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

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Running Header: Lower Famennian cyrtospiriferid brachiopods from Armenia

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

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

Introduction

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

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

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

Geological and stratigraphic setting

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

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

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

Material and methods

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

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

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

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;

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

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

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

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

Pentagonospirifer abrahamyanae new species

Figures 3–5; Table 1

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

Diagnosis.—Shell medium-sized (up to 36.7 mm in width, 34.1 mm in length, 29.2 mm in thickness) (Table 1), wider than long, aequibiconvex to ventribiconvex, widest at hinge line, highest at about midlength, with acute cardinal extremities; anterior margin emarginate; anterior commissure uniplicate; ventral interarea triangular, high, apsacline; pseudodeltidium with distinct, stacked sets of growth lamellae and with a minute, ovate foramen positioned apically; dorsal fold and ventral sulcus wide, and well-defined; tongue high, subtriangular to subcircular 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: $p <$

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

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

Subfamily Cyrtiopsinae Ivanova, 1972

Genus *Tornatospirifer* new genus

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

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, apsacine; 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

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

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

Tornatospirifer armenicus (Abrahamyan, 1974)

Figures 6–9; Table 2

- 1952 *Cyrtospirifer murchisonianus*; Arakelyan, p. 40, 42.
- 1957 *Cyrtospirifer murchisonianus* (de Koninck); Abrahamyan, p. 73, pl. 9, fig. 1; text-fig. 14.1.
- 1964 *Cyrtospirifer murchisonianus* (de Koninck); Arakelyan, p. 75, 77, 94.
- 1973 *Cyrtospirifer murchisonianus* (de Koninck); Abrahamyan et al., p. 218.
- 1974 *Cyrtiopsis senceliae armenica* ssp. n.; Abrahamyan, p. 61, pl. 21, fig. 1; pl. 22, fig. 4.
- 1975 *Cyrtiopsis senceliae armenica*; Abrahamyan et al., p. 24.
- 1978 *Cyrtiopsis senceliae armenica* Abrahamyan; Brice in Brice et al., p. 24.
- 1979 *Cyrtiopsis armenica* (Abrahamyan); Aristov et al., p. 88, 91.
- 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 Djavank 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

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

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

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

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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Figures captions

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

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

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

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

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

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

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

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

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

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

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

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

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