

Aramazdospirifer orbelianus (Abich, 1858) n. comb.,
a new cyrtospiriferid brachiopod genus
and a biostratigraphically important species
from the lower Famennian
(Upper Devonian) of Armenia

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Aramazdospirifer orbelianus (Abich, 1858) (neotype) in ventral and dorsal views.

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***Aramazdospirifer orbelianus* (Abich, 1858) n. comb., a new cyrtospiriferid brachiopod genus and a biostratigraphically important species from the lower Famennian (Upper Devonian) of Armenia**

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ABSTRACT

The new genus *Aramazdospirifer* n. gen. (Cyrtospiriferidae) is erected to include *Spirifer orbelianus* Abich, 1858 from the lower Famennian of Central Armenia as its type species and to refute long-standing claims related to the affinities of the latter. The micro-ornament and internal structure of this species are investigated and documented for the first time, on the basis of recently collected material from the Ertych horizon of three different sections. Additionally, a neotype is selected for Abich's species as the type material is lost. *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. is a biostratigraphically important species for the lower Famennian strata of the Lesser Caucasus. It appears to be restricted to the South-Armenian Block; reports outside this Gondwanan area are discussed and discarded.

KEY WORDS

Brachiopoda,
Spiriferida,
lower Famennian,
Gondwana,
Armenia,
neotypification,
new genus,
new combination.

RÉSUMÉ

Aramazdospirifer orbelianus (Abich, 1858) n. comb., un nouveau genre de brachiopode cyrtospiriferide et une espèce biostratigraphique importante du Famennien inférieur (Dévonien supérieur) d'Arménie.

Le nouveau genre *Aramazdospirifer* n. gen. (Cyrtospiriferidae) est ici érigé, afin d'inclure *Spirifer orbelianus* Abich, 1858 du Famennien inférieur d'Arménie centrale comme son espèce type et réfuter ainsi des hypothèses antérieures sur les affinités de cette espèce. La micro-ornementation et la structure interne de celle-ci sont étudiées et documentées pour la première fois, sur la base de matériel récemment récolté dans trois coupes différentes au sein de l'horizon Ertych. En outre, un néotype est sélectionné pour cette espèce décrite initialement par Abich, étant donné que le matériel type est perdu. *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. est une espèce biostratigraphiquement importante du Famennien inférieur du Petit Caucase. Cette espèce semble être restreinte au bloc Sud-Arménien; des rapports la mentionnant à l'extérieur du domaine gondwanien sont discutés et écartés.

MOTS CLÉS

Brachiopodes,
Spiriferida,
Famennien inférieur,
Gondwana,
Arménie,
néotypification,
genre nouveau,
combinaison nouvelle.

INTRODUCTION

The Upper Devonian sedimentary sequences of Armenia are highly fossiliferous and contain a diverse and well-preserved brachiopod fauna (Abrahamyan 1957, 1964, 1974; Arakelyan 1964; Serobyán *et al.* 2021), which remains largely undocumented from a taxonomic and biostratigraphic point of view. Re-investigation of this fauna is crucial to better understand Late Devonian changes in brachiopod diversity and palaeobiogeographic distribution. In Armenia, Devonian outcrops were first examined by the famous German geologist Hermann Abich, considered as the “Father of Caucasian Geology” (Milanovsky 2007). Abich (1858) described a number of new brachiopod species from the Lesser Caucasus, notably the spiriferid species *Spirifer orbelianus* Abich, 1858. The latter was erroneously reported afterwards in the Franco-Belgian Basin by Gosselet (1874), and later in different parts of the world (see Sartenaer 1974 for a review, and references below). Due to its great potential for biostratigraphic correlations of lower Famennian successions throughout the Lesser Caucasus, re-investigation of *S. orbelianus* is a necessary task as its affinities at the genus level still remain unclear, in spite of the extensive taxonomic studies led by Abrahamyan (1957, 1974) and Afanasjeva (*in* Alekseeva *et al.* 2018a). The purpose of the present study is to reassess the taxonomy of *S. orbelianus* on the basis of recently collected material from the lower Famennian of Central Armenia, with implications for its palaeobiogeographic distribution.

STRATIGRAPHIC AND PALAEOGEOGRAPHIC SETTINGS

In the southern part of Central Armenia crops out a c. 1 500 m-thick Middle Devonian-lower Carboniferous sequence of platform carbonate deposits (Fig. 1). They record the earliest depositional history of Palaeozoic sediments in the area; they were accumulated on a Gondwanan passive margin that was facing the Palaeotethys, situated to the North; this part of Gondwana was later individual-

ized as the South-Armenian Block, following its northward migration and opening of Neotethys further to the South (Sosson *et al.* 2010). The Middle Devonian-lower Carboniferous sequences of Armenia constitute a continuous succession of mixed carbonate-siliciclastic deposits, developed in a shallow water environment. The Upper Devonian-lower Carboniferous sequences were subdivided by Abrahamyan (1964) and Arakelyan (1964) into twelve “formations”. However, in practice, most of them have very similar lithological characteristics and they cannot be recognized in the field without knowledge of their brachiopod assemblages. Thus, they have a biostratigraphic rather than lithostratigraphic significance (see Serobyán *et al.* 2019). It is worth noting that Abrahamyan *et al.* (1975) described these stratigraphic units as “horizons” and no longer used the term “formation”. In Armenia, Famennian deposits are more widespread than the Frasnian ones. The latter consist mainly of marly and sandy limestones, biogenic limestones rich in brachiopods and corals (a few gastropods and cephalopods were also found) with interbedded sandstones and quartzites, whereas the Famennian is chiefly represented by biogenic and sandy limestones, quartzites and shales. The first Devonian biostratigraphical zonal scheme based on brachiopods was established by Rzhonsnitskaya (1948). Afterwards, in her groundbreaking monograph, Abrahamyan (1957) discussed the occurrence and stratigraphic distribution of the brachiopod species she dealt with; she thus proposed a new continuous biostratigraphic zonal scheme characterized by marker species or species assemblages (Fig. 2). This was a major step forward, as the existing Devonian brachiopod biostratigraphic scheme available at the time for the region was very rudimentary. As the Upper Palaeozoic sedimentary sequences of Armenia continue into Nakhichevan, the stratigraphic and faunal similarities in terms of brachiopods allowed Mamedov & Rzhonsnitskaya (1985) to use and refine Abrahamyan's zonal scheme for the entire region of the Lesser Caucasus (or Transcaucasia). Subsequently, their zonal scheme was updated by Rzhonsnitskaya & Mamedov (2000) and correlated with the international conodont biozonation based on the conodont study of Aristov (1994) carried out in Nakhichevan.

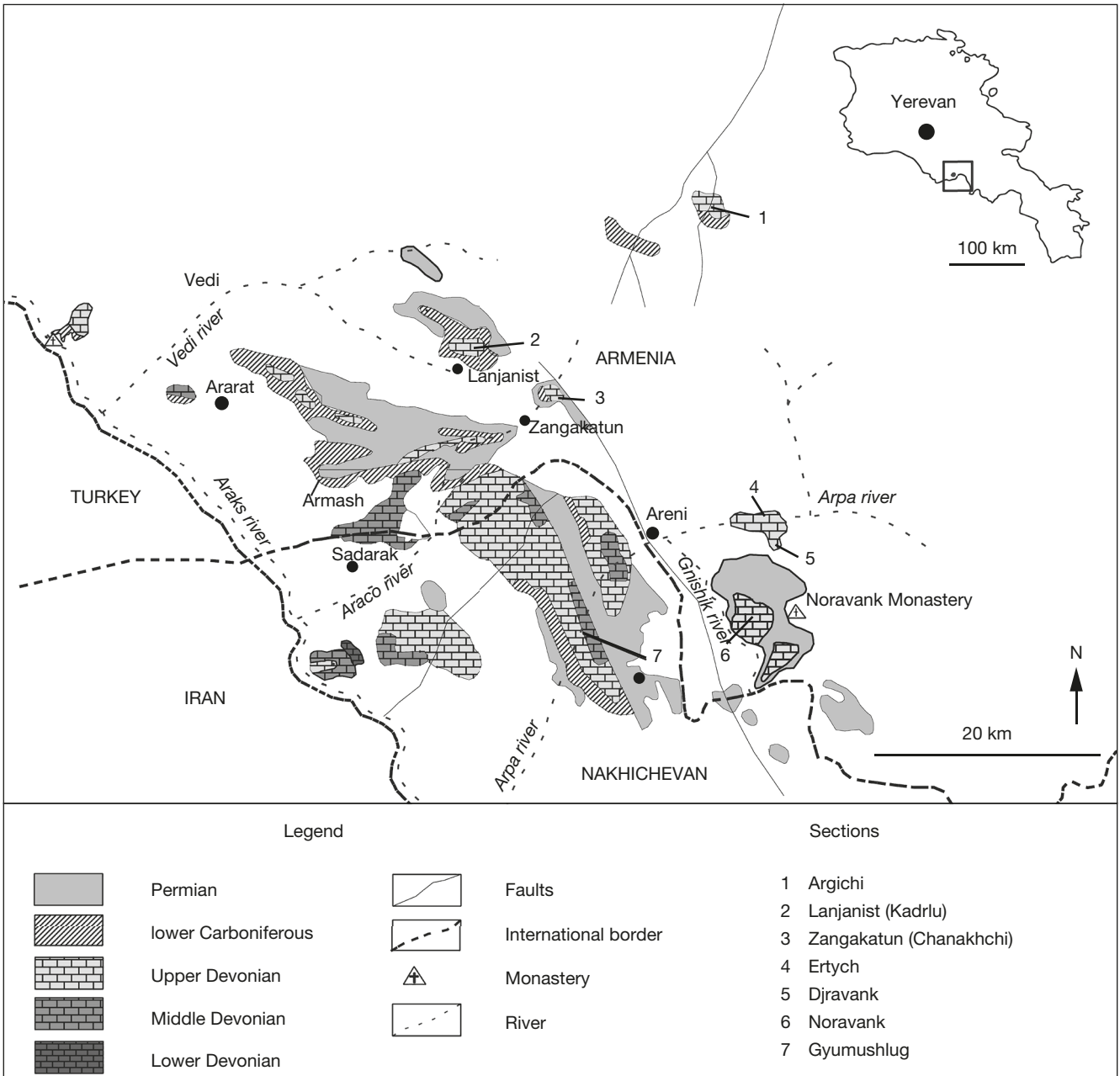


Fig. 1. — Schematic geological map of the South-Armenian Block; distribution of the Upper Devonian-lower Carboniferous deposits with localization of the sections containing *Aramazdospirifer orbelianus* (Abich, 1858) n. comb.

ABBREVIATIONS

IGSNASRAGM Institute of Geological Sciences of the National Academy of Sciences of Armenia, Yerevan;
 RBINS Royal Belgian Institute of natural Sciences, Brussels;
 USTL University of Lille, Lille.

MATERIAL AND METHODS

The examined material was collected from the Noravank, Ertych and Djrvank sections (Fig. 1) during several field seasons organized in 2018 and 2019. It comes from marly limestones and shales of the lower Famennian Ertych horizon

(Fig. 2), which can be correlated with the ‘*Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) and the ‘*Cyrtiopsis orbelianus-Cyrtiopsis armenicus* Zone of Rzhonsnitskaya & Mamedov (2000). In total, 80 articulated brachiopod shells and 15 dissociated valves were collected, the main part of which is derived from a soft, weathered surface that provided well-preserved, nearly sediment-free specimens. The bulk of the specimens illustrated and investigated herein is housed at the Geological Museum of the IGSNASRAGM. Some specimens are deposited at the RBINS and others at the USTL.

The recently collected material was compared with Abrahamyan’s specimens, collected in Armenia during the 1940s to 1980s, most of which are now stored at the IGSNASRAGM.

Stage	Sub-stage	Arakelyan (1964)	Abrahamyan (1957)	Rzhonsnitskaya & Mamedov (2000)
Famennian	lower	Ertych	' <i>Cyrtospirifer</i> ' <i>orbelianus</i>	' <i>Cyrtospirifer</i> ' <i>orbelianus</i> - ? <i>Cyrtiopsis armenicus</i>
		Noravank	<i>Cyrtospirifer lonsdalii</i> <i>Productella herminae</i> <i>Camarotoechia arpaensis</i> etc.	<i>Mesoplica meisteri</i> - <i>Cyrtospirifer asiaticus</i>
Frasnian	Upper	Baghrsagh		<i>Cyrtospirifer subarchiaci</i> <i>Cyphoterorhynchus arpaensis</i>

FIG. 2. — Biostratigraphic scheme of the lower Famennian of the Lesser Caucasus (Transcaucasus) correlated with the major lithostratigraphic units.

The internal structure of the newly collected articulated specimens identified as *A. orbelianus* (Abich, 1858) n. comb. found in the three sections (Fig. 1) was investigated by using the standard technique of serial sections and acetate peels. The latter were assembled between microscope slides and photographed under a binocular microscope Olympus SZX 12. Afterwards, the photographs were transferred to CorelDRAW X7 software and internal details were drawn using a digital drawing tablet. Furthermore, in order to capture the fine details of the internal structure, the ground specimens were photographed directly under a Canon EOS 700D camera that was attached on a Zeiss SteREO Discovery V20 Microscope. Intact brachiopod specimens were coated with magnesium oxide or ammonium chloride sublimate before being photographed. All images have been further processed using Adobe Photoshop CS6. Additionally, the IGSNASRAGM 3895/PS 3001 specimen was coated with gold and the digitization of the micro-ornament of the latter was performed by ZEISS EVO Scanning Electron Microscope. RBINS specimens selected for scanning electron microscopy were observed using a low vacuum SEM, an ESEM FEI Quanta 200, but not coated with gold.

SYSTEMATIC PALAEOONTOLOGY

The supraspecific classification adopted herein follows Carter *et al.* (2006) for the Order Spiriferida. The synonymy list only concerns the report of the species in the South-Armenian Block.

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily CYRTOSPIRIFEROIDEA
Termier & Termier, 1949

Family CYRTOSPIRIFERIDAE Termier & Termier, 1949
Subfamily CYRTOSPIRIFERINAE Termier & Termier, 1949

Aramazdospirifer n. gen.

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DIAGNOSIS. — Shell of medium-size, ventribiconvex, subpentagonal, wider than long to longer than wide, with mucronate cardinal

extremities; generally widest at hinge line; ventral interarea moderately high, apsacline; delthyrium wide and most of its height covered by a pseudodeltidium, the latter is composed of several distinct plates, with submesothyrid foramen; fold and sulcus moderately wide, well-defined, median longitudinal elevation developed in sulcus and frequently on fold; ribs numerous, usually simple on flanks, increasing by bifurcation in sulcus and on fold; micro-ornament capillate both on ribs and in interspaces; dental plates long, strong and intrasinal; delthyrial plate well-developed; unsupported ctenophoridium with numerous vertical lamellae; crural plates short; dorsal myophragm present.

TYPE SPECIES. — *Spirifer orbelianus* Abich, 1858.

OTHER SPECIES. — It is currently difficult to assign other species to *Aramazdospirifer* n. gen. with certainty in the absence of taxonomical revisions of the diverse cyrtospiriferide fauna from the Famennian of the ex-USSR. *Spirifer* (*Cyrtospirifer*) *aperturatus* von Schlotheim *sensu* Nalivkin (1930) described in the Central Kara-Tau and along the headwaters of the Naryn river (Kazakhstan) likely belongs to the new genus, although the latter has a less globular shell, subcircular tongue and lacks median and longitudinal elevations in sulcus and fold. It is worth noting that the real *aperturatus* from Germany and the Franco-Belgian basin differs from Nalivkin's species and does not belong to *Aramazdospirifer* n. gen. (see Paeckelmann 1942; Vandercammen 1959). It is also probable that *Cyrtospirifer* (*Cyrtospirifer*) *pentagonalis* Sidjachenko (1962) described from the Famennian of Central Kara-Tau should be assigned to *Aramazdospirifer* n. gen. as it shares many common features with the new genus. More precisely its inflated and subpentagonal shell that is ornamented with closely spaced and flattened ribs, acute to mucronate cardinal extremities and apsacline triangular ventral interarea that fit well with the diagnosis of the new genus. Nevertheless, the micro-ornament, the internal morphology and the type of pseudodeltidium of the latter species is unknown. Finally, *Cyrtospirifer aquilinus* Romanowski *sensu* Nalivkin (1930) described from the Central Kara-Tau and along the headwaters of the Naryn river (Kazakhstan) might also be assigned to the new genus, although it lacks median and longitudinal elevations in sulcus and on fold. However, its micro-ornament and internal morphology is unknown. All these uncertainties preclude the possibility of a definite assignment to *Aramazdospirifer* n. gen.

ETYMOLOGY. — In honor of Aramazd, who was the chief god in pre-Christian Armenian mythology.

REMARKS

Aramazdospirifer n. gen. is included in the superfamily Cyrtospiriferioidea based on the presence of dental plates, a ctenophoridium, a well-developed delthyrial plate, and capillate ornamentation. Although a thorough revision of this superfamily, recommended by Ma & Day (2000), is still pending, *Aramazdospirifer* n. gen. is assigned to the family Cyrtospiriferidae, as defined by Johnson (2006), due to the development of ribs in the sulcus and on fold. Additionally, its wide hinge line argues for its assignment to the subfamily Cyrtospiriferinae rather than to the Cyrtiopsinae.

Afanasjeva in Alekseeva *et al.* (2018a) examined some specimens collected from the Armenian sections and reassigned Abich's species to the late Givetian? – early Frasnian genus *Uchtospirifer* Liashenko, 1957 known from South Timan (Russia). *Aramazdospirifer* n. gen. shares indeed several external and internal characters with *Uchtospirifer* Liashenko, 1957 *sensu* Sokiran (2006). More particularly, both genera display a subpentagonal shell that is ornamented with closely spaced and flattened ribs (also in sulcus and on fold), an apsacline

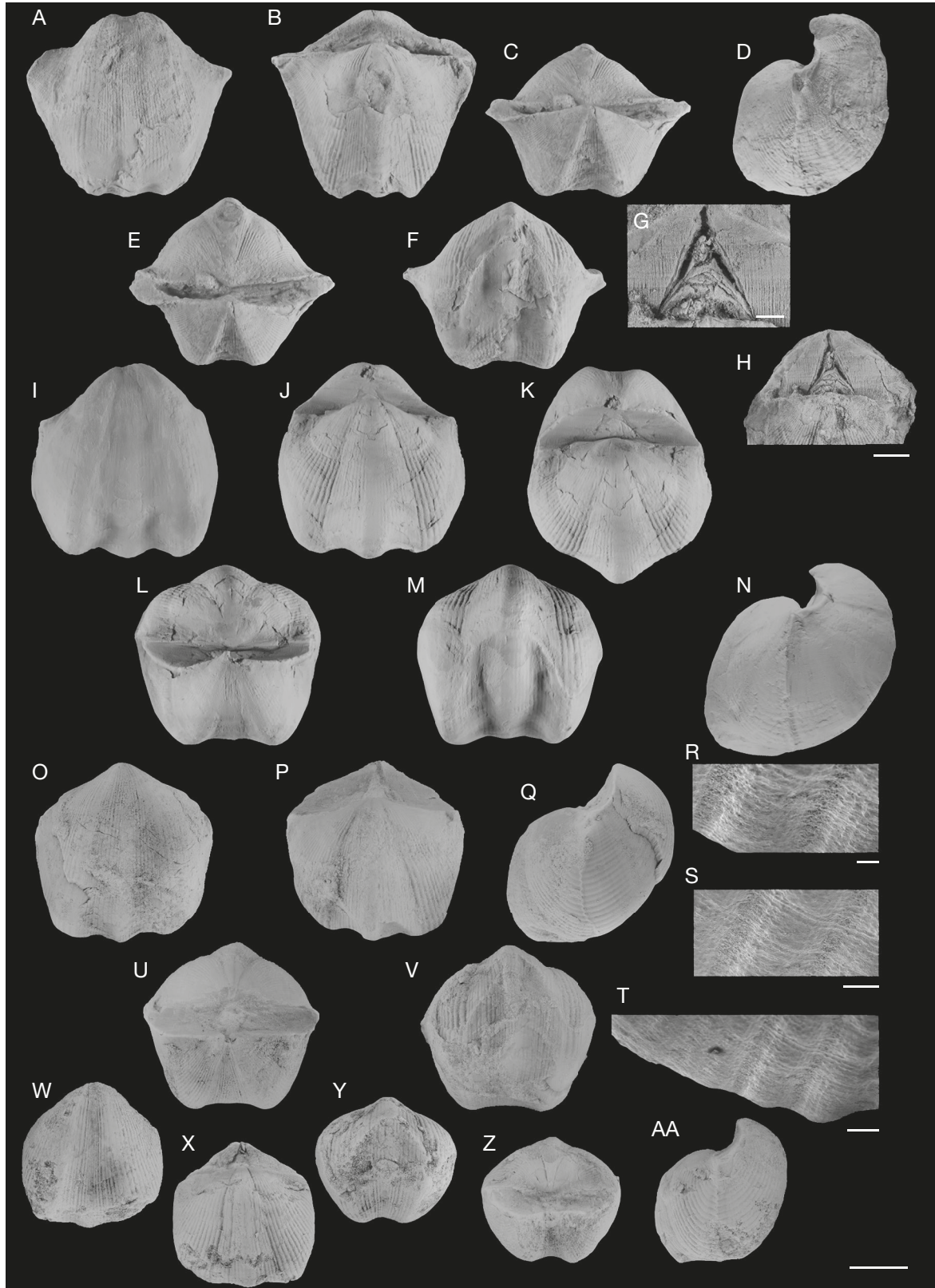


FIG. 3. — *Aramazdospirifer orbelianus* (Abich, 1858) n. comb.: **A-F, R-T**, almost complete specimen (IGSNASRAGM 3895/PS 3001) from the Djiravank section in ventral, dorsal, posterior, lateral, posterodorsal and anterior views (**A-F**), close-up of micro-ornament (capillae and growth lines) on dorsal valve (close to anterior margin; **R-T**); **G, H**, incomplete specimen (IGSNASRAGM 3896/PS 3002) from the Noravank section, close-up of the ventral interarea (pseudodeltidium; **G**); **I-N**, almost complete specimen (IGSNASRAGM 3897/AB97/48; neotype, Noravank section) in ventral, dorsal, posterodorsal, posterior, anterior and lateral views; **O-Q, U-V**, almost complete specimen (IGSNASRAGM 3898/PS 3004) from the Ertych section in ventral, dorsal, lateral, posterior and anterior views; **W-AA**, almost complete juvenile specimen (IGSNASRAGM 3899/PS 3005) from the Djiravank section in ventral, dorsal, anterior, posterior and lateral views. Scale bars: A-F, I-Q, U-AA, 10 mm; G, 2 mm; H, 5 mm; R, 200 μ m; S, 400 μ m; T, 500 μ m.

TABLE 1. — Measurements and ratios in mm of *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. Abbreviations: **dL**, length of the dorsal valve; **L**, length of the shell; **T**, thickness of the shell; **W**, width of the shell; **Ws**, width of the sulcus.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	60	54	53	55	53	54	53	55	53
Mean value	30.47	30.77	25.9	14.57	24.08	1.01	0.86	0.48	1.27
Standard deviation	3.2916	3.9919	4.4912	2.0632	2.7598	0.1058	0.1096	0.0625	0.1078
Standard error±	±0.4249	±0.543	±0.6169	±0.2782	±0.3791	±0.0144	±0.015	±0.0084	±0.0148
Min	22	21.3	14.9	9	18.6	0.78	0.57	0.34	1.09
Max	39	39.1	35.1	20	29.1	1.21	1.21	0.6	1.52

and triangular ventral interarea, divergent dental plates, and an unsupported ctenophoridium. However, *Aramazdospirifer* n. gen. differs from *Uchtospirifer* by its much more inflated shell, acute to mucronate cardinal extremities, wider hinge line, clearly defined longitudinal and median elevation in sulcus and similar elevation often developed on fold, and the type of pseudodeltidium formed by several distinct plates. Furthermore, it is worth noting that *Aramazdospirifer* n. gen. has narrower ribs perceptible along the whole length of its sulcus and fold, whereas the median ribs of *Uchtospirifer* are variably developed, sometimes flattened to imperceptible or absent. Moreover, the micro-ornament of the new genus lacks the tubercles observed on *Uchtospirifer*.

Externally *Aramazdospirifer* n. gen. resembles also to the Famennian genus *Wenjukovispirifer* Oleneva, 2016 mainly in terms of its rounded subpentagonal outline, ventribiconvex lateral profile, acute to mucronate cardinal extremities, wide hinge line, well-defined and triangular ventral interarea, wide sulcus and fold bearing bifurcating ribs that are narrower than those present on the flanks. However, *Aramazdospirifer* n. gen. differs by its median and longitudinal elevation in sulcus and similar elevation frequently displayed on fold, and its pseudodeltidium that is formed by several distinct plates with minute submesothryrid foramen. Additionally, *Aramazdospirifer* n. gen. lacks pustules that are observed in *Wenjukovispirifer*. It is difficult to compare the internal morphology of these genera as Oleneva (2016) did not illustrate any serial sections. Nevertheless, she mentioned the presence of a median septum situated in the ventral interior of *Wenjukovispirifer*, a character that is not observed in *Aramazdospirifer* n. gen.

The new genus differs strongly from *Cyrtospirifer* Nalivkin in Frederiks 1924, by its more globular, longitudinally elongated and inflated shell, well-developed pseudodeltidium, longitudinal and median elevation in sulcus and similar elevation often developed on fold and the type of micro-ornament. Internally, these genera appear to be similar, though *Aramazdospirifer* n. gen. possesses an unsupported ctenophoridium, while the latter is supported by an apical callosity in many *Cyrtospirifer* representatives.

Aramazdospirifer n. gen. is distinguished externally from *Lamarckispirifer* Gatinaud, 1949 *sensu* Ma & Day (2007), known from the lower Famennian of South China (Ma & Day 1999), by its more rounded and inflated shell, longitudinal and median elevation in sulcus and analogous elevation often developed on fold and its high tongue. Additionally, *Aramazdospirifer* n. gen. lacks a median furrow on fold of the dorsal

valve and the *hayasakai*-type micro-ornament. Internally, the most substantial difference is the presence of a dorsal median septum in *Lamarckispirifer*, while this character is absent in *Aramazdospirifer* n. gen.

Aramazdospirifer n. gen. can be distinguished from the genus *Pseudocyrtiopsis* Ma & Day, 1999, known from the lower Famennian of South China, by its shell outline, longitudinal and median elevation in sulcus and analogous elevation often developed on fold, simple and flattened ribs, lack of well-developed pustules in ribs and interspaces. Internally, *Aramazdospirifer* n. gen. differs by its unsupported ctenophoridium.

Aramazdospirifer orbelianus (Abich, 1858) n. comb.
(Figs 3-7; Table 1)

Spirifer orbelianus Abich, 1858: 438, 440, 524-525, pl. 1, figs 2, 3; pl. 2, figs 4, 5.

Cyrtospirifer orbelianus — Rzhonsnitskaya 1948: 1480. — Arakelyan 1952: 40, 42. — Abrahamyan 1957: 70, pl. 8, fig. 3. — Arakelyan 1964: 75, 77, 82, 94. — Abrahamyan *et al.* 1973: 218. — Abrahamyan 1974: 60, pl. 22, figs 2, 3.

Spirifer orbelianus — Sartenaer 1974: 10 (only the Armenian specimens).

Cyrtiopsis orbelianus — Arakelyan *et al.* 1975: 24. — Rzhonsnitskaya & Mamedov 2000: 331, table 1.

Uchtospirifer orbelianus — Afanasjeva in Alekseeva *et al.* 2018a: 41, pl. 30, fig. 4; text-fig. 103. — Grechishnikova in Alekseeva *et al.* 2018b: 832, 855.

NEOTYPE. — Abich (1858) did not designate a type specimen for his new species among the four ones he illustrated. Abich's collection is stored in the Saint Petersburg Mining Institute Museum, but all the spiriferides collected by Abich are lost (D. Bezgodova, personal communication, 2019). Therefore, the single specimen illustrated by Abrahamyan (1957: pl. 8; fig. 3) is hereby designated as the neotype and figured in Figure 3I-N. It is stored at the Geological Museum in Yerevan under the collection number IGSNASRAGM 3897/AB97/48.

TYPE LOCALITY AND HORIZON. — Marly/sandy limestone layers (Abrahamyan 1957, 10th limestone layer of the Amaghu section, appendix 1) of the Ertych horizon, Noravank section (formerly Amaghu), Central Armenia.

OCCURRENCE AND AGE. — This species is one of the most biostratigraphically valuable species in Armenia for the recognition of the lower Famennian and is used for the definition of a brachiopod zone, namely the '*Cyrtospirifer orbelianus* Zone of Abrahamyan

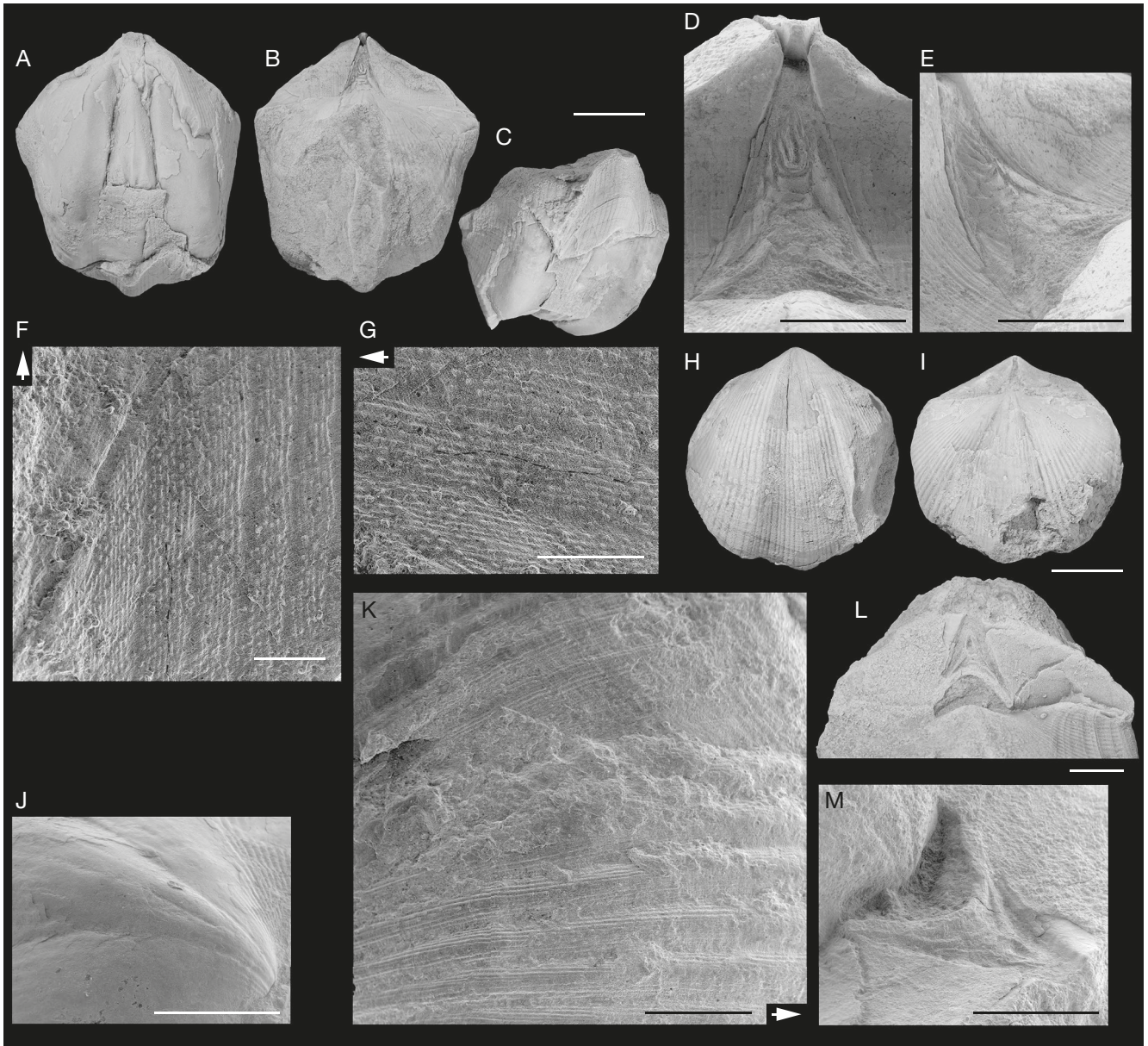


FIG. 4. — *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. the Ertych section: **A-G**, almost complete specimen (RBINS a13459) in ventral (muscle field and long intrasinal dental plates are visible), dorsal and anterolateral views, close-up of the pseudodeltidium, and detail of the capillate micro-ornament observed in sulcus near the anterior margin; **H-K**, incomplete specimen (RBINS a13460) in ventral (slightly inclined showing the intrasinal dental plates and the median fold in sulcus) and dorsal views, close-up of the myophragm, and detail of the capillate micro-ornament observed on the left flank of the dorsal valve; **L, M**, poorly preserved articulated specimen (RBINS a13461), view of the ventral area showing the pseudodeltidium and close-up of the latter. The **arrows** indicate the anterior margin. Scale bars: A-C, H, I, 10 mm; D, E, J, L, M, 5 mm; K, 2 mm; F, G, 1 mm.

(1957), as well as the ‘*Cyrtiopsis orbelianus*–‘*Cyrtiopsis armenicus* Zone of Rzhonsnitskaya & Mamedov (2000) (Fig. 2). Initially, Abrahamyan (1957) reported this species from sequences considered as constituting the lower part of the upper Famennian. Following the extensive stratigraphic study of Abrahamyan (1964) and Arakelyan (1964), it appeared that the previously reported *orbelianus* bearing sequences are actually early Famennian in age. Therefore, Abrahamyan (1974) specified that *A. orbelianus* n. comb. is restricted to the lower Famennian (possibly corresponding to the equivalent of the *Palmatolepis crepida*–*P. glabra pectinata* conodont zones of Spalletta *et al.* (2017)). Previously this species has been observed in Armenia in the Argichi, Lanjanist (Kadrly), Chanakchi (Zangakatun), Ertych and Noravank sections (Fig. 1) (Abrahamyan 1957; Arakelyan 1964) and doubtfully in the Gyumushlug section of Nakhichevan (Fig. 1; Abrahamyan 1957). It is worth noting

that only two poorly preserved specimens of possible *A. orbelianus* n. comb. have been found so far in Nakhichevan by Abrahamyan (1957) (IGSNASRAGM collections). Nevertheless, both specimens lack longitudinal and median elevations, and display an erect beak, which are not characters present in *A. orbelianus* n. comb. Moreover, further sampling in several sections exposing the lower Famennian strata in Nakhichevan, including the Gyumushlug section, did not reveal the presence of Abich’s species (e.g. Arakelyan 1964; Aristov *et al.* 1979; Feliks *et al.* 1980; Grechishnikova 1986).

MATERIAL EXAMINED. — Eighty articulated specimens, ten ventral and five dorsal valves from the marly/sandy limestones of the Ertych horizon of the Djiravank (sixty articulated specimens and ten ventral valves), Noravank (type locality; twelve articulated specimens and four dorsal valves) and Ertych (eight articulated specimens and one

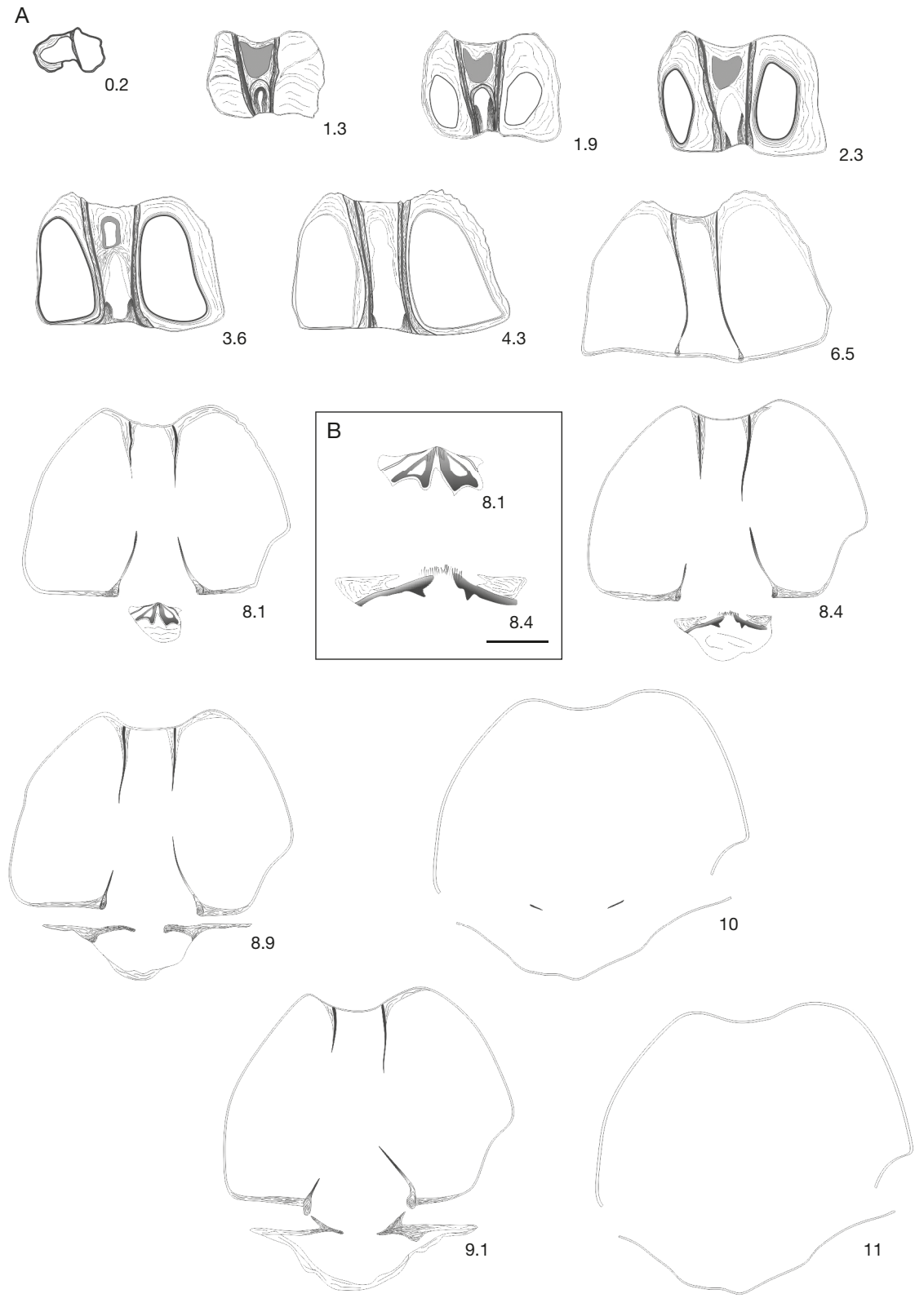


FIG. 5. — Transverse serial sections of *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. from the Džravank section. Numbers refer to distances in mm from the tip of the ventral umbo. Scale bars: A, 5 mm; B, 2.5 mm.

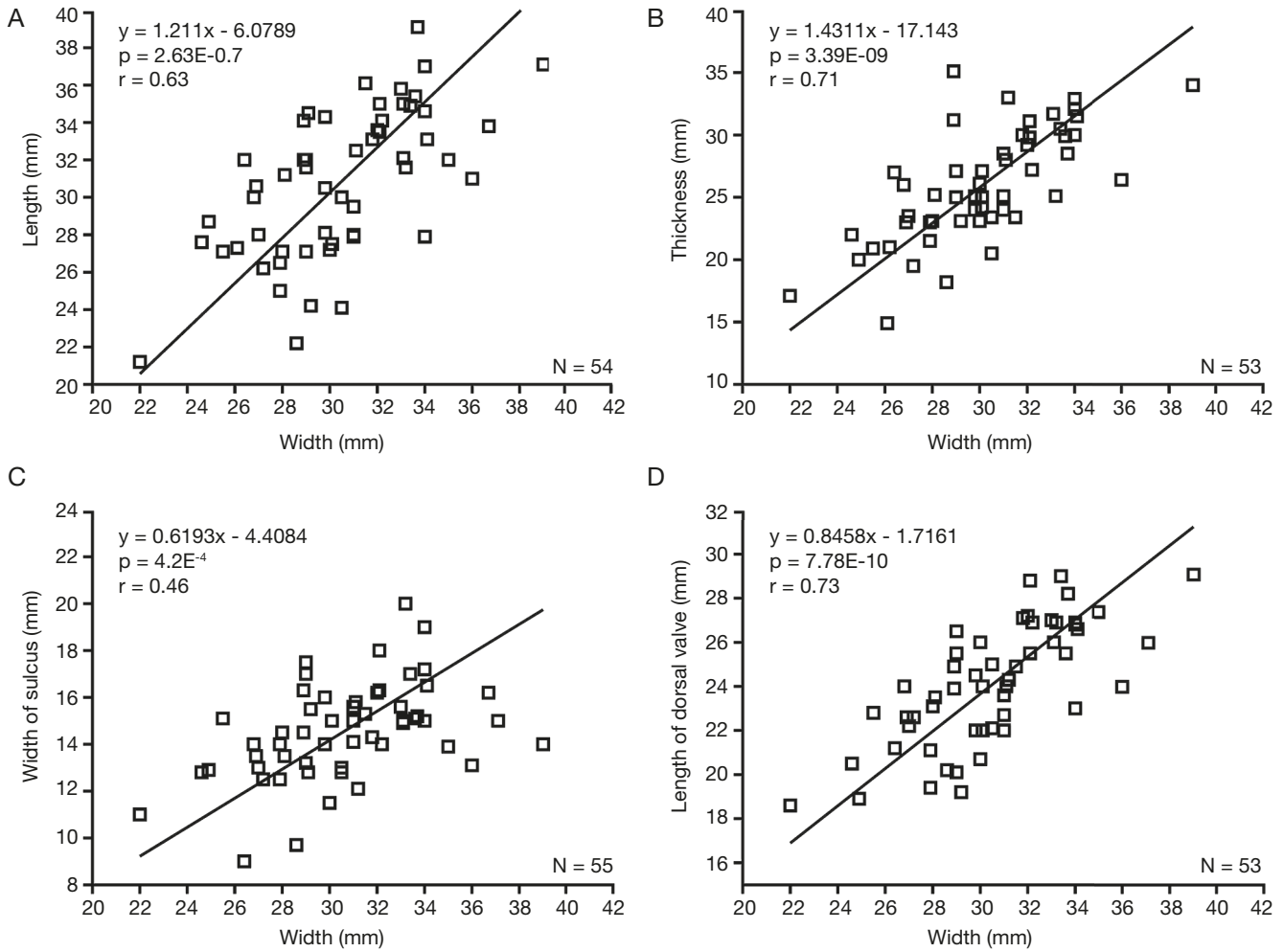


FIG. 6. — Scatter diagrams of *Aramazdospirifer orbelianus* (Abich, 1858) n. comb.: **A**, relation between shell width and length; **B**, relation between shell width and thickness; **C**, relation between shell width and width of sulcus; **D**, relation between shell width and length of dorsal valve. Abbreviations: **N**, number of specimens measured; **p**, probability value; **r**, coefficient of correlation.

dorsal valve) sections. Three articulated specimens in Abrahamyan’s collection (IGSNASRAGM) from the Noravank section and two ventral valves from the Gyumushlug section (Nakhichevan).

DESCRIPTION

Shell medium-sized (up to 39 mm in width and 39.1 mm in length), wider than long to longer than wide, generally ventribiconvex, rounded subpentagonal in outline, widest at hinge line, highest at about midlength; cardinal extremities acute to mucronate, but strongly extended in some specimens; anterior margin strongly excavated by sulcus, emarginate; anterior commissure uniplicate.

Ventral valve strongly inflated, rounded pentagonal in outline, with convex flanks sloping steeply towards lateral commissures; highest at about midlength or slightly posteriorly; umbo strongly inflated, large and prominent; beak erect (85-90°), interarea apsacline, triangular, moderately high, well-defined, concave; delthyrium wide, with most of its height covered by pseudodeltidium, the latter formed by several distinct plates; foramen minute, rounded to ovate; sulcus wide, shallow to moderately deep, originating from

beak, widening and becoming deeper anteriorly, sulcus margins gentle. Sulcus bears a longitudinal and median elevation which inconspicuously originates in the posterior part of the valve; it widens, thickens and becomes more conspicuous anteriorly (highest and widest at the anterior margin); tongue high, perpendicular to commissural plane with its distal part sometimes bent dorsally, subogival in outline.

Dorsal valve wider than long, inflated with flanks sloping moderately to strongly towards lateral commissures, subquadrangular to subtrapezoidal in outline; highest in the anterior third of the valve, but gradually decreasing towards the anterior margin; interarea linear (up to 3 mm high), slightly concave, orthocline; fold well-defined, wide, moderately high, inconspicuously originating from beak, widening and becoming higher anteriorly, often bearing a longitudinal and median elevation starting from dorsal beak. Ornamentation of up to 35 rounded (generally 28-30, 5-6 ribs per 5 mm at anterior margin near sulcus and fold), simple, flattened, low ribs on each flank, becoming fainter towards posterolateral margins; in sulcus and on fold, up to 25 ribs, increasing by bifurcations, much narrower than

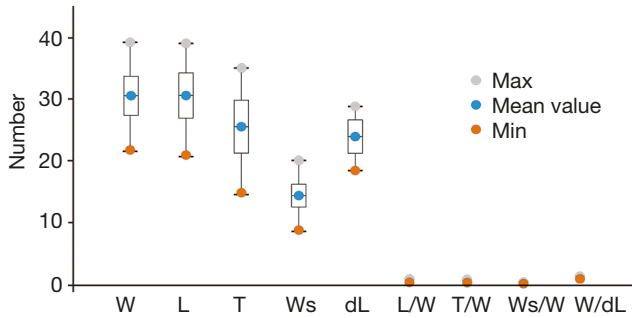


FIG. 7. — Measurements and ratios in mm of *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. Abbreviations: **dL**, length of the dorsal valve; **L**, length of the shell; **T**, thickness of the shell; **W**, width of the shell; **Ws**, width of the sulcus.

those present on flanks; interspaces as wide as ribs on flanks, but wider than ribs in sulcus and on fold; micro-ornament of capillae both on ribs and in interspaces with concentric growth lines sometimes thickened as growth varices.

Ventral valve interior with thin, long, intrasinal and divergent dental plates, becoming much less divergent to almost parallel more anteriorly, converging dorsally in umbonal region (as seen in transverse section); delthyrial plate well-developed, thick (particularly in large specimens); umbonal callus well-developed, central and lateral apical cavities large and filled in by callus; teeth relatively small, subrectangular. Dorsal valve interior with unsupported ctenophoridium composed of up to 33 well developed, relatively long lamellae; hinge plate divided; outer hinge plates slightly concave, crural bases dorsally convergent; spiral cones not preserved in the sectioned specimens.

Variability

The shell shape varies from almost globular forms with thickness exceeding as width and length, having narrower, shallow sulcus to transversely elongated wider forms with broad sulcus and relatively less inflated valves. The beak angle, the height of the longitudinal elevation and the number of ribs are also shifting.

Ontogeny

Juvenile forms differ from adults in having less inflated valves, straight beaks, shallower sulcus, weak fold, fainter ribs, inconspicuous elevations developed only anteriorly and the less convex delthyrial plate. The size distribution during growth represented by the length/width, thickness/width, width of sulcus/width and length of dorsal valve/width plots (Fig. 6) shows a continuous and progressive growth with no distinct grouping. The relative proportions of *Aramazdospirifer orbelianus* n. comb. represented by sufficient material remain constant (linear regression: $y = ax + b$; significant probability value: $p < 0.001$ *** whatever the degree of development of individuals [Fig. 6]). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve. To complete the scatter plots, the measurements (in mm) of numerous individuals of *Aramazdospirifer orbelianus* n. comb. are also

presented in Table 1 and Figure 7. The length of the dorsal valve shows less dispersed values (Fig. 7).

DISCUSSION

Aramazdospirifer orbelianus n. comb. was named by Abich (1858) in honor of the Orbelian family, one of the strongest dynasties in medieval Armenia, characterized by a long history of political influence documented in inscriptions throughout the provinces of Vayots Dzor and Syunik. Abich found this species in the lower Famennian sequence exposed at Noravank although he did not explicitly mention this locality. Abich (1858: 524) indicated that “*Sp. Orbelianus* ist bis jetzt nur in dem Baranco des Erhebungstales von Gyneschik [= Gnishik], in den Schichten h and k Profils pag. 440, und zwar in sehr grossen Mengenverhältnissen gefunden worden”, i.e., the author found this species in large numbers only in the h (impure limestones) and k (limestones with glauconitic sand) horizons of the profile exposed on the slopes of the valley of the Gnishik river (Fig. 1). These are apparently the marly/sandy limestone layers constituting the lower Famennian sequence exposed below the Noravank monastery, which is one of the most notable monasteries built by the Orbelian dynasty. Abich’s species was later reported by Gosselet (1874, 1880, 1894) in northern France and southern Belgium, from sequences accumulated close to the Givetian-Frasnian boundary. However, according to Sartenaer (1974) and Mottequin (2019), the Franco-Belgian material was erroneously identified as *Spirifer orbelianus* and needs further investigation. Reed (1922) reported a single specimen from Pamir, identified as *S. orbelianus* and stated that the species displays all the superficial features typical for Abich’s species. Nonetheless, his single illustrated specimen has rounded cardinal extremities, coarser ribs with very narrow interspaces and fewer ribs in sulcus and on fold; it also lacks a median longitudinal elevation. We thus consider this specimen as distinct from Abich’s species and in need of re-examination. Bonnet (1947: 32, 39) noted the presence of *Spirifer orbelianus* in Frasnian strata of Armenia, but this occurrence remains highly questionable as he did not illustrate his material (Sartenaer 1974). Gatinaud (1949) erected the genus *Lamarckispirifer* and assigned many species to it, including Abich’s species, but as noted by Ma & Day (2007), the latter species differs externally by its inflated shell and cannot be attributed to that genus. During the “golden era” of Palaeozoic studies in Armenia (1950s to 70s) *A. orbelianus* n. comb. was reported extensively by Abrahamyan (1957, 1974), Abrahamyan *et al.* (1973) and Arakelyan (1952, 1964). Abrahamyan (1957) assumed that *A. orbelianus* n. comb. could be a sister species of ‘*Cyrtiopsis armenicus*’ as the latter appeared in a slightly younger horizon. Therefore, Abrahamyan (1974) incorrectly assigned both species to the lower Famennian genus *Cyrtiopsis* Grabau, 1923. Sartenaer (1974) discussed several reports of *A. orbelianus* n. comb. from Africa, the Franco-Belgian basin and Iran. He rightly concluded that none of

them corresponds to Abich's species. In sum, *A. orbelianus* n. comb. is known only from the South-Armenian Block (Central Armenia and possibly Nakhichevan).

CONCLUSIONS

The taxonomic revision of *Spirifer orbelianus* Abich, 1858, based on material collected from its type locality in Central Armenia and complemented by the specimens described by Abrahamyan (1957), led us to define the new cyrtospiriferine genus *Aramazdospirifer* n. gen. *Aramazdospirifer orbelianus* (Abich, 1858) n. comb. is one of the most useful species for the biostratigraphy of the lower Famennian in the Lesser Caucasus due to its short stratigraphic range and abundance. In addition to its type species, which appears to be endemic in the South-Armenian Block, several other Famennian species described from Central Kazakhstan and the East European Platform may be also considered for assignment to the genus *Aramazdospirifer* n. gen., although they are in need of a modern taxonomic reassessment. Further studies on Armenian material are still needed in order to complement the recent revisions of the Famennian brachiopod faunas from the area of northern Gondwana that now corresponds to the Lesser Caucasus, Afghanistan and Iran (Alekseeva *et al.* 2018a, b; Mottequin & Brice 2019; Serobyán *et al.* 2021).

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