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► **To cite this version:**

Vahram Serobyan, Taniel Danelian, Catherine Crônier, Araik Grigoryan, Bernard Mottequin. New and revised cyrtospiriferid (Spiriferida) brachiopods from the lower Famennian (Upper Devonian) of Armenia. *Journal of Paleontology*, 2022, 96 (4), pp.839-858. 10.1017/jpa.2022.9 . hal-04418661

HAL Id: hal-04418661

<https://hal.science/hal-04418661>

Submitted on 26 Jan 2024

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1 **New and revised cyrtospiriferid (Spiriferida) brachiopods from the lower**
2 **Famennian (Upper Devonian) of Armenia**

3

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15

16 **Running Header:** Lower Famennian cyrtospiriferid brachiopods from Armenia

17

18 **Abstract.**—The Upper Devonian sedimentary sequences of Central Armenia, which mainly
19 consist of shallow water, mixed carbonate-siliciclastic deposits, contain abundant and diverse
20 brachiopods that are dominated by spiriferides. Based on newly collected material from the
21 lower Famennian *orbelianus* brachiopod zone (coeval to the *crepida* conodont zone) of Armenia,
22 we here introduce two new cyrtospiriferid genera and fully document their type species,

23 including their intraspecific variability. *Pentagonospirifer* n.gen. is a monospecific genus
24 assigned to the subfamily Cyrtospiriferinae that is currently known only from the lower
25 Famennian of Armenia; it is likely that its type species, *P. abrahamyanae* n. sp., evolved from
26 the species *Cyrtospirifer verneuili sensu* Abrahamyan, known from the Frasnian and lower
27 Famennian of Armenia. The second new genus, *Tornatospirifer* n. gen. is assigned to the
28 subfamily Cyrtiopsinae and defined on the basis of one of the most biostratigraphically valuable
29 cyrtospiriferid species, namely *T. armenicus* (Abrahamyan, 1974), described previously from the
30 lower Famennian *orbelianus* Zone of Armenia. It is likely that it evolved from a Frasnian
31 ancestral stock of *Tiocyrspis* Sartenaer, 1994, known from north-western Europe, which
32 probably migrated during the early Frasnian to the north Gondwanan margin. A neotype is
33 selected for Abrahamyan's species as the type material is lost. Epibionts (*Cornulites*, *Hederella*)
34 are also documented.

35

36 **Introduction**

37

38 Cyrtospiriferidae are spire-bearer brachiopods that originated in the Middle Devonian (Givetian)
39 (Paeckelmann, 1942; Grechishnikova, 1996; Schemm-Gregory, 2011; Gourvennec, 2019). They
40 diversified rapidly during the Frasnian and proliferated on tropical/subtropical platforms during
41 the Late Devonian (Ma and Day, 1999) until their extinction at the end of the Famennian during
42 the Hangenberg event (Carter and Gourvennec, 2006; Mottequin et al., 2014). Thanks to their
43 richness in brachiopods, the Upper Devonian sedimentary sequences of Armenia can provide
44 interesting insights to improve our understanding of their changes in diversity in relation to well-
45 known extinction events (Abrahamyan, 1957, 1964, 1974; Arakelyan, 1964; Alekseeva et al.,

46 2018a, b; Serobyan et al., 2021). However, although Upper Devonian–Lower Carboniferous
47 brachiopods of the Lesser Caucasus (Armenian and Nakhichevan; Fig. 1) were studied
48 systematically by Abrahamyan (1957, 1964, 1974), Grechishnikova (1986, 1996) and more
49 recently by Alekseeva et al. (2018a, b) and Serobyan et al. (2019, 2021) they still remain largely
50 undocumented from a taxonomic and biostratigraphic point of view. This is particularly true for
51 the cyrtospiriferids, among which most species were described previously without examination
52 of the most fundamental features in brachiopod taxonomy, such as their internal structure and
53 type of micro-ornament, which are significant for their supraspecific classification.
54 Consequently, many of them were mistakenly referred to genera such as *Cyrtospirifer* Nalivkin
55 in Fredericks, 1924 and *Cyrtiopsis* Grabau, 1923.

56 Based on recently collected material from a single brachiopod biozone (the *orbelianus*
57 Zone) from four different localities in Armenia (Fig. 1), the prime objective of this contribution
58 is to reassess the taxonomy of two lower Famennian cyrtospiriferid species, one of which was
59 documented in the second half of the 20th century and used in the biostratigraphy of the lower
60 Famennian sequences of the Lesser Caucasus. Taking this opportunity, taxonomic aspects of the
61 family Cyrtospiriferidae are discussed, as well as evolutionary and paleobiogeographic
62 implications of the newly erected genera. Finally, two types of encrusters are documented for the
63 first time from the Armenian material and the epibiont-host relationship is discussed.

64

65 **Geological and stratigraphic setting**

66

67 The Upper Devonian sedimentary sequences of Armenia have a restricted geographic
68 distribution and occur mainly in the southern part of Central Armenia, but they continue
69 westwards in Nakhichevan (Fig. 1). They consist essentially of marly and sandy biogenic
70 limestones, rich in brachiopods, and intercalations of quartzose sandstones (arenites), fine-
71 grained sandstones and shales. The carbonate-siliciclastic sequences of both areas belong to the
72 South Armenian Block (SAB; Sosson et al., 2010), which was part at the time of the northern
73 margin of the Gondwana megacontinent. These sedimentary sequences are considered to have
74 been accumulated in rather shallow water platform environments (Arakelyan, 1964; Ginter et al.,
75 2011). The Frasnian and Famennian deposits were subdivided into a number of ‘formations’ by
76 Arakelyan (1964) (e.g., Baghrsagh, Noravank, Ertych; Fig. 2). However, the latter were defined
77 mainly based on their brachiopod assemblages, they thus bear a biostratigraphic rather than
78 lithostratigraphic significance (see discussion in Serobyan et al., 2019). Consequently, they are
79 here regarded as horizons and not as lithostratigraphic formations.

80 The biostratigraphical zonal scheme of the Upper Devonian rocks of the Lesser Caucasus
81 was first established by Rzhonsnitskaya (1948), who simply subdivided the Devonian into two
82 parts: Lower and Upper. Later, Abrahamyan (1957) introduced a new continuous
83 biostratigraphic scheme, mainly for the Famennian, composed of taxon-range and assemblage
84 biozones (Fig. 2). Abrahamyan’s biozones were further revised by Mamedov and
85 Rzhonsnitskaya (1985) and updated by Rzhonsnitskaya and Mamedov (2000), who correlated
86 them also with the conodont biozonation of Aristov (1994), which was carried out in
87 Nakhichevan. In addition, Grechishnikova et al. (1980, 1982) and Grechishnikova and Levitskii
88 (2011), and more recently updated by Grechishnikova in Alekseeva et al. (2018a, b), contributed
89 also to the biostratigraphy of the Middle Devonian–Lower Carboniferous sequences of the

90 Lesser Caucasus. However, in spite of these studies, the brachiopod biostratigraphy of the
91 Middle–Upper Devonian sequences of the Lesser Caucasus still remain poorly understood.
92 Moreover, these studies cause sometimes confusion, as it can be illustrated with the following
93 example; Aristov (1994) recognized two conodont zones across the Givetian–Frasnian boundary:
94 *Ancyrodella binodosa* and *A. rotunbiloba*; he further specified that the *binodosa* Zone may be
95 correlated with the lower part of *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis*
96 brachiopod Zone, whereas its upper part should be coeval with the *rotunbiloba* conodont Zone.
97 However, Rzhonsnitskaya and Mamedov (2000) raised the lower boundary of the *Cyrtospirifer*
98 *subarchiaci*–*Cyphoterorhynchus arpaensis* brachiopod zone to the early Frasnian. Afterwards,
99 Alekseeva et al. (2018a) considered this brachiopod zone to be late Frasnian in age, without
100 giving any further evidence. Another example that requires future clarification concerns the
101 lower Famennian brachiopod biozonation. Abrahamyan (1957) and Grechishnikova et al. (1980,
102 1982) recognized only one brachiopod zone within this substage, namely the *Cyrtospirifer*
103 *orbelianus* and the *Mesoplica meisteri* zones, respectively. However, Rzhonsnitskaya and
104 Mamedov (2000) established two biozones for the same interval: the lowermost Famennian
105 *Mesoplica meisteri*–*Cyrtospirifer asiaticus* and the lower Famennian *Cyrtiopsis orbelianus*–*C.*
106 *armenicus* Zones. Finally, Alekseeva et al. (2018a) followed the biostratigraphic scheme of
107 Grechishnikova et al. (1980) and considered that the lower Famennian of the Lesser Caucasus is
108 represented by only one brachiopod zone; however, they re-named it as *Mesoplica meisteri*–
109 *Cyrtospirifer asiaticus* Zone. The biostratigraphic scheme of Rzhonsnitskaya and Mamedov
110 (2000) was followed by Ginter et al. (2011), who described chondrichthyan remains from the
111 Upper Devonian–Lower Carboniferous succession of Armenia, some of which were recovered
112 from the Frasnian–Famennian interval of the Ertych and Noravank sections. Besides

113 chondrichthyans, these authors reported also conodonts from the *Cyrtiopsis orbelianus*–*C.*
114 *armenicus* Zone of the Noravank section, among which, some elements indicate the lower
115 Famennian *crepida* Zone (see Ginter et al., 2011; text-fig. 4).

116

117 **Material and methods**

118

119 The examined material was collected from the *Cyrtospirifer orbelianus* brachiopod Zone of
120 Abrahamyan (1957) cropping out in four different localities (Fig. 1); this brachiopod zone is
121 correlated with the *crepida* conodont Zone (Fig. 2).

122 The internal morphology of specimens was investigated by using the standard technique
123 of serial sections and acetate peels, in addition to numerous photographs of ground specimens
124 taken with a Canon EOS 700D camera, in order to catch the very minute details related to the
125 development of internal features. Shells selected for scanning electron microscopy were coated
126 with gold and their micro-ornament was observed with the help of a ZEISS EVO 10 Scanning
127 Electron Microscope hosted with the Paleontology team of Lille University. The larger
128 specimens were coated with magnesium oxide before being photographed.

129 *Repositories and institutional abbreviations.*—Most of the specimens illustrated and investigated
130 herein are deposited at the Geological Museum of the Institute of Geological Sciences of the
131 National Academy of Sciences of Armenia, Yerevan (IGSNASRAGM/PS). The prefix PS
132 indicates the laboratory of Paleontology and Stratigraphy. A few specimens are housed at the
133 public paleontological collection of Lille University (France).

134

135 **Systematic paleontology**

136

137 The supraspecific classification of this study follows the one proposed by Carter et al. (1994) and
138 Johnson (2006).

139

140

Order Spiriferida Waagen, 1883

141

Suborder Spiriferidina Waagen, 1883

142

Superfamily Cyrtospiriferoidea Termier and Termier, 1949

143

Family Cyrtospiriferidae Termier and Termier, 1949

144

Subfamily Cyrtospiriferinae Termier and Termier, 1949

145

Genus *Pentagonospirifer* new genus

146

147 *Type species.*—*Pentagonospirifer abrahamyanae* n. gen. n. sp., by monotypy.

148

149 *Diagnosis.*—Shell medium-sized, aequibiconvex to ventribiconvex, with acute to slightly
150 mucronate cardinal extremities; widest at hinge line; ventral interarea triangular, high, variably
151 concave, apsacline; pseudodeltidium with distinct, stacked sets of growth lamellae, with apical
152 foramen; dorsal fold and ventral sulcus wide, well-defined; ribs numerous, usually simple on
153 flanks, increasing by bifurcation in sulcus and on fold; micro-ornament of capillae with pustules
154 on them and closely spaced growth lines; dental plates long, always intrasinal; delthyrial
155 thickening is formed by a development of strong apical callus on delthyrial plate, around dental
156 plates and floor of ventral valve; ctenophoridium unsupported.

157

158 *Occurrence.*—Lower Famennian of Armenia.

159

160 *Etymology.*—*Pentagonus, a, um* (Latin): five-angled; *spirifer* is a common suffix used in the
161 spiriferide group. The name draws attention to the pentagonal ventral valve of the genus.

162

163 *Remarks.*—*Pentagonospirifer* n. gen. is assigned to the subfamily Cyrtospiriferinae
164 (Cyrtospiriferidae) on the basis of its wide hinge line, high interarea and acute cardinal
165 extremities.

166 The new genus resembles to some extent to some representatives of the lower Famennian
167 genus *Sinospirifer* Grabau, 1931 as revised by Ma and Day (2003, 2007), Ma et al. (2003) by its
168 wide hinge line, acute cardinal extremities, a massive apical callus developed in the ventral
169 interior and its unsupported ctenophoridium; however, *Pentagonospirifer* n. gen. has a higher
170 ventral interarea, a minute foramen near the apex, more ribs in sulcus and on fold, and pustules
171 developed only on capillae. Internally, the most significant difference concerns the dental plates
172 that are intrasinal and devoid of thickening in *Pentagonospirifer* n. gen., whereas *Sinospirifer*
173 possesses greatly thickened extrasinal dental plates.

174 Externally, *Pentagonospirifer* n. gen. appears to be closely related to *Wenjukovispirifer*
175 Oleneva, 2016, known from the Famennian of the European Platform, and more particularly by
176 its rounded subpentagonal outline, inflated shell, high ventral interarea, well-developed sulcus
177 and fold, an ornamentation composed of simple, and low ribs separated by narrower interspaces;

178 however, the new genus is distinguished by its relatively aequibiconvex lateral profile, its
179 pseudodeltidium with distinct, stacked sets of growth lamellae and its minute foramen developed
180 apically. It is worth noting that the internal structure of *Wenjukovispirifer* is not known as yet;
181 therefore, further comparison is hampered. Nevertheless, Oleneva (2016) did mention the
182 presence of a ventral septum (=myophragm?) in the ventral interior of *Wenjukovispirifer*, which
183 was not observed in *Pentagonospirifer* n. gen. Moreover, no strong apical callus on the delthyrial
184 plate is mentioned for *Wenjukovispirifer*, a feature observed in *Pentagonospirifer*.

185 The new genus may be distinguished from the late Givetian to early Famennian? genus
186 *Cyrtospirifer* Nalivkin in Frederiks, 1924, as revised by Ma and Day (2003), by its more
187 longitudinally elongated shell, the presence of a robust pseudodeltidium and its micro-ornament.
188 Internally, *Pentagonospirifer* n. gen. mainly differs by the presence of strong apical callosity
189 developed on the delthyrial plate.

190 *Pentagonospirifer* n. gen. displays many external similarities (e.g., rounded
191 subpentagonal outline, acute cardinal extremities, widest at hinge line, well-developed sulcus and
192 fold with ribs fainter than those on flanks) with *Pripyatispirifer* Pushkin, 1996 from the lower
193 Famennian of Belarus and possibly from the lower Frasnian of Nakhichevan (Afanasjeva in
194 Alekseeva et al., 2018b), but differs from the latter by its larger shell size, high ventral interarea
195 and by its minute apical foramen. Besides, the new genus differs by its micro-ornament
196 composed of capillae with pustules on them as *Pripyatispirifer* representatives lack plicae and
197 pustules on ribs. It is difficult to compare precisely the internal morphology of these genera as
198 Pushkin (1996) did not illustrate transverse sections, but based on Pushkin's illustration (1996, p.
199 47, fig. 2), the cardinal process of *Pripyatispirifer* appears to be trilobed, which is quite an
200 unusual case, thus different from that of *Pentagonospirifer* n. gen.

201 *Pentagonospirifer* n. gen. differs mainly from *Eodmitria* Brice, 1982, known from the
202 lower–middle Frasnian of Western Europe (Belgium, France and Germany) and Turkey (Brice,
203 1982; Sartenaer, 1982; Gourvennec, 2006), by its more inflated shell, high ventral interarea and
204 well-defined fold and sulcus. Furthermore, the micro-ornament of *Pentagonospirifer* n. gen.
205 consists of capillae with pustules on them (only on ribs), whereas the micro-ornament of
206 *Eodmitria* is papillose. It is worth noting that both genera have quite similar internal
207 morphologies, with the exception of the disposition of dental plates, which are intrasinal in
208 *Pentagonospirifer*, while they are extrasinal in *Eodmitria*.

209 *Pentagonospirifer* n. gen. is distinguished externally from *Pseudocyrtiopsis* Ma and Day,
210 1999 from the lower Famennian of South China, by its larger and more inflated shell (due to the
211 greater thickness of the dorsal valve), its bifurcating ribs in sulcus and on fold, its finer and more
212 numerous ribs on flanks, as well as the lack of capillae that are developed in the interspaces of
213 *Pseudocyrtiopsis* representatives. Internally, *Pentagonospirifer* n. gen. mainly differs by the
214 presence of a strong apical callosity developed on the delthyrial plate and by its unsupported
215 ctenophoridium.

216 *Pentagonospirifer* n. gen. differs from *Plicapustula* Ma and Day, 2007, from the lower
217 Famennian of South China and North America, by its more inflated and transversely elongated
218 shell, well-developed pseudodeltidium with a minute foramen near the apex, bifurcating ribs
219 across the whole width of sulcus and by the presence of capillae on ribs. Moreover, no strong
220 apical callus on the delthyrial plate is mentioned for *Plicapustula*, a feature observed in
221 *Pentagonospirifer* n. gen.

222 *Pentagonospirifer* n. gen. is distinguished externally from *Lamarckispirifer* Gatinaud,
223 1949 from the lower Famennian of South China as revised by Ma and Day (2007), by its inflated
224 shell, its high and subogival tongue, the larger number of ribs on flanks and fold and in sulcus,
225 and by the absence of a median furrow on fold that is generally present in *Lamarckispirifer*.
226 Moreover, *Pentagonospirifer* n. gen. differs by the presence of a strong apical callus developed
227 on the delthyrial plate and by its unsupported ctenophoridium.

228

229 *Pentagonospirifer abrahamyanae* new species

230 Figures 3–5; Table 1

231

232 *Holotype*.—An almost complete articulated specimen that is partly covered by encrusters in its
233 sulcus (IGSNASRAGM 3928/PS3073; Fig. 3.11–3.18), lower Famennian *orbelianus* Zone of
234 Djravank section (7 km southeast from Areni, Vayots Dzor Province, Central Armenia (Fig. 1)).

235

236 *Diagnosis*.—Shell medium-sized (up to 36.7 mm in width, 34.1 mm in length, 29.2 mm in
237 thickness) (Table 1), wider than long, aequibiconvex to ventribiconvex, widest at hinge line,
238 highest at about midlength, with acute cardinal extremities; anterior margin emarginate; anterior
239 commissure uniplicate; ventral interarea triangular, high, apsacline; pseudodeltidium with
240 distinct, stacked sets of growth lamellae and with a minute, ovate foramen positioned apically;
241 dorsal fold and ventral sulcus wide, and well-defined; tongue high, subtriangular to subcircular
242 in outline; ribs numerous, usually simple on flanks, increasing by bifurcation in sulcus and on

243 fold; micro-ornament of capillae with pustules on them and closely spaced growth lines; dental
244 plates long, extending to about 30% of the shell length, slightly convergent, diverging dorsally in
245 the umbonal region, always intrasinal; delthyrial thickening is formed by a development of
246 strong apical callus on delthyrial plate, around dental plates and floor of ventral valve;
247 ctenophoridium unsupported, slightly convex, with numerous vertical lamellae.

248

249 *Occurrence.*—This species occurs in the lower Famennian Ertych horizon of Arakelian (1964),
250 the *Cyrtospirifer orbelianus* brachiopod Zone of Abrahamyan (1957) and the *Cyrtiopsis*
251 *orbelianus*–*Cyrtiopsis armenicus* brachiopod zone of Rzhonsnitskaya and Mamedov (2000) (see
252 Fig. 2). The Ertych horizon is also correlated with the *crepida* conodont Zone.

253

254 *Description.*—Shell medium-sized, wider than long, generally aequibiconvex to slightly
255 ventribiconvex, rounded subpentagonal in outline, widest at hinge line, highest at about
256 midlength; cardinal extremities acute; anterior margin emarginate; anterior commissure
257 uniplicate. Ventral valve strongly inflated, with convex flanks sloping steeply towards lateral
258 commissures; highest in the posterior third of the valve, then decreasing progressively towards
259 anterior margin; umbo strongly inflated, large and prominent; beak straight to suberect; interarea
260 apsacline, triangular, high, generally slightly concave (occasionally perpendicular to
261 commissural plane) well-defined; delthyrium wide, covered by a pseudodeltidium for most of its
262 height, the latter being formed by distinct, stacked sets of growth lamellae; foramen minute,
263 ovate near the apex; sulcus relatively wide, shallow to moderately deep, originating from beak,

264 with rounded lateral boundaries, round-to flat-bottomed at front; tongue high, perpendicular to
265 commissural plane or slightly bent dorsally, subtriangular to subcircular in outline.

266 Dorsal valve wider than long, strongly inflated, with flanks sloping moderately towards
267 lateral commissures, subtrapezoidal in outline; highest in the anterior third of the valve
268 (occasionally near midlength at the juvenile growth stages), but progressively decreasing towards
269 anterior margin; interarea linear, flat to slightly concave, orthocline; fold moderately high to
270 high, wide, originating from beak, round-topped at front.

271 Ornamentation of up to 29 rounded (5 ribs per 5 mm at anterior margin near sulcus and
272 fold), simple, flattened, low ribs on each flank, becoming fainter towards posterolateral margins;
273 in sulcus and on fold, up to 25 ribs, increasing by bifurcation, much narrower than those present
274 on flanks; ribs twice wider than interspaces on the entire shell; micro-ornament of fine capillae
275 only on ribs with pustules on them and with closely spaced growth lines sometimes thickened as
276 growth varices.

277 Ventral valve interior (Fig. 4) with relatively thin, long, intrasinal and slightly divergent
278 dental plates, becoming subparallel more anteriorly, converging dorsally in umbonal region (as
279 seen in transverse section); delthyrial thickening formed by accretion of strong apical callus from
280 the internal faces of the dental plates and floor of ventral valve; delthyrial plate thin; lateral
281 apical cavities posteriorly infilled; teeth relatively small, subcircular.

282 Dorsal valve interior (Fig. 4) with flat to slightly concave, unsupported ctenophoridium
283 composed of up to 27 well-developed relatively long lamellae; dental sockets shallow; hinge
284 plate divided; crural bases mediodorsally oriented; spiral cones not preserved in the sectioned
285 specimens.

286

287 *Etymology.*—The species name refers to Marina Semenovna Abrahamyan (1922–1999), who
288 contributed greatly to the taxonomy and biostratigraphy of the Upper Devonian–Lower
289 Carboniferous brachiopods of the Lesser Caucasus.

290

291 *Material examined.*—Forty-eight articulated specimens and nine dissociated valves from the
292 Ertych horizon of the sections Ertych (nine articulated specimens and two ventral valves),
293 Djravank (twenty-eight articulated specimens and five ventral valves) and Noravank (eleven
294 articulated specimens and two ventral valves). One of the examined specimens (IGSNASRAGM
295 3965/PS 3071) is encrusted by two cornulitid tubeworms, which displays the external features of
296 the genus *Cornulites* von Schlotheim, 1820 (Fig. 3.2, 3.19), whereas the encrusters observed on
297 IGSNASRAGM 3928/PS 3034 (Fig. 3.11, 3.15, 3.18) appear to be colonial organisms belonging
298 to the genus *Hederella* Hall, 1883.

299

300 *Shell ontogeny.*—The examination of a few juvenile specimens shows that almost all superficial
301 features (e.g., aequibiconvex shell covered by numerous rib, well-developed sulcus and fold,
302 relatively high ventral interarea, high tongue) may be observed since the early growth stages; the
303 only difference to separate juveniles from adults is their shell size. The size distributions during
304 the growth, as represented by the width/length, the width/thickness, the width/width of sulcus
305 and the width/length of dorsal valve plots, show a continuous and progressive growth with no
306 distinct grouping (Fig. 5). The relative proportions of the latter are represented by sufficient
307 material remaining constant (linear regression: $y = ax + b$; significant probability value: $p <$

308 0.01***) whatever the degree of development of individuals (Fig. 5). Moreover, the correlation
309 is positive with width varying proportionally with length, thickness, width of sulcus and the
310 length of dorsal valve. However, the width /length of the dorsal valve ratio shows less dispersed
311 values (Fig. 5.4). To complete the scatter plots, the measurements (in mm) of numerous
312 individuals of *P. abrahamyanae* n. gen. n. sp. are also represented in Table 1.

313
314 *Remarks.*— Despite the great faunal similarities between the Upper Devonian sequences of
315 Armenia and Nakhichevan, the literature review of papers devoted to the brachiopods described
316 in Nakhichevan (e.g., Grechishnikova, 1986, 1996; Grechishnikova in Alekseeva et al., 2018 b)
317 did not reveal specimens that could be assigned to *Pentagonospirifer abrahamyanae* n. gen. n.
318 sp. The main difference of the latter species from other early Famennian cyrtospiriferids of
319 Armenia is the presence of delthyrial thickening that is formed by a development of strong apical
320 callus on delthyrial plate, around dental plates and floor of ventral valve. It is worth noting
321 that until now, among the spiriferides described in Armenia, encrusters are observed only in the
322 specimens of this species.

323

324 Subfamily Cyrtiopsinae Ivanova, 1972

325 Genus *Tornatospirifer* new genus

326

327 *Type species.*—*Cyrtiopsis senceliae armenica* Abrahamyan, 1974.

328

329 *Other species.*—*Cyrtiopsis caucasia* Grechishnikova, 1986 is considered here as a junior
330 synonym of the type species of *Tornatospirifer* n. gen. as we observed all superficial features
331 that were supposed to separate the latter from Abrahamyan's species. *Cyrtiopsis senceliae*
332 Sartenaer *sensu* Sidjachenko (1962) and *Cyrtospirifer (Cyrtospirifer) helenae* Sidjachenko, 1962
333 from the Famennian of Central and southeastern Kara-Tau (Kazakhstan) are allocated to this
334 genus although the pseudodeltidium and micro-ornament of the latter are unknown due to poor
335 preservation. *Spirifer (Cyrtospirifer) archiaci* Murchison *sensu* Nalivkin (1937) also from
336 Central Kara-Tau is tentatively assigned to this genus; however, its internal morphology and
337 micro-ornament are unknown. *Spirifer murchisonianus* de Koninck [sic] *sensu* Reed (1922: pl.
338 10, figs. 3–12, pl. 11, figs. 1–7) from the Famennian (excluding the lowermost and uppermost
339 Famennian according to Sartenaer, 1970) of Pamir (Tajikistan) also probably belongs to this new
340 genus. Sartenaer (1956a, 1965) clearly demonstrated that *Spirifer murchisonianus* de Koninck is
341 a nomen nudum. Although Reed (1922) did not illustrate serial sections, he mentioned the
342 presence of dental plates and dorsal median septum (he apparently observed the development of
343 a callus supporting the ctenophoridium) that fit well with the diagnosis of *Tornatospirifer* n. gen.
344
345 *Diagnosis.*—Shell medium-sized, ventribiconvex, rounded subpentagonal, brachythyrid with
346 obtuse or rounded cardinal extremities (though the latter are worn in most of the studied
347 specimens); ventral interarea triangular, high, apsacline; delthyrium relatively wide, covered by a
348 pseudodeltidium formed by several distinct plates; fold and sulcus wide, well-defined; ribs
349 numerous, simple on flanks, increasing by bifurcation in sulcus and on fold; micro-ornament of
350 closely spaced growth lines, capillae occurring only on ribs and numerous pustules developed

351 only on capillae; dental plates long, strong, intrasinal; delthyrial plate well-developed;
352 ctenophoridium supported by an apical callosity; hinge plates divided.

353

354 *Occurrence.*—Lower Famennian of Armenia and Nakhichevan, Famennian of Central Kara-Tau
355 (Kazakhstan) and probably Famennian of Pamir (Tajikistan).

356

357 *Etymology.*—*Tornatus*, *a, um* (Latin): rounded; *spirifer* is a common suffix used in the
358 spiriferide genera. The name refers to the rounded subpentagonal shell shape.

359

360 *Remarks.*—*Tornatospirifer* n. gen. is placed within the subfamily Cyrtiopsinae due to its
361 brachythyrid shell and obtuse or rounded cardinal extremities.

362 *Tornatospirifer* n. gen. is closely related to the genus *Tiocyrspis* Sartenaer, 1994, which is
363 known from the upper Frasnian of Belgium and Germany; however, the former displays more
364 inflated ventral valve and higher ventral interarea. Moreover, *Tornatospirifer* n. gen. possesses
365 delthyrial plate, a character that is not observed in *Tiocyrspis*.

366 *Tornatospirifer* n. gen. mainly differs externally from *Cyrtiopsis* Grabau, 1923 *sensu* Ma
367 and Day (1999) from the lower Famennian of China, by its high ventral interarea, its
368 pseudodeltidium composed of several distinct plates and by its clearly defined sulcus contrary to
369 those with rounded lateral boundaries occurring in *Cyrtiopsis* representatives. The essential
370 internal difference between the two genera is the presence of a well-developed delthyrial plate in
371 *Tornatospirifer* n. gen., which is absent in *Cyrtiopsis*.

372 *Tornatospirifer* n. gen. shares several external and internal characters with the genus
373 *Uchtospirifer* Ljashenko, 1957 *sensu* Sokiran (2006). More particularly, both genera display a

374 brachythyrid shell that is subpentagonal in outline and ornamented with closely spaced and
375 flattened ribs, an apsacline and triangular ventral interarea, as well as intrasinal and divergent
376 dental plates. However, *Tornatospirifer* n. gen. differs by its more globular shell, the type of its
377 pseudodeltidium (formed by several distinct plates), the development of ribs in sulcus and on
378 fold that are not transforming into capillae, flattening or disappearing as it is observed in
379 *Uchtospirifer* representatives. Internally *Tornatospirifer* n. gen. is distinguished by its supported
380 ctenophoridium whereas the latter is unsupported in *Uchtospirifer*.

381 *Tornatospirifer* n. gen. differs from the lower Famennian genus *Pseudocyrtiopsis* Ma and
382 Day, 1999 from South China, by its general shape and outline, bifurcating ribs in sulcus and on
383 fold as well as lack of capillae that are developed in the interspaces of *Pseudocyrtiopsis*
384 representatives. Although, it is also worthwhile to stress that these genera have quite similar
385 internal morphology (e.g., strong, divergent dental plates, a well-developed delthyrial plate and a
386 supported ctenophoridium).

387 *Tornatospirifer* n. gen. is distinguished externally from *Ghorispirifer* Mottequin and
388 Brice, 2019, known from the upper–uppermost Famennian of Afghanistan and Iran by its high
389 ventral interarea and by its micro-ornament, which is composed of capillae and numerous
390 pustules only on ribs, whereas *Ghorispirifer* has capillae with pustules both on ribs and in
391 interspaces. The most substantial difference lies in the ventral internal morphology. In
392 *Tornatospirifer* n. gen. the dental plates are connected by a well-developed delthyrial plate which
393 is absent in *Ghorispirifer*.

394 *Tornatospirifer* n. gen. is distinguished externally from the widespread genus
395 *Dichospirifer* Brice 1971, as revised by Mottequin and Brice (2019), by its high ventral interarea,
396 well-defined fold and sulcus, its simple ribs on flanks. Furthermore, the micro-ornament of the

397 new genus consists of capillae with dense pustules only on ribs whereas capillae with rare
398 pustules are observed both on ribs and in interspaces in *Dichospirifer*. The internal morphology
399 of both genera is quite similar with the exception of the delthyrial plate, which is massive and
400 well-developed in *Tornatospirifer* n. gen., when *Dichospirifer* possesses a rudimentary one, and
401 secondly the ctenophoridium of the latter genus is bilobed posteriorly, which is not the case of
402 the new genus.

403 The new genus is distinguished from the Famennian genus *Dmitria* Sidjachenko, 1961,
404 by its well-developed sulcus and fold, its high and subogival tongue, its high ventral interarea
405 and by the presence of numerous pustules developed on capillae. Internally, *Tornatospirifer* n.
406 gen. mainly differs by its delthyrial plate, which is absent in *Dmitria* representatives.

407

408 *Tornatospirifer armenicus* (Abrahamyan, 1974)

409 Figures 6–9; Table 2

410

411 1952 *Cyrtospirifer murchisonianus*; Arakelyan, p. 40, 42.

412 1957 *Cyrtospirifer murchisonianus* (de Koninck); Abrahamyan, p. 73, pl. 9, fig. 1; text-fig. 14.1.

413 1964 *Cyrtospirifer murchisonianus* (de Koninck); Arakelyan, p. 75, 77, 94.

414 1973 *Cyrtospirifer murchisonianus* (de Koninck); Abrahamyan et al., p. 218.

415 1974 *Cyrtiopsis senceliae armenica* ssp. n.; Abrahamyan, p. 61, pl. 21, fig. 1; pl. 22, fig. 4.

416 1975 *Cyrtiopsis senceliae armenica*; Abrahamyan et al., p. 24.

417 1978 *Cyrtiopsis senceliae armenica* Abrahamyan; Brice in Brice et al., p. 24.

418 1979 *Cyrtiopsis armenica* (Abrahamyan); Aristov et al., p. 88, 91.

419 1986 *Cyrtiopsis caucasia*; Grechishnikova, p. 55, pl. 1, figs. 3–4; text-fig. 2.

420 2018a *Cyrtiopsis caucasia* Grechishnikova; Grechishnikova in Alekseeva et al., p. 855.
421 2018b *Cyrtiopsis caucasia* Grechishnikova; Afanasjeva in Alekseeva et al., p. 1005, pl. 29, figs.
422 5–6; text-fig. 101.

423 2019 *Cyrtiopsis senceliae armenica* Abrahamyan; Mottequin and Brice 2019, p. 56.

424

425 *Neotype*.—After extensive search at the Geological Museum of Yerevan, none of the syntypes
426 illustrated by Abrahamyan (1974: pl. 21, fig. 1; pl. 22, fig. 4) was found in Abrahamyan's
427 collection; they are therefore considered as lost. Consequently, one of the recently collected
428 specimens from the Ertych horizon (lower Famennian) of the Shamamidzor section (type
429 locality) (Lanjanist village, Ararat province, West Central Armenia; Fig. 1) is hereby designated
430 as the neotype (IGSNASRAGM 3980/PS 3048 and figured in Figure 7.1–7.8).

431

432 *Occurrence*.—This species characterizes the lower Famennian *Cyrtospirifer orbelianus* Zone of
433 Abrahamyan (1957), as well as the *Cyrtiopsis orbelianus*–*Cyrtiopsis armenicus* Zone of
434 Rzhonsnitskaya and Mamedov (2000) (Fig. 2) both in Armenia and Nakhichevan. *T. armenicus*
435 is known only in the Ertych horizon; in addition to our results from the Shamamidzor, Ertych,
436 Djravank and Noravank sections, it was also found in the Zangakatun section (Armenia), studied
437 by Abrahamyan (1957) and Arakelyan (1964) and in the Gyumushlug section in Nakhichevan
438 studied by Abrahamyan (1957) and Grechishnikova (1986) (Fig. 1).

439

440 *Description*.—Shell medium-sized (reaching 33.7 mm in width, 31.3 mm in length and 27.5 mm
441 in thickness) (Table 2), slightly wider than long, ventribiconvex, rounded subpentagonal in
442 outline, widest at about midlength; cardinal extremities obtuse or rounded (although the latter are

443 poorly preserved in our examined material); anterior margin gently emarginate to straight;
444 anterior commissure uniplicate.

445 Ventral valve strongly inflated, rounded subpentagonal in outline, with convex flanks
446 sloping moderately towards lateral commissures; highest in the posterior third of the valve, then
447 decreasing progressively towards anterior margin; umbo markedly inflated, large; beak acute,
448 straight to suberect; interarea apsacline, triangular, high, well-defined, slightly concave;
449 delthyrium relatively wide, covered by pseudodeltidium formed by several distinct plates with an
450 ovate foramen at its top (Abrahamyan, 1974: pl. 22, fig. 4) (Fig. 7.9); sulcus well-defined, wide,
451 moderately deep, originating from beak, widening and becoming deeper anteriorly, flat- to
452 round-bottomed at front; tongue wider than high, perpendicular to commissural plane or slightly
453 bent dorsally, high, subcircular to subogival in outline.

454 Dorsal valve wider than long, moderately inflated with convex flanks sloping gently to
455 moderately towards lateral commissures, rounded rectangular in outline; highest at about
456 midlength or more anteriorly to it, then decreasing gradually towards anterior margin; interarea
457 linear, nearly flat, orthocline; fold well-delimited, wide, moderately high, originating from beak,
458 widening and becoming relatively higher anteriorly, round-topped at front.

459 Flanks covered by 26 to 32 rounded (5–6 ribs per 5 mm at anterior margin near sulcus
460 and fold), simple, flattened, low ribs, becoming weaker towards posterolateral margins; in sulcus
461 and on fold, up to 25 ribs, mainly increasing by bifurcations, generally in their middle part;
462 interspaces narrower than ribs; micro-ornament (Fig. 7.7–7.8) of closely spaced growth lines
463 (irregularly thickened as growth varices), capillae occurring only on ribs and numerous pustules
464 developed on capillae.

465 Ventral valve interior (Fig. 8) with long, intrasinal posteriorly thickened and divergent
466 (19–25 degrees) dental plates; delthyrial plate thick; central and lateral apical cavities large and
467 poorly filled in by callus; teeth small, subrectangular.

468 Dorsal valve interior (Fig. 8) with ctenophoridium consisting of up to 36 well-developed,
469 relatively long lamellae, and supported by a short pseudoseptum; hinge plates divided; outer
470 hinge plate slightly concave; crural bases dorsally convergent; spiralia oriented posterolaterally
471 with at least 18 whorls per spiral cone.

472
473 *Material examined.*—Forty-one articulated specimens, ten ventral and six dorsal valves from the
474 sections Ertych (five articulated specimens and two dorsal valves), Djravank (eighteen
475 articulated specimen and three ventral valves), Noravank (twelve articulated specimens, two
476 ventral and two dorsal valves), and Shamamidzor (six articulated specimens, five ventral and two
477 dorsal valves).

478
479 *Shell ontogeny.*—The examination of juvenile forms suggests that the latter differ from adults in
480 having inconspicuous umbones, small acute beaks, fainter ribs and flat ventral interarea. The
481 tongue of specimens at young stages is subogival in outline, then progressively becoming
482 subcircular with age. Sulcus and fold well-developed since early growth stage. The size
483 distribution during growth, as represented by the width/length, width/thickness, width/width of
484 sulcus and width/length of dorsal valve plots, show a continuous and progressive growth with no
485 distinct groupings (Fig. 9). The relative proportions of *Tornatospirifer armenicus* (Abrahamyan,
486 1974) represented by sufficient material remain constant (linear regression: $y = ax + b$; significant
487 probability value: $p < 0.01^{***}$) whatever the degree of development of individuals (Fig. 9).

488 Moreover, there is a positive correlation in the variation of the shell's width proportionally with
489 length, thickness, width of sulcus and the length of dorsal valve. The width/length of the dorsal
490 valve shows less dispersed values (Fig. 9.4). To complete the scatter plots, the measurements (in
491 mm) of numerous individuals of *Tornatospirifer armenicus* (Abrahamyan, 1974) are also
492 presented in Table 2.

493
494 *Remarks.*—Arakelyan (1952) initially identified this species as *Cyrtospirifer purchisonianus* (de
495 Verneuil, 1845), a lower Frasnian representative of the genus *Uchtospirifer* from Russia
496 (Ljashenko, 1959; Sartenaer, 1965). It was first illustrated by Abrahamyan (1957), who also
497 examined its internal morphology, without resolving the taxonomic confusion. Many years later,
498 the relatively detailed study of Abrahamyan (1974) established that it should be assigned to the
499 genus *Cyrtiopsis*, considering it as a subspecies of *Cyrtiopsis senceliae* Sartenaer, 1956b (=
500 '*Pseudocyrtiopsis*' *senceliae*, see discussions in Ma and Day (1999) and Mottequin and Brice
501 (2019)), as species known from the lower Famennian of southern Belgium, one of the paratypes
502 of which (Sartenaer, 1956b: pl. 1, fig. 4) was re-illustrated recently by Mottequin and Brice
503 (2019: fig. 5.16–20). In fact, '*P.*' *senceliae* is clearly distinct from the Armenian material as its
504 mucronate shell is longer than wide (different outline) and displays notably a fold divided
505 longitudinally into three subequal parts. Brice in Brice et al. (1978) considered *Cyrtiopsis*
506 *senceliae armenica* Abramyan, 1974 as a synonym of *Ghorispirifer chakhaensis* (Brice, 1971)
507 known from the upper and uppermost Famennian of Afghanistan and Iran. However, as
508 explained by Mottequin and Brice (2019), this opinion cannot be accepted as the material from
509 Armenia may be easily distinguished from *G. chakhaensis* by its different outline (*G.*
510 *chakhaensis* displays a rounded or ovate outline with rounded posterolateral commissures,

511 whereas the specimens from Armenia display a rounded subpentagonal outline and almost
512 straight posterolateral commissures), its pseudodeltidium formed by several distinct plates, its
513 high ventral interarea, having more ribs in sulcus and on fold and lacking numerous pustules
514 developed on capillae. Moreover, *T. armenicus* has a delthyrial plate, which is absent in *G.*
515 *chakhaensis*. Afterwards, Aristov et al. (1979) raised Abrahamyan's (1974) subspecies to the
516 species level. Grechishnikova (1986) erected *Cyrtiopsis caucasia* from the lower Famennian of
517 Nakhichevan and indicated the similarity to *C. senceliae armenicus* coming from the same
518 locality (Gyumushlug section; Fig. 1). The author compared her material with Abrahamyan's
519 (1974) subspecies and mentioned that *C. caucasia* differs from the former by its triangular shell
520 outline, smaller size, ventral triangular interarea and prominent ventral beak. Grechishnikova
521 (1986: pl. 1, fig. 3) illustrated only the holotype, which was re-illustrated by Afanasjeva in
522 Alekseeva et al. (2018b: pl. 29, fig. 5). The latter compared Grechishnikova's species and *C.*
523 *senceliae* from Western Europe, China [*sic*] as well as Armenia, and indicated that the former
524 differs by its subtriangular shell outline. Thus, she implicitly considered either that
525 Abrahamyan's (1974) subspecies is still a subspecies of Sartenaer's (1956b) species, or simply
526 that she does not recognize *armenicus* as a valid subspecies. However, all of the external features
527 mentioned by both Grechishnikova (1986) and Afanasjeva in Alekseeva et al. (2018a, b), which
528 were supposed to point the differences, are also observed in Abrahamyan's species with the
529 exception of the subtriangular shell outline that is not even observed in their material, as the
530 holotype of *C. caucasia* is rounded subpentagonal in outline. Consequently, they certainly should
531 be considered as intraspecific variations. Thus, we consider *Cyrtiopsis caucasia* as a junior
532 synonym of Abrahamyan's species. As seen above, a great attention has been paid to this species
533 because of its peculiar external morphology and potential utility for recognition the lower

534 Famennian strata in the Lesser Caucasus; however, its affinities at the genus level were unknown
535 so far.

536

537 **Discussion**

538

539 *Definition of the family Cyrtospiriferidae and the likely origin of the two new genera.*—In
540 the classification put forward by Carter et al. (1994), one of the main distinguishing features of
541 the superfamily Cyrtospiriferoidea is the presence of a delthyrial plate. In the same classification
542 and taken into account the width of the hinge line and type of cardinal extremities, the family
543 Cyrtospiriferidae is divided into two subfamilies: the Cyrtospiriferinae Termier and Termier,
544 1949 and the Cyrtiopsinae Ivanova, 1972, with *Cyrtospirifer* Nalivkin in Fredericks, 1924 and
545 *Cyrtiopsis* Grabau, 1923 as their type genera, respectively. However, following the taxonomic
546 revision conducted by Ma and Day (1999) it was realized that the genus *Cyrtiopsis* is devoid of
547 any delthyrial plate, which contradicts one of the main criteria in the definition of the
548 superfamily Cyrtospiriferoidea proposed by Carter et al. (1994). Therefore, Ma and Day (2000,
549 p. 450) revised the family Cyrtospiriferidae to include genera that are devoid of a delthyrial
550 plate. Later, Ma and Day (2003) noted that some genera possess a posterior ventral shell
551 thickening that could be considered as equivalent to a delthyrial plate and therefore they could
552 also be included in the family Cyrtospiriferidae. Although Johnson (2006), while defining the
553 superfamily Cyrtospiriferoidea, argued that its representatives generally possess a delthyrial
554 plate, it is obvious that the concept of this superfamily also requires revision to include those
555 members, which are devoid of any delthyrial plate. Moreover, amongst all genera assigned to the
556 subfamily Cyrtiopsinae, a delthyrial plate is observed only in the genus *Pseudocyrtiopsis* Ma and

557 Day (1999), a genus erected to include those cyrtospiriferid species that resemble somehow to
558 *Cyrtyopsis* Grabau, 1923, but also differ from it by their wide hinge line and the presence of a
559 delthyrial plate. Although both Ma and Day (1999) and later Gourvenec and Carter (2007)
560 attributed *Pseudocyrtyopsis* to the subfamily Cyrtyopsinae, this genus displays a high ventral
561 interarea, a wide hinge line and mucronate cardinal extremities. These morphological characters
562 are suggestive of its assignment to the Cyrtospiriferinae, according to Johnson's (2006)
563 classification. Thus, it appears that *Tornatospirifer* n. gen. and not *Pseudocyrtyopsis* Ma and Day
564 (1999) is the only genus of the subfamily Cyrtyopsinae, which possesses a delthyrial plate. In
565 conclusion, in spite of the extensive taxonomic studies led by Carter et al. (1994), Ma and Day
566 (1999, 2000, 2003, 2007), Ma et al. (2003) and Johnson (2006), the superfamily
567 Cyrtospiriferoidea, as well as the family Cyrtospiriferidae and its subfamilies, still require a
568 thorough revision in order to further understand the phylogenetic relationships amongst the
569 different species and genera assigned to this interesting and diverse group of spire-bearing
570 brachiopods.

571 It is likely that the new species *Pentagonospirifer abrahamyanae* evolved from a
572 *Cyrtospirifer* stock. Adult shells of both genera resemble each other in terms of their size,
573 rounded subpentagonal outline, acute cardinal extremities and apsacline ventral interareas. It is
574 possible that *P. abrahamyanae* evolved from *Cyrtospirifer verneuili* (Murchison, 1840) *sensu*
575 Abrahamyan (1957), which has been reported by the latter author from both the Frasnian and
576 lower Famennian deposits of Armenia. Morphologic trends leading to *Pentagonospirifer* would
577 have involved longitudinal elongation and inflation of the shell, development of a more complex
578 pseudodeltidium (composed of several plates) and micro-ornament (fine capillae only on ribs
579 with pustules on them) and a strong medial callosity on the delthyrial plate. We tentatively

580 regard *Tornatospirifer armenicus* (Abrahamyan, 1974) and the newly defined genus
581 *Tornatospirifer* as having evolved from *Tiocyrspis* Sartenaer, 1994. The latter genus is the oldest
582 cyrtiopsine representative and, it is only known from the upper Frasnian of Germany and
583 Belgium (Sartenaer, 1994); *Tornatospirifer* differs from *Tiocyrspis* mainly by its more complex
584 pseudodeltidium and by possessing a delthyrial plate.

585

586 *Paleobiogeographic considerations.*—The Late Devonian was characterized by a high eustatic
587 sea level and prolonged cosmopolitanism (Johnson et al., 1985). Brachiopod provincialism was
588 overall low at the time, presumably due to favorable patterns in oceanic current circulation that
589 led to substantial interchange between previously isolated faunas (Brock and Yazdi, 2000).
590 However, as shown through the studies of Gaetani (1965, 1968), Brice (1971), and Brice et al.
591 (1973, 1999) a single bioprovince may be individualized for the Upper Devonian brachiopod
592 assemblages found along the northern margin of Gondwana. Serobyán et al. (2021) concurred
593 recently with this viewpoint based on the study of lower Famennian rhynchonellides and
594 athyrides from Armenia; these authors argued for a rather uniform early Famennian brachiopod
595 bioprovince that was developed between Pamir (to the east) and the Anatolide-Tauride
596 microplate (to the west) (Fig. 10).

597 The brachiopods studied herein belong to the rhynchonelliforms that used to have a
598 benthic mode of life and produced lecithotrophic larvae, with a free-swimming larval stage
599 (Williams et al., 1996; Carlson, 2016). Both the monospecific genus *Pentagonospirifer* n. gen.
600 and the type species of *Tornatospirifer* (*T. armenicus*) appear to be restricted to the lower
601 Famennian of the South Armenian Block. However, at least two (and possibly three) previously
602 described species from the Kara-Tau region of Central Kazakhstan have been assigned by us to

603 the newly defined genus *Tornatospirifer* n. gen.; another questionably assigned species (*P. (?)*
604 *murchisonianus* de Koninck [sic] *sensu* Reed, 1922) is known from Pamir (Tajikistan) (Fig. 10);
605 morphologically it strongly resembles *Tornatospirifer armenicus* (Abrahamyan, 1974) and
606 therefore phylogenetically the two species may be closely related. Thus, *Tornatospirifer* species
607 had a quite wide latitudinal distribution during the Famennian, across the Paleo-Tethys ocean.
608 Moreover, if our hypothesis is correct for the evolutionary origin of *Tornatospirifer* from a
609 *Tiocyrspis* ancestral stock situated in Western Europe, we may tentatively consider that its
610 origination and migration took place during the earliest Famennian to both the Central
611 Kazakhstan block and the northern Gondwanan margin (SAB). Nevertheless, in order to achieve
612 robust conclusions in terms of the biogeographic distribution of Upper Devonian brachiopods,
613 modern taxonomic revisions are necessary on the brachiopod fauna described during the second
614 half of 20th century from areas of the former Soviet Union (Nalivkin, 1937, 1941; Martinova,
615 1961; Sidjachenko, 1962).

616

617 *Brachiopod encrusters: patterns and likely interaction with their host.*—Paleozoic encrusters
618 were common elements of shelly substrates during the Devonian time. More particularly, as
619 noted by Musabelliu and Zaton (2018) the lower Famennian marked an increase in cornulitid
620 abundance and morphological disparity. These epifaunal suspension feeders may be helpful for
621 paleoecological interpretations; they inhabited only in waters of normal salinity (Vinn et al.,
622 2019) as it is also the case of most brachiopod species. However, their biological affinities,
623 morphological peculiarities and paleobiodiversity remain largely undocumented. This is the very
624 first report documenting the presence of encrusters and their encrustation patterns on Upper
625 Devonian brachiopods from the Lesser Caucasus (Armenia and Nakhichevan). Indeed, no

626 observation or mention of any kind has been made before on this aspect (e.g. Abrahamyan, 1957,
627 1964, 1974; Arakelyan, 1964; Grechishnikova, 1986, 1996; Alekseeva et al., 2018a, b).

628 In our material, one specimen (IGSNASRAGM 3965/PS 3071) of *Pentagonospirifer*
629 *abrahamyanae* n. gen. n. sp. was found to be encrusted by two cornulitid tubeworms on its dorsal
630 valve, near the anterior margin, although one of them is only partly preserved (Fig. 3.2, 3.19).
631 The latter displays the external features of the genus *Cornulites* von Schlotheim, 1820, the
632 representatives of which are considered as hard-substrate encrusters; they are known since the
633 Middle Ordovician and up to the Late Carboniferous (Vinn, 2010). The tube of *Cornulites* sp. is
634 oriented with its aperture directed towards the brachiopod anterior commissure; this polarity
635 suggests the way in which the tubeworm was attached on the brachiopod shell and its subsequent
636 growth direction so that to “steal” some food transported by the weak currents produced by the
637 feeding activity of the brachiopod host (Richards, 1974). Moreover, the brachiopod shell
638 displays distinct shell malformations that were obviously caused by the growth of the cornulitid
639 tubeworm, affecting thus the shell-secreting epithelium of the host. Obviously, by feeding on the
640 food brought by the weak currents produced by the brachiopod lophophore, the cornulitid had a
641 clear negative impact on the host, as a deviation in the growth pattern is observed on the shell of
642 the latter. It is likely that the small size of the host is not due to its young age, but due to the
643 negative impact of the encrustors. In this regard, it is reasonable to consider this cornulitid
644 tubeworm as an ectoparasite (Richards, 1974) and not as a commensal in relation to its owner.
645 Encrusters observed on a second brachiopod specimen of *Pentagonospirifer abrahamyanae* n.
646 gen. n. sp. (IGSNASRAGM 3928/PS 3034; Fig. 3.11, 3.15, 3.18) were likely colonial organisms;
647 they may be assigned to *Hederella* Hall, 1883, an enigmatic encrusting metazoan that is known
648 from the Silurian to the Permian, although it is more common in the Devonian record (Tapanila,

649 2005). Although it resembles cyclostome bryozoans, it is not considered as a bryozoan because
650 of its branching patterns, lack of an astogenetic gradient, skeletal microstructure, and wide range
651 in tube diameters (Wilson and Taylor, 2001). It is likely that it was some kind of a lophophorate-
652 grade animal of uncertain affinity (Taylor and Wilson, 2008).

653

654 **Conclusions**

655

656 The taxonomic examination of two cyrtospiriferid species, based on newly collected material
657 from the lower Famennian of Armenia led us to define two new genera: *Pentagonospirifer*
658 (Cyrtospiriferinae) and *Tornatospirifer* (Cyrtiopsinae). *Tornatospirifer* n. gen. appears to be the
659 only genus within the subfamily Cyrtiopsinae, which possesses a delthyrial plate. This indicates
660 that although most of cyrtiopsine genera lack a delthyrial plate, the presence or absence of this
661 internal structure should not be used in the definition of the Cyrtiopsinae in classifications that
662 possibly will be established after a thorough revision of the whole superfamily
663 Cyrtospiriferoidea, as recommended by Ma and Day (2000). *Cyrtiopsis caucasia*
664 Grechishnikova, 1986 is hereby considered as a junior synonym of *Tornatospirifer armenicus*
665 (Abrahamyan, 1974), which is one of the most biostratigraphically valuable species for the
666 recognition of lower Famennian strata in the Lesser Caucasus. Both illustrated species appear to
667 be restricted to the lower Famennian of the SAB arguing for its relative isolation within the
668 northern margin of Gondwana.

669

670 **Acknowledgments**

671
672 V. Serobyanyan is grateful to the French Embassy in Yerevan and the MOB-LIL-EX International
673 Mobility Grant Programme of the University of Lille for funding his studies in France. T.
674 Danelian and A. Grigoryan would like to thank the Erasmus + Programme for funding their staff
675 mobility in 2018 and 2019, respectively. C. Crônier acknowledges the financial support of the
676 Lille Institute on Environmental Sciences (IRePSE). Fieldwork was also facilitated by the
677 logistic support of the Institute of Geological Sciences (Armenian Academy of Sciences). The
678 authors thank the Région Hauts-de-France, and the Ministère de l'Enseignement Supérieur et de
679 la Recherche (CPER Climibio), and the European Fund for Regional Economic Development for
680 their financial support. Sylvie Régnier (UMR Evo-Eco-Paleo, ULille) is gratefully acknowledged
681 for the high-quality SEM pictures obtained on specimens deposited at IGSNASRAGM. The
682 authors are also grateful to Andrzej Baliński for his advice on spiriferides from the Eastern
683 European Platform. This work is a contribution to the IGCP project n° 652 'Reading Geologic
684 Time in Paleozoic Sedimentary Rocks'. The manuscript benefited from the reviews of A.
685 Baliński and of an anonymous reviewer, and from the editorial help of J. Jin, to whom all we are
686 much indebted.

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926

927 **Figures captions**

928

929 **Figure 1.** Schematic geological map and distribution of Upper Paleozoic sequences in the Lesser
930 Caucasus (Central Armenia and Nakhichevan), including the location of sections mentioned in
931 the present study (after Serobyanyan et al., 2019, modified).

932

933 **Figure 2.** Biochronostratigraphic framework of the Frasnian–lower Famennian sedimentary
934 sequences in the Lesser Caucasus, including the biostratigraphic horizons established by
935 Arakelyan (1964) and brachiopod biozones of Abrahamyan (1957) in Central Armenia and of
936 Grechishnikova et al. (1980) and Rzhonsnitskaya and Mamedov (2000) in Nakhichevan. It also
937 includes the regional conodont zonation established by Aristov (1994) in Nakhichevan and the
938 standard conodont zones of Ziegler and Sandberg (1990).

939

940 **Figure 3.** *Pentagonospirifer abrahamyanae* n. gen. n. sp. from the lower Famennian of Armenia.
941 The arrows indicate the anterior margin. (1–5, 19). IGSNASRAGM 3965/PS 3071 (Djravank
942 section), almost complete juvenile specimen in ventral, dorsal, lateral, posterior and anterior
943 views (1–5), and close-up of cornulitid tubeworm (19). (6–10). IGSNASRAGM 3966/PS 3072
944 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior
945 views. (11–18). IGSNASRAGM 3967/PS 3073 (holotype, Djravank section), almost complete
946 specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views (11–15), close-up
947 of the ventral interarea (delthyrium) showing the pseudodeltidium composed of several distinct,
948 stacked sets of growth lamellae with an ovate foramen near the apex (16–17) and close-up of
949 *Hederella* encrustation patterns near the front (18). (20–26). IGSNASRAGM 3968/PS 3074
950 (Ertych section), partly exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal
951 and anterior views (21–26), and close-up of the micro-ornament (capillae with pustules) on
952 ventral valve (25–26). Scale bars: 10 mm (1–15, 20–24), 5mm (16–17), 400 µm (25), 200 µm
953 (26).

954
955 **Figure 4.** Transverse serial sections of *Pentagonospirifer abrahamyanae* n. gen. n. sp.,
956 (IGSNASRAGM 3964/PS 3070), Djravank section. Numbers refer to distance in mm measured
957 from the top of the ventral umbo. Scale bars: 5 mm.

958
959 **Figure 5.** Scatter diagrams of *Pentagonospirifer abrahamyanae* n. gen. n. sp. 1, Relation
960 between shell width and length. 2, Relation between shell width and thickness. 3, Relation
961 between shell width and width of sulcus. 4, Relation between shell width and length of dorsal

962 valve. Abbreviations: N , number of specimens measured; $y=ax+b$, linear model; r , coefficient of
963 correlation; p^{***} , significant probability value.

964

965 **Figure 6.** *Tornatospirifer armenicus* (Abrahamyan, 1974) from the lower Famennian of
966 Armenia. (1–6). IGSNASRAGM 3978/PS 3084 (Djrvank section), almost complete specimen
967 in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. (7–12). IGSNASRAGM
968 3979/PS 3085 (Noravank section), almost complete specimen in ventral, dorsal, lateral, posterior,
969 posterodorsal and anterior views. (13–18). IGSNASRAGM 3980/PS 3086 (Djrvank), partly
970 exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. Scale
971 bar: 10 mm (1–18).

972

973 **Figure 7.** *Tornatospirifer armenicus* (Abrahamyan, 1974) from the lower Famennian of
974 Armenia. (1–8). IGSNASRAGM 3981/PS 3087 (neotype, Shamamidzor section), partly
975 exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views (1–6),
976 and close-up of the micro-ornament (capillae with pustules) on dorsal valve (7–8). (9).
977 IGSNASRAGM 3982/PS 3088 (Djrvank section), incomplete specimen, close-up of the ventral
978 interarea (delthyrium) showing partly preserved pseudodeltidium with an ovate foramen near the
979 apex. Scale bars: 10 mm (1–6), 2.5 mm (9), 400 μm (7), 200 μm (8).

980

981 **Figure 8.** Transverse serial sections of *Tornatospirifer armenicus* (Abrahamyan, 1974)
982 (IGSNASRAGM 3977/PS 3083), Djrvank section. Numbers refer to distances in mm measured
983 from the top of the ventral umbo.

984

985 **Figure 9.** Scatter diagrams of *Tornatospirifer armenicus* (Abrahamyan, 1974). 1, Relation
986 between shell width and length. 2, Relation between shell width and thickness. 3, Relation
987 between shell width and width of sulcus. 4, Relation between shell width and length of dorsal
988 valve. Abbreviations: N , number of specimens measured; $y=ax+b$, linear model; r , coefficient of
989 correlation; p^{***} , significant probability value.

990

991 **Figure 10.** Late Devonian paleogeographic reconstruction of the Paleotethys Ocean and its
992 surrounding continents, including the position of the South-Armenian Block along the northern
993 margin of the Gondwana megacontinent (redrawn and modified after Denayer and Hoçgör 2014,
994 based on the maps of Stampfli et al., 2002).

995

996 **Table 1.** Measurements in mm and ratios of *Pentagonospirifer abrahamyanae* n. gen. n. sp.
997 Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width
998 of the sulcus, dL–length of the dorsal valve.

999

1000 **Table 2.** Measurements in mm and ratios of *Tornatospirifer armenicus* (Abrahamyan, 1974)
1001 Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width
1002 of the sulcus, dL–length of the dorsal valve.