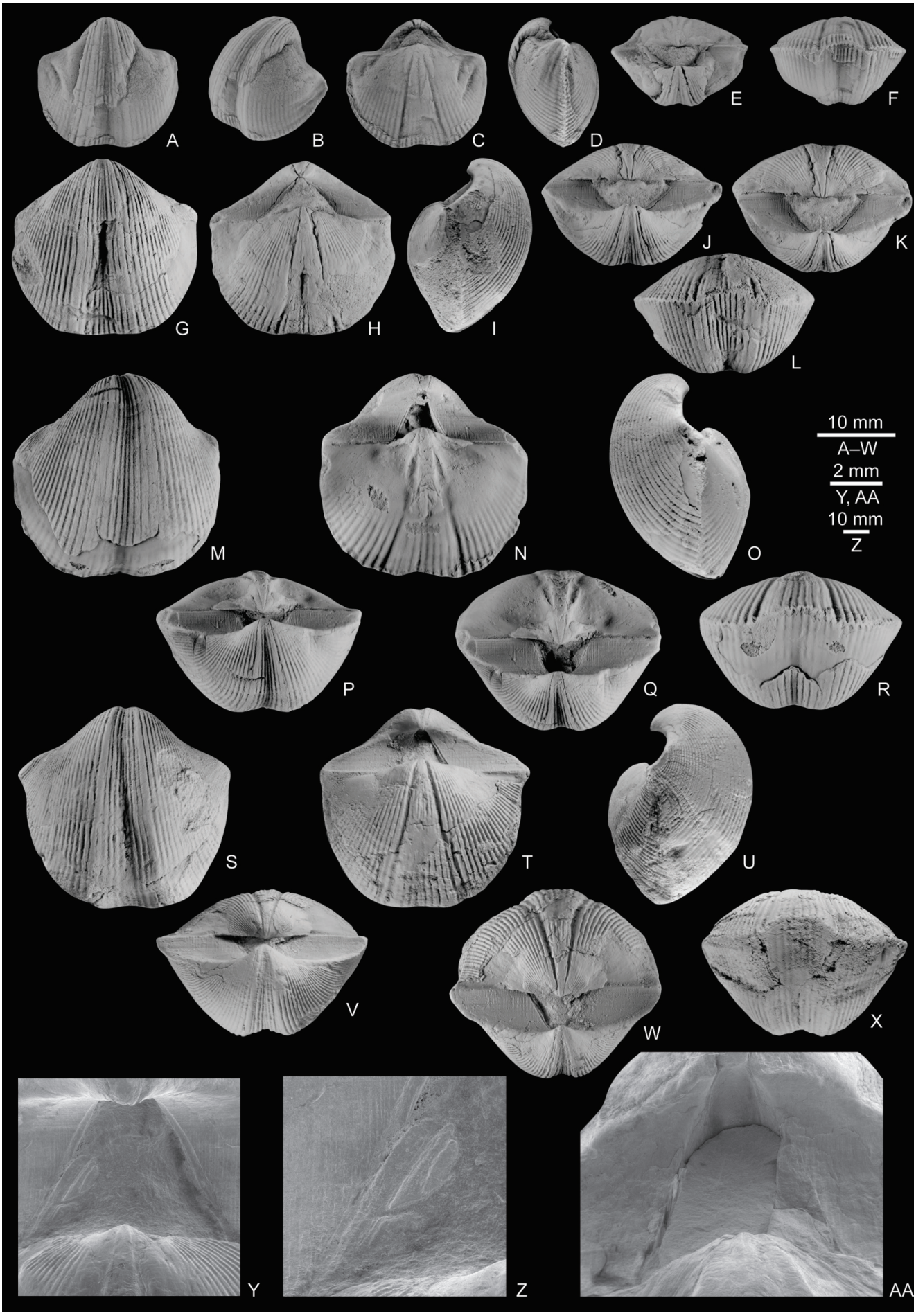

FIGURE 13

Derivation of the name: The species name refers to Ruben Arakelyan (1919–1978), who was the Head of the Laboratory of Regional geology and Stratigraphy of the Institute of Geological Sciences of Armenian SSR (1960s–1970s) and contributed greatly to the stratigraphy and biostratigraphy of the Lesser Caucasus.

Holotype: An almost complete articulated specimen (IGSNASRAGM 3971/PS 3077; Fig. 13.G–L) from the Frasnian.

Material: Fifty-two articulated specimens and five dissociated valves from the Frasnian limestone beds of the Ertych (Er19/1 - IGSNASRAGM 3969/PS 3075, IGSNASRAGM 3972/AR 3078, IGSNASRAGM 3974/PS 3080, IGSNASRAGM 3975/PS 3081; Er19/2 - IGSNASRAGM 3976/PS 3082.1, IGSNASRAGM 3976/PS 3082.2, IGSNASRAGM 3976/PS 3082.3; Er19/3 - IGSNASRAGM 3976/PS 3082.4, IGSNASRAGM 3976/PS 3082.5, IGSNASRAGM 3976/PS 3082.6), Djravank (Dj19/8 - IGSNASRAGM 3970/PS 3076, IGSNASRAGM 3976/PS 3082, IGSNASRAGM 3976/PS 3082.7, IGSNASRAGM 3976/PS 3082.8; Dj19/9 - IGSNASRAGM 3976/PS 3082.9; Dj19/10 - IGSNASRAGM 3976/PS 3082.10; Dj19/11 - IGSNASRAGM 3976/PS 3082.11, IGSNASRAGM 3976/PS 3082.12, IGSNASRAGM 3976/PS 3082.13) and Noravank (Nv19/38 - IGSNASRAGM 3971/PS 3077 (holotype), IGSNASRAGM 3973/PS 3079, IGSNASRAGM 3976/PS 3082.14, IGSNASRAGM 3976/PS 3082.15, IGSNASRAGM 3976/PS 3082.16, IGSNASRAGM 3976/PS 3082.17; Nv19/50 - IGSNASRAGM 3976/PS 3082.18, IGSNASRAGM 3976/PS 3082.19, IGSNASRAGM 3976/PS 3082.20, IGSNASRAGM 3976/PS 3082.21, IGSNASRAGM 3976/PS 3082.22, IGSNASRAGM 3976/PS 3082.23, IGSNASRAGM 3976/PS 3082.24, IGSNASRAGM 3976/PS 3082.25, IGSNASRAGM 3976/PS 3082.26, IGSNASRAGM 3976/PS 3082.27, IGSNASRAGM 3976/PS 3082.28, IGSNASRAGM 3976/PS 3082.29, IGSNASRAGM 3976/PS 3082.30, IGSNASRAGM 3976/PS 3082.31, IGSNASRAGM 3976/PS 3082.32, IGSNASRAGM 3976/PS 3082.33, IGSNASRAGM 3976/PS 3082.34, IGSNASRAGM 3976/PS 3082.35, IGSNASRAGM 3976/PS 3082.36, IGSNASRAGM 3976/PS 3082.37, IGSNASRAGM 3976/PS 3082.38, IGSNASRAGM 3976/PS 3082.39, IGSNASRAGM 3976/PS 3082.40, IGSNASRAGM 3976/PS 3082.41, IGSNASRAGM 3976/PS 3082.42, IGSNASRAGM 3976/PS 3082.43, IGSNASRAGM 3976/PS 3082.44, IGSNASRAGM 3976/PS 3082.45, IGSNASRAGM 3976/PS 3082.46, IGSNASRAGM 3976/PS 3082.47, IGSNASRAGM 3976/PS 3082.48, IGSNASRAGM 3976/PS 3082.49) sections.

Type horizon: Bed Nv19/38 (Fig. 2), Frasnian nodular limestones.

Type locality: Noravank section (6 km southeast from Areni, Vayots Dzor Province, Southwest Central Armenia) (Fig. 1, 2).

Diagnosis: Shell medium- to large-sized (up to 51.2 mm in width, 49.5 mm in length, 37.2 mm in thickness) (Tab. 5), ventribiconvex, subpentagonal, wider than long, with mucronate cardinal extremities; widest at hinge line; highest at midlength or more posteriorly; anterior margin flat to slightly emarginate; anterior commissure uniplicate; ventral interarea moderately high, triangular, apsacline; delthyrium wide, closed by robust pseudodeltidium, the latter lacks growth lines; fold and sulcus narrow, slightly to moderately developed; tongue very low, more or less rounded in outline; costae numerous, low, rounded and increasing by bifurcation in sulcus and on fold; dental plates robust, divergent but converging dorsally in umbonal region, extrasinal posteriorly then becoming subsinal or intrasinal anteriorly and extending to about 30% of the shell length; delthyrial plate short; ctenophoridium composed of numerous vertical lamellae and supported by a strong callosity; hinge plates divided.

Description. Shell medium- to large-sized, wider than long, sharply ventribiconvex, rounded subpentagonal in outline, widest at hinge line; cardinal extremities slightly mucronate; anterior margin flat to slightly emarginate; anterior commissure weakly uniplicate.

Ventral valve strongly inflated, rounded pentagonal in outline, with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then quickly decreasing towards anterior margin; umbo strongly inflated, large and prominent; beak small, erect to incurved; interarea apsacline, moderately high, well-defined, concave; delthyrium wide, the type of delthyrial cover is unknown as only some of the remnants are partially preserved in one of the collected specimens (IGSNASRAGM 3975/PS 3081; Fig. 13Y–Z); sulcus very narrow, shallow, originating from beak, well-defined, with gentle margins, round-bottomed at front; tongue very low, more or less rounded in outline, perpendicular to commissural plane.

Dorsal valve wider than long, inflated with flanks sloping gently towards lateral commissures, subquadrangular to subtrapezoidal in outline; highest at about midlength or slightly posteriorly, then decreasing gradually towards anterior margin; interarea linear (up to 1.5 mm high), slightly concave, orthocline; fold well-delimited, low, relatively narrow, originating from beak, round-topped at front.

Ornamentation of up to 30 rounded (generally 26–29; 4–5 costae per 5 mm at anterior margin near sulcus and fold), low, flattened, simple costae on each flank, becoming progressively fainter towards posterolateral margins; in sulcus and on fold, up to 15 costae (generally 10–12) increasing by bifurcation and intercalation, narrower than those present on flanks; costae 2–2.5 wider than interspaces on the flanks and nearly as wide as interspaces in sulcus and on fold; micro-ornament of closely spaced growth lines sometimes thickened as growth varices (though it is worth mentioning that the preservation of current material does not permit to document the presence (or otherwise) of other structures (capillae, etc.).

Ventral valve interior (Fig. 15) with strong dental plates, extrasinal posteriorly but subsinal or intrasinal anteriorly, generally divergent (21–26 degrees) but converging dorsally in umbonal region (as seen in transverse section); delthyrial plate short (Fig. 13AA); central apical cavity filled in by a stout

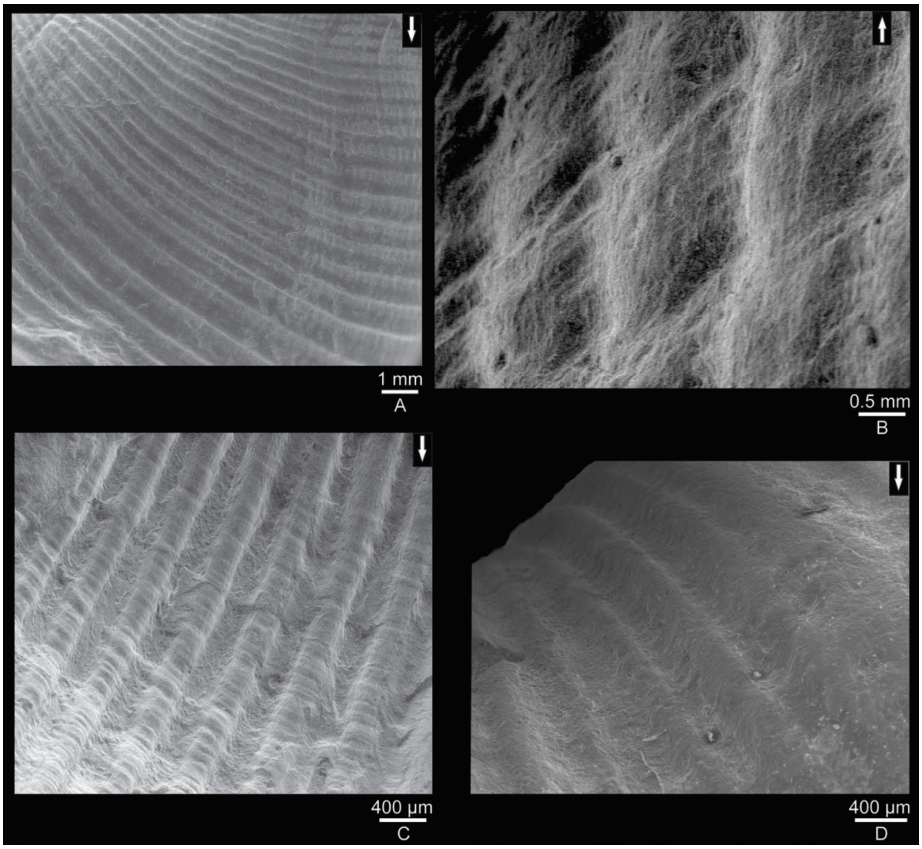

Fig. 14 - *Angustisulcispirifer arakelyani* n. gen., n. sp. from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). The arrows indicate the lateral margin. A–C) IGSNASRAGM 3975/PS 3081 (Ertych), details of the micro-ornament from the lateral oblique view (A–B) and close to the anterior margin (C) showing only the growth lines that are still visible in more internal layers of the shell. D) IGSNASRAGM 3976/PS 3082 (Djravank), close-up of the ornament displaying the faint costae in the sulcus.

and knob-like callosity on its floor (Fig. 15, serial sections 4.9–6.5); lateral apical cavities large and moderately filled in by callus; teeth relatively small, but stout.

Dorsal valve interior with ctenophoridium (Fig. 15) composed of up to 25 well-developed, long lamellae and supported by a strong apical callus; myophragm low, long (Fig. 14C); hinge plates divided; crural bases dorsally convergent; spiralia oriented posterolaterally, with at least 15 whorls per spiral cone.

Shell ontogeny. Juvenile forms differ from adults by their inconspicuous umbones, suberect beak, low fold and poorly developed sulcus. The beak inclination angle increases progressively with ontogenetic growth. The size distributions during growth, as illustrated by the various plots of Figure 16, show a continuous and progressive growth with possibly three-four distinct growth stages. However, the factors that caused this grouping effect remain unknown. The relative proportions of *Angustisulcispirifer arakelyani* n. gen., n. sp. represented by sufficient material remain constant (linear regression: $y = ax+b$; significant probability value: $p < 0.001$*** whatever the degree of development of individuals (Fig. 16)). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve. To complete the scatter plots, the measurements of numerous individuals of *A. arakelyani* n. gen., n. sp. are also represented in Tab. 5.

Remarks. This species is one of the most biostratigraphically valuable species in Armenia for the recognition of the Frasnian strata. However, it has mistakenly been confused with *Spirifer verneuili* var. *subarchiaci* Martelli, 1902 (= *Plicapustula subarchiaci* (Martelli, 1902) *sensu* Ma & Day (2007)) from the middle Famennian of southeastern China since Arakelyan (1952). The Armenian material differs from Martelli's (1902) species by its more globular and inflated shell as well as by its poorly developed fold and sulcus. Internally, the new species is distinguished by its short delthyrial plate and strong dental plates.

Angustisulcispirifer arakelyani n. gen., n. sp. is very close to *Uchtospirifer subarchiaci* (Martelli, 1902) sensu Afanasjeva in Alekseeva et al. (2018b) from the Frasnian of Nakhichevan (e.g., subpentagonal shell outline, ventribiconvex lateral profile, inflated umbones, ventral triangular and apsacline interarea, shallow sulcus and low fold, simple costae on flanks, bifurcating in sulcus and on fold, the pres-

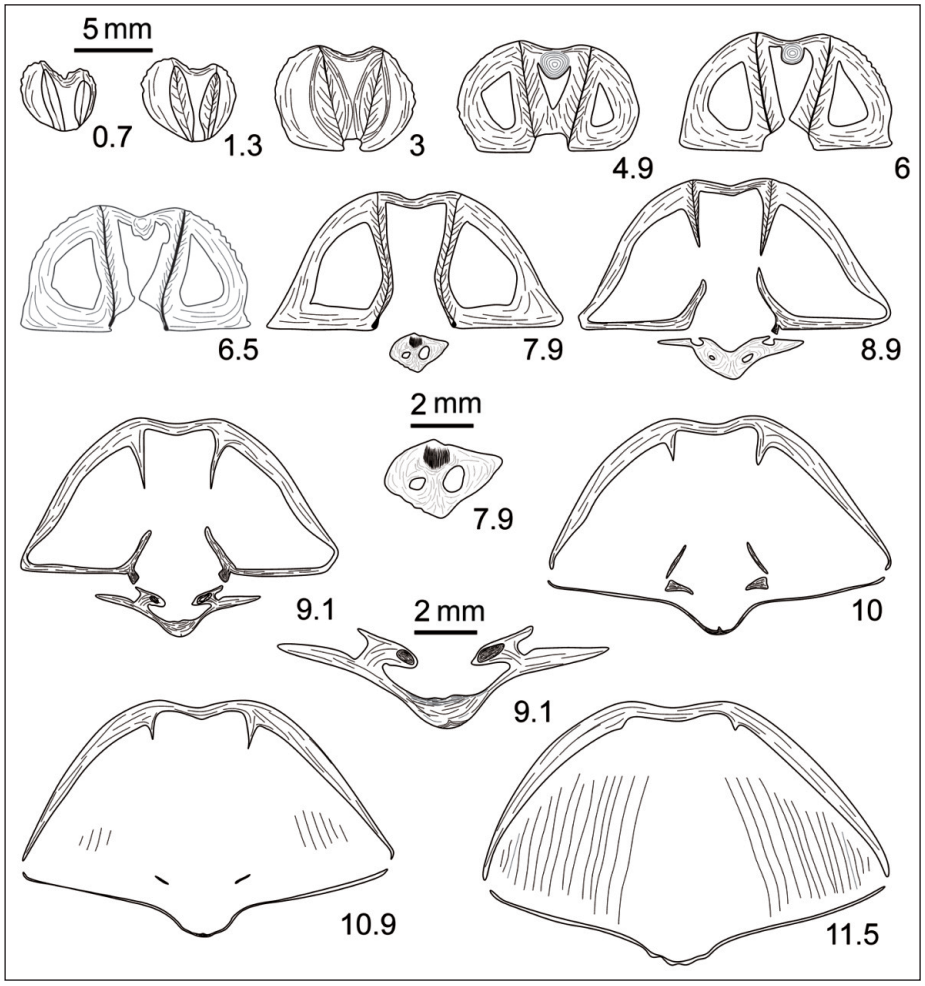

Fig. 15 - Transverse serial sections of *Angustisulcispirifer arakelyani* n. gen, n. sp. from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Ertych, Central Armenia). (IGSNASRAGM 3969/PS 3075). Numbers refer to distances in mm from the tip of the ventral umbo.

ence of a well-developed delthyrial plate and myophragm), which is also evidently confused with Martelli's (1902) species and needs to be re-investigated. However, the Armenian material is distinguishable by its wider hinge line, higher ventral interarea and less inflated shell. The internal features of the material studied by Afanasjeva in Alekseeva et al. (2018b: text-fig. 102) remain incompletely illustrated as only one serial section showing the ventral interior was provided; thus, further evidences are needed to point out other similarities and differences concerning internal morphology of these two species.

The new species shares several similarities (e.g., subpentagonal shell outline, ventribiconvex lateral profile, mucronate cardinal extremities, widest at hinge line, inflated umbones, triangular and apsacline interarea, simple costae on flanks, bifurcating in sulcus and on fold) with two species recognised from the Famennian of Central Kara-Tau, namely *Cyrtospirifer* (*C.*) *kursaensis* Sidjachenko, 1962 and

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	52	50	50	50	50	50	50	50	50
Mean value	28.86	26.91	22.44	20.6	8.8	0.92	0.67	0.3	0.71
Standard deviation	7.0307	7.0832	21.55	5.7482	3.1153	0.0495	0.049	0.051	0.04
Standard error±	±0.975	±1.002	±1.1783	±0.8129	±0.4406	±0.007	±0.007	±0.0071	±0.006
Min	18.4	15.9	11.5	12	3	0.77	0.55	0.15	0.58
Max	51.2	49.5	37.2	38.1	19.8	0.98	0.76	0.39	0.77

Tab. 5 - Measurements in mm and ratios of *Angustisulcispirifer arakelyani* n. gen., n. sp. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus, dL–length of the dorsal valve.

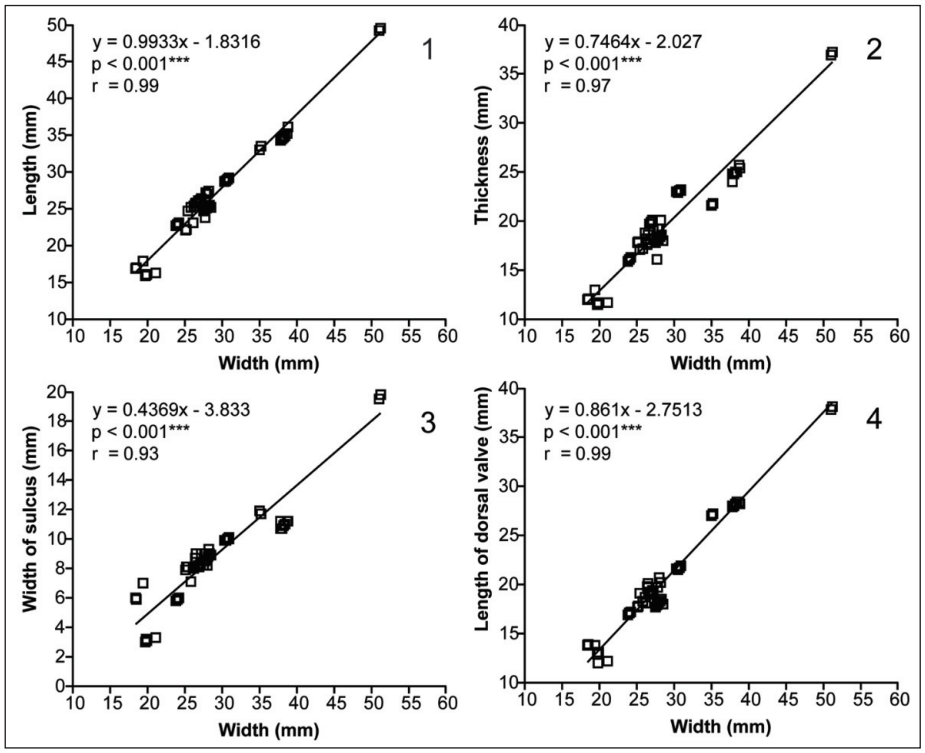

Fig. 16 - Scatter diagrams of *Angustisulcispirifer arakelyani* n. gen., n. sp. 1) Relation between shell width and length. 2) Relation between shell width and thickness. 3) Relation between shell width and width of sulcus. 4) Relation between shell width and length of dorsal valve. Abbreviations: *n*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

C. (*C.*) *limatus* Solkina in Sidjachenko (1962), but it also differs from them by its weakly developed fold and sulcus, very low tongue more or less rounded in outline, and by the presence of a stout and knob-like callosity developed in the ventral valve.

The re-examination of Arakelyan (1952, 1964) and Abrahamyan et al. (1973)'s material demonstrates that the species used to recognise the Frasnian strata in Armenia and Nakhichevan by these authors was *A. arakelyani* n. gen., n. sp. and not *Uchtospirifer subarchiaci* (Martelli, 1902) sensu Afanasjeva in Alekseeva et al. (2018b). Moreover, as we have never found the latter species in the recently collected fauna from Armenia we suggest using the new species to recognise the Frasnian strata in Armenia.

Occurrence. This species is found in all three studied sections (Tab. 1). Previously, it was reported from the Baghrsagh and Danzik sections in Nakhichevan and from the Noravank section in Armenia (Arakelyan 1964).

Cyrtospiriferinae gen. indet.

Fig. 17–19; Tab. 6

Material: Eight articulated specimens and six dissociated valves from the Frasnian limestone beds of the Ertych (Er19/2 - IGSNASRAGM 3954/PS 3060, IGSNASRAGM 3955/PS 3061, IGSNASRAGM 3957/PS 3063, IGSNASRAGM 3958/PS 3064, IGSNASRAGM 3958/PS 3064.1, IGSNASRAGM 3958/PS 3064.2, IGSNASRAGM 3958/PS 3064.3, IGSNASRAGM 3958/PS 3064.4) and Djravank (Dj19/10 - IGSNASRAGM 3956/PS 3062, IGSNASRAGM 3958/PS 3064.5, IGSNASRAGM 3958/PS 3064.6, IGSNASRAGM 3958/PS 3064.7, IGSNASRAGM 3958/PS 3064.8, IGSNASRAGM 3958/PS 3064.9) sections.

Description. Shell medium-sized (attaining 41.1 mm in width, 23.2 mm in length and 22.5 mm in thickness) (Tab. 6), wider than long, equibiconvex to ventribiconvex, transversely elongated in outline; widest at hinge line (most specimens are incomplete); cardinal extremities acute to mucronate; anterior margin straight to emarginate; anterior commissure uniplicate.

Ventral valve strongly inflated, with convex flanks sloping moderately to strongly towards lateral commissures; highest in the posterior third of the valve or at midlength, then decreasing quickly towards anterior margin; umbo inflated, prominent; beak straight to erect; interarea apsacline, triangular, moderately high, slightly to clearly concave; delthyrium wide, with a kind of protuberance in its central part (Fig. 17M); sulcus originating from beak, wide, shallow to moderately deep, round-bottomed at front, tongue low to moderately high, wide, subtrapezoidal to subcircular in outline.

Dorsal valve inflated with flanks sloping gently towards lateral commissures, subtrapezoidal in

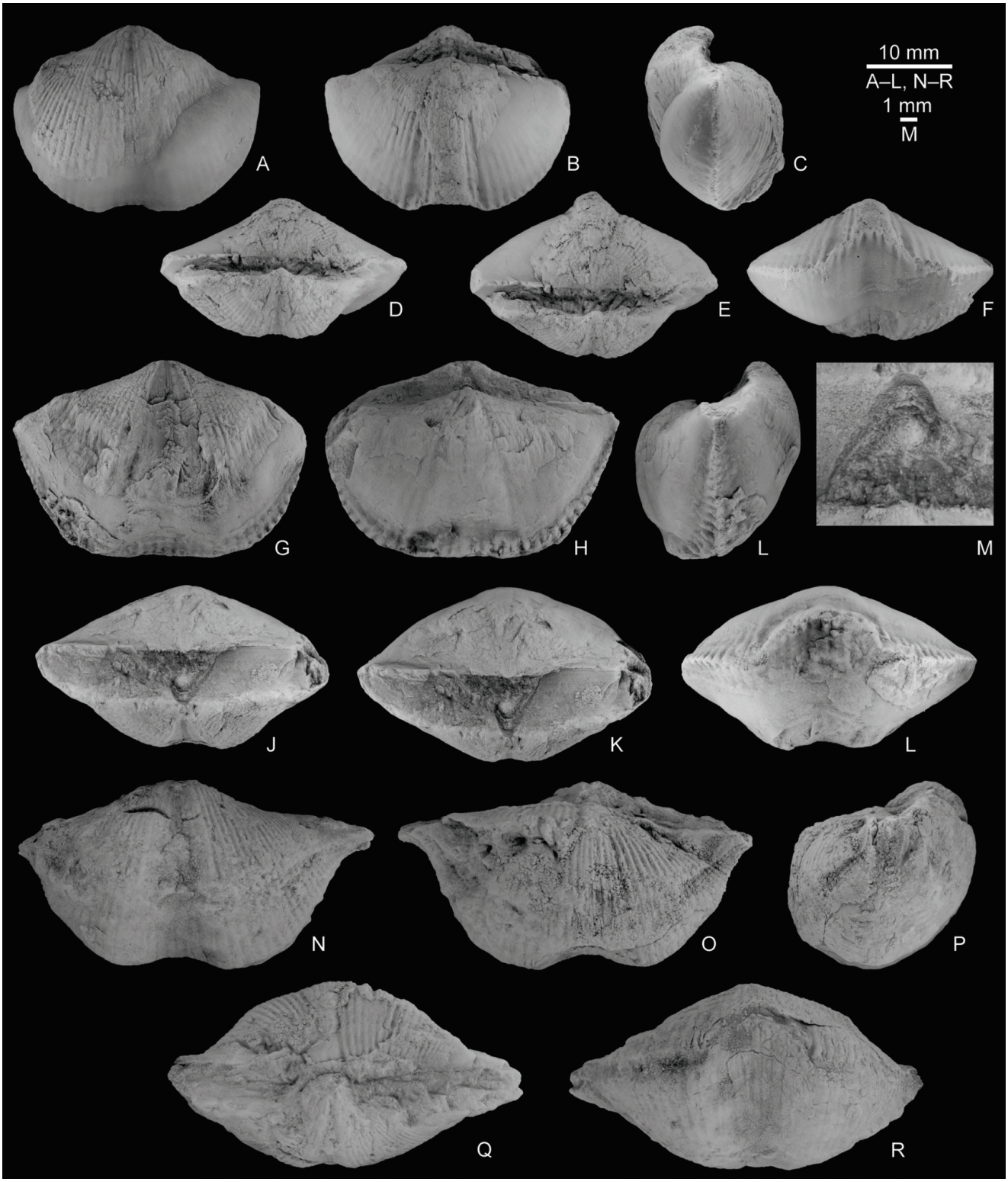

Fig. 17 - Cyrtospiriferinae gen. indet. from the Frasnian *Ripidiorhynchus gnishikensis*– *Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Central Armenia). A–F) IGSNASRAGM 3955/PS 3061 (Ertych), corroded specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. G–M) IGSNASRAGM 3956/PS 3062 (Djravank), almost complete specimen in ventral, dorsal, lateral, posterior, posterolateral and anterior views (G–L), and close-up of the ventral interarea showing the partly preserved central foramen (M). N–R) IGSNASRAGM 3958/PS 3064 (Ertych section), corroded specimen in ventral, dorsal, lateral, posterior and anterior views.

outline; highest at about midlength or more anteriorly to it, but gradually decreasing towards the anterior margin; interarea nearly flat, linear, orthocline; fold low, relatively wide to wide, well-delimit-

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	14	11	9	11	8	11	9	11	8
Mean value	36.24	22.06	18.52	11.46	17.5	0.6	0.5	0.31	0.47
Standard deviation	3.6515	0.4272	2.1701	1,3156	2.3084	0.0618	0.0453	0.043	0.0271
Standard error±	±0.9759	±0.1288	±0.7233	±0.3967	±0.8161	±0.0184	±0.0151	±0.013	±0.0096
Min	29	21.6	16.4	9	12	0.53	0.44	0.26	0.41
Max	41.8	23.2	22.2	13.4	19.8	0.75	0.57	0.38	0.51

Tab. 6 - Measurements in mm and ratios of Cyrtospiriferinae gen. indet. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus, dL–length of the dorsal valve.

ed (except in the specimen figured in Fig. 17N–R), starting from beak and widening anteriorly, round-topped at front.

Up to ca. 20 (3–4 costae per 5 mm at anterior margin near sulcus and fold) simple, low costae on flanks with top rounded; interspaces narrower than costae; in sulcus and on fold, up to 11 costae narrower than those on flanks, increasing by bifurcation; micro-ornament poorly preserved.

Remarks. The examined material is assigned to the family Cyrtospiriferidae, as defined by Johnson (2006), based on the presence of dental plates, a ctenophoridium, ornamentation and development of costae in sulcus and on fold. Additionally, its wide hinge line and acute to mucronate cardinal extremities argues for its assignment to the subfamily Cyrtospiriferinae rather than to Cyrtiopsinae. However, the insufficiency of our material precludes a definitive generic identification. It is also important to emphasize that the examination of two serially sectioned specimens shows that the internal morphology of our material is quite variable from one specimen to another. Most notably, although the central and lateral apical cavities of both serially sectioned specimens are infilled by stout callosity, both possess greatly thickened, subsinal or extrasinal and divergent dental plates converging dorsally in umbonal region and stout teeth, one of them (Fig. 18) displays a thick delthyrial plate, whereas the other shows a septal pillow made by delthyrial thickening formed by accretion of strong apical callus from the internal faces of the dental plates (Fig. 19). Moreover, the ctenophoridium observed in the former specimen is supported by strong callosity, whereas the latter specimen has an unsupported ctenophoridium. However, these differences are provisionally regarded here as representing intraspecific variability pending additional and better preserved specimens. Additionally, it is worth stressing that both specimens display divided hinge plates and dorsally convergent crural bases.

Conodonts and age dating

Conodonts examined in this study come from the lower limestone interval of the Djravank section (Fig. 2). Samples Dj19/8 and 19/9 include conodont elements of *Polygnathus webbi* Stauffer, 1938, *Icriodus excavatus* Weddige, 1984 and *Polygnathus*? *linguiformis* Hinde, 1879. This record suggests an age range from the *norrisi* (latest Givetian) to Upper *rhenana* (late Frasnian) biozones. The lowermost conodont bearing sample Dj19/10 contains some diagnostic elements referable to *Polygnathus aequalis* morphotype II Klapper & Lane 1985, which suggests an assignment to the *transitans* (latest early Frasnian) conodont biozone or younger. Taking these data into consideration, the age of the lower brachiopod bearing limestone interval is within the age range from *transitans* (latest early Frasnian) to Upper *rhenana* (late Frasnian).

Discussion

Biostratigraphy

Brachiopod assemblages have already been used in the establishment of Upper Devonian biostratigraphic schemes in the Lesser Caucasus. A rudimentary Devonian biostratigraphical zonal scheme based on brachiopods was first established by Rzhonsnitskaya (1948), who simply subdivided the Devonian into two parts: Lower and Upper. Later, Abrahamyan (1957, 1964, 1974) developed a new continuous biostratigraphic scheme characterized by taxon-range and assemblage biozones (Fig. 20). Grechishnikova et al. (1980, 1982), Mamedov & Rzhonsnitskaya (1985) and Rzhonsnitskaya &

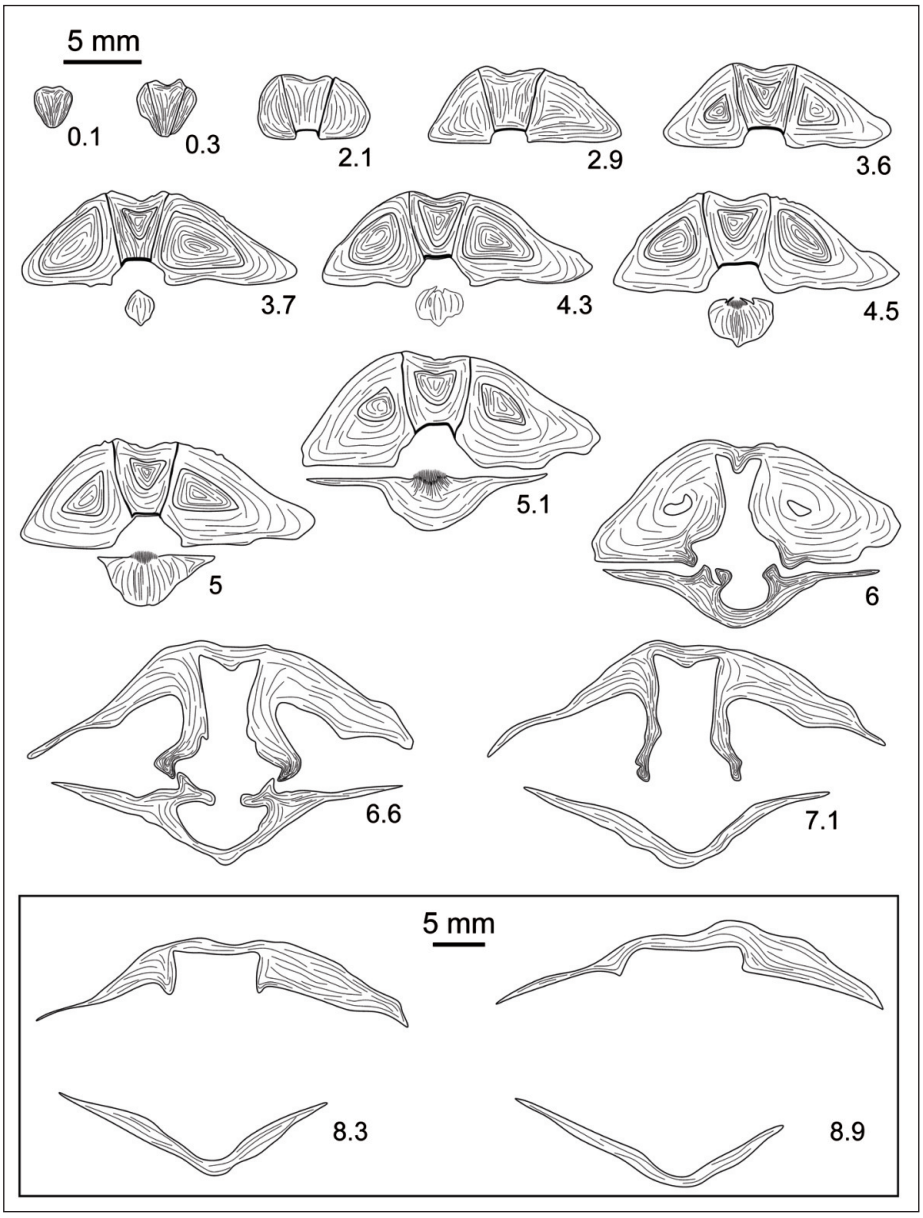

Fig. 18 - Transverse serial sections of Cyrtospiriferinae gen. indet. (IGSNASRAGM 3954/PS 3060) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone (Ertych, Central Armenia). Numbers refer to distances in mm from the tip of the ventral umbo.

Mamedov (2000), further applied Abrahamyan's zonal scheme in Nakhichevan, while improving and complementing it for some intervals. Rzhonsnitskaya & Mamedov (2000) updated their brachiopod biozonal scheme and correlated it with the conodont biozonation established by Aristov (1994) in Nakhichevan. The latter authors also introduced a long unzoned interval between their Frasnian and lower Famennian zones (Fig. 20). More recently, Alekseeva et al. (2018a, b) followed the zonal scheme of Grechishnikova et al. (1980) and recognised only one brachiopod zone for the lower Famennian, and they used species characteristic of two different zones in the biozonation of Mamedov & Rzhonsnitskaya (1985) and Rzhonsnitskaya & Mamedov (2000). Finally, Serobyan et al. (2022a, b) recognised the lower Famennian *Aramazdospirifer orbelianus–Tornatospirifer armenicus* brachiopod assemblage Zone. Also, it should be noted that Mirieva (2010) described eight rhynchonellide assemblage and taxon-range biozones from the Upper Devonian successions of the Lesser Caucasus based exclusively on rhynchonellide brachiopod occurrences. However, the presence of some species used by Mirieva (2010) for the recognition of the substages of the Frasnian and Famennian is disputable; moreover, many of her biozones are based on species that are taxonomically poorly discriminated. For instance, she considered *Eoparaphorhynchus triaequalis* (Gosselet, 1877) as a characteristic species for almost all biozones spanning the lower to uppermost Famennian. But, as shown by Pakhnevich (2012), the specimens collected from Armenia and Nakhichevan, identified as *E. triaequalis*, differ from Gosselet's

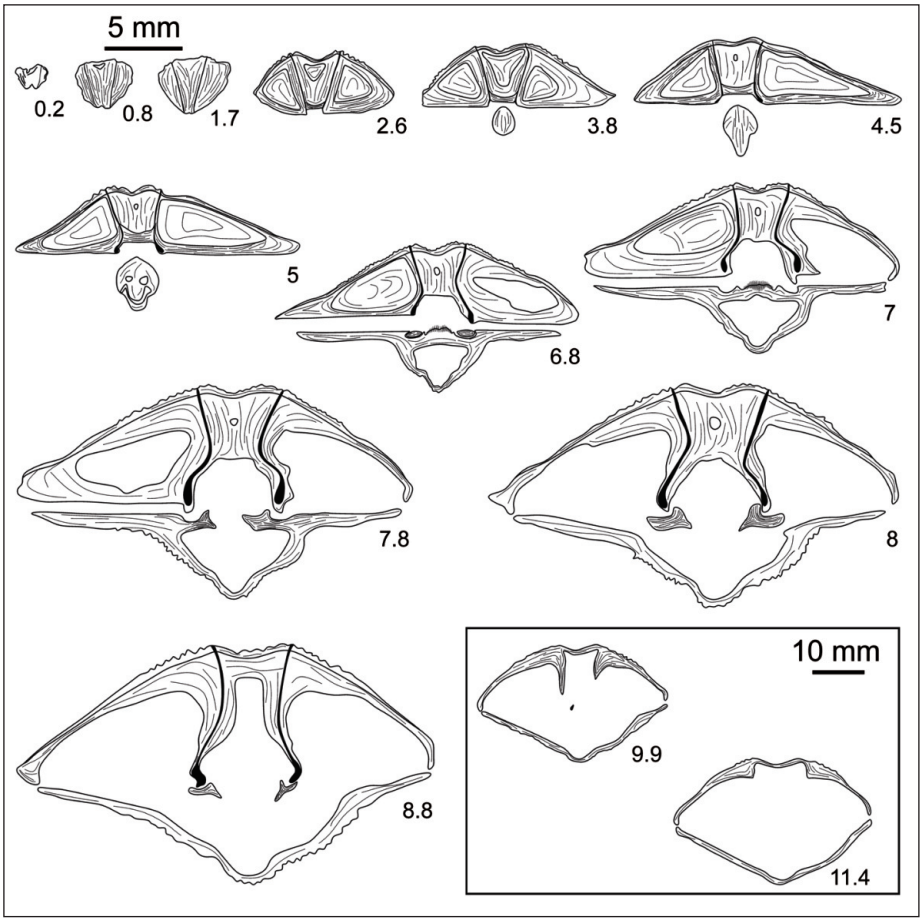

Fig. 19 - Transverse serial sections of Cyrtospiriferinae gen. indet. (IGSNASRAGM 3957/PS 3063) from the Frasnian *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod assemblage Zone of the Ertych section (Central Armenia). Numbers refer to distances in mm from the tip of the ventral umbo.

Stage	Substage	Conodont zones		Brachiopod zones				
		Standard (Ziegler & Sandberg, 1990)	Local zones established in Nakhichevan (Aristov, 1994)	Abrahamyan (1957)	Grechishnikova et al. (1982)	Rzhonsnitskaya & Mamedov (2000)	Mirieva (2010)	Serobyan et al. (2022b) & current study
Famennian	lower	*crepida*	*Polygnathus brevilaminus Icriodus cornutus*	*Cyrtospirifer orbelianus*	*Cyrtospirifer asiaticus –Mesoplica meisteri*	*Cyrtiopsis orbelianus– Cyrtiopsis armenicus*	*Ripidiorhynchus kotalensis*	*Aramazdospirifer orbelianus– Tornatospirifer armenicus*
		triangularis	*Polygnathus brevilaminus*			*Mesoplica meisteri– Cyrtospirifer asiaticus*	*Ripidiorhynchus griasica*	
Frasnian	upper	*linguiformis*	Unzoned	*Cyrtospirifer lonsdalii, Productella herminae, Camarotoechia radiata arpaensis* and five other species	Unzoned	Unzoned	Unzoned	Unzoned
		rhenana						*Ripidiorhynchus gnishikensis– Angustisulcispirifer arakelyani*
	middle	*jamieae*						
		hassi						
		punctata			*Cyrtospirifer subarchiaci– Cyphoterorhynchus arpaensis*	*Cyrtospirifer subarchiaci– Cyphoterorhynchus arpaensis*	*Cyphoterorhynchus koraghensis*	
	lower	*transitans*	*Ancyrodella rotunbiloba*					
		falsiovalis						
Giv.	Up.		*Ancyrodella binodosa*					

Fig. 20 - Biochronostratigraphic framework of the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus, including correlation of the newly established brachiopod assemblage biozone with the biozones of Serobyan et al. (2022b) and Abrahamyan (1957) in Central Armenia, and of Grechishnikova et al. (1982), Rzhonsnitskaya & Mamedov (2000) and Mirieva (2010) in Nakhichevan. The figure also includes the regional conodont zonation established by Aristov (1994) in Nakhichevan and the standard conodont zones of Ziegler & Sandberg (1990). Abbreviations: Giv., Givetian; Up., Upper.

(1877) species by the presence of punctae on the shell walls. For this reason he erected the new monospecific genus *Sharovaella* with its type species *Sharovaella mirabilis* and specified that the latter occurs only in the lower Famennian. Serobyan et al. (2019) revised the descriptions of eight trigonirhynchiid brachiopod species known from the Upper Devonian of Armenia and highlighted the biochronological potential of trigonirhynchiid brachiopods in dating accurately the upper Frasnian and parts of the lower and upper Famennian in the Lesser Caucasus. The biostratigraphic significance of rhynchonellides was later stressed by Pakhnevich (2020), who summarised the existing data on their occurrences. He noted that the Lower–Middle Devonian rhynchonellide assemblages of the Lesser Caucasus are mainly dominated by the representatives of the family Hebetoechiidae in contrast to those of the Frasnian and Famennian, which are dominated by the family Trigonirhynchiidae. Pakhnevich (2020) further specified that their diversity decreased afterwards and that they became a minor component of lower Carboniferous brachiopod assemblages, with no real utility for the biostratigraphy.

The brachiopod assemblages recovered from our studied sections (see Tab. 1) may be correlated with the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov (2000), which has been established in Nakhichevan, as several species from this zone are also identified in our material (e.g. *Ripidiorhynchus gnishikensis*, *Cyphoterorhynchus koraghensis* and *Atrypa* (*Planatrypa*) *ertichensis*). However, as neither of the two index species *Cyphoterorhynchus arpaensis* (Abrahamyan, 1957) or *Cyrtospirifer subarchiaci* sensu Rzhonsnitskaya & Mamedov (2000) (=*Angustisulcispirifer subarchiaci* [sic]), were found in our sections, we suggest introducing a new local biozone for the studied sections in Armenia. This zone is based on the species *Ripidiorhynchus gnishikensis* and *Angustisulcispirifer arakelyani* n. gen., n. sp., as they are both abundant in the lower limestone interval of all three studied sections (see Tab. 1). Moreover, *R. gnishikensis* has also been described in Nakhichevan (Pakhnevich in Alekseeva et al. 2018a). Consequently, we here establish a new brachiopod assemblage zone, namely the *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani*, for which neither the base, nor the top can be defined at this stage. Any of these two species may allow to recognise this local biozone in the studied sections. Given the conodonts retrieved at the Djravank section, the age of this zone is constrained to the Frasnian, between the latest early Frasnian and late Frasnian (between the *transitans* and the upper *rhenana* conodont zones). Within the interval corresponding to the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone, Aristov (1994) recognised two conodont zones: *Ancyrodella binodosa* and *A. rotundiloba*. He noted that the *A. binodosa* Zone corresponds to the lower part of *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone, whereas the *rotundiloba* Zone is coeval to the upper part of *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone. The author further specified that the most important taxa for the recognition of the Givetian–Frasnian boundary, namely *Ancyrodella binodosa* and *A. rotundiloba*, are extremely rare in the studied sections, which excludes the possibility to determine their first and last appearances. Therefore, he suggested to temporarily place the Givetian–Frasnian boundary within the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone. Nonetheless, Rzhonsnitskaya & Mamedov (2000) raised the lower boundary of the latter brachiopod zone to the lower Frasnian. We concur with the viewpoint of Rzhonsnitskaya & Mamedov (2000), since Aristov's (1994) main point for considering the lower part of the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone as Givetian in age was based on the presence of *A. binodosa*, a conodont species that may also occur in the lower Frasnian (e.g., Reissner 1989; Gouwy et al. 2007); thus, no data on conodonts were presented by Aristov (1994) to explicitly support a Givetian age. Furthermore, as Aristov (1994) reported *A. rotundiloba*, a species that does not range above the *punctata* Zone (Ziegler & Sandberg 1990: 17), in the upper part of the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone, it is reasonable to assume that the age of this biozone is likely to be covering the lower–middle Frasnian interval and the latter may be correlated with the *falsiovalis–punctata* conodont zones.

Brachiopod palaeobiogeography

Unlike the Emsian and Middle Devonian, which was characterized by cooler climatic conditions and global faunal endemism, especially among marine invertebrates, the early and middle Frasnian was a time of globally warm climatic conditions

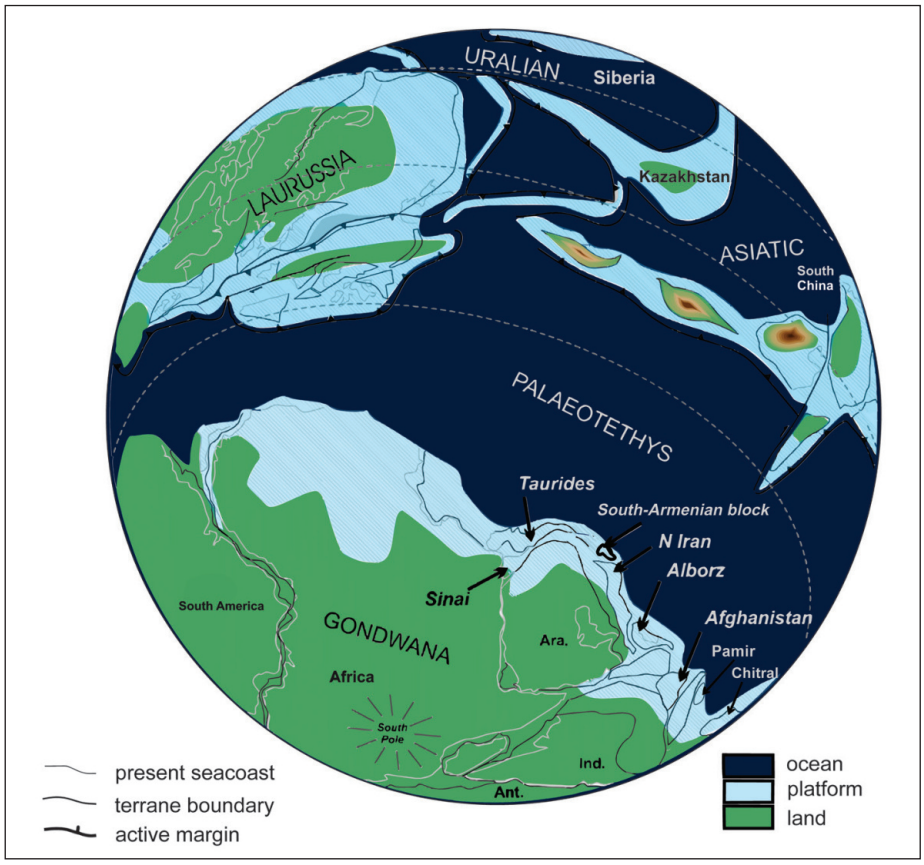

Fig. 21 - Late Devonian palaeogeographic reconstruction of the Palaeotethys Ocean and its surrounding continents, including the position of the South Armenian Block along the northern margin of the Gondwana megacontinent (redrawn and modified after Denayer & Hoşgör 2014, based on the maps of Stampfli et al. 2002). Abbreviations: Ant., Antarctica; Ara., Arabia; Ind., India.

(Joachimski et al. 2009) and of high sea level (Vail et al. 1977; Johnson et al. 1985). The combination of these environmental conditions, in addition to continental or terrane amalgamation, and favorable oceanic circulation patterns, have probably led to changes in Devonian marine biogeography from a high level of provinciality during the Early Devonian to a low one during the Late Devonian (Oliver 1976; McGhee 1996; Copper 1998; Rode & Lieberman 2004). Generally, the Late Devonian has long been recognised as an interval of strong faunal cosmopolitanism, during which marine faunas attained wide geographic coverage, as exemplified by benthic organisms, notably brachiopods (Johnson 1971; Racki 1998; Rode & Lieberman 2004). However, Gaetani (1965, 1968), Brice (1971), and Brice et al. (1973, 1999) documented a striking similarity among the Late Devonian brachiopod faunas thriving on the shallow-water carbonate platform of the northern margin of Gondwana, namely from Armenia to NW Pakistan. They further pointed out that a single bioprovince may be individualized for the Late Devonian brachiopod assemblages described along this realm. The quantitative analysis presented by Brock & Yazdi (2000) improved the understanding of palaeobiogeographic affinities of Late Devonian brachiopods from Iran, and also confirmed the latter findings. More recently, Serobyan et al. (2021) concurred with this viewpoint based on the brachiopod fauna they described in Armenia, as well as the available data from the region, and advocated a rather uniform early Famennian brachiopod bioprovince that was developed between Pamir (to the east) and the Anatolide-Tauride microplate (to the west). In this context, *Cyphoterorhynchus koraghensis* (Reed, 1922), described in this study, is of particular palaeobiogeographic significance, since the latter is found in Armenia, Afghanistan, Chitral (NW Pakistan), Iran, and probably Turkey, all of which were situated only along the northern margin of the Gondwanan megacontinent (Fig. 21). It is also worth emphasising here that the genus *Cyphoterorhynchus* Sartenaer, 1964 has a wider palaeobiogeographic distribution extending from Chitral westward to Libya and Spain. Unlike *Cyphoterorhynchus*, the genus *Ripidiorhynchus* Sartenaer, 1966a occurs both in Gondwana and Laurussia megacontinents. More particularly, Racki (1993) reported some rhynchonellide specimens from the upper Givetian of Poland (Góra Zamkowa and Stokówka), which he identified as *Ripidiorhynchus* aff. *pskovensis* (Nalivkin 1941). The author further specified that although he tentatively assigned these

specimens to *R. pskovensis* [=*Ripidiorhynchus livonicus* (Buch, 1834), according to Sokiran (2002)], they may also represent a new species, as well as the oldest record of this genus. Later, Sokiran (2002) revised this material and, on its basis, erected a new species, *Ripidiorhynchus chencinensis*. Two representatives of the genus *Ripidiorhynchus*, namely *Ripidiorhynchus aldogus* (Nalivkin, 1941) and *Ripidiorhynchus griasicus* (Nalivkin, 1934) occur in the lower Frasnian strata of the Main Devonian Field (Northwestern region of the East European Platform (EEP)), whereas *Ripidiorhynchus livonicus* (Buch, 1834) and *Ripidiorhynchus huotinus* (de Verneuil, 1845) occur in the lower Famennian of the Central Devonian Field (Central region of the EEP) (see references in Sokiran 2002). Therefore, it is reasonable to assume that although it first occurred in the upper Givetian strata of Poland, this genus later expanded to the north-western region of the platform due to the early Frasnian transgression and later to the south-east, migrating towards the northern margin of Gondwana; it thus colonised the SAB carbonate platform in the course of the early and middle Frasnian. In the present study, three atrypide species are described, of which *Atrypa* (*Planatrypa*) *ertichensis* (Abrahamyan, 1959) and *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992 appear to be restricted to the SAB, since they have been documented only from Armenia and Nakhichevan. However, they belong to genera/subgenera that can rather be considered cosmopolitan because they are known worldwide. The third species, left in open nomenclature, is assigned to *Spinatrypa* well-known notably from the Givetian–Frasnian shallow water carbonate/siliciclastic deposits of North America (see references in Day & Copper 1998), Western Europe (Copper 1965, 1967b; Mottequin 2003, 2008) and Lesser Caucasus (Komarov 1997). The newly created genus *Angustisulcispirifer*, in addition to its type species *A. arakelyani* n. gen., n. sp., described in the lower–middle Frasnian interval of Armenia, and a species from Nakhichevan, may also include two more species reported from the Famennian of Central Kara-Tau (Kazakhstan). In addition to the recent data, also considering that Serobyan et al. (2022a, b), who identified three cyrtospiriferid genera (*Aramazdospirifer*, *Pentagonospirifer* and *Tornatospirifer*) from the early Famennian of Armenia and assigned several species from Kara-Tau to them, one can note the similarity between the Late Devonian brachiopod faunas from Kara-Tau and synchronous faunas from Armenia. Furthermore, this observation seems to be especially true for cyrtospiriferids.

Conclusions

Recent brachiopod sampling from Central Armenia allowed to identify an assemblage composed of seven species. Based on the presence of species *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959), *Cyphoterorhynchus koraghensis* (Reed, 1922), *Atrypa* (*Planatrypa*) *ertichensis* (Abrahamyan, 1959) and *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992, this assemblage may be tentatively considered as lateral equivalent of the lower–middle Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone established in Nakhichevan. However, as neither of the two index species of the latter zone were found in the sections studied in Armenia, a new local brachiopod assemblage zone is introduced, namely the *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani*. The latter is dated as of latest early Frasnian to late Frasnian in age based on conodonts identified in the Djravank section. Revision of the rhynchonellide, atrypide and cyrtospiriferide brachiopods recovered from the latter zone revealed some species that were previously unknown from this interval and also several new features in the species that were already known, but poorly illustrated, and consequently led us to define a new genus and a new species. Most notably, *Angustisulcispirifer arakelyani* n. gen., n. sp. is erected to solve a long-standing taxonomic confusion associated with *Cyrtospirifer subarchiaci* Martelli (1902) sensu Arakelyan (1952), a taxonomically poorly known, but at the same time biostratigraphically valuable species. *Atrypa* (*Planatrypa*) *ertichensis* (Abrahamyan, 1959) appears to possess frills, an ornamental feature rarely observed in this (sub)genus and considered unknown in this species. Two spinatrypinid shells ascribed to *Spinatrypa* Stainbrook, 1951 represent the first report of the genus *Spinatrypa* in the Frasnian of the Lesser Caucasus, since representatives of this genus were reported previously only in the Middle Devonian (Eifelian–Givetian) of Nakhichevan. The palaeobiogeographic distribution of the rhynchonellides and atrypides within the Frasnian of Armenia suggests that the brachiopod communities thriving on the shallow water carbonate platform of the SAB included some apparently endemic species (e.g., *Ri-*

pidiorhynchus gnishikensis, *Desquamatia* (*Seratrypa*) *abramianae*, *Atrypa* (*Planatrypa*) *ertichensis*, but also species (*Cyphoterorhynchus koraghensis*), which was common in other parts of the Gondwanan northern margin extending eastwards to Iran, Afghanistan and Chitral, and probably westwards to Turkey. However, although some Frasnian brachiopods from Central Armenia are described here, it appears that new surveys are urgently needed to understand Late Devonian changes in brachiopod diversity.

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