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

3

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19

20 *Keywords:* Atrypida; Rhynchonellida; Spiriferida; Frasnian; Gondwana; Lesser Caucasus.

21

22 *Abstract.* An assemblage of seven brachiopod species belonging to the orders Rhynchonellida,  
23 Atrypida and Spiriferida are studied from three distinct localities of Central Armenia. The  
24 examined material is recovered from an interval of shallow water nodular limestones and  
25 provides insights into the diversity of Frasnian brachiopods on that part of the northern margin of  
26 Gondwana preserved within the South Armenian Block. The revision of *Atrypa (Planatrypa)*  
27 *ertichensis*, a biostratigraphically significant species for the Frasnian of the Lesser Caucasus  
28 (Armenia and Nakhichevan), revealed the presence of frills, an ornamental feature rarely  
29 observed in this (sub)genus and considered unknown in this species. Taxonomic discussion  
30 involves also the selection of neotypes for *Ripidiorhynchus gnishikensis* and *Atrypa (Planatrypa)*  
31 *ertichensis*. The newly described species, *Angustisulcispirifer arakelyani* n. gen., n. sp., appears

32 to be one of the most biostratigraphically characteristic for the Frasnian of Armenia. The  
33 intraspecific morphological variability of *Cyphoterorhynchus koraghensis* concerns especially  
34 the presence or absence of crenulations of the teeth and dental sockets. The size variability of *C.*  
35 *koraghensis* and *Desquamatia (Seratrypa) abramianae* is documented quantitatively for the first  
36 time and it shows a continuous and progressive growth without any distinct groupings; the  
37 former is a palaeobiogeographically important species for the Frasnian strata of the northern  
38 Gondwana margin. Pending the revision of the Pakistani and Iranian material, a plaster cast of  
39 the lectotype of *C. koraghensis* from the Frasnian of Kuragh in Chitral (northwest Pakistan), the  
40 holotype as well as one of the paratypes of *Cyphoterorhynchus koraghensis interpositus* from the  
41 Frasnian (Bahram Formation) of the Ozbak-Kuh region in eastern Iran are illustrated herein.  
42 Finally, a new Frasnian brachiopod zone, namely the *Ripidiorhynchus gnishikensis*–  
43 *Angustisulcispirifer arakelyani* assemblage Zone is here introduced for the studied sections.  
44 Although, its base and top cannot be identified, it is constrained to the Frasnian based on  
45 conodonts identified in the Djravank section. It may be considered as a partly lateral equivalent  
46 of the *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone established in  
47 Nakhichevan.

48

49 *Running Header.* Frasnian brachiopods from Armenia

50

## 51 **Introduction**

52

53 During the Devonian, brachiopods were the most abundant and diverse group of filter-  
54 feeding organisms, thriving in shallow-water tropical and subtropical marine environments  
55 (Sepkoski 1981; Ma & Day 1999; Curry & Brunton 2007). However, they were severely affected  
56 in the course of the Frasnian–Famennian (F–F) biotic crisis due to different global change events  
57 that generated major sea-level changes and marine anoxia (McGhee 1996; Racki 1998; Racki &  
58 House 2002; Huang et al. 2018). Regional taxonomic and biostratigraphic studies of these shell-  
59 forming sessile marine invertebrates are important to better understand the regional impact of  
60 Late Devonian crisis events to their diversity, evolution and palaeobiogeographic distribution.

61 The Upper Devonian sequences of the Lesser Caucasus (Armenia and Nakhichevan; Fig.  
62 1) are represented by shallow water, mixed carbonate-siliciclastic deposits. They constitute the

63 South Armenian Block, which was then part of the northern margin of Gondwana (Sosson et al.  
64 2010). More particularly, during the Late Devonian, this realm was part of a considerable  
65 carbonate platform that was positioned within a tropical zone of the southern hemisphere (Brock  
66 & Yazdi 2000; Scotese 2014; Golonka 2020). The Upper Devonian sequences in Armenia are  
67 highly fossiliferous and contain a diverse and well-preserved brachiopod fauna. Thus, their fossil  
68 record may provide valuable insights to the brachiopod diversity of the northern margin of  
69 Gondwana.

70 The Devonian outcrops in the area were first studied by the famous German geologist  
71 Hermann Abich in 1858, who also described several new brachiopod species from them, notably  
72 the cyrtospiriferid *Spirifer orbelianus* Abich, 1858, which was recently revised and reassigned to  
73 the newly erected genus *Aramazdospirifer* Serobyán et al. (2022a). Few other papers dealt with  
74 Devonian brachiopods in the first part of the 20<sup>th</sup> century (e.g., Frech & Arthaber 1900; Bonnet  
75 1947). Following World War II, Upper Devonian–Carboniferous brachiopods and their  
76 biostratigraphy were studied systematically by Abrahamyan during the years 1949 to 1974. In  
77 her groundbreaking monography, Abrahamyan (1957) described and illustrated 36 brachiopod  
78 species from the Famennian–Tournaisian interval. Later, Abrahamyan (1959) wrote an article  
79 mainly devoted to the Frasnian species, where she described some rhynchonellides and atrypides,  
80 which were partly revised by her afterwards (Abrahamyan, 1974), in addition to newly studied  
81 Frasnian species. However, as shown by some recent papers dealing with the Devonian  
82 brachiopods of the Lesser Caucasus (Alekseeva et al. 2018a, b; Serobyán et al. 2019, 2021,  
83 2022a, b), in contrast to the Famennian brachiopods, the Frasnian ones have received relatively  
84 little attention and remain largely undocumented from a taxonomic point of view, not to mention  
85 their palaeoecological, palaeobiogeographic, or evolutionary understandings.

86 Consequently, the main objective of this paper is to revise and update the systematic  
87 classification of the Frasnian brachiopods from Armenia. This revision is mainly based on newly  
88 collected material from three distinct localities in Central Armenia (Ertych, Džravank and  
89 Noravank; Fig. 1), and is supplemented by brachiopod specimens stored in the collections  
90 assembled by Abrahamyan and Arakelyan, between 1940 and 1980. Furthermore, the  
91 biostratigraphy of the Frasnian–lower Famennian brachiopods from the Lesser Caucasus is also  
92 discussed. The incapacity to use previously established biozones led us to introduce a new local  
93 brachiopod assemblage zone for the Frasnian sequences of Armenia, which is constrained by

94 conodonts to the Frasnian and correlated with likely lateral equivalents in Nakhichevan. We  
95 finally discuss the palaeobiogeographic affinities of the studied Frasnian brachiopods.

96

### 97 **Stratigraphic setting**

98

99 An over 1500 m-thick pile of Middle Devonian–Lower Carboniferous deposits is present in the  
100 Lesser Caucasus (Fig. 1). The Middle Devonian part has a restricted distribution in Armenia and  
101 crops out only along the border with Nakhichevan, whereas the Upper Devonian part has a  
102 relatively wider distribution, but correlating the different sections still remains complicated due  
103 to biostratigraphic uncertainties. The Upper Devonian sequences consist essentially of marly and  
104 sandy biogenic limestones, rich in brachiopods, and intercalations of arenitic and fine-grained  
105 sandstones and shales. Only a few sections exposing the Frasnian–lower Famennian shallow-  
106 water facies are known in Armenia and further research is necessary. The sections covering this  
107 particular stratigraphic interval, which were studied in the last decades, provide valuable  
108 information on different fossil groups, such as corals (Sytova et al. 1974), chondrichthyan  
109 microremains (Ginter et al. 2011), conodonts (Grigoryan et al. 2019), and trilobites (Crônier et  
110 al. 2021), but limited information is available on lithostratigraphy. The F–F sequences are  
111 exposed mainly below the monastery of Noravank and around the locality Ertych (Fig. 1). The  
112 latter consist chiefly of two distinct nodular limestone intervals, rich in brachiopods, which are  
113 separated by an interval of black shales that is overlain by mature sandstones (Fig. 2). The  
114 brachiopods of the upper limestone interval were recently revised and documented by Serobyan  
115 et al. (2021, 2022a, b) and Serobyan & Mottequin (2022). The brachiopod assemblage of the  
116 lower limestone interval is the subject of this paper.

117

### 118 **Material and methods**

119

120 The examined material was collected during several field seasons organised during 2018–  
121 2022 from three sections (Fig. 3) cropping out in the Vayots Dzor Province of Southwest Central  
122 Armenia. Two of them, Ertych and Noravank sections, were already studied by Arakelyan  
123 (1964) and Ginter et al. (2011), respectively, while the Djravank section was only briefly  
124 presented in Grigoryan et al. (2019). The latter is situated ca. 9 km east of the little town of Areni

125 (39°43.670' N, 45°16.145' E). The studied section crops out along a mountainous path leading to  
126 a small abandoned church. Here the lower limestone sequence is observed with its entire  
127 thickness of 22 m, intercalated between sandstones and shales at the base and shales at the top.  
128 The Ertych section is situated on the southern bank of the Arpa River (ca. 8.5 km east of Areni),  
129 in an abandoned quarry (39°43.850' N, 45°16.300' E). Here, only the upper 10 m of limestones  
130 are observed, overlain stratigraphically by a thick sequence of blackish shales. Finally, in the  
131 Noravank section, situated just below the famous monastery (39°41.110' N 45°13.730' E) only  
132 the upper 12 m of the limestone interval could be observed, overlain in their turn by shales. Most  
133 of the specimens illustrated and investigated herein are deposited at the Geological Museum of  
134 the Institute of Geological Sciences of the National Academy of Sciences of Armenia, Yerevan  
135 (prefixed IGSNASRAGM/PS). The prefix PS indicates the laboratory of Paleontology and  
136 Stratigraphy. A few specimens are housed at the public palaeontological collection of the Lille  
137 University, France. Additional illustrated specimens are curated at the Royal Belgian Institute of  
138 Natural Sciences in Brussels (prefixed RBINS), notably one plaster cast of a sample curated at  
139 the Geological Survey of India (Kolkata) (prefixed GSI). The internal morphology of the  
140 specimens was investigated by using the standard technique of serial sections and acetate peels.  
141 In order to capture the fine details related to the development of internal features, the serially  
142 sectioned specimens were photographed directly under a Canon EOS 700D camera that was  
143 attached to a Zeiss SteREO Discovery V20 Microscope. Specimens deposited at the  
144 IGSNASRAGM were coated with magnesium oxide before being photographed by a Canon EOS  
145 700D camera, equipped with the Canon EFS 60 mm macro lens. RBINS material was  
146 photographed using an Olympus OM-D E-M10 Mark II digital camera, equipped with the  
147 Olympus M.Zuiko Digital ED 60 mm macro lens, and coated with ammonium chloride.

148 Conodonts were obtained from three samples of the lower limestone interval of the  
149 Djravank section (Fig. 3) after processing with formic acid at the Institute of Geological Sciences  
150 (Yerevan). Several tens of conodont elements were recovered and picked up in Yerevan. Some  
151 of them were mounted on SEM stubs and gold coated for ca. 2 minutes. They were photographed  
152 by a ZEISS EVO 10 Scanning Electron Microscope hosted with the Palaeontology team of Lille  
153 University (UMR 8198 Evo-Eco-Paleo). Samples Dj19/8 and 19.9 include conodont elements of  
154 *Polygnathus webbi*, *Icriodus excavatus* and *Polygnathus ?linguiformis*. This record suggests an  
155 age range from *norrisi* (uppermost Givetian) to Upper *rhenana* (upper Frasnian) biozones. The

156 lowermost conodont bearing sample Dj19/10 contains some diagnostic elements referable to  
157 *Polygnathus aequalis* morphotype II, which suggests *transitans* (uppermost of lower Frasnian)  
158 conodont biozone or younger. Taking these data into consideration, the age of the lower  
159 brachiopod bearing interval is within the age range from *transitans* (uppermost of lower  
160 Frasnian) to Upper *rhenana* (upper Frasnian).

161

## 162 **Systematic palaeontology**

163

164 The beds from which brachiopods were collected are indicated in Figure 3. Table 1 provides the  
165 occurrence of the identified brachiopod species in the three studied sections. The supraspecific  
166 classification used herein follows Savage (2002, 2007) for the Order Rhynchonellida instead of  
167 the one adopted by Sartenaer (2001, 2003), wherein the Subfamily Ripidiorhynchinae Savage,  
168 1996 is elevated to the family level with *Ripidiorhynchus* Sartenaer, 1966a as its only  
169 representative. Likewise, the supraspecific classification follows Copper (2002) for the order  
170 Atrypida, except otherwise stated, and Carter et al. (1994) and Johnson (2006) for the Order  
171 Spiriferida.

172

173 Order **Rhynchonellida** Kuhn, 1949

174 Superfamily Rhynchotrematoidea Schuchert, 1913

175 Family Trigonirhynchiidae Schmidt, 1965

176 Subfamily Ripidiorhynchinae Savage, 1996

177 Genus *Ripidiorhynchus* Sartenaer, 1966a

178

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

181

182 *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959)

183 Fig. 4–5; Tab. 2

184

185 1959 *Camarotoechia strugi* Nal. subsp. *gnishikensis* Abrahamyan, p. 6, pl. 2, fig. 5–7.

186 1964 *Camarotoechia strugi* Nal. subsp. *gnishikensis* Abrahamyan, 1959 - Arakelyan, pp. 67, 70,  
187 74, 92, 93.

188 1975 *Ripidiorhynchus (Camarotoechia) strugi* var. *gnishikensis* (Abr.) - Arakelyan et al., p. 22.

189 2018a *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) - Pakhnevich in Alekseeva et al., pp.  
190 852, 905, pl. 6, fig. 6a–d; pl. 14, fig. 6 and 18; text-fig. 50.

191 2019 *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) - Serobyanyan et al., p. 7.

192

193 **Neotype:** Although Abrahamyan (1959: pl. 2, fig. 5–7) designated a holotype among the three  
194 specimens she illustrated, neither the holotype nor other specimens examined in her publication  
195 were traced within Abrahamyan's brachiopod collections stored at the IGSNASRAGM and are  
196 therefore considered as lost. Consequently, the single specimen figured in Figure 4 is hereby  
197 designated as the neotype (IGSNASRAGM 3927/PS 3033).

198

199 **Type horizon:** Frasnian nodular limestones.

200

201 **Type locality:** Djavank section (ca. 9 km east of Areni, Vayots Dzor Province, Southwest  
202 Central Armenia) (Fig. 1, 3).

203

204 **Material:** Nine articulated specimens and four ventral valves from the Ertych (four articulated  
205 specimens and two ventral valves) and Djavank (five articulated specimens and two ventral  
206 valves) sections.

207

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

212

213 Ventral valve gently inflated in both lateral and posterior profiles with flanks sloping  
214 gently towards lateral commissures; highest near umbo then, decreasing progressively towards  
215 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



216 round bottomed at front; tongue high and wide, with sharp borders, subtrapezoidal in outline,  
217 perpendicular to commissural plane or slightly bent dorsally.

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

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

226 Ventral valve interior (Fig. 5) with thin, long dental plates converging ventrally; teeth  
227 massive, subrectangular in outline; central apical cavity wide.

228 Dorsal valve interior (Fig. 5) with low and very short septum; septalium deep, Y-shaped  
229 and covered anteriorly; hinge plate united.

230

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

242

243 **Occurrence.** *Ripidiorhynchus gnishikensis* was first described in Armenia by Abrahamyan  
244 (1959), in the Frasnian sequences of the Gnishik section (Fig. 1). Later it was reported by  
245 Arakelyan (1964) in the Frasnian sequences of the Baghrsagh and Danzik sections (Fig. 1) as  
246 well as in the lower Famennian of the Noravank, Ertych and Gyumushlug sections (Fig. 1)

247 within a brachiopod assemblage including Frasnian spiriferides. Presumably Arakelyan (1964)  
248 confused *R. gnishikensis* with a lower Famennian representative of that genus as Abrahamyan's  
249 species occurred only in the Frasnian. Unfortunately, the specimens identified as *R. gnishikensis*  
250 by Arakelyan cannot be traced within his collections and are considered as lost, which excludes  
251 any possibility of re-examination. However, Arakelyan et al. (1975) mentioned *R. gnishikensis*  
252 amongst the biostratigraphically significant species characterising the Frasnian in Armenia.  
253 Afterwards, Pakhnevich in Alekseeva et al. (2018a) examined numerous specimens from several  
254 localities in Nakhichevan and specified that it actually occurs within the *Cyrtospirifer*  
255 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov  
256 (2000) (coeval with the *falsiovalis*–*punctata* conodont zones), confirming the viewpoint of  
257 Arakelyan et al. (1975) that *R. gnishikensis* is restricted to the Frasnian strata. Additionally, it is  
258 judicious to remind here that recent sampling also revealed the presence of this species only in  
259 the Frasnian strata.

260

261 Genus *Cyphoterorhynchus* Sartenaer, 1964

262

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

265

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

270

271 *Cyphoterorhynchus koraghensis* (Reed, 1922)

272 Fig. 6–8, 9A–E; Tab. 3

273

274 1922 *Uncinulus (Uncinulina) koraghensis* Reed, p. 40, 120, 123–125, pl. 7, fig. 10–13 (see also  
275 for synonymy before 1922).

276 ?1922 *Uncinulus (Uncinulina) koraghensis* var. *pentagonalis* Reed, p. 42, 120, 123, 125, pl. 7,  
277 fig. 14–17.

278 ?1922 *Uncinulus (Uncinulina) koraghensis* var. *transiens* Reed, p. 43, 120, 123, 125, pl. 7, fig.  
279 18–20.  
280 ?1922 *Uncinulus (Uncinulina) koraghensis* var. *ponderosa* Reed, p. 44, 120, 123, 125, pl. 7, fig.  
281 21–22a; pl. 8, fig. 1, 1a.  
282 1952 *Uncinulus (Uncinulus) koraghensis* Reed - Arakelyan, p. 36.  
283 1964 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Sartenaer, p. 51, pls. 4–5.  
284 1966b *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Sartenaer, p. 28–29, 34–37 (see  
285 also for synonymy of Iranian material).  
286 1971 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922) - Brice, p. 47, 309–315, 318, 323,  
287 336, pl. 3, fig. 1a–d, 6a–d; text-fig. 13A; tab. 5.  
288 1975 *Cam. [Camarotoechia] karaghensis [sic] koraghensis* Reed - Arakelyan et al., p. 24.  
289 2000 *Cyphoterorhynchus koraghensis* Reed, 1922 - Rzhonsnitskaya & Mamedov, p. 330.  
290 2002 *Cyphoterorhynchus koraghensis* (Reed, 1922) - Savage, p. 1076, fig. 728, 1 a–n (copy of  
291 Sartenaer, 1964, pl. 4, fig. 4 a–b, d–e).  
292 2010 *Cyphoterorhynchus koraghensis* Reed - Mirieva, p. 74, 75, tab. 1.

293

294 **Lectotype:** As Reed (1922) did not designate any holotype amongst the specimens he illustrated,  
295 Sartenaer (1964) designated the specimen (GSI 12115) figured by Reed (1922: pl. 7, fig. 10–10a)  
296 as the lectotype of this species (see also Sartenaer, 1966b). The plaster cast of the lectotype, sent  
297 by B.C. Roy to P. Sartenaer in 1965, is illustrated herein (Fig. 9A–E).

298

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

301

302 **Material examined:** Twenty-five articulated specimens and four ventral valves from the Ertych  
303 (eighteen articulated specimens and two ventral valves) and Djravank (eleven articulated  
304 specimens and two ventral valves) sections.

305

306 **Description.** Shell medium-sized, attaining up to 27 mm in width, 24.3 mm in length and 18.5  
307 mm in thickness (Tab. 3), transversally ovate in outline, wider than long, widest and highest at

308 about midlength, strongly dorsibiconvex, anterior margin emarginate; anterior commissure  
309 uniplicate and serrate.

310       Ventral valve slightly inflated with flanks sloping gently towards lateral commissures;  
311 beak suberect; foramen minute, permesothyrid; sulcus wide, shallow to moderately deep,  
312 generally well-defined by sulcus bounding costae, imperceptibly starting from midlength or more  
313 anteriorly, deepening gradually towards anterior margin, flat- to round-bottomed at front; tongue  
314 high, perpendicular to commissural plane, subtrapezoidal in outline.

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

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

326       Ventral valve interior (Fig. 7) with short, stout and subparallel dental plates situated close  
327 to the walls; teeth massive, subrectangular in outline; central apical cavity wide; lateral apical  
328 cavities poorly infilled by callosity.

329       Dorsal valve interior (Fig. 7) with high and long septum; septalium V-shaped, not deep,  
330 relatively narrow and covered anteriorly; hinge plates united anteriorly to septalium; crural bases  
331 stout, diverging dorsally.

332  
333 **Shell ontogeny.** The size distributions of *C. koraghensis* during growth, as represented by the  
334 width/length, the width/thickness and the width/width of sulcus plots, show a continuous and  
335 progressive growth with no distinct grouping (Fig. 8). The relative proportions of *C. koraghensis*  
336 represented by sufficient material remain constant (linear regression:  $y = ax+b$ ; significant  
337 probability value:  $p < 0.001^{***}$ ) whatever the degree of development of individuals (Fig. 8).  
338 Moreover, the correlation is positive with width varying proportionally with length, thickness

339 and width of sulcus. To complete the scatter plots, the measurements of numerous individuals of  
340 *C. koraghensis* are also presented in Tab. 3.

341  
342 **Remarks.** According to the article 45.6.4 of the International Code of Zoological Nomenclature  
343 (ICZN 1999), the epithets, which were used for the varieties of *Uncinulus* (*Uncinulina*)  
344 *koraghensis* introduced by Reed (1922) (see synonymy list), must be considered as of  
345 subspecific rank in his publication. In erecting the genus *Cyphoterorhynchus*, Sartenaer (1964)  
346 estimated that these varieties (sic) could fall within the limits of the variability of the species and  
347 stressed that further specimens from a tighter sampling were needed to decide on this matter.  
348 Sartenaer (1966b), after having examined the plaster casts of Reed's (1922) illustrated  
349 specimens, definitely considered that the varieties (sic) enter in the limits of the variability of the  
350 species. Nevertheless, Sartenaer (1966b) complicated the situation in erecting  
351 *Cyphoterorhynchus koraghensis interpositus* from the Frasnian (Bahram Formation) of the  
352 Ozbak-Kuh region in eastern Iran, of which the holotype (Fig. 9F–K) and one of the paratypes  
353 (Fig. 9L–P) are illustrated here. Indeed, he considered that some of the specimens from the type  
354 locality of *C. koraghensis*, including some paralectotypes, may belong to his new subspecies and  
355 thus ignored the names introduced by Reed (1922). Moreover, he indicated that the two *C.*  
356 *koraghensis* subspecies and *C. arpaensis* (Abrahamyan 1957) occur in the same beds within the  
357 Iranian sections, which is puzzling biologically speaking as the subspecies must be  
358 geographically or stratigraphically separated from each other. Pakhnevich in Alekseeva et al.  
359 (2018a) recently placed Sartenaer's (1966b) subspecies in synonymy with *C. arpaensis*. We do  
360 not comment further on the validity of the subspecies *interpositus*, leaving it temporarily aside  
361 from the nominal subspecies, as only the study of large collections of *Cyphoterorhynchus*  
362 specimens from the Kuragh Ridge and the revision of the Pakistani material investigated by Reed  
363 (1922), which is curated at the GSI, will shed new light on the taxonomical issues related to *C.*  
364 *koraghensis*. This is the reason for which we have placed Reed's (1922) varieties (= subspecies)  
365 into doubtful synonymy, pending their revision, but these could simply be morphotypes or even  
366 ecotypes of the same species.

367         The material investigated herein fits well with Sartenaer's (1964) description of *C.*  
368 *koraghensis* although the teeth and dental sockets of the studied specimens lack the crenulations  
369 observed in the Chitral specimens. This species, which has already been recognised within the

370 Frasnian of Central Armenia (Arakelyan 1952; Arakelyan et al. 1975) and Nakhichevan (Mirieva  
371 2010; Rzhonsnitskaya & Mamedov 2000), is also known from the middle and upper Frasnian of  
372 northwestern Pakistan (Chitral; Reed 1922), Afghanistan (Brice 1971; Kuhn, 1977) and Iran  
373 (Sartenaer 1966b), thus from Gondwanan terranes. Furthermore, Gourvennec (2006) illustrated a  
374 single specimen from the Upper Devonian (probably from the lower Frasnian) of Eastern Taurus  
375 (Turkey) and identified it as *C. koraghensis*. Although he did not examine its internal structure,  
376 this assignment seems to be the most satisfactory as it does not differ externally from Reed's  
377 species. Moreover, his assignment can be further supported by the resemblance of Devonian  
378 brachiopod assemblage recovered by him from the Eastern Taurus (Turkey) with those described  
379 in Afghanistan, Iran, Pakistan and the Lesser Caucasus.

380 *C. koraghensis* displays strong similarities with *C. arpaensis* (Abrahamyan, 1957);  
381 however the latter differs by its subcircular tongue and having fainter and fewer costae on flanks  
382 and in sulcus and on fold. *C. arpaensis* is one of the most biostratigraphically valuable species in  
383 the Lesser Caucasus and used for the definition of a Frasnian brachiopod zone, namely the  
384 *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya & Mamedov  
385 (2000). However, our recent sampling did not reveal the presence of this species in the Frasnian  
386 of our studied sections. Although Abrahamyan (1957) did not designate a type specimen among  
387 the two she illustrated, Pakhnevich in Alekseeva et al. (2018a) considered the only photographed  
388 specimen (Abrahamyan 1957: pl. 5, fig. 6) as the holotype. According to the Article 73 of the  
389 International Code of Zoological Nomenclature (ICZN 1999), the holotype of a new species can  
390 only be fixed in the original publication and by the original author, and thus Abrahamyan's  
391 specimen selected by Pakhnevich cannot be considered as the valid holotype. Moreover, the  
392 specimen chosen by Pakhnevich from Abrahamyan (1957)'s publication is lost. Therefore, a  
393 neotype must be designated among the specimens of Abrahamyan (1957)'s collection, which is  
394 currently stored at the IGSNASRAGM.

395 Contrary to Pakhnevich's statement (in Alekseeva et al. 2018a: 910), *Cyphoterorhynchus*  
396 *arpaensis* does not occur in the Frasnian of Belgium, where the genus has never been recovered.  
397 Furthermore, *Cyphoterorhynchus* seems to be a Gondwana-restricted genus as, besides the  
398 aforementioned areas, it is also known from Australia (e.g. Sartenaer 1964; Roberts et al. 1972;  
399 Dring 1980), Libya (Mergl & Massa 1992, 2000) and southern Spain (Pardo & García-Alcalde  
400 1984) (see Brock & Yazdi 2000: fig. 5).

401  
402 **Occurrence.** In Armenia, recent samplings revealed the presence of this species only in the  
403 Frasnian interval. Previous reports of it by Arakelyan (1952) and Arakelyan et al. (1975) from  
404 the lower Famennian strata of the Gyumushlug section (Fig. 1) need to be considered as dubious,  
405 as the position of the Frasnian–Famennian boundary is not known yet due to the absence of the  
406 diagnostic conodont species. Moreover, Reed’s (1922) species was reported only in the Frasnian  
407 of Nakhichevan by Rzhonsnitskaya & Mamedov (2000) and Mirieva (2010).

408  
409 Order **Atrypida** Rzhonsnitskaya, 1960  
410 Suborder **Atrypidina** Moore, 1952  
411 Superfamily Atrypoidea Gill, 1871  
412 Family Atrypidae Gill, 1871  
413 Subfamily Atrypinae Gill, 1871  
414 Genus *Atrypa* Dalman, 1828  
415 Subgenus *Atrypa (Planatrypa)* Struve, 1966

416  
417 **Type species:** *Atrypa (Planatrypa) collega* Struve, 1966, from the Junkerberg beds, middle  
418 Eifelian, Eifel (Germany).

419  
420 *Atrypa (Planatrypa) ertichensis* (Abrahamyan, 1959)

421 Fig. 10A–F

422  
423 1959 *Atrypa tubaecostata* Paeck. var. *ertichensis* Abrahamyan, p. 7, pl. 1, fig. 1–3.  
424 1974 *Spinatrypa ertichensis* - Abrahamyan, p. 57, pl. 17, fig. 4.  
425 1985 *Spinatrypina ertichensis* - Mamedov & Rzhonsnitskaya, p. 148.  
426 1997 *Atrypa (Planatrypa) ertichensis* - Komarov, p. 87, pl. 1, fig. 5.  
427 2018a *Atrypa (Planatrypa) ertichensis* - Grechishnikova in Alekseeva et al., p. 24, 26.

428  
429 **Type material:** Abrahamyan (1959: p. 7, pl. 1, fig. 1a–d) selected the articulated specimen  
430 (IGSNASRAGM 270/3–54) from the Frasnian of Ertych section (Armenia) as the holotype.  
431 Although Abrahamyan’s collection is stored at the Geological Museum in Yerevan, many of her

432 specimens were lost in 2010 (when the entire museum with its collections was moved to another  
433 building), as was the holotype of *Atrypa (Planatrypa) ertichensis*. Currently, the type material  
434 stored at the museum consists of three specimens, of which one (IGSNASRAGM  
435 3936/AB205/4–54), illustrated by Abrahamyan (1959: p. 8, table 1, fig. 2a–d) is designated here  
436 as the neotype. In addition, here we illustrate for the first time one of the paratypes  
437 (IGSNASRAGM 3936/AB270/82/3–54) (Fig. 10.A–F).

438

439 **Additional material:** Two partly exfoliated articulated specimens.

440

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

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

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

453       Ornamentation of tubular-imbricate, coarse costae originating at beaks and becoming  
454 fainter towards lateral cardinal extremities; costae increasing principally by bifurcation on  
455 ventral valve and by intercalation on dorsal valve; 65–72 costae on the entire shell; generally 5–6  
456 costae per 5 mm at anterior margin; growth lamellae more crowded near the anterior and lateral  
457 margins, extending into frills (Fig. 10A).

458       Internal morphology not observed.

459

460 **Remarks.** Initially described by Abrahamyan (1959), this species was mistakenly considered as  
461 a variety of *Atrypa tubaecostata* Paeckelmann, 1913, a late Givetian species assigned to  
462 *Exatrypa* by Copper (1967a), based on some external differences observed in the Armenian



463 material such as a larger size, a more inflated dorsal valve and the presence of sulcus. However,  
464 Abrahamyan (1974) transferred it to *Spinatrypa* Stainbrook, 1951 and raised it at the species  
465 level, whereas Mamedov & Rzhonsnitskaya (1985) attributed it to *Spinatrypina* Rzhonsnitskaya,  
466 1964. Afterwards, Komarov (1997) re-assigned it to *Atrypa* (*Planatrypa*) Struve, 1966 owing to  
467 the general shell shape, external ornamentation and absence of dental plates. Although Komarov  
468 (1997) did not insist on the absence of dental nuclei, his illustrations of internal features clearly  
469 demonstrate that these structures are not developed and support this subgeneric assignment (see  
470 Copper 2002). However, the examination of Abrahamyan's species revealed the presence of  
471 frills, an ornamental feature that was considered unknown in Struve's (1966) subgenus by  
472 Copper (2002), but their presence in this subgenus was challenged notably by Komarov (1997),  
473 Halamski & Baliński (2013) and Halamski et al. (2022). As Baliński & Halamski (2023) noted  
474 the existence of species presenting intermediate characters that cannot be assigned definitely to  
475 one of the subgenera previously recognised within *Atrypa* (see Copper 2002) or to *Kyrtatrypa*  
476 Struve, 1966, we presently follow Komarov's (1997) subgeneric assignment, pending a  
477 reassessment of some features used in (sub)generic distinctions among atrypides, which is well  
478 beyond the scope of this work.

479

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

487

488 Subfamily Spinatrypinae Copper, 1978

489 Genus *Spinatrypa* Stainbrook, 1951

490

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

493

494 *Spinatrypa* sp.

495 Fig. 10G–L

496

497 **Material:** Two partly exfoliated articulated specimens from the Ertych section.

498

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

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

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

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

516       Internal morphology unknown.

517

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

524

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

528  
529 **Type species:** *Desquamatia* (*Seratrypa*) *pectinata* Copper, 1967a, from the lower Frasnian of  
530 Germany (Bergisches Land).

531  
532 *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992  
533 Fig. 11–13; Tab. 4

534  
535 1992 *Desquamatia* (*Seratrypa*) *abramianae* Komarov, p. 99, pl. 1, fig. 3–4.  
536 1997 *Desquamatia* (*Seratrypa*) *abramianae* - Komarov, p. 151, pl. 4, fig. 5–8; pl. 5, fig. 1–6.  
537 2018a *Desquamatia* (*Seratrypa*) *abramianae* - Alekseeva et al., pp. 852–853.

538  
539 **Holotype:** The holotype (Komarov 1992: pl. 1, fig. 3) is from the Frasnian *Cyrtospirifer*  
540 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov  
541 (2000) of the Danzik section, left bank of the Arpa River, Nakhichevan. It is currently housed at  
542 the Vernadsky State Geological Museum (Moscow), under the registration no. VI-223/3a.

543  
544 **Material:** Twenty-three articulated specimens and four ventral valves from the Ertych (twelve  
545 articulated specimens and two ventral valves), Djravank (eleven articulated specimens) and  
546 Noravank (two ventral valves) sections.

547  
548 **Description.** Shell medium-sized (up to 39.6 mm in width, 37.7 mm in length and 27.9 mm in  
549 thickness) (Tab. 4), wider than long to longer than wide, sharply dorsibiconvex, relatively  
550 equidimensional, widest at about mid-length or more posteriorly to it, semi-elliptic to semi-  
551 rounded in outline; hinge line shorter than greatest width; anterior margin slightly rounded to  
552 straight; anterior commissure undulose to slightly uniplicate.

553 Ventral valve inflated posteriorly with flanks sloping moderately towards the lateral  
554 commissures; highest in the posterior third of the valve, then decreasing progressively towards  
555 the anterior margin; umbo inflated, prominent; beak acute, incurved; interarea very small,

556 concave, hypercline; foramen and deltidial plates unobserved due to deficient preservation;  
557 sulcus very shallow and only perceptible at front, flat- to slightly round-bottomed at front;  
558 tongue low, wider than high, semi-rounded to semi-elliptic, not perpendicular to commissural  
559 plane.

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

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

566 Ventral valve interior (Fig. 12) with stout but short dental plates; dental nuclei relatively  
567 large, well-marked; teeth massive, simple; central apical cavity not filled in by callosities.

568 Dorsal valve interior (Fig. 12) with a weak cardinal process in form of a pad, enclosed  
569 within the cardinal pit; dental sockets not deep, divided by a median crest; crural bases stout;  
570 crura ventrally directed; jugal processes and spiral cones not observed.

571

572 **Shell ontogeny.** Juveniles display a thinner shell with rectimarginate anterior commissure and  
573 semi-elliptic as well as very low tongue. Although not developed in juveniles, a sulcus occurs in  
574 older shells. Beak inclination angle does not change with age because juveniles also have an  
575 incurved beak. The size distributions of *Desquamatia (Seratrypa) abramiana* during growth, as  
576 represented by the scatter plots of the width/length, the width/thickness and the width/width of  
577 sulcus, show a continuous and progressive growth with no distinct grouping (Fig. 13). The  
578 relative proportions of *D. (S.) abramiana* represented by sufficient material remain constant  
579 (linear regression:  $y = ax + b$ ; significant probability value:  $p < 0.001$ \*\*\* whatever the degree of  
580 development of individuals (Fig. 13). Moreover, the correlation is positive with width varying  
581 proportionally with length, thickness and width of sulcus. To complete the scatter plots, the  
582 measurements of numerous individuals of *D. (S.) abramiana* are also presented in Tab. 4.

583

584 **Remarks.** Although Komarov (1992, 1997) examined numerous specimens from Nakhichevan  
585 identified as *Desquamatia (Seratrypa) abramiana*, this species was previously known only from

586 illustrations of a few partially exfoliated samples of which only the ventral internal features were  
587 documented. Our better-preserved material has allowed a complete redescription of this taxon.

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

606

607 **Occurrence.** This species was originally reported from to the Frasnian *Cyrtospirifer*  
608 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya & Mamedov  
609 (2000) in Nakhichevan (Komarov 1992, 1997). It is recorded herein for the first time from the  
610 Frasnian strata of the Ertych, Djravank and Noravank sections (Fig. 1).

611

612 Order **Spiriferida** Waagen, 1883

613 Suborder **Spiriferidina** Waagen, 1883

614 Superfamily Cyrtospiriferoidea Termier & Termier, 1949

615 Family Cyrtospiriferidae Termier & Termier, 1949

616 Subfamily Cyrtospiriferinae Termier & Termier, 1949

617

618 Genus *Angustisulcispirifer* n. gen.

619

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

622

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

626

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

634

635 **Comparison with related genera.** *Angustisulcispirifer* n. gen. is included in the Superfamily  
636 Cyrtospiriferoidea on account of its dental plates, delthyrial plate and ctenophoridium.  
637 *Angustisulcispirifer* n. gen. is assigned to the Family Cyrtospiriferidae, as defined by Johnson  
638 (2006), based on costate sulcus and fold. It is further placed within the Subfamily  
639 Cyrtospiriferinae as defined by Johnson in Carter et al. (1994) and Johnson (2006) due to its  
640 wide hinge line and its slightly mucronate cardinal extremities.

641 The new genus is distinguished externally from *Cyrtospirifer* Nalivkin in Fredericks,  
642 1924, as revised by Ma & Day (2003), by its more globular, longitudinally elongated and  
643 ventrally inflated shell as well as poorly developed fold and sulcus. Internally,  
644 *Angustisulcispirifer* n. gen. differs by its short delthyrial plate and robust dental plates.

645 *Angustisulcispirifer* n. gen. resembles to some extent the genus *Uchtospirifer* Ljashenko,  
646 1957 as revised by Sokiran (2006), known from the lpper Givetian?–lower Frasnian of Russia  
647 and Poland, based on its strongly ventribiconvex profile, subpentagonal shell with flanks closely

648 ornamented by low, flattened costae and high ventral interarea, but the former displays wide  
649 hinge line (*vs.* short hinge line for *Uchtospirifer*), mucronate cardinal extremities (*vs.* rounded  
650 ones for *Uchtospirifer*), narrow sulcus and fold (*vs.* moderately wide ones for *Uchtospirifer*), and  
651 low tongue. Additionally, the new genus has costae in sulcus and on fold that are not transformed  
652 into capillae, flattening or disappearing as it is observed in *Uchtospirifer* representatives.  
653 Internally, *Angustisulcispirifer* n. gen. differs by its supported ctenophoridium.

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

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

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

672

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

674

675 **Other included species.** As the morphological characters of *Cyrtospirifer* (*C.*) *kursaensis*  
676 Sidjachenko, 1962 and *C. (C.) limatus* Solkina in Sidjachenko (1962) from the Famennian of  
677 Central Kara-Tau (Kazakhstan) fit well with the diagnosis of the new genus, the latter may be  
678 tentatively assigned to it, though the type of pseudodeltidium as well as the micro-ornament of

679 both species are undocumented. *Uchtospirifer subarchiaci* (Martelli, 1902) sensu Afanasjeva in  
680 Alekseeva et al. (2018b) (not *Plicapustula subarchiaci* (Martelli, 1902), see Ma & Day 2007) is  
681 also included in the new genus. Moreover, it most likely belongs to the same phylogenetic  
682 lineage as *A. arakelyani* n. gen., n. sp. because both species display strong similarities.

683

684 *Angustisulcispirifer arakelyani* n. gen., n. sp.

685 Fig. 14–17; Tab. 5

686

687 1952 *Cyrtospirifer subarchiaci* [*sic*] Martelli - Arakelyan, p. 31, 36.

688 1957 *Cyrtospirifer subarchiaci* (Martelli) - Abrahamyan, p. 9.

689 1964 *Cyrtospirifer subarchiaci* (Martelli) - Arakelyan, p. 67, 70, 74, 92.

690 1973 *Cyrtospirifer subarchiaci* (Martelli) - Abrahamyan et al., p. 217.

691 1975 *Cyrtospirifer subarchiaci* (Martelli) - Arakelyan et al., p. 22.

692

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

697

698 **Holotype:** An almost complete articulated specimen (IGSNASRAGM 3971/PS 3077; Fig. 16.G–  
699 L) from the Frasnian.

700

701 **Material:** Fifty-two articulated specimens and five dissociated valves from the Frasnian  
702 limestone beds of the Noravank (twenty-five articulated specimens and three ventral valves),  
703 Ertych (ten articulated specimens) and Djravank (seven articulated specimens and two ventral  
704 valves) sections.

705

706 **Type horizon:** Frasnian nodular limestones.

707

708 **Type locality:** Noravank section (6 km southeast from Areni, Vayots Dzor Province, Southwest  
709 Central Armenia) (Fig. 1, 3).



710

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

722

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

726       Ventral valve strongly inflated, rounded pentagonal in outline, with convex flanks  
727 sloping steeply towards lateral commissures; highest in the posterior third of the valve, then  
728 quickly decreasing towards anterior margin; umbo strongly inflated, large and prominent; beak  
729 small, erect to incurved; interarea apsacline, moderately high, well-defined, concave; delthyrium  
730 wide, the type of delthyrial cover is unknown as only some of the remnants are partially  
731 preserved in one of the collected specimens (IGSNASRAGM 3975/PS 3081; Fig. 14.Y–Z);  
732 sulcus very narrow, shallow, originating from beak, well-defined, with gentle margins, round-  
733 bottomed at front; tongue very low, more or less rounded in outline, perpendicular to  
734 commissural plane.

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

740       Ornamentation of up to 30 rounded (generally 26–29; 4–5 costae per 5 mm at anterior

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

748         Ventral valve interior (Fig. 16) with strong dental plates, extrasinal posteriorly but  
749 subsinal or intrasinal anteriorly, generally divergent (21–26 degrees) but converging dorsally in  
750 umbonal region (as seen in transverse section); delthyrial plate short (Fig. 14.AA); central apical  
751 cavity filled in by a stout and knob-like callosity on its floor (Fig. 16, serial sections 4.9–6.5);  
752 lateral apical cavities large and moderately filled in by callus; teeth relatively small, but stout.

753         Dorsal valve interior with ctenophoridium (Fig. 16) composed of up to 25 well-  
754 developed, long lamellae and supported by a strong apical callus; myophragm low, long (Fig.  
755 15.C); hinge plates divided; crural bases dorsally convergent; spiralia oriented posterolaterally,  
756 with at least 15 whorls per spiral cone.

757

758 **Shell ontogeny.** Juvenile forms differ from adults by their inconspicuous umbones, suberect  
759 beak, low fold and poorly developed sulcus. The beak inclination angle increases progressively  
760 with ontogenetic growth. The size distributions during growth, as illustrated by the various plots  
761 of Figure 17, show a continuous and progressive growth with possibly three–four distinct growth  
762 stages. However, the factors caused this grouping effect remain unknown. The relative  
763 proportions of *Angustisulcispirifer arakelyani* n. gen., n. sp. represented by sufficient material  
764 remain constant (linear regression:  $y = ax + b$ ; significant probability value:  $p < 0.001^{***}$   
765 whatever the degree of development of individuals (Fig. 17)). Moreover, the correlation is  
766 positive with width varying proportionally with length, thickness, width of sulcus and the length  
767 of dorsal valve. To complete the scatter plots, the measurements of numerous individuals of *A.*  
768 *arakelyani* n. gen., n. sp. are also represented in Tab. 5.

769

770 **Remarks.** This species is one of the most biostratigraphically valuable species in Armenia for  
771 the recognition of the Frasnian strata. However, it has mistakenly been confused with *Spirifer*

772 *verneuili* var. *subarchiaci* Martelli, 1902 (= *Plicapustula subarchiaci* (Martelli, 1902) sensu Ma  
773 & Day (2007)) from the middle Famennian of southeastern China since Arakelyan (1952). The  
774 Armenian material differs from Martelli's (1902) species by its more globular and inflated shell  
775 as well as by its poorly developed fold and sulcus. Internally, the new species is distinguished by  
776 its short delthyrial plate and strong dental plates.

777 *Angustisulcispirifer arakelyani* n. gen., n. sp. is very close to *Uchtospirifer subarchiaci*  
778 (Martelli, 1902) sensu Afanasjeva in Alekseeva et al. (2018b) from the Frasnian of Nakhichevan  
779 (e.g., subpentagonal shell outline, ventribiconvex lateral profile, inflated umbones, ventral  
780 triangular and apsacline interarea, shallow sulcus and low fold, simple costae on flanks,  
781 bifurcating in sulcus and on fold, the presence of a well-developed delthyrial plate and  
782 myophragm), which is also evidently confused with Martelli's (1902) species and needs to be re-  
783 investigated. However, the Armenian material is distinguishable by its wider hinge line, higher  
784 ventral interarea and less inflated shell. The internal features of the material studied by  
785 Afanasjeva in Alekseeva et al. (2018b: text-fig. 102) remain incompletely illustrated as only one  
786 serial section showing the ventral interior was provided; thus, further evidences are needed to  
787 point out other similarities and differences concerning internal morphology of these two species.  
788 The new species shares several similarities (e.g., subpentagonal shell outline, ventribiconvex  
789 lateral profile, mucronate cardinal extremities, widest at hinge line, inflated umbones, triangular  
790 and apsacline interarea, simple costae on flanks, bifurcating in sulcus and on fold) with two  
791 species recognised from the Famennian of Central Kara-Tau, namely *Cyrtospirifer* (*C.*)  
792 *kursaensis* Sidjachenko, 1962 and *C. (C.) limatus* Solkina in Sidjachenko (1962), but it also  
793 differs from them by its weakly developed fold and sulcus, very low tongue more or less rounded  
794 in outline, and by the presence of a stout and knob-like callosity developed in the ventral valve.

795 The re-examination of Arakelyan (1952, 1964) and Abrahamyan et al. (1973)'s material  
796 demonstrates that the species used to recognise the Frasnian strata in Armenia and Nakhichevan  
797 by these authors was *A. arakelyani* n. gen., n. sp. and not *Uchtospirifer subarchiaci* (Martelli,  
798 1902) sensu Afanasjeva in Alekseeva et al. (2018b). Moreover, as we have never found the latter  
799 species in the recently collected fauna from Armenia we suggest using the new species to  
800 recognise the Frasnian strata in Armenia.

801

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

805

806 *Cyrtospiriferinae* gen. indet.

807 Fig. 18–20; Tab. 6

808

809 **Material:** Eight articulated specimens and six dissociated valves from the Frasnian limestone  
810 beds of the Ertych (six articulated specimens and two ventral valves) and Djravank (two  
811 articulated specimens and four ventral valves) sections.

812

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

817       Ventral valve strongly inflated, with convex flanks sloping moderately to strongly  
818 towards lateral commissures; highest in the posterior third of the valve or at midlength, then  
819 decreasing quickly towards anterior margin; umbo inflated, prominent; beak straight to erect;  
820 interarea apsacline, triangular, moderately high, slightly to clearly concave; delthyrium wide,  
821 with a kind of protuberance in its central part (Fig. 18.M); sulcus originating from beak, wide,  
822 shallow to moderately deep, round-bottomed at front, tongue low to moderately high, wide,  
823 subtrapezoidal to subcircular in outline.

824       Dorsal valve inflated with flanks sloping gently towards lateral commissures,  
825 subtrapezoidal in outline; highest at about midlength or more anteriorly to it, but gradually  
826 decreasing towards the anterior margin; interarea nearly flat, linear, orthocline; fold low,  
827 relatively wide to wide, well-delimited (except in the specimen figured in Fig. 18N–R), starting  
828 from beak and widening anteriorly, round-topped at front.

829       Up to ca. 20 (3–4 costae per 5 mm at anterior margin near sulcus and fold) simple, low  
830 costae on flanks with top rounded; interspaces narrower than costae; in sulcus and on fold, up to  
831 11 costae narrower than those on flanks, increasing by bifurcation; micro-ornament poorly  
832 preserved.

833 **Remarks.** The examined material is assigned to the family Cyrtospiriferidae, as defined by  
834 Johnson (2006), based on the presence of dental plates, a ctenophoridium, ornamentation and  
835 development of costae in sulcus and on fold. Additionally, its wide hinge line and acute to  
836 mucronate cardinal extremities argues for its assignment to the subfamily Cyrtospiriferinae  
837 rather than to Cyrtiopsinae. However, the insufficiency of our material precludes a definitive  
838 generic identification. It is also important to emphasize that the examination of two serially  
839 sectioned specimens shows that the internal morphology of our material is quite variable from  
840 one specimen to another. Most notably, although the central and lateral apical cavities of both  
841 serially sectioned specimens are infilled by stout callosity, both possess greatly thickened,  
842 subsinal or extrasinal and divergent dental plates converging dorsally in umbonal region and  
843 stout teeth, one of them (Fig. 19) displays a thick delthyrial plate, whereas the other shows a  
844 septal pillow made by delthyrial thickening formed by accretion of strong apical callus from the  
845 internal faces of the dental plates (Fig. 20). Moreover, the ctenophoridium observed in the  
846 former specimen is supported by strong callosity, whereas the latter specimen has an  
847 unsupported ctenophoridium. However, these differences are provisionally regarded here as  
848 representing intraspecific variability pending additional and better preserved specimens.  
849 Additionally, it is worth to stress that both specimens display divided hinge plates and dorsally  
850 convergent crural bases.

851

## 852 **Discussion**

### 853 ***Biostratigraphy***

854 Brachiopod assemblages have already been used in the establishment of Upper Devonian  
855 biostratigraphic schemes in the Lesser Caucasus. A rudimentary Devonian biostratigraphical  
856 zonal scheme based on brachiopods was first established by Rzhonsnitskaya (1948), who simply  
857 subdivided the Devonian into two parts: Lower and Upper. Later, Abrahamyan (1957, 1964,  
858 1974) developed a new continuous biostratigraphic scheme characterized by taxon-range and  
859 assemblage biozones (Fig. 21). Grechishnikova et al. (1980, 1982), Mamedov & Rzhonsnitskaya  
860 (1985) and Rzhonsnitskaya & Mamedov (2000), further applied Abrahamyan's zonal scheme in  
861 Nakhichevan, while improving and complementing it for some intervals. Rzhonsnitskaya &  
862 Mamedov (2000) updated their brachiopod biozonal scheme and correlated it with the conodont  
863 biozonation established by Aristov (1994) in Nakhichevan. The latter authors also introduced a

864 long unzoned interval between their Frasnian and lower Famennian zones (Fig. 21). More  
865 recently, Alekseeva et al. (2018a, b) followed the zonal scheme of Grechishnikova et al. (1980)  
866 and recognised only one brachiopod zone for the lower Famennian, and they used species  
867 characteristic of two different zones in the biozonation of Mamedov & Rzhonsnitskaya (1985)  
868 and Rzhonsnitskaya & Mamedov (2000). Finally, Serobyán et al. (2022a, b) recognised the  
869 lower Famennian *Aramazdospirifer orbelianus*–*Tornatospirifer armenicus* brachiopod  
870 assemblage Zone. Also, it should be noted that Mirieva (2010) described eight rhynchonellide  
871 assemblage and taxon-range biozones from the Upper Devonian successions of the Lesser  
872 Caucasus based exclusively on rhynchonellide brachiopod occurrences. However, the presence  
873 of some species used by Mirieva (2010) for the recognition of the substages of the Frasnian and  
874 Famennian is disputable; moreover, many of her biozones are based on species that are  
875 taxonomically poorly discriminated. For instance, she considered *Eoparaphorhynchus*  
876 *triaequalis* (Gosselet, 1877) as a characteristic species for almost all biozones spanning the lower  
877 to uppermost Famennian. But, as shown by Pakhnevich (2012), the specimens collected from  
878 Armenia and Nakhichevan, identified as *E. triaequalis*, differ from Gosselet's (1877) species by  
879 the presence of punctae on the shell walls. For this reason he erected the new monospecific  
880 genus *Sharovaella* with its type species *Sharovaella mirabilis* and specified that the latter occurs  
881 only in the lower Famennian. Serobyán et al. (2019) revised the descriptions of eight  
882 trigonirhynchiid brachiopod species known from the Upper Devonian of Armenia and  
883 highlighted the biochronological potential of trigonirhynchiid brachiopods in dating accurately  
884 the upper Frasnian and parts of the lower and upper Famennian in the Lesser Caucasus. The  
885 biostratigraphic significance of rhynchonellides was later stressed by Pakhnevich (2020), who  
886 summarised the existing data on their occurrences. He noted that the Lower–Middle Devonian  
887 rhynchonellide assemblages of the Lesser Caucasus are mainly dominated by the representatives  
888 of the family Hebetoechiidae in contrast to those of the Frasnian and Famennian, which are  
889 dominated by the family Trigonirhynchiidae. Pakhnevich (2020) further specified that their  
890 diversity decreased afterwards and that they became a minor component of Lower Carboniferous  
891 brachiopod assemblages, with no real utility for the biostratigraphy.

892 The brachiopod assemblages recovered from our studied sections (see Tab. 1) may be  
893 correlated with the *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone of  
894 Rzhonsnitskaya & Mamedov (2000), which has been established in Nakhichevan, as several

895 species from this zone are also identified in our material (e.g. *Ripidiorhynchus gnishikensis*,  
896 *Cyphoterorhynchus koraghensis* and *Atrypa (Planatrypa) ertichensis*). However, as neither of  
897 the two index species *Cyphoterorhynchus arpaensis* (Abrahamyan, 1957) or *Cyrtospirifer*  
898 *subarchiaci* sensu Rzhonsnitskaya & Mamedov (2000) (= *Angustisulcispirifer subarchiaci* [sic]),  
899 were found in our sections, we suggest introducing a new local biozone for the studied sections  
900 in Armenia. This zone is based on the species *Ripidiorhynchus gnishikensis* and  
901 *Angustisulcispirifer arakelyani* n. gen., n. sp., as they are both abundant in the lower limestone  
902 interval of all three studied sections (see Tab. 1). Moreover, *R. gnishikensis* has also been  
903 described in Nakhichevan (Pakhnevich in Alekseeva et al. 2018a). Consequently, we here  
904 establish a new brachiopod assemblage zone, namely the *Ripidiorhynchus gnishikensis*–  
905 *Angustisulcispirifer arakelyani*, for which neither the base, nor the top can be defined at this  
906 stage. Any of these two species may allow to recognise this local biozone in other sections.  
907 Given the conodonts retrieved at the Djavank section, the age of this zone is constrained to the  
908 Frasnian, between the uppermost part of the lower Frasnian and the upper Frasnian (between the  
909 *transitans* and the upper *rhenana* conodont zones). Within the interval corresponding to the  
910 *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone, Aristov (1994)  
911 recognised two conodont zones: *Ancyrodella binodosa* and *A. rotundiloba*. He noted that the *A.*  
912 *binodosa* Zone corresponds to the lower part of *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus*  
913 *arpaensis* brachiopod Zone, whereas the *rotundiloba* Zone is coeval to the upper part of  
914 *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone. The author further  
915 specified that the most important taxa for the recognition of the Givetian/Frasnian boundary,  
916 namely *Ancyrodella binodosa* and *A. rotundiloba*, are extremely rare in the studied sections,  
917 which excludes the possibility to determine their first and last appearances. Therefore, he  
918 suggested to temporarily place the Givetian/Frasnian boundary within the *Cyrtospirifer*  
919 *subarchiaci*–*Cyphoterorhynchus arpaensis* Zone. Nonetheless, Rzhonsnitskaya & Mamedov  
920 (2000) raised the lower boundary of the latter brachiopod zone to the lower Frasnian. We concur  
921 with the viewpoint of Rzhonsnitskaya & Mamedov (2000), since Aristov (1994)'s main point for  
922 considering the lower part of the *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis*  
923 brachiopod Zone as Givetian in age was based on the presence of *A. binodosa*, a conodont  
924 species that may also occur in the lower Frasnian (e.g., Reissner 1989; Gouwy et al. 2007); thus,  
925 no data on conodonts were presented by Aristov (1994) to explicitly support a Givetian age.

926 Furthermore, as Aristov (1994) reported *A. rotundiloba*, a species that does not range above the  
927 *punctata* Zone (Ziegler & Sandberg 1990: 17), in the upper part of the *Cyrtospirifer*  
928 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone, it is reasonable to assume that the  
929 age of this biozone is likely to be covering the lower–middle Frasnian interval and the latter may  
930 be correlated with the *falsiovalis*–*punctata* conodont zones.

931

### 932 ***Brachiopod palaeobiogeography***

933 Unlike the late Early–Middle Devonian, which was characterized by cooler climatic conditions  
934 and global faunal endemism, especially among marine invertebrates, the early and middle  
935 Frasnian (early Late Devonian) was a time of globally warm climatic conditions (Joachimski et  
936 al. 2009) and of high sea level (Vail et al. 1977; Johnson et al. 1985). The combination of these  
937 environmental conditions, in addition to continental or terrane amalgamation, and favorable  
938 oceanic circulation patterns, have probably led to changes in Devonian marine biogeography  
939 from a high level of provinciality during the Early Devonian to a low one during the Late  
940 Devonian (Oliver 1976; McGhee 1996; Copper 1998; Rode & Lieberman 2004). Generally, the  
941 Late Devonian has long been recognised as an interval of strong faunal cosmopolitanism, during  
942 which marine faunas attained wide geographic coverage, as exemplified by benthic organisms,  
943 notably brachiopods (Johnson 1971; Racki 1998; Rode & Lieberman 2004). However, Gaetani  
944 (1965, 1968), Brice (1971), and Brice et al. (1973, 1999) documented a striking similarity among  
945 the Late Devonian brachiopod faunas thriving on the shallow-water carbonate platform of the  
946 northern margin of Gondwana, namely from Armenia to NW Pakistan. They further pointed out  
947 that a single bioprovince may be individualized for the Late Devonian brachiopod assemblages  
948 described along this realm. The quantitative analysis presented by Brock & Yazdi (2000)  
949 improved the understanding of palaeobiogeographic affinities of Late Devonian brachiopods  
950 from Iran, and also confirmed the latter findings. More recently, Serobyan et al. (2021)  
951 concurred with this viewpoint based on the brachiopod fauna they described in Armenia, as well  
952 as the available data from the region, and advocated a rather uniform early Famennian  
953 brachiopod bioprovince that was developed between Pamir (to the east) and the Anatolide-  
954 Tauride microplate (to the west). In this context, *Cyphoterorhynchus koraghensis* (Reed, 1922),  
955 described in this study, is of particular palaeobiogeographic significance, since the latter is found  
956 in Armenia, Afghanistan, Chitral (NW Pakistan), Iran, and probably Turkey, all of which were



957 situated only along the northern margin of the Gondwanan megacontinent (Fig. 22). It is also  
958 worth emphasising here that the genus *Cyphoterorhynchus* Sartenaer, 1964 has a wider  
959 palaeobiogeographic distribution extending from Chitral westward to Libya and Spain. Unlike  
960 *Cyphoterorhynchus*, the genus *Ripidiorhynchus* Sartenaer, 1966a occurs both in Gondwana and  
961 Laurussia megacontinents. More particularly, Racki (1993) reported some rhynchonellide  
962 specimens from the upper Givetian of Poland (Góra Zamkowa and Stokówka), which he  
963 identified as *Ripidiorhynchus* aff. *pskovensis* (Nalivkin 1941). The author further specified that  
964 although he tentatively assigned these specimens to *R. pskovensis* [= *Ripidiorhynchus livonicus*  
965 (Buch, 1834), according to Sokiran (2002)], they may also represent a new species, as well as the  
966 oldest record of this genus. Later, Sokiran (2002) revised this material and, on its basis, erected a  
967 new species, *Ripidiorhynchus chencinensis*. Two representatives of the genus *Ripidiorhynchus*,  
968 namely *Ripidiorhynchus aldogus* (Nalivkin, 1941) and *Ripidiorhynchus griasicus* (Nalivkin,  
969 1934) occur in the lower Frasnian strata of the Main Devonian Field (Northwestern region of the  
970 East European Platform (EEP)), whereas *Ripidiorhynchus livonicus* (Buch, 1834) and  
971 *Ripidiorhynchus huotinus* (de Verneuil, 1845) occur in the lower Famennian of the Central  
972 Devonian Field (Central region of the EEP) (see references in Sokiran 2002). Therefore, it is  
973 reasonable to assume that although it first occurred in the upper Givetian of Poland, this genus  
974 later expanded to the north-western region of the platform due to the early Frasnian transgression  
975 and later to the south-east, migrating towards the northern margin of Gondwana; it thus  
976 colonised the SAB carbonate platform in the course of the early and middle Frasnian. In the  
977 present study, three atrypide species are described, of which *Atrypa (Planatrypa) ertichensis*  
978 (Abrahamyan, 1959) and *Desquamatia (Seratrypa) abramiana* Komarov, 1992 appear to be  
979 restricted to the SAB, since they have been documented only from Armenia and Nakhichevan.  
980 However, they belong to genera/subgenera that can rather be considered cosmopolitan because  
981 they are known worldwide. The third species, left in open nomenclature, is assigned to  
982 *Spinatrypa* well-known notably from the Givetian–Frasnian shallow water carbonate/siliciclastic  
983 deposits of North America (see references in Day & Copper 1998), Western Europe (Copper  
984 1965, 1967b; Mottequin 2003, 2008) and Lesser Caucasus (Komarov 1997). The newly created  
985 genus *Angustisulcispirifer*, in addition to its type species *A. arakelyani* n. gen., n. sp., described  
986 in the lower–middle Frasnian interval of Armenia, and a species from Nakhichevan, may also  
987 include two more species reported from the Famennian of Central Kara-Tau (Kazakhstan). In

988 addition to the recent data, also considering that Serobyán et al. (2022a, b), who identified three  
989 cyrtospiriferid genera (*Aramazdospirifer*, *Pentagonospirifer* and *Tornatospirifer*) from the early  
990 Famennian of Armenia and assigned several species from Kara-Tau to them, one can note the  
991 similarity between the Late Devonian brachiopod faunas from Kara-Tau and synchronous faunas  
992 from Armenia. Furthermore, this observation seems to be especially true for cyrtospiriferids.

993

## 994 **Conclusions**

995

996 Recent brachiopod sampling from Central Armenia allowed to identify an assemblage composed  
997 of seven species. Based on the presence of species *Ripidiorhynchus gnishikensis* (Abrahamyan,  
998 1959), *Cyphoterorhynchus koraghensis* (Reed, 1922), *Atrypa (Planatrypa) ertichensis*  
999 (Abrahamyan, 1959) and *Desquamatia (Seratrypa) abramianae* Komarov, 1992, this assemblage  
1000 may be tentatively considered as lateral equivalent of the lower–middle Frasnian *Cyrtospirifer*  
1001 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod Zone established in Nakhichevan.  
1002 However, as neither of the two index species of the latter zone were found in the sections studied  
1003 in Armenia, a new local brachiopod assemblage zone is introduced, namely the *Ripidiorhynchus*  
1004 *gnishikensis*–*Angustisulcispirifer arakelyani*. The latter is dated as of latest early Frasnian to late  
1005 Frasnian in age based on conodonts identified in the Djravank section. Revision of the  
1006 rhynchonellide, atrypide and cyrtospiriferide brachiopods recovered from the latter zone revealed  
1007 some species that were previously unknown from this interval and also several new features in  
1008 the species that were already known, but poorly illustrated, and consequently led us to define a  
1009 new genus and a new species. Most notably, *Angustisulcispirifer arakelyani* n. gen., n. sp. is  
1010 erected to solve a long-standing taxonomic confusion associated with *Cyrtospirifer subarchiaci*  
1011 Martelli (1902) sensu Arakelyan (1952), a taxonomically poorly known, but at the same time  
1012 biostratigraphically valuable species. *Atrypa (Planatrypa) ertichensis* (Abrahamyan, 1959)  
1013 appears to possess frills, an ornamental feature rarely observed in this (sub)genus and considered  
1014 unknown in this species. Two spinatrypinid shells ascribed to *Spinatrypa* Stainbrook, 1951  
1015 represent the first report of the genus *Spinatrypa* in the Frasnian of the Lesser Caucasus, since  
1016 representatives of this genus were reported previously only in the Middle Devonian (Eifelian–  
1017 Givetian) of Nakhichevan. The palaeobiogeographic distribution of the rhynchonellides and  
1018 atrypides within the Frasnian of Armenia suggests that the brachiopod communities thriving on

1019 the shallow water carbonate platform of the SAB included some apparently endemic species  
1020 (e.g., *Ripidiorhynchus gnishikensis*, *Desquamatia (Seratrypa) abramiana*, *Atrypa (Planatrypa)*  
1021 *ertichensis*, but also species (*Cyphoterorhynchus koraghensis*), which was common in other  
1022 parts of the Gondwanan northern margin extending eastwards to Iran, Afghanistan and Chitral,  
1023 and probably westwards to Turkey. However, although some Frasnian brachiopods from Central  
1024 Armenia are described here, it appears that new surveys are urgently needed to understand Late  
1025 Devonian changes in brachiopod diversity.

1026

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1028

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1043

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