University of Lille
UMR CNRS 8198 – Evo-Eco-Paleo
Doctoral School – 104
Sciences of Matter, Radiation
and the Environment

National Academy of Sciences of the Republic of Armenia
Institute of Geological Sciences
Laboratory of Paleontology and Stratigraphy

Thesis

Joint PhD

For obtaining the title of

Doctor of the University of Lille

Specialisation: Geosciences, Ecology, Palaeontology and Oceanography

and of

Doctor of the Institute of Geological Sciences of Armenia

Specialisation: Geology, Paleontology, Stratigraphy

by

SEROBYAN Vahram

Upper Devonian brachiopods and sedimentary sequences from Armenia; biodiversity, stratigraphy and paleobiogeography

Thesis directed by

Taniel Danelian, Araik Grigoryan and Catherine Crônier

Defended on September 24th September 2021

Members of the jury:

CRASQUIN Sylvie	CNRS-Sorbonne University, France, *Reviewer**
DAY James	Illinois State University, USA, *Reviewer**
DANELIAN Taniel	University of Lille, France, *Director*
SERVAIS Thomas	CNRS-Univ. of Lille, France, *Examiner and Jury President*
MELIKSETIAN Khachatur	Institute of Geological Sciences, Armenia, *Examiner*
GRIGORYAN Araik	Institute of Geological Sciences, Armenia *Director*
HAIRAPETIAN Vachik	Islamic Azad University, Iran, *Examiner*
Invited	
CRONIER Catherine	University of Lille, France, *Co-director*
MOTTEQUIN Bernard	Royal Belgian Institute of Natural Sciences, *Examiner*

Université de Lille
UMR CNRS 8198 – Evo-Eco- Paléo
Ecole doctorale–104
Sciences de la Matière,
du Rayonnement et de
l'Environnement

l'Académie nationale des sciences de la République d'Arménie
l'Institut des Sciences Géologiques
Le laboratoire de Paléontologie et Stratigraphie

THÈSE

en Cotutelle

Pour obtenir le grade de

Docteur de l'Université de Lille

Spécialité: Géosciences, Ecologie, Paléontologie, Océanographie

Et de

Docteur de l'Institut des sciences géologiques d'Arménie

Spécialité: Géologie, Paléontologie, Stratigraphie

par

SEROBYAN Vahram

Brachiopodes du Dévonien supérieur et séquences sédimentaires d'Arménie; biodiversité, stratigraphie et paléobiogéographie

---

Thèse dirigée par

Taniel Danelian, Araik Grigoryan et Catherine Crônier

Soutenue le 24 septembre 2021

Membres du jury:

CRASQUIN Sylvie	CNRS-Sorbonne Université, France, *Rapporteur**
DAY James	Université d'État de l'Illinois, Etats-Unis, *Rapporteur**
DANELIAN Taniel	Université de Lille, France, *Directeur de thèse*
SERVAIS Thomas	CNRS-Univ. de Lille, France, *Examinateur, Président de Jury*
MELIKSETIAN Khachatur	Institut des sciences géologiques, Arménie, *Examinateur*
GRIGORYAN Araiyk	Institut des sciences géologiques, Arménie, *Directeur de thèse*
HAIRAPETIAN Vachik	Université islamique Azad, Iran, *Examinateur*
Invité	
CRONIER Catherine	Université de Lille, France, *Co-directeur de thèse*
MOTTEQUIN Bernard	Institut Royal des Sci. Nat. de Belgique, *Examinateur*

Université de Lille
CNRS-UMR 8198 Évo-Éco-Paléo
Bâtiment SN5
Avenue Paul Langevin
Cité Scientifique
59655 Villeneuce d’Ascq cedex
France

Abstract

The Upper Devonian carbonate-siliciclastic sedimentary sequences and brachiopods from three distinct sections (Ertych, Djravank and Noravank) of Central Armenia are here examined. Paleoenvironmental interpretation is performed based on bio- and lithofacies to reconstruct the depositional environments in which the sedimentary sequences were accumulated. Moreover, the studied sections are correlated lithostratigraphically, as well as biostratigraphically by focusing on their brachiopod assemblages. Twenty-six brachiopod species are described on the basis of recently collected material from the Frasnian–Famennian (F–F) succession. Four new brachiopod genera (*Aramazdospirifer, Angustisulcispirifer, Pentagonospirifer* and *Tornatospirifer*) and five new species (*Ripidiorhynchus djravankensis, Cyrtospirifer pseudoasiaticus, Pseudocyrtiopsis areniensis, Pentagonaspirifer abrahamyanae* and *Angustisulcispirifer arakelyani*) are introduced. All brachiopod species are examined according to modern taxonomic concepts and illustrated both externally and internally, with the exception of some rare species. The intraspecific morphological variability of the described species is documented quantitatively. The previously suggested biostratigraphic scheme for brachiopods of the F–F interval of the Lesser Caucasus (Armenia and Nakhichevan) is revised. More particularly, the *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod Zone, of Frasnian age, characterizes the peloidal grainstones of the Interval 1 that accumulated as a highstand system tract, while the lower Famennian *Aramazdospirifer orbelianus–Tornatospirifer armenicus* Zone is found in the packstones/grainstones of the Interval 4, which was deposited during a transgressive event. The present study also documents the diversity of brachiopods reported from the Frasnian–lower Famennian sequences of the Lesser Caucasus; the synthesis of all previous and current data suggests that a major change in diversity took place amongst rhynchonellides, atrypides and spiriferides. From a paleobiogeographic viewpoint, the studied fauna clearly shares affinities with contemporaneous brachiopods known from other parts of the north-Gondwanan margin, especially from those areas that extend eastwards of the South

Armenian Block (SAB) into Afghanistan and Pamir, although there are also many endemic elements. Finally, the paleobiogeographic significance of the four newly defined genera is discussed, including the re-assignment to them of several other Famennian species known previously from Nakhichevan, Pamir (Tajikistan), Central Kazakhstan and the East European Platform.

Keywords: Brachiopoda; Rhynchonellida; Atrypida; Athyrida; Spiriferida; Frasnian; Famennian; Kellwasser Biocrisis; Gondwana; Lesser Caucasus; South Armenian Block; Armenia; Nakhichevan.

Résumé

Les séries sédimentaires carbonatées-terrigènes et les brachiopodes du Dévonien supérieur d'Arménie centrale ont été ici étudiées à partir de trois coupes distinctes (Ertych, Djravank et Noravank). Leur interprétation paléoenvironnementale a été réalisée à partir des bio- et lithofaciès afin de reconstituer leurs milieu de dépôt. De plus, les coupes étudiées ont été corrélées lithostratigraphiquement, ainsi que biostratigraphiquement, en se basant sur leurs assemblages à brachiopodes. Vingt-six espèces de brachiopodes sont décrites sur la base d'un matériel récemment collecté. Quatre nouveaux genres de brachiopodes (*Aramazdospirifer, Angustisulcispirifer, Pentagonospirifer* et *Tornatospirifer*), ainsi que cinq nouvelles espèces (*Ripidiorhynchus djravankensis, Cyrtospirifer pseudoasiaticus, Pseudocyrtiopsis areniensis, Pentagonaspirifer abrahamyanae* et *Angustisulcispirifer arakelyani*) sont introduits. Toutes les espèces de brachiopodes sont examinées selon des concepts taxonomiques modernes; leurs caractéristiques internes et externes sont illustrées, à l'exception de quelques rares espèces. La variabilité morphologique intraspécifique des espèces décrites est documentée quantitativement. Le schéma biostratigraphique proposé auparavant pour l'intervalle Frasnien–Famennien du Petit Caucase (Arménie et Nakhichevan) est révisé. Plus particulièrement, la zone à *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani*, d'âge Frasnien, est proposée pour la faune trouvée dans les calcaires à péloïdes accumulés dans un cortège à haut niveau marin, alors que la zone à *Aramazdospirifer orbelianus–Tornatospirifer armenicus*, d'âge Famennien inférieur, est caractérisée par des packstones/grainstones de l'intervalle 4, déposés lors d'un événement transgressif. La présente étude documente également la diversité des brachiopodes signalée dans le Petit Caucase à travers l'intervalle Frasnien–Famennien inférieur et souligne un renouvellement majeur de faune parmi les rhynchonellides, les atrypides et les spiriférides. D'un point de vue paléobiogéographique, la faune étudiée a clairement des affinités avec celles connues dans d'autres régions de la marge nord-Gondwanienne, notamment celles qui s'étendent vers l'est du SAB (Bloc sud arménien) jusqu'en Afghanistan et le Pamir, bien qu'il existe également de nombreux éléments endémiques. De plus, la signification paléobiogéographique des quatre nouveaux genres est discutée, y compris de plusieurs autres espèces du Famennien qui leur sont réaffectés et qui étaient connues auparavant du Nakhichevan, du Pamir (Tadjikistan), du Kazakhstan central et de la Plate-forme d'Europe de l'Est.

Mots-clés: Brachiopodes; Rhynchonellida; Atrypida; Athyrida; Spiriferida; Frasnien; Famennien; Crise biologique de Kellwasser; Gondwana; Petit Caucase; Bloc sud arménien; Arménie; Nakhichevan.

Ամփոփում

Սույն աշխատանքում ուսումնասիրված են կենտրոնական Հայաստանի երեք կտրվածքների (Էրտիչ, Ջրավանք և Նորավանք) վերին դևոնի կարբոնատ-սիլիկատային (կրաքարեր, ավազաքարեր և քվարցիտներ) նստվածքային հաջորդականություններն ու բրախիոպոդները: Նստվածքային հաջորդականությունների նստվածքակուտակման պայմանների վերականգնումը իրականացվել է կենսա- և լիթոֆացիաների ուսումնասիրությունների հիման վրա: Ավելին, ուսումնասիրված կտրվածքները կորելացվել են, ինչպես լիթոշերտագրական, այնպես էլ կենսաշերտագրական տեսանկյունից՝ բրախիոպոդային համալիրների վրա հիմնվելով: Աշխատանքում նույնականացվել և նկարագրվել է բրախիոպոդների քսանվեց տեսակ, որոնք գտնվել են Ֆրան–Ֆամենի (F–F) հաջորդական նստվածքներից: Բրախիոպոդների մանրակրկիտ ուսումնասիրության արդյունքում առաջարկվել է չորս նոր սեռ (*Aramazdospirifer*, *Angustisulcispirifer*, *Pentagonospirifer* և *Tornatospirifer*) և հինգ նոր տեսակ (*Ripidiorhynchus djravankensis*, *Cyrtospirifer pseudoasiaticus*, *Pseudocyrtiopsis areniensis*, *Pentagonaspirifer abrahamyanae* և *Angustisulcispirifer arakelyani*): Բրախիոպոդների բոլոր տեսակները հետազոտվել են ժամանակակից տաքսոնոմիական դասակարգումների համաձայն. աշխատանքում ներկայացված է վերջիններիս ինչպես արտաքին, այնպես էլ ներքին կառուցվածքը, բացի մի շարք հազվագյուտ տեսակների, որոնք ուսումնասիրված են միայն արտաքնապես: Ուսումնասիրված ուսոտանիների ներտեսակային մորֆոլոգիական փոփոխականությունը փաստագրված է քանակապես առաջին անգամ: Վերանայվել է Փոքր Կովկասի (Հայաստան և Նախիջևան) ֆրան–ֆամեն միջակայքի բրախիոպոդների նախկինում առաջարկված կենսաշերաատագրական սխեման: Մասնավորապես, առաջարկվել է օգտագործել երկու նոր բրախիոպոդային զոնա՝ *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* և *Aramazdospirifer orbelianus–Tornatospirifer armenicus*: *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* զոնան բնորոշում է ծովի բարձր մակարդակի ժամանակ

կուտակված ֆրանի հասակի նստվածքային առաջացումները՝ կազմված ավազային կրաքարերից և բնորոշում է ինտերվալ 1-ը: *Aramazdospirifer orbelianus–Tornatospirifer armenicus* զոնան բնորոշում է ստորին ֆամենի հասակի Ինտերվալ 4-ը, որի նստվածքակուտակումը տեղի է ունեցել տրանսգրեսիայի ընթացքում: Սույն աշխատանքում ուսումնասիրվել են նաև Փոքր Կովկասի ֆրան–ստորին ֆամենի հաջորդական նստվածքներից հայտնաբերված բրախիոպոդների կենսաբազմազանության փոփոխությունները: Նախկին աշխատանքների և ներկա տվյալների վերանայումը ցույց է տալիս, որ ֆրան–ֆամեն միջակայքում rhynchonellide, atrypide և spiriferide խմբերի բրախիոպոդների կենսաբազմազանության մեջ տեղի են ունեցել զգալի փոփոխություններ: Հնակենսաշխարհագրական տեսանկյունից, ուսումնասիրված ֆաունան հստակորեն կապված է Գոնդվանայի հյուսիսային հատվածի այլ տեղամասերում հայտնաբերված հասակակից բրախիոպոդային համալիրների հետ, հատկապես Հարավ Հայկական Բլոկից դեպի արևելք՝ մինչև Աֆղանստան և Պամիր ընկած տարածքները: Թեև հարկ է նշել, որ Հարավ Հայկական Բլոկում հայտնաբերվել են նաև բրախիոպոդի էնդեմիկ տեսակներ: Աշխատանքում քննարկվում է նոր առաջարկված չորս ցեղերի հնակենսաշխարհագրական տարածման առանձնահատկությունները՝ հաշվի առնելով այն հանգամանքը, որ նախկին աշխատություններում՝ Նախիջևանից, Պամիրից (Տաջիկստան), Կենտրոնական Ղազախստանից և Արևելյան Եվրոպայի պլատֆորմից բերված ֆամենի մի շարք տեսակներ սույն աշխատությունում վերագրվեցին նոր առաջարկված ցեղերին:

Հանգուցային բառեր. Brachiopoda; Rhynchonellida; Atrypida; Athyrida; Spiriferida; Ֆրան; Ֆամեն; Կելվասարի կենսաբազմազանության ճգնաժամ; Գոնդվանա; Փոքր Կովկաս; Հարավ Հայկական Բլոկ; Հայաստան; Նախիջևան:

Acknowledgements /Remerciements

I am grateful to the French Embassy in Armenia for providing me a 15 month grant over three years, which allowed the launch of this co-tutorial PhD. I am also grateful to the University of Lille for providing me a 4 month MOBLILEX International Mobility Grant and to the Erasmus + International Credit Mobility Programme for funding the last year of my PhD studies in France. I would like to thank the Institute of Geological Sciences (Armenian Academy of Sciences) for its logistic support to organize the fieldwork over the years 2017–2020. I also want to express my gratitude to Dr. K. Meliksetian for his continuous support and for the opportunity that was given to me to work on this very interesting topic under the supervision of Prof. T. Danelian, Prof. C. Crônier and Dr. A. Grigoryan. I want to thank them all for their tremendous support, their advice and their proofreading. In addition, I am grateful to T. Danelian for his advice on scientific writing. Also, I want to thank very much C. Crônier, who taught me some special technical skills in the laboratory. I would like to thank A. Grigoryan for his great support on the field during all these years and for his advice related to stratigraphy. I would like to express my deep gratitude to Dr. B. Mottequin (Institut Royal des Sciences Naturelles de Belgique) for his advice and guidance in relation to the taxonomy of brachiopods. I am also grateful to Prof. F. Boulvain for his advice and guidance in the study of sedimentary facies, sequence stratigraphic analysis and paleoenvironmental interpretations. I would like to acknowledge S. Régnier for help with the SEM and the high quality pictures we obtained. I would also like to thank J. Cuvelier for searching and providing me the special literature I needed from the libraries of other universities. I am thankful to Prof. X. Vekemans and F. Holvoote for all their help with administrative tasks related to my PhD studies or those that were necessary for me to attend scientific conferences and fieldwork. Many thanks to the Paleontology team of the Evo-Eco-Paléo laboratory for all these three nice years I spent in France, for welcoming me so warmly and for the good time and laughs we had during the coffee breaks and lunches.

Contents

Introduction

The Late Devonian (383-359 Ma) marked a critical period in the history of biodiversity, as it coincided with a number of significant geo- and bio-events of which the most astounding is the Frasnian–Famennian (F–F) biocrisis, considered as one of the “Big Five” mass extinctions events known from the Phanerozoic (see McGhee, 1996, 2013; Walliser, 1996; Baliński, 2002; Racki and House, 2002). It is also referred to as the two-step “Kellwasser Event” (e.g., Schindler, 1993; Gereke and Schindler, 2012); it is subdivided into the Lower and Upper Kellwasser Event (LKE and UKE, respectively); this separation is based on its appearance in Germany and in other study localities, where it forms two distinct black shale layers (referred to as the Lower and Upper Kellwasser Horizons) (Buggisch, 1991; Riquier et al., 2006; Schindler, 1990a; Schindler, 1990b). The LKE is found within the Lower *gigas*/*Palmatolepis rhenana* conodont Zone, whereas the UKE is found at the top of the *Palmatolepis linguiformis* conodont Zone (Becker et al., 2012; Klapper et al., 1994). The UKE marks a global biotic event corresponding to a major ecosystem perturbation at the F–F boundary. Most notably, it resulted in the decimation of the low-latitude metazoan reef systems (Sorauf and Pedder, 1986; Copper, 2002), as well as benthic (e.g. trilobites, ostracods and brachiopods) and nektonic (e.g. ammonoids, tentaculites and conodonts) marine communities (McGhee, 1996; Walliser, 1996; Ma et al., 2016). Although most paleontologists agree that the marine biosphere experienced severe losses at the F–F boundary, a consensus still remains elusive regarding the mechanism (extinction versus lack of origination) and severity of the crisis (compared to other times of biotic crisis). One of the main challenges in attaining this consensus is a parallel lack of consensus about the cause of the extinction/depletion. Most notably as noted by Racki (2005), Stigall (2012) and Stanley (2016) the main cause of this biotic crisis and the resulting disruption of the epeiric carbonate factory appears to be not the elevated extinction rates, but reduced speciation rates and, therefore this event should be considered as representing a massive diversity depletion event and not as a mass extinction event; thus they suggest it to be defined as the F–F Biodiversity Crisis. It is also worth to emphasize that this biocrisis affected mostly shallow water marine ecosystems, resulting in a permanent decline of shallow water coral/stromatoporoid reef communities and the elimination of some brachiopod clades related to tropical and subtropical settings (McGhee, 1996; Racki, 1998; Huang et al., 2018).

The Upper Devonian sequences of Central Armenia and Nakhichevan (Fig. 1) are represented by shallow water, mixed carbonate-siliclastic deposits; they are remarkable in terms of their completeness and richness in fossil remains (Abrahamyan 1957, 1964, 1974; Arakelyan 1964; Alekseeva et al., 2018a, b). They have attracted the interest of pioneer geologists such as the famous German geologist Hermann Abich, who first described in 1858 Devonian outcrops and a new spiriferide species ('*Spirifer*' *orbelianus*) from Armenia (Serobyan et al., in press). In this country, Upper Devonian–Lower Carboniferous brachiopods were systematically studied by Abrahamyan during the years 1949 to 1974. One of her most important publications dates back to 1957, in which she described and illustrated 36 brachiopod species (including eight new ones) from the Famennian–Tournaisian interval. The latter brachiopods were partly revised by Abrahamyan (1974) in addition to newly studied Frasnian species. However, despite the extensive taxonomic studies led by Abrahamyan (1957, 1974) and more recently by Alekseeva et al. (2018a, b), who mainly focused on brachiopods from Nakhichevan (Fig. 1), brachiopods from this area still remain largely undocumented from a taxonomic and biostratigraphic point of view. This is especially true for the Upper Devonian brachiopods, many of which were described without any examination of their most fundamental features such as their internal morphology, their pseudodeltidium and their type of micro-ornament, all of which are significant for their supraspecific classification. Re-investigation of this fauna is crucial to better understand Late Devonian changes in brachiopod diversity and their paleobiogeographic distribution.

Thus, in order to understand the changes in brachiopod biodiversity during the critical Frasnian–Famennian transitional interval, the prime objective of my study has been to adress this question on the basis of the taxonomic re-examination of F–F brachiopods from Armenia mainly based on recently collected fresh material, which was additionally complemented by specimens that were collected during the 1940s to 1980s by Abrahamyan and Arakelyan, both from Armenia and Nakhichevan (Fig. 1). My study also integrates and taxonomically updates the fauna known from Nakhichevan and studied by Grechishnikova (1986), Mirieva (2010) and Alekseeva et al. (2018a, b). It is worth noting that in addition to previously reported species, I also describe several new, previously unknown taxa. The paleobiogeographic distribution of the studied brachiopods is also discussed and compared with Upper Devonian assemblages coming from other regions of the Gondwanan northern margin, East European Platform (EEP) and Kara-Tau (Central Kazakhstan). Besides, the taxonomic overview, an updated occurrence table is represented in this study, which is combined with biostratigraphic and lithological analysis of the studied sections.

Chapter 1 presents briefly the geological and stratigraphic setting of this study based on the published literature, while Chapter 2 details the quantity of brachiopod material used during my PhD and the methods I have applied to study it.

Chapter 3 presents the lithostratigraphy of the three sections (Ertych, Djravank and Noravank) that provided the collected brachiopod material. I have attempted to describe, through thin section observations, the succession of facies encountered in each section, after which I provide for them a sequence stratigraphic analysis and a paleoenvironmental interpretation.

Chapter 4 forms the core of my dissertation and it is devoted to the systematic paleontology of the encountered Upper Devonian brachiopods. Those species and genera that are presented in detail in two published/accepted papers were not included, as the final manuscripts of these 2 papers are presented as appendices at the end of this Thesis. Appendix 1, published by Serobyan et al. 2021 in the *Journal of Paleontology*, documents and discusses the taxonomy of six rhynchonellide and one athyride species recovered from the lower Famennian interval of Armenia. Appendix 2, accepted for publication in the *Comptes Rendus Palevol* (Serobyan et al., in press) documents and discusses in detail the taxonomy of one of the most biostratigraphically important species of the lower Famennian in the Lesser Caucasus, *Aramazdospirifer orbelianus* (Abich, 1858), while at the same time introduced *Aramazdospirifer* as a new genus.

Chapter 5 is subdivided into five parts. The Subchapter 5.1 presents the stratigraphic distribution of early–middle Frasnian and early Famennian brachiopods in the intervals 1 and 4 in the three main stratigraphic sections, while the Subchapter 5.2 outlines a synthesis of data on the brachiopod biostratigraphy in the Lesser Caucasus and defines two new brachiopod biozones. The Subchapter 5.3 outlines the nature of early–middle Frasnian to early Famennian brachiopod biostratigraphic record and the changes in diversity throughout this interval, whereas the Subchapter 5.4 describes the paleobiogeographic distribution of the brachiopods found in the three sections studied, and finally the Subchapter 5.5 summarizes the occurrences of epibionts including cornulitids and Hederella observed in the early Famennian cyrtospiriferids.

Chapter 1

Geological, stratigraphic and paleogeographic setting

In the southern part of Central Armenia crops out a ca. 1,500 m-thick Middle Devonian–Lower Carboniferous sequence of platform carbonate deposits (Fig. 1). They record the earliest depositional history of Paleozoic sediments in the area; they were accumulated on a Gondwanan passive margin that was facing the Paleotethys, situated to the north (Fig. 2); this part of Gondwana was later individualized as the South Armenian Block, following its northward migration and opening of Neotethys further to the South (Sosson et al., 2010). The Upper Devonian sequences of Armenia are composed of mixed carbonate-siliciclastic sediments and consist essentially of marly and sandy biogenic limestones, rich in brachiopods, and intercalations of quartzites, sandstones and shales. These sedimentary sequences are considered to be deposited in rather shallow-water continental platform environments (Arakelyan, 1964; Ginter et al., 2011). The Upper Devonian of Armenia is represented by both Frasnian and Famennian deposits, which were subdivided into a number of 'formations' by Abrahamyan (1964) and Arakelyan (1964) (e.g., Baghrsagh, Noravank, Ertych; Fig. 3). 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 Serobyan et al., 2019a, b); they are here regarded as regional stages and not as lithostratigraphic formations. The first Devonian biostratigraphical zonal scheme based on brachiopods was established by Rzhonsnitskaya (1948), who simply subdivided the Devonian into two parts: Lower and Upper Devonian. Later, Abrahamyan (1957) introduced a new continuous biostratigraphic scheme, mainly for the Famennian, which was composed of taxon-range and assemblage biozones (Fig. 3). 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 Paleozoic sedimentary sequences of Armenia continue into Nakhichevan (Fig. 1), the stratigraphic and faunal similarities in terms of brachiopods allowed Mamedov and 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 and Mamedov (2000) and correlated with the international

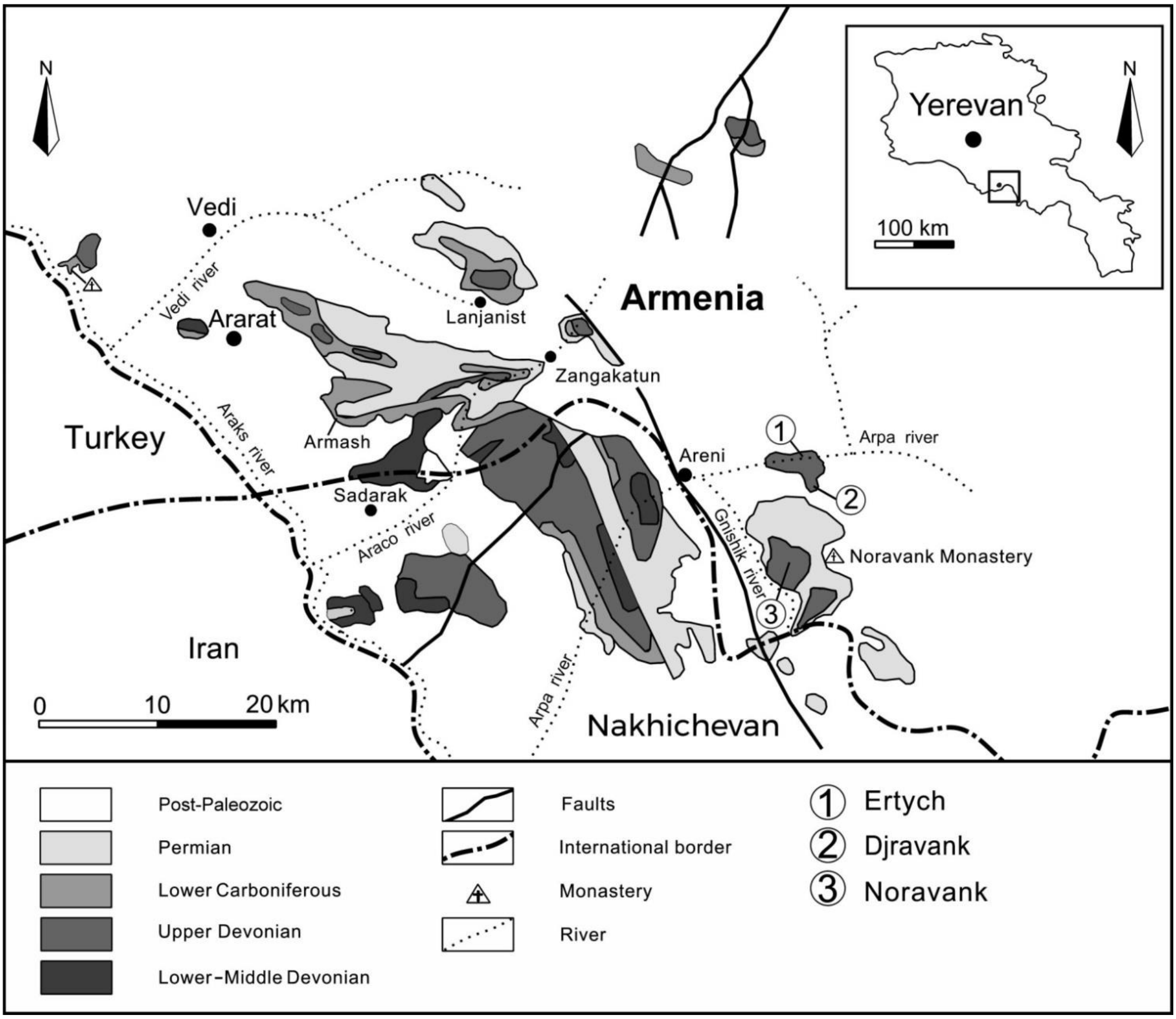


Figure 1. Schematic geological map and distribution of the Upper Paleozoic sequences in the Lesser Caucasus (Central Armenia and Nakhichevan), including the location of the three sections mentioned in the present study (modified after Serobyan et al., 2019a).

conodont biozonation, based on the conodont study of Aristov (1994) (Fig. 3) carried out in Nakhichevan. In addition to these studies, Grechishnikova et al. (1980, 1982, 1983), Grechishnikova and Levitskii (2011) also contributed to the systematic paleontology and biostratigraphy of Middle Devonian–Lower Carboniferous brachiopods of the Lesser Caucasus, mainly focusing on sections situated in Nakhichevan (Fig. 1); the latter studies were more recently updated by Grechishnikova in Alekseeva et al. (2018a). However, these studies not only

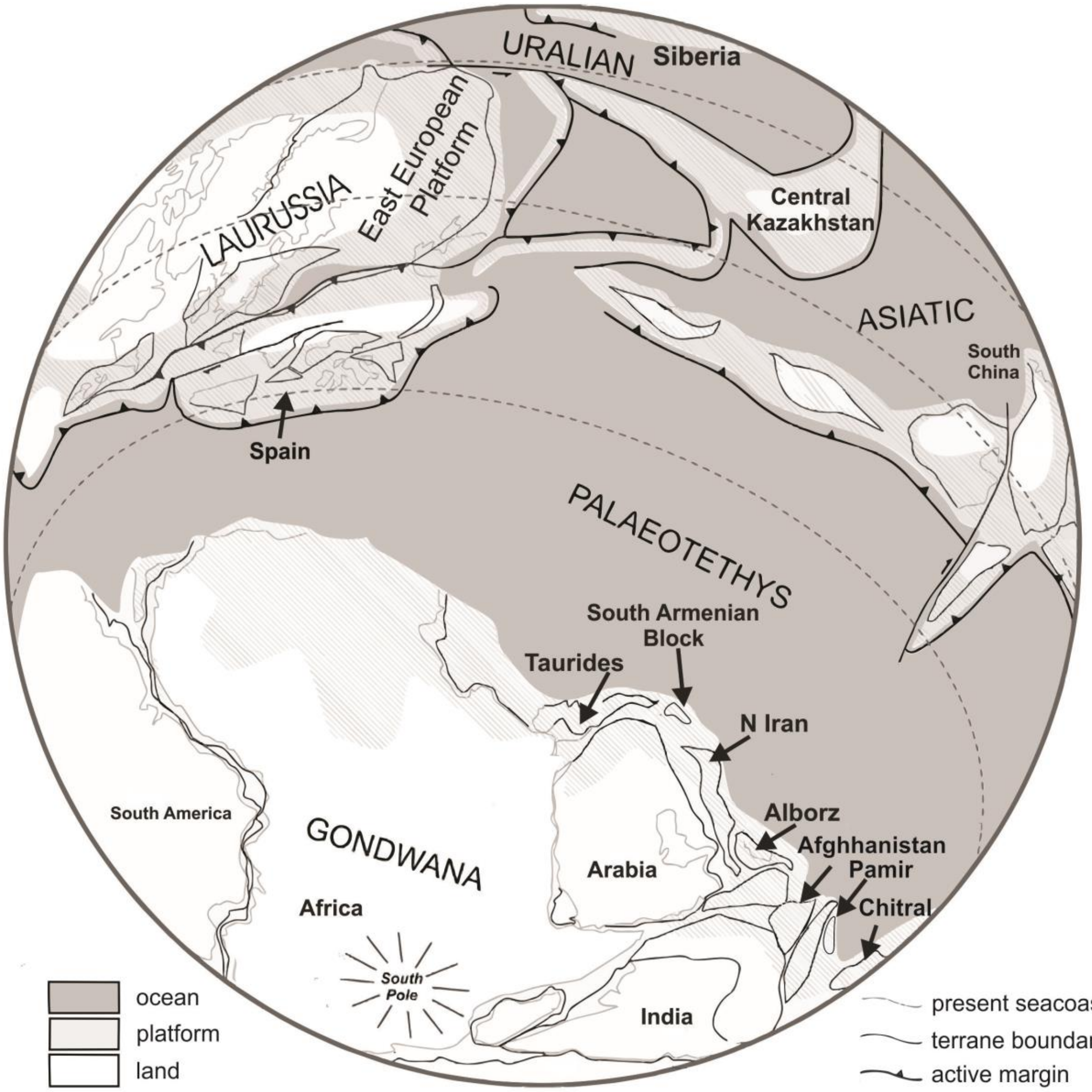


Figure 2. Late Devonian paleogeographic reconstruction of the Paleotethys ocean and its surrounding continents, including the position of the South Armenian Block along the northern margin of the Gondwana megacontinent (redrawn and modified after Denayer and Hoşgör, 2014, based on the maps of Stampfli et al., 2002).

complement each other, but they sometimes cause confusion, which is especially true for the Givetian–Frasnian and Frasnian–Famennian intervals. More particularly, across the Givetian–Frasnian boundary, Aristov (1994) recognized two conodont zones: *Ancyrodella binodosa* and *A. rotunbiloba*. The author further specified that the *binodosa* Zone corresponds to the lower part of *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone, whereas the *rotunbiloba* Zone is coeval to the upper part of *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone. He placed the Givetian–Frasnian boundary within the *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone. However, Rzhonsnitskaya and Mamedov (2000) raised the lower boundary of the latter brachiopod zone to the lower Frasnian. Afterwards, Alekseeva et al. (2018a) considered this brachiopod zone to be late Frasnian in age without giving any further evidence. It is certain that this assumption must be re-considered after a thorough study of conodonts, but before, it is reasonable to suppose that the age of this biozone is likely to be covering the lower–middle (lower part) Frasnian interval. Regarding to the lower Famennian, Abrahamyan (1957) and Grechishnikova et al. (1980) recognized only one brachiopod zone within this substage of the Lesser Caucasus, namely the *Cyrtospirifer orbelianus*. Whereas, Rzhonsnitskaya and Mamedov (2000) established two biozones: the lowest Famennian *Mesoplica meisteri–Cyrtospirifer asiaticus* and the lower Famennian *Cyrtiopsis orbelianus–C. armenicus*. Ginter et al. (2011),

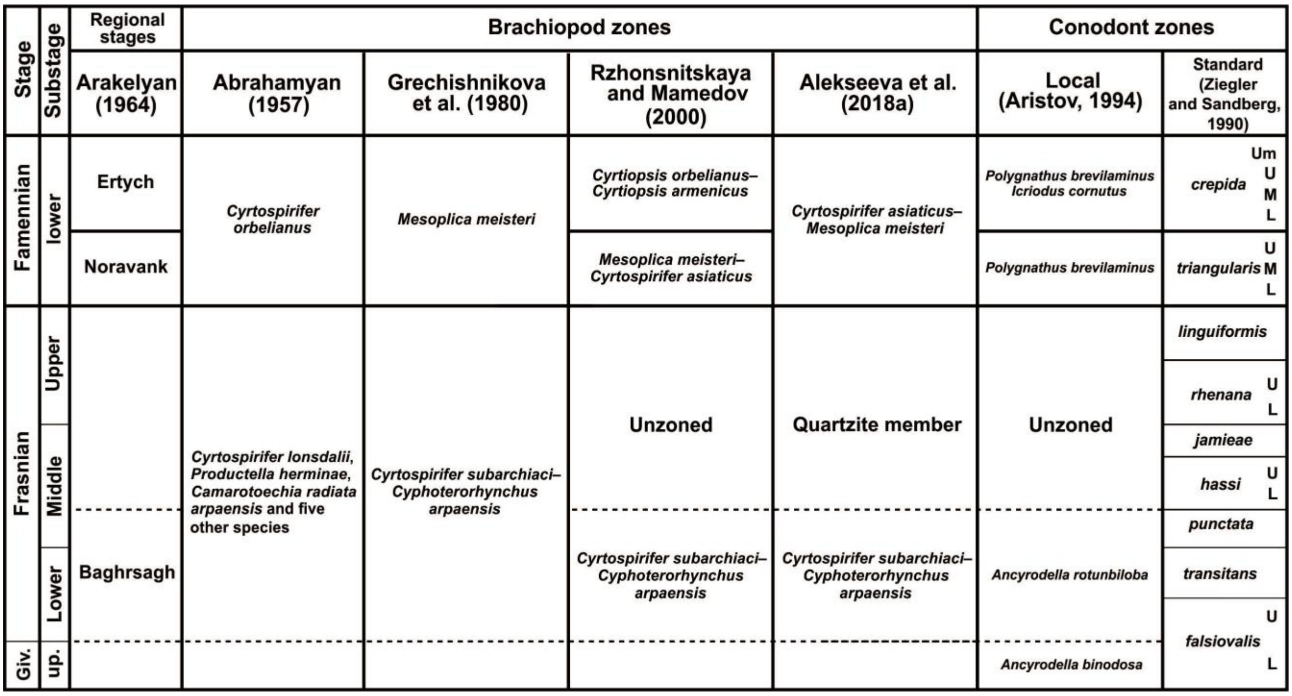


Figure 3. Biochronostratigraphic framework of the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus, including the regional stages established by Arakelyan (1964) and brachiopod biozones of Abrahamyan (1957) in Central Armenia and of Grechishnikova et al. (1980) and Rzhonsnitskaya 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).

described chondrichthyan remains from Armenia, some of which were recovered from the F–F interval of the Ertych and Noravank sections. It is worth emphasizing that they followed the biostratigraphic scheme of Rzhonsnitskaya and Mamedov (2000). Besides chondrichthyans, Ginter et al. (2011) reported conodonts above the layer of algal limestone (=oncolitic grainstone in the present study; Nv17/4) of the Noravank section, among which, some elements indicated the lower Famennian *crepida* Zone (see Ginter et al., 2011; text-fig. 4). Alekseeva et al. (2018a, b) followed the biostratigraphic scheme of Grechishnikova et al. (1980) and considered that the lower Famennian of the Lesser Caucasus is represented by only one brachiopod zone, but re-named it the *Mesoplica meisteri–Cyrtospirifer asiaticus* Zone. Finally, Grigoryan et al. (2019) described a conodont assemblage from the upper part of the Djravank section suggesting an early Famennian age.

Chapter 2

Material and methods

The examined material was collected from the Frasnian–lower Famennian interval of Ertych, Djravank and Noravank sections (Fig. 1) during several field seasons organized in 2017–2020. Although, during 2017–2020, I visited also several other outcrops, the current study is focused on these three sections only as they comprise well-exposed and highly fossiliferous sedimentary sequences and, thus, can provide valuable insights into events that occurred during the Late Devonian. The sections consist of shallow water carbonate-siliciclastic sediments. The limestone classification adopted herein follows Dunham (1962), which divides carbonate rocks based on their texture and mud content, and Dott (1964) for sandstone classification. The latter is a widely used classification of sandstones which divides them on the basis of their percentage in mud matrix and then subdivdes them into types based on their grain composition.

Macrofossils (predominantly brachiopods) were collected bed-by-bed from marly/sandy limestones and shales by splitting them out of the rock. In total 1888 articulated brachiopod shells and 325 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 material sampled by our care in the field was complemented with specimens that were collected during the 1940s to 1980s by Abrahamyan and Arakelyan, both from Armenia and Nakhichevan.

The internal structure of the newly collected articulated specimens 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. All ground specimens were selected among recently collected material as historical specimens cannot be sectioned; thus, the latter have been used only for measurements. Statistical analysis, i.e., ANCOVA (test for comparison of several models of simple linear regression) was applied in order to determine if the regression line slopes of our four samples are significantly different. Statistical analysis was performed under the free PAST 3 software. Almost complete articulated specimens were coated with magnesium oxide before being photographed with a Canon EOS 700D camera. Specimens selected for scanning electron microscopy were coated with gold and a ZEISS EVO Scanning Electron Microscope was used to image micro-ornamentation. Afterwards, in order to enhance contrast and brightness, all images were further processed using Adobe Photoshop CS6. Specimens selected for scanning electron microscopy and studied at the Royal Belgian Institute were observed using a low vacuum SEM, an ESEM FEI Quanta 200, but not coated with gold.

Repositories and institutional abbreviations.—Most of the illustrated material is housed at the Geological Museum of the Institute of Geological Sciences of the National Academy of Sciences of Armenia, Yerevan (IGSNASRAGM/PS), unless otherwise stated. The prefix PS indicates the Laboratory of Paleontology and Stratigraphy. The prefix IGSNASRAGM/AB points to the specimens belonging to Abrahamyan's collection. Part of the studied material is housed at the public paleontological collection of the University of Lille (USTL), France. The prefix RBINS is used for some specimens deposited at the Royal Belgian Institute of Natural Sciences, Brussels. Specimens cited in Brice (1967) are stored at the Laboratoire de Paléontologie de la Faculté Libre des Sciences des Lille (collections De Lapparent and Brice). The material studied by Erlanger (1993) is housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow and is catalogued under the prefix PIN and collection no. 3744. The material examined by Komarov (1997) is curated at the Vernadsky State Geological Museum, Moscow (VSGM) and is catalogued under the prefix VI and collection no. 223.

Chapter 3

The studied sections: lithostratigraphy, sequence stratigraphy and paleoenvironmental interpretation

3.1 The Ertych section

The section shows Frasnian–lower Famennian sequences situated at the southern bank of the Arpa river (ca. 8.5 km east of Areni), near the ruins of Ertych village. The base of this section, here referred to as Interval 1, mainly consists of limestone layers with a total thickness of ca. 13 m (Figs. 4.1–4.2). These limestones are nodular at the base and contain abundant brachiopod fauna, whereas in the upper part of this interval, they become well-bedded with scarce brachiopods. These grain-supported carbonate rocks (Er19/1/1, Er19/1/3, Er19/1/4; Fig. 7.1–7.6) constituting the Interval 1 are defined as peloidal bioclastic grainstones and include different fragments of brachiopod shells (e.g., Fig. 7.1, 7.4), dasycladacean algae (Fig. 7.2), gastropods (Fig. 7.3), crinoids (Fig. 7.5) and sea urchins (Fig. 7.6). In thin section, the layer Er19/1/3 contains iron dolomite (Fig. 7.4). The Interval 1 yielded abundant brachiopod fauna; a few hundred specimens were recovered from this interval. The base of the overlying Interval 2 corresponds to 7 m of black shales (Figs. 4.3) followed upwards by 2 m thick calcareous sandstones (quartz-wacke) (Er19/5; Figs. 4.3, 8.1–8.2) that contain poorly preserved rhynchonellide brachiopods and fish bones (Fig. 8.2). The total thickness of Interval 2 is ca. 35 m; it is chiefly composed of alternations of bioturbated sandstones (quartz-wacke) and black shales (Fig. 4.4–4.5). The overlying Interval 3 is primarily composed of coarse grained siliciclastic rocks and a few layers of shale. More particularly, its base is represented by sandstones which appear to be quite mature and representing facies that are intermediate between quartzite and sandstone (Fig. 8.3), whereas its middle part is constituted of quartzites and two layers of shales (Figs. 5.1); those shale layers are very rich in macro-plant remains (Fig. 5.3). The upper part of Interval 3 includes a few layers of sandstones, some of which are bioturbated (unbranched vertical narrow burrows are observed, resulting from the reworking of sediments by some organisms) and contain calcareous cement as well as many fish bones (e.g., Er19/98; Fig. 8.7–8.8), and shales; these sandstone layers are characterized as quartz-wacke. It is worth noting that the

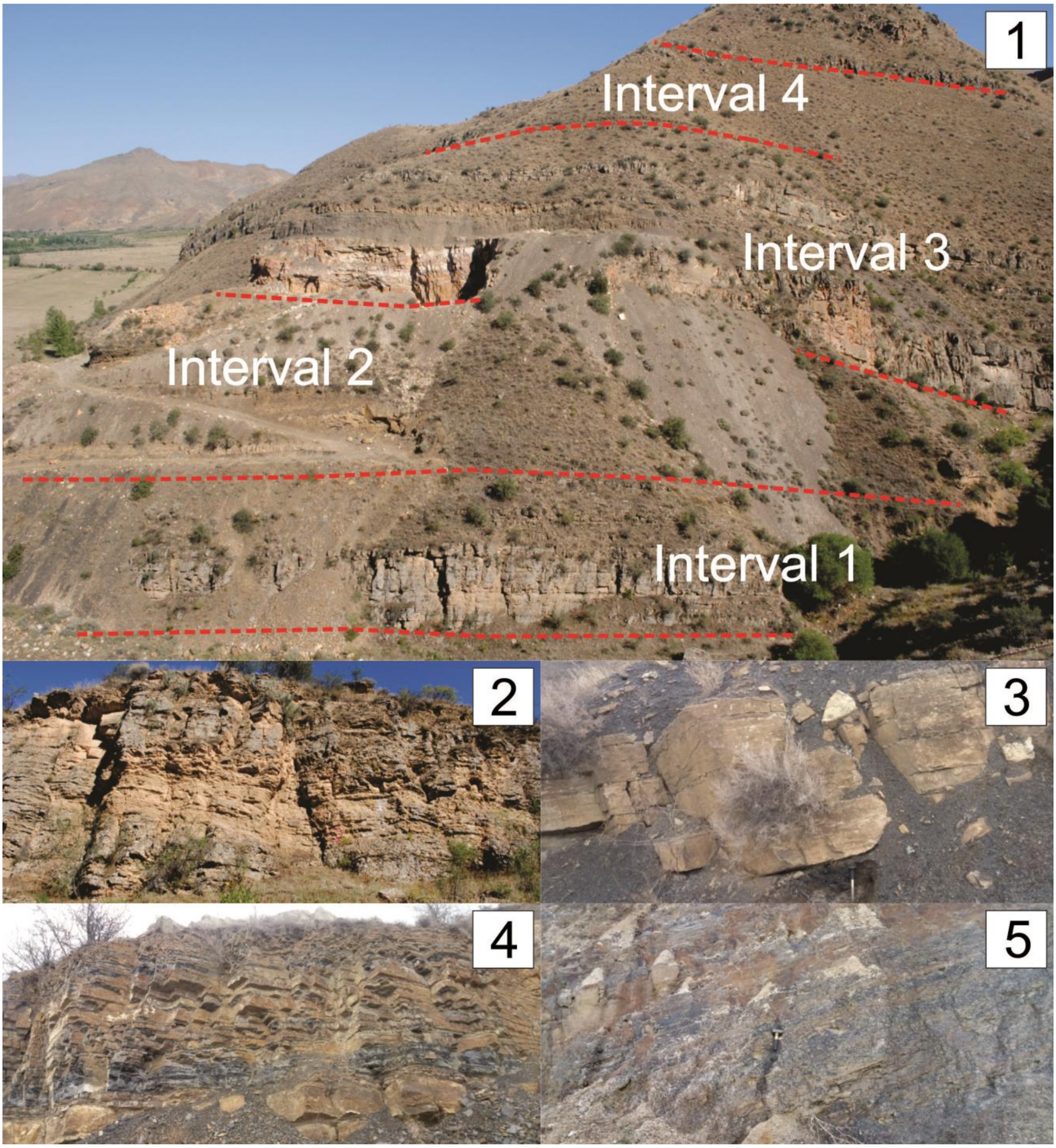


Figure 4. (**1**) Southeastern view of the Ertych section. (**2**) The base of the section (**Interval 1**) displays nodular limestones, rich in brachiopods. (**3**) Calcareous sandstone (quartz-wacke) layer situated at the lower part of Interval 2 (Er1/5) and intercalated in black shale layers of which the lower one is ca. 8 m thick. (**4**) Intercalation of sandstones and black shales constituting the middle part of Interval 2. (**5**) Organic rich black shales of the upper part of Interval 2.

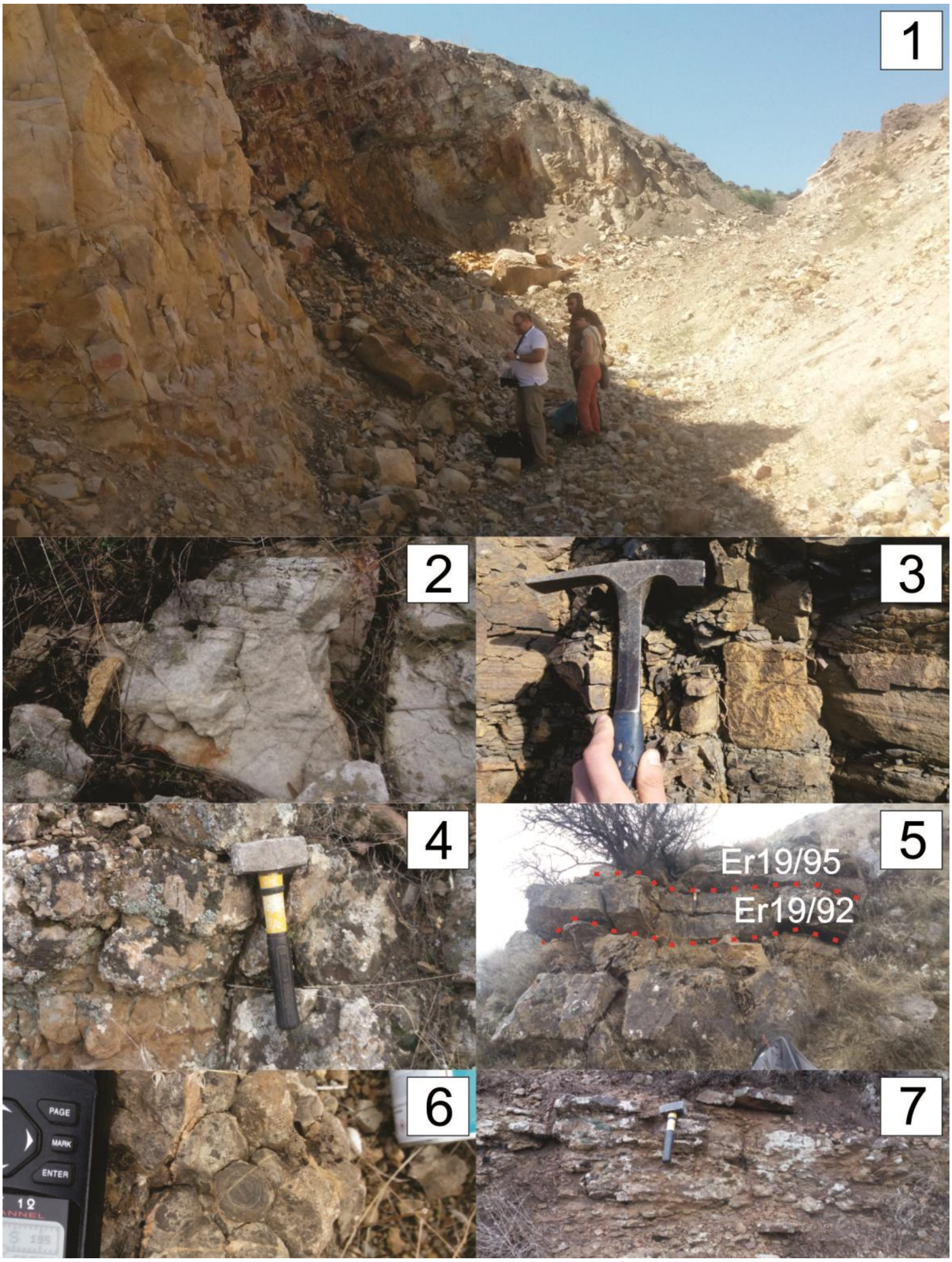


Figure 5. Field views of the Ertych section. (**1**) Quartzite quarry explored at the Interval 3. (**2**) Close-up of quartzites cropping out in the quarry. (**3**) Black shale layers observed between the two quartzite beds and containing macro-plant remains. (**4**) Bioturbated sandstone (quartz-wacke) at the upper part of Interval 3. (**5**). Base of Interval 4 comprising oncolitic (Er19/92) and peloidal (Er19/95) grainstones. (**6**) Oncolitic grainstone (Er19/92) forming approximately spherical structures. (**7**) Organic rich grainstone/packstone layers bearing abundant early Famennian brachiopods typical for the *orbelianus* Zone of Abrahamyan (1957) and constituting the upper part of Interval 4.

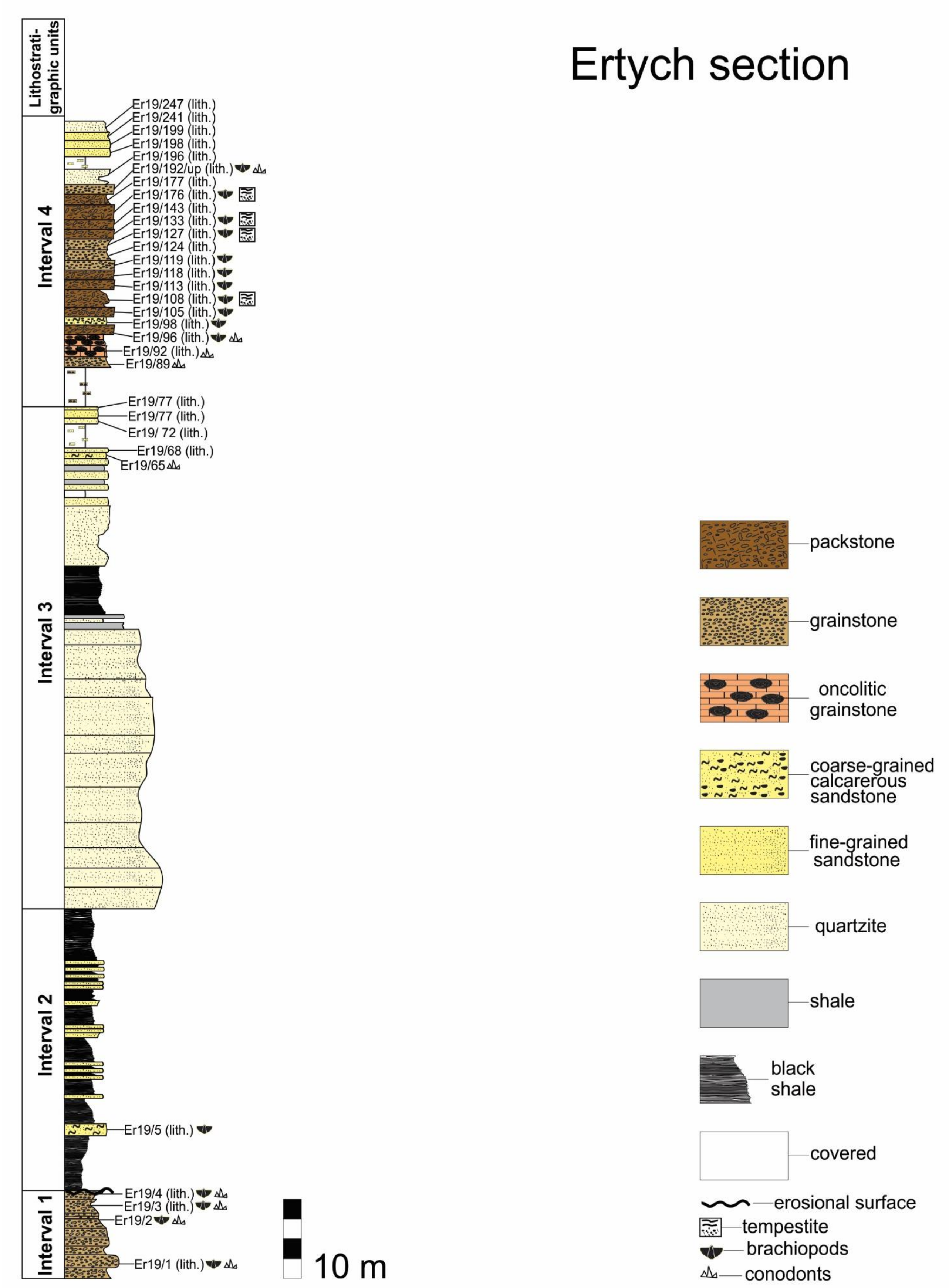


Figure 6. Lithostratigraphy of the Ertych section.

grains of the sandstones are irregularly shaped and their sphericity is quite low; thus, the grains constituting these sandstones are poorly sorted. No brachiopod specimen was recovered from this interval. The overlying Interval 4 is distinguished by the interbedding of different types of carbonate rocks. More particularly, the base of this interval consists of well-bedded and recrystallized limestone layers described as grainstone, which are covered by ca. 50 cm-thick, clearly distinct oncolitic grainstone with peloids (Figs. 5.5–5.6). The latter is overlain by tentaculite packstone layers (Er19/105, Fig. 9.1–9.3; Er19/108, 9.4–9.5), which, in addition to tentaculites, also include different fragments of brachiopods, bivalves, bryozoans, trilobites, fish bones and lithoclasts. These packstone layers appear to represent storm deposits as they are mostly composed of poorly sorted and broken fragments of animals, living at different depths. The packstone layers cropping out above, such as Er19/113 (9.6), Er19/119 (9.7) and Er19/124 (9.8) differ from the latter by possessing a large amount of fine and poorly sorted quartz grains. This interval of packstones is overlain by bioclastic grainstone layers (e.g., Er19/127, Er19/133, Er19/143) that probably correspond to storm deposits as they are composed of displaced and broken fossils such as brachiopods, trilobites (10.1), fish bones (10.2), dasycladacean algae and ostracods (10.5–10.6), which are usually encountered at different depths, and some of them also include quartz grains and peloides (e.g., 10.3–10.4) transported from a shallower environment. The overlying Er19/176 constitutes a coquina-bed (packstone facies) with peloides, fragments of tentaculites, brachiopod spines (10.7) and ostracods (10.8), whereas, the ensuing layer Er19/192 is identified as peloidal grainstone with crinoids (quite well sorted). The interval ends with relatively well-sorted and fine-grained quartzite and sandstone (quartz-wacke) layers (Fig. 11.2–11.4). The grainstone/packstone layers of Interval 4, which crop out above the oncolitic grainstone yielding abundant brachiopods; a few hundred specimens were collected that are dominated by spiriferides and rhynchonellides.

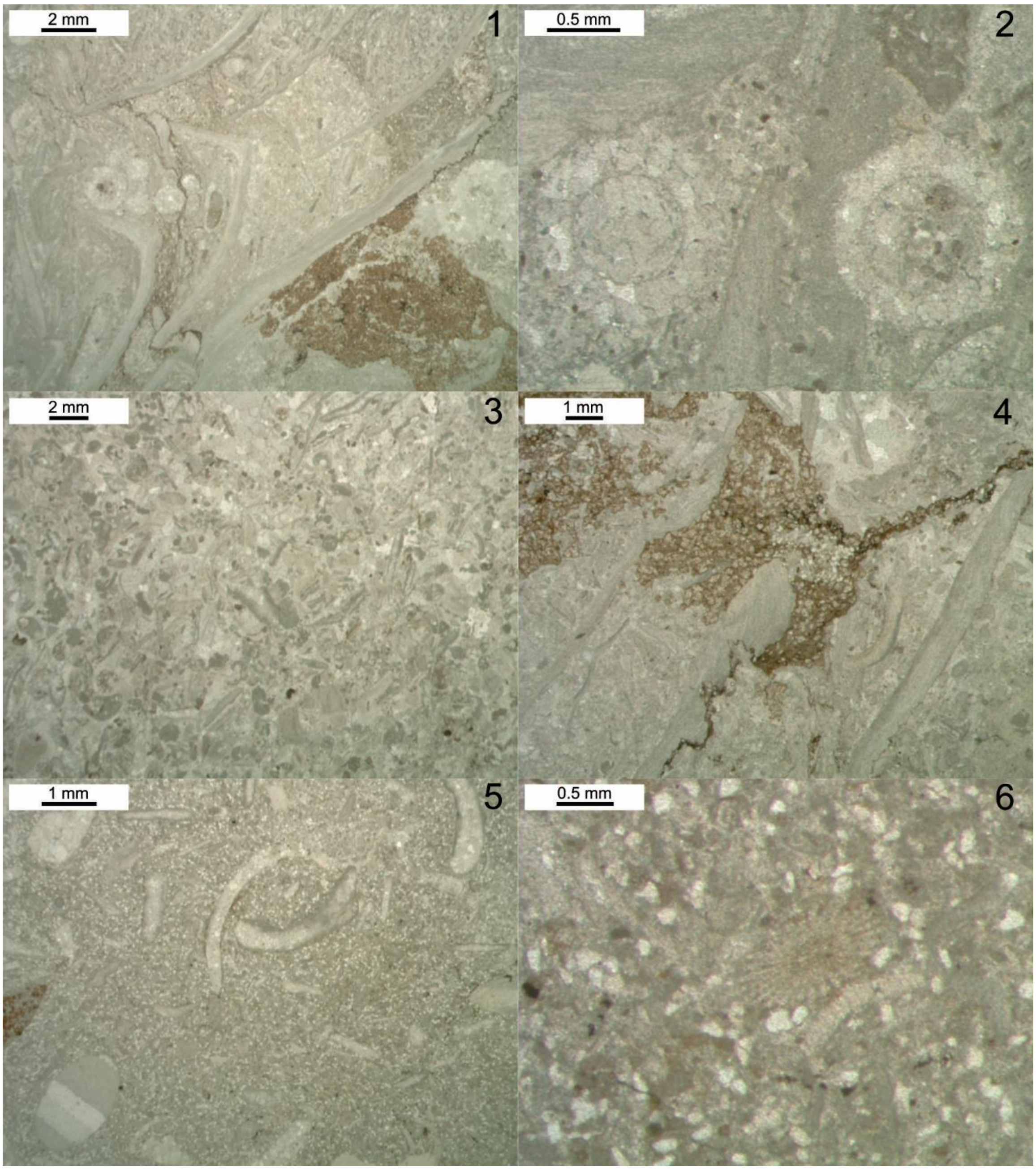


Figure 7. Photomicrographs of thin sections from Interval 1 of the Ertych section. (**1-2**) Er19/1/1, peloidal bioclastic grainstone with shell fragments of brachiopods (**1**), and close-up of dasycladacean algae (**2**). (**3-4**) Er19/1/3, peloidal bioclastic grainstone (**3**) and close-up of iron dolomite (probably of late diagenesis) (**4**). (**5-6**) Er19/1/4, peloidal bioclastic grainstone with mollusk fragments and quartz grains (**5**) and close-up of a sea urchins spine (in transverse section) (**6**).

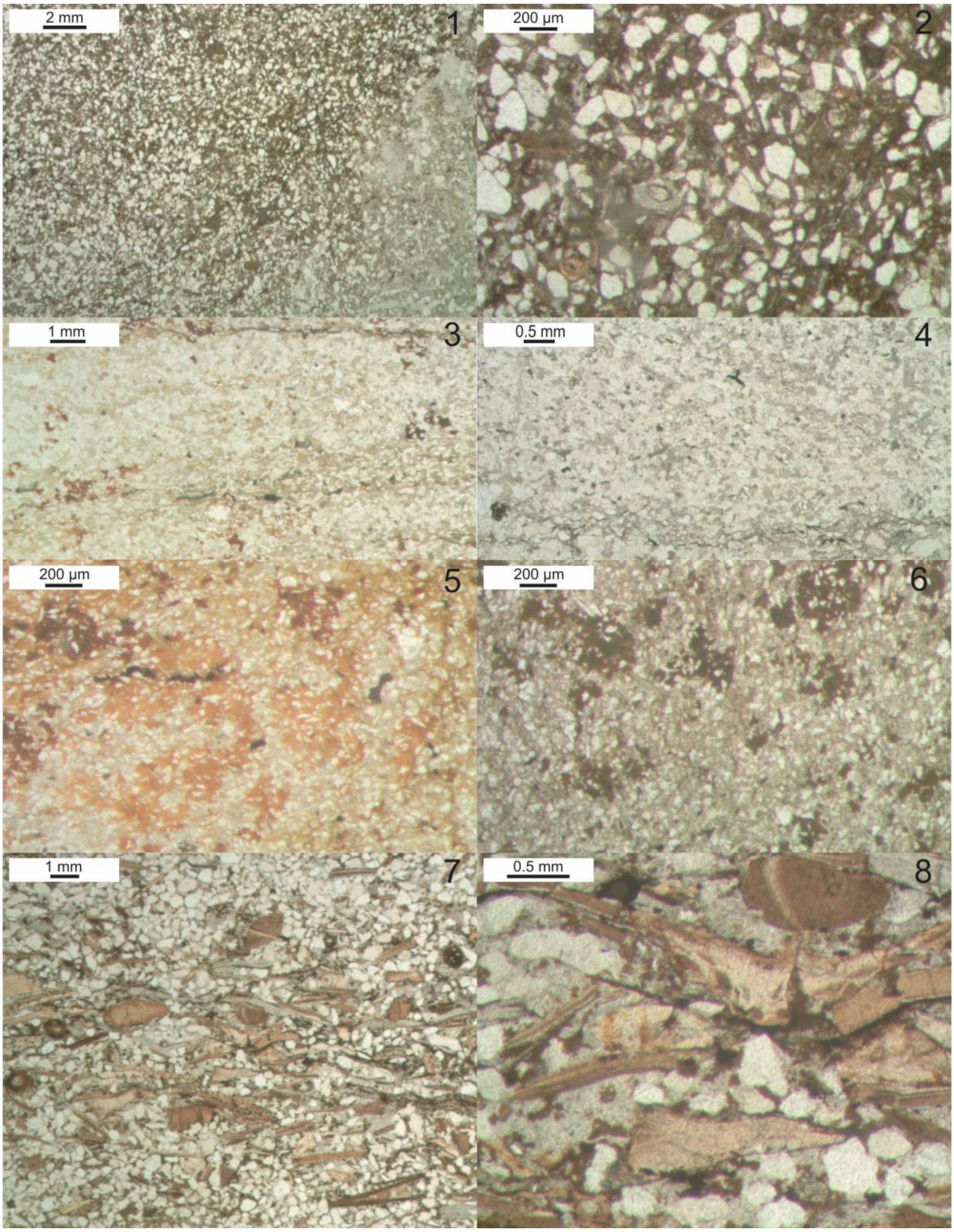


Figure 8. Photomicrographs of thin sections from Interval 2 of the Ertych section. (**1-2**) Er19/1/5, sandstone (quartz-wacke) with fish bones. (**3**) Er19/68, siliciclastic rock intermediate between quartzite and sandstone. (**4**) Er19/72, fine-grained quartzite. (**5**) Er19/77 fine-grained bioturbated sandstone (quartz-wacke). (**6**) Er19/78, fine-grained sandstone with a lot of matrix (quartz-wacke). (**7-8**) Er19/98, coarse sandstone (quartz-wacke) with calcareous cement and a lot of fish bones, well-sorted bone layer (**7**) and close-up of the phosphatus concentration (**8**).

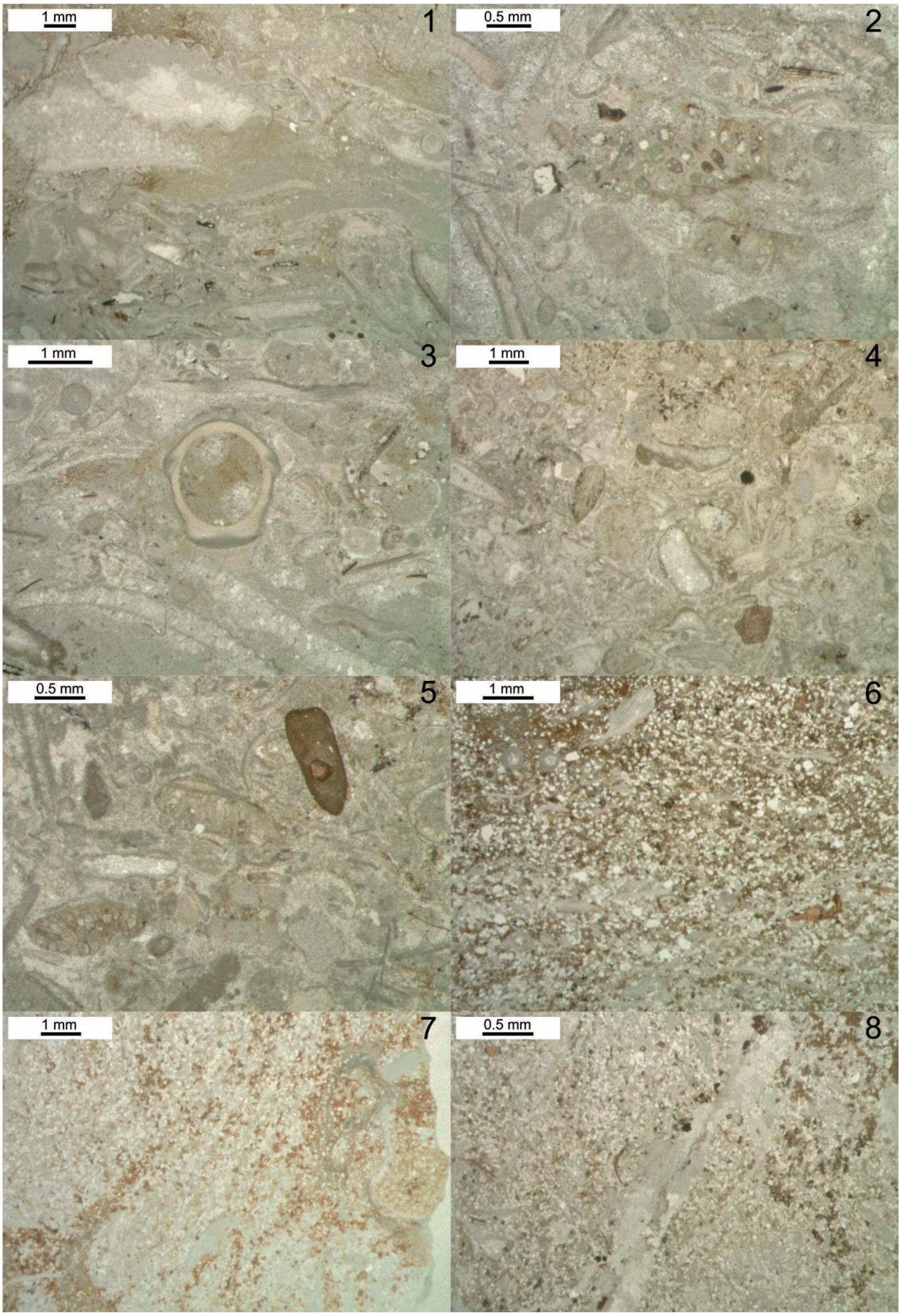


Figure 9. Photomicrographs of thin sections from the lower part of Interval 4 of the Ertych section. (**1-3**) Er19/105, spectacular tentaculite packstone (**1**) that also contains bryozoans, fragments of bivalves (**2**), trilobites and brachiopod spines (**3**). (**4-5**) Er19/108, tentaculite packstone, a storm deposit that in ddition to tentaculites, also includes trilobite and fish bone fragments, (**4**) bryozoans and lithoclasts (**5**). (**6-8**) Er19/113 (**6**), Er19/119 (**7**) and Er19/124 (**8**) packstone with quartze grains and different fragments of brachiopods.

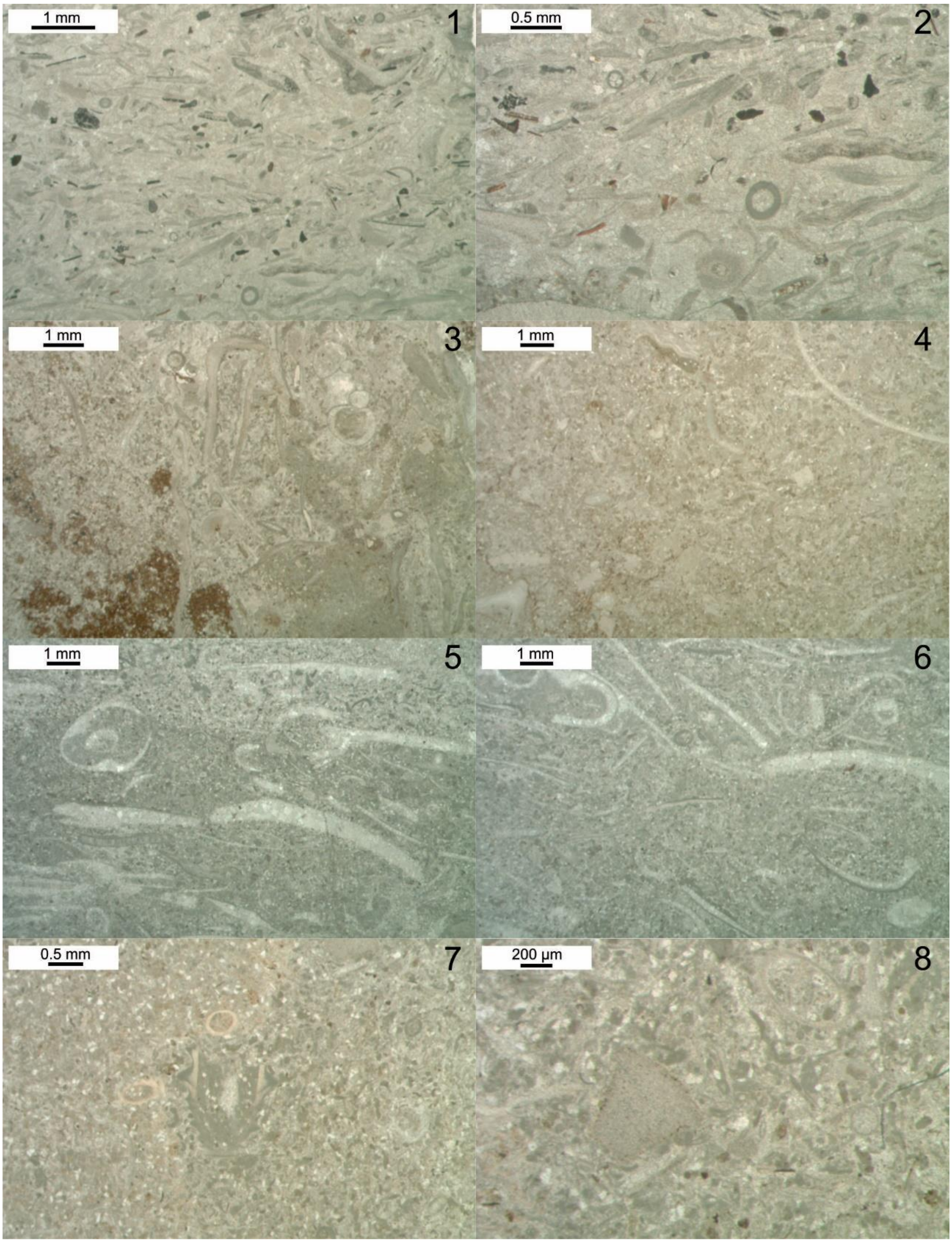


Figure 10. Photomicrographs of thin sections from the upper part of Interval 4 of the Ertych section. (**1-2**) Er19/127, bioclastic grainstone (tempestite) mainly composed of different fragments of brachiopods, fish and trilobites. (**3-4**) Er19/133, bioclastic grainstone (tempestite), which also contains peloids, brachiopod spines, trilobite and dasycladacean algae. (**5-6**) Er19/143, bioclastic grainstone containing different fragments of brachiopods, dasycladacean algae (**5**) and ostracods (**6**). (**7-8**) Er19/176, coquina-bed, packstone with fragments of tentaculites, brachiopod spines (**7**) and ostracods (**8**).

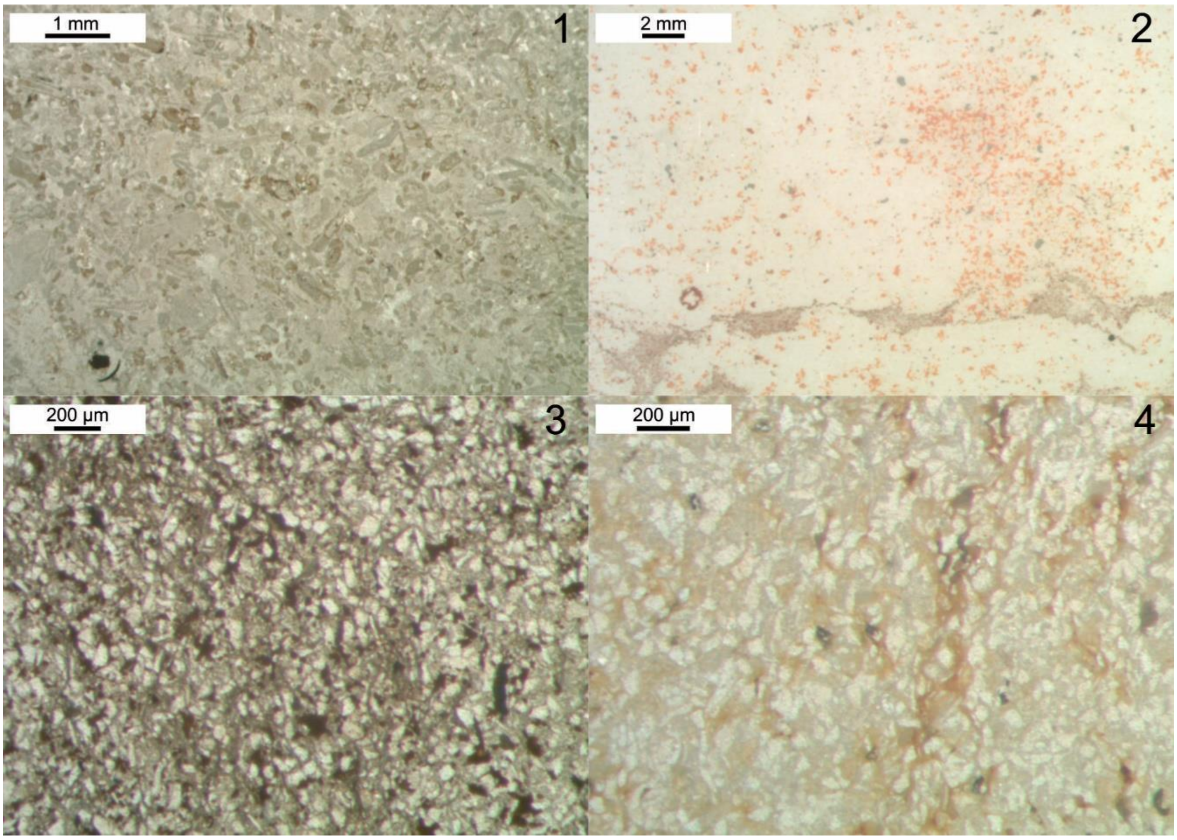


Figure 11. Photomicrographs of thin sections from the upper part of Interval 4 of the Ertych section. (**1**) Er19/192, grainstone with peloids (quite well sorted). (**2**) Er19/196, fine-grained quartzite, (well sorted). (**3**) Er19/198, fine-grained sandstone (quartz-wacke). (**4**) Er19/241, fine-grained sandstone with matrix (quartz-wacke).

3.2 The Djravank section

The section displays Frasnian to lower Famennian sequences that crop out along a mountain path (Fig. 12.1) that starts from the ruins of the Ertych village and leads to a tiny church hidden in the mountains, at the locality known as Djravank (Fig. 1). The section is exposed ca. 500 meters to the

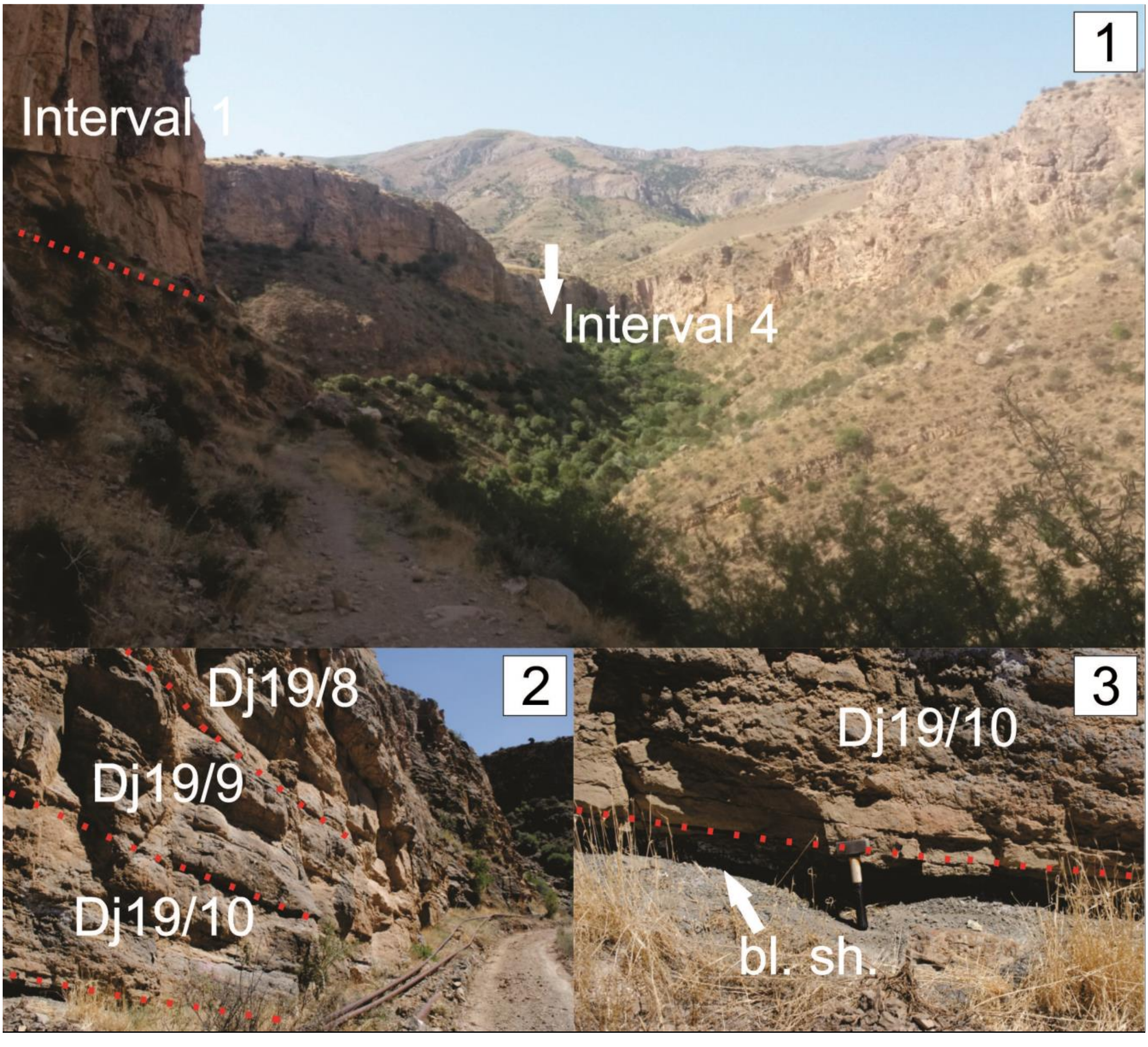


Figure 12. Djravank section (lower part). (**1**) The mountain path originates from the ruins of the Ertych village and leads to the studied section; the arrow indicates the location of Interval 4. (**2**) Peloidal grainstone beds that constitute the base of the section (Dj19/10, Dj19/9 and Dj19/8). (**3**) A black shale (bl. sh.) layer cropping out below the layer Dj19/10, which is very rich in rhynchonellides and above which the atrypides disappear.

south-southwest of the Ertych section, on the left slope of a valley upon which the Djravank church was built. It consists mainly of sandstones, quartzites, shales and massive limestones, but the top is distinguished by the interbedding of different types of carbonate rocks (Fig. 13) including a layer of oncolitic limestone. The base of the section, here referred to Interval 1, shows a ca. 25 m-thick continuous carbonate sequence composed of brachiopod rich well-bedded limestones displaying a more or less clear nodular aspect (Fig. 12.1–12.3).

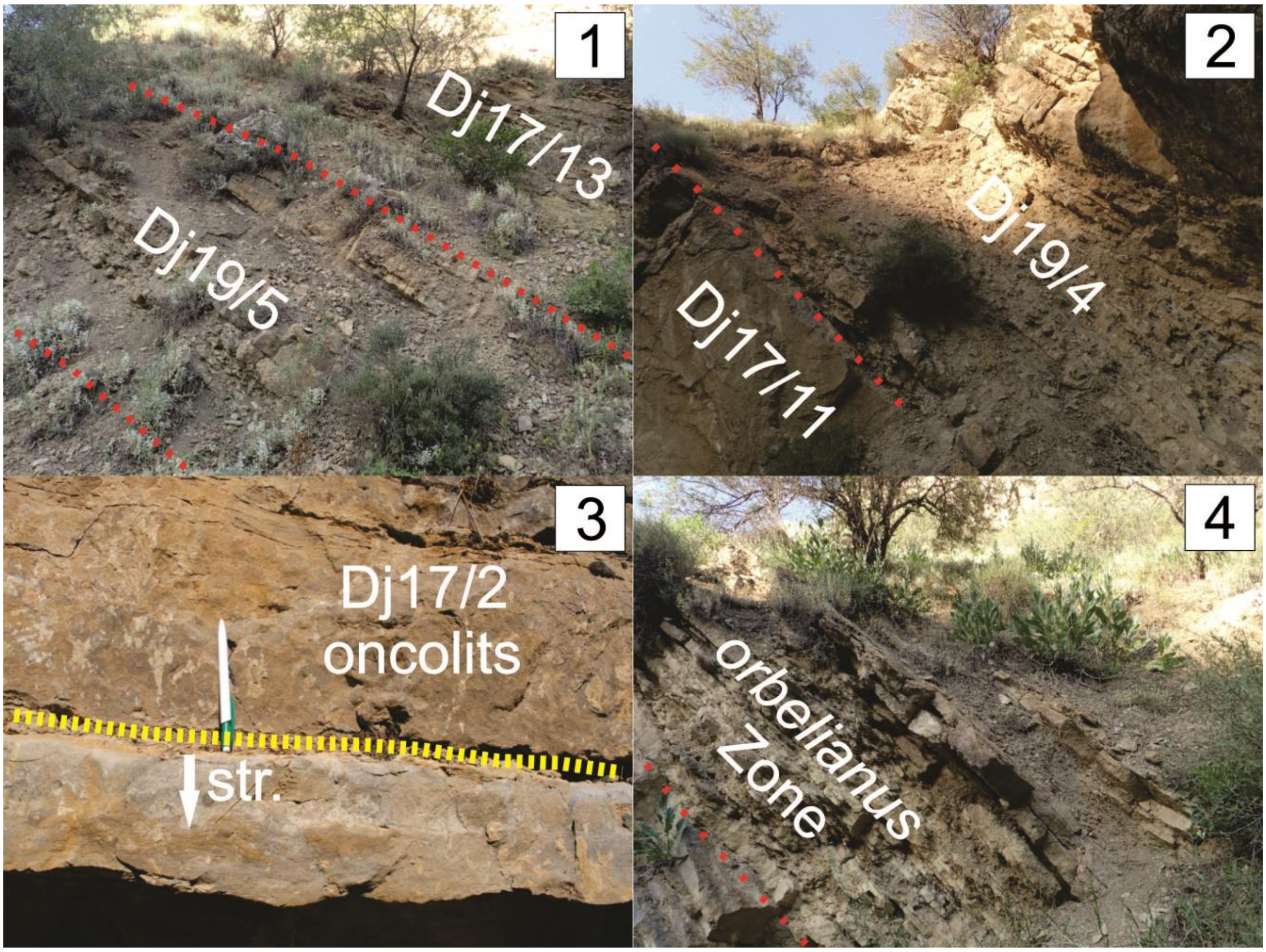


Figure 13. Djravank section (upper part). (**1**). The muddy and shelly limestone layers Dj19/5 and Dj17/3, which constitute the lower part of Interval 4; (**2**). Middle part of Interval 4 represented by different kinds of carbonate rocks of which some are resistant and well-bedded (e.g., Dj 19/H) and the rest are less resistant, nodular and more shelly (e.g., Dj 19/I). (**3**). Successive layers of stromatoporoid which is indicated by an arrow and overlapped by an oncolitic layer (Dj17/2). (**4**). Marly and sandy nodular limestones cropping out at the top of Interval 4 that lithologically corresponds to the Ertych Regional Stage of Arakelyan (1964) and bearing brachiopod fauna of the *orbelianus* Zone of Abrahamyan (1957).

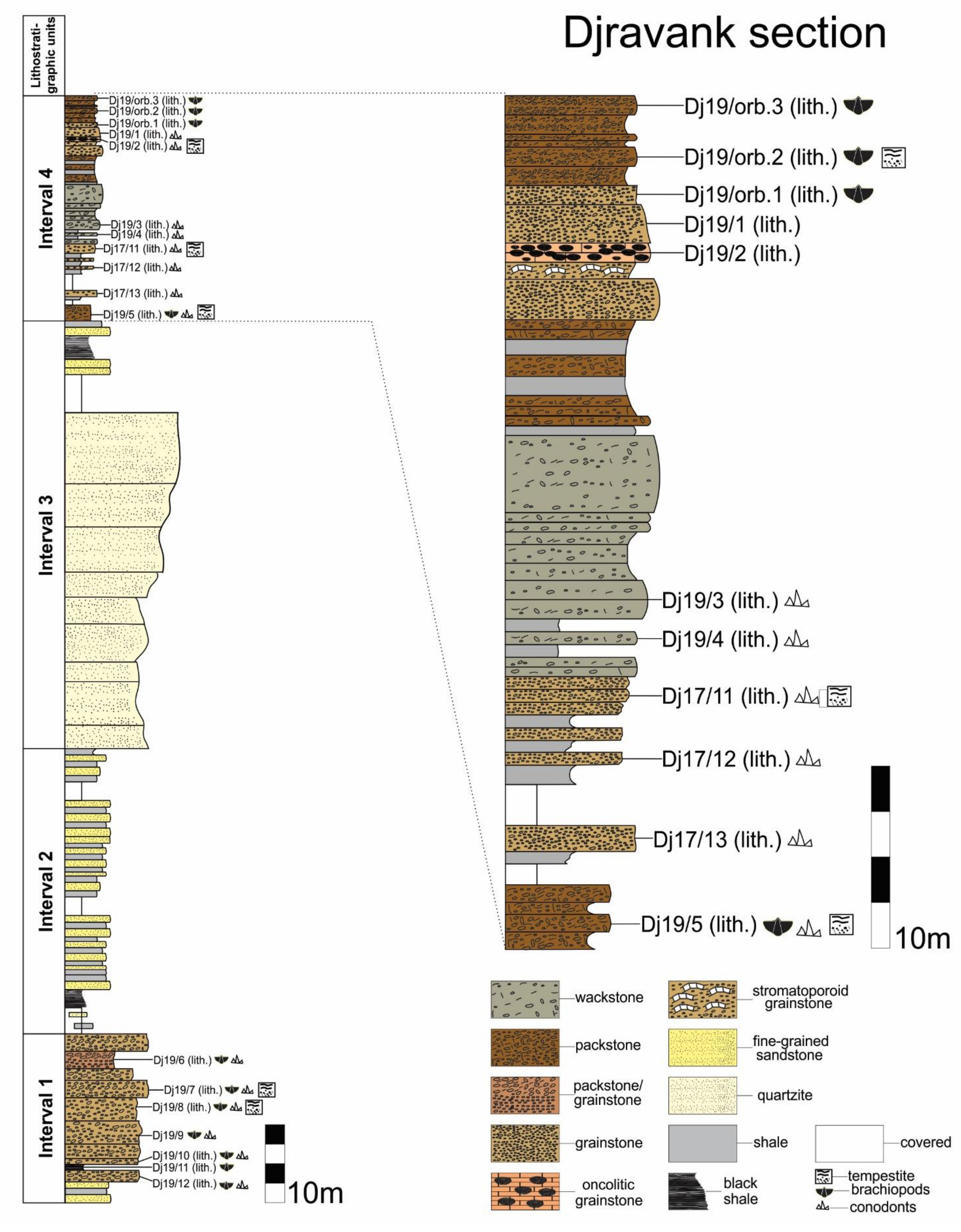


Figure 14. Lithostratigraphy of the Djravank section.

In addition to peloides, these limestone layers also contain ostracods (Fig. 15.1), brachiopod spines (Fig. 15.2), bryozoans (Figs. 15.2, 15.5), fragments of cyanobacterial mats (Fig. 15.4) and dasycladacean algae (Fig. 15.6). They consist of displaced body fossils and display strong bioturbation (e.g., 15.5–15.6). These bioturbaion patterns seem to be open tubes produced by animals burrowing in a stable, stiff substrate, subsequently filled with sediment transported by storm-generated currents (Wanless et al., 1988). Thus, they are here defined as peloidal bioclastic grainstones and considered to be storm deposition (tempestite). This massive graintone is interrupted by a distinct black shale layer (Fig. 12.3) below which, the grainstones are dominated by rhynchonellides, atrypides and productides, whereas the limestones cropping out above this layer contain no atrypide brachiopods. It is also important to highlight here that this black shale layer is rich in rhynchonellide brachiopods which confirms the viewpoints of Racki (1993), who aptly noted that the rhynchonellides were well-adapted to Late Devonian hypoxic habitats. Above the black shale layer, the limestones become dominated by spiriferides. Several hundred brachiopod specimens are taken from the Interval 1 to describe the brachiopod assemblage. The Interval 1 is overlain by intercalations of sandstones and shales, which in turn are covered by massive quartzites. Although this part of the section is partly covered by huge blocks of Eocene rocks, we could observe from place to place rocks resembling the facies of Intervals 2 and 3. The top of this section, which is termed Interval 4, is distinguished by the interbedding of different types of carbonate rocks. More particularly, the base (Dj19/5; Figs. 13.1, 16.3–16.4) represents a coquina-bed facies with fragments of stromatoporoids and cyanobacteria, which probably come from lagoonal and reefal environments, ostracods (Fig. 16.3) and a large bryozoan (Fig. 16.4). This externally very fragile layer is highly rich in rhynchonellide brachiopods (*Ripidiorhynchus djravankensis* n. sp.). Stratigraphically above, there is a change in facies that is observable in the field due to the resistance of the rocks (Fig. 13.1–13.2). The first bioturbated wackestone facies is observed within the layer Dj19/4 (Fig. 16.5–16.6), which clearly differs from the Dj19/5 and other layers outcropping below by being mud-supported and including a huge numbers codiacean algae

(*Umbella*). These limestone layers in their turn change to bioclastic grainstones since the layer Dj17/13 (Fig. 16.7–16.8); the latter includes brachiopod spines, crinoids and cyanobacterial mats (16.8). It should be noted that, unlike the base, the upper part of this interval is devoid of mud-supported carbonate rocks. Most notably, the layers of Dj17/12 (Fig. 17.1–17.2) and Dj17/11 (Fig. 17.3) are of bioclastic grainstone facies and appear to be storm deposits. Successive layers of stromatoporoids are observed on the ca. 25 cm layer Dj17/3, which unfortunately could not be observed in the sampled rocks and thin section. The skeleton was made of horizontal layers (the laminae) supported by upright rod-like structures (Fig. 13.3). These laminar stromatoporoids grew up to 30 mm in height and 60 mm in width. However, the photomicrograph of thin sections reveals a lot of *Umbella* (Fig. 17.4). The overlying Dj17.2 layer can be defined as oncolitic grainstone and obviously differs from all layers observed within this interval; thus in addition to Dj17/3, this oncolitic grainstone layer can be used as a marker bed. Dj17/2 is overlapped by peloidal grainstone layers of Dj17/1 and Dj17/orb. Dj17/orb. is very rich in brachiopods and yielded several hundred brachiopod specimens. At the first view, rhynchonellide and spiriferide brachiopods appear to be dominant within this assemblage. Dj17/orb is closing the Interval 4. It is also worth noting that the whole section is uncomformably covered by the Eocene algal limestones.

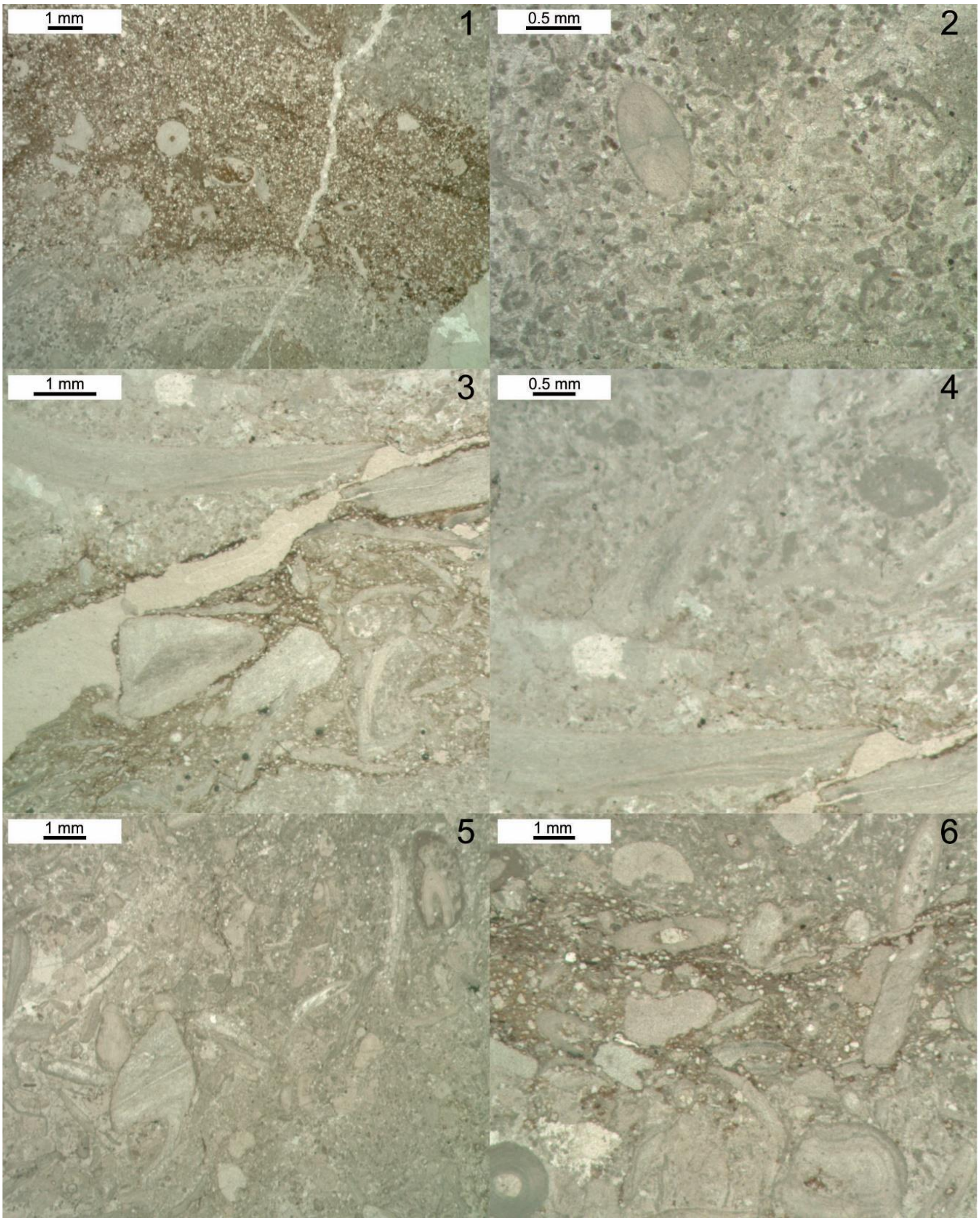


Figure 15. Photomicrographs of thin sections of Interval 1 of the Djravank section. (**1-2**) Dj19/10, peloidal bioclastic grainstone that displays strong bioturbation and quartz graines that partially replaced the host deposits (**1**) and close-up of a brachiopod spine (**2**). (**3-4**) Dj19/8, bioturbated coquina beds-grainstone containing shelly material (**3**) as well as fragments of cyanobacterial mats (**4**), and representing storm deposits. (**5-6**) Dj19/7, bioclastic grainstone, storm deposits comprising of brachiopod spines (of which the one of top right is encrusted by bryozoan and after reworked) (**5**), gastropods and fragment of dasycladacean algae (**6**).

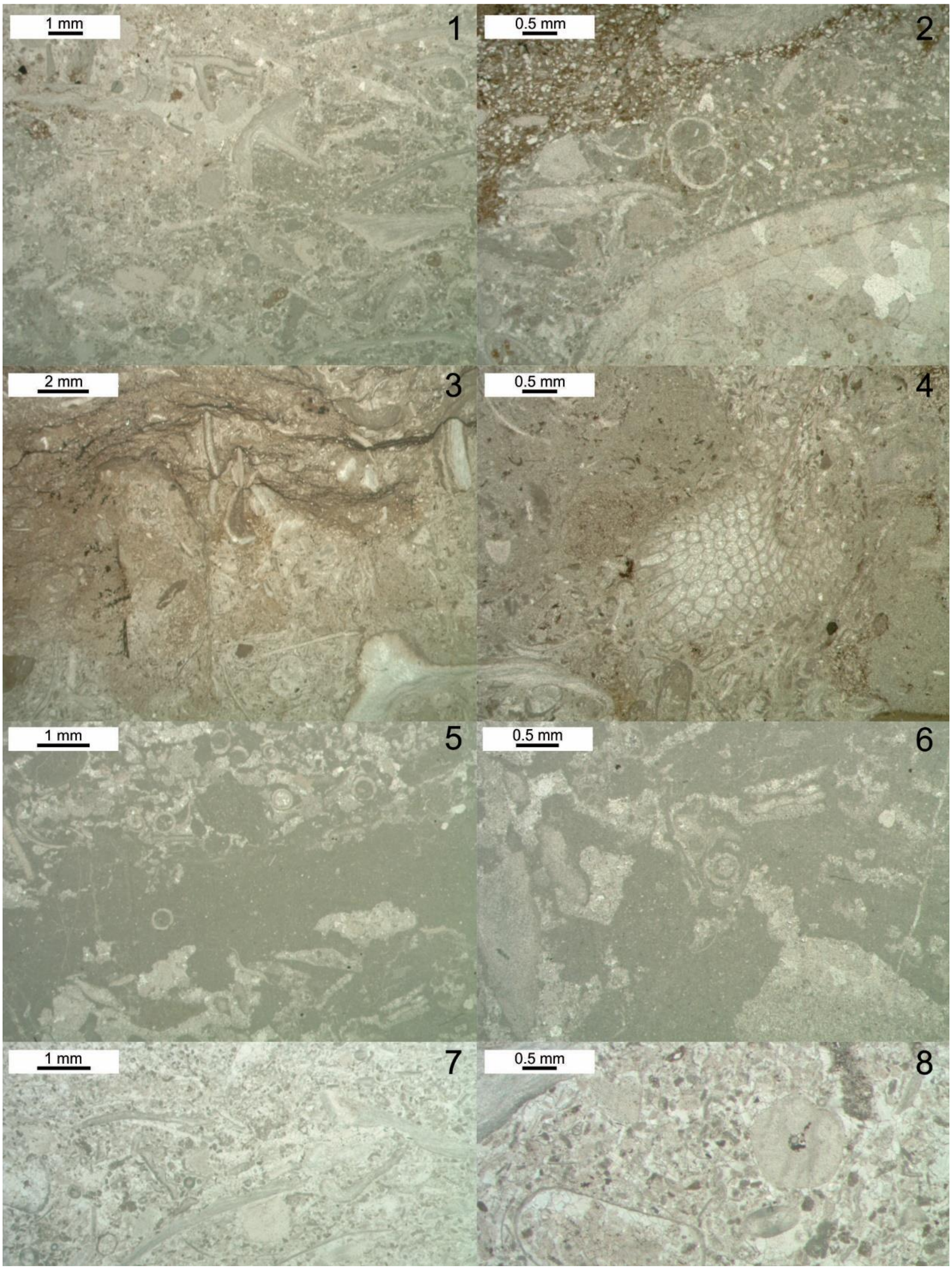


Figure 16. Photomicrographs of thin sections of intervals 1 and 4 of the Djravank section. **Interval 1**. (**1-2**) Dj19/6, grainstone facies with mixed peloid/brachiopod assemblage (**1**) that also includes ostracods, byozoans and gastropods (**2**). **Interval 4**. (**3-4**) Dj19/5, coquina-bed facies with fragments of stromatoporoids and cyanobacteria, ostracods (**3**) and a large brozoan (**4**). (**5-6**) Dj19/4, bioturbated wackestone with codiacean algae *Umbella* and sparite-filled fenestrae, (**5**) and close-up of one of those *Umbella* (**6**). (**7-8**) Dj17/13, bioclastic grainstone including fragments of brachiopods (**7**), crinoids and cyanobacteria (*Girvanella*) (**8**).

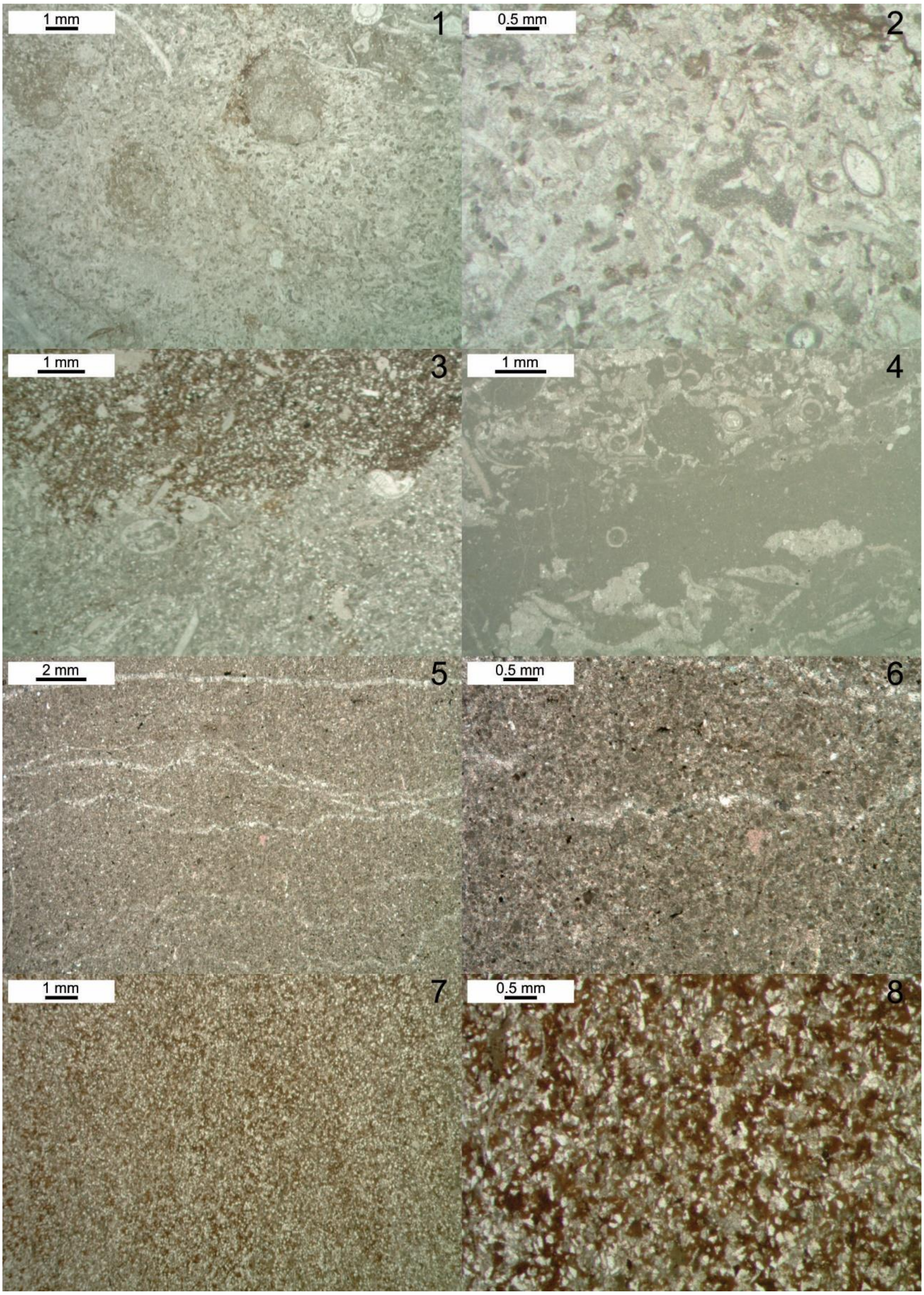


Figure 17. Photomicrographs of thin sections of the upper part of Interval 4 of the Djravank section. (**1-2**) Dj17/12, bioclastic grainstone displaying burrows and including codiacean algae *Umbella* (**1**), ostracods and fragments of cyanobacterial mats (**2**). (**3**) Dj17/11, bioclastic peloidal grainstone, tempestite. (**4**) Dj17/3, lagunal facies with *Umbella*. (**5-6**) Dj17/1, peloidal grainstone. (**7-8**) Dj17/orb, peloidal grainstone.

3.3 The Noravank section

Frasnian–Famennian carbonate and-siliciclastic deposits are perfectly exposed in a narrow gorge made by the Amaghu River, below the Noravank Monastery (Fig. 18.1) and constitute the Noravank section which has long been considered as the stratotype for the eponymous regional stage. Although the Noravank section is one of the most important sections in this area for documenting both the faunal turnover and lithological changes that occurred in the Late Devonian, this section has never been studied in detail and remains poorly known. Previously this section has been investigated by different paleontologists and stratigraphers (e.g., Abrahamyan, 1957; Arakelyan, 1964; Ginter et al., 2011) through almost the same profile; however, the data they provided regarding both the lithology and stratigraphy contradict each other. More particularly many stratigraphic intervals are overextended, overlooked and represented with incorrect stratigraphic positions. This could be explained by the difficult structural context of the section, as it is composed of folded and faulted sequences which are difficult to follow and observe in the field.

The lower part of the section (Interval 1) consists of ca. 12 m-thick limestones (Fig. 18.1–18.4) that are mainly identified here as peloidal bioclastic grainstones and also include some layers apparently representing storm deposits. The layers Nv19/1 and Nv19/20 represent peloidal bioclastic grainstones, which are composed of brachiopod spines, gastropods (Fig. 21.1, 21.4) and rare cyanobacterial mats (Fig. 21.2). These grainstone layers are well-bedded and clearly distinct (Nv19/1–Nv19/20; Fig. 19.2), whereas the layers cropping out above become more nodular and less resistant (Fig. 19.3); this part of interval is composed of tempestites such as the layers Nv19/38 (Fig. 21.3–21.4), Nv19/50 (Fig. 22.1–22.4). These tempestites consist of different broken fragments of brachiopods, crionoids, bryozoans, trilobites, cyanobacterial mats, tentaculites and lithoclasts that are reworked after the deposition. The overlying layer Nv19/60 also includes some *Umbella* (Fig. 22.6) which are not observed in the grainstones cropping out below that level, whereas the Nv19/74

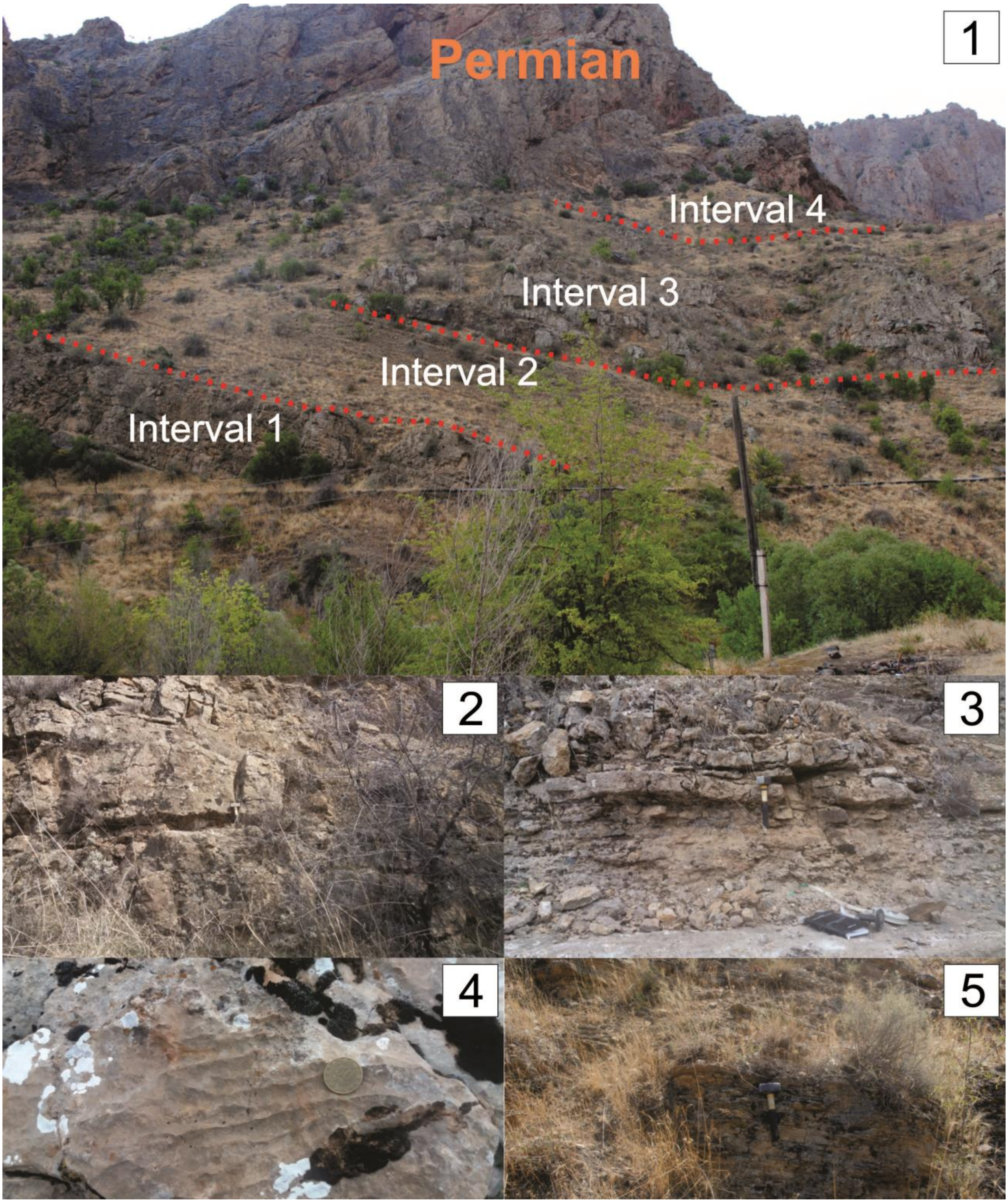


Figure 18. Field photographs of the Noravank section. (**1**) Frasnian–Famennian siliciclastic-carbonate sequences exposed in a deep valley, on a slope of the Gnishik river, below the Noravank Monastery, which is covered by massive sandy limestones of Permian age. (**2**) Close view of the Frasnian base of the section (Nv19/1–Nv19/19), which is represented by well-bedded limestone beds (lower part of Interval 1). (**3**). Nodular limestones (Nv19/20) of Interval 1 wherein the last atrypide specimen was found. (**4**) The upper part (Nv19/74) of Interval 1. (**5**) Intercalations of shales and sandstones that represent the base of Interval 2.

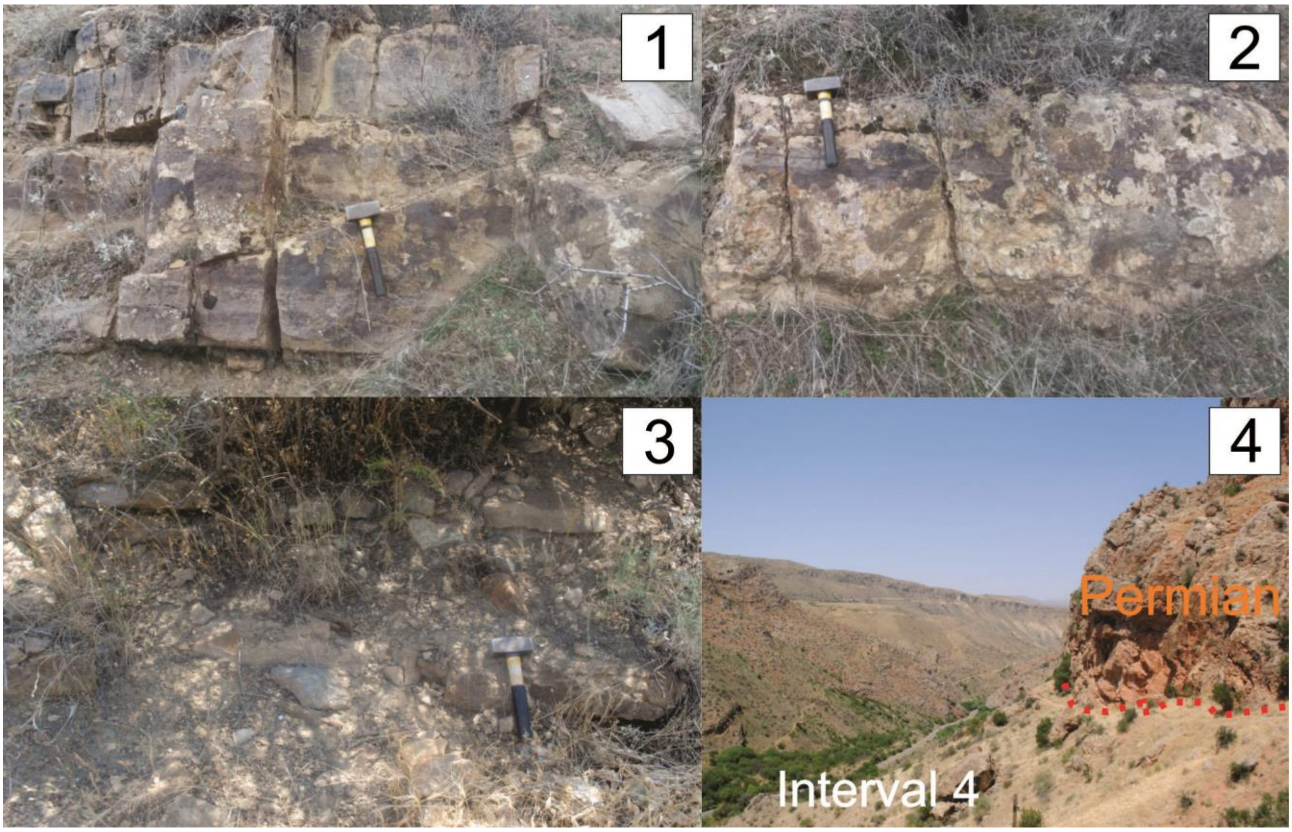


Figure 19. Noravank section. (**1**–**2**). Quartzite beds of Interval 3. (**3**). Slightly visible limestone layer (Nv19/218) that represents the base of Interval 4. (**4**). View of the top of Interval 4 consisting of Famennian marly and sandy limestones layers, which are unconformably overlain by sandy limestones of Permian age.

contains some fragments of tentactulites (Fig. 22.7), sea urchins and gastropods (Fig. 22.8). At this level, we found the last atrypide brachiopod specimens, which are partly exfoliated. A possible erosional surface separates the top of Interval 1 from the overlying shales of the Interval 2. Hundreds of brachiopod specimens are recovered from the Interval 1, most notably, from the layers Nv19/1, Nv19/6, Nv19/20, Nv19/38 and Nv19/74.

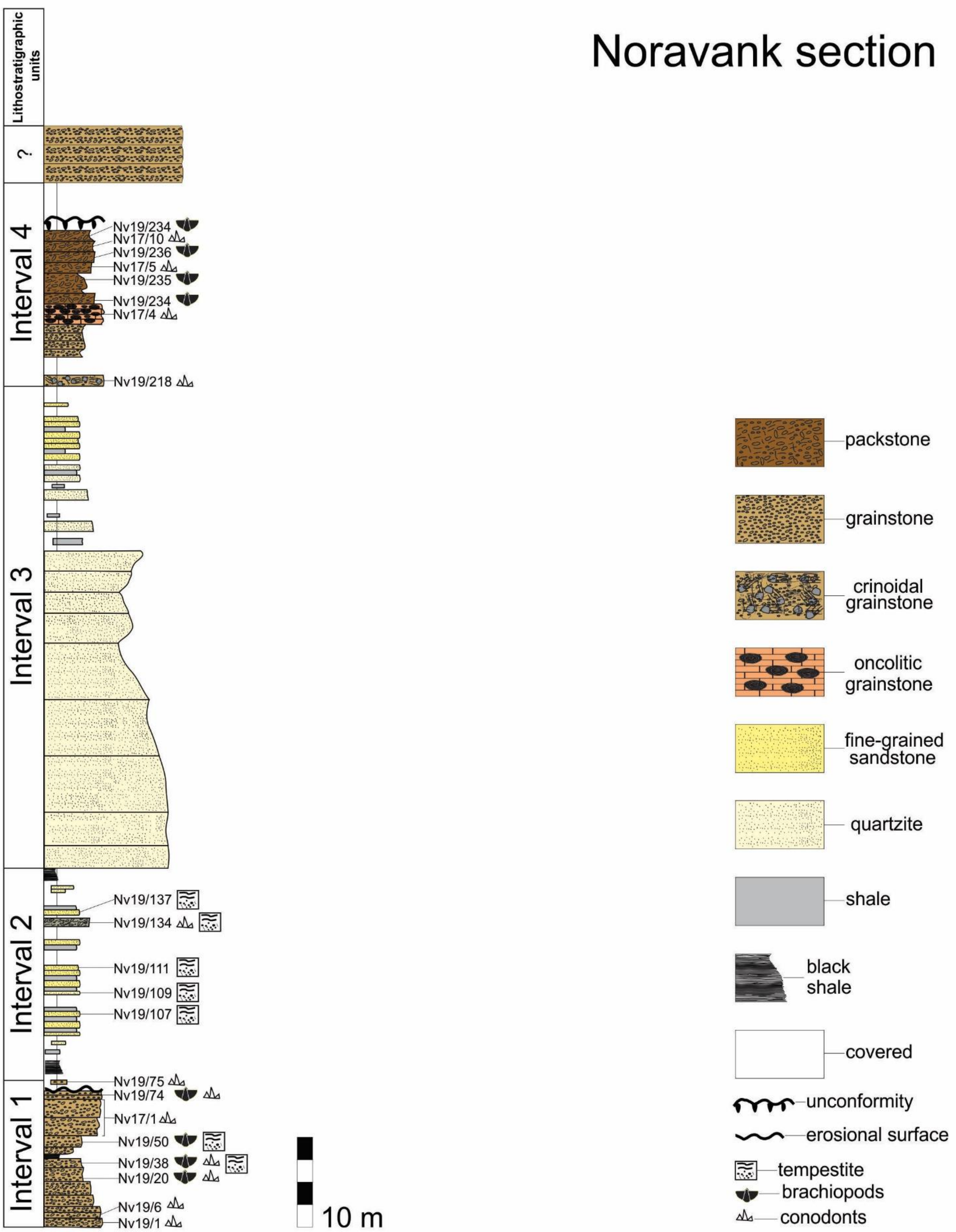


Figure 20. Lithostratigraphy of the Noravank section.

At the place, where we observed and sampled the Interval 1, the layers that crop out above the layer Nv19/74 and constitute the ensuing interval were folded and not convenient for measurements as well as sampling. Therefore, in order to avoid errors, it was decided to observe the section 20 meters to the east (to the direction of the Noravank monastery, in front of a small bridge) where we described more or less horizontally laying layers. The overlying Interval 2 is ca. 25 m-thick and mainly composed of intercalations of shales, sandstones and a single layer of bryozoan packstone. The sandstone (quartz-wacke) layers of this interval, such as Nv19/107 (Fig. 23.1–23.2), Nv19/109 (Fig. 23.3–23.4) and Nv19/111 (Fig. 23.5–23.6) are mainly bioturbated and clayey. Additionally, it is also worth mentioning that some of these sandstone layers, like the Nv19/109 contain also some fish bones (Fig. 23.4). The single carbonate layer Nv19/134 of Interval 2 is described as bryozoan packstone of storm deposits and besides bryozoans, which are represented in this layer by at least two species, includes fragments of brachiopods, trilobites, ostracods and fish bones (Fig. 24.1–24.2). The top of Interval 2 is represented by shale that it overlain by a massive interval of quartzites and sandstones, which together form the Interval 3. The lower and middle parts of this interval are mainly composed of massive quartzite whereas the upper part includes layers of sandstones and very thin layers of shales. The upper part of this interval is partly covered by scree which precludes the possibility to trace the beginning of the subsequent Interval. Thus, I consider the first limestone layer termed Nv19/218 (Fig. 24.5–24.6) as the base of Interval 4, because it represents clearly different facies. The latter is a crinoidal grainstone layer. The Interval 4 (Figs. 19.1, 20.4) chiefly consists of peloidal bioclastic grainstones, packstones and a single layer of oncolitic grainstone. The Nv17/4 is an oncolitic grainstone layer with peloides and bioclasts which form layered and approximately spherical structures (Fig. 25.1–25.4) composed of cyanobacterial growth. This layer is quite distinct and differs from other carbonate layers cropping out both below or above by its spherical structure. Nv17/4 is overlapped by packstones (Nv17/1.bis; Fig. 25.5–25.6) which contains a lot of sand grains, fragments of bivalves, brachiopod spines and bryozoans. The Interval 4 is topped by peloidal bioclastic grainstone layers. Abundant brachiopods are described from the packstone/grainstone layers outcropping above the oncolitic layer (Nv17.4). The top of the section is covered by massive red limestones of Permian age (Ginter et al., 2011), which are unconformably overlying the Upper Devonian (lower Famennian) rocks (Figs. 18.1, 19.4, 20).

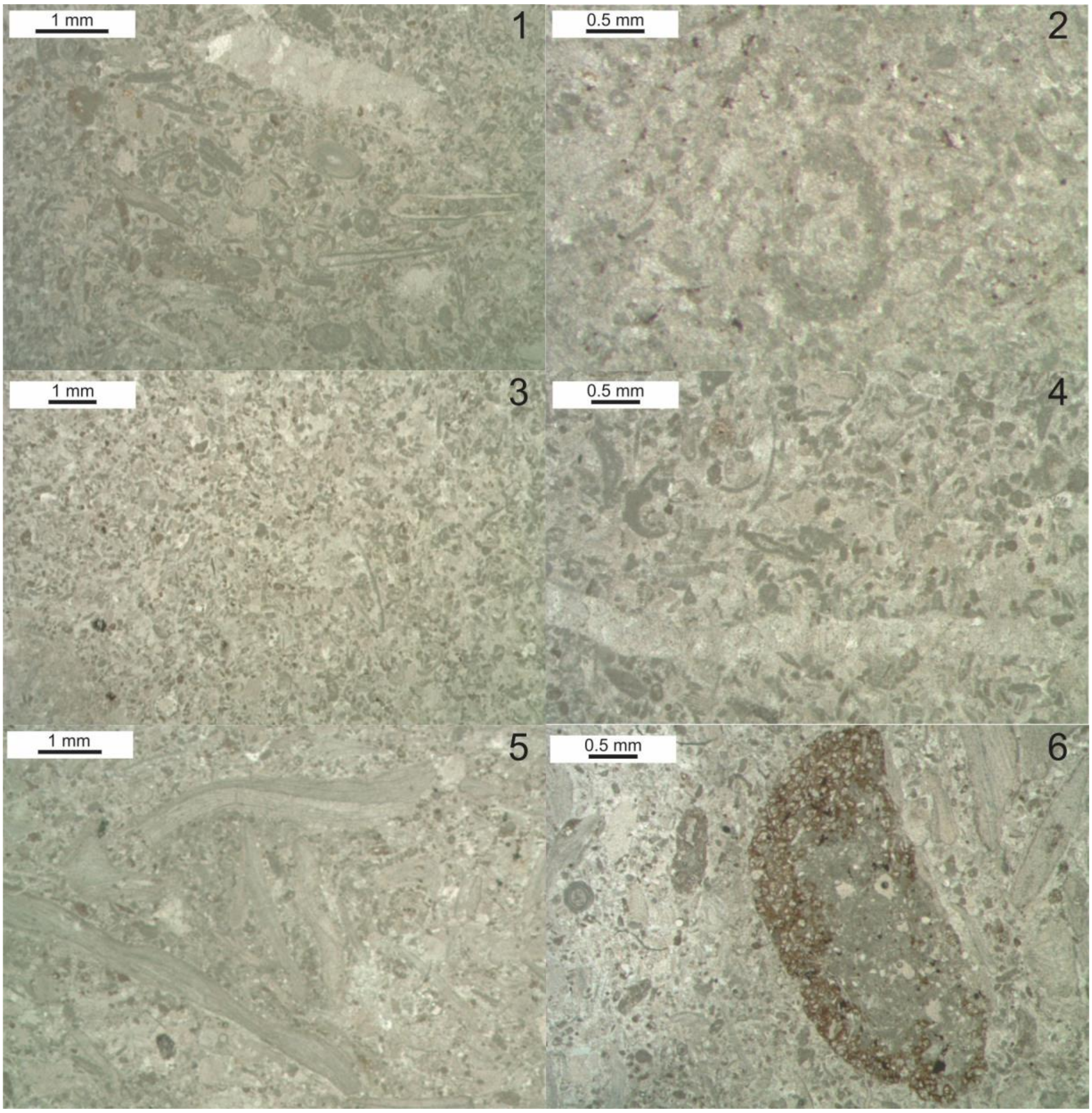


Figure 21. Photomicrographs of thin sections from Interval 1 of the Noravank section. (**1-2**) Nv19/1, bioclastic peloidal grainstone with brachiopod spines, gastropods (**1**) and fragments of cyanobacterial mats (**2**). (**3-4**) Nv19/20, bioclastic peloidal grainstone (same facies as in Nv19/1). (**5-6**) Nv19/38, bioclastic peloidal grainstone, storm deposition, composed of different shell fragments of brachiopods, crinoids (**5**), lithoclasts that are reworked afterwards and cyanobacterial mats (**6**).

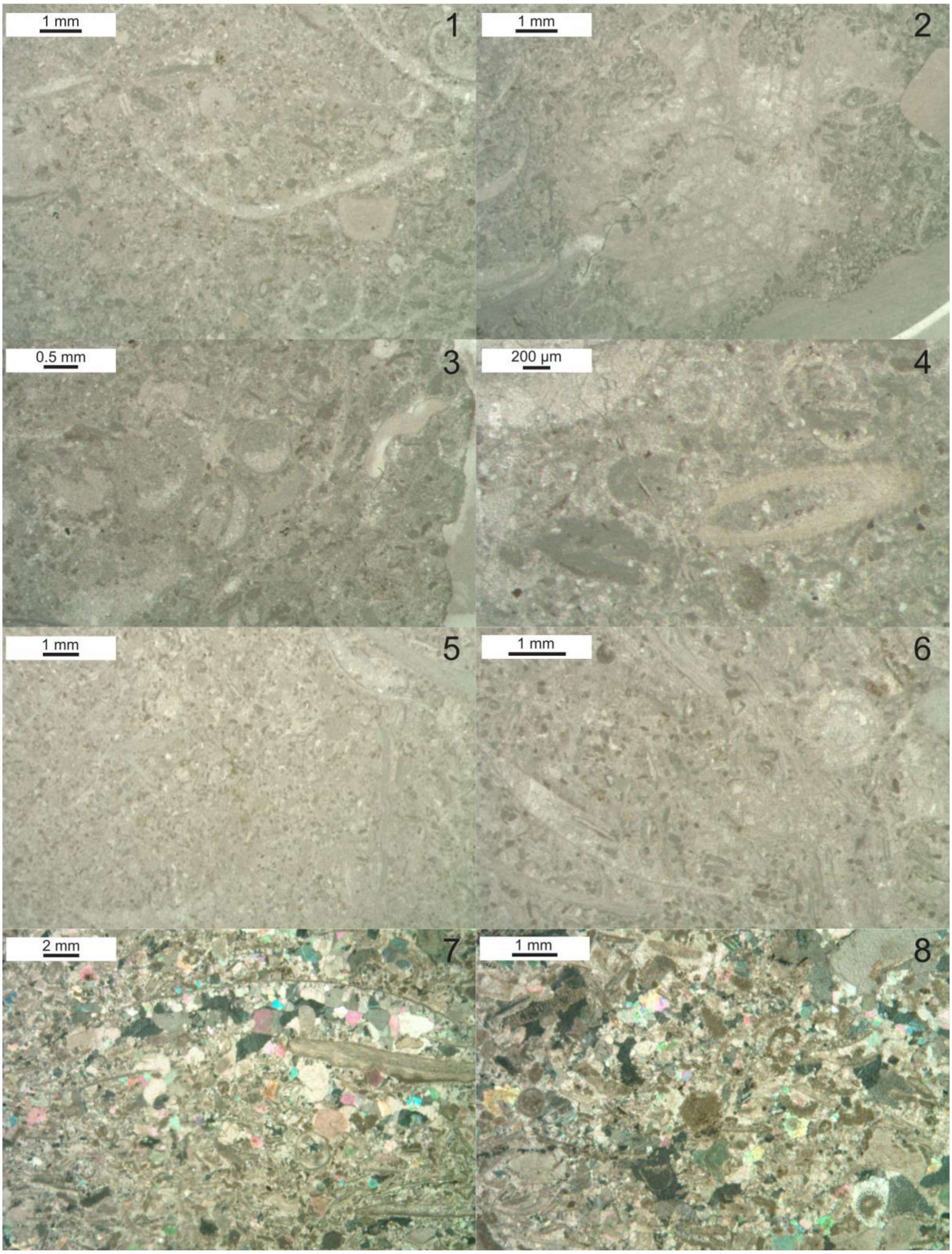


Figure 22. Photomicrographs of thin sections from Interval 1 of the Noravank section. (**1-4**) Nv19/50, bioclastic peloidal grainstone (tempestite) with different fragments of brachiopods, crinoids (**1**), bryozoan (**2**), trilobite (**3**), fragments of cyanobacterial mats and tentaculites (**4**). (**5-6**) Nv19/60, bioclastic peloidal limestone with fragments of brachiopods (5) and a few codiacean algae *Umbella* (6). (**7-8**) Nv19/74, bioclastic peloidal grainstone with a few fragments of tentaculites (**7**), sea urchins and gastropods (**8**).

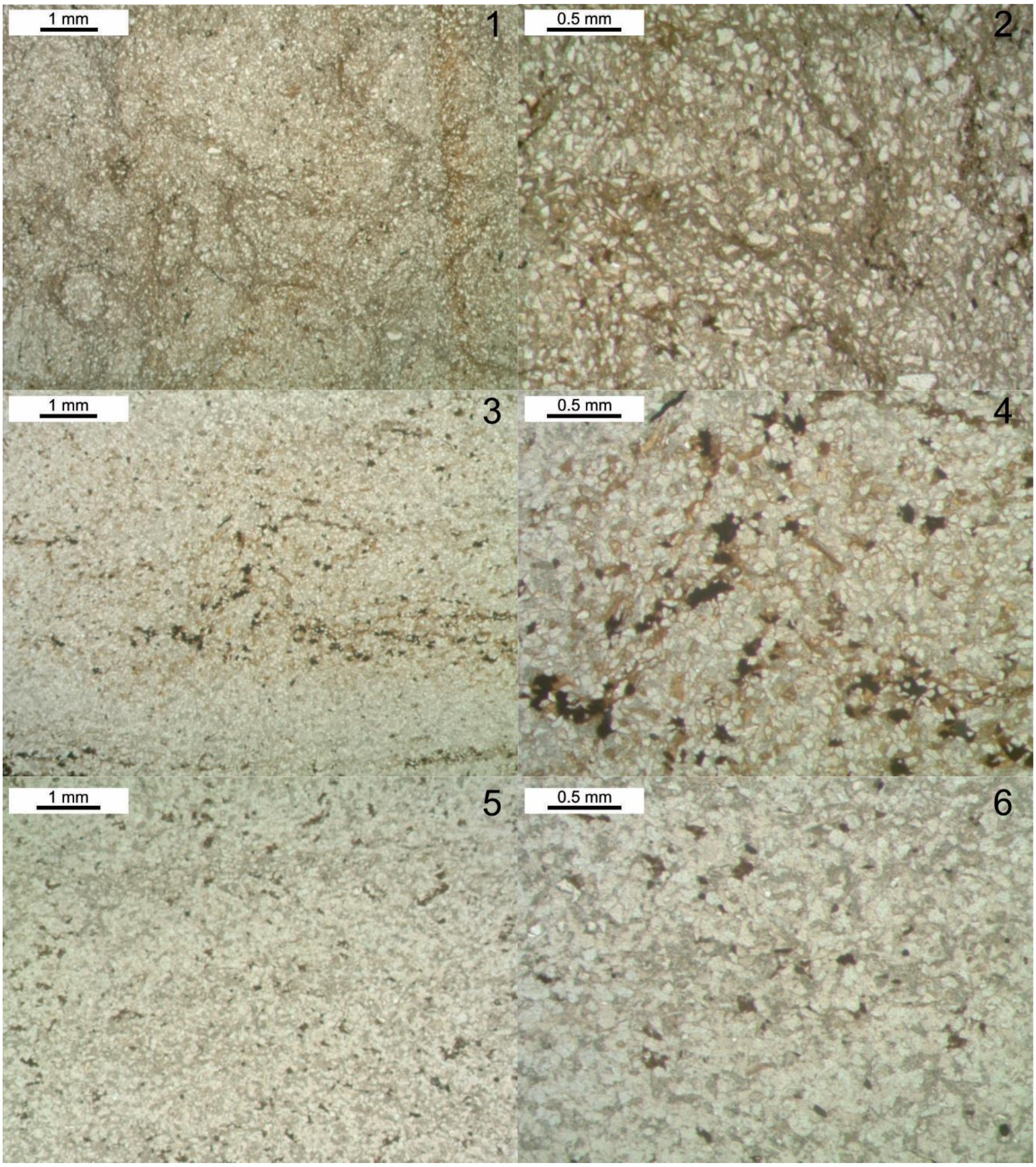


Figure 23. Photomicrographs of thin sections from Interval 2 of the Noravank section. (**1-2**) Nv19/107, bioturbated clayey sandstone (quartz-wacke). (**3-4**) Nv19/109, bioturbated clayey sandstone (quartz-wacke) with a little phosphate concentration. (**5-6**) Nv19/111, bioturbated sandstone (quartz-wacke).

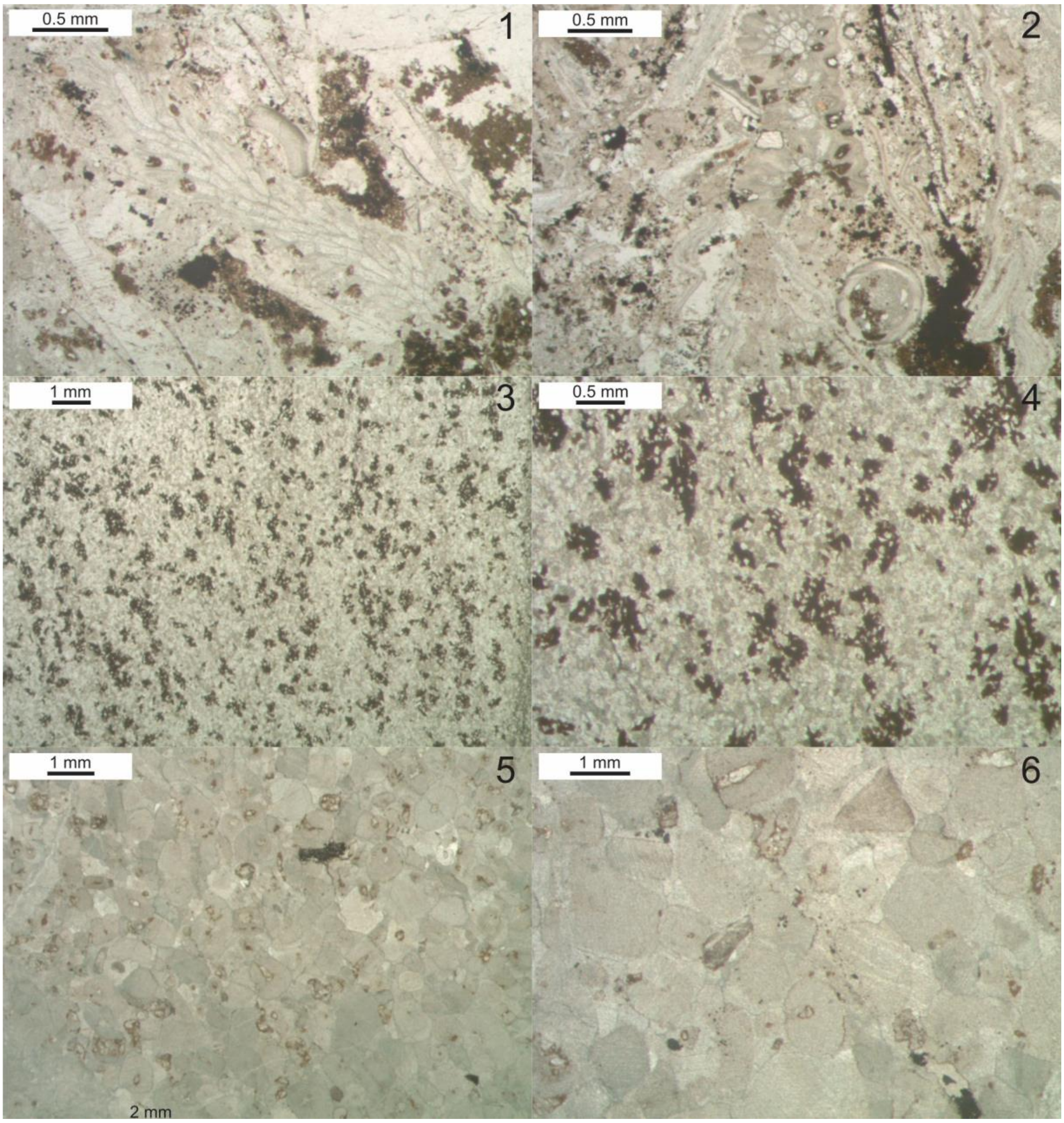


Figure 24. Selected photomicrographs of thin sections from Intervals 2 and 4 of the Noravank section. (**1-2**) Nv19/134 (Interval 2), bryozoan packstone of storm deposit that also contains fragments of brachiopods and trilobites (**2**). (**3-4**) Nv19/137 (Interval 2), bioturbated clayey sandstone (lithic-wacke, storm deposit). (**5-6**) Nv19/218 (Interval 4), crinoidal grainstone.

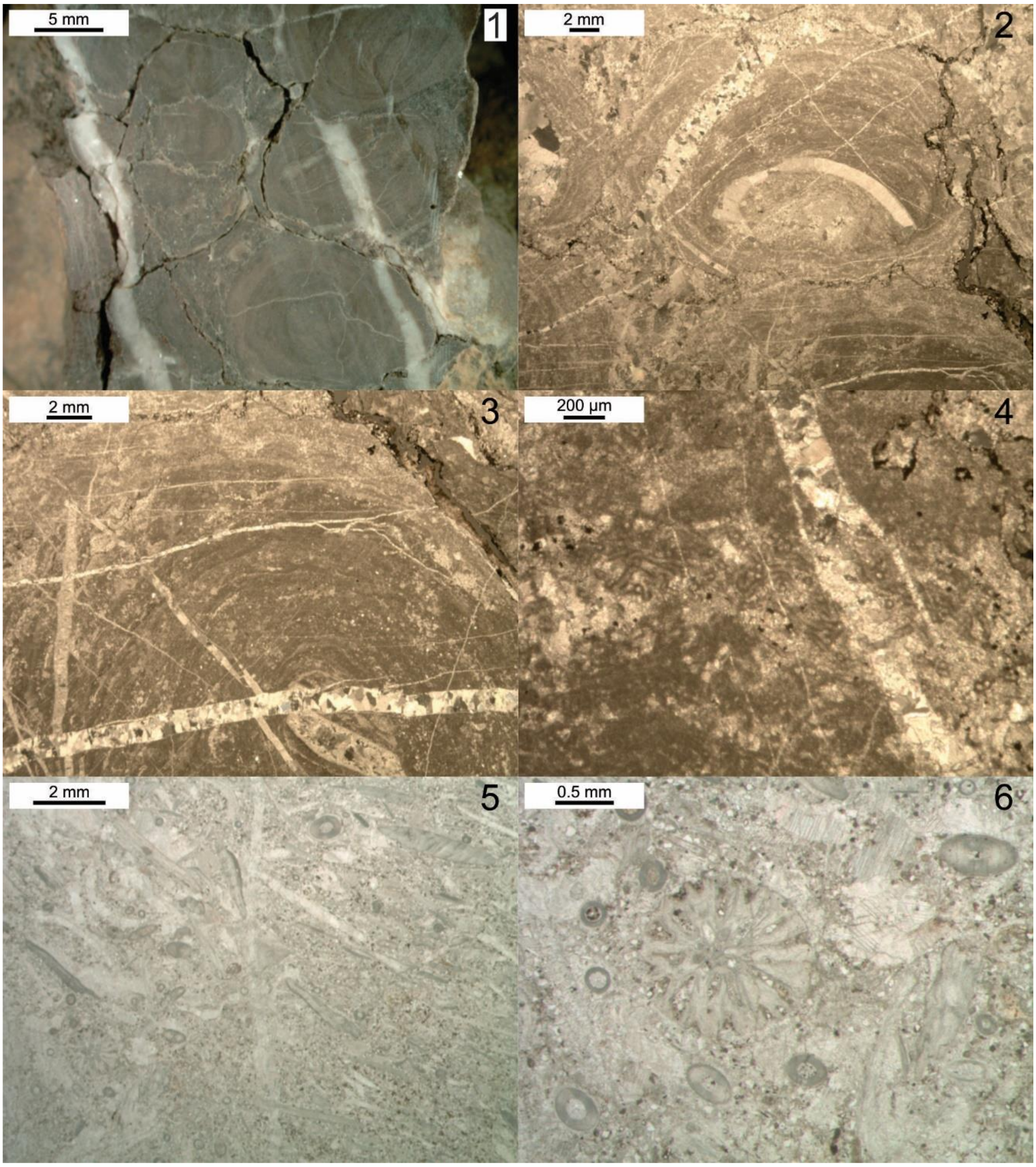


Figure 25. Interval 4 of the Noravank section. (**1-4**) Nv17/4, oncolitic grainstone with peloids and bioclast; polished slab (**1**) and photomicrographs of thin sections showing the oncolites, formed by layered and approximately spherical structures (**2-3**) composed of cyanobacterial growth (**4**). (**5-6**) Nv17/1. bis (Interval 4), packstone with a lot of sand (**5**), brachiopod spines and bryozoan fragments (**6**).

3.4 Lithostratigraphic correlations

The three studied sections from Central Armenia (Ertych, Djravank and Noravank) show that they are very similar in their lithostratigraphic evolution. We establish above four lithostratigraphic intervals (Fig. 26) that have been correlated throughout these sections. The **Interval 1** is mainly composed of ca. 12 m-thick bioclastic and peloidal grainstones and a few layers of tempestite (e.g., Fig. 21.3–21.4, Fig. 22.3–22.4). These grainstones contain peloides, shell fragments of brachiopods, gastropods, ostracods, dasycladacean algae, rare bryozoans and cyanobacteria. The tempestites are more common within the Interval 1 of Djravank and Noravank sections than in the Ertych section. In addition to peloides and quartz grains, these storm deposits contain abraded fragments of brachiopods, gastropods, ostracods and less commonly tentaculites that were sorted mechanically and hydrodynamically. The **Interval 2** is chiefly composed of black shales, calcareous and clayey bioturbated sandstones (quartz-wacke) (and a single layer of bryozoan packstone observed only in the Noravank section). Hummocky cross-stratification (HCS) is observed within this interval in all three sections. The sandstones of Interval 2 consist of grains that are fine, irregularly shaped and connected each other by clayey material (e.g., Fig. 24.3–24.4); thus, they are identified as lithic-wacke. Some layers also contain fish bones. The total thickness of **Interval 3** is ca. 25–30 m. It is mainly composed of quartzites in its lower and middle part and of sandstones and shales in its upper part. Two intercalating shale layers are observed between the thick quartzite beds of the lower–middle part of this interval within the Ertych section; they contain abundant and well-preserved macro-plant remains (e.g., Fig. 5.1). The ensuing **Interval 4** is mainly distinguished by the alternation of different types of carbonate rocks including a layer of oncolitic limestone. The base of this interval in the Noravank section is represented by a distinct layer of crinoidal grainstone (Nv19/218), which is covered by black shales and bioclastic grainstones. In the middle part of this interval a distinct layer of oncolitic grainstone (Fig. 24.1–24.4) crops out, which consists of

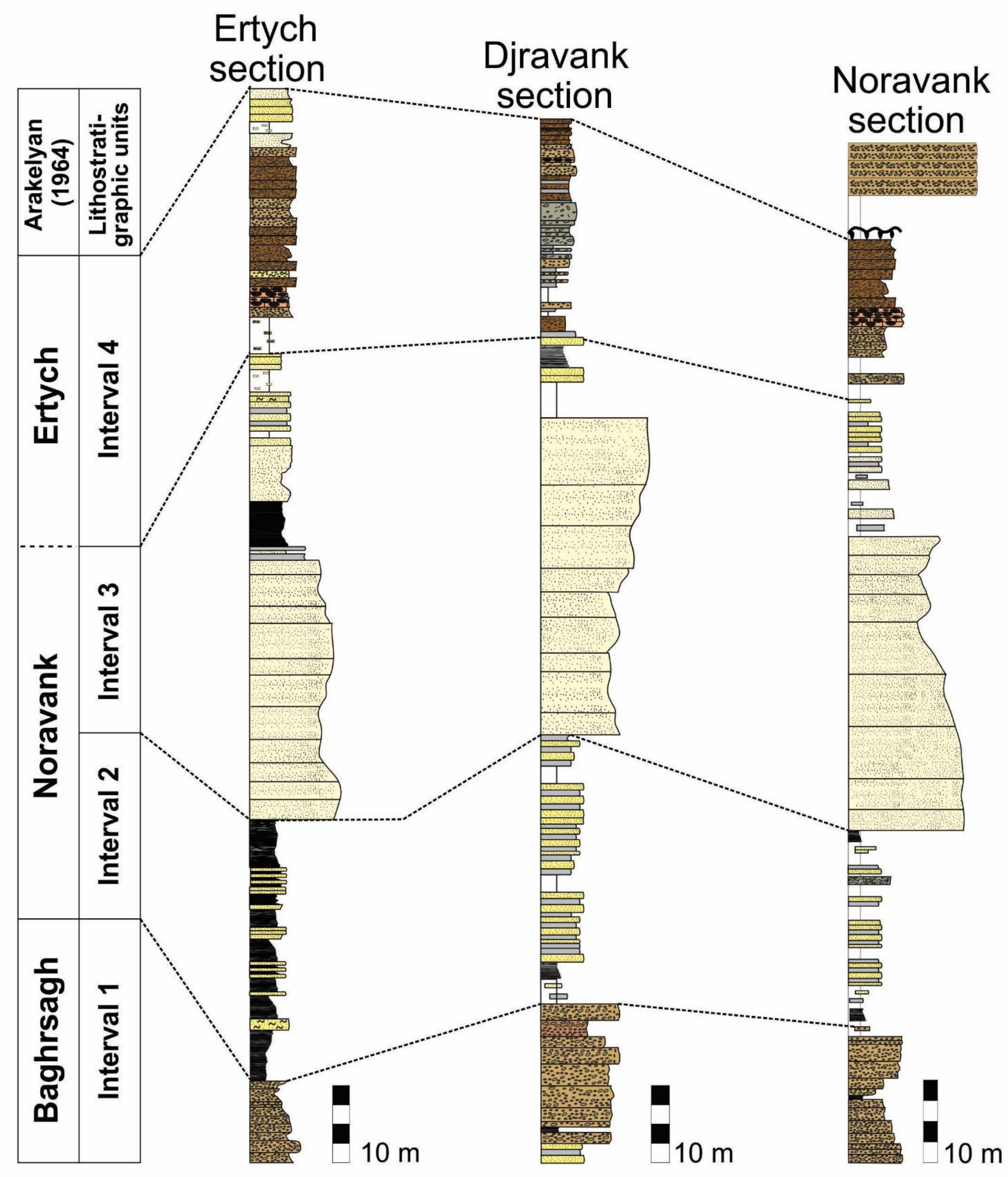


Figure 26. Lateral correlation between the three studied sections.

successive layers of calcium carbonate precipitated due to the activity of cyanobacteria. In addition to cyanobacterial mats, this oncolitic grainstone layer includes peloides and codiacean algae (*Umbella*). The top of the section is unconformably covered by Permian sandy limestones (e.g., Figs. 18.1, 19.4). In contrast to the Noravank section, Interval 4 of the Ertych section is devoid of a crinoidal limestone or alternatively these are not exposed. The base of Interval 4 in the Ertych section is represented by ca. 1 m of bioclastic grainstones that are overlain by an oncolotic grainstone layer (Er19/92; Fig. 5.5–5.6); the latter is identical with the Nv17/4 observed within the Interval 4 of the Noravank section. The middle–upper parts of Interval 4 in Ertych section consist of tentaculite/bryozoan packstone (e.g., Er19/105, Fig. 9.1–8.9; Er19/108, Fig. 9.4–9.5) with a few layers of bioclastic grainstone (e.g., Er19/127, 10.1–10.2) and coquina beds (e.g., Er19/176, 10.7–10.8) as is the case of this interval within the Noravank section. However, the Interval 4 of the Ertych section is topped by fine-grained clayey sandstone (lithic-wacke) and quartzite layers, which are not observed either in the Noravank or in the Djravank sections. The Interval 4 of the Djravank section differs slightly from its equivalent in the Ertych and Noravank sections by possessing more muddy material in its carbonates as observed in the layers Dj19/5 (Fig. 16.3–16.4) and Dj19/4 (Fig. 16.5–16.6) cropping out in the lower–middle parts. Its second peculiarity lies in the layer below the oncolitic grainstones (Dj19/2), which includes successive layers of stromatoporoids (Fig. 13.3) that was not observed below the oncolitic layer of the other two sections.

Although these four intervals vary slightly in thickness and lithological composition depending on the section, their general composition is quite similar. Most importantly, these intervals are easy to distinguish in the field and they have a fairly wide geographic distribution (the Ertych and Djravank sections are less than a kilometer apart and both of them are ca. 5 Km away from the Noravank section); thus they are mappable and may be more useful for future geological mapping than the “formations” introduced by Arakelyan (1964), which as discussed by Serobyan et al. (2019a, b) are defined based on their fossil assemblages (mainly brachiopods) and not on their lithology.

3.5 Sequence stratigraphy and paleoenvironmental interpretation

The intervals constituting our studied sections have similar lithostratigraphic composition; thus it can be reasonably assumed that these intervals were developed under the same depositional environment (e.g., depth, carbonate production). More particularly, the stratigraphic development of sedimentary rocks of Interval 1 in all three sections clearly displays an aggradational stacking pattern that is interpreted as representing a highstand system tract (HST). The lithological composition and the fossil fauna described in the Interval 1 allow considering that it was accumulated in an internal ramp environment. However, the erosional surface (ES) observed at the top of this interval (e.g., Nv19.74) and the overlying black shales observed in all sections, which can be considered as a maximum flooding surface (MFS), mark a change in depositional trend (Catuneanu, 2002, 2017). The deposition of Interval 2, apparently records a deepening-upward (transgressive) trend. Hummocky cross-stratification (HCS) is observed within this interval in all three sections, which is an important sedimentary structure mainly found in sandstones formed by the wave action at the shoreface-offshore transition (middle ramp) (Woolfe, 1993). It is a form of cross-bedding described mainly in sandstones, which usually characterizes a wave dominated facies and formed at a depth of water below fair weather wave base (FWWB) and above storm wave base (SWB). Consequently, the presence of HCS structure suggests that the sedimentary rocks of Interval 2 were deposited on a median ramp environment (Dott, 1982). While, the vertical buildup of massive quartzite and sandstone layers of Interval 3 indicate an aggradational sedimentary pattern accompanied with a HST. It is likely that these fine-grained quartzites were accumulated in a very shallow environment, more precisely in an inner ramp environment. However, the sandstones and shales cropping out in the upper part of this interval indicate a change in environment; most likely the shale layers developed in the upper part of this interval coincided with a TST and a trend in deepening. Unfortunately, no MFS was detected within this interval to indicate the layer which

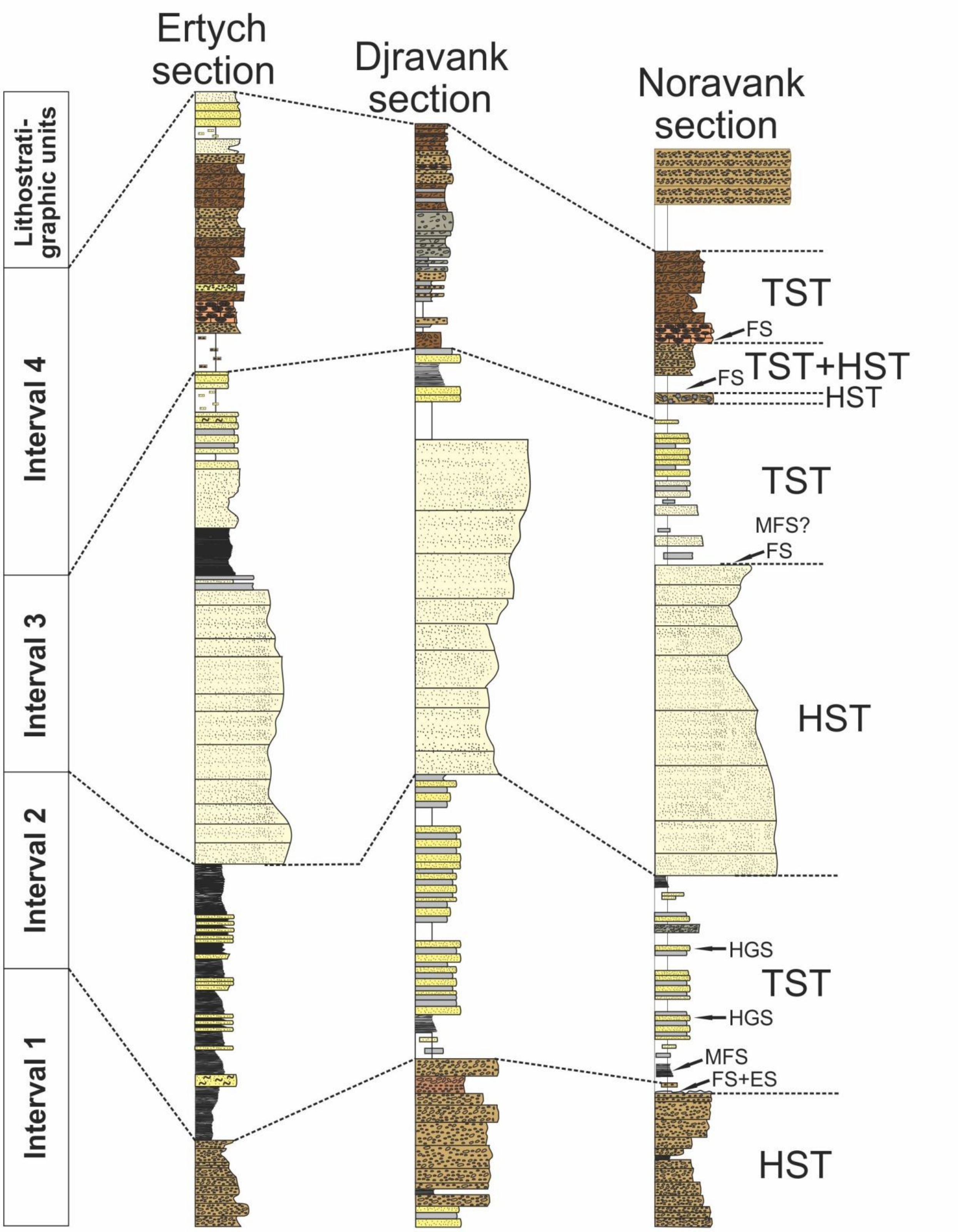


Figure 27. Sequence stratigraphic interpretation of the studied sections.

exactly marks the end of a HST and beginning of a TST. The base of Interval 4 in the Noravank section is represented by a distinct layer of crinoidal grainstone (Nv19/218), which clearly points to a change in depositional environment and matches with a HST. The Nv19/218 is covered by black shales (flooding surface?) and bioclastic grainstones. This crinoidal layer is not observed in the Ertych and Djravank sections. This oncolitic grainstone layer that is observed in all sections, in addition to cyanobacterial mats also includes peloides and *Umbella* typical of fresh water environment, which allows me to assume that it was formed in a shallow inner lagoon type of environment. Evidently, Nv17/4 records a significant drop in sea level. The accumulation of the upper part of Interval 4 in a lagoonal environment is further evidenced by the sparite-filled fenestrae observed within the layer Dj19/4, which also containes plenty of *Umbella*. However, the overlying tentaculite/bryozoan packstones feature deeper facies, apparantly associated with a transgression that generally results from a rising relative sea level (Catuneanu, 2006, 2017).

Chapter 4

Systematic paleontology

The supraspecific classification adopted herein follows Savage et al. (2002) and Savage (2007) for the Order Rhynchonellida (instead of the one suggested by Sartenaer (2001, 2003)), Copper (2002) for the order Atrypida, Alvarez and Rong (2002) for the Order Athyrida and Carter et al. (1994) Johnson (2006) for the Order Spiriferida. The term Athyrida is used here according to the recommendation made by Copper and Jin (2017).

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonirhynchiidae Schmidt, 1965

Subfamily Trigonirhynchiinae Schmidt, 1965

Genus *Sartenaerus* Özdikmen, 2008

See Serobyan et al. (2021), p. 530.

Sartenaerus baitalensis (Reed, 1922)

See Serobyan et al. (2021), p. 530, Figs. 3–4.

Sartenaerus charakensis (Brice, 1967)

See Serobyan et al. (2021), p. 533, Figs. 5.1–5.10, 6.

Genus *Porthmorhynchus* Sartenaer, 2001

Porthmorhynchus? sp.

See Serobyan et al. (2021), p. 536, Figs. 5.11–5.15, 7.

Subfamily Ripidiorhynchinae Savage, 1996

Genus *Ripidiorhynchus* Sartenaer, 1966a

Type species.—*Terebratula livonica* von Buch, 1834.

Ripidiorhynchus gnishikensis (Abrahamyan, 1959)

Plate 1.1–1.5; Figures 28, 30; Table 1

1959 *Camarotoechia strugi* Nal. subsp. *gnishikensis* n. subsp.; Abrahamyan, p. 6, pl. 2, figs. 5–7.

1964 *Camarotoechia strugi* Nal, subsp. *gnishikensis* Abrahamyan, 1959; Arakelyan, p. 63, 67, 70, 74, 77, 92, 93.

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

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

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

Neotype.—Although Abrahamyan (1959: pl. 2, figs. 5–7) designated a holotype among the three specimens she illustrated, neither the holotype nor other specimens examined in her publication can be traced within Abrahamyan's collection stored at the IGSNASRAGM and are considered as lost. Therefore, the single specimen (IGSNASRAGM 3927/PS 3033) figured in Plate 1.1–1.5 is hereby designated as the neotype.

Occurrence.—*Ripidiorhynchus gnishikensis* was first described in Armenia by Abrahamyan (1959), in the Frasnian sequences of the Gnishik section (Fig. 1). Later it was reported by Arakelyan (1964) in the Frasnian Baghrsagh Regional Stage of the Baghrsagh and Danzik sections as well as in the lowest Famennian Noravank Regional Stage of the Noravank, Ertych and Gyumushlug sections (Fig. 1) within a brachiopod assemblage composed of Frasnian spiriferide brachiopods. Presumably Arakelyan (1964) confused *R. gnishikensis* with a lower Famennian representative of that genus, most likely with *R. djravankensis* n. sp. as Abrahamyan's species occurred only in the Frasnian.

Unfortunately, the specimens identified as *R. gnishikensis* by Arakelyan cannot be traced within his collection and are considered as lost, which precludes the opportunity of re-examination and revealing this taxonomic confusion. However Arakelyan et al. (1975) mentioned *R. gnishikensis* amongst the biostratigraphically significant species characterizing the Frasnian in Armenia. Afterwards, Pakhnevich in Alekseeva et al. (2018a) examined a huge material from several localities in Nakhichevan and specified that it actually occurs in the Baghrsagh Regional Stage, correlated with the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* brachiopod Zone of Rzhonsnitskaya and Mamedov (2000), confirming the viewpoint of Arakelyan et al. (1975). Additionally, it is judicious to remind here that recent sampling also revealed the presence of this species only in the Frasnian sequences.

Description.—Shell small-sized (up to 17.9 mm in width, 16.2 mm in length, 13.7 mm in thickness) (Table 1), slightly wider than long, rounded subtriangular in outline, sharply dorsibiconvex; widest at midlength or slightly anteriorly to it, highest near umbones; anterior margin slightly rounded to emarginate; anterior commissure uniplicate, serrate.

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

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

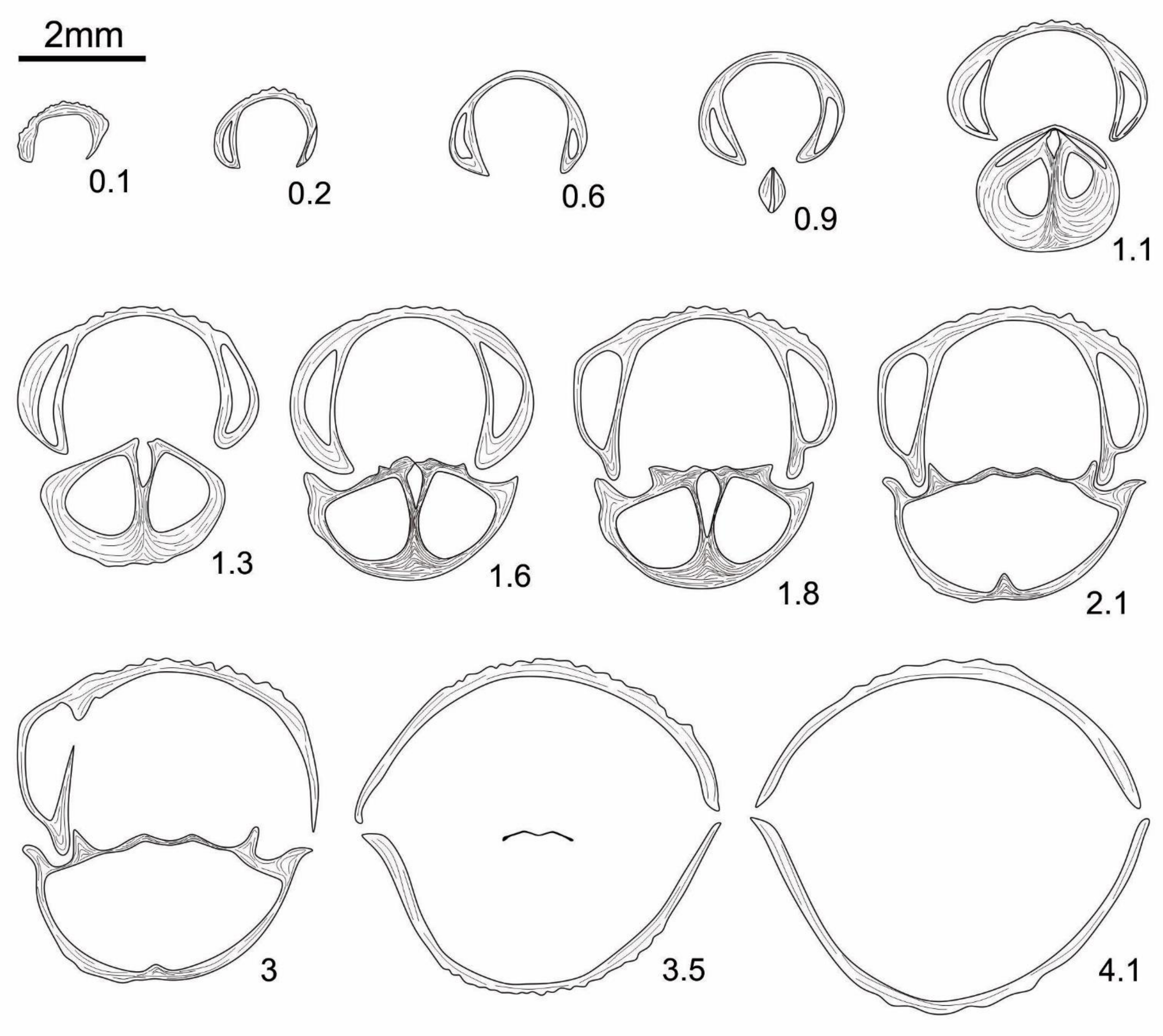


Figure 28. Transverse serial sections of *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) (IGSNASRAGM 3926/PS 3032) from the Frasnian *Cyrtospirifer subarchiaci–Cyprhoteorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo.

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

Ventral valve interior (Fig. 28) with thin, long dental plates converging ventrally; teeth massive, subrectangular in outline; central apical cavity wide. Dorsal valve interior (Fig. 28) with low and very short septum; septalium deep, Y-shaped and covered anteriorly; hinge plate united.

Material.—Nine articulated specimens and four ventral valves from the Ertych (four articulated specimens and two ventral valves) and Djravank (five articulated specimens and two ventral valves) sections.

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

Table 1. Measurements in mm and ratios of *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

Remarks.—*Ripidiorhynchus gnishikensis* was described initially by Abrahamyan (1959) as a subspecies of *Camarotoechia strugi* Nalivkin, 1941 based on some external differences observed within the Armenian material such as the finer ribs and a lower trapezoidal tongue. Note that Nalivkin's (1941) species was considered by Sokiran (2002) as a synonym of *R. livonicus* (von Buch, 1834). Based on the detailed study of material from Nakhichevan, Pakhnevich (in Alekseeva et al., 2018a) raised the subspecies *gnishikensis* to the species level assigning it at the same time to the genus *Ripidiorhynchus*, based on the general shape and outline, the well-developed sulcus and fold beginning at some distance from the beaks, the ventrally convergent dental plates as well as the presence of a low septum and a covered septalium.

Ripidiorhynchus djravankensis n. sp.

Plate 1.6–1.20; Figures 29–30; Table 2

Holotype.—An almost complete articulated specimen (IGSNASRAGM 3931/PS 3037; Pl. 1.16–3.20) from the layer Dj19/5 (Fig. 14); Djravank section (7 km southeast from Areni, Vayots Dzor Province, Central Armenia) (Fig. 1).

Diagnosis.—Shell medium-sized (up to 19.5 mm in width, 17.1 mm in length and 14.7 mm in thickness) (Table 2), sharply dorsibiconvex, wider than long, transversally ovate in outline; anterior margin emarginate; anterior commissure uniplicate; sulcus well-defined, deep, originating at midlength; fold high, wide, starting at some distance from the umbo; tongue high to very high, subtrapezoidal; flanks with 8–10 low to moderately high, angular ribs; 3–4 ribs in sulcus, 4–5 ribs on fold; dental plates short, convergent ventrally; teeth massive; dorsal median septum short; septalium narrow, covered anteriorly; hinge plates united.

Occurrence.—Sartenaer (2001) discussed and discarded several reports pointing out the presence of *Ripidiorhynchus* representatives in the lower Famennian of Afghanistan (Brice and Lang, 1968; Brice, 1971; Farsan, 1986) and New Mexico (Cooper and Dutro, 1982; Dutro, 1986). He explained that previous authors mistakenly attributed some species to this genus coming from sections where the Frasnian–Famennian boundary is poorly constrained and concluded that no evidence points the presence of *Ripidiorhynchus* in the Famennian. Moreover, Sartenaer (2001) rejected its presence in Iran (Gaetani, 1965) and Afghanistan (Farsan, 1986). Nevertheless, Sokiran (2006) revised a few *Ripidiorhynchus* species from the EEP including the type species *R. livonicus* from the uppermost part of the lower Frasnian (*Palmatolepis transitans* Zone of Ziegler and Sandberg, 1990) and two species from the lower Famennian interval (*P. crepida*–*P. rhomboidea* zones of Ziegler and Sandberg, 1990). She thus provided an accurate age asserting the presence of the genus in the lower

Famennian, at least in the EEP. The newly defined species *R. djravankensis* n. sp. hereby confirms that the genus *Ripidiorhynchus* crossed the Frasnian–Famennian boundary. This is also the first ever record of this genus in the lower Famennian of the northern margin of Gondwana. However, it is worth noting that the latter species appears to have a very restricted paleogeographic and stratigraphic distribution as among the three investigated contemporaneous sections, it has been reported only from the Djravank section and only within the Dj19/5 layer (Figs. 13.1, 14).

Description.—Shell medium-sized, wider than long, transversally ovate in outline, sharply dorsibiconvex; widest and highest at about midlength; anterior margin emarginate, anterior commissure strongly uniplicate and serrate.

Ventral valve regularly convex in both lateral and posterior profiles with flanks sloping gently towards lateral commissures; highest at about midlength or more posteriorly to it, then decreasing towards anterior margin; umbo inflated, relatively prominent, beak small, acute, suberect to erect; palintropes small, curved; no deltidial plates observed; sulcus well-defined by its bounding ribs, wide, deep to very deep, originating at midvalve, rapidly deepening anteriorly, flat-bottomed at front; tongue high to very high, subtrapezoidal in outline, with sharp margins, perpendicular to commissural plane or slightly bent dorsally.

Dorsal valve strongly inflated, strongly curved in posterior and lateral views with convex flanks sloping steeply towards lateral commissures; highest more anteriorly to midlength; fold high to very high, wide, well-defined, inconspicuously starting from the posterior half of the valve, flat- to slightly round-topped at front.

Ornamentation of sharp, subangular, low to moderately high ribs, originating at beaks, becoming fainter towards lateral cardinal extremities; ribs in sulcus and on fold slightly wider than those present on flanks; 3–4 ribs in sulcus, 4–5 ribs on fold, 8–10 ribs on flanks, occasionally one pair of faint ribs developed on the flanks of the fold and on the margins of the sulcus; interspaces as wide as ribs, growth lines numerous, irregularly spaced.

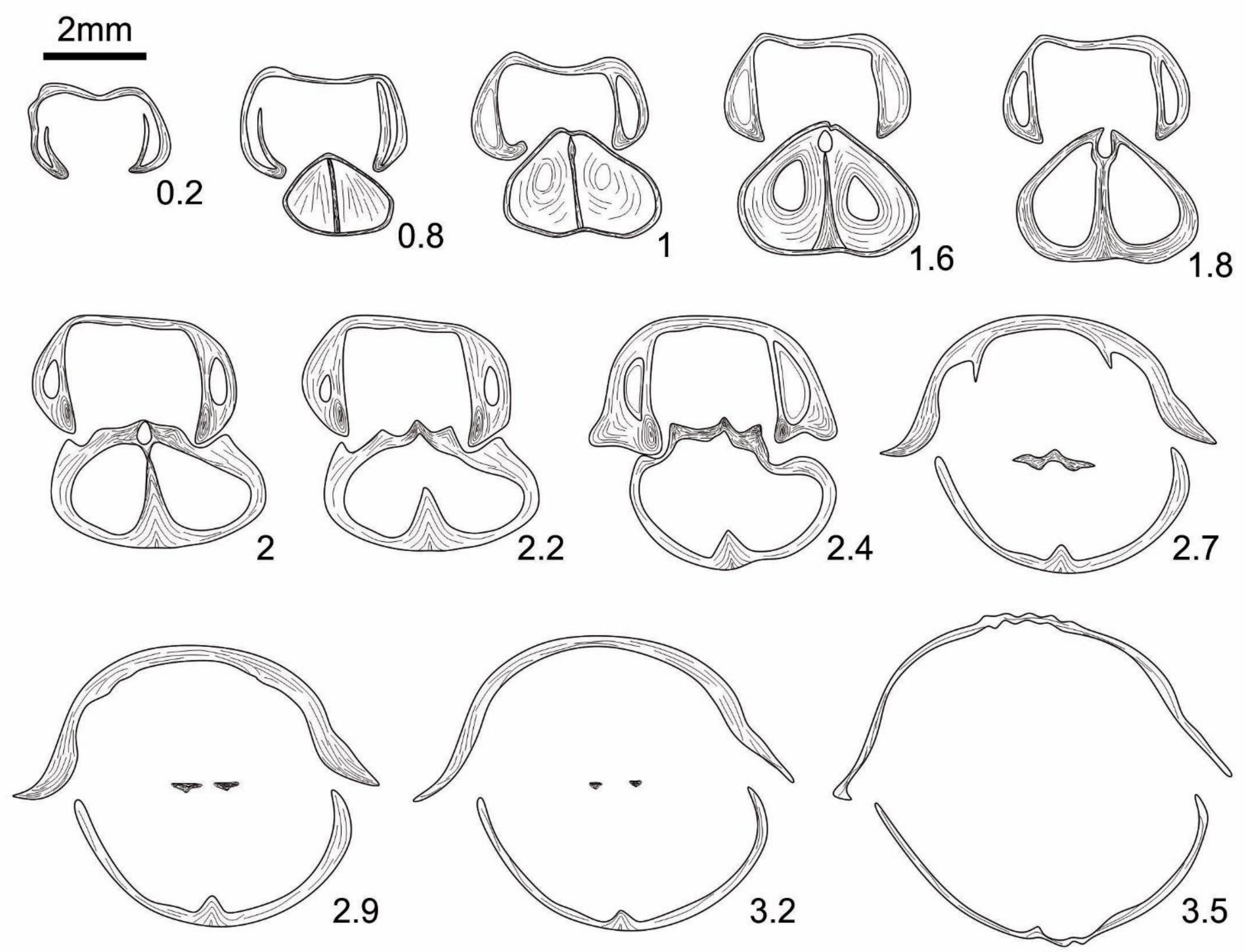


Figure 29. Transverse serial sections of *Ripidiorhynchus djravankensis* n. sp. (IGSNASRAGM 3928/PS 3034) from the lowest Famennian Noravank Regional Stage, Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo.

Ventral valve interior (Fig. 29) with stout, short intrasinal dental plates, slightly converging ventrally; teeth massive, subrectangular in outline; central apical cavity wide; lateral apical cavities moderately filled in by callus.

Dorsal valve interior (Fig. 29) with low, stout septum supporting a deep, Y-shaped, and anteriorly covered septalium; hinge plates united.

Etymology.—In reference to the type locality of the species (Djravank section) (Fig. 1).

Material examined.—Twenty-seven articulated specimens, seven ventral and six dorsal valves from the Djravank section.

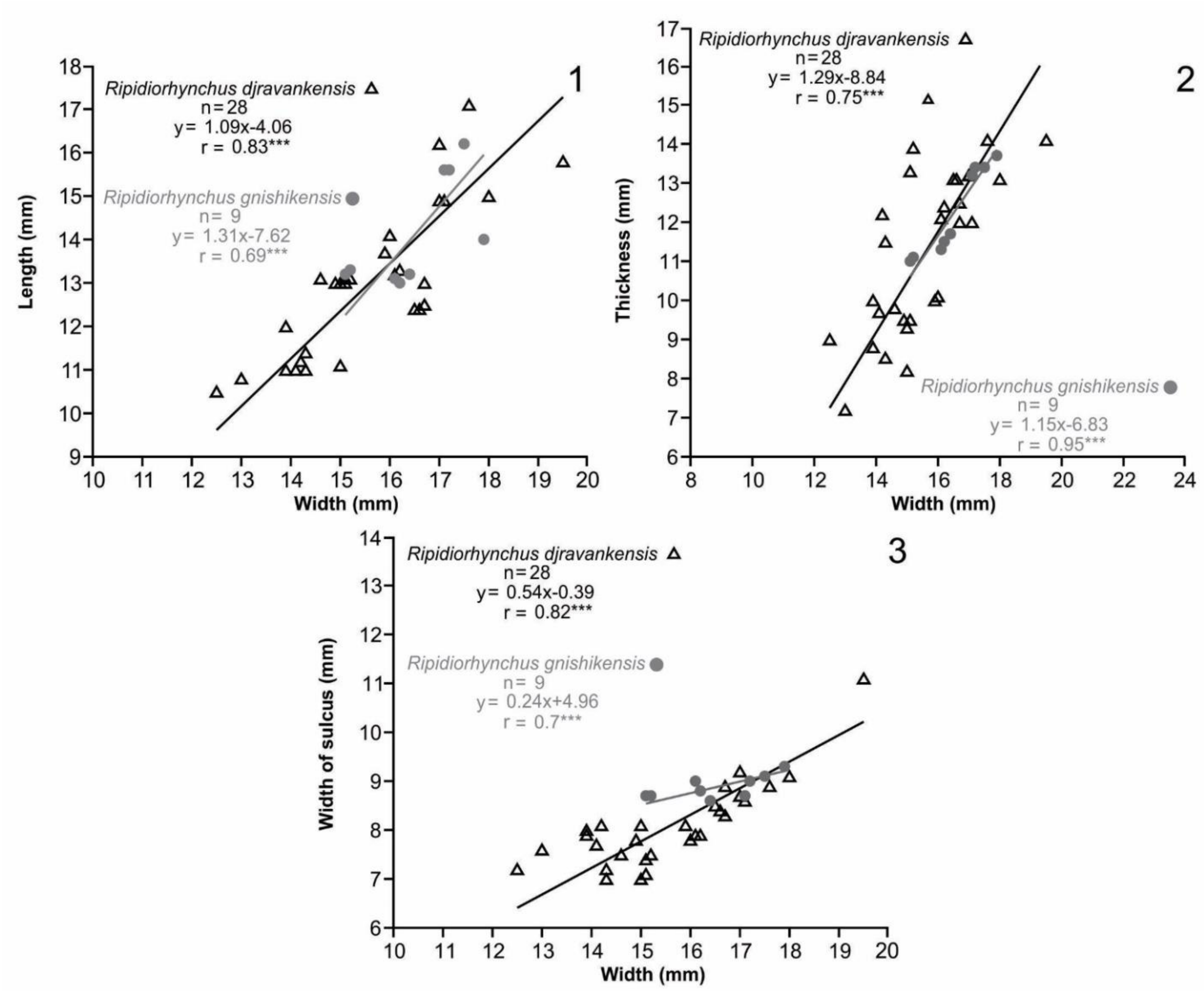


Figure 30. Scatter diagrams exhibiting the relation between shell width/ length (**1**), shell width/thickness (**2**), and shell width/width of sulcus (**3**) of *Ripidiorhynchus djravankensis* n. sp. and *R. gnishikensis* (Abrahamyan, 1959). Abbreviations: *n*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation.

Shell ontogeny.—The size distribution of *R. djravankensis* n. sp. during the growth, as represented by the scatter plots of the width/length, the width/thickness and the width/width of sulcus, shows a continuous and progressive growth with no distinct stages (Fig. 30). The relative proportions 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. 30). With an exception of the thickness, the correlation is positive with width varying proportionally with length and width of sulcus. The shell outline highly varies in its thickness, more often having a shell with thickness exceeding length; the fold height is also impermanent, shifting from high to very high and thus changing also the tongue height. To complete the scatter plots, the measurements (in mm) of numerous individuals of *R. djravankensis* n. sp. are represented in Table 2.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	29	29	29	29	29	29	29
Mean value	15.59	12.99	11.22	8.09	0.83	0.72	0.52
Standard deviation	1.5679	1.7159	2.0184	0.8526	0.0586	0.0931	0.0339
Standard error±	±0.2912	±0.3186	±0.3748	±0.1583	±0.0109	±0.0173	±0.0063
Min	12.5	10.5	7.2	7	0.74	0.55	0.47
Max	19.5	17.1	14.7	11.1	0.97	0.91	0.58

Table 2. Measurements in mm and ratios of *Ripidiorhynchus djravankensis* n. sp. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

Remarks.—The external and internal features of the newly defined species match well with the diagnosis of *Ripidiorhynchus* Sartenaer, 1966a.

R. djravankensis n. sp. differs from *R. livonicus* (Buch, 1834), which was revised by Sokiran (2006), from lower Frasnian Sargaevo Horizon of northwestern Russia (Sartenaer, 1966a), Latvia, and Lithuania, by its wider and deeper sulcus, its wider fold that is flat- to slightly round-topped at front, and fewer and coarser ribs. Internally, the new species differs by the development of relatively stout callosities in lateral apical cavities and by narrow septalium.

R. djravankensis n. sp. looks like the lower–middle Frasnian species *R. aldogus* (Nalivkin, 1941) as revised by Sokiran (2006), occurring within the Snetogorsk and Pskov beds of northwestern Russia, but the new species differs by having more developed sulcus and fold, a suberect to erect beak as well as a high tongue.

R. djravankensis n. sp. is close to two species recognized within the Zadonsk Horizon of central Russia, namely *R. cernosemicus* (Nalivkin, 1934) and *R. huotinus* (de Verneuil, 1845), but it differs from the former by its more globular shell outline, more convex lateral profile and having fewer ribs. *R. djravankensis* n. sp. is distinguished from the latter by its wider fold and sulcus, suberect to erect beak and having fewer ribs.

R. djravankensis n. sp. is easily distinguished from *R. griasicus* (Nalivkin, 1934) *sensu* Sokiran (2006) reported from the lower Famennian Elets Horizon (central Russia), by its more inflated shell, well-developed sulcus and fold as well as high tongue.

R. djravankensis n. sp. is differing from *R. chencinensis* Sokiran, 2006 reported from the uppermost Givetian of the Holy Cross Mountains (Poland), by its higher and wider tongue, by the presence of one pair of faint ribs developed on the flanks of the fold and on the margins of the sulcus, and the absence of a strong median rib in sulcus and of two opposed ribs on fold which is commonly observed in *R. chencinensis*.

R. djravankensis n. sp. is separable from *R. gnishikensis* (Abrahamyan, 1959), which was recently illustrated by Pakhnevich in Alekseeva et al. (2018a), by its larger and transversally ovate shell (see above).

Genus *Cyphoterorhynchus* Sartenaer, 1965

Type species.—*Uncinulus* (*Uncinulina*) *koraghensis* Reed, 1922.

Cyphoterorhynchus koraghensis koraghensis (Reed, 1922)

Plate 2.1–2.15; Figures 31–32; Table 3

1902 *Rhynchonella*, species; Hudleston, p. 14, pl. 3, fig. 10a–c.

1911 *Rhynchonella* (*Camarotoechia*) cf. *Omaliusi* Gosselet; Reed, p. 104, pl. 8, figs. 2, 2a.

1911 *Rhynchonella* (*Wilsonia*?) cf. *Dumonti* Gosselet; Reed, p. 40, pl. 7, figs. 10–22; pl. 8, figs. 1, 1a.

1922 *Uncinulus* (*Uncinulina*) *koraghensis* sp. nov.; Reed, p. 40, 120, 123–125, pl. 7, figs. 10–13.

1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *pentagonalis*; Reed, p. 42, 120, 123, 125, pl. 7, figs. 14–17.

1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *transiens*; Reed, p. 43, 120, 123, 125, pl. 7, figs. 18–20.

1922 *Uncinulus* (*Uncinulina*) *koraghensis* var. *ponderosa*; Reed, p. 44, 120, 123, 125, pl. 7, figs. 21–22a; pl. 8, figs. 1, 1a.

1952 *Uncinulus* (*Uncinulus*) *koraghensis* Reed; Arakelyan, p. 36.

1963 '*Uncinulus*' *koraghensis* var. *transiens* Reed; de Lapparent and Le Maître, p. 188.

1965 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922); Sartenaer, p. 51, pls. 4–5.

1966b *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922); Sartenaer, p. 28–29, 34–37.

1971 *Cyphoterorhynchus koraghensis* (Reed F. R. C., 1922); Brice, p. 47, 309–315, 318, 323, 336, pl. 3, figs. 1a–d, 6a–d; text-fig. 13A; table 5.

1975 *Cam.* [*Camarotoechia*] *karaghensis* [*sic*] *koraghensis* Reed; Arakelyan et al., p. 24.

2000 *Cyphoterorhynchus koraghensis* Reed, 1922; Rzhonsnitskaya and Mamedov, p. 330.

2000 *Cyphoterorhynchus koraghensis interpositus* Sartenaer; Jafarian, table 1, text-fig. 3, pl. 1, fig. 5a–c.

2002 *Cyphoterorhynchus koraghensis* (Reed, 1922); Savage, p. 1076, fig. 728, 1 a–n (copy of Sartenaer, 1965, pl. 4, fig. 4 a–b, d–e).

2010 *Cyphoterorhynchus koraghensis* Reed; Mirieva, p. 74, 75, table 1.

Lectotype.—Reed (1922) did not designate a holotype amongst the specimens he illustrated. Sartenaer (1965) designated the specimen figured by Reed (1922, pl. 7, fig. 10–10a) as the lectotype (see also Sartenaer, 1966b).

Occurrence.—In Armenia, recent samplings revealed the presence of this species only in the Frasnian sequences. It now appears obvious that the reports of this species by Arakelyan (1952) and Arakelyan et al. (1975) within the lower Famennian of the Gyumushlugh section have to be reinterpreted in the light of the current definition of the Frasnian–Famennian boundary although it is currently not located with precision in Armenia in the absence of the diagnostic conodonts. Reed's species was reported in the Frasnian of Nakhichevan by Rzhonsnitskaya and Mamedov (2000) and Mirieva (2010).

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

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

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

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

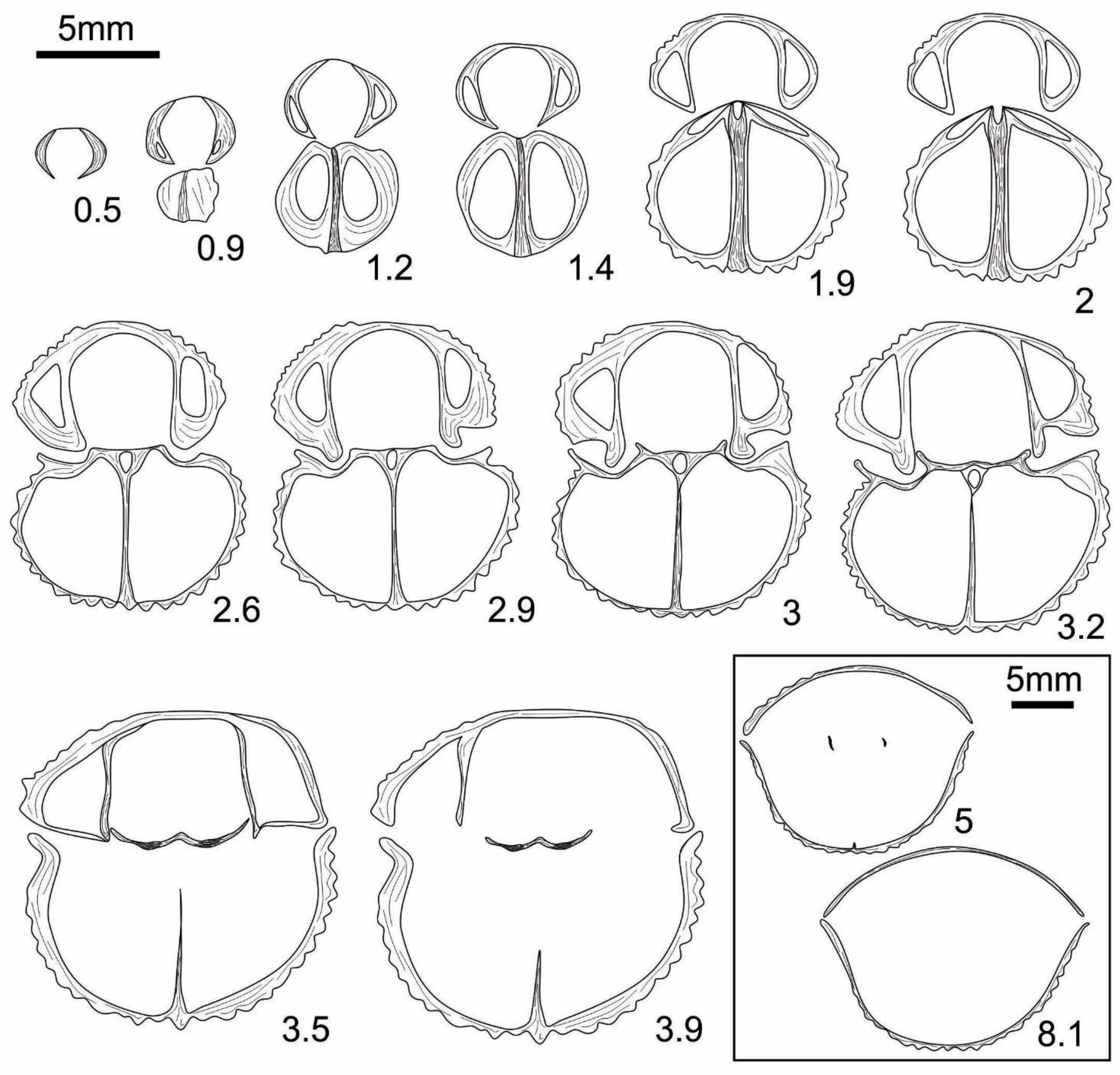


Figure 31. Transverse serial sections of *Cyphoterorhynchus koraghensis koraghensis* (Reed, 1922) (IGSNASRAGM 3932/PS 3038) from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo.

Ventral valve interior (Fig. 31) with short, stout and subparallel dental plates situated close to the walls; teeth massive, subrectangular in outline; central apical cavity wide; lateral apical cavities poorly infilled by callosity.

Dorsal valve interior (Fig. 31) with high and long septum; septalium V-shaped, not deep, relatively narrow and covered anteriorly; hinge plates united anterior of septalium; crural bases stout, diverging dorsally.

Material examined.—Twenty-nine articulated specimens and four ventral valves from the Ertych (18 articulated specimens and two ventral valves) and Djravank (eleven articulated specimens and two ventral valves) sections.

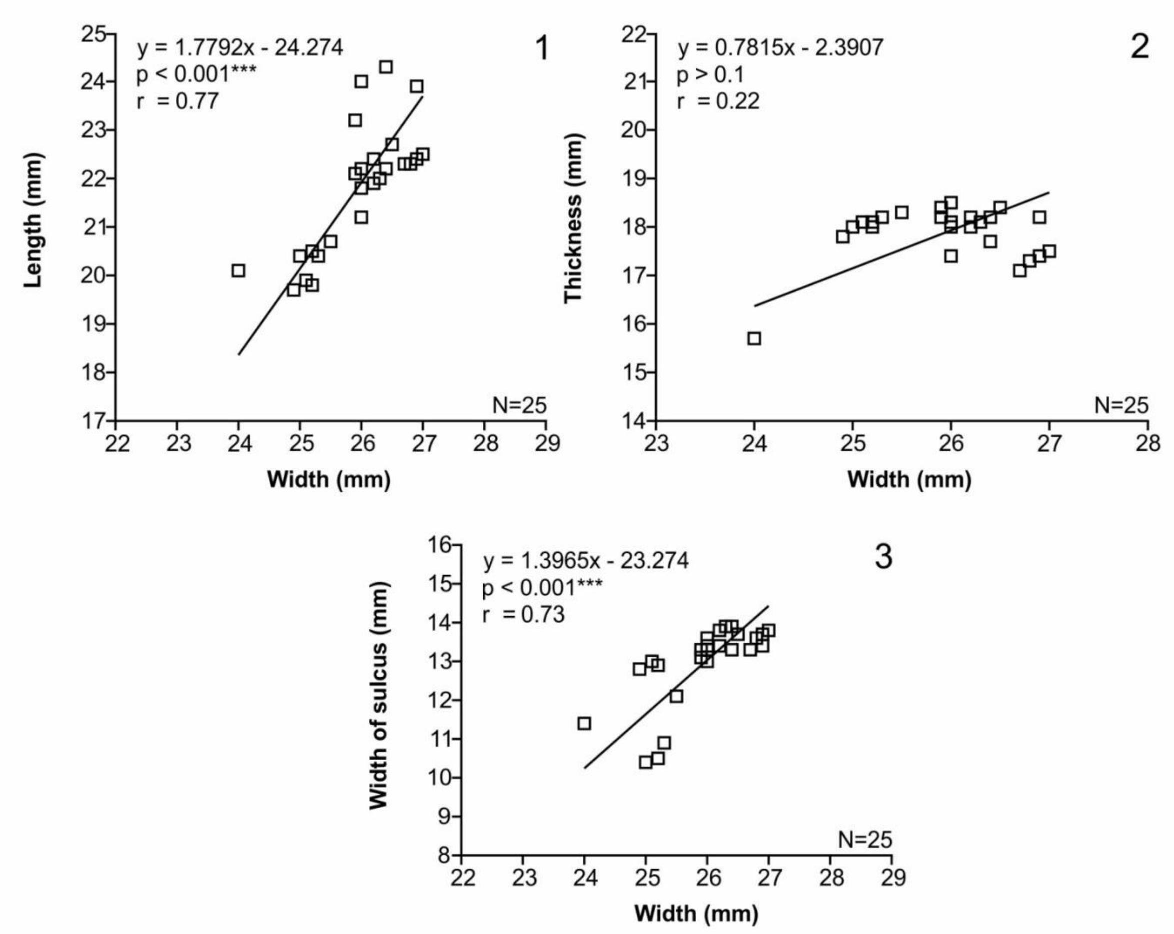


Figure 32. Scatter diagrams of *Cyphoterorhynchus koraghensis koraghensis* (Reed, 1922). 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. Abbreviations: *n*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

Shell ontogeny.—The size distributions of *C. k. koraghensis* during growth, as represented by the scatter plots of the width/length, the width/thickness and the width/width of sulcus, show a continuous and progressive growth with no distinct grouping (Fig. 32). The relative proportions of *C. k. koraghensis* represented by sufficient material remain constant (linear regression: y = ax+b; significant probability value: p < 0.01***) whatever the degree of development of individuals. Moreover, the correlation is positive with width varying proportionally with length, thickness and width of sulcus (Fig 32). To complete the scatter plots, the measurements (in mm) of numerous individuals of *C. k. koraghensis* are also presented in Table 3.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	25	25	25	25	25	25	25
Mean value	25.93	21.8	17.88	12.94	0.84	0.69	0.5
Standard deviation	0.7482	1.3312	0.5847	1.0448	0.0361	0.0266	0.0321
Standard error±	±0.1496	±0.2662	±0.1169	±0.209	±0.0072	±0.053	±0.0064
Min	24	19.7	15.7	10.4	0.79	0.63	0.42
Max	27	24.3	18.5	13.9	0.92	0.72	0.53

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

Remarks.—Both external and internal features of the Armenian material fit well with Reed (1922)'s description of *Cyphoterorhynchus koraghensis*, which is known from the middle–upper Frasnian strata of different parts of the Gondwanan terranes. More precisely, it was described in Chitral (northwestern Pakistan; Reed, 1922), Afghanistan (Brice, 1971), Iran (Sartenaer, 1966b) and probably Turkey (Gourvennec, 2006). However, it should be stressed that the teeth and dental sockets of Armenian material lack crenulation, contrary to what it is observed in specimens from Chitral. Gourvennec (2006) illustrated a single specimen from the Upper Devonian (probably from the lower Frasnian) of Eastern Taurus (Turkey) and identified it as *C. koraghensis*. Although he did not examine its internal structure, this assignment seems to be the most satisfactory as it does not differ superficially from Reed's material. Moreover, his assignment can be further supported by the resemblance of Devonian brachiopods of Turkey with those described in Afghanistan, Iran, Pakistan and the Lesser Caucasus.

According to Sartenaer (1966b), *C. k. koraghensis* differs from *C. k. interpositus* Sartenaer, 1966b, which is a transitional form between the nominal species and *C. arpaensis* (Abrahamyan, 1957), by its transversely ovate shell outline, coarser and fewer ribs. It is also worth emphasizing that Pakhnevich in Alekseeva et al. (2018a) considered the latter subspecies to be synonym of *C. arpaensis*, since he observed in Abrahamyan's species the main characteristics (e.g. number of costae, shell width), which were supposed to distinguish the subspecies.

C. k. koraghensis is distinguished externally from *C. arpaensis* (Abrahamyan, 1957) by its suptrapezoidal tongue, serrate anterior and lateral commissures as well as coarser and fewer ribs. The latter is one of the most biostratigraphically valuable species in the Lesser Caucasus and used for the definition of a Frasnian brachiopod zone, namely the *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000). However, our recent sampling did not reveal the presence of this species in the Frasnian of our studied sections, which possibly means that in Armenia it occurs in older strata. Although Abrahamyan (1957) did not designate a type specimen among the two she illustrated, Pakhnevich in Alekseeva et al. (2018a) considered the only photographed specimen (Abrahamyan, 1957: pl. 5, fig. 6) as the holotype.

According to the Article 73 of the International Commission on Zoological Nomenclature (1999), the holotype of a new species can only be fixed in the original publication and by the original author, and thus Abrahamyan's specimen selected by Pakhnevich cannot be considered as the valid holotype. Moreover, the specimen chosen by Pakhnevich from Abrahamyan (1957)'s publication is lost. Therefore, a lectotype must be designated among the specimens of Abrahamyan (1957)'s collection, which is currently stored at the IGSNASRAGM.

Contrary to Pakhnevich (in Alekseeva et al., 2018: p. 910)'s statement, *Cyphoterorhynchus arpaensis* does not occur in the Frasnian of Belgium, where the genus has never been recovered. In addition, it is worth stressing that the genus is also known from Libya (Mergl and Massa, 2000) and Spain (Pardo and García Alcalde, 1984), thus only in Gondwanan terranes.

Genus *Gesoriacorostrum* Sartenaer, 2003

Gesoriacorostrum? sp.

See Serobyan et al. (2021), p. 536, Figs. 8–9.

Superfamily Rhynchoporoidea Muir-Wood, 1955

Family Rhynchoporidae Muir-Wood, 1955

Subfamily Greirinae Erlanger, 1993

Genus *Greira* Erlanger, 1993

Greira transcaucasica Erlanger, 1993

See Serobyan et al. (2021), p. 538, Figs. 10–11.

Genus *Sharovaella* Pakhnevich, 2012

Sharovaella? sp.

See Serobyan et al. (2021), p. 542, Figs. 12–13.

Order Atrypida Rzhonsnitskaya, 1960

Suborder Atrypidina Moore, 1952

Superfamily Atrypoidea Gill, 1871

Family Atrypidae Gill, 1871

Subfamily Atrypinae Gill, 1871

Genus *Atryparia* Copper, 1966

Subgenus *Atryparia* (*Costatrypa*) Copper, 1973

Type species.—*Atrypa varicostata* Stainbrook, 1945.

Atryparia (*Costatrypa*) *ertichensis* (Abrahamyan, 1959)

Plate 3.1–3.7

1959 *Atrypa tubaecostata* Paeck. var. *ertichensis* n. var. Abrahamyan, p. 7, pl. 1, figs. 1–3.

1974 *Spinatrypa ertichensis*; Abrahamyan, p. 57, pl. 17, fig. 4.

1985 *Spinatrypina ertichensis*; Mamedov and Rzhonsnitskaya, p. 148.

1997 *Atrypa* (*Planatrypa*) *ertichensis*; Komarov, p. 87, pl. 1, fig. 5.

2018a *Atrypa* (*Planatrypa*) *ertichensis*; Grechishnikova in Alekseeva et al., p. 24, 26.

Holotype.—An articulated specimen (270/3–54; the holotype is the 270th collected specimen by Abrahamyan in 1954, from the 3th layer of Ertych section) from the Frasnian of Ertych section, Armenia (Abrahamyan, 1959; pl. 1, fig. 1a–d). It is currently housed at IGSNASRAGM and is catalogued under collection no. 3/1. In fact, in addition to the holotype, there is another specimen of the type of material that was marked with the same number as the holotype, but was not illustrated by Abrahamyan (1959). Therefore, it was decided to illustrate the second specimen to demonstrate its original mark and the difference between it and the real holotype.

Occurrence.—Although Abrahamyan (1959) initially described this species from the Frasnian strata of Armenian sections, Komarov (1997) specified that it mainly occurs in the upper Givetian *Adolfia zickzack* Zone of Rzhonsnitskaya and Mamedov (2000) and occasionally in the lower part of the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone. However, as it was turned out later *Adolfia zickzack* Zone of Rzhonsnitskaya and Mamedov (2000) is early Frasnian in age based on conodonts and rugoe corals (see Grechishnikova in Alekseeva et al. (2018a); p. 24–25). Thus, it appears that *Atryparia* (*Costatrypa*) *ertichensis* (Abrahamyan, 1959) occurs in the lower Frasnian of the Lesser Caucasus.

Description.—Shell medium-sized (up to 30.1 mm in width, 29.7 mm in length and 16.9 mm in thickness), strongly dorsibiconex, shield-shaped to semi-elliptic in outline; hinge line shorter than the maximum width; the maximum height and width of the shell in the posterior third of the shell; anterior margin rounded to straight; anterior commissure undulose to slightly uniplicate.

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

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

Ornamentation of tubular-imbricate, coarse ribs originating at beaks and becoming fainter towards lateral cardinal extremities; ribs increasing principally by bifurcation on the ventral valve and by intercalation on the dorsal valve; 65–72 ribs on the entire shell; generally 5–6 ribs per 5 mm at anterior margin; growth lamellae more crowded near the anterior and lateral margins, extending into frills (Pl. 3.1).

Internal morphology not observed.

Material.—Three articulated specimens of Abrahamyan's collection and two newly recovered specimens from the Frasnian of Ertych section.

Remarks.—Initially described by Abrahamyan (1959), this species was mistakenly considered as a variety of *Atrypa tubaecostata* Paeckelmann, 1931, based on some external differences observed in the Armenian material such as larger size, inflated dorsal valve and the presence of sulcus. However, in 1974, Abrahamyan raised it at the species level, but its affinities at the genus level still remain unclear. Mamedov and Rzhonsnitskaya (1985) attributed the latter to the genus *Spinatrypina*, but again without study of its main fundamental features such as the ornament and internal morphology. Afterwards, Komarov (1997) re-assigned it to *Atrypa* (*Planatrypa*) owing to the general shell shape, external ornamentation and absence of dental plates from the ventral interior. However, the frilly ornamentation described on Abrahamyan's species (see Pl. 3.6), argues its assignment to the Upper Devonian *Atryparia* (*Costatrypa*) Copper, 1973 rather than Middle Devonian *Atrypa* (*Planatrypa*) Struve, 1966. Additionally, it is worth noting that the examination of some of the type specimens of Abrahamyan's species established that the specimens described in Nakhichevan by Komarov (1997) are conspecific with the ones of Armenian sections.

Subfamily Spinatrypinae Copper, 1978

Genus *Spinatrypa* Stainbrook, 1951

Subgenus *Spinatrypa* (*Spinatrypa*) Stainbrook, 1951

Type species.—*Atrypa hystrix* var. *occidentalis* Hall, 1858.

Spinatrypa (*Spinatrypa*) sp.

Plate 3.8–3.13

Occurrence.—The specimens were collected from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) of Ertych section (Fig. 1).

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

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

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

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

Internal morphology unknown.

Material.—Two partly exfoliated articulated specimens.

Remarks.—*Spinatrypa* (*Spinatrypa*) Stainbrook, 1951 is mainly known from the upper Givetian–upper Frasnian shallow water carbonate/siliciclastic deposits of Northern America and Weastern Europe. Our material is closely related to the subgenus *Spinatrypa* (*Spinatrypa*) based on its size, semi-elliptic outline, strongly dorsibiconvex profile, slightly uniplicate anterior commissure, subtrapezoidal tongue, coarse and undulose ornamentation. However, it is doubtfully assigned to this subgenus as the insufficiency of our material precludes the possibility to examine its internal morphology. Complementary material is needed to reach a more confident identification. Additionally, it is also pertinent to stress that this is the first documentation of this subgenus in the Frasnian of the Lesser Caucasus.

Subfamily Variatrypinae Copper, 1978

Genus *Desquamatia* Alekseeva, 1960

Subgenus *Desquamatia* (*Seratrypa*) Copper, 1967

Type species.—*Dequamatia* (*Seratrypa*) *pectinata* Copper, 1967.

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

Plate 4; Figure 33–34; Table 4

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

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

Holotype.—The holotype (VI-223/3a; Komarov, 1992: pl. 1, fig. 3) is from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov

(2000) of the Danzik section, left bank of the Arpa River, Nakhichevan. It is currently housed at the VSGM.

Occurrence.—This species is only found in the SAB. More particularly, according to Komarov (1992, 1997), it is restricted to the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Nakhichevan. Our examined material comes from the same Frasnian strata of the Ertych, Djravank and Noravank sections (Fig. 1).

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

Ventral valve inflated posteriorly with flanks sloping moderately towards the lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards the anterior margin; umbo inflated, prominent; beak acute, erect; interarea very small, concave, anacline to hypercline; foramen and deltidial plates unobserved due to deficient preservation; sulcus very shallow and perceptible only at front, flat- to slightly round-bottomed at front; tongue low, wider than high, semi-rounded to semi-elliptic, not perpendicular to commissural plane.

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

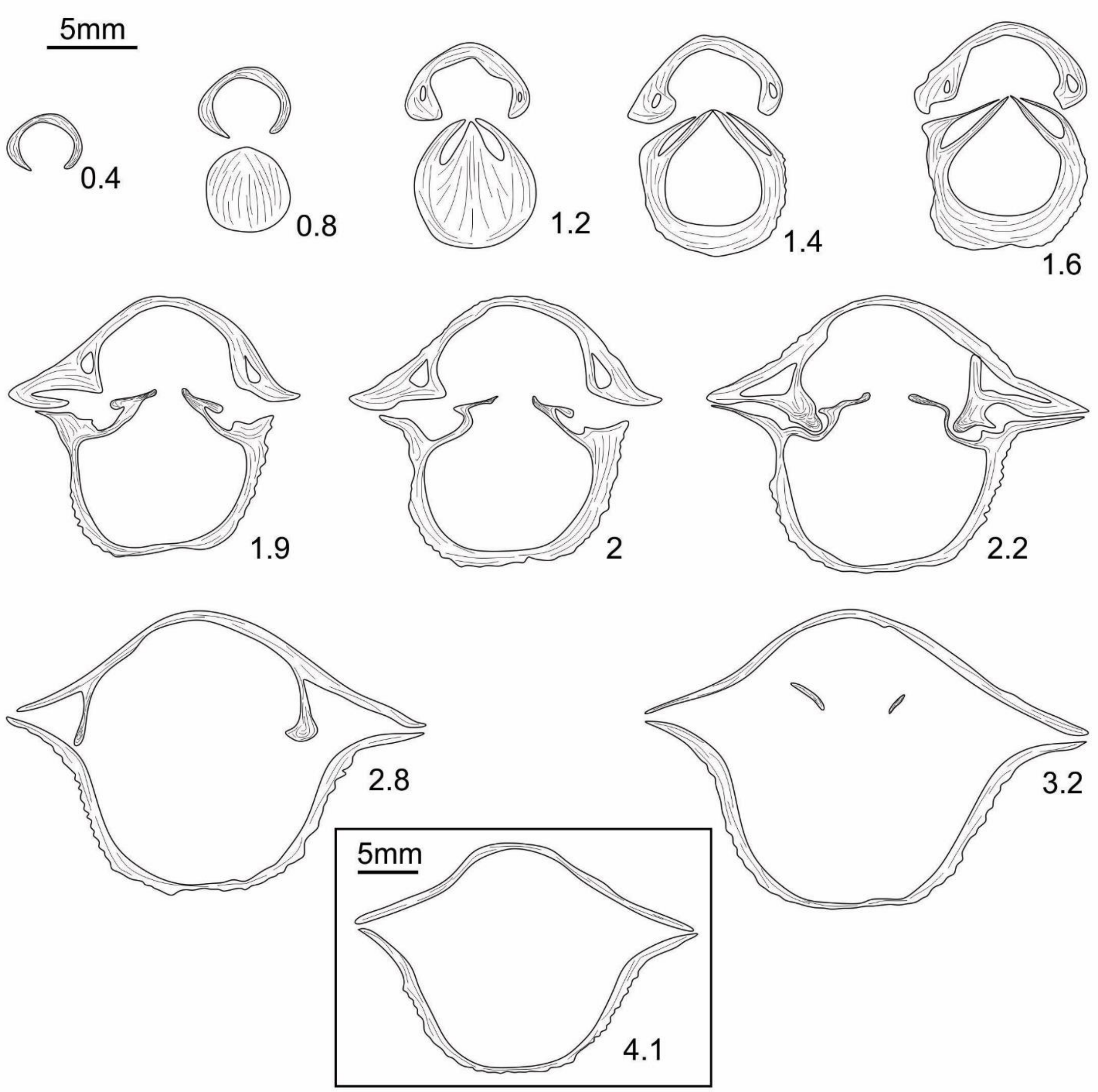


Figure 33. Transverse serial sections of *Desquamatia (Seratrypa) abramianae* Komarov, 1992 (IGSNASRAGM 3938/PS 3044), from the Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo. Scale bars: 5 mm.

Ornamentation of fine, tubular ribs increasing by bifurcation and intercalation on both valves; generally 125–140 ribs on the entire shell, 5–6 ribs per 5 mm at anterior margin; growth lamellae more crowded near the lateral and anterior margins.

Ventral valve interior (Fig. 33) with stout but short dental plates; dental nuclei relatively large, well-marked; teeth massive, simple; central apical cavity not filled in by callosities.

Dorsal valve interior (Fig. 33) with a weak cardinal process in form of a pad, enclosed within the cardinal pit; dental sockets not deep, divided by a median crest; crural bases stout; crura ventrally directed; jugal processes and spiral cones not observed.

Material.—Twenty-three articulated specimens and four ventral valves: 12 articulated specimens and two ventral valves come from the Ertych section, 11 articulated specimens from the Djravank section, and two ventral valves from the Noravank section.

Shell ontogeny.—Juveniles display a thinner shell with rectimarginate anterior commissure and semi-elliptic as well as very low tongue. Although not developed in juveniles, a sulcus occurs in older shells. Beak inclination angle does not change with age because juveniles also have an erect beak. The size distributions of *Desquamatia* (*Seratrypa*) *abramianae* during growth, as represented by the scatter plots of the widht/length, the width/thickness and the width/width of sulcus, show a continuous and progressive growth with no distinct grouping (Fig. 34). The relative proportions of *D.* (*S.*) *abramianae* represented by sufficient material remain constant (linear regression: $y = ax+b$; significant probability value: $p < 0.001$*** whatever the degree of development of individuals (Fig. 34). Moreover, the correlation is positive with width varying proportionally with length, thickness and width of sulcus. To complete the scatter plots, the measurements (in mm) of numerous individuals of *D.* (*S.*) *abramianae* are also presented in Table 4.

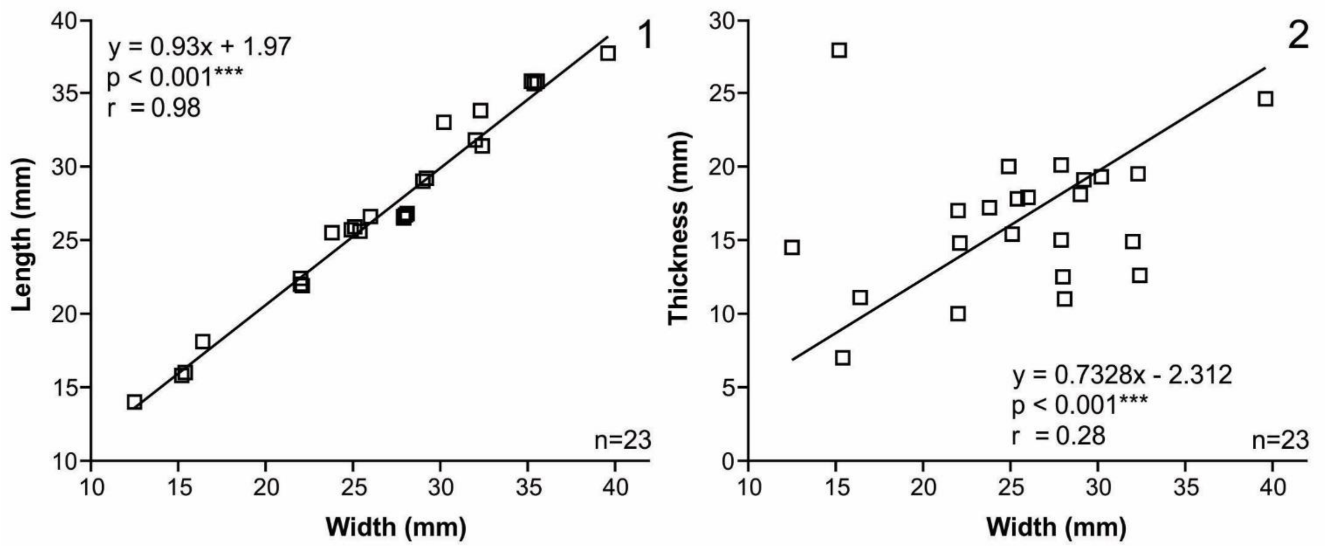


Figure 34. Scatter diagrams of *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992. 1, Relation between shell width and length. 2, Relation between shell width and thickness. Abbreviations: *N*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

	W	L	T	L/W	T/W
Number of individuals	23	23	23	23	23
Mean value	25.5	25.7	16.4	1.01	0.64
Standard deviation	6.42	5.9774	4.706	0.05	0.0756
Standard error±	±1.3388	±1.2464	±0.981	±0.0104	±0.0158
Min	12.5	14	7	0.95	0.52
Max	39.6	37.7	27.9	1.12	0.76

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

Remarks.—Although Komarov (1992, 1997) examined a huge collection of specimens identified as *Desquamatia* (*Seratrypa*) *abramianae*, he illustrated only a few partly exfoliated specimens, which were primarily devoid of most fundamental features such as ornamentation. Moreover, it is pertinent to highlight here that Komarov represented only a few serial sections displaying the ventral interior, whereas the dorsal one remains unknown. Therefore, we herein represent the close-up of its ornamentation, the internal morphology of both valves in details and different measurements as well as ratios in order to permit to perform statistics to document the intraspecific variation of this species. Additionally, it is worth noting that our material appears to be conspecific with the specimens illustrated by Komarov (1992, 1997) from the Frasnian strata of Nakhichevan.

Order Athyrida Boucot, Johnson, and Staton, 1964

Suborder Athyridina Boucot, Johnson, and Staton, 1964

Superfamily Athyroidea Davidson, 1881

Family Athyridae Davidson, 1881

Subfamily Cleiothyridininae Alvarez, Rong, and Boucot, 1998

Genus *Crinisarina* Cooper and Dutro, 1982

Crinisarina pseudoglobularis Serobyan et al., 2021

See Serobyan et al. (2021), p. 543, Figs. 14–15.

Order Spiriferida Waagen, 1883

Suborder Spiriferidina Waagen, 1883

Superfamily Cyrtospiriferoidea Termier and Termier, 1949

Family Cyrtospiriferidae Termier and Termier, 1949

Subfamily Cyrtospiriferinae Termier and Termier, 1949

Cyrtospiriferinae gen. et sp. 1

Plate 5.1–5.6

Occurrence—The single specimen examined here is recovered from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in the Ertych section.

Description.—Shell medium-sized (up to 26.9 mm in width, 21.7 mm in length and 16.9 mm in thickness), wider than long, ventribiconvex, rounded transverse in outline; hinge line narrower than widest; highest in the posterior third of the valve; cardinal extremities obtuse or slightly mucronate; anterior margin nearly straight; anterior commissure slightly uniplicate.

Ventral valve strongly inflated, with convex flanks sloping steeply towards lateral commissures; umbo inflated, prominent; beak erect, acute; interarea apsacline, triangular, low to moderately high, well-defined, delthyrium unobserved; sulcus very narrow, shallow, originating from beak, poorly delimited, flat- to slightly round-bottomed at front; tongue very low, semi-elliptic in outline.

Dorsal valve inflated, semi-circular to semi-elliptic in outline, with flanks sloping gently to moderately towards lateral commissure; highest in the posterior third of the valve, then decreasing gradually towards anterior margin; umbo prominent, protruding beyond the posterior margin with an acute beak, interarea linear, orthocline; fold unobserved due to poorly preservation state.

Ornament of low, flattened ribs that are poorly preserved.

Internal morphology unknown.

Material examined.—One single exfoliated articulated specimen.

Remarks.— This very restricted material is attributed to the Family Cyrtospiriferidae as defined by Johnson (2006) because of its inflated shell and the development of ribs in the sulcus and on fold. It is further assigned to the Subfamily Cyrtospiriferinae based on its wide hinge line and rounded transverse outline. However, the lack of knowledge about the internal features and the micro-ornament of this specimen precludes a generic assignment. Cyrtospiriferinae gen. et sp. 1 differs from Cyrtospiriferinae gen. et sp. 2 (Pl. 5.7–5.9) by its more rounded shell, inflated ventral valve, nearly straight anterior margin as well as narrow and shallow sulcus.

Cyrtospiriferinae gen. et sp. 2

Plate 5.7–5.9

Occurrence.—The specimens were collected from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) of the Ertych section (Fig. 1).

Material.—Two partly exfoliated ventral valves.

Remarks.—These poorly preserved ventral valves (up to 32 mm in width) are inflated and characterized by a transversely oval outline, with a deep sulcus originating from the beak. The ornamentation consists of simple, low ribs which are slightly wider than those present on flanks (Pl. 11.9). Additional material is required to reach a better identification.

Genus *Cyrtospirifer* Nalivkin in Fredericks, 1924

Type species.—*Spirifer verneuili* Murchison, 1840.

Remarks.—Abrahamyan (1957: pl. 9, figs. 2–3) illustrated some specimens identified as *Cyrtospirifer verneuili* (Murchison, 1840) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Central Armenia and indicated that in this country, this species occurs in the Frasnian–uppermost Famennian interval. Although Abrahamyan (1957) didn't illustrate the internal morphology and type of micro-ornament of her material, this assigment seems to be the most satisfactory as the specimens she illustrated are closely related to the type material described from Ferques (France). Later, Abrahamyan (1974) illustrated a single specimen from the upper Famennian of Armenia and assigned it to *C. verneuili*. However, it is evident that this specimen does not share affinities with Murchison's species as it displays more rounded outline as well as small and mucronate cardinal extremities, which is not the case of *C. verneuili*. It is judicious to remind here that the type material of Murchison's species is described from the Frasnian strata of Ferques. Therefore, the occurrence of *C. verneuili* in the upper Famennian of Armenia must be excluded and Abrahamyan (1974)'s specimen should be re-investigated. It is also noteworthy that recent sampling did not reveal the presence of this species in the three sections studied.

Cyrtospirifer? sp. 1

Plate 5.10–5.11

Occurrence.—The specimens were collected from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) of the Ertych section (Fig. 1).

Material.—Two partly exfoliated articulated specimens.

Remarks.— This very restricted material is attributed to the Family Cyrtospiriferidae as defined by Johnson (2006) because of its inflated shell and the development of ribs in the sulcus and on fold. It is further assigned to the Subfamily Cyrtospiriferinae based on its wide hinge line and rounded transverse outline. However, the lack of knowledge about the internal features and the micro-ornament of this specimen precludes a generic assignment.

Cyrtospirifer? sp. 2

Plate 5.12–5.16; Figure 35

Occurrence— The specimens are recovered from the lower Famennian *Cyrtospirifer orbelianus* brachiopod Zone of Abrahamyan (1957), which corresponds to the *Cyrtiopsis orbelianus*–*Cyrtiopsis armenicus* brachiopod Zone of Rzhonsnitskaya and Mamedov (2000).

Description.—Shell medium-sized (attaining 34 mm in width, 17.9 mm in length and 20.1 mm in thickness), wider than long, markedly ventribiconvex, rounded subtrapezoidal in outline; widest at hinge line; highest close the hinge line; cardinal extremities probably acute (broken); anterior margin nealy straigth; anterior commissure uniplicate.

Ventral valve highly inflated, with convex flanks sloping steeply towards lateral commissures; highest near the hinge line, then decreasing gradually towards anterior margin; umbo inflated, prominent; beak small, acute, erect; interarea very high, well-defined, catacline, triangular, generally slightly concave; delthyrium wide, almost completely covered by a pseudodeltidium that is poorly preserved; sulcus wide, relatively deep, originating from beak, round-bottomed at front; tongue not high, relatively wide, not perpendicular to commissural plane, subcircular to subogival in outline.

Dorsal valve moderately inflated with flanks sloping gently towards lateral commissures; highest in the posterior third of the valve, then progressively declining towards the anterior margin; interarea nearly flat, linear, orthocline; fold wide, well-delimited, moderately high, starting from beak and widening anteriorly, round-topped at front.

Up to 22 simple, low ribs on flanks with top rounded; in sulcus and on fold, at least 10 ribs (poorly preserved) increasing by bifurcations and narrower than those on flanks; interspaces narrower than ribs; micro-ornament is not preserved.

Ventral interior (Fig. 35) with relatively stout dental plates, intrasinal or subsinal posteriorly but extrasinal more anteriorly; delthyrial plate well-developed, situated close to the delthyrial thickening formed by accretion of strong apical callosities; lateral apical cavities moderately infilled.

Dorsal valve interior (Fig. 35) with unsupported ctenophoridium consisting of relatively short lamellae; hinge plates divided; crural bases dorsally convergent; spiralia unknown.

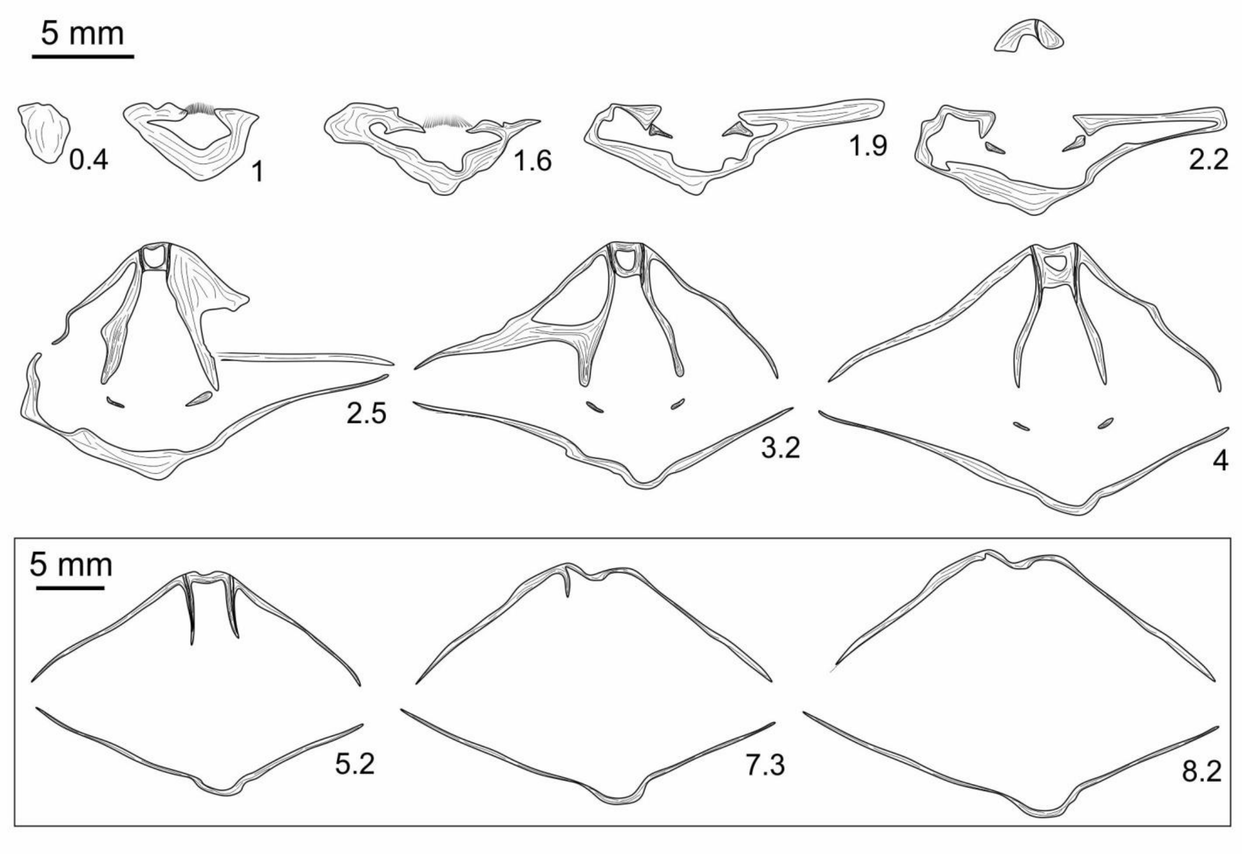


Figure 35 . Transverse serial sections of *Cyrtospirifer*? sp. 2 (IGSNASRAGM 3945/PS 3051) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Armenia, Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo.

Material.—Two articulated specimens from the Djravank section.

Remarks.—Our material is closely related to the genus *Cyrtospirifer* based on its rounded subtrapezoidal outline, widest at hinge line, ventribiconvex profile, well-developed fold and sulcus, the type of ornamentation (low, simple ribs on flanks and fainter as well as bifurcating ribs in sulcus and on fold) and the presence of a well-developed delthyrium. However, it is doubtfully assigned to this genus as the orientation of its dental plates (converging ventrally), the development of delthyrium near the umbonal region and the presence of an apical callosity in the ventral interior are in contradiction with the diagnosis of the genus. Although its external morphology resembles *Cyrtospirifer*? sp. 1 in terms of general shape and outline, this very restricted material is separated as the internal structure of *Cyrtospirifer*? sp. 1 is unknown and it comes from the Frasnian strata. Additionally, it is worth mentioning that *Cyrtospirifer*? sp. 2 is much smaller than *Cyrtospirifer*? sp. 1 and has fewer ribs. Additional material is needed to reach a more confident identification.

Cyrtospirifer sp. 1

Plate 5.17–5.21; Figure 36

Occurrence.—The specimens were collected from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) of the Djravank section (Fig. 1).

Description.—Shell medium-sized (up to 27 mm in width, 20.6 mm in length and 17.6 mm in thickness), wider than long, ventribiconvex, subtrapezoidal in outline, highest at about midlength; anterior margin straight; anterior commissure uniplicate.

Ventral valve strongly inflated, with convex flanks sloping steeply to moderately towards lateral commissures; highest at about midlength or slightly posteriorly, then decreasing progressively towards anterior margin; umbo inflated, prominent; beak erect; interarea apsacline, strongly concave, low; delthyrium unobserved (concealed by sediment); sulcus narrow, shallow to relatively deep, originating from beak, flat-bottomed at front, well-defined by bounding ribs; tongue low, subtrapezoidal in outline, perpendicular to commissural plane or slightly bent dorsally.

Dorsal valve slightly inflated with flanks sloping gently towards lateral commissures, subquadrangular to subtrapezoidal in outline; highest at midlength, then decreasing gradually towards anterior margin; interarea linear, orthocline; fold low, well-delimited, inconspicuously originating from beak, round to flat-topped at front.

Ornamentation of up to 16 rounded (5 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 4–5 ribs, slightly narrower than those present on flanks; ribs slightly wider than interspaces on flanks; micro-ornament poorly preserved, only a few capillae observed in interspaces of the ventral valve.

Ventral valve interior (Fig. 36) with stout, long, extrasinal and markedly divergent dental plates, converging dorsally in umbonal region (as seen in transverse section); delthyrial plate short; central apical cavity large, poorly filled in by callus; lateral apical cavities slightly filled by callus; teeth massive, subrectangular in outline.

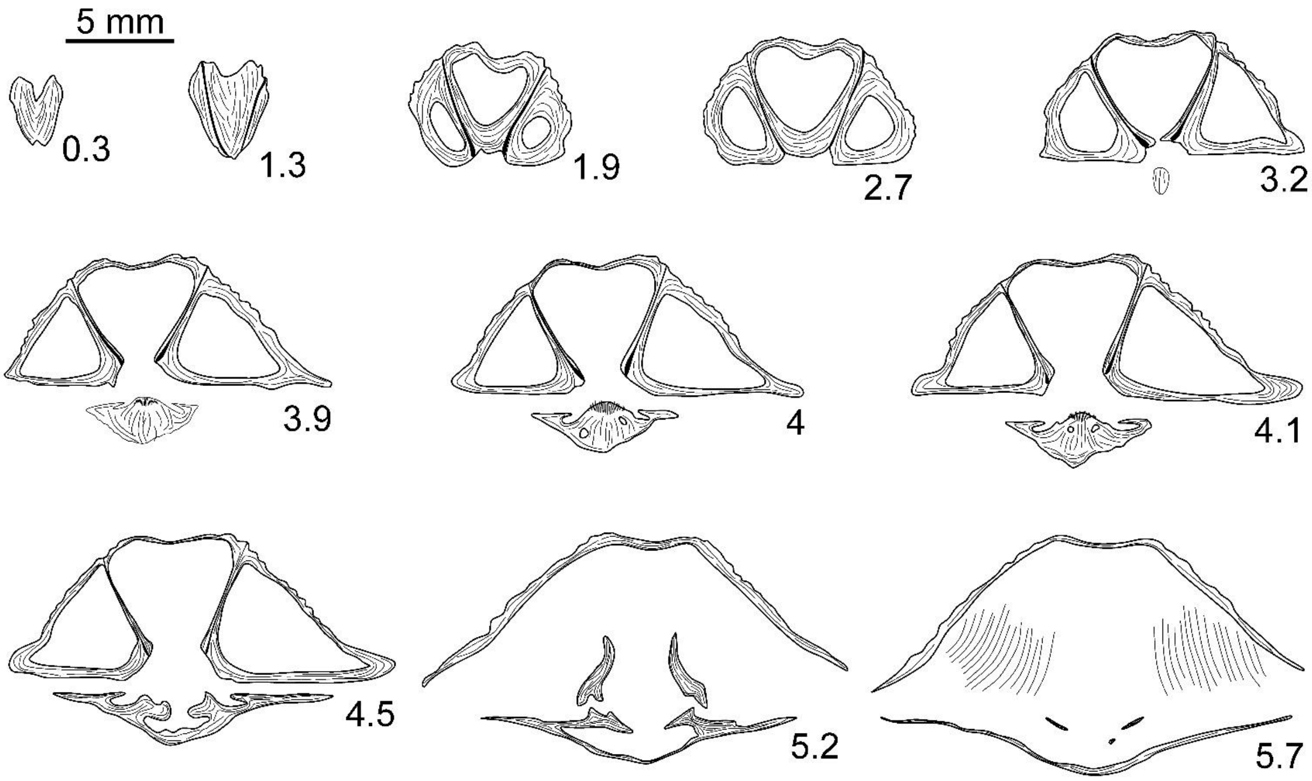


Figure 36. Transverse serial sections of *Cyrtospirifer* sp. indet. 1 (IGSNASRAGM 3947/PS 3053) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Armenia, Ertych section. Numbers refer to distances in mm from the tip of the ventral umbo.

Dorsal valve interior (Fig. 36) with supported ctenophoridium that is composed of up to 19 well-developed, relatively long lamellae; hinge plate divided; crural bases stout; spiralia oriented posterolaterally with at least 15 whorls per spiral cone.

Material.—Two partly exfoliated articulated specimens.

Remarks.—The external and internal features observed (e.g., ventribiconvex profile, subtrapezoidal outline, concave and apsacline ventral interarea, well-developed fold and sulcus, long and extrasinal dental plates, the presence of delthyrial plate, supported ctenophoridium) in the two studied specimens indicate affinities to the genus *Cyrtospirifer* Nalivkin in Fredericks, 1924. However, further specimens are needed to reach a more confident identification at the species level.

Cyrtospirifer pseudoasiaticus n. sp.

Plate 6; Figures 37–38; Table 5

Holotype.—An almost complete articulated specimen (IGSNASRAGM 3952/PS 3058; Pl. 6.11–6.16) from the lower Famennian *orbelianus* Zone of Abrahamyan (1957), which is correlated with the Ertych Regional Stage (Fig. 3); Ertych section (6 km southeast from Areni, Vayots Dzor Province, Central Armenia) (Fig. 1).

Diagnosis.—Shell medium-sized (up to 30 mm in width, 21.5 mm in length and 21.2 mm in thickness) (Table 5), wider than long, ventribiconvex (rarely equibiconvex), rounded transverse in outline with obtuse cardinal extremities; hinge line narrower than widest, anterior margin emarginate; anterior commissure uniplicate; fold and sulcus relatively wide; tongue high, subogival to subcircular in outline; micro-ornament of closely spaced capillae occurring both on ribs and in interspaces and numerous pustules developed on capillae; dental plates divergent; delthyrial plate well-developed; teeth stout; ctenophoridium unsupported; dental sockets shallow; crural spiralia oriented posterolaterally.

Occurrence.—This species is found only in Armenia. More precisely it is described from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957), which is correlated with the Ertych Regional Stage of Arakelyan (1964) (Fig. 2).

Description.—Shell medium-sized, wider than long, ventribiconvex (rarely equibiconvex), rounded transverse in outline with obtuse cardinal extremities; hinge line narrower than widest; highest in the posterior third of shell; anterior margin emarginate; anterior commissure uniplicate.

Ventral valve strongly inflated with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards anterior margin; umbo strongly inflated, prominent; beak straight; interarea well-defined, apsacline, triangular, high, generally slightly concave; delthyrium wide, covered by a pseudodeltidium for most of its height, the latter is formed by several distinct plates; foramen minute, ovate, near the apex; sulcus relatively wide, moderately deep, originating from beak, round-bottomed at front; tongue high, subogival to subcircular in outline, generally not perpendicular to commissural plane.

Dorsal valve subtrapezoidal to rounded subrectangular in outline, inflated, with convex flanks sloping gently to moderately towards lateral commissures; highest at about midlength or slightly posteriorly to it, then decreasing gradually towards anterior margin (but that is not displayed in the specimen of IGNASRAGM 3951/PS 3057 as it is broken); umbo inflated, projecting slightly beyond the posterior margin; interarea linear, orthocline; fold wide, well-delimited, high, originating from beak, round-topped at front.

On flanks, up to 25 (5 ribs per 5–6 mm at anterior margin near sulcus and fold) usually simple, rounded ribs becoming fainter towards lateral cardinal extremities; in sulcus and on fold, up to 20 (usually 16–18) ribs increasing by bifurcations (Pl. 6.16), much narrower than those present on flanks; interspaces narrower than ribs; micro-ornament (Pl. 6.17) of closely spaced growth lines (irregularly thickened as growth varices), capillae occurring both on ribs and in interspaces, and numerous pustules developed on capillae.

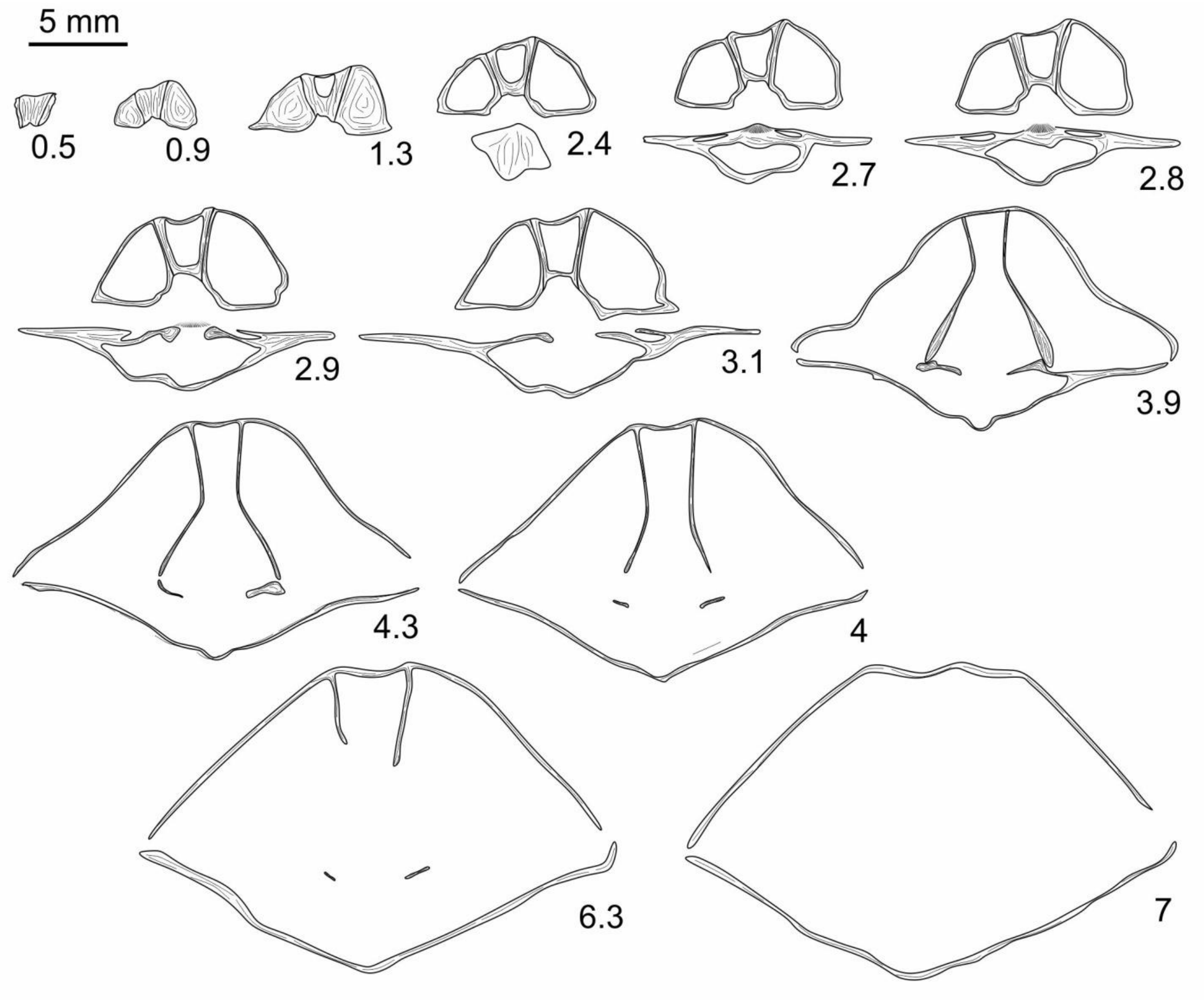


Figure 37. Transverse serial sections of *Cyrtospirifer pseudoasiaticus* n. sp. (IGSNASRAGM 3949/PS 3055) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Armenia, Ertych section. Numbers refer to distances in mm from the tip of the ventral umbo.

Ventral valve interior (Fig. 37) with relatively thin, long, divergent dental plates extrasinal posteriorly then becoming subsinal anteriorly; delthyrial plate well-developed; central and lateral apical cavities poorly infilled by callosities; teeth stout.

Dorsal valve (Fig. 37) with unsupported ctenophoridium composed of numerous vertical lamellae (ca. 28–30); hinge plates divided; dental sockets shallow; crural bases mediodorsally oriented; spiralia oriented posterolaterally with at least 20 whorls per spiral cone.

Etymology.—In reference to the confusion made with the spiriferide species *Cyrtospirifer asiaticus* Brice, 1971.

Material.—Twenty-eight articulated specimens and six dissociated valves from the Ertych Regional Stage of the Ertych (twelve articulated specimens and two ventral valves) and Djravank (sixteen articulated specimens and four ventral valves) sections.

Shell ontogeny.—Although our material does not include juveniles, the examination of relatively small specimens (youth stages of growth) show that the latter display all external morphological characters that are typical for this species. The size distributions during the growth, as represented by the width/length, the width/thickness, the width/width of sulcus and the width/ length of dorsal valve plots, show a continuous and progressive growth with no distinct grouping (Fig. 38). The relative proportions of *Cyrtospirifer pseudoasiaticus* n. sp. represented by sufficient material remain constant (linear regression: $y = ax+b$; significant probability value: $p < 0.001$*** whatever the degree of development of individuals). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve.

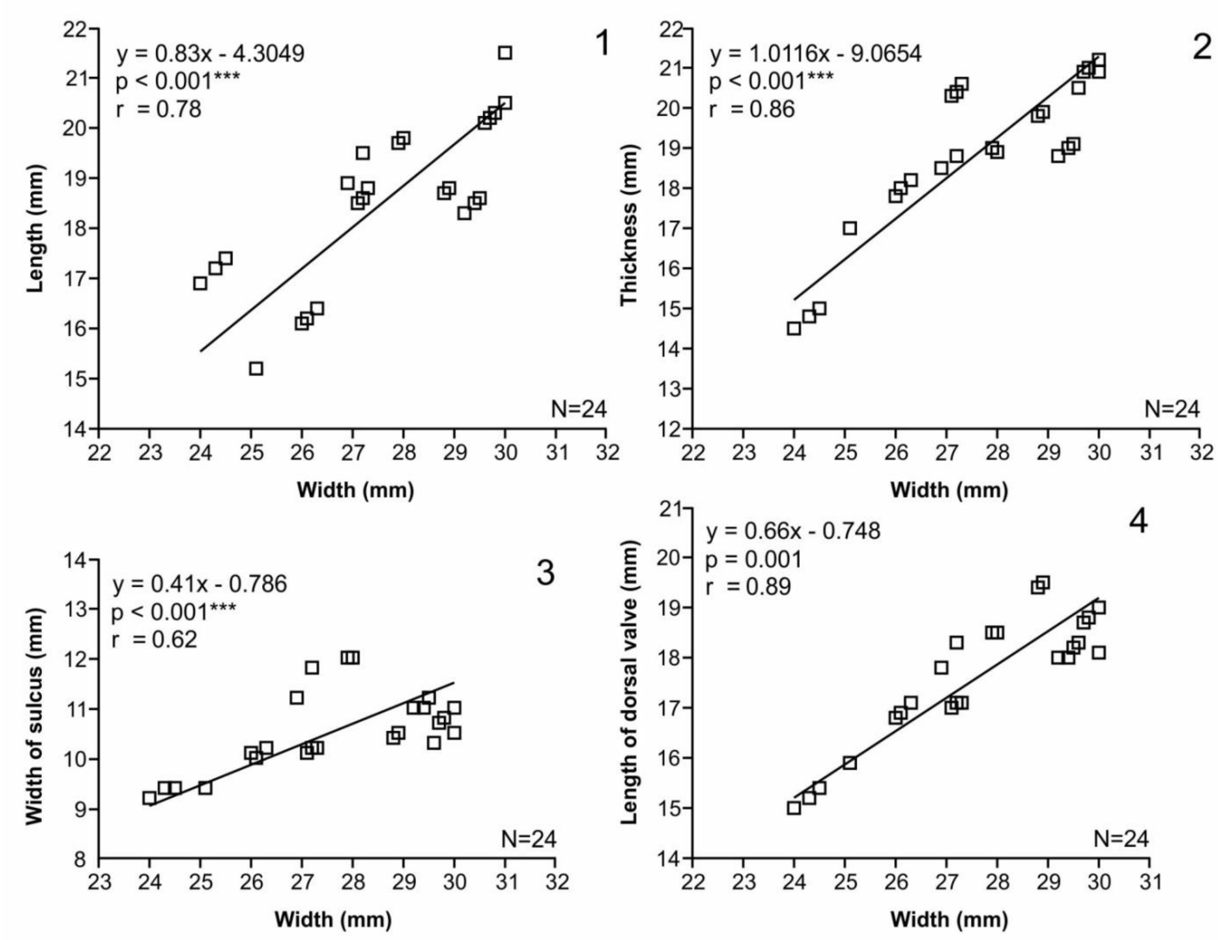


Figure 38. Scatter diagrams of *Cyrtospirifer pseudoasiaticus* n. sp. 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. 4, Relation between shell width and length of dorsal valve. Abbreviations: *N*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	24	24	24	24	24	24	24	24	24
Mean value	27.6	18.5	18.9	10.5	17.6	0.67	0.68	0.38	0.64
Standard deviation	1.92	1.5887	1.94	0.79	1.2771	0.0365	0.04	0.2636	0.021
Standard error±	±0.3922	±0.324	±0.3967	±0.16	±0.26	±0.007	±0.008	±0.0048	±0.0042
Min	24	15.2	14.5	9.2	15	0.61	0.6	0.35	0.6
Max	30	21.5	21.2	12	19.5	0.72	0.75	0.43	0.67

Table 5. Measurements in mm and ratios of *Cyrtospirifer pseudoasiaticus* 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.

To complete the scatter plots, the measurements (in mm) of numerous individuals of *Cyrtospirifer pseudoasiaticus n. sp.* are also presented in Table 5.

Remarks.—Our material is assigned to *Cyrtospirifer* Nalivkin in Fredericks, 1924 based on its rounded transverse outline, ventribiconvex profile, apsacline and triangular ventral interarea, well-developed fold and sulcus bearing bifurcating ribs, flanks ornamented by low and flattened ribs, the type of micro-ornament (composed of capillae occurring both on ribs and in interspaces, and bearing numerous pustules), long dental plates extrasinal or positioned at sinal border and its well-developed delthyrial plate. However, it is worth noting that our specimens display short hinge line, obtuse cardinal extremities and a pseudodeltidium formed by several distinct plates, features which are not frequently observed in cyrtospiriferids. We herein provide a comparison of *C. pseudoasiaticus* n. sp. with other *Cyrtospirifer* representatives but only with those which are described regarding to current standards as previously several species were lumped into the genus *Cyrtospirifer*, which after revision may be proven to belong to different genera (Ma and Day, 2003).

C. pseudoasiaticus n. sp. differs externally from *C. verneuili* (Murchison, 1840) as revised by Ma and Day (2003), from the uppermost Givetian–upper Frasnian of Western Europe, by its relatively short hinge line, obtuse cardinal extremities, pseudodeltidium formed by several distinct plates and the type of micro-ornament (consisting of capillae and pustules on ribs and in interspaces). Internally, the new species is distinguished by its unsupported ctenophoridium.

The new species displays strong similarities to *C. whitneyi* (Hall, 1858) from the middle–upper Frasnian of USA and Canada, most notably to those specimens illustrated by Ma and Day (2003: pl. 9, figs. 12–18); however, the former differs externally by its more inflated shell, type of pseudodeltidium (formed by several distinct plates) and having relatively less densely crowded pustules on capillae and in interspaces.

C. pseudoasiaticus n. sp. seems to be similar to *C. asiaticus* Brice, 1971, a relatively poorly known species, originally described from the lower Famennian of Afghanistan; however *C.*

pseudoasiaticus n. sp. is separable by its comparably less globular shell, short hinge line, obtuse cardinal extremities and foramen near the apex. Internally, the new species differs by its unsupported ctenophoridium. It is also pertinent to remind here that according to Ma and Day (2007) Brice's species might be belonging to *Sinospirifer* Grabau, 1931; this assumption was based on its central hypothyrid foramen and type of its micro-ornament (consisting of numerous small pustules originating from capillae present both on ribs and in interspaces).

The new species differs superficially from *C. placitus* Stainbrook, 1945 occurring in the upper Frasnian of USA by its comparatively short hinge line, lack of sharply extended cardinal extremities, type of pseudodeltidium and well-developed micro-ornament. It should be emphasized that internally *C. pseudoasitaticus* n. sp. is differing by its unsupported ctenophoridium, whereas the latter is sometimes supported in Stainbrook's species.

C. pseudoasitaticus n. sp. is externally separable from *C. thalattodoxa* Crickmay, 1952 as revised by Ma and Day (2003) from the middle Frasnian of Canada and USA by its deeper sulcus, straight beak, subogival to subcircular tongue round-topped at front and the type of pseudodeltidium. Moreover, the micro-ornament of the new species differs by the presence of capillae both on ribs and in interspaces whereas the latter is not observed in *C. thalattodoxa*. Internally, the new species is readily distinguished by its smaller teeth, thinner dental plates and by the absence of strong apical of callosities in the ventral interior.

C. pseudoasitaticus n. sp. is separable from *C. disjunctus* (Sowerby, 1840) *sensu* Sokiran (2013), by its smaller size, lack of sharply extended cardinal extremities and bifurcating ribs on flanks. Moreover, the micro-ornament of *C. disjunctus* consists of densely spaced concentric growth lines, whereas only a few concentric growth lines are observed in *C. pseudoasitaticus* n. sp. It is difficult to compare the internal morphology of these species as Sowerby (1840) did not show his serial sections.

The new species may be distinguished from *C. vjacheslavi* Sokiran, 2013 occurring in the middle Frasnian of EEP by its transversely elongated shell, obtuse cardinal extremities, higher ventral interarea, straight beak and non-bifurcating ribs on flanks. Moreover, *C. pseudoasitaticus* n. sp. differs by the presence of capillae on ribs and in interspaces whereas Sokiran's species devoid capillae. Internally, the new species is differing by its shorter delthyrial plate and smaller teeth. It is pertinent to remind here that Sokiran (2013) erected her species based on the specimens, which were previously identified as *Spirifer disjunctus* (Sowerby, 1840) (e.g., Murchison et al., 1845; Nalivkin, 1947; Ljaschenko, 1959).

C. pseudoasitaticus n. sp. differs externally from *C. schelonicus* Nalivkin, 1941 as illustrated by Sokiran (2006) from the middle Frasnian of East European Platform (EEP) by its smaller size, relatively short hinge line and by the lack of markedly extended cardinal extremities. Internally, the new species differs by its thin dental plates, smaller teeth and unsupported ctenophoridium.

C. pseudoasitaticus n. sp. is distinguishable from *C. rudkinensis* Ljaschenko, 1959 *sensu* Sokiran (2006) from the middle Frasnian of EEP by its smaller size, relatively short hinge line, lack of sharply extended cardinal extremities, high ventral interarea and wide delthyrium. Internally, the new species differs by its unsupported ctenophoridium and small teeth.

The new species is separable from *C. mylaensis* Sokiran, 2006 from the middle Frasnian of EEP by its smaller size, less globular shell outline, obtuse cardinal extremities, relatively high fold and by the presence of pustules developed on capillae both on ribs and in interspaces. The most significant internal difference is the presence of strong callosities developed in central apical cavity of Sokiran's species, whereas the apical cavity of our material is poorly filled in.

It is difficult currently to compare the new species with other cyrtospiriferids described in the EEP by means of pseudodeltidium and micro-ornament as the latter features are rarely preserved in the EEP material.

Genus *Sinospirifer* Grabau, 1931

Type species.—*Spirifer verneuili* var. *subextensus* Martelli,1902

Sinospirifer sp. 1

Plate 7.1–7.13; Figure 39; Table 6

Occurrence.—The specimens were collected from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) of the Ertych section (Fig. 1).

Description.—Shell medium-sized (reaching 38.1 mm in width, 23.2 mm in length and 22 mm in thickness) (Table 6), wider than long, sharply ventribiconvex, rounded transverse in outline; widest at hinge line; (not the case of the specimen figured in Pl. 7.1–7.6, as it is exfoliated); cardinal extremities acute; anterior margin straight to emarginate; anterior commissure uniplicate.

Ventral valve strongly inflated, with convex flanks sloping moderately to strongly towards lateral commissures; highest in the posterior third of the valve or at midlength, then decreasing progressively towards anterior margin; umbo inflated, prominent; beak straight to erect; interarea well-defined, apsacline, triangular, moderately high, slightly to clearly concave; delthyrium wide, almost completely covered by a pseudodeltidium that is penetrated by a central foramen or pedicle tube (Pl. 7.13); sulcus originating from beak, wide, moderately deep, round-bottomed at front, tongue low, wide, perpendicular to commissural plane or slightly bent dorsally, subtrapezoidal to subcircular in outline.

Dorsal valve inflated with flanks sloping gently towards lateral commissures; highest at about midlength or more anteriorly to it, but gradually decreasing towards the anterior margin; interarea nearly flat, linear, orthocline; fold low, wide, well-delimited, starting from beak and widening anteriorly, round-topped at front.

On flanks, up to c. 20 (3–4 ribs per 5 mm at anterior margin near sulcus and fold) usually simple, rounded ribs becoming fainter towards lateral cardinal extremities; ribs wider than interspaces on flanks; micro-ornament not preserved.

Ventral valve interior (Fig. 39) with long, strong, subsinal or extrasinal, greatly thickened and divergent dental plates, converging dorsally in umbonal region (as seen in transverse section); delthyrial plate well-developed, massive; median ridge short; lateral apical cavities large and greatly filled in by callus; teeth stout.

Dorsal valve interior (Fig. 39) with ctenophoridium consisting of up to 30 well-developed, relatively long lamellae, and supported by strong callosity; hinge plates divided; crural bases dorsally convergent; at least 20 whorls per spiral cone (not illustrated).

Material.—Six articulated specimens and six dissociated valves from the Baghrsagh Regional Stage of the Ertych (four articulated specimens and two ventral valves) and Djravank (two articulated specimens and four ventral valves) sections.

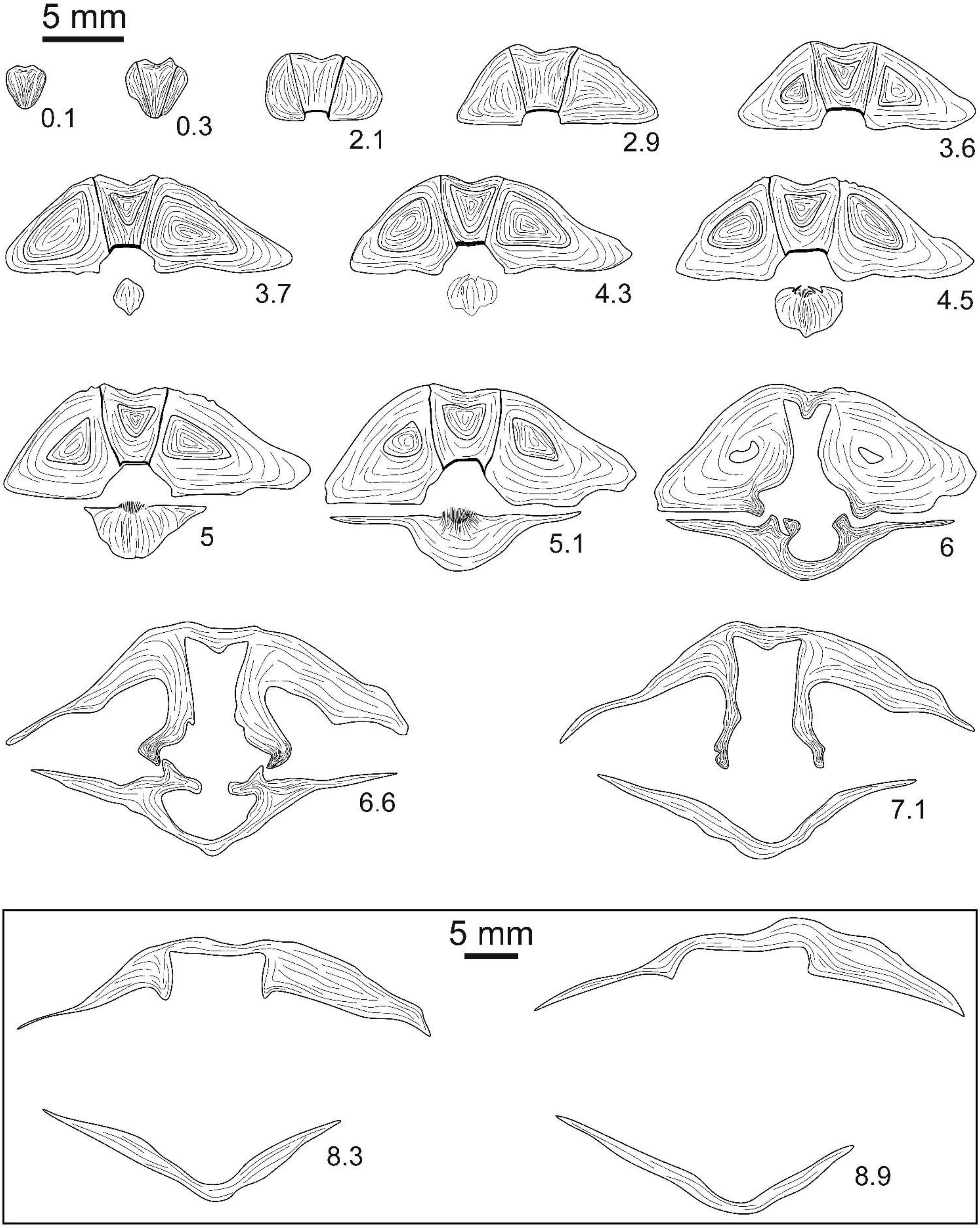


Figure 39. Transverse serial sections of *Sinospirifer* sp. 1 (IGSNASRAGM 3954/PS 3060) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) of the Ertych section (Fig. 1). Numbers refer to distances in mm from the tip of the ventral umbo.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	6	6	6	6	6	6	6	6	6
Mean value	34.1	20.57	19.27	16	0.6	0.58	0.47	0.31	0.47
Standard deviation	4.637	3.65	2.5696	3.4641	0.033	0.1616	0.05	0.054	0.05
Standard error±	±2.677	±2.107	±1.4836	±2.01	±0.0189	±0.09	±0.0287	±0.312	±0.0287
Min	29	16.4	16.9	12	0.57	0.44	0.41	0.26	0.41
Max	38.1	23.2	22	18	0.63	0.76	0.51	0.37	0.51

Table 6. Measurements in mm and ratios of *Sinospirifer* sp. 1. 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.

Remarks.—*Sinospirifer* Grabau, 1931 is mainly known from the Famennian of China and East European Platform (Ma et al., 2002, 2003; Ma and Day, 2007), but also from Western Europe (Mottequin, 2005). Our material is assigned to the genus *Sinospirifer* rather than to *Cyrtospirifer* based on its central foramen or pedicle tube penetrating the pseudodeltidium, greatly thickened subsinal or extrasinal dental plates and the presence of delthyrial thickening formed by a development of strong apical callosity. Thus, this study establishes for the first time the presence of this genus within the Frasnian strata in Armenia.

Sinospirifer sp. 2

Plate 7.14–7.18; Figure 40

Occurrence.—The specimens were collected from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpensis* Zone of Rzhonsnitskaya and Mamedov (2000) of the Ertych section (Fig. 1).

Description.—Shell medium-sized (attaining 41.1 mm in width, 23.2 mm in length and 22.5 mm in thickness), wider than long, equibiconvex, transversely elongated in outline; widest at hinge line; highest more posteriorly to midlength; cardinal extremities acute; anterior margin emarginate; anterior commissure uniplicate.

Ventral valve inflated with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards anterior margin; umbo inflated, large and prominent; beak and foramen unobserved; interarea triangular, moderately high, apsacline; sulcus shallow to moderately deep, originating from beak, with rounded lateral boundaries, round-bottomed at front; tongue wider than high, low to moderately high, subcircular to subogival in outline.

Dorsal valve inflated with flanks sloping moderately towards lateral commissures, subtrapezoidal in outline; highest in the anterior third of the valve, then progressively decreasing towards anterior margin; interarea linear, flat, orthocline; fold low, relatively wide, originating from beak, round-topped at front.

Up to 28 simple, low ribs on flanks with top rounded; interspaces narrower than ribs; in sulcus and on fold, up to 11 ribs narrower than those on flanks, increasing by bifurcation; micro-ornament poorly preserved, only a few capillae persist in interspaces and on ribs of the right flank of dorsal valve (Pl. 7.15).

Ventral interior (Fig. 40) with greatly thickened, extrasinal and divergent dental plates converging dorsally in umbonal region (as seen in transverse section) and extending up to 35% of the valve length; delthyrial thickening formed by accretion of strong apical callus from the internal faces of the dental plates and floor of ventral valve; delthyrial plate long, thick; central and lateral apical cavities infilled by stout callosity; teeth stout.

Dorsal valve interior (Fig. 40) with unsupported ctenophoridium consisting of relatively short lamellae; dental sockets shallow; hinge plates divided; crural bases dorsally convergent; spiralia unobserved.

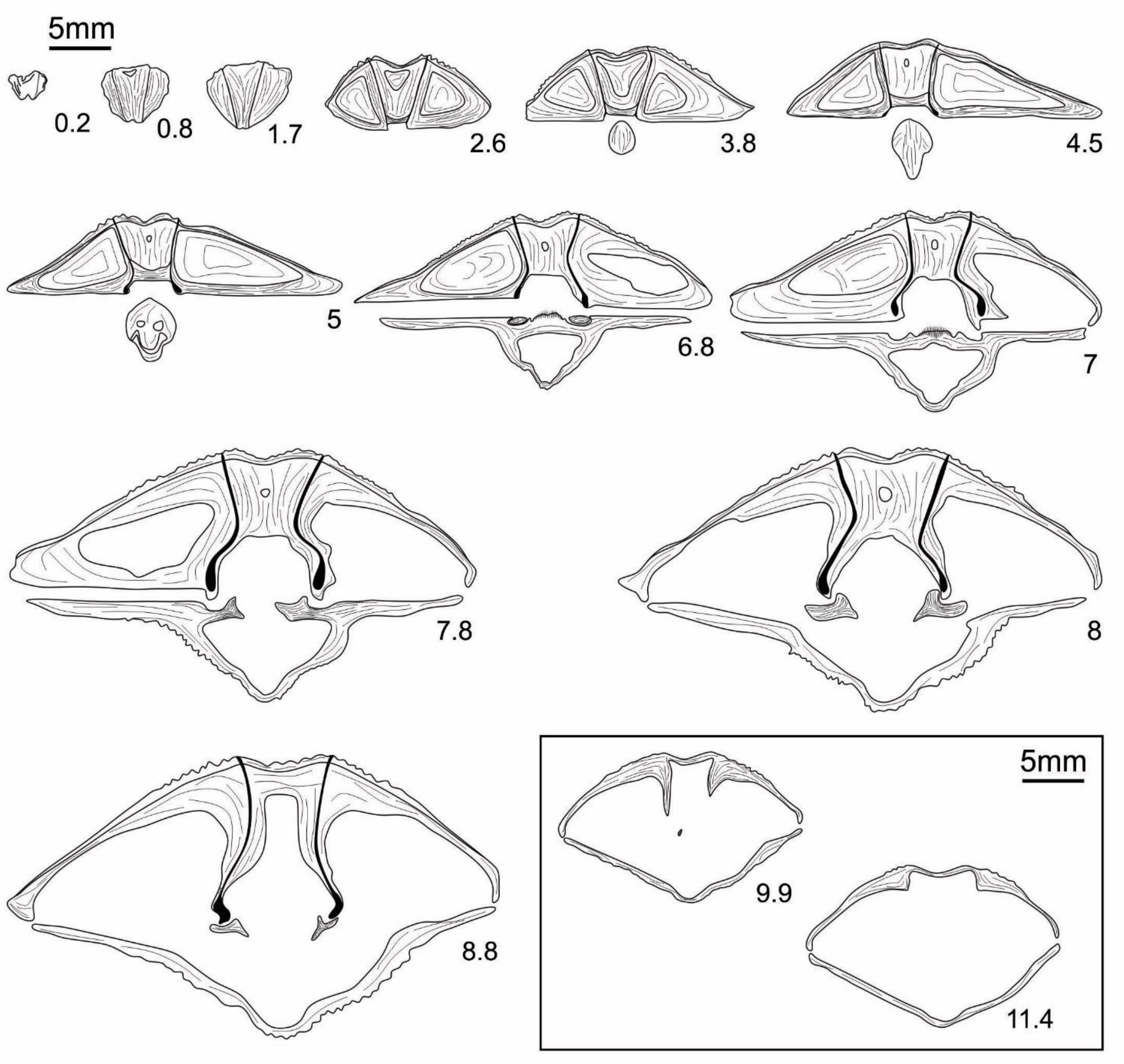


Figure 40. Transverse serial sections of *Sinospirifer* sp. 2 (IGSNASRAGM 3957/PS 3063) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpensis* Zone of Rzhonsnitskaya and Mamedov (2000) (Fig. 3) of the Ertych section (Fig. 1). Numbers refer to distances in mm from the tip of the ventral umbo.

Material.—Two partly exfoliated articulated specimens.

Remarks.—The greatly thickened and extrasinal dental plates, development of a strong apical callus in the ventral interior and unsupported ctenophoridium observed in our material suggests an assignment to the genus *Sinospirifer* Grabau, 1931. However, the poor state of preservation and insufficiency of our material precludes the possibilities to reach a more confident identification until the species level. *Sinospirifer* sp. 2 seems to be very close to *Sinospirifer* sp. indet. 1 but differs from the latter by its more inflated and equibiconvex shell, extended cardinal extremities (although they are poorly preserved in the former), large number of ribs and by its unsupported ctenophoridium. However, further material is needed to compare these species more comprehensively.

Genus *Pseudocyrtiopsis* Ma and Day, 1999

Type species.—*Cyrtiopsis spiriferoides* Grabau, 1931.

Remarks.— Ma and Day (1999) created the genus *Pseudocyrtiopsis* to include those cyrtospiriferide species that resemble to some extent to *Cyrtiopsis* Grabau, 1923, but differs from the latter due to wide hinge line and the presence of delthyrial plate. Although both Ma and Day (1999) and later Gourvennec and Carter (2007) attributed *Pseudocyrtiopsis* to the Subfamily Cyrtiopsinae, this genus displays high ventral interarea, wide hinge line and mucronate cardinal extremities, which suggest its assignment to the Subfamily Cyrtospiriferinae, following the classification proposed by Carter et al. (2006).

Pseudocyrtiopsis areniensis new species

Plate 8; Figures 41–42; Table 7

Holotype.—An almost complete articulated specimen (IGSNASRAGM 3963/PS 3069; Pl. 8.22–8.27) from the lower Famennian *orbelianus* Zone of Abrahamyan (1957), which is correlated with the Ertych Regional Stage (Fig. 3); Djravank section (7 km southeast from Areni, Vayots Dzor Province, Central Armenia) (Figs. 1).

Diagnosis.— Shell medium-sized (reaching 37.1 mm in width, 30.2 mm in length and 29.2 mm in thicknes (Table 7), wider than long, ventribiconvex to dorsibiconvex; cardinal extremities mucronate; anterior margin emarginate; anterior commissure uniplicate; widest at hinge line; ventral interarea triangular, high, apsacline; pseudodeltidium composed of several distinct plates, with a minute, ovate foramen near the apex; dorsal fold and ventral sulcus wide and well-defined; tongue high, subcircular to subogival in outline; ribs numerous, simple on flanks, increasing by bifurcation in sulcus and on fold; micro-ornament of capillae both on ribs and in interspaces with numerous pustules developed on them; dental plates long, robust, divergent, subsinal or extrasinal posteriorly then becoming intrasinal more anteriorly, delthyrial plate thick; ctenophoridium unsupported, slightly convex, with numerous vertical lamellae.

Occurrence.—This species is found only in the Ertych Regional Stage, which corresponds to the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) and to the *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone of Rzhonsnitskaya and Mamedov (2000) (Fig. 3).

Description.—Shell medium-sized (reaching 37.1 mm in width, 30.2 mm in length and 29.2 mm in thicknes (Table 7), wider than long, ventribiconvex to dorsibiconvex, rounded subpentagonal in outline, widest at hinge line, highest at about midlength or more anteriorly to it; cardinal extremities mucronate; anterior margin emarginate; anterior commissure uniplicate.

Ventral valve markedly inflated, with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards anterior margin; umbo strongly inflated, large and prominent; beak straigth; interarea apsacline, triangular, high, well-defined; delthyrium wide, covered by pseudodeltidium except for a subtrapezoial opening at its base; pseudodeltidium formed by several (at least six) distinct plates; foramen minute, ovate, near the apex; sulcus wide, shallow to moderately deep, originating from beak, with rounded lateral boundaries, round-bottomed at front; tongue high to very high, subcircular to subogival in outline, generally bent dorsally.

Dorsal valve inflated, with flanks sloping gently to moderately towards lateral commissures, subtrapezoidal to subquadrangular in outline; interarea linear, orthocline, concave; fold low to moderately to high, wide, well-delimited, originating from beak, round-topped at front.

Ornamentation of up to 25 rounded (4–5 ribs per 5 mm at anterior margin near sulcus and fold), low, flattened, simple ribs on each flank, becoming progressively fainter towards posterolateral margins; in sulcus and on fold, up to 21 ribs (generally 15–17) increasing by bifurcations, narrower than those present on the flanks; micro-ornament of capillae occurring both on ribs and in interspaces and bearing numerous pustules (Pl. 8.9); growth lines closely spaced, sometimes thickened as growth varices.

Ventral valve interior (Fig. 41) with long, robust and divergent dental plates, subsinal or extrasinal posteriorly but becoming intrasinal more anteriorly; delthyrial plate thick; teeth relatively small, subquadrangular in outline; central and lateral apical cavities large and moderately filled in by callus; teeth relatively small but stout.

Dorsal valve interior with unsupported ctenophoridium (Fig. 41) composed of numerous well-developed, long lamellae; myophragm low; hinge plates divided; crural bases dorsally convergent; spiralia not observed.

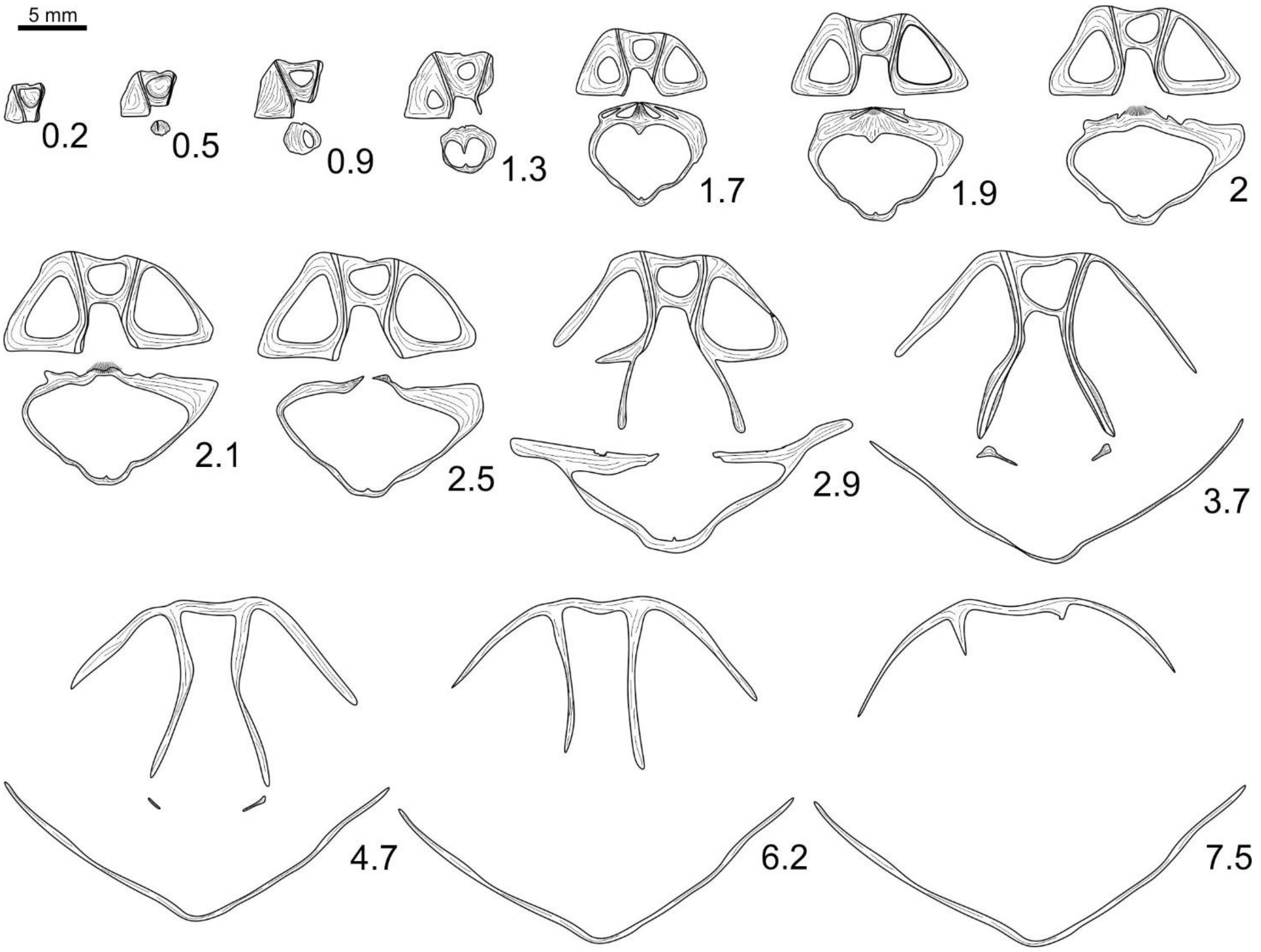


Figure 41. Transverse serial sections of *Pseudocyrtiopsis areniensis* n. sp. (IGSNASRAGM 3959/PS 3065) from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) of the Djravank section (Fig. 1). Numbers refer to distances in mm from the tip of the ventral umbo.

Etymology.—Areni is the name of the center of Areni Municipality of the Vayots Dzor Province, where the species was found.

Material.—Twenty-four articulated specimens and ten dissociated valves from the Ertych Regional Stage of the Ertych (ten articulated specimens and four ventral valves), Djravank (eleven articulated specimens and four ventral valves) and Noravank (three articulated specimens and two ventral valves) sections.

Shell ontogeny.—Although our material does not include juveniles, the examination of relatively small specimens (young stages of growth) show that the latter display all the external morphological characters also visible on the adults that are typical for this species. The size distributions during the growth, as represented by the width/length, the width/thickness, the width/width of sulcus and the width/length of dorsal valve plots, show a continuous and progressive growth with no distinct grouping (Fig. 42). The relative proportions of *Pseudocyrtiopsis areniensis* n. sp. represented by sufficient material remain constant (linear regression: y = ax+b; significant probability value: p < 0.001*** whatever the degree of development of individuals (Fig. 42)). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve.

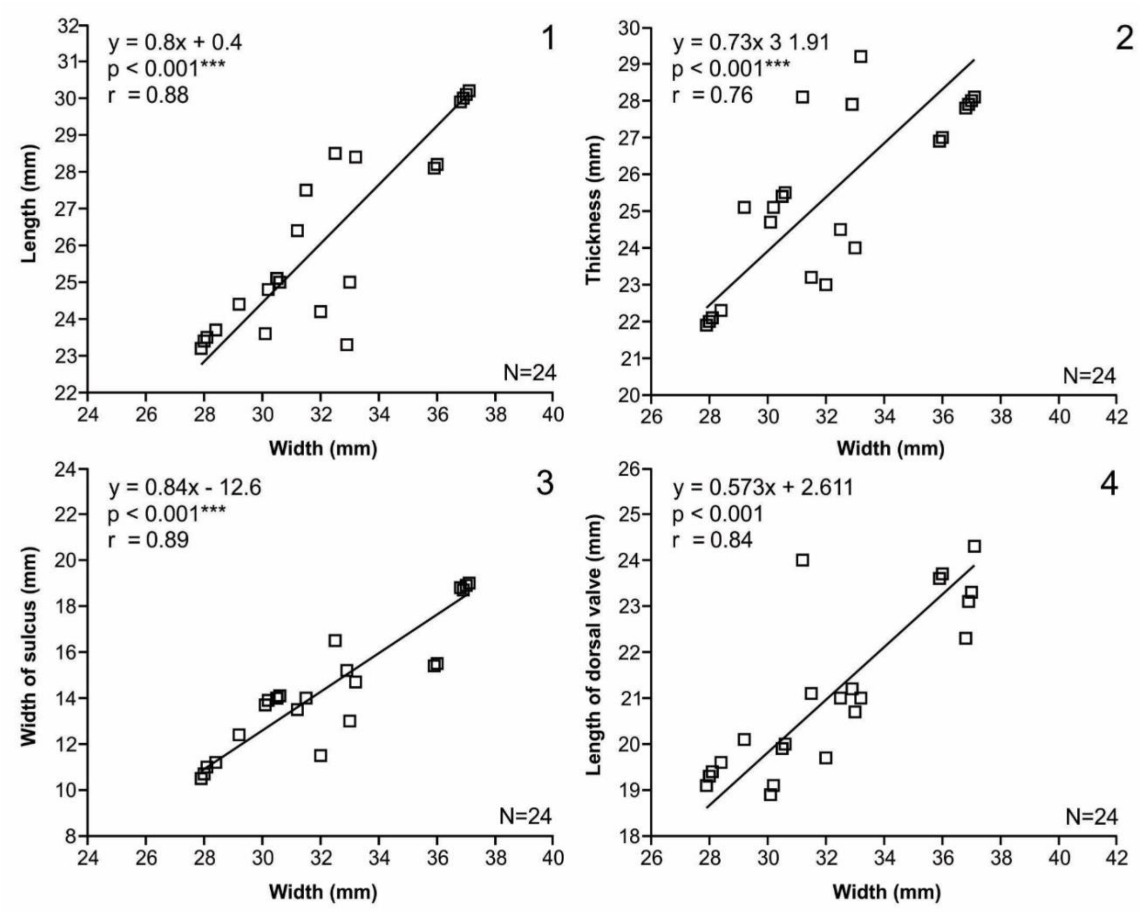


Figure 42. Scatter diagrams of *Pseudocyrtiopsis areniensis* n. sp. 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. 4, Relation between shell width and length of dorsal valve. Abbreviations: *N*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

To complete the scatter plots, the measurements (in mm) of numerous individuals of *Pseudocyrtiopsis areniensis* n. sp. are also presented in Table 7.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	24	24	24	24	24	24	24	24	24
Mean value	32.08	26.11	25.4	14.3	21	0.81	0.79	0.44	0.66
Standard deviation	3.0778	2.4661	2.2571	2.5866	1.765	0.038	0.05	0.45.	0.034
Standard error±	±0.6283	±0.503	±0.4607	±0.528	±0.36	±0.0076	±0.01	±0.009	±0.007
Min	27.9	23.2	21.9	10.5	18.9	0.71	0.72	0.36	0.61
Max	37.1	30.2	29.2	19	24.3	0.88	0.9	0.51	0.77

Table 7. Measurements in mm and ratios of *Pseudocyrtiopsis areniensis* 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.

Remarks.—The external and internal features observed (e.g. rounded subpentagonal outline, wide hinge line, mucronate cardinal extremities, high and apsacline ventral interarea, the type of pseudodeltidium and micro-ornament, strong dental plates, well-developed delthyrial plate) in the studied specimens indicate affinities to genus *Pseudocyrtiopsis* Ma and Day, 1999, which has so far only been documented from China (Ma and Day, 1999) and dubiously from Belgium (Mottequin and Brice, 2019).

Pseudocyrtiopsis areniensis n. sp. may be distinguished from *Pseudocyrtiopsis spiriferoides* (Grabau, 1931) as revised Ma and Day (1999), by its more inflated shell, higher tongue and the lack of primary sinal pairs of ribs that are much stronger than others.

The new species differs from *Pseudocyrtiopsis kunlunensis* (Wang and Zhu in Jin et al., 1979) by its more inflated, globular shell, high to very high, subcircular to subogival tongue and by the larger number of ribs on fold and in sulcus.

Genus *Aramazdospirifer* Serobyan et al.

See Serobyan et al. (in press)

Aramazdospirifer orbelianus (Abich, 1858)

See Serobyan et al. (in press), Figs. 3–6, Table 1.

Genus *Pentagonospirifer* new genus

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

Diagnosis.—Shell medium-sized, equibiconvex to ventribiconvex, with acute to slightly mucronate cardinal extremities. Widest at hinge line. Ventral interarea triangular, high, variably concave, apsacline. Pseudodeltidium composed of several distinct plates, with apical foramen. Dorsal fold and ventral sulcus wide, well-defined. Ribs numerous, usually simple on flanks, increasing by bifurcation in sulcus and on fold. Micro-ornament of capillae with pustules on them and closely spaced growth lines. Dental plates long, always intrasinal. Delthyrial thickening is formed by a development of strong apical callus on delthyrial plate, around dental plates and floor of ventral valve. Ctenophoridium unsupported.

Occurrence.—Lower Famennian of Armenia.

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

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

The new genus resembles to some extent some representatives of the lower Famennian genus *Sinospirifer* Grabau, 1931 by its wide winge line, acute cardinal extremities, development of a massive apical callus in the ventral interior and its unsupported ctenophoridium; however, *Pentagonospirifer* n. gen. has a higher ventral interarea, a minute foramen near the apex, more ribs in sulcus and on fold and pustules developed only on capillae. Internally, the most significant difference concerns the dental plates that are intrasinal and devoid of thickening in *Pentagonospirifer* n. gen., whereas *Sinospirifer* possesses greatly thickened extrasinal dental plates

Externally, *Pentagonospirifer* n. gen. is close to *Wenjukovispirifer* Oleneva, 2016, known from the Famennian of EEP, by its rounded subpentagonal outline, inflated shell, high ventral interarea, well-developed sulcus and fold, ornamentation composed of simple, low ribs separated by narrower interspaces; however, the new genus is distinguished by its relatively equibiconvex 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; 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, *sensu* 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 the lower Famennian genus *Pripyatispirifer* Pushkin, 1996, but differs 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. Although, 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.

Pentagonospirifer n. gen. differs mainly from *Eodmitria* Brice, 1982, known from the lower–middle Frasnian of Western Europe (Belgium, France and Germany) and Turkey, by its more inflated shell, high ventral interarea and well-defined fold and sulcus. Furthermore, the micro-ornament of *Pentagonospirifer* n. gen. consists of capillae with pustules on them (only on ribs) whereas the micro-ornament of *Eodmitria* is papillose. It is worth emphasizing that both genera have quite similar internal morphologies, with the exception of dispositon of dental plates, which are intrasinal in the new genus, while Brice's genus has extrasinal ones. *Pentagonospirifer* n. gen. is distinguished externally from *Pseudocyrtiopsis* Ma and Day, 1999 from the lower Famennian of South China, by its larger and more inflated shell (due to the greater thickness of the dorsal valve), its bifurcating ribs in sulcus and on fold, its finer and more numerous ribs on flanks, as well as the lack of capillae that are developed in the interspaces of *Pseudocyrtiopsis* representatives. Internally, *Pentagonospirifer* n. gen. mainly differs by the presence of a strong apical callosity developed on the delthyrial plate and by its unsupported ctenophoridium.

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

Plate 9, Figures 43–44; Table 8

Holotype.—An almost complete articulated specimen that is partly covered by encrusters in its sulcus (IGSNASRAGM 3928/PS3073; Plate. 9.11–9.18), 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 8), wider than long, equibiconvex 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 fold; micro-ornament of capillae with pustules on them and closely spaced growth lines; dental plates long, extending to about 30% of the shell length, slightly convergent, diverging dorsally in the umbonal region, always intrasinal; delthyrial thickening is formed by a development of strong apical callus on delthyrial plate, around dental plates and floor of ventral valve; ctenophoridium unsupported, slightly convex, with numerous vertical lamellae.

Occurrence.—This species occurs in the lower Famennian Ertych Regional Stage that is correlated with the *Cyrtospirifer orbelianus* brachiopod Zone of Abrahamyan (1957) and the *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* brachiopod Zone of Rzhonsnitskaya and Mamedov (2000) (see Fig. 3).

Description.—Shell medium-sized, wider than long, generally equibiconvex to slightly ventribiconvex, rounded subpentagonal in outline, widest at hinge line, highest at about midlength; cardinal extremities acute; anterior margin emarginate; anterior commissure uniplicate.

Ventral valve strongly inflated, with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards anterior margin; umbo strongly inflated, large and prominent; beak straight to suberect; interarea apsacline, triangular, high, generally slightly concave (occasionally perpendicular to commissural plane) well-defined; delthyrium wide, covered by a pseudodeltidium for most of its height, the latter being formed by distinct, stacked sets of growth lamellae; foramen minute, ovate, near the apex; sulcus relatively wide, shallow to moderately deep, originating from beak, with rounded lateral boundaries, round-to flat-bottomed at front; tongue high, perpendicular to commissural plane or slightly bent dorsally, subtriangular to subcircular in outline.

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

Ornamentation of up to 29 rounded (5 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 bifurcation, much narrower than those present on flanks; ribs twice wider than interspaces on the entire shell; micro-ornament of fine capillae only on ribs with pustules on them and with closely spaced growth lines sometimes thickened as growth varices.

Ventral valve interior (Fig. 43) with relatively thin, long, intrasinal and slightly divergent dental plates, becoming subparallel more anteriorly, converging dorsally in umbonal region (as seen in transverse section); delthyrial thickening formed by accretion of strong apical callus from the internal faces of the dental plates and floor of ventral valve; delthyrial plate thin; lateral apical cavities posteriorly infilled; teeth relatively small, subcircular.

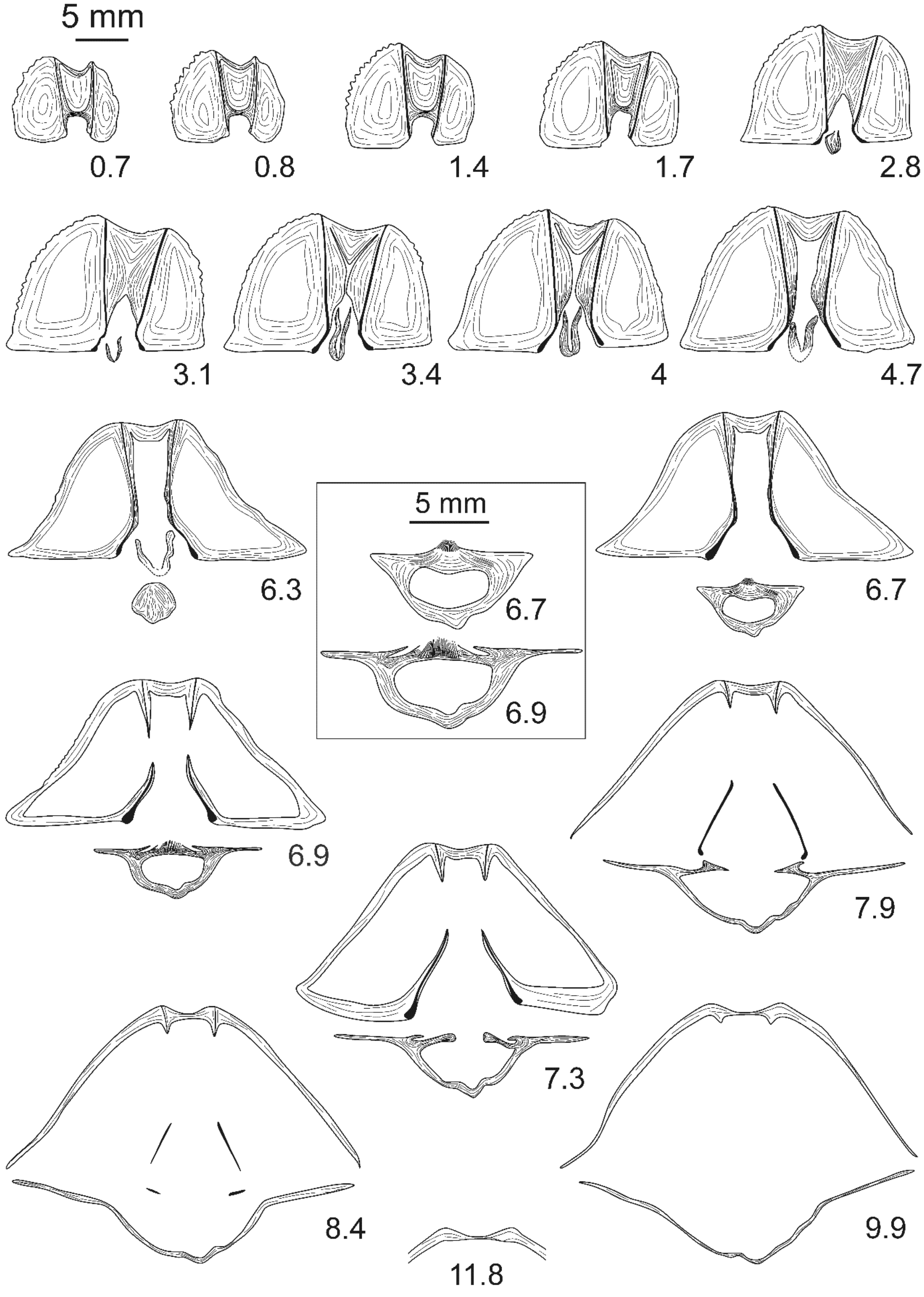


Figure 43. Transverse serial sections of *Pentagonospirifer abrahamyanae* n. gen., n. sp. (IGSNASRAGM 3964/PS 3070), from the Djravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Dorsal valve interior (Fig. 43) with flat to slightly concave, unsupported ctenophoridium composed of up to 27 well-developed relatively long lamellae; dental sockets shallow; hinge plate divided; crural bases mediodorsally oriented; spiral cones not preserved in the sectioned specimens.

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

Material examined.—Forty-eight articulated specimens and nine dissociated valves from the Ertych Regional Stage of the Ertych (nine articulated specimens and two ventral valves), Djravank (twenty-eight articulated specimens and five ventral valves) and Noravank (eleven articulated specimens and two ventral valves) sections.

Shell ontogeny.—Examination of a few juvenile specimens shows that almost all superficial features (e.g., equibiconvex shell covered by numerous ribs, well-developed sulcus and fold; relatively high ventral interarea, high tongue) can be observed since the early growth stages; the only difference to separate juveniles from adults is their shell size. The size distributions during the growth, as represented by the width/length, the width/thickness, the width/width of sulcus and the width/length of dorsal valve plots, show a continuous and progressive growth with no distinct grouping (Fig. 44). The relative proportions of the latter is 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. 44)). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve. However, the

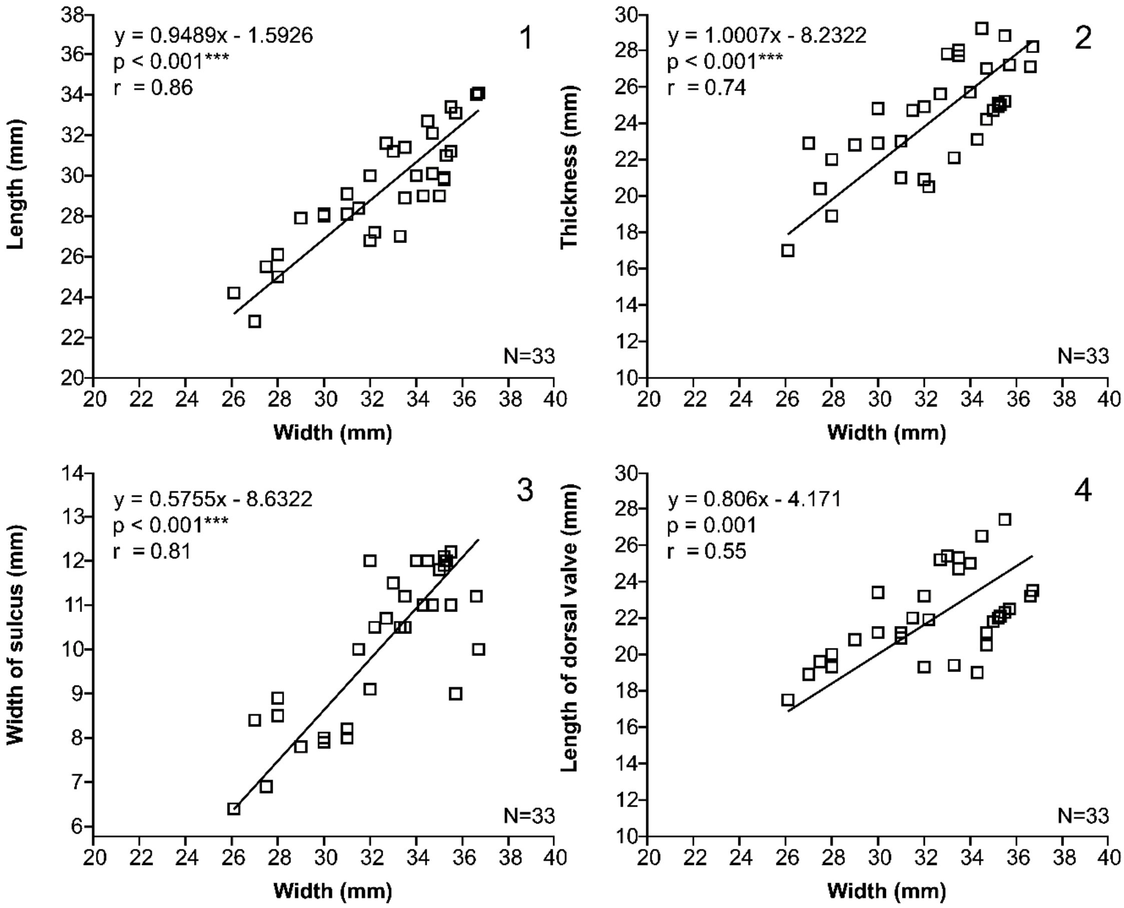


Figure 44. Scatter diagrams of *Pentagonospirifer abrahamyanae* n. gen., n. sp. 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. 4, Relation between shell width and length of dorsal valve. Abbreviations: *N*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	33	33	33	33	33	33	33	33	33
Mean value	32.46	29.3	24.3	22.1	0.9	0.9	0.75	0.68	0.31
Standard deviation	3.087	2.8113	2.97	2.3882	0.05	0.05	0.07	0.0688	0.034
Standard error±	±0.5374	±0.489	±0.5161	±0.4157	±0.231	±0.0087	±0.0118	±0.012	±0.0059
Min	26.1	22.8	17	9.2	17.5	0.81	0.64	0.55	0.25
Max	36.7	34.1	29.2	16.5	27.4	1.04	0.92	0.87	0.38

Table 8. 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.

length/width of the dorsal valve ratio shows less dispersed values (Fig. 44). To complete the scatter plots, the measurements (in mm) of numerous individuals of *P. abrahamyanae* n. gen., n. sp. are also represented in Table 8.

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 one of the striking features of *P. abrahamyanae* n. gen. n. sp. is its suitability for brachiopod encrusters, since until now, among the spiriferides described in Armenia, encrusters are observed only in the specimens of this species.

Genus *Angustisulcispirifer* new genus

Type species.—*Angustisulcispirifer arakelyani* n. gen., n. sp., Frasnian, Central Armenia.

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

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

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

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

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

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

Angustisulcispirifer n. gen. resembles to some extent the genus *Uchtospirifer* Ljashenko, 1957 as revised by Sokiran (2006) from the upper Givetian?–lower Frasnian strata of Russia and possibly upper Givetian of Poland, based on its ventribiconvex profile, subpentagonal shell with flanks closely ornamented by low, flattened ribs and high ventral interarea, but the former displays wide hinge line (*vs*. short hinge line for *Uchtospirifer*), mucronate cardinal extremities (*vs*. rounded ones for *Uchtospirifer*), narrow sulcus and fold (*vs*. moderately wide ones for *Uchtospirifer*). Additionally, the new genus has ribs in sulcus and on fold that are not transformed into capillae, flattening or disappearing as it is observed in *Uchtospirifer* representatives. Internally, *Angustisulcispirifer* n. gen. differs by its supported ctenophoridium.

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

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

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

Angustisulcispirifer arakelyani new species

Plates 10–11, Figures 45–46; Table 9

1952 *Cyrtospirifer subarchiachi* [*sic*] Martelli; Arakelyan, p. 31, 36.

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

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

1973 *Cyrtospirifer subarchiaci* (Martelli); Abrahamyan et al., 217.

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

Holotype.—An almost complete articulated specimen (IGSNASRAGM 3971/PS 3077; Pl. 10.7–10.12) from the Baghrsagh Regional Stage (Frasnian) of the Noravank section (6 km southeast from Areni, Vayots Dzor Province, Southwest Central Armenia) (Fig. 1).

Diagnosis.—Shell medium- to large-sized (up to 51.2 mm in width, 49.5 mm in length, 37.2 mm in thickness) (Table 9), ventribiconvex, subpentagonal, wider than long, with mucronate cardinal extremities; widest at hinge line; highest at midlength or more posteriorly; anterior margin flat to slightly emarginate; anterior commissure uniplicate; ventral interarea moderately high, triangular, apsacline; delthyrium wide, closed by robust pseudodeltidium, the latter lacks growth lines; fold and sulcus narrow, slightly to moderately developed; tongue very low, more or less rounded in outline; ribs numerous, low, rounded and increasing by bifurcation in sulcus and on fold; micro-ornament of closely spaced growth lines (though the presence of capillae and pustules is not excluded); dental plates robust, divergent but converging dorsally in umbonal region, extrasinal posteriorly then becoming subsinal or intrasinal anteriorly and extending to about 30% of the shell length; central apical cavity moderately filled in by callus that is rounded in shape, lateral apical cavities large and moderately filled by callus; delthyrial plate short; ctenophoridium composed of numerous vertical lamellae and supported by a strong callosity; hinge plates divided.

Occurrence.—This species characterizes the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) (Fig. 3). Previously, it was reported from the Baghrsagh and Danzik sections in Nakhichevan and from the Noravank section in Armenia (Arakelyan, 1964) (Fig. 1).

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

Ventral valve strongly inflated, rounded pentagonal in outline, with convex flanks sloping steeply towards lateral commissures; highest in the posterior third of the valve, then progressively decreasing towards anterior margin; umbo strongly inflated, large and prominent; beak small, erect to incurved; interarea apsacline, moderately high, well-defined, concave; delthyrium wide, the type of delthyrial cover is unkown as only some of the remnants are partially preserved in one of the collected specimens (IGSNASRAGM 3975/PS 3081; Pl. 10.25–10.26); sulcus very narrow, shallow, originating from beak, well-defined, with gentle margins, round-bottomed at front; tongue very low, more or less rounded in outline, perpendicular to commissural plane.

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

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

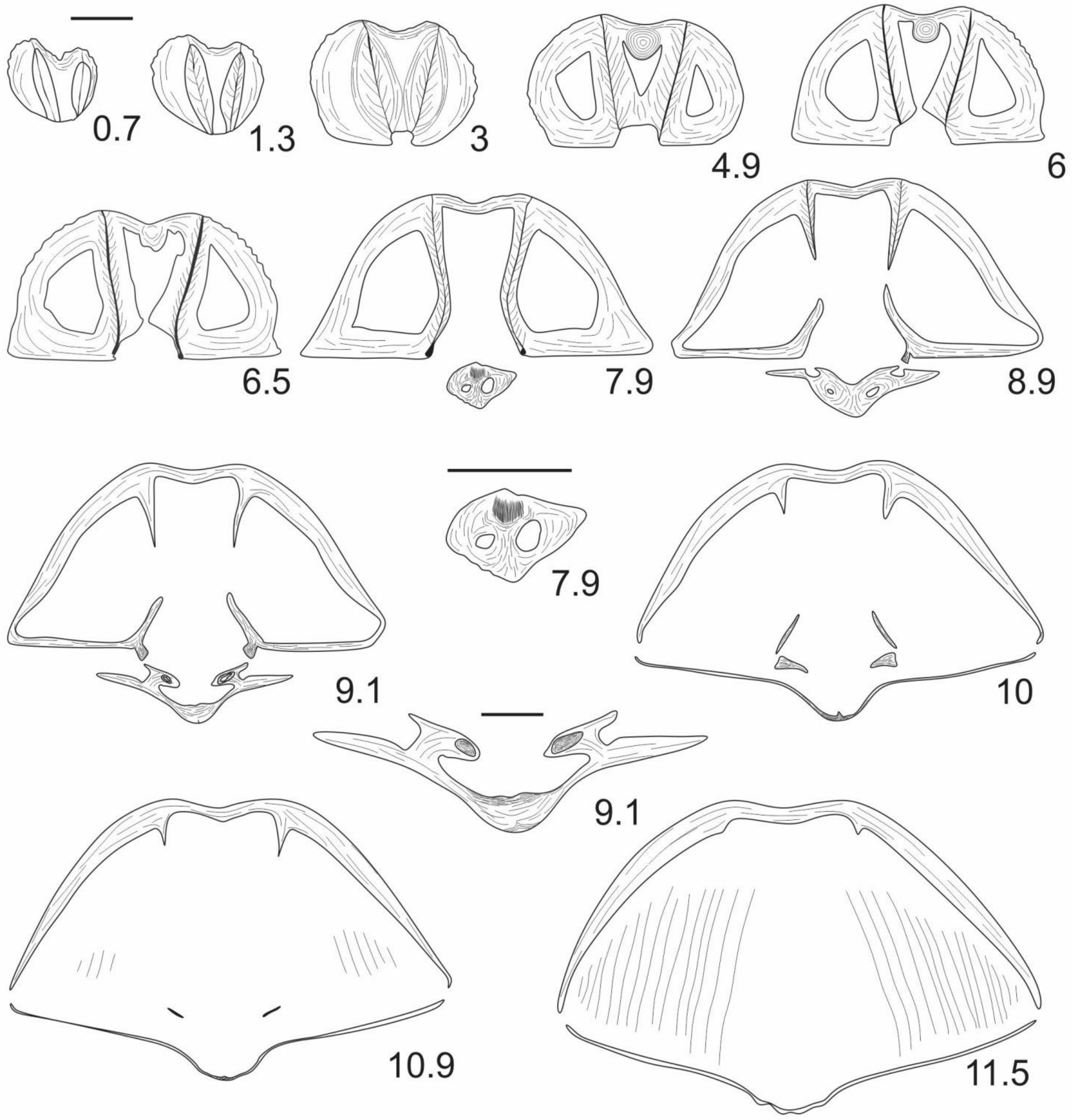


Figure 45. Transverse serial sections of *Angustisulcispirifer arakelyani* n.gen, n. sp. (IGSNASRAGM 3969/PS 3075) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), Noravank section. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

Ventral valve interior (Fig. 45) with strong dental plates, extrasinal posteriorly but subsinal or intrasinal anteriorly, generally divergent (21–26 degrees) but converging dorsally in umbonal region (as seen in transverse section); delthyrial plate short (Pl. 10.27); central apical cavity filled in by a stout and knob-like callosity on its floor (Fig. 45, serial sections 4.9–6.5); lateral apical cavities large and moderately filled in by callus; teeth relatively small, but stout.

Dorsal valve interior with ctenophoridium (Fig. 45) composed of up to 25 well-developed, long lamellae and supported by a strong apical callus; myophragm low; hinge plates divided; crural bases dorsally convergent; spiralia oriented posterolaterally, with at least 15 whorls per spiral cone.

Material.—Forty-two articulated specimens and five dissociated valves from the limestone beds of the Baghrsagh Regional Stage of the Noravank (twenty-five articulated specimens and three ventral valves), Ertych (ten articulated specimens) and Djravank (seven articulated specimens and two ventral valves) sections.

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

Shell ontogeny.—Juvenile forms differ from adults by their inconspicuous umbones, suberect beak, low fold and poorly developed sulcus. The beak inclination angle increases progressively with ontognetic growth. The size distributions during growth, as illustrated by the various plots of Figure 46, show a continuous and progressive growth with possibly three-four distinct growth stages. However, the factors caused this grouping effect remain unknown. The relative proportions of *Angustisulcispirifer arakelyani* n. gen., n. sp. represented by sufficient material remain constant (linear regression: $y = ax+b$; significant probability value: $p < 0.001$*** whatever the degree of development of individuals (Fig. 46)). 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 *A. arakelyani* n. gen., n. sp. are also represented in Table 9.

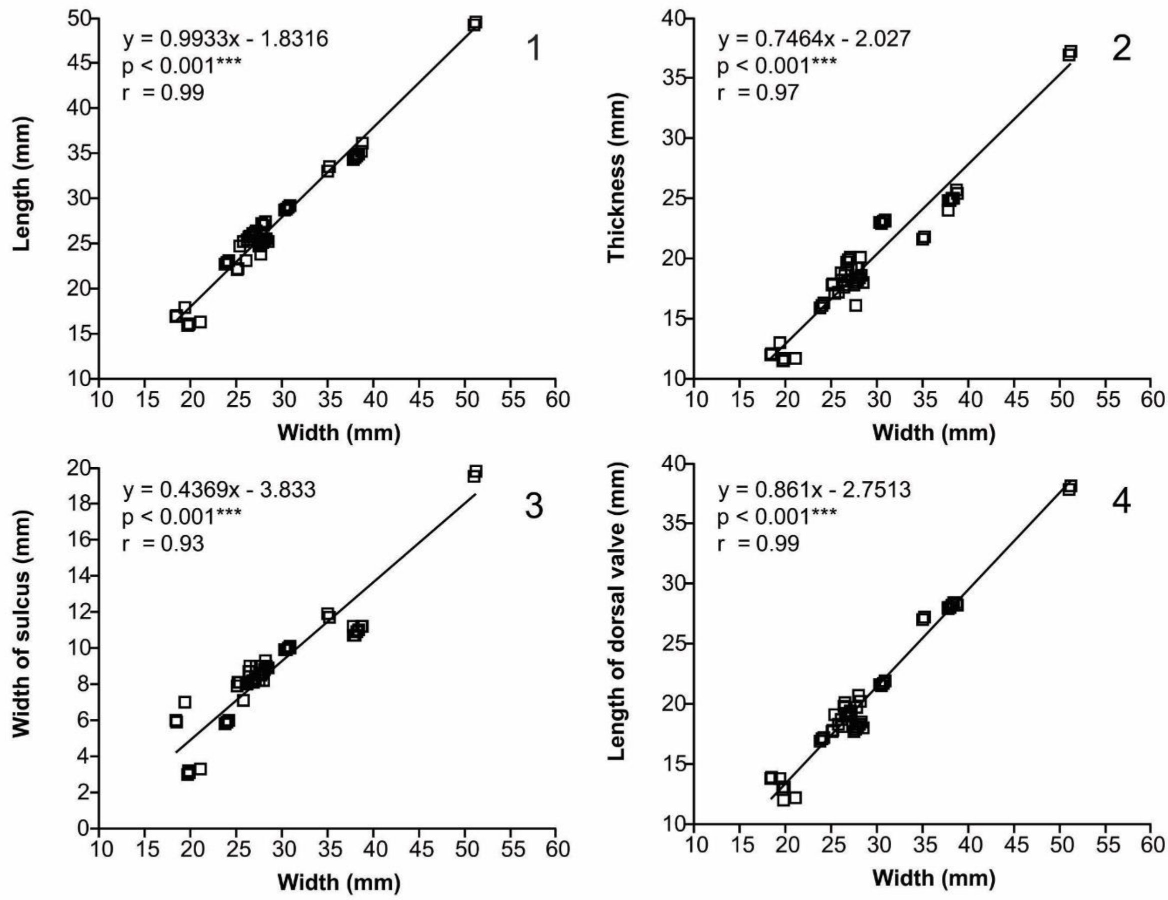


Figure 46. Scatter diagrams of *Angustisulcispirifer arakelyani* n. gen., n. sp. 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. 4, Relation between shell width and length of dorsal valve. Abbreviations: *n*, number of specimens measured; $y=ax+b$, linear model; *r*, coefficient of correlation; *p****, significant probability value.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	50	50	50	50	50	50	50	50	50
Mean value	29	26.91	22.44	20.6	8.8	0.92	0.67	0.3	0.71
Standard deviation	7.131	7.0832	21.55	5.7482	3.1153	0.0495	0.049	0.051	0.04
Standard error±	±1.0084	±1.002	±1.1783	±0.8129	±0.4406	±0.007	±0.007	±0.0071	±0.006
Min	18.4	15.9	11.5	12	3	0.77	0.55	0.15	0.58
Max	51.2	49.5	37.2	38.1	19.8	0.98	0.76	0.39	0.77

Table 9. Measurements in mm and ratios of *Angustisulcispirifer arakelyani* n. gen., n. sp. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus, dL–length of the dorsal valve.

Remarks.—Although the biostratigraphic significance of *Angustisulcispirifer arakelyani* n. gen., n. sp. has been known for a while, the latter was never illustrated and its internal characters were not examined so far. Moreover, *A. arakelyani* n. gen., n. sp. was mistakenly confused with *Spirifer verneuili* var. *subarchiaci* Martelli, 1902 (= *Plicapustula subarchiaci* (Martelli, 1902) *sensu* Ma and Day (2007)) from the middle Famennian of southeastern China, since Arakelyan (1952) used this taxon name until now. The Armenian material differs from Martelli's species by its more globular and inflated shell as well as by its poorly developed fold and sulcus. Internally, the new species is distinguished by its short delthyrial plate and strong dental plates.

Comparison with the other species.—*Angustisulcispirifer arakelyani* n. gen., n. sp. is very close to *Uchtospirifer subarchiaci* (Martelli, 1902) *sensu* Afanasjeva in Alekseeva et al. (2018b) from the Frasnian of Nakhichevan (e.g., subpentagonal shell outline, dorsibiconvex lateral profile, inflated umbones, ventral triangular and apsacline interarea, shallow sulcus and low fold, simple ribs on flanks, bifurcating in sulcus and on fold, the presence of a well-developed delthyrial plate and myophragm), which is also evidently confused with Martelli's species and needs to be re-investigated. However, the Armenian material is distinguishable by its wide hinge line, higher ventral interarea and less inflated shell. It is worth noting that Afanasjeva in Alekseeva et al.

(2018b: text-fig. 102) illustrated the internal morphology of her material by only one serial section showing only the ventral interior and thus further evidences are needed to point out other similarities and differences concerning internal morphology of these two species.

The new species shares several similarities with two species recognized from the Famennian of Central Kara-Tau, namely *Cyrtospirifer* (*C.*) *kursaensis* Sidjachenko, 1962 and *C.* (*C.*) *limatus* Solkina in Sidjachenko (1962), but it also differs from them by its weakly developed fold and sulcus, very low tongue more or less rounded in outline, and by the presence of a stout and knob-like callosity developed in the ventral valve.

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

Subfamily Cyrtiopsinae Ivanova, 1972

Genus *Tornatospirifer* new genus

Type species.—*Cyrtiopsis senceliae armenica* Abrahamyan, 1974, lower Famennian, Armenia.

Other species.—*Cyrtiopsis caucasia* Grechishnikova, 1986 is considered here as a junior synonym of the type species of *Tornatospirifer* n. gen. as we observed all superficial features that were supposed to separate the latter from Abrahamyan's species. *Cyrtiopsis senceliae* Sartenaer *sensu* Sidjachenko (1962) and *Cyrtospirifer* (*Cyrtospirifer*) *helenae* Sidjachenko, 1962 from Central and southeastern Kara-Tau (Kazakhstan) are allocated to this genus although the pseudodeltidium and micro-ornament of the latter are unknown due to poor preservation. *Spirifer* (*Cyrtospirifer*) *archiaci*

Murchison *sensu* Nalivkin (1937) also from Central Kara-Tau may be considered for assignment to this genus, but it is impossible to assign it with certainty as its internal morphology and micro-ornament are unknown. *Spirifer murchisonianus* de Koninck *sensu* Reed (1922: pl. 10, figs. 3–12; pl. 11, figs. 1–7) from the Famennian (excluding the lowermost and uppermost Famennian according to Sartenaer, 1970) of Pamir (Tajikistan) probably belongs to the new genus. Although Reed (1922) did not illustrate serial sections, he mentioned the presence of dental plates and dorsal median septum (he apparently observed the development of a callus supporting the ctenophoridium) that fit well with the diagnosis of *Tornatospirifer* n. gen.

Diagnosis.—Shell medium-sized, ventribiconvex, rounded subpentagonal, brachythyrid with obtuse or rounded cardinal extremities (though the latter are worn in most of the studied specimens); ventral interarea triangular, high, apsacline; delthyrium relatively wide, covered by a pseudodeltidium formed by several distinct plates; fold and sulcus wide, well-defined; ribs numerous, simple on flanks, increasing by bifurcation in sulcus and on fold; micro-ornament of closely spaced growth lines, cappilae occurring only on ribs and numerous pustules developed only capillae; dental plates long, strong, intrasinal; delthyrial plate well-developed; ctenophoridium supported by an apical callosity; hinge plates divided.

Occurrence.—Lower Famennian of Armenia and Nakhichevan, probably the Famennian of Pamir (Tajikistan) and likely the Famennian of Central and southeastern Kara-Tau (Kazakhstan).

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

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

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

Tornatospirifer n. gen. shares several external and internal similarities with the genus *Uchtospirifer* Ljashenko, 1957 *sensu* Sokiran (2006). More particularly, both genera display a brachythyrid shell, subpentagonal in outline and ornamented with closely spaced and flattened ribs, an apsacline and triangular ventral interarea, as well as intrasinal and divergent dental plates. However, *Tornatospirifer* n. gen. is differing by its more globular shell, the type of pseudodeltidium (formed by several distinct plates), the development of ribs in sulcus and on fold that are not transforming into capillae, flattening or disappearing as it is observed in *Uchtospirifer* representatives. Internally *Tornatospirifer* n. gen. is distinguished by its supported ctenophoridium whereas the latter is unsupported in *Uchtospirifer*.

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

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

Tornatospirifer n. gen. mainly differs externally from *Dichospirifer* Brice 1971, as revised by Mottequin and Brice (2019), by its high ventral interarea, 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)

Plates 12–13; Figures 47–48; Table 10

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.

2018a *Cyrtiopsis caucasia* Grechishnikova; Grechishnikova in Alekseeva et al., p. 855.

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

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

Neotype.—After extensive search at the Geological Museum of Yerevan, none of the syntypes illustrated by Abrahamyan (1974: pl. 21, fig. 1, pl. 22, fig. 4) was recovered from Abrahamyan's collection; they are therefore considered as lost. Consequently, one of the recently collected specimens from the Ertych Regional Stage (lower Famennian) of the Shamamidzor section (type locality) (Lanjanist village, Ararat province, West Central Armenia; Fig. 1) is hereby designated as the neotype (IGSNASRAGM 3980/PS 30488) and figured in Plate 13.1–13.8.

Occurrence.—This species defines the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957), as well as the *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone of Rzhonsnitskaya and Mamedov (2000) (Fig. 3) both in Armenia and Nakhichevan. Formerly, *T. armenicus* was documented from the Ertych Regional Stage of the Ertych, Noravank, Shamamidzor and Zangakatun sections in Armenia (Abrahamyan, 1957; Arakelyan, 1964) and from the Gyumushlug section in Nakhichevan (Abrahamyan, 1957; Grechishnikova, 1986) (Fig. 1).

Description.—Shell medium-sized (reaching 33.7 mm in width, 31.3 mm in length and 27.5 mm in thickness) (Table 10), slightly wider than long, ventribiconvex, rounded subpentagonal in 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) (Pl. 13.9); 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 (Pl. 13.7–13.8) of closely spaced growth lines (irregularly thickened as growth varices), capillae occurring only on ribs and numerous pustules developed on capillae.

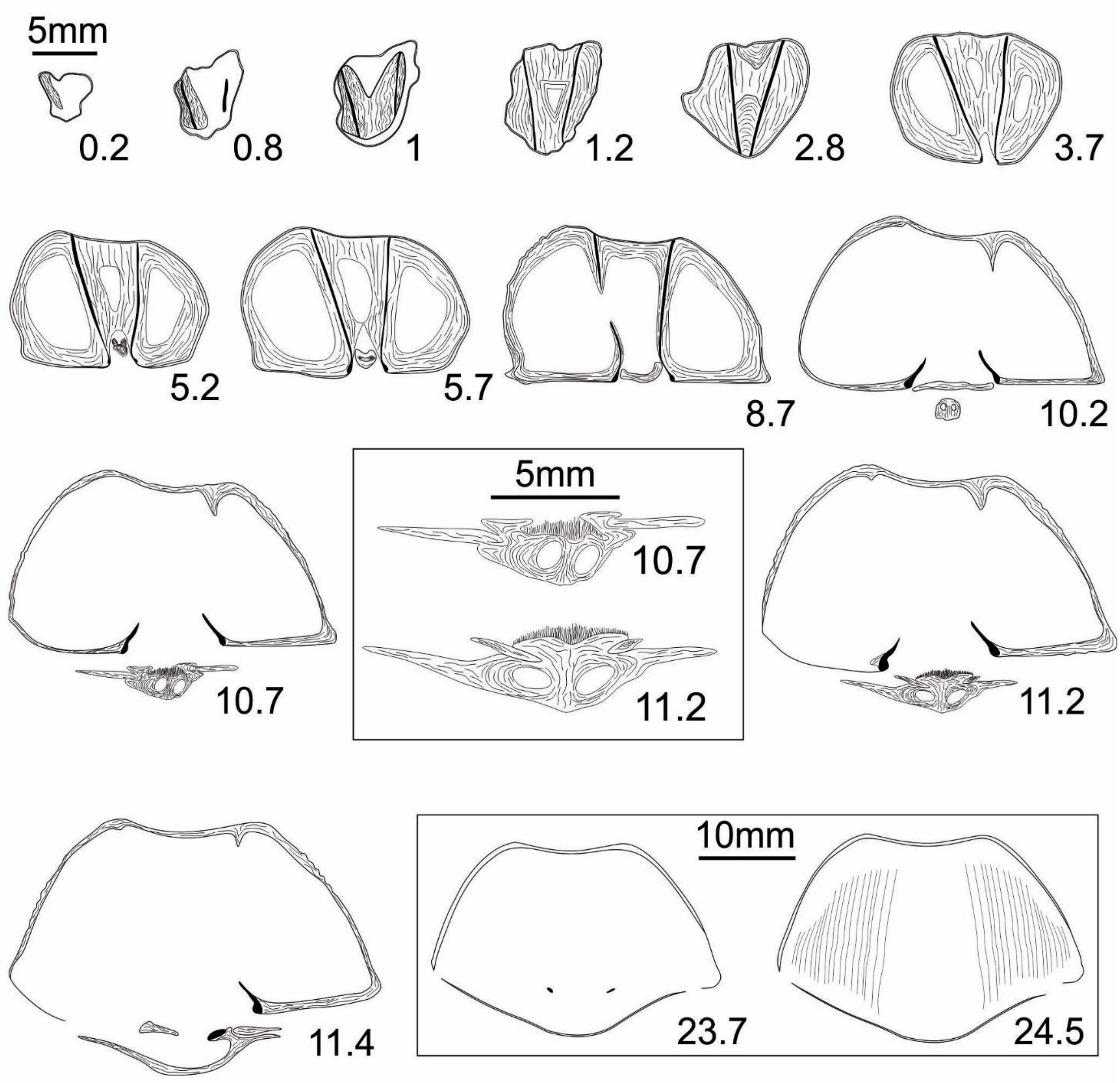


Figure 47. Transverse serial sections of *Tornatospirifer armenicus* (Abrahamyan, 1974) (IGSNASRAGM 3977/PS 3083), Djravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Ventral valve interior (Fig. 47) 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. 47) 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 Ertych (five articulated specimens and two dorsal valves), Djravank (18 articulated specimen and three ventral valves) and Noravank (12 articulated specimens, two ventral and two dorsal valves), and Shamamidzor (six articulated specimens, five ventral and two dorsal valves) sections.

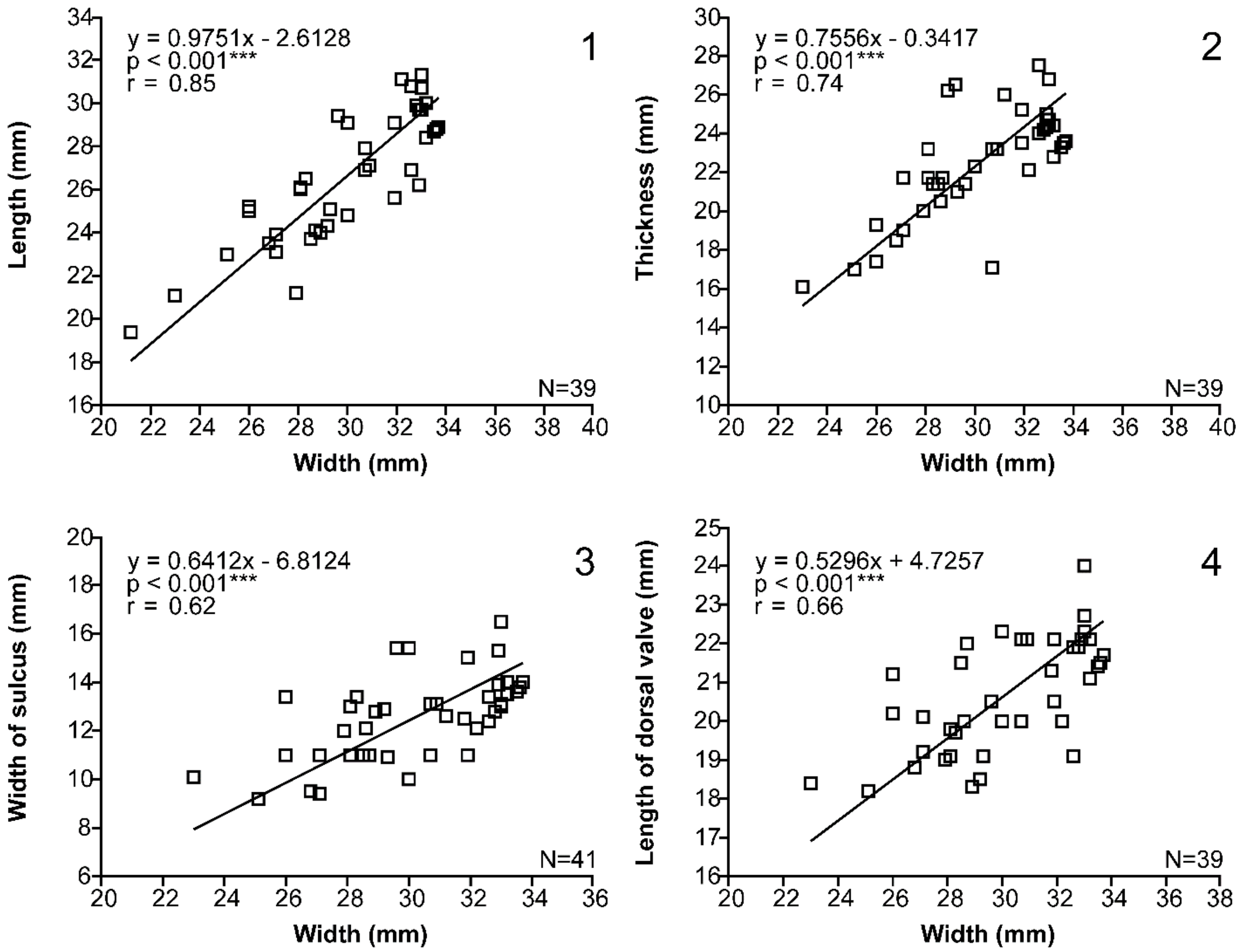


Figure 48. Scatter diagrams of *Tornatospirifer armenicus* (Abrahamyan, 1974). 1, Relation between shell width and length. 2, Relation between shell width and thickness. 3, Relation between shell width and width of sulcus. 4, Relation between shell width and length of dorsal valve. Abbreviations: *N*, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

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 grow stage. The size distribution during the growth, as represented by the width/length, the width/thickness, the width/width of sulcus and the width/length of dorsal valve plots, shows a continuous and progressive growth with no distinct grouping (Fig. 48). 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. 48)). Moreover, the correlation is positive with width varying proportionally with length, thickness, width of sulcus and the length of dorsal valve. The length/width of the dorsal valve shows less dispersed values (Fig. 48). To complete the scatter plots, the measurements (in mm) of numerous individuals of *Tornatospirifer armenicus* (Abrahamyan, 1974) are also presented in Table 10.

	W	L	T	Ws	dL	L/W	T/W	Ws/W	W/dL
Number of individuals	42	39	39	41	40	39	39	41	39
Mean value	29.97	26.57	22.44	12.54	20.7	0.89	0.74	0.42	0.69
Standard deviation	3.0263	3.0372	2.846	1.7461	1.46	0.0545	0.064	0.0466	0.0504
Standard error±	±0.467	±0.486	±0.4557	±0.2727	±0.231	±0.0087	±0.0103	±0.0073	±0.0081
Min	21.2	19.4	16.1	9.2	18.2	0.76	0.56	0.35	0.59
Max	33.7	31.3	27.5	16.5	24	0.99	0.91	0.52	0.82

Table 10. 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.

Remarks.—Arakelyan (1952) initially identified this species as '*Cyrtospirifer murchisonianus*', a lower Frasnian representative of the genus *Uchtospirifer* from Russia (Ljashenko, 1959; Sartenaer, 1965b). 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* and she considered it as a subspecies of *Cyrtiopsis senceliae* Sartenaer, 1956 (= '*Pseudocyrtiopsis*' *senceliae,* see discussions in Ma and Day (1999) and Mottequin and Brice (2019)) known from the lower Famennian of southern Belgium, of which one of the paratypes (Sartenaer 1956: 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 statement cannot be accepted as the material from Armenia can be easily distinguished from *G. chakhaensis* by its outline (*G. chakhaensis* displays a rounded or ovate outline with rounded posterolateral commissures whereas the Armenian species displays rounded subpentagonal outline and almost straight posterolateral commissures), its pseudodeltidium formed by several distinct plates, its high ventral interarea, having more ribs in sulcus and on fold and lacking numerous pustules developed on capillae. Moreover, *T. armenicus* has a delthyrial plate, which is absent in *G. chakhaensis*. Afterwards, Aristov et al. (1979) raised Abrahamyan's (1974) subspecies to the species level. Grechishnikova (1986) erected *Cyrtiopsis caucasia* from the lower Famennian of Nakhichevan and indicated the similarity to *C. senceliae armenicus* coming from the same locality (Gyumushlug section; Fig. 1). The author compared her material with Abrahamyan's (1974) subspecies and mentioned that *C. caucasia* differs from the former by its triangular shell outline, smaller size, ventral triangular interarea and prominent ventral beak. Grechishnikova (1986: pl. 1. fig. 3) illustrated only the holotype, which was re-illustrated by Afanasjeva in Alekseeva et al. (2018b: pl. 29, fig. 5). The latter compared Grechishnikova's species and *C. senceliae* from Western Europe, China [*sic*] as well as Armenia, and indicated that the former differs by its subtriangular shell outline. Thus, she implicitly considered either that Abrahamyan's (1974) subspecies is still a subspecies of Sartenaer's (1956) species, or simply that she does not recognize *armenicus* as a valid subspecies. However, all of the external features mentioned by both Grechishnikova (1986) and Afanasjeva in Alekseeva et al. (2018b), which were supposed to point the differences, are also observed in Abrahamyan's species except the subtriangular shell outline that is not even observed in their material, as the holotype of *C. caucasia* is rounded subpentagonal in outline. Consequently, they certainly should be considered as intraspecific variations. Thus, we consider *Cyrtiopsis caucasia* as a junior synonym of Abrahamyan's species. As seen above, a great attention has been paid to this species 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.

Chapter 5

Brachiopod diversity, stratigraphy and paleobiogeography

5.1 Diversity and stratigraphic distribution of brachiopods in the studied sections

The Upper Devonian succession in our 3 studied sections yielded abundant and diverse brachiopod fauna. The brachiopods were primarily collected from Intervals 1 and 4; the other 2 intervals are mainly composed of siliciclastic/shaly rocks and did not really yield any brachiopods. The examination of these brachiopod specimens, both externally and internally, led us to identify altogether twenty-six species (Fig. 49). In total, twenty-one brachiopod species are described in the **Ertych section** among which ten come from the Interval 1 and eleven from the Interval 4. More particularly, rhynchonellides are scarce in the Interval 1, as it contains only two species: *Cyphoterorhynchus koraghensis koraghensis* (Reed, 1922) and *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959), whereas they are more diverse and abundant in the Interval 4 and represented by four species: *Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967), *Greira transcaucasica* Erlanger, 1993 and *Sharovaella*? sp (Fig. 49). The atrypide brachiopods occur only in the Interval 1 (Fig. 49); they are represented by three species: *Atryparia* (*Costatrypa*) *ertichensis* (Abrahamyan, 1959), *Spinatrypa* (*Spinatrypa*) sp. and *Desquamatia* (*Seratrypa*) *abramianae* Komarov, 1992. All three atrypide species appear not to be encountered above the layer Er19/4 and thus they occur only in the Interval 1 (Fig. 49). The Order Athyrida is represented by only one species *Crinisarina pseudoglobularis* Serobyan et al., 2021, which appears at the base of Interval 4 and then immediately becomes highly abundant. The abundance of this species decreased in the middle part of interval and again increased at the top (Fig. 49). In contrast to atrypide and athyride brachiopods, the spiriferides are relatively diverse both in the Interval 1 and Interval 4. In particular, the Interval 1 includes five species (Cyrtospiriferinae gen. et sp. 1,

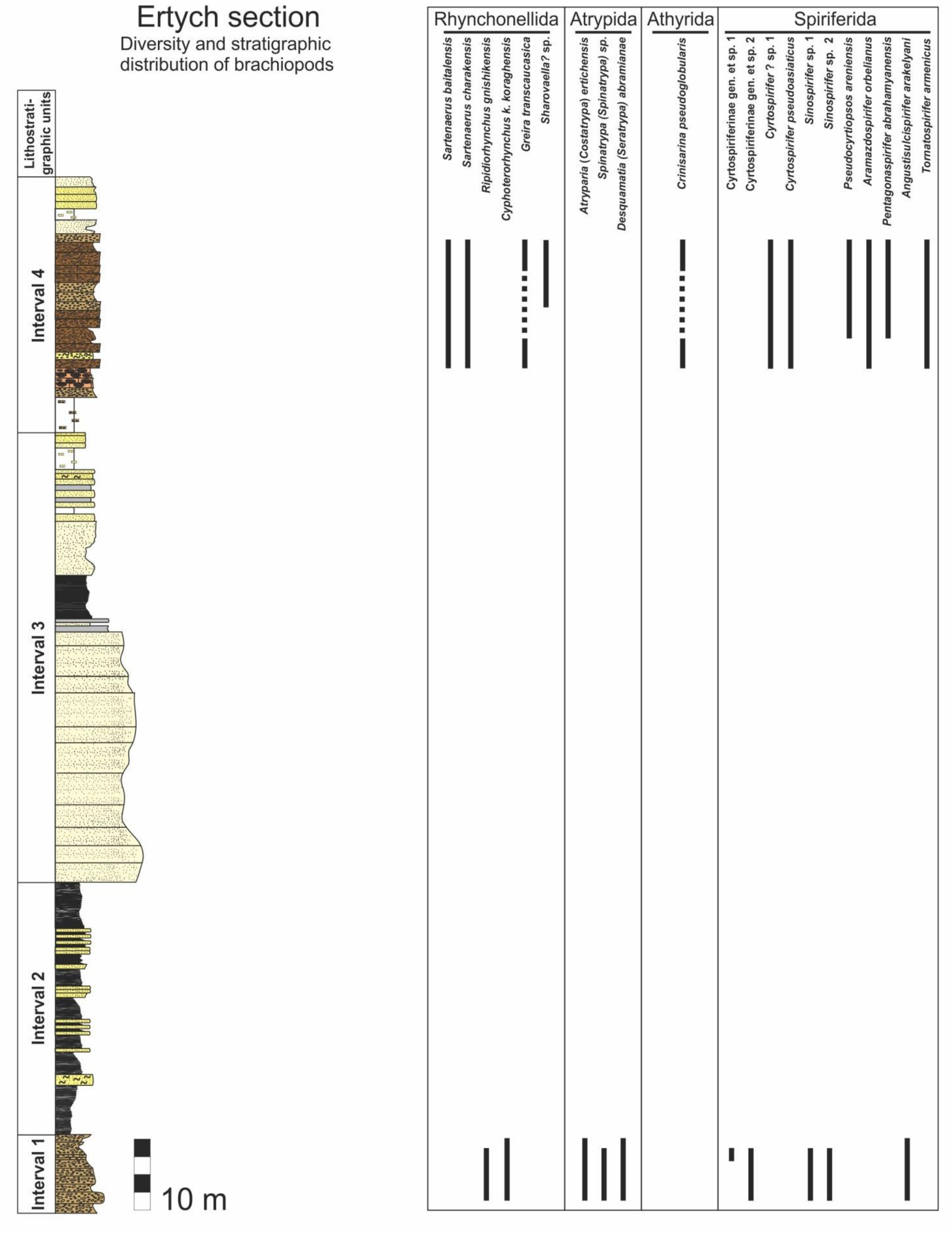


Figure 49. Diversity and stratigraphic distribution of brachiopods of the Ertych section.

Cyrtospiriferinae gen. et sp. 2, *Sinospirifer* sp. 1, *Sinospirifer* sp. 2, *Angustisulcispirifer arakelyani* n. gen., n. sp.), while the Interval 4 bears six spiriferides (*Cyrtospirifer*? sp., *Cyrtospirifer pseudoasiaticus* n. sp., *Pseudocyrtiopsis areniensis* n. sp., *Aramazdospirifer orbelianus* (Abich, 1858), *Pentagonaspirifer abrahamyanae* n. gen., n. sp. and *Tornatospirifer armenicus* (Abrahamyan, 1974)). Thus, spiriferides are more diverse and rich in the Interval 4 than in the Interval 1 (Fig. 49). Additionally, it should be noted that none of the spiriferides of Interval 1 were traced above this interval (Fig. 49). The sedimentary sequences of the **Djravank section** bear similar brachiopod faunas as those of the Ertych section (Fig. 50). In general, twenty species are described in this section, six of which were recovered from the Interval 1 and fourteen from the Interval 4. Most notably, the Interval 1 of Djravank section includes those two rhynchonellides (*Cyphoterorhynchus koraghensis koraghensis* (Reed, 1922) and *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959)), which are described at the base of the Ertych section. Regarding the Interval 4, in addition to those rhynchonellides (*Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967) and *Greira transcaucasica* Erlanger, 1993) observed in the Ertych section, I found three other species (*Porthmorhynchus*? sp., *Gesoriacorostrum*? sp., *Ripidiorhynchus djravankensis* n. sp.). Furthermore, it is worthwhile to emphasize that *Sharovaella*? sp. was not found in the Djravank section. The Order Atrypida is represented by only a single species *Desquamatia* (*Seratrypa*) *abramianae* Komararov, 1992 occurring only in the Interval 1. The spiriferides of Djravank section are represented by nine species. Most notably, the Interval 4 encloses seven species, when the Interval 1 includes only two spiriferides. Additionally, it is important to note that *Cyrtospirifer*? sp. 2 and *Cyrtospirifer* sp. 1 are found only in this section. In the Djravank section the Order Athyrida is represented by only one species *Crinisarina pseudoglobularis* Serobyan et al., 2021 that occurs within the Interval 4 as is the case of the Ertych section. Brachiopods found in the **Noravank section** are only represented by fourteen species, of which ten are documented from the Interval 4 and only four from the Interval 1 (Fig. 51). More particularly, the Interval 1 includes only one rhynchonellide species (*Cyphoterorhynchus*

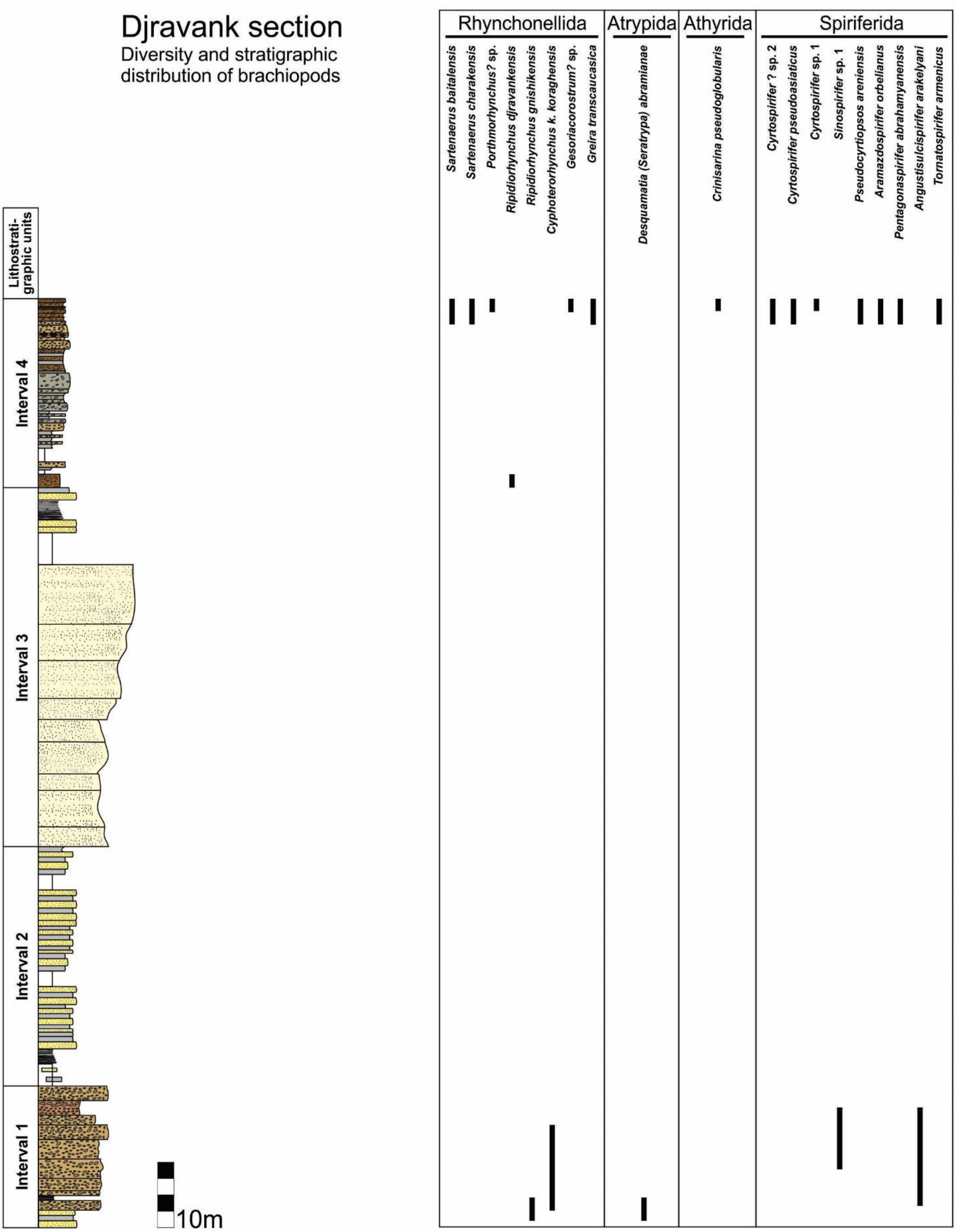


Figure 50. Diversity and stratigraphic distribution of brachiopods of the Djravank section.

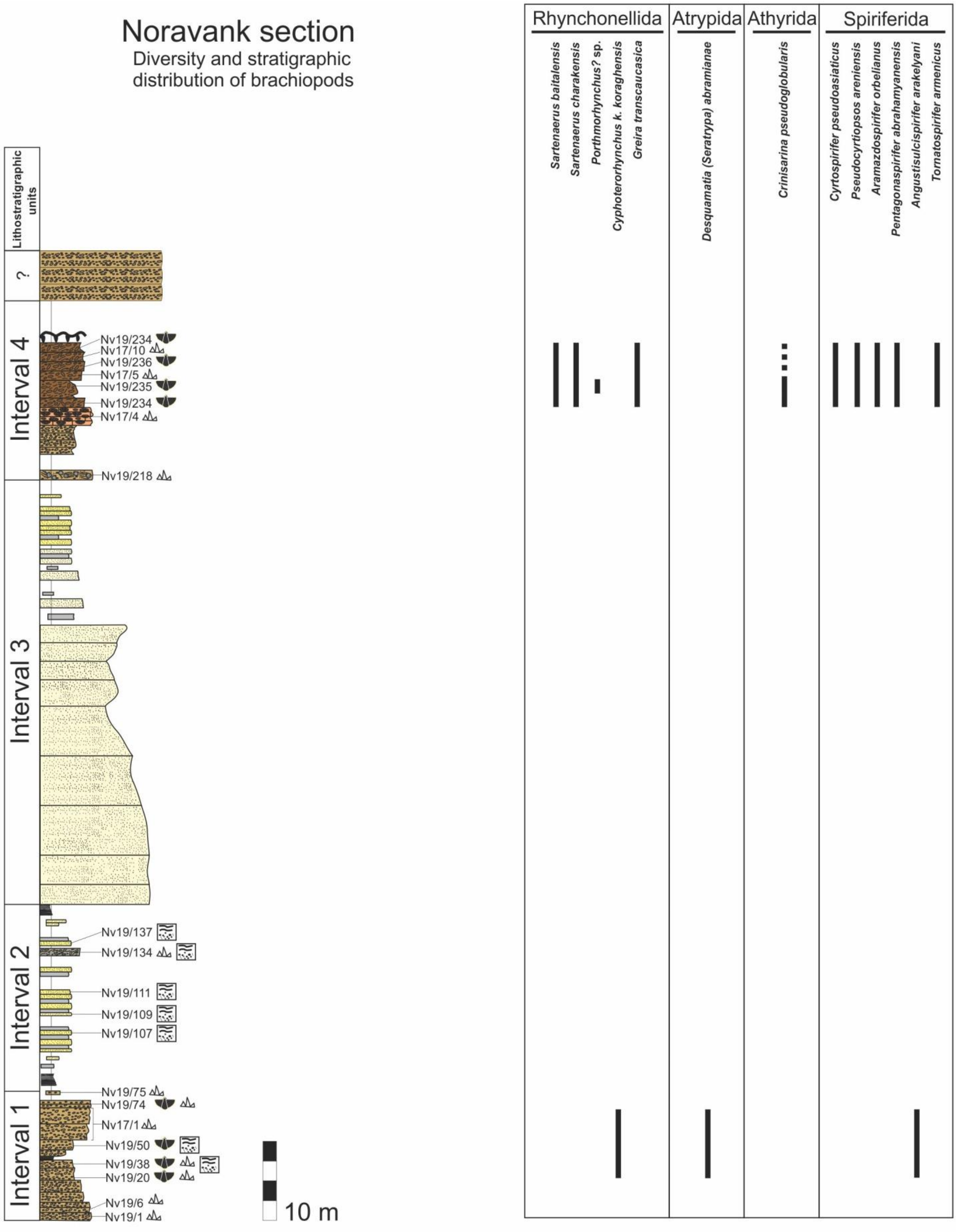


Figure 51. Diversity and stratigraphic distribution of brachiopods of the Noravank section.

koraghensis koraghensis (Reed, 1922), while the Interval 4 contains four (*Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967), *Greira transcaucasica* Erlanger, 1993 and *Porthmorhynchus*? sp.). The Order Atrypida is represented by a single species (*Desquamatia* (*Seratrypa*) *abramianae* Komararov, 1992) in the Interval 1, as is the case of the Djravank section. The spiriferides are also relatively scarce by only six species of which only one occurs in the Interval 1 and those 5 in the Interval 4 (Fig. 51). The species documented from these three sections belong to the orders Rhynchonellida, Atrypida, Athyrida and Spiriferida. Interestingly, none of the species of Interval 1 is documented also in the Interval 4 (Figs. 49–51).

5.2 Bio- and chronostratigraphy

The Devonian brachiopod assemblages are extensively applied in biostratigraphic correlations of shallow water successions in the Lesser Caucasus. However, the biostratigraphic framework of the Lesser Caucasus based on brachiopods still remains largely undocumented. This is probably due to the poorly constrained stratigraphic sections and the lack of standard biostratigraphic markers such as conodonts, which precludes detailed dating. The brachiopods recovered from our studied sections belong to two distinct assemblages (Fig. 52). The first assemblage is described in the Interval 1, which may be correlated with the assemblage of Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) as it contains several taxa that are typical for the latter zone (e.g., *Ripidiorhynchus gnishikensis*, *Cyphoterorhynchus koraghensis koraghensis*, *Atryparia* (*Costatrypa*) *ertichensis*). Rzhonsnitskaya and Mamedov (2000)'s zone is correlated with the *transitans*–*punctata* conodont zones. Consequently, it can be reasonably assumed that the brachiopod assembalge described from the Interval 1 also corresponds to the *transitans*–*punctata* conodont zones. However, neither *Cyphoterorhynchus arpaensis* (Abrahamyan, 1957) nor *Cyrtospirifer subarchiaci sensu* Rzhonsnitskaya and Mamedov (2000) (=*Angustisulcispirifer subarchiaci* [sic!]) was not revealed by the recent sampling in our sections. Therefore, I suggest using *Ripidiorhynchus gnishikensis* and *Angustisulcispirifer arakelyani* n. gen., n. sp. for defining this biozone in Armenia, as the latter species are abundant and restricted in the Frasnian strata. Moreover, *R. gnishikensis* has been also described in Nakhichevan (Pakhnevich 2018 in Alekseeva et al., 2018a). Consequently, I thereby establish a new assemblage brachiopod zone, namely the *Ripidiorhynchus gnishikensis*–*Angustisulcispirifer arakelyani* that may be correlated with the *transitans*–*punctata* zones (Fig. 53). Biostratigraphically speaking, this biozone corresponds to the Baghrsagh Regional Stage of Arakelyan (1964) as the limestone layers, where the assemblage was found, include brachiopod species (e.g., *Angustisulcispirifer arakelyani*, *Cyphoterorhynchus koraghensis koraghensis Atryparia* (*Costatrypa*) *ertichensis*), which Arakelyan

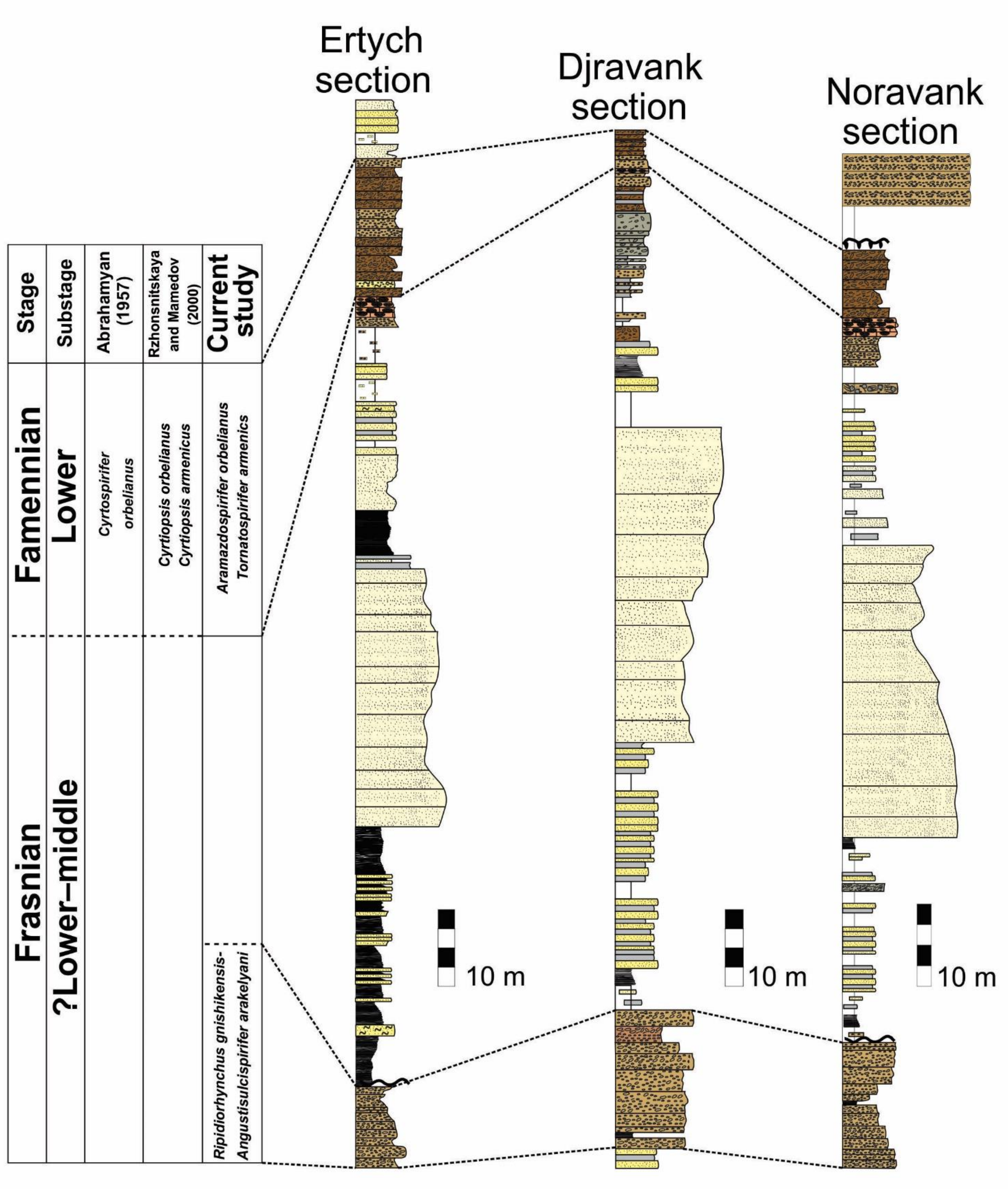


Figure 52. Biochronostratigraphic framework and the correlation of three studies section based on the newly established brachiopod biozones and the biozonation schemes of Abrahamyan (1957) in Central Armenia and Rzhonsnitskaya and Mamedov (2000) in Nakhichevan.

considered the most significant while establishing the latter horizon. The Intervals 2 and 3 are mostly composed of siliciclastic rocks and yielded a few poorly preserved rhynchonellids, which were impossible to identify. These intervals together appear to constitute the Noravank Regional Stage. Only at the transition between the intervals 3 and 4, a rhynchonellide species *Ripidiorhynchus djravankensis* n. sp. is described, but it is impossible to speak about a biozone as this species is observed only in the Djravank section. The second brachiopod assemblage comes from the Interval 4 (Fig. 52), which is lower Famennian in age. First of all, it is worth to emphasize that there are different brachiopod biozones established for the lower Famennian (Fig. 53). More particularly, in the scheme of Abrahamyan (1957), the lower Famennian is characterized by the *Cyrtospirifer orbelianus* taxon-range Zone (Fig. 52). Grechishnikova et al. (1980) also recognized a single biozone within the lower Famennian interval, but termed it *Mesoplica meisteri* Zone. This scheme was further updated by Alekseeva et al. (2018a) and renamed the *Cyrtospirifer asiaticus*–*Mesoplica meisteri* Zone (Fig. 53). In contrast to these authors, Rzhonsnitskaya and Mamedov (2000) recognized two brachiopod biozones: the lowest Famennian *Mesoplica meisteri*–*Cyrtospirifer asiaticus* and the lower Famennian *Cyrtiopsis orbelianus*–*Cyrtiopsis armenicus* zones (Fig. 53). The examination of the brachiopod assemblage from the Armenian sections shows that the lower Famennian is represented herein by only one biozone, which is devoid of *Mesoplica meisteri* (Peetz, 1901) [=*Ardiviscus meisteri* (Peetz, 1901)] and *Cyrtospirifer asiaticus* (Brice, 1971). Instead, it is highly rich in *Aramazdospirifer orbelianus* (Abich, 1858) and *Tornatospirifer armenicus* (Abrahamyan, 1974) species, both of which appear together within the same level: above the oncolitic grainstone layer (e.g., Er19/92, Nv17/4), wherein Ginter et al. (2011) described conodont elements indicating the *crepida* conodont Zone. Therefore, I propose to use both species for recognizing the lower Famennian strata (*crepida* Zone) in the Armenian sections, taking into account their taxonomic update. It is also worth to remind here that the *crepida* Zone is coeval to the *Polygnathus brevilaminus*–*Icriodus cornutus* conodont Zone of Aristov (1994). This biozone corresponds to the Ertych Regional Stage of Arakelyan (1964).

Figure 53. Biochronostratigraphic framework of the lower/middle Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus, including the correlation of the newly established brachiopod biozones in Central Armenia with the biozones of Abrahamyan (1957) in Central Armenia and of Grechishnikova et al. (1980), Rzhonsnitskaya and Mamedov (2000), Alekseeva et al. (2018a, b) 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).

Stage	Sub-stage	Regional stages	Brachiopod zones					Conodont zones	
		Arakelyan (1964)	Abrahamyan (1957)	Grechishnikova et al. (1980)	Rzhonsnitskaya and Mamedov (2000)	Alekseeva et al. (2018 a, b)	Current study	Local (Aristov, 1994)	Standard (Ziegler and Sandberg, 1990)
Famennian	lower	Ertych	*Cyrtospirifer orbelianus*	*Mesoplica meisteri*	*Cyrtiopsis orbelianus*–*Cyrtiopsis armenicus*	*Cyrtospirifer asiaticus*–*Mesoplica meisteri*	*Aramazdospirifer orbelianus*–*Tornatospirifer armenicus*	*Polygnathus brevilaminus Icriodus cornutus*	*crepida* Um U M L
		Noravank			*Mesoplica meisteri*–*Cyrtospirifer asiaticus*			*Polygnathus brevilaminus*	*triangularis* U M L
Frasnian	upper		*Cyrtospirifer lonsdalii*, *Productella herminae*, *Camarotoechia radiata arpaensis* and five other species	*Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis*	Unzoned	Quartzite member		Unzoned	*linguiformis*; *rhenana* U L
	middle								*jamieae*; *hassi* U L
	lower	Baghrsagh			*Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis*	*Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis*	*Ripidiorhynchus gnishikensis*–*Angustisulcispirifer arakelyani*	*Ancyrodella rotunbiloba*	*punctata*; *transitans*; *falsiovalis* U
Giv.	up.							*Ancyrodella binodosa*	*falsiovalis* L

5.3 Diversity and assemblages of brachiopods across the F–F interval

The consequences of the Kellwasser Biocrisis on the brachiopods from the Lesser Caucasus and their post-crisis recovery remain largely undocumented until now. Moreover, in the absence of standard biostratigraphic markers such as conodonts, the precise location of the F–F boundary remains unclear. However, it is possible to assess the diversity of the brachiopods prior to this crisis and after it, on the basis of current results that are additionally complimented by published data (Fig. 54), keeping in mind that the conodont biozonation adopted herein dates back to Aristov (1994). Additionally, it is worth noting that only those occurrences are included, which are illustrated and/or further confirmed by other studies; however, some of them might need modern taxonomic reassessment. In this study, twenty-six brachiopod species are described from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), which corresponds to the *transitans–punctata* conodont zones and from the lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone of Rzhonsnitskaya and Mamedov (2000), equivalent to the *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957). The latter biozone is correlated with the *crepida* conodont Zone. There are also twenty-six other species documented previously by Abrahamyan (1957, 1974), Arakelyan (1964) and Alekseeva et al. (2018a, b) from F–F interval, which were not found during our field trips. Up to now, all the described brachiopod species belong to the orders Orthotetida, Productida, Rhynchonellida, Atrypida, Athyrida and Spiriferida. More particularly, the only representative of the Order Orthotetida in the Lesser Caucasus was documented by Abrahamyan (1957) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone. It appears that *Schuchertella* sp. did not cross the F–F boundary (Fig. 54). Whereas the order Productida was more diverse with six species, of which two (*Devonoproductus* sp., *Productella subaculeata* (Murchison, 1840)) were described in the Frasnian

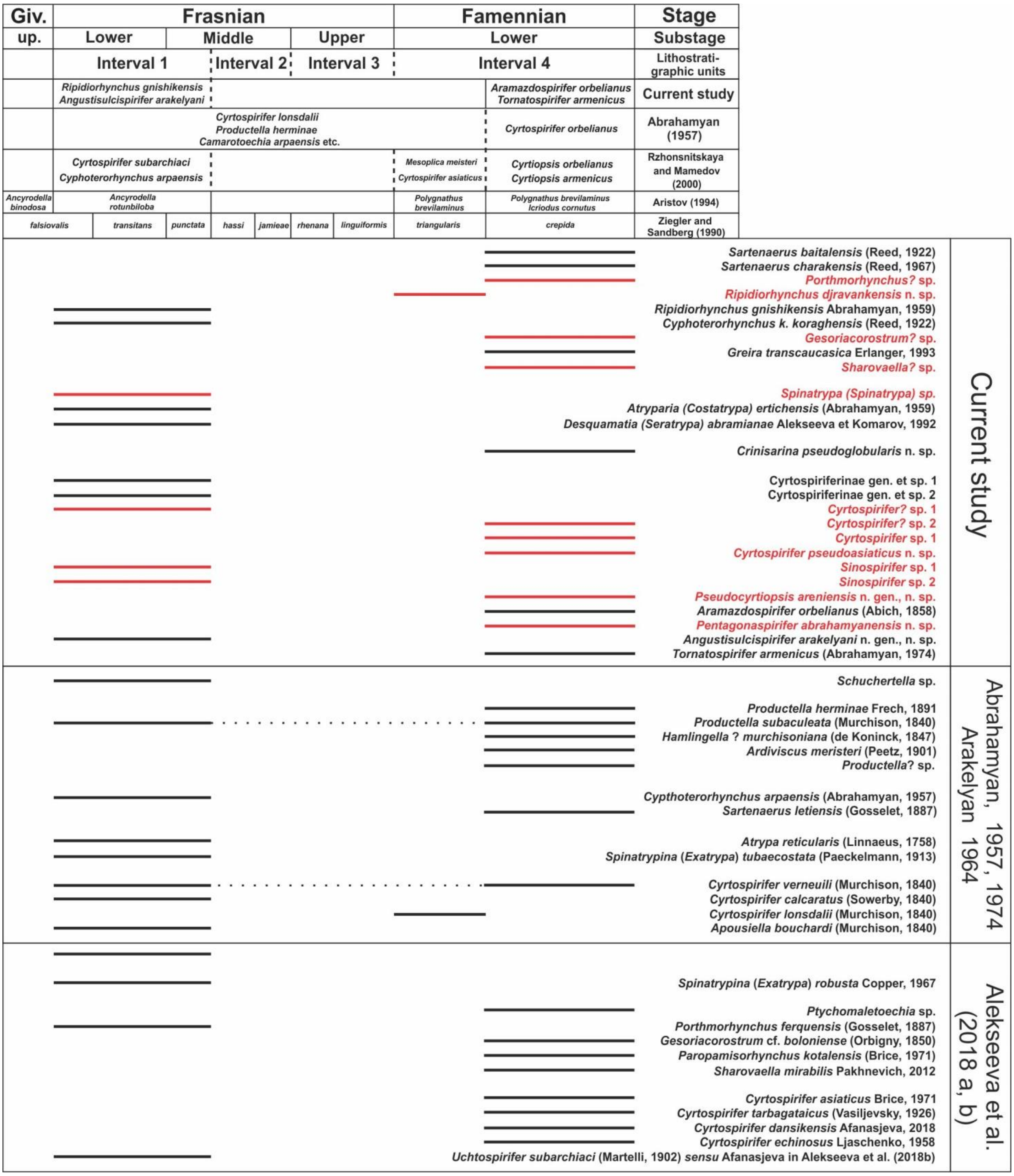


Figure 54. Biostratigraphic distribution of brachiopods reported from the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus that includes the described both in the current study and those which were known before from the studies of Abrahamyan (1957, 1974), Arakelyan (1964) and Alekseeva et al. (2018a, b). Red color indicates the species that were unknown before this study.

and five species (*Productella subaculeata* (Murchison, 1840), *Productella herminae* Frech, 1891, *Productella*? sp., *Ardiviscus meristeri* (Peetz, 1901) and *Hamlingella* ? *murchisoniana* (de Koninck, 1847)) *sensu* Abrahamyan (1974) in the lower Famennian *Cyrtiopsis orbelianus*–*Cyrtiopsis armenicus* Zone; *Productella subaculeata* (Murchison, 1840) appears to overcome the F–F boundary successfully (Fig. 54). Two rhynchonellide species *Cyphoterorhynchus koraghensis koraghensis* (Reed, 1922) and *Ripidiorhynchus gnishikensis* (Abrahamyan, 1959) are described in this study from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in addition to *Cyphoterorhynchus arpaensis* (Abrahamyan, 1957) and *Porthmorhynchus ferquensis* (Gosselet, 1887), which were described previously by Abrahamyan (1957) and Pakhnevich in Alekseeva et al. (2018a). Therefore, it appears that the rhynchonellides are represented by only two subfamilies Trigonirhynchiinae and Ripidiorhynchinae in the Frasnian of the Lesser Caucasus. Although, *R. gnishikensis* disappeared in the Frasnian, the genus evidently crossed the F–F boundary in the Armenian sections and was represented in the lower Famennian by *R. djravankensis* n. sp., which apparently originated from the former species. In spite of a low diversity of rhynchonellides in the Frasnian, the lower Famennian marks a comparably high diversity, where the latter became one of the dominant groups with eleven species. Most notably, *R. djravankensis* n. sp. is described within the Noravank Regional Stage, while the other ten species come from the Ertych Regional Stage, which is correlated with the *orbelianus* Zone. This assemblage includes three species (*Sartenaerus baitalensis* (Reed, 1922), *S. charakensis* (Brice, 1967) and *S. letiensis* (Gosselet, 1887)) belonging to the Famennian genus *Sartenaerus* Özdikmen, 2008, one species (*Ptychomaletoechia* sp.) to the Famennian–Tournaisian genus *Ptychomaletoechia* Sartenaer, 1961 and two species (*Porthmorhynchus ferquensis* (Gosselet, 1887 and *Porthmorhynchus*? sp.) refer to *Porthmorhynchus* Sartenaer, 2001, which is mainly known from the middle–upper Frasnian. These genera are included in the Subfamily Trigonirhynchiinae. The subfamilies Ripidiorhynchinae and Greirinae here consist of two genera (Fig. 55), of which the

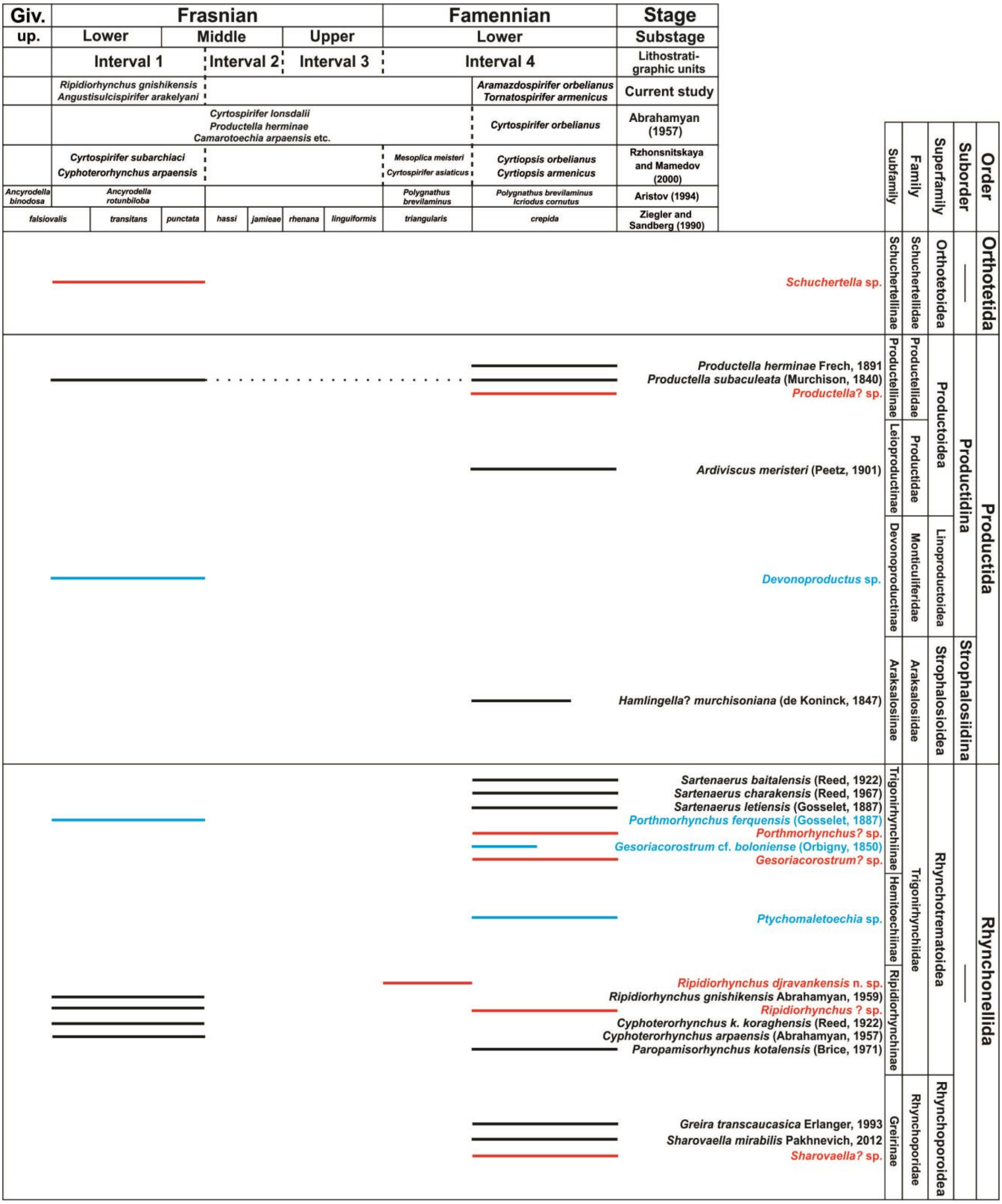


Figure 55. Biostratigraphic distribution of brachiopod species belonging to the order Orthotetida, Productia and Rhynchonellida reported from the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus. Red color indicates species which are known from Armenia based on the data of Abrahamyan (1957, 1974) and Arakelyan (1964); blue color indicates species reported from Nakhichevan (Alekseeva et al., 2018a, b); black color points those species that are known both from Armenia and Nakhichevan.

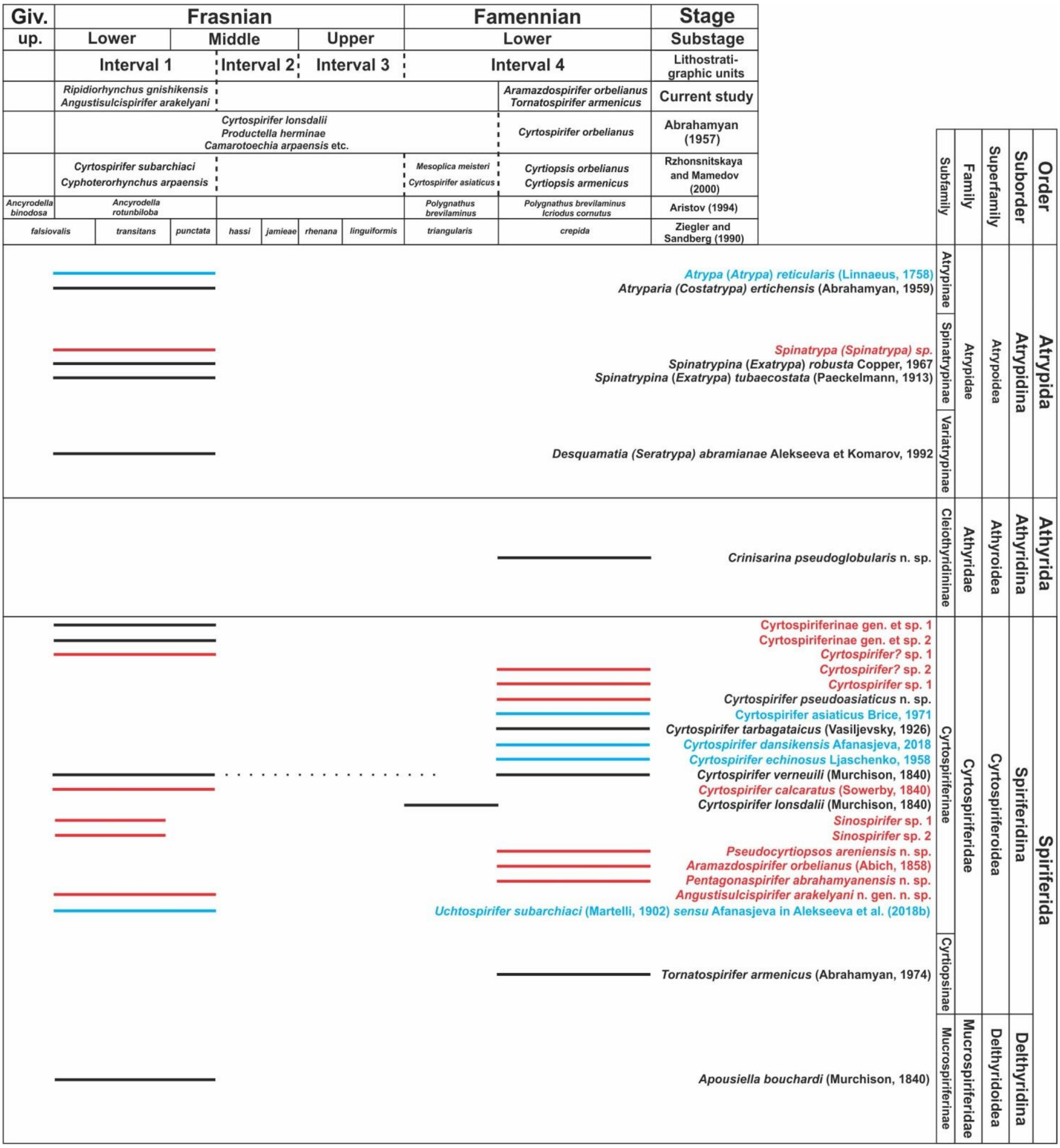


Figure 56. Biostratigraphic distribution of brachiopod species belonging to the orders Atrypida, Athyrida and Spiriferida, reported from the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus. Red color indicates species which are known from Armenia based on the data of Abrahamyan (1957, 1974) and Arakelyan (1964); blue color indicates species reported from Nakhichevan (Alekseeva et al., 2018a, b); black color points those species that are known both from Armenia and Nakhichevan.

former includes *Paropamisorhynchus* Sartenaer, 2001 and *Gesoriacorostrum* Sartenaer, 2003 that are represented by three species (*Paropamisorhynchus kotalensis* (Brice, 1971), *Gesoriacorostrum boloniense* (Orbigny, 1850) and *Gesoriacorostrum*? sp.), while the latter comprises of *Greira* Erlanger, 1993 and *Sharovaella* Pakhnevich, 2012 that also include three species (*Greira transcaucasica* Erlanger, 1993, *Sharovaella mirabilis* Pakhnevich, 2012 and *Sharovaella*? sp.). Thus, it can be inferred that in the Lesser Caucasus, the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone is represented by only two rhynchonellide genera, whereas the lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone in addition to the genus *Ripidiorhynchus*, which crossed the F–F boundary, also includes seven genera (Fig. 54–55).

Six representatives of the Order Atrypida are documented from the Frasnian strata of the Lesser Caucasus, of which all vanished near the F–F boundary (Fig. 56). These species are allocated to *Atryparia* (*Costatrypa*), *Spinatrypa* (*Spinatrypa*), *Desquamatia* (*Seratrypa*) genera/subgenera, which in turn belong to the subfamilies Atrypinae, Spinatrypinae and Variatrypinae. It is also worth noting that Komarov (1997), who in his groundbreaking monograph dealt exclusively with atrypides of the Lesser Caucasus, described eighteen atrypides in the Eifelian, twelve within the Givetian and only six in the lower Frasnian. This signifies that the depletion of atrypides diversity in the Lesser Caucasus commenced since the Givetian and continued in the course of the Frasnian and the diversity of atrypides was already low near the F–F boundary.

Crinisarina pseudoglobularis Serobyan et al., 2021 records the earliest history of the Order Athyrida in the Lesser Caucasus. This species appeared in the lower Famennian Ertych Regional Stage and became extremely abundant within a short stratigraphic interval.

In contrast to atrypides and athyrides, the spiriferides were present both in the Frasnian and in the lower Famennian strata (Figs. 54, 56). Moreover, they are the most diverse and abundant group of the Frasnian–lower Famennian interval with twenty-two species, of which ten are from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone and twelve species are described from the lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone. Among the Frasnian species, only *Cyrtospirifer verneuili* (Murchison, 1840) *sensu* Abrahamyan (1957) seems to cross the F–F boundary; however, the occurrence of this species must be further confirmed by recent sampling. The Frasnian species, which were identified until the species level, belong to the genera *Cyrtospirifer* Nalivkin in Fredericks, 1924, *Sinospirifer* Grabau, 1931 and *Angustisulcispirifer* n. gen., which in their turn are allocated to the Subfamily Cyrtospiriferinae. Thus, although the diversity of cyrtospiriferids was relatively high at the species level, it was quite low at the genus and subfamily levels. The spiriferides of the lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* Zone belong to *Cyrtospirifer* Nalivkin in Fredericks, 1924, *Pseudocyrtiopsis* Ma and Day, 1999, *Aramazdospirifer* n. gen., *Pentagonaspirifer* n. gen. and *Tornatospirifer* n. gen. With an exception of the latter genus, which is assigned to the Subfamily Cyrtiopsinae, all the lower Famennian genera are included in the Subfamily Cyrtospiriferinae. It is evident that the diversity of spiriferides was higher in the lower Famennian not only at the species level but also at the genus and subfamilies levels.

As highlighted above, a major turnover is observed among the orders Orthotetida, Productida, Rhynchonellida, Atrypida, Athyrida and Spiriferida at the transition between the Frasnian Baghrsagh and the lower Famennian Ertych regional stages (Figs. 54–56), since twenty-one species went extinct and only one productide and one spiriferide species seem to cross the F–F boundary and moreover their occurrences in the lower Famennian strata need to be confirmed. This drop of diversity is regarded as the record of the Kellwasser Biocrisis in the Lesser Caucasus. Although, all clades were severely affected by the F–F Biocrises, the post-crisis diversification of productides, rhynchonellides and spiriferides appears to be quick in the course of the lower Famennian, which marks the appearance of two species within the Noravank Regional Stage and twenty-five in the Ertych Regional Stage. This is not the case of the Order Athyrida as only one single athyride species originated within the Ertych Regional Stage. However, it is worth to emphasize that at this stage, it is difficult to determine whether the Frasnian brachiopods disappeared due to the lack of origination or by a global trigger in the SAB, especially in the absence of conodont data. More evidences and an updated conodont biozonation are needed to understand both consequences and aftermaths of the Kellwasser Biocrises in the Lesser Caucasus.

Evidently, the Frasnian–lower Famennian succession of the Lesser Caucasus bears two distinct brachiopod assemblages, of which the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* assemblage consists of species belonging to at least five orders Orthotetida, Productida, Rhynchonellida, Atrypida and Spiriferida (Fig. 57.1). This assemblage

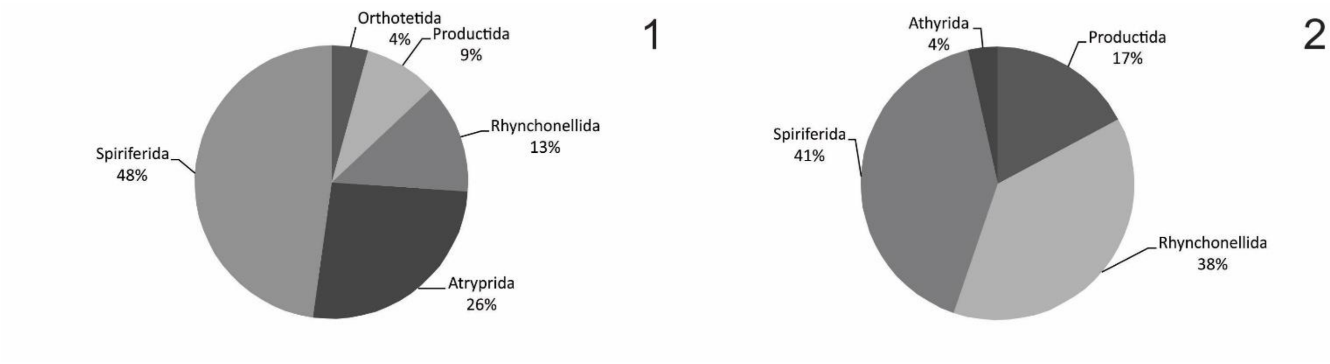


Figure 57. The composition of brachiopod assemblages described in the Lesser Caucasus and represented by percentages on pie charts at the order level. (**1**) The Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* assemblage. (**2**) The lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* assemblage.

includes twenty-three species, among which the spiriferides predominate, accounting for 48 % (11 species) of the total number of species, while the atrypides account for 26 % (6 species), rhynchonellides 13 % (3), prudoctides 9 % (2 species) and orthotetides only 4 % (1 species) (Fig. 57.1). The lower Famennian *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* assemblage includes twenty-nine species belonging to the orders Productida, Rhynchonellida, Spiriferida and Athyrida (Fig. 57.2). The latter assemblage is dominated by the spiriferides and rhynconellides, accounting for 41 % (12 species) and 38 % (11 species) of the total number of species, respectively. At the same time, the productides make up 17 % (5 species) and the athyrides only 4 % (1 species).

Although, the Frasnian assemblage includes species of five brachiopod orders, one more than the lower Famennian, while comparing these two assemblages, it becomes evident that the lower Famennian contains more diversified brachiopod fauna then the Frasnian at the subfamily, genus and species levels. The brachiopod orders constituting these assemblages differ in diversity from one assemblage to another one. Interestingly, the spiriferids were predominant in both assemblages, whereas the rhynchonellides, being relatively scarce in the Frasnian, flourished within the lower Famennian as is the case of productides.

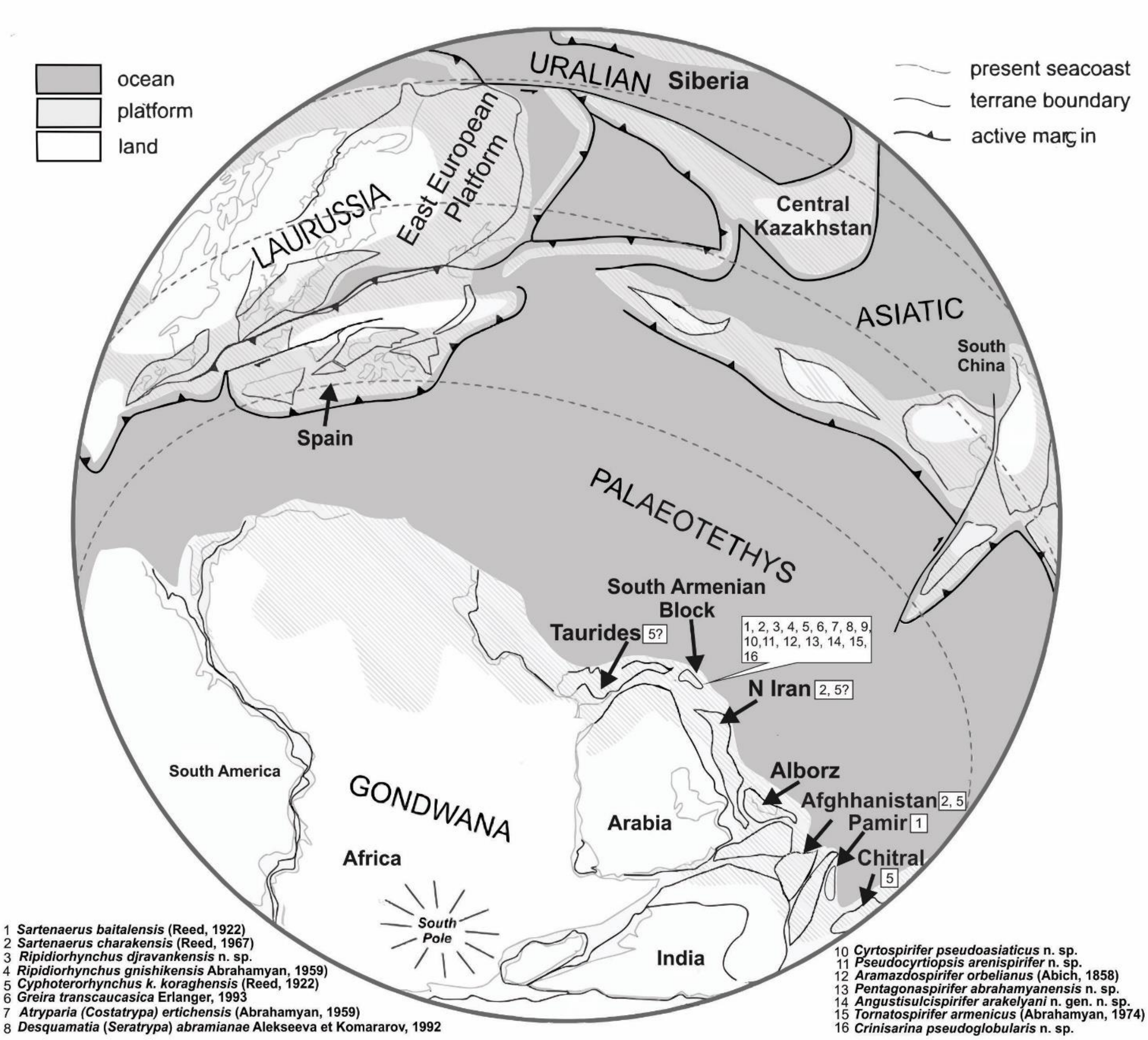
5.4 Brachiopod encrustation patterns

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 of cornulitid abundance and morphological disparity. These epifaunal suspension feeders may be helpful for palecological interpretations as being fully marine, they were very sensitive to water salinity and inhabited only in water of normal salinity (Vinn et al., 2019) as it is also the case of most brachiopod species. However, their biological affinities, morphological peculiarities, paleobiodiversity remain largely undocumented. In our material, one of the brachiopod specimens (IGSNASRAGM 3965/PS 3071) belonging to *Pentagonospirifer abrahamyanae* n. gen., n. sp. is encrusted by two cornulitid tubeworms at its dorsal valve, near the anterior margin, though one of them is only partly preserved (Pl. 9.2, 9.19). The latter resembles the external features of the genus *Cornulites* Schlotheim, 1820, which representatives are considered as hard-substrate encrusters and known from the Middle Ordovician to the Upper Carboniferous (Vinn, 2010). The tube of ?*Cornulites* sp. is oriented with its aperture directed towards the brachiopod anterior commissure suggesting attachment to living shell and subsequent growth for “stealing” some food from currents, produced by the feeding activity of the brachiopod host (Richards, 1974). Moreover, the shell of this brachiopod displays distinct shell malformations caused by cornulitid growth affecting the host’s shell-secreting epithelium. Obviously, feeding on the food brought by the currents produced by the lophophores of this brachiopod, this cornulitid species had a clear negative effect on the brachiopods, such as a deviation in the growth of its shell. It is likely that the small size of this brachiopod is due to the negative effects of these encrustors, and not related to age. In this regard, it is reasonable to consider this cornulitid species as an ectoparasite and not as a commensal in relation to its owner. This is also the case of cornulitids observed on one of the specimen of *Cyrtopspirifer pseudoasiaticus* n. sp. (IGSNASRAGM 3951/PS 3057; Pl. 6.18), though they are only partially preserved. The encrusters observed on the second specimen of *Pentagonospirifer* *abrahamyanae* n. gen., n. sp. (IGSNASRAGM 3928/PS 3034; Pl. 9.11, 9.15, 9.18) are colonial organisms referred to *Hederella* Hall, 1883 that is a still enigmatic encrusting metazoan known from the Silurian to the Permian and were most common in the Devonian period. It is similar to cyclostome bryozoans, but it is not a bryozoan because of its branching patterns, lack of an astogenetic gradient, skeletal microstructure, and wide range in tube diameters (Wilson and Taylor, 2001). Possibly, it is some lophophorate-grade animal of uncertain affinity. Additionally, it should be emphasized that the Upper Devonian brachiopods from the Lesser Caucasus were never investigated with respect to encrustation patterns and this is the very first report documenting their presence on the lower Famennian spiriferids of Armenia.

5.5 Paleobiogeography

Although a precise paleolatitudinal evaluation of the Late Devonian position of the South Armenian Block is still hampered due to the remagnetization of Upper Paleozoic rocks following the Late Cretaceous obduction of ophiolites (Meijers et al., 2015), existing paleogeographic reconstructions place the SAB at the junction between the Iranian terranes (to the east) and the Anatolide-Tauride microplate (to the west). It was thus an integral part of the northern passive margin of Gondwana, facing the Paleotethys ocean to the north (Figs. 58–59). Thus, during the Late Devonian it was part of a huge platform that was positioned within the southern hemisphere tropical carbonate development zone (Brock and Yazdi, 2000). The SAB was later individualized during the Triassic, as an independent microcontinent, as it migrated northwards following the opening of Neotethys further to the south (Sosson et al., 2010). However, some authors consider that during the Mesozoic, the SAB had the same kinematic trajectory as the Tauride plate and therefore it was part of it (Rolland et al., 2020).

The taxonomic assessment of brachiopods collected from the Frasnian–lower Famennian interval cropping out in the Ertych, Djravank and Noravank sections of Central Armenia allows us to recognize the presence of nine rhynchonellide, three atrypide, one athyride and thirteen spiriferide species. As rhynchonelliform brachiopods have a benthic mode of life and produce lecithotrophic larvae, their paleobiogeographic patterns have the potential to reveal past geographic boundaries and oceanographic connections, although caution should be exercised on questions of taxonomic consistency, comparison of assemblages of similar age and biofacies (Brock and Yazdi, 2000). In that respect the two species of the Famennian genus *Sartenaerus* found in the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) (*S. baitalensis* and *S. charakensis*) are of particular paleobiogeographic significance as they point to a likely wide Frasnian–lower Famennian brachiopod bioprovince developed along the northern Gondwana margin, from the SAB to Afghanistan and Pamir (Fig. 58). However, it should be stressed that in spite of the



.

Figure 58. Late Devonian paleobiogeographic distribution of brachiopod species described in this study (the paleomap is redrawn and modified after Denayer and Hoçgör, 2014, based on the maps of Stampfli et al., 2002).

well-constrained age of the occurrence of *S. baitalensis* in the Lesser Caucasus (the species occurs only in the *Cyrtospirifer orbelianus* Zone) this is not the case for the occurrence of *S. baitalensis* in Pamir (Reed, 1922). Finally, the apparent absence of both species in other parts of the northern Gondwanan margin, especially in Morocco, may be due to the presence of deeper (cephalopod-bearing) facies for this interval and therefore it may reflect a paleoenvironmental rather than paleobiogeographical signal.

In this study, two species of *Ripidiorhynchus* genus are described, *R. gnishikensis* (Abrahamyan, 1959) from the Frasnian and *R.djravankensis* n. sp., from the lower Famennian, of which the latter was probably originated from the former as both species share several common superficial and internal features. Racki (1993) noted the presence of this genus in the upper Givetian of Poland, while several *Ripidiorhynchus* representatives were reported from the lower Frasnian of Main Devonian Field (northwestern Russia), lower Famennian of East European Platform (Eastern Europe) (see references in Sokiran, 2006) as well as from the Frasnian of Nakhichevan (Pakhnevich 2018 in Alekseeva et al., 2018a). Therefore, it is judicious to assume that firstly occurred in the upper Givetian of Poland, this genus was later expanded to the north-western region of platform due to the early Frasnian transgression and later to the south-east, migrating towards the northern margin of Gonwana; it thus colonized the Frasnian carbonate platform of SAB and persisted until the lower Famennian strata within the Armenian Djravank section.

This is the first time that the genus *Porthmorhynchus* is recognized (although doubtfully) from the Armenian sections. It is also worth stressing that the genus is known so far only from the Frasnian, as its type species *P. ferquensis* is known from the middle–upper Frasnian of northern France (Boulonnais region) and Nakhichevan (Pakhnevich in Alekseeva et al., 2018a). The other species assigned to this genus (*P. elburzensis*) is known from the upper Frasnian of the Alborz Mts (northern Iran; (Gaetani, 1965)). Thus, the doubtful report of this genus from the lower Famennian *Cyrtospirifer orbelianus* Zone of Armenia is significant, although it requires further study to confirm its presence. *Greira transcaucasica* is one of the oldest punctate rhynchonellide species and, as it is only known from the SAB, this may represent an interesting case of endemicity.

The atrypide brachiopods display a high level of endemicity at the species level, since among the three described species, two (*Atryparia* (*Costatrypa*) *ertichensis* (Abrahamyan, 1959), *Desquamatia*

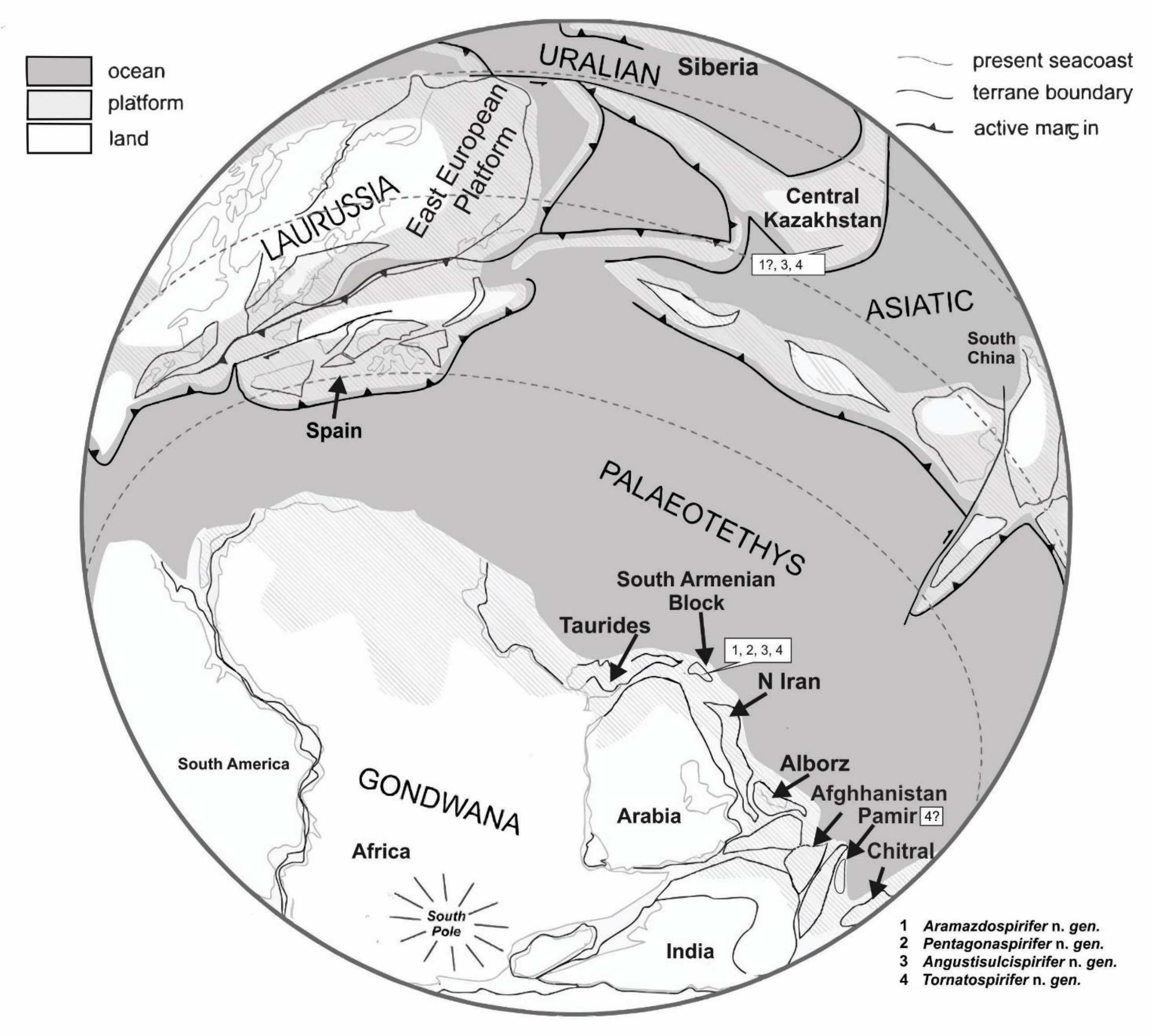


Figure 59. Paleobiogeographic distribution of the newly established genera (the paleomap redrawn and modified after Denayer and Hoçgör, 2014, based on the maps of Stampfli et al., 2002).

(*Seratrypa*) *abramianae* Komarov, 1992) seem to be restricted to the SAB. However, the genera/subgenera (*Atryparia* (*Costatrypa*), *Spinatrypa* (*Spinatrypa*), *Desquamatia* (*Seratrypa*)) that include these three described species are known worldwide. The single athyride species recognized (*Crinisarina pseudoglobularis* Serobyan et al., 2021) represents also the first ever report of genus *Crinisarina* in the SAB and indeed in the entire northern margin of Gondwana, although it cannot be excluded that *Crinisarina* representatives are present in the Famennian of North Africa (Algeria and Morocco), where taxonomical studies have been mostly dedicated to the rhynchonellides, productidines and spiriferides, whereas the other elements of the brachiopod faunas received scant attention (see references in Mottequin et al., 2015). Alike other species of *Crinisarina* (see discussion in Mottequin, 2008), it is likely that *C. pseudoglobularis* Serobyan et al., 2021 had a preference for soft substrates, comprised of argillaceous sediments, on which it was attached with a thin pedicle. This corresponds well to our own observations, as this species was found mainly in shaly intervals. If among the rhynchonellides some species were described in other parts of the Gondwanan northern margin, the spiriferides display low level of cosmopolitanism and might be significant for the paleobiogeography only at the genus level. More particularly, in addition to type species, which appear to be endemic in the SAB, the newly described lower Famennian genera *Aramazdospirifer* n. gen., *Pentagonaspirifer* n. gen., *Tornatospirifer* and the Frasnian *Angustisulcispirifer* n. gen likely include several other Famennian species described from Pamir (Tajikistan), Central Kazakhstan and the East European Platform, although the latter species are in need of a modern taxonomic reassessment (Fig. 59). The new species of *Pseudocyrtiopsis areniensis* represents the first ever report of the genus *Pseudocyrtiopsis* Ma and Day (1999) in the lower Famennian strata of SAB. This discovery highlights an important radiation of this kind, since until now it was known only from China and possibly from Belgium. Ma and Day (2007) indicated that the genus *Sinospirifer* Grabau, 1931 first occurs in the lower Famennian, as observed in the Russian Platform, South China, southwestern USA (western North America) and possibly eastern North America, but it appears that the latter genus was already present in the Frasnian.

Conclusions

1. The examination of the Frasnian-Famennian sedimentary sequences in Central Armenia revealed that the ‘formations’ established by Arakelyan (1964) have very similar lithological characteristics and that they cannot be distinguished without knowledge of their brachiopod assemblages; thus, they have a biostratigraphic rather than lithostratigraphic significance. The four intervals introduced in the present study may serve as a basis for future establishment of more formal lithostratigraphic formations, useful for mapping purposes.
2. The three studied sections (Ertych, Djravank and Noravank) have similar lithostratigraphic successions and contain shallow water mixed carbonate-siliciclastic deposits that were subdivided into four distinct intervals. It is likely that the Interval 1, composed mainly of bioclastic/peloidal grainstones and a few layers of tempestites, accumulated in an inner ramp environment at a time of high sea level, whereas the deposition of Interval 2, composed of bioturbated sandstones and black shales, took place on the median part of a ramp during a transgressive event. The Interval 3 is primarily composed of quartzites, sandstones and a few layers of shale; it displays an aggradational sedimentary pattern and reflects a HST, while the overlying Interval 4 represents a carbonate interval is composed at its base of grainstones or wackestones facies (depending on section); this Interval contains in its upper part, an oncolitic layer that was accumulated in a lagoonal environment and which indicates a dramatic sea level drop. This interval ends in our studied sections with grainstones/packstones, the composition of which suggests a deepening-upward (transgressive) trend.
3. Twenty-six species of Rhynchonellide, Atrypide, Athyride and Spiriferide brachiopods are documented and described in detail. They constitute two distinct assemblages: the first one (*Ripidiorhynchus gnishikensis–Angustisulcispirifer*) is described from the Interval 1, which may be correlated with the Baghrsagh Regional Stage, whereas, the second one (*Aramazdospirifer orbelianus–Tornatospirifer armenicus*) is recovered from the Interval 4 and may be correlated with the Ertych Regional Stage.

4. The taxonomic reassessment of the newly collected brachiopods led us to erect a number of new species and genera, but also to update previous assignments based on newly observed features that were poorly illustrated or unknown until now. Most notably, *Spinatrypa ertichensis* Abrahamyan, 1974 is revised and re-assigned to *Atryparia* (*Costatrypa*) Copper, 1973 mainly based on its frilly ornamentation. *Cyrtospirifer* Nalivkin in Fredericks, 1924 is one of the main components of Frasnian–Famennian assemblages in Armenia; it appears to include four species, of which *Cyrtospirifer pseudoasiaticus* n. sp., one of the most abundant species in the lower Famennian sequence, is new to science. The genus *Pseudocyrtiopsis* is transferred from the Subfamily Cyrtiopsinae to the Subfamily Cyrtospiriferinae based on some features (high ventral interarea, wide hinge line and mucronate cardinal extremities) that are observed in *Pseudocyrtiopsis areniensis* n. sp. Four new genera are erected: *Aramazdospirifer Pentagonaspirifer*, *Angustisulcispirifer* and *Tornatospirifer*. *Aramazdospirifer* and *Tornatospirifer* include two of the most biostratigraphically important species of the lower Famennian in the Lesser Caucasus, *Aramazdospirifer orbelianus* (Abich, 1858) and *Tornatospirifer senceliae armenica* (Abrahamyan, 1974), respectively.
5. The examination of brachiopod assemblages confirms the presence of a number of species known previously (e.g., *Sartenaerus baitalensis*, *Ripidiorhynchus gnishikensis*, *Spirifer orbelianus*, *Cyrtiopsis senceliae armenica*) from the South Armenian Block. However, I here provide for the first time a detailed description of the internal structure of *Sartenaerus baitalensis*, which is the type species of a biostratigraphically and paleogeographically important genus. Thus, the brachiopod record from Armenia firmly establishes the presence of the Famennian genus *Sartenaerus* in the lower Famennian (it was previously known since the middle Famennian; Mottequin et al., 2014). It is also the first documentation of *S. charakensis* in the Armenian sections; moreover, its stratigraphic range is extended here down to the *Cyrtospirifer orbelianus* Zone (it was previously known from the *ghorensis*–*pamiricus* Zone). Two species belonging to the genus *Ripidiorhynchus* Sartenaer, 1966a are

described: *R. gnishikensis* (Abrahamyan, 1959) and *R. djravankensis* n. sp., the latter establishes the first record of this genus within the lower Famennian of the SAB. This study also documents for the first time the presence of the subgenera *Atryparia* (*Costatrypa*) Copper, 1973 and *Spinatrypa* (*Spinatrypa*) Stainbrook, 1951, in the Frasnian of the SAB. The athyride species (*Crinisarina pseudoglobularis* Serobyan et al., 2021) represents the first report of the genus *Crinisarina* in the SAB and indeed in the entire north Gondwanan realm. Remarkably, the genus *Sinospirifer* Grabau, 1931, which was previously known from the Famennian of China, East European Platform (Ma et al., 2002, 2003; Ma and Day, 2007) and Western Europe (Mottequin, 2005), is reported here since the Frasnian. Its paleobiogeographic distribution is thus wider than previously thoughtIt is likely that in addition to their type species, the newly erected genera *Aramazdospirifer*, *Pentagonaspirifer*, *Angustisulcispirifer* and *Tornatospirifer* include several other Famennian species described from Pamir (Tajikistan), Central Kazakhstan and the East European Platform, although the latter species are in need of a modern taxonomic reassessment. The paleobiogeographic distribution of the rhynchonellides, atrypides, spiriferides and athyrides within the Frasnian–lower Famennian sequences of Armenia suggests that the brachiopod communities thriving on the shallow water carbonate platform of the SAB included also species that were common to other parts of the Gondwanan northern margin extending eastwards to Afghanistan and Pamir, but also some apparently endemic species (e.g., *R. gnishikensis*, *R. djravankensis*, *G. transcaucasica*, *Aramazdospirifer orbelianus*, *Pentagonospirifer abrahamyanae*).

6. A comparison between the brachiopod assemblages recorded in the Intervals 1 (Baghrsagh Regional Stage) and 4 (Ertych Regional Stage) reveals some interesting differences in diversity and assemblages structure. The assemblages are very different. More particularly, the rhynchonellides, atrypides and spiriferides species assemblages are very different, as with the exception of *Cyrtospirifer verneuilli* (Murchison 1840) *sensu* Abrahamyan (1957),

none of the Frasnian species crossed the Frasnian–Famennian boundary. However, the early Famennian diversification of the productides, rhynchonellides and spiriferides appears to be high in the Armenian fossil record, which is not the case of athyrides as only one species is observed within the lower Famennian.

References

Abich, H., 1858, Vergleichende geologische Grundzüge der Kaukasischen, Armenischen und Nordpersischen Gebirge: Prodromus einer Geologie der Kaukasischen Länder: Mémoires de l'Académie impériale des Sciences de Saint-Pétersbourg, 6[ème] série, Sciences mathémathiques et physiques, v. 7, p. 359–534.

Abrahamyan, M.S., 1954, Novye vidy brakhiopod iz famenskikh otlozheniy Armyanskoy SSR: Izvestiya Akademii Nauk Armyanskoy SSR, v. 7, p. 65–71. [in Russian]

Abrahamyan, M.S., 1957, Brakhiopody verkhnefamenskikh i etrenskikh otlozheniy yugo-zapadnoy Armenii: Yerevan, Izdatelstvo Akademii Nauk Armyanskoy SSR, 142 p. [in Russian]

Abrahamyan, M.S., 1964, Karbon, *in* Mkrtchian, S.S., Vardaniants, L.A., Gabrielian, A.A, Maghakian, I.G., and Paffenholz, C.N., eds., Geologiya Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, v. 2, p. 96–118. [in Russian]

Abrahamyan, M.S., 1959, Novyye vidy brakhiopod iz verkhnego devona Armenii: Izvestiya Akademii Nauk Armyanskoy SSR, v. 12, p. 4–10. [in Russian and in Armenian]

Abrahamyan, M.S., 1974, Opisanie fauny, Devonskaya sistema, Tip Brachiopoda, Brakhiopody, *in* Akopian, V.T., ed., Atlas iskopaemoy fauny Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk, p. 48–67. [in Russian]

Abrahamyan, M.S., Arakelyan, R.A., and Azizbekov, Sh.A., 1973, Malyy Kavkaz (Yuzhnoe Zakavkaz'ya), *in* Rzhonsnitskaya, M.A., ed., Kavkazskaya geosinklinal'naya oblast i Predkavkaz'e, *in* Nalivkin, D.V., Rzhonsnitskaya, M.A., Markovski, B.P., eds., Stratigrafiya SSSR, Devonskaya sistema: Moscow, Nedra 1, p. 210–219. [in Russian]

Abrahamyan, M.S., Arakelyan, R.A., and Papoyan, A.S., 1975, Granitsa Devona i Nizhnego Karbona, *in* Stratigrafiya Karbona i Geologiya Uglenosnykh Formatsii SSSR. Moscow, Nedra, Moscow, p. 49–55. [in Russian]

Alekseeva, R.E., 1960, A new subgenus *Atrypa* (*Desquamatia*) subgen. nov. of the family Atrypidae Gill (brachiopods): Doklady Akademii Nauk SSSR 131, p. 421–424. [in Russian]

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., and Pakhnevich, A.V., 2018a, Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia: Paleontological Journal, v. 5, p. 829–967.

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., and Pakhnevich, A.V., 2018b, Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia (Ending): Paleontological Journal, v. 52, p. 969–1085.

Alvarez, F., Rong, J.Y., and Boucot, A.J., 1998, The classification of athyridid brachiopods: Journal of Paleontology, v. 72, p. 827–855.

Alvarez, F., and Rong, J.Y., 2002, Athyridida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda 4 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H1475–H1601.

Arakelyan, R.A., 1952, Stratigrafiya paleozoyskikh otlozheniy yugo-zapadnoy Armenii i prilegayushchikh chastey Nakhichevanskoy ASSR: Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk., 142 p. [in Russian]

Arakelyan, R.A., 1964, Devon, *in* Mkrtchian, S.S., Vardaniants, L.A., Gabrielian, A.A., Maghakian, I.G., and Paffenholz, C.N., eds., Geologiya Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, v. 2, p. 46–96. [in Russian]

Arakelyan, R.A., Malxasyan, E.G., Mkrtchyan, C.C., and Paffenholz, C.N., 1975, Geologicheskiy ocherk Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk, 175 p. [in Russian]

Aristov, V.A., 1994, Konodonty devona–nizhnego karbona Evrazii: soobshhestva, zonalnoye raschleneniye, korrelyatsiya raznofatsialnykh otlozheniy: Trudy Geologicheskogo Instituta Rossiyskoy Akademii Nauk, v. 484, 1–193. [in Russian]

Aristov, V.A., Grechishnikova, I.A., Tschigova, V.A., and Felix, V.P., 1979, Subdivision and correlation of the Famennian and the lower Tournaisian deposits of Transcaucasia (on brachiopods, conodonts and ostracods): Geological Survey of Belgium, Professional Paper, v. 161, p. 91–95.

Baliński, A., 2002, Frasnian–Famennian brachiopod extinction and recovery in southern Poland: Acta Palaeontologica Polonica v. 47, 289–305.

Baranov, V.V., Sokiran, E., and Blodgett, R.B., 2016, Late Devonian (Famennian) brachiopods, conodonts, biogeography and sedimentary geology of Bel'kovsky Island (Russian Arctic): New Mexico Museum of Natural History and Science Bulletin, v. 74, p. 25–40.

Becker, R., Gradstein, F., Hammer, O., 2012, The Devonian period, *in* Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G., eds., The Geologic Time Scale 2012: Amsterdam, Elsevier, p. 559–601.

Bonnet, P., 1947, Description géologique de la Transcaucasie méridionale (chaînes de l'Araxe moyen): Mémoires de la Société géologique de France, nouvelle série, v. 25, p. 1–62.

Boucot, A.J., Johnson, J.G., and Staton, R.D., 1964, On some atrypoid, retzioid, and athyridoid Brachiopoda: Journal of Paleontology, v. 38, p. 805–822.

Buch, L., 1834, Über Terebrateln, mit einem Versuch, sie, zu classificiren und zu beschreiben: Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin, p. 21–144.

Brice, D., 1967, Deux nouvelles espèces de Rhynchonelloidea dans le Dévonien supérieur d'Afghanistan central: Annales Société Géologique du Nord, v. 87, p. 95–105.

Brice, D., 1971, Etude paléontologique et stratigraphique du Dévonien de l'Afghanistan: Notes et Mémoires du Moyen Orient, v. 11, p. 1–364.

Brice, D., 1982, *Eodmitria*, genre nouveau de brachiopode Cyrtospiriferidae du Frasnien Inférieur et Moyen: Geobios, v. 15, p. 575–581.

Brice, D., and Lang, J., 1968, Sur un nouveau gisement du Dévonien supérieur à Iraq (Bamian, Afghanistan): Comptes Rendus de la Société Géologique de France, v. 4, p. 1–120.

Brice, D., Colleau, A., and Lapparent A.F. de, 1969, Sur la stratigraphie du Dévonien de Robat-e-Paï (Afghanistan occidental): Comptes Rendus de la Société Géologique de France, v. 268, p. 2856–2858.

Brice, D., and Meats, P., 1972, Le genre *Ripidiorhynchus* (Rhynchonellida-Brachiopodes) dans le Dévonien de Ferques (Boulonnais). Annales de la Société géologique du Nord, v. 91, p. 15–228.

Brice, D., Jenny, J., Stampfli, G., and Bigey, F., 1978, Le Dévonien de l'Elbourz oriental: stratigraphie, paléontologie (Brachiopodes et Bryozoaires), paléogéographie: Rivista Italiana di Paleontologia e Stratigrafia, v. 84, p. 1–56.

Brice, D., Mistiaen, B., and Rohart, J.C., 1999, New data on distribution of brachiopods, rugose corals and stromatoporoids in the Upper Devonian of central and eastern Iran: Paleobiogeographic implications: Annales de la Société géologique du Nord, v. 2, p. 21–32.

Brice, D., and Deville, P., 2007, Brachiopodes du Dévonien d'Afghanistan, types et figurés (A3.01–B14) du catalogue systématique des collections de l'Université Catholique de Lille: Annales Société Géologique du Nord, v. 14, p. 9–21.

Brock, G.A., and Yazdi, M., 2000, Palaeobiogeographic affinities of Late Devonian brachiopods from Iran: Records of the western Australian Museum, Supplement, p. 321–334.

Buggisch, W., 1991, The global Frasnian-Famennian Kellwasser event: Geologische Rundschau, v. 80, p. 49–72.

Buckman, S.S., 1906, Brachiopod nomenclature: Epithyris, Hypothyris, Cleiothyris Phillips, 1841: Annals and Magazine of Natural History (series7), v. 18, p. 321–327.

Brunton, C.H.C., and Tilsley, C.J.W., 1991, A check list of brachiopods from Treak Cliff, Derbyshire, with reference to other Dinantian (Lower Carboniferous) localities: Proceedings of the Yorkshire Geological Society, v. 48, p. 287–295.

Carter, J.L., 2006, Spiriferoidea, *in*, Kaesler, R.L., ed., Treatise on invertebrate paleontology. Pt. H. Brachiopoda 5 (revised). Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. H1769–H1811.

Carter, J.L., Johnson, J.G., Gourvennec, R., and Hou, H.F., 1994, A revised classification of the spiriferid brachiopods: Annals of the Carnegie Museum, v. 63, no. 4, p. 327–374.

Catuneanu, O., 2002, sequence stratigraphy of clastic systems: concepts, merits, and pitfalls: Journal of African Earth Sciences, v. 35, p. 1–43.

Catuneanu, O., 2006, Principles of Sequence Stratigraphy: Amsterdam, Elsevier, 375 p.

Catuneanu, O., 2017. Sequence stratigraphy: guidelines for a standard methodology, *in* Montenari, M., ed., Stratigraphy and Timescales, v. 2: UK, Academic Press, p. 1–57.

Cooper, G.A., and Dutro, J.T., 1982, Devonian brachiopods of New Mexico: Bulletins of American Paleontology, v. 82–83, p. 1–215.

Copper, P., 1966, European Mid–Devonian correlations: Nature, v. 209, p. 982–984.

Copper, P., 1967, Frasnian Atrypidae (Bergisches Land, Germany): Palaeontographica A 126, p. 116–140.

Copper, P., 1973, New Siluro–Devonian atrypoid brachiopods: Journal of Paleontology, v. 47, p. 484–500.

Copper, P., 1978, Devonian Atrypoids from western and northern Canada, *in* Stelck, C.R., Chatterton, B.D.E., eds., Western and Artic Canadian Biostratigraphy: Geological Association of Canada, Special Paper 18, p. 289–331.

Copper, P., 2002a, Atrypida, *in* Kaesler R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, 4 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H921–H1688.

Copper, P., 2002b, Reef development at the Frasnian/Famennian mass extinction boundary: Palaeogeograpy Palaeoclimatology Palaeoecology, v. 181, p. 27–65.

Copper, P., and Jin, J., 2017, Early athyride brachiopod evolution through the Ordovician–Silurian mass extinction and recovery, Anticosti Island, eastern Canada: Journal of Paleontology, v. 91(6), p. 1123–1147.

Crickmay, C.H., 1952, Discrimination of late Upper Devonian: Journal of Paleontology, v. 26, p. 585–609.

Davidson, T., 1881, On genera and species of spiral-bearing Brachiopoda from specimens developed by Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire: Geological Magazine, v. 8, p. 1–13.

Denayer, J. and Hoşgör, I., 2014, Lower Carboniferous rugose corals from the Arabian Plate: An insight from the Hakkari area (SE Turkey): Journal of Asian Earth Sciences, v. 79, p. 345–357.

d'Orbigny, A., 1850, Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnés Faisant Suite au Cours Elémentaire de Paléontologie et de Géologie Stratigraphiques: Paris, Victor Masson, v. 1, 394 p.

Dott, R.H., 1964, Wacke, Greywacke and Matrix-What Approach to Immature Sandstone Classification?: Journal of Sedimentary Petrology, v. 34, p. 625–632.

Dott, R. H., and Bourgeois, J., 1982, Hummocky Stratification: Significance of Its Variable Bedding Sequences: Geological Society of America Bulletin, v. 93, p. 663–680.

Dunham, R. J., 1962, Classification of carbonate Rocks according to depositional texture, *in* Ham, W. E., ed., Classification of carbonate Rocks: American Association of Petroleum Geologists Memoir, p. 108–121.

Dutro, J.F., 1986, The Late Devonian extinction event as recorded by articulate brachiopod ranges in the United States of America: Biostratigraphie du Paléozoique, v. 4, p. 455–464.

Erlanger, O.A., 1993, *Greira* gen. nov.– Drevneyshiy rod poristykh rinkhonellid: Paleontologicheskiy Zhurnal, v.1, p. 118–122. [in Russian]

Farsan, N.M., 1986, Frasnian mass extinction – A single catastrophic event or cumulative? Faunistic investigations at the Frasnian–Famennian boundary in South-central Asia: Lecture Notes in Earth Sciences, v. 8, p. 189–197.

Feliks, V.P., Grechishnikova, I.A., Levitskii, E.S., Nagiev, V.N., 1980, Novyye dannyye o geologii rudnika Gyumyushlung: Izvestiya Vysshikh Uchebnykh Zavedeniy. Geologiya i razvedka, v. 2, 69–73. [in Russian]

Frech, F., 1891, Ueber das Devon del Ostalpen II: Zeitschrift der Deutschen Geologischen Gesellschaft v. 43, p. 672–687.

Frederiks, G.N., 1924, Paleontologicheskiye etyudy. 2. O Verkhne-Kamennougol'nykh spiriferidakh Urala: Izvestiya Geologicheskogo Komiteta v. 38, p. 295–324. [in Russian]

Gaetani, M., 1965, Brachiopods and mollusks from Geirud Formation, Member A (Upper Devonian and Tournaisian): The geology of the Upper Djadjerud and Lar Valleys (North Iran): 2. Palaeontology, Rivista Italiana di Paleontologia e Stratigrafia v. 71, p. 679–770.

Gaetani, M., 1968, Lower Carboniferous brachiopods from Central Elburz: Rivista Italiana di Paleontologia e Stratigrafia, v. 74, no. 3, p. 665–744.

Gatinaud, G., 1949, Contribution à l'étude des Brachiopodes Spiriferidae. I.–Exposé d'une nouvelle méthode d'étude de la morphologie externe des Spiriferidae à sinus plissé: Bulletin du Museum National d'Histoire, Naturelle, v. 2, p. 487–492.

Gereke, M., Schindler, E., 2012, The "Time-Specific Facies and biological crises-the Kellwasser Event interval near the Frasnian/Famennian boundary (Late Devonian): Palaeogeography Palaeoclimatology Palaeoecology 367–368, p. 19–29.

Gill, T., 1871, Arrangement of the families of molluscs prepared for the Smithsonian Institution: Smithsonian Miscellaneous Collections, v. 227, p. 1–49.

Ginter, M., Hairapetian, V., and Grigorian, A, 2011, Chondrichthyan microfossils from the Famennian and Tournaisian of Armenia: Acta Geologica Polonica, v. 61, p. 153–173.

Gosselet, J., 1874, Carte géologique de la bande méridionale des calcaires dévoniens de l'Entre Sambre–et–Meuse: Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux–Arts de Belgique, 2ème série, v. 37, p. 81–114.

Gosselet, J., 1880, Esquisse géologique du Nord de la France et des contrées voisines. 1er fascicule: Lille, Terrains primaires, Imprimerie Six-Horemans, 167 p.

Gosselet, J., 1877, Note (1ère) sur le Famennien: Quelques documents pour l'étude des schistes de Famenne: Annales de la Société géologique du Nord, v. 4, p. 303–320.

Gosselet, J., 1887, Note sur quelques rhynchonelles du terrain dévonique supérieur: Annales de la Société géologique du Nord, v. 14, p. 188–221.

Gosselet, J., 1894, Étude sur les variations du Spirifer Verneuili et sur quelques espèces voisines. Mémoires de la Société géologique du Nord, v. 4, p. 1–61.

Gourvennec, R., 2006, Upper Devonian Brachiopods from Eastern Taurus (Turkey): Geologica Croatica, v. 59, no. 1, p. 1–17.

Gourvennec, R., and Carter, J.L., 2007, Spiriferida and Spiriferinida, *in*, Kaesler, R.L., ed., Treatise on Invertebrate Palaeontology. Pt. H, Brachiopoda 6 (Revised). Boulder, Colorado and Lawrence, Kansas. Geological Society of America (and University of Kansas Press), p. H2772–H2796.

Grabau, A.W., 1923, Stratigraphy of China. Part 1. Palaeozoic and older: Geological Survey of China, Beijing, p. 200 (201–528 [1924]).

Grabau, A.W., 1931, Devonian Brachiopoda of China, I: Devonian Brachiopoda from Yunnan and other districts in South China: China Geological Survey, Palaeontologia Sinica Ser. B 3, p. 1–545.

Grechishnikova, I.A., 1986, Novyye devonskiye spiriferidy Zakavkaz'ya: Zapiski Gornogo Instituta, v. 107, p. 52–60. [in Russian]

Grechishnikova, I.A., Levitskii, V.S., and Feliks, V.P., 1980, K biostratigrafii srednego Devona Zakavkaz'ya: Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel Geologii, v. 55, p. 39–50.

Grechishnikova, I.A., Aristov, V.A., Reitlinger, E.A., and Chizhova, V.A., 1982, Biostratigrafiya pogranichnykh otlozhenii devona i karbona Zakavkaz'ya (opornye razrezy): Severo-Vostochnyy Kompleksnyy Nauchno-Issledovatel'skiy Institut Dal'nevostochnogo Nauchnogo Tsentra Akademii Nauk SSSR, p. 1–38. [in Russian]

Grechishnikova, I.A., and Levitskii, E.S., 2011, The Famennian–Lower Carboniferous Reference Section Geran-Kalasi (Nakhichevan Autonomous Region, Azerbaijan): Stratigraphy and Geological Correlation, v. 19, p. 21–43.

Grigoryan A., Serobyan, V, Randon. C., Mayilyan, R., Avagyan, N., Danelian, T., 2019, A Famennian (Late Devonian) conodont assemblage from brachiopod-rich limestones of the Djravank section (southern Armenia): Proceedings of National Academy of Sciences of the Republic of Armenia, Earth Sciences, v. 72, p. 3–12.

Hall, J, 1858, Report on the geological survey of the state of Iowa; embracing the results of investigations made during portions of the years 1855–1857, *in* Hall, J and Whitney, J.D., eds., Palaeontology, vol. 1, part 2. Published by authority of the legislature of Iowa, Des Moines, p. 473–724.

Hall, J., 1883, Bryozoans of the Upper Heldelberg and Hamilton Groups: Transactions of the Albany Institute, v. 10, p. 145–197.

Huang, C., Song, J., Shen, J., Gong, Y., 2018, The influence of the Late Devonian Kellwasser events on deep-water ecosystems: evidence from palaeontological and geochemical records from South China: Palaeogeography Palaeoclimatology Palaeoecology, v. 504, p. 60–74.

International Commission on Zoological Nomenclature, 1999, International Code of Zoological Nomenclature, 4th edition: London, International Trust for Zoological Nomenclature.

Ivanova, E.A., 1972, Osnovnyye zakonomernosti evolyutsii spiriferid (Brachiopoda): Paleontological Journal, v. 3, p. 309–320. [in Russian]

Jafarian, M.A., 2000, Late Devonian index brachiopoda of North-East Esfahan in correlation with other regions: Journal of Sciences Islamic Republic of Iran, v. 11, p. 221–231.

Johnson, J.G., 2006, Cyrtospiriferoidea (part), *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda 5 (revised). Boulder, Colorado, Lawrence, Geological Society of America (and University of Kansas Press), p. H1722–H1732.

Jin, Y-G., Ye, S.-L., Xu, H.-K., and Sun, D.-L,1979, Brachiopoda, *in* Sinica, eds, Paleontological Atlas of Northwestern China, Qinghai Province, Lower Paleozoic-Cenozoic: Beijing, Geological press, v. 1, p. 60–225. [in Chinese]

Klapper, G., Feist, R., Becker, R., House, M., 1994 [1993], Definition of the Frasnian-Famennian stage boundary: Episodes, v. 16, p. 433–441.

Knipper, A.L., and Khain, E.V., 1980, Structural position of ophiolites of the Caucasus: Ofioliti, Special Issue, v. 2, p. 297–314.

Komarov, V.N., 1992, Novye Desquamatia (Brachiopod) vidy iz devonskikh otlozheniy Zakavkaz’ye: Byulleten’ Moskovskogo Obshchestva Ispytateley Prirody, v. 67, no. 1, p. 91–101. [in Russian]

Komarov, V.N., 1997, Devonskie atripidy Zakavkaz’ya: Moscow, 198 p. [in Russian]

Koninck, L.-G. de, 1887, Faune du calcaire carbonifère de la Belgique. Sixième partie. Brachiopodes: Annales du Musée royal d’Histoire naturelle de Belgique, v. 14, p. 1–154.

Kuhn, O., 1949, Lehrbuch der Paläozoologie: Stuttgart, E.Schweizerbart’sche Verlagbuchhandlung, 326 p.

Lapparent, A.F. de, and Le Maître, D., 1963, Sur le Dévonien du Koh-i-Baba en Afghanistan: Comptes Rendus de la Société Géologique de France, v. 6, p. 1–188.

Ljashenko, A.I., 1957, Novyi rod Devonskikh brakhiopod Uchtospirifer: Doklady Akademii Nauk SSSR 117, p. 885–888. [in Russian]

Ljashenko, A.I., 1959, Atlas brakhiopod i stratigrafiya Devonskikh otlozhenii tsentral’nykh oblastei Russkoi Platformy: Moskva, Gostoptehizdat, 451 p. [in Russian]

Luehe, M., 1911, Acanthocephala: Register der Acanthocephalan und parasitischen Plattwürmer, geordnet nach ihren Wirten, *in* Susswasser-fauna Deutschlands (Brauer), Heft 16, p. 1–116.

Ma, X.-P., Day, J., 1999, The late Devonian brachiopod *Cyrtiopsis davidsoni* Grabau 1923, and related forms from central Hunan of South China: Journal of Paleontology, v. 73, no. 4, p. 608–624.

Ma, X.-P., and Day, J., 2000, Revision of Tenticospirifer Tien, 1938, and morphologically similar spiriferid brachiopod genera from the Late Devonian (Frasnian) of Eurasia, North America, and Australia: Journal of Paleontology, v. 74, no. 3, p. 444–463.

Ma, X.-P., and Day, J., 2003, Revision of North American and selected Eurasian Late Devonian (Frasnian) species of Cyrtospirifer and Regelia (Brachiopoda): Journal of Paleontology, v. 77, no. 2, p. 267–292.

Ma, X.-P., and Day, J., 2007., Morphology and revision of Late Devonian (Early Famennian) Cyrtospirifer (Brachiopoda) and related genera from South China and North America: Journal of Paleontology, v. 81, no. 2, p. 286–311.

Ma, X.-P, Sun, Y.-L., Hao, W.-C., and Liao, W.-H, 2002, Rugose corals and brachiopods across the Frasnian–Famennian boundary in central Hunan, South China: Acta Palaeontologica Polonica, v. 47, n. 2, p. 373–396.

Ma, X.-P., Gong, Y.-M., Chen, D.-Z., Racki, G., Chen, X.-Q., Liao, W.-H., 2016, The Late Devonian Frasnian–Famennian event in South China–patterns and causes of extinctions, sea level changes, and isotope variations: Palaeogeography Palaeoclimatology Palaeoecology, v. 448, p. 224–244.

Mamedov, A.B., and Rzhonsnitskaya, M.A., 1985, Devonian of the south Transcaucasus: Zonal subdivision, boundaries of series and stages, correlation: Courier Forschungsinstitut Senckenberg, v. 75, p. 135–156.

Martelli, A., 1902, Il Devoniano superiore dello Schensi (Cina): Bollettino della Societa` Geologica Italiana Bulletino, 21, p. 349–370.

McGhee, G.R., 1996, The Late Devonian mass extinction. The Frasnian/Famennian Crisis: New York, Columbia University Press, 303 p.

McGhee, G.R., 2013, When the Invasion of Land Failed: the Legacy of the Devonian Extinctions: New York, Columbia University Press, 356 p.

McMahon, C.A., and Hudlestone, W.H., 1902, Fossiis from the Hindu Khoosh: London, Geological Magazine, v. 9, p. 3–8, 49–58.

Meijers, M.J.M., Smith, B., Kirscher, U., Mensink, M., Sosson, M., Rolland, Y., Grigoryan, A., Sahakyan, L., Avagyan, A., Langereis, C., and Müller, C., 2015, A paleolatitude reconstruction of the South Armenian Block (Lesser Caucasus) for the Late Cretaceous: Constraints on the Tethyan Realm: Tectonophysics, v. 644–645, p. 197–219.

Mergl, M., and Massa, D, 2000, A palaeontological review of the Devonian and Carboniferous succession of the Murzuq Basin and the Djado Sub-Basin, *in* Sola, M.A., and Worsldey, D., eds, Geological Exploration in Murzuq Basin: Elsevier, Amsterdam, p. 41–88.

Merriam, C.W., 1940, Devonian stratigraphy and paleontology of the Roberts Mountains Region, Nevada: Geological Society of America, Special Papers, v. 25, p. 1–114.

Mirieva, G.T., 2010. Zonal'noye raschleneniye otlozheniy verkhnego Devona Yuzhnogo Zakavkaz'ya (Nakhchyvanskoy AR) po rinkhonellidam: Evolyutsiya organicheskogo mira i bioticheskiye krizisy: Materially 56 sessii Paleontologicheskogo obshchestvo pri RAN, Saint Petersburg Russia, p. 74–76. [in Russian]

Modzalevskaya, T.L., 2012, New Upper Devonian species of the suborder Athyrididina Boucot, Johnson et Staton from Belarus: Paleontological Journal, v. 46, p. 360–369.

Moore, R.C., 1952, Brachiopods, *in* Moore, R.C., Lalicker, C.G., Fischer, A.G., eds., Invertebrate Fossils: New York, McGraw-Hill, p. 197–267.

Mottequin, B., 2005, Les Brachiopodes de la transition Frasnien/Famennien dans le Bassin de Namur-Dinant (Belgique). Systématique-Paléoécologie-Biostratigraphie Extinctions: Ph.D. thesis, University of Liège, Liège, Belgium, 427 p.

Mottequin, B., 2008, Late middle Frasnian to early Famennian (Late Devonian) strophomenid, orthotetid and athyridid brachiopods from southern Belgium: Journal of Paleontology, v. 82, p. 1052–1073.

Mottequin, B., and Brice, D., 2019, Reappraisal of some Upper Devonian (Famennian) spiriferide brachiopods from the Band-e Bayan Domain (Afghanistan): Geobios, v. 52, p. 47–65.

Mottequin, B., Brice, D., and Legrand-Blain, M., 2014, Biostratigraphic significance of brachiopods near the Devonian–Carboniferous boundary: Geological Magazine, v. 151, p. 216–228.

Mottequin, B., Malti, F.Z., Benyoucef, M., Crônier, C., Samar, L., Randon, C., and Brice, D., 2015, Famennian rhynchonellides (Brachiopoda) from deep-water facies of the Ougarta Basin (Saoura Valley, Algeria): Geological Magazine, v. 152, p. 1009–1024.

Mottequin, B., and Brice, D., 2016, Upper and uppermost Famennian (Devonian) brachiopods from north-western France (Avesnois) and southern Belgium: Geologica Belgica, v. 19, p. 121–134.

Muir-Wood, H.M., 1955, A history of the classification of the phylum Brachiopoda: London, British Museum (Natural History), 124 p.

Murchison, R.I., 1840, Description de quelques-unes des coquilles fossiles les plus abondantes dans les couches de´voniennes du Bas-Boulonnais: Bulletin de la Société Géologique de France 11, p. 250–256.

Murchison, R., Verneuil, E., and Keyserling, A., 1845, Géologie de la Russie d'Europe et des Montagnes de l'Oural : Paléontologie, v. 2, p. 1–512.

Musabelliu, S., and Zaton, M., 2018, Patterns of cornulitid encrustation on the Late Devonian brachiopod shells from Russia: Proceedings of the Geologists Association, v. 129, p. 227 –234.

Nalivkin, D.V., 1930, Brakhiopody verkhnego i srednego devona Turkestana: Trudy Geologicheskogo Komiteta. Novaya seriya, 180, p. 1–22. [in Russian]

Nalivkin, D.V., 1934, Opisaniye fauny, *in* Markovskii, B.P, ed., and Nalivkin, D.V., eds., Zadonskie i Eleckie sloi: Trudy Glavnoye geologo gidro-geodezicheskoye upravleniye, v. 313, p. 17–55. [in Russian]

Nalivkin, D.V., 1937, Brakhiopody verkhnego i srednego devona i nizhnego karbona Severo-Vostochnogo Kazakhstana: Tsentral'nyi Nauchno-Issledovatel'skii Geologo-Razvedochnyi Institut (TSNIGRI), Trudy 99, p. 1–200. [in Russian]

Nalivkin, D.V., 1941, Brakhiopody glavnogo devonskogo polya, *in* Borisiak, A.A., and Gekker, R.F., eds., Fauna Glavnogo devonskogo polya: Moskva, Paleontologicheskiy Institut AN SSSR, v. 1, p. 139–221. [in Russian]

Nalivkin, D.V., 1947, Class Brachiopoda: Brachiopods, in Atlas rukovodyashchikh form iskopaemykh faun SSSR: Leningrad, Gosgeolizdat, 1947, v. 3, p. 63–134. [in Russian]

Nicollin, J.-P., and Brice, D., 2004, Biostratigraphical value of some Strunian (Devonian, uppermost Famennian) Productidina, Rhynchonellida, Spiriferida, Spiriferinida brachiopods.: Geobios, v. 37, p. 53–437.

Oleneva, N.V., 2016, Devonian Brachiopods of the Orders Spiriferida and Spiriferinida of the European Russia and Transcaucasia: Systematics, Shell Microstructure: Paleontological Journal, v. 50, no. 11, p. 1207–1296.

Özdikmen, H., 2008, Nomenclatural changes for a family group name and twelve genus group names: Munis Entomology and Zoology, v. 3, p. 217–230.

Paeckelmann, W., 1942, Beiträge zur Kenntnis devonischer Spiriferen: Abhandlungen des Reichsamts für Bodenforschung, v. 197, p. 1–188.

Pakhnevich, A.V., 2012, New Devonian punctate rhynchonellids (Brachiopoda) from Transcaucasia: Paleontological Journal, v. 6, p. 560–567.

Pardo, M.V., and García-Alcalde, J.L., 1984, Bioestratigrafía del Devónico de la Región de Almadén (Ciudad Real, España): Universidad de Oviedo, Trabajos de Geología, v. 14, p. 79–109.

Peetz, H. von, 1901, Beiträge zur Kenntniss der Fauna aus den devonischen Schichten am Rande des Steinkohlen-Bassins von Kusnetzk (West-Siberien): Saint-Pétersbourg, Travaux de la Section Geologique du Cabinet de sa Majesté, v. 4, 394 p.

Phillips, J., 1836, Illustrations of the Geology of Yorkshire: Part 2, the Mountain Limestone District: London, John Murray, 253 p.

Pushkin, V.I., 1996, *Pripyatispirifer*, a new Lower Famennian genus from Belarus: Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, v. 66, p. 43–51.

Racki, G., 1993, Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains: Acta Palaeontologica Polonica, v. 37, p. 87–182.

Racki, G., 1998, Frasnian–Famennian biotic crisis: undervalued tectonic control?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 177–198.

Racki, G., and House, M.R., 2002, Late Devonian biotic crisis: ecological, depositional and geochemical records: Palaeogeographi Palaeoclimatologi Palaeoecology, v. 181, p. 1–374.

Racki, G., 2005, Toward understanding Late Devonian global events: few answers, many questions, *in* Over, D.J., Morrow, J.R., Wignall, P.B., eds., Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards an Integrated Approach, v. 20. p. 5–36.

Reed, F.R.C., 1911, Devonian fossils from Chitral, Persia, Afghanistan and the Himalayas: Geoloical Survey of India Rec., v. 41, p. 86–114.

Reed, F.R.C., 1922, Devonian fossils from Chitral and the Pamirs. Memoirs of the Geological Survey of India: Palaeontologica Indica, New Series, v. 6, no. 2, p. 1–134.

Richards, P.R., 1974, Ecology of the Cornulitidae: Journal of Paleontology, Tulsa, v. 48, no. 3, p. 514–523.

Riquier, L., Tribovillard, N., Averbuch, O., Devleeschouwer, X., Riboulleau, A., 2006, The Late Frasnian Kellwasser horizons of the Harz Mountains (Germany): two oxygen deficient periods resulting from different mechanisms: Chemical Geology, v. 233, p. 137–155.

Rolland, Y., Hassig, M., Bosch, D., Brugier, O., Melis, R., Galoyan, G., Topuz, G., Sahakyan, L., Avagyan, A., and Sosson, M., 2020, The East Anatolia-Lesser Caucasus ophiolite: An exceptional case of large-scale obduction, synthesis of data and numerical modelling: Geoscience Frontiers, v. 11, p. 83–108.

Rzhonsnitskaya, M.A., 1948, Devonskiye otlozheniya Zakavkaz'ya: Doklady Akademy Nauk SSSR, v. 59, p. 1477–1480. [in Russian]

Rzhonsnitskaya, M.A., 1960, Order Atrypida, *in* Orlov, Y.A., ed., Osnovy Paleontologii: Moscow, Akademia Nauk SSSR, v. 7, p. 257–264. [in Russian]

Rzhonsnitskaya, M.A., and Mamedov, A.B., 2000, Devonian stage boundaries in the southern Transcaucasus: Courier Forschungsinstitut Senckenberg, v. 225, p. 329–333.

Sartenaer, P., 1956, Signification et importance du genre Cyrtiopsis dans les dépôts Famenniens inferieurs. Deuxième note: Cyrtiopsis senceliae nov. sp: Bulletin de l'Institut royal des Sciences naturelles de Belgique, v. 32, p. 1–12.

Sartenaer, P., 1961, Late Upper Devonian (Famennian) rhynchonelloid brachiopods: Bulletin de l'Institut royal des Sciences naturelles de Belgique, Naturelle, v. 37, p. 1–15.

Sartenaer, P., 1965a, Rhynchonelloidea de Shogran et Kuragh (Chitral). Italian Expeditions to the Karakorum (K2) and Hindu Kush: Brill, Leiden, Scientific Reports, IV.-Paleontology, v. 1, p. 55–66.

Sartenaer, P., 1965b, Signification et importance du genre Cyrtiopsis dans les dépôts famenniens inférieurs. Quatrième Note. Position systématique et stratigraphique du lectotype de l'espèce Spirifer Murchisionanus De Verneuil E., 1845: Bulletin de la Société belge de Géologie, Paléontologie, Hydrogéologie, v. 73, no. 3, p. 366–392.

Sartenaer, P., 1966a, *Ripidiorhynchus*, nouveau genre de Brachiopode Rhynchonellide du Frasnien: Bulletin de l'Institut royal des Sciences naturelles de Belgique, Naturelle, v. 42, no. 30, p. 1–15.

Sartenaer, P., 1966b, Frasnian Rhynchonellida from the Ozbak-Kuh and Tabas Regions (east Iran): Iran Geological Survey, Report 6, no. 2, p. 25–54.

Sartenaer, P., 1970, Nouveaux genres Rhynchonellides (Brachiopodes) du Paléozoïque: Bulletin de l'Institut royal des Sciences naturelles de Belgique, v. 46, no., 32, p. 1–32.

Sartenaer, P., 1974, Signification stratigraphique du 'niveau des monstres' du Frasnien franco–belge: Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, v. 50, p. 1–19.

Sartenaer, P., 2001, Revision of the rhynchonellid brachiopod genus *Ripidiorhynchus* Sartenaer: Geologica Belgica, v. 3, p. 191–213.

Sartenaer, P., 2003, *Gesoriacorostrum*, a new Middle Frasnian rhynchonellid (brachiopod) genus from Boulonnais (N France): Geologica Belgica, v. 6, p. 181–192.

Sartenaer, P., and Plodowski, G., 2003, Reassessment of the Strunian genus *Araratella* Abrahamian, Plodowski and Sartenaer 1975 in the Northern Gondwanaland (Rhynchonellida, Brachiopoda): Courier Forschungsinstitut Senckenberg, v. 242, p. 329–348.

Savage, N.M., 1996, Classification of Paleozoic rhynchonellid brachiopods, *in* P. Copper, P., and Jin, J., eds., Proceedings of the Third International Brachiopod Congress: A.A. Balkema, Rotterdam, p. 60–249.

Savage, N.M., 2007, Rhynchonellida (part), *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, 6 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H19–H2703.

Savage, N.M., Manceñido, M.O., Owen, E.F., Carlson, S.J., Grant, R.E., Dagys, A.S., and Sun, D.L., 2002, Rhynchonellida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, 4 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H376–H1027.

Schindler, E., 1990, Die Kellwasser-Krise (hohe Frasne-Stufe, Ober Devon): Gottinger Arbeiten zur Geologie und Paläontologie, v. 46, p. 1–115.

Schindler, E., 1990b, The late Frasnian (Upper Devonian) Kellwasser Crisis, *in* Kauffman, E.G., Walliser, O.H., eds., Extinction Events in Earth History: Proceedings of the Project 216: Global Biological Events in Earth History: Springer Berlin Heidelberg, Berlin, Heidelberg, p. 151–159.

Schindler, E., 1993, Event-stratigraphic markers within the Kellwasser Crisis near the Frasnian/Famennian boundary (Upper Devonian) in Germany: Palaeogeography Palaeoclimatology Palaeoecology, v. 104, p. 373–379.

Schmidt, H., 1965, Neue Gattungen Paläozoischer Rhynchonellacea (Brachiopoda): Senckenbergiana lethaea, v. 45, no. 6, p. 1–25.

Schuchert, C., 1913, Class 2: Brachiopoda, *in* Eastman, C.R., ed., Text–book of Paleontology, v. 1, Part 1, 2nd edition: London, MacMillan and Co., Ltd., p. 355–420.

Serobyan, V., Grigoryan, A., Mottequin, B., Mayilyan, R., Crônier, C., and Danelian, T., 2019a, Biostratigraphy of the Upper Devonian trigonirhynchiid brachiopods (rhynchonellida) from Armenia: Proceedings of National Academy of Sciences of the Republic of Armenia, Earth Sciences, v. 72, p. 3–18.

Serobyan, V., and Mayilyan, R., 2019b, Progress in paleontology and stratigraphy of Upper Paleozoic sedimentary sequences of Armenia: Collection of scientific articles of YSU SSS, Natural and Physical-Mathematical Sciences, v. 1, p. 118–125.

Serobyan, V., Danelian, T., Crônier, C., Grigoryan, A., and Mottequin, B., 2021, Lower Famennian (Upper Devonian) rhynchonellide and athyride brachiopods from the South Armenian Block: Journal of Paleontology, v. 95, p. 527–552.

Serobyan, V., Danelian, T., Crônier, C., Grigoryan, A., and Mottequin, B., (in press) Aramazdospirifer orbelianus (Abich, 1858), a new cyrtospiriferid brachiopod genus and a biostratigraphically important species from the lower Famennian (Upper Devonian) of Armenia: Comptes Rendus Palevol.

Sidjachenko, A.I., 1962, Spiriferidy i stratigrafiya famenskikh otlozheniy tsentral'nogo i yugo-vostochnogo Karatau: Moskva, Akademiya Nauk SSSR, Sibirskoje otdelenie, 147 p. [in Russian]

Sokiran, E.V., 2002, Frasnian–Famennian extinction and recovery of rhynchonellid brachiopods from the East European Platform: Acta Palaeontologica Polonica, v. 47, p. 339–354.

Sokiran, E.V., 2006, Early–Middle Frasnian cyrtospiriferid brachiopods from the East European Platform: Acta Palaeontologica Polonica, v. 51, p. 759–772.

Sokiran, E.V., 2013, *Cyrtospirifer vjacheslavi*, a New Cyrtospiriferid Species (Cyrtospiriferidae, Brachiopoda) from the Middle Frasnian of the East European Platform: Paleontological Journal, v. 47, p. 581–587.

Sorauf, J.E., Pedder, A.E.H., 1986, Late Devonian rugose corals and the Frasnian–Famennian crisis: Canadian Journal of Earth Sciences, v. 23, p. 1265–1287.

Sosson, M., Rolland, Y., Müller, C., Danelian, T., Melkonyan, R., Kekelia, S., Adamia, S., Babazadeh, V., Kangarli, T., Avagyan, A., Galoyan, G., and Mosar, J., 2010, Subductions, obduction and collision in the Lesser Caucasus (Armenia, Azerbaijan, Georgia), new insights. *in* Sosson, M., Kaymakci, N., Stephenson, E.A., Bergerat, F., and Starostenko, V., eds., Sedimentary Basin Tectonics from the Black Sea and Caucasus to the Arabian Platform: London, Geological Society, Special Publication, v. 340, p. 329–352.

Sowerby, J., de C., 1840, On the distribution and classification of theolder or Paleozoic deposits of the North of Germany and Belgium and their comparison with formations of the same age in the British Isles, *in* Sedgwick, A., and Murchison, R. I., eds., Organic Remains Engraved and Described by James de Carle Sowerby.: Transactions of the Geological Society of London, 2nd ser., v. 5, no. 3, p. 50–58.

Spaletta, C., Perri, M.C., Over, D.J., Corradini, C., 2017, Famennian (Upper Devonian) conodont zonation: revised global standard: Bulletin of Geosciences, v. 92, p. 31–57.

Stainbrook, M.A., 1945, Brachiopoda of the Independence Shale of Iowa: Geological Society of America Memoir, v. 14, p. 1–74.

Stainbrook, M.A., 1947, Brachiopoda of the Percha Shale of New Mexico and Arizona: Journal of Paleontology, v. 21, p. 297–328.

Stainbrook, M.A., 1951, Substitution for the preoccupied name Hystricina: Journal of the Washington Academy of Sciences 41, 196 p.

Stampfli, G., Von Raumer, J.F., and Borel, G.D., 2002, Paleozoic evolution of pre-Variscan terranes: From Gondwana to the Variscan collision, *in* Martinez Catalan, J.R., Hatcher, R.D., Jr., Arenas, R., and Diaz Garcia, F., eds, Variscan-Appalachian dynamics: The buildings of the late Paleozoic basement: Boulder, Colorado, Geological Society of America, Special Paper, v. 364, p. 263–280.

Stanley, S.M., 2016, Estimates of the magnitudes of major marine mass extinctions in earth history: Proceedings of the National Academy of Sciences, v. 113, E6325–E6334.

Stigall, A.L., 2012, Speciation collapse and invasive species dynamics during the Late Devonian "Mass Extinction": GSA Today, v. 22, p. 4–9.

Struve, W., 1966, Beiträge zur Kenntnis devonischer Brachiopoden, 15. Einige Atrypinae aus dem Silurium und Devon: Senckenbergiana lethaea, v. 47, p. 123–163.

Termier, H., and Termier, G., 1949, Essai sur l'évolution des Spiriféridés: Notes et Mémoires, Service géologique, Division des Mines et de la Géologie (Maroc), v. 74, no. 2, p. 85–112.

Vandercammen, A., 1959, Essai d'étude statistique des Cyrtospirifer du Frasnien de la Belgique: Institut royal des Sciences naturelles de Belgique, Mémoire, v. 145, p. 1–175.

Verneuil, E., 1845., Geologie de la Russie d'Europe et des Montagnes de l'Oural: Paris, Paleontologie, v. 2, p. 1–512.

Vinn, O., 2010, Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms: Palæogeography, Palæoclimatology, Palæoecology, Amsterdam, v. 292, p. 211–221.

Vinn, O., Musabelliu, S., and Zaton, M., 2019, Cornulitids from the Upper Devonian of the Central Devonian Field, Russia: GFF, v. 141, p. 68–76.

Von Schlotheim, E.F, 1820, Die Petrefakten-Kunde auf ihrem jetzigen Standpunkte durch die Beshreibung seiner Sammlung versteinerter und fossiler Ueberreste des their-und Planzenreichs der Voiwelt erlaeutert: Gotha, 437 p.

Waagen, W.H., 1883, Salt Range fossils, I. *Productus*-Limestone Fossils: Brachiopoda. Palaeontologia Indica, Series, 13–14, p. 391–546.

Walliser, O., 1996, Global events in the Devonian and Carboniferou, *in*, Walliser, O., ed., Global Events and Event Stratigraphy in the Phanerozoic: Berlin, Springer-Verlag, p. 225–250.

Wanless, H.R., Tedesco, L.P., Tyrrell, K.M., 1988, Pro duction of subtidal and surficial tempestites by Hurricane Kate, Caicos Platform, British West Indies: Journal of Sedimentary Petrology, v. 58, p. 739–750.

Woolfe, K.J., (1993), "Devonian depositional environments in the Darwin Mountains: Marine or non-marine?": Antarctic Science, v. 5, p. 211–220.

Wilson, M.A., and Taylor, P.D., 2001, "Pseudobryozoans" and the problem of encruster diversity in the Paleozoic: PaleoBios, v. 21 ((supplement to no. 2)), p. 134–135.

Ziegler, W., and Sandberg, C.A., 1990, The Late Devonian standard conodont zonation: Courier Forschungsinstitut Senckenberg, v. 121, p. 1–115.

Paleontological plates

Plate 1

Ripidiorhynchus gnishikensis (Abrahamyan, 1959) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**1–5**). IGSNASRAGM 3927/PS 3033 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views.

Ripidiorhynchus djravankensis n. sp. from the lowest Famennian Noravank Regional Stage of Djravank section in Armenia.

(**6–10**). IGSNASRAGM 3929/PS 3035, almost complete juvenile specimen in ventral, dorsal, lateral, posterior, and anterior views.

(**11–15**). IGSNASRAGM 3930/PS 3036, partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views.

(**16–20**). IGSNASRAGM 3931/PS 3037, almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bar: 5 mm.

Plate 1

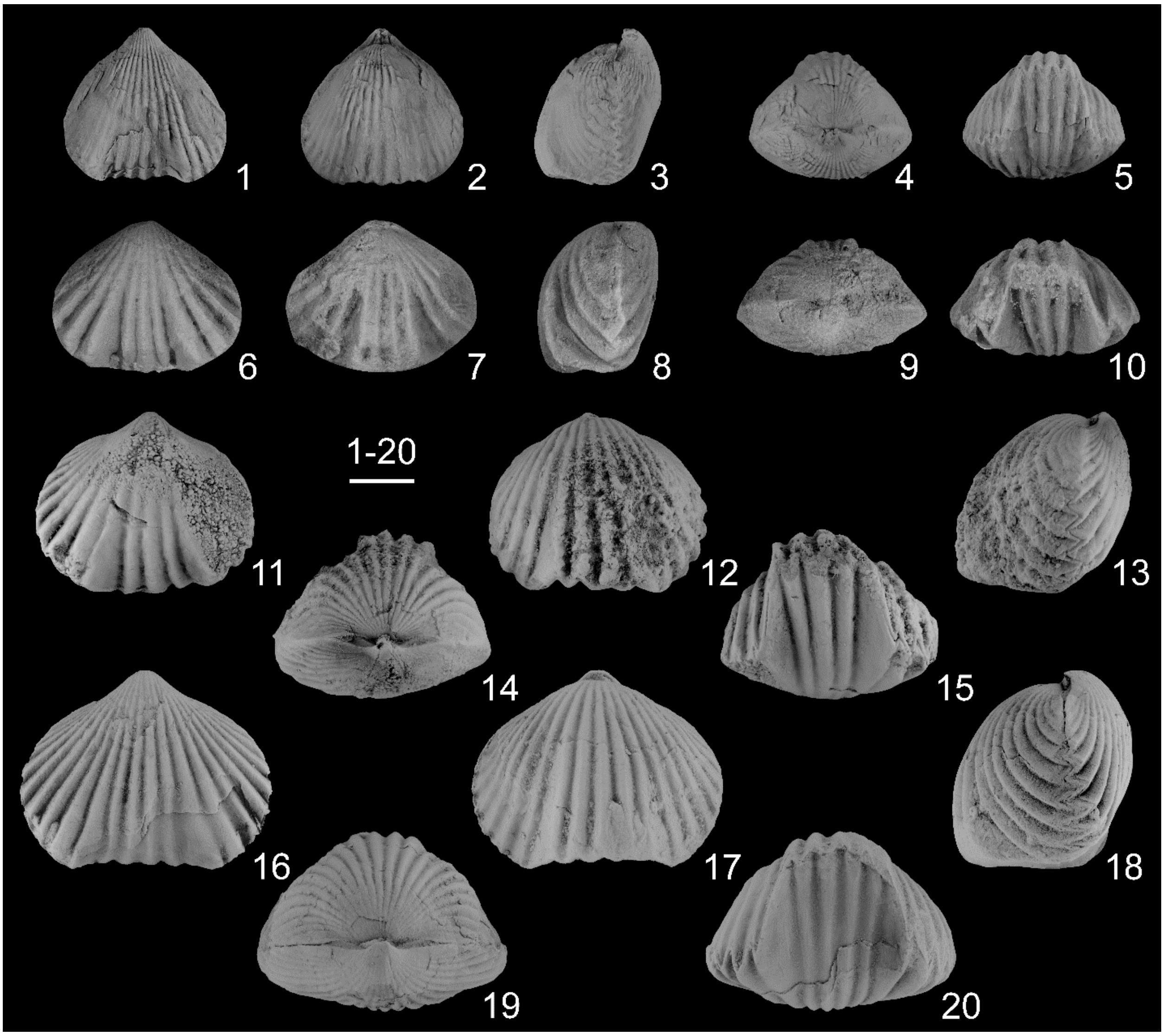


Plate 2

Cyphoterorhynchus koraghensis koraghensis (Reed, 1922) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**1–5**). IGSNASRAGM 3933/PS 3039 (Ertych section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views.

(**6–10**). IGSNASRAGM 3934/PS 3040 (Djravank), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views.

(**11–15**). IGSNASRAGM 3935/PS 3041 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bar: 5 mm.

Plate 2

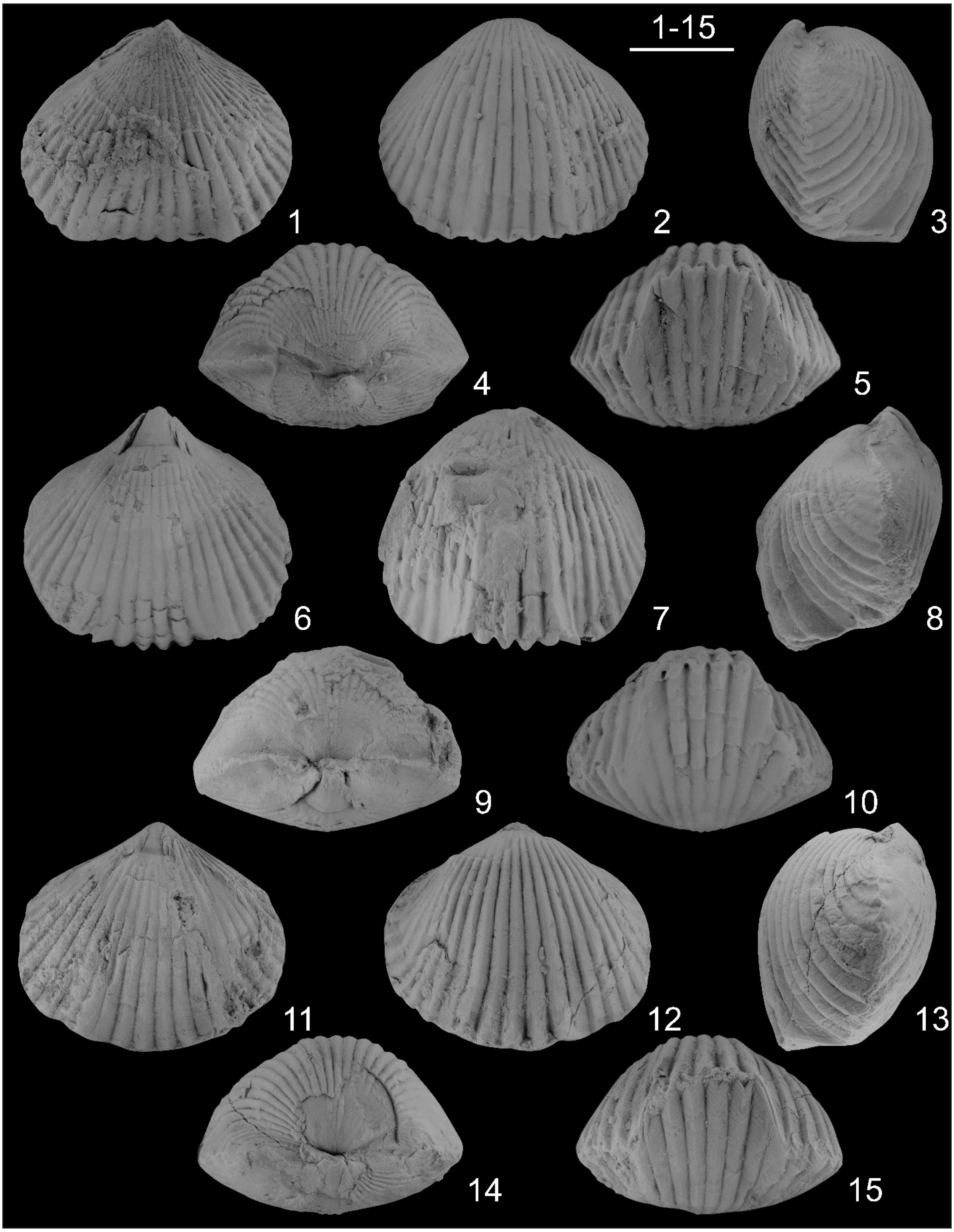


Plate 3

Atryparia (*Costatrypa*) *ertichensis* (Abrahamyan, 1959) from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**1–7**). IGSNASRAGM 3936/AB270/3–54 (paralectotype, Ertych section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (**1–5**), close-up of ornament showing the bifurcation on the ventral valve (**6**), and Abrahamyan's original handwritten mark on the dorsal valve of the specimen (**7**). Scale bars: 10 mm (1–5), 2 mm (6).

Spinatrypa (*Spinatrypa*) sp. from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**8–13**). IGSNASRAGM 3937/PS 3043 (Ertych section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (**21–25**), and close-up to the micro-ornament displaying the growth lines covered by concentric microlines (**26**). Scale bars: 10 mm (8–12), 2 mm (13).

Plate 3

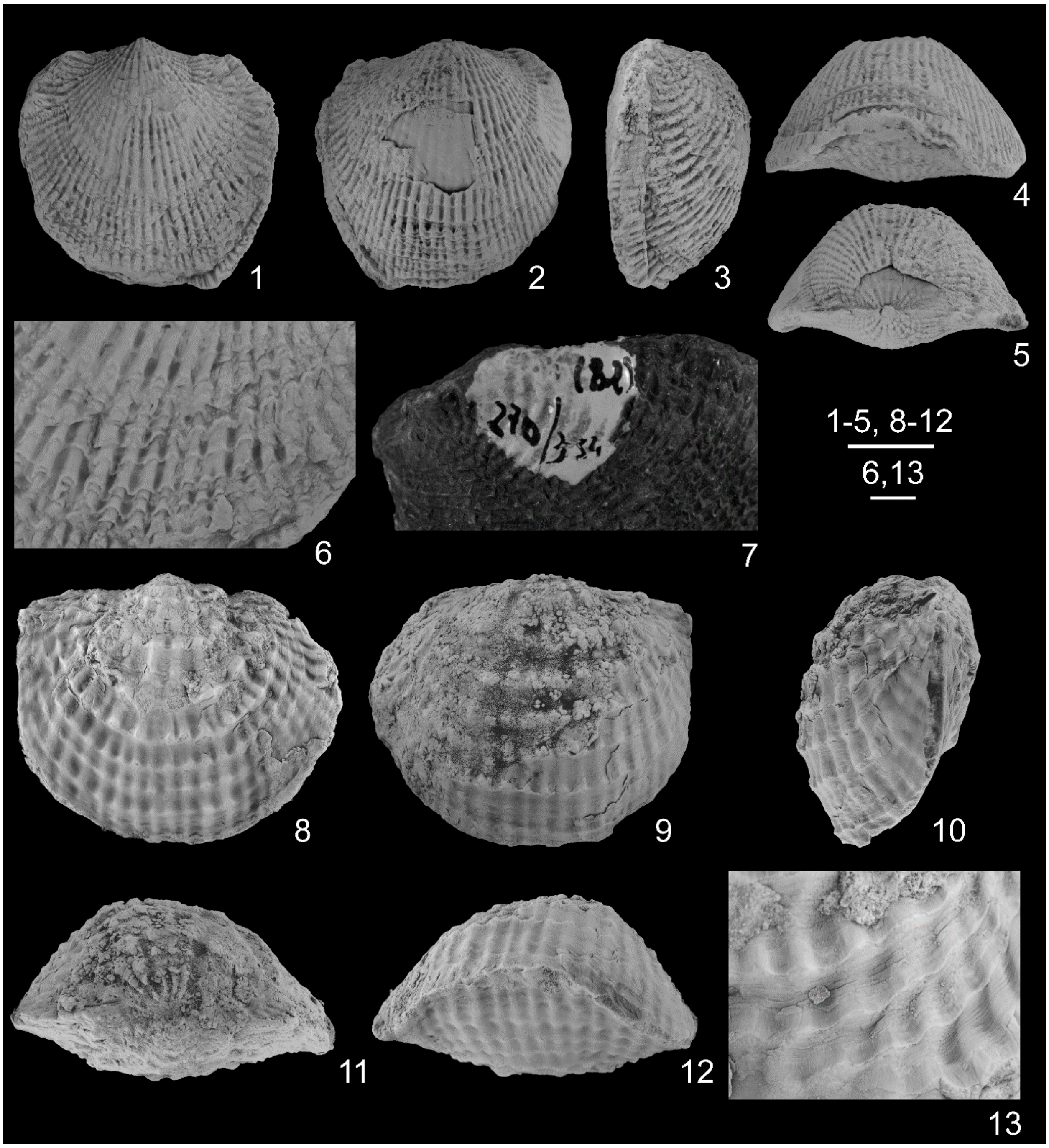


Plate 4

Desquamatia (*Seratrypa*) *abramianae* Alekseeva et Komararov, 1992 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**1–5**). IGSNASRAGM 3939/PS 3045 (Noravank section), partly corroded juvenile specimen in ventral, dorsal, lateral, posterior and anterior views.

(**6–10**). IGSNASRAGM 3940/PS 3046 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views.

(**11–16**). IGSNASRAGM 3941/PS 3047 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (**11–15**), and close-up (**16**) of tubular ribs increasing by bifurcation and intercalation on the ventral valve. Scale bars: 10 mm (1–15), 2 mm (16).

Plate 4

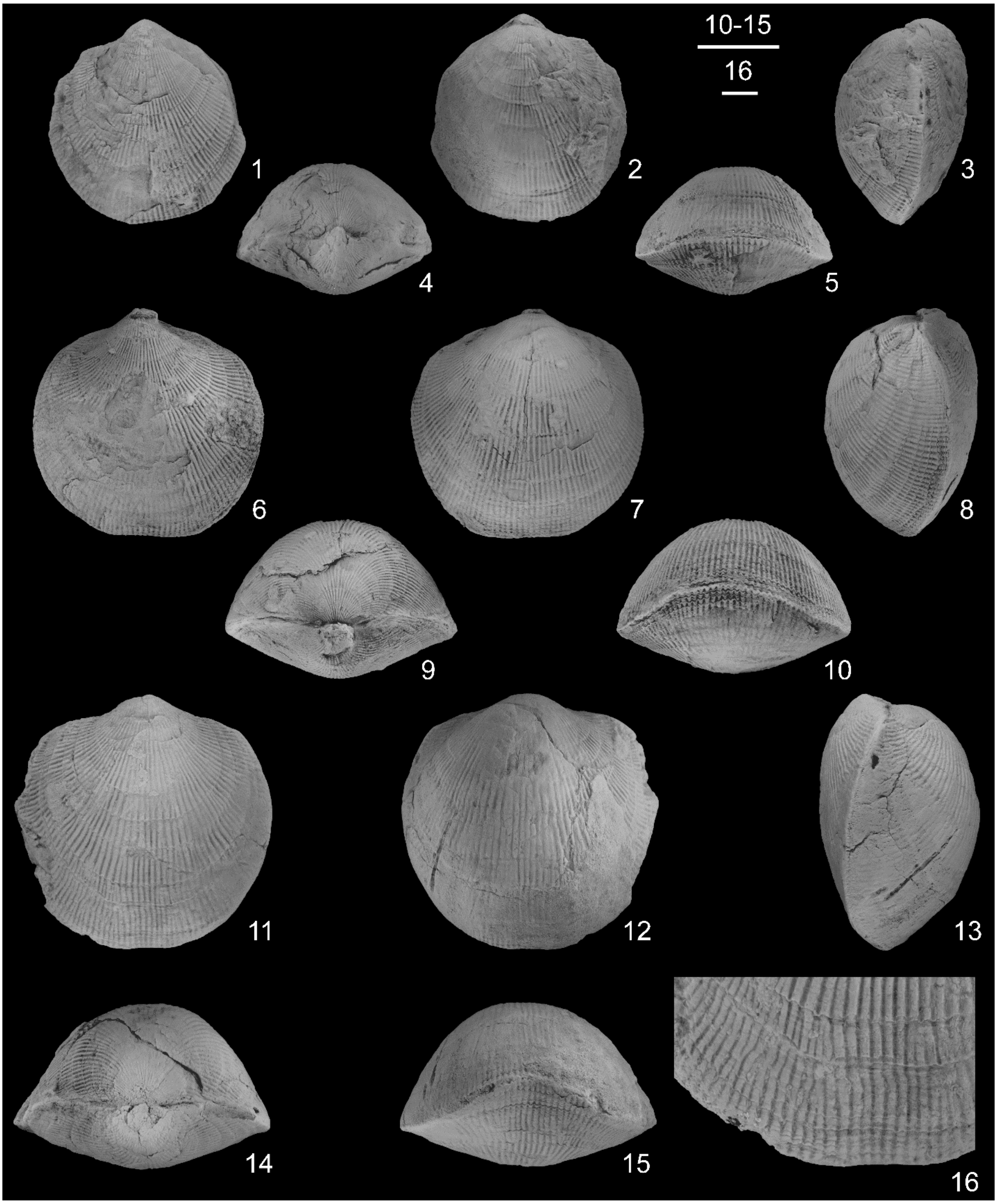


Plate 5

Cyrtospiriferinae gen. et sp. 1 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchusarpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(1–6). IGSNASRAGM 3942/PS 3048 (Ertych section), partly corroded specimen in ventral, dorsal, lateral, posterior and anterior views **(1–5**), and close-up of the ornament displaying the poorly preserved ribs near at the front **(6**).

Cyrtospiriferinae gen. et sp. 2 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**7–9**). IGSNASRAGM 3943/PS 3049 (Djravank section), incomplete ventral valve in orthogonal and lateral views (**7–8**), and close-up of the ornament showing the ribs in the sulcus (**9**).

Cyrtospirifer? sp. 1 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000) in Armenia.

(**10–11**). IGSNASRAGM 3944/PS 3050 (Ertych section), incomplete ventral valve in orthogonal and posterior views.

Cyrtospirifer? sp. 2 from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) in Armenia.

(**12–16**). IGSNASRAGM 3946/PS 3052 (Djravank section), corroded specimen in ventral, dorsal, lateral, posterior and anterior views.

Cyrtospirifer sp. 1 from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) in Armenia.

(**17–21**). IGSNASRAGM 3948/PS 3054 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bars: 10 mm (1–5, 7–8, 10–21), 2 mm (9), 0.5 mm (6).

Plate 5

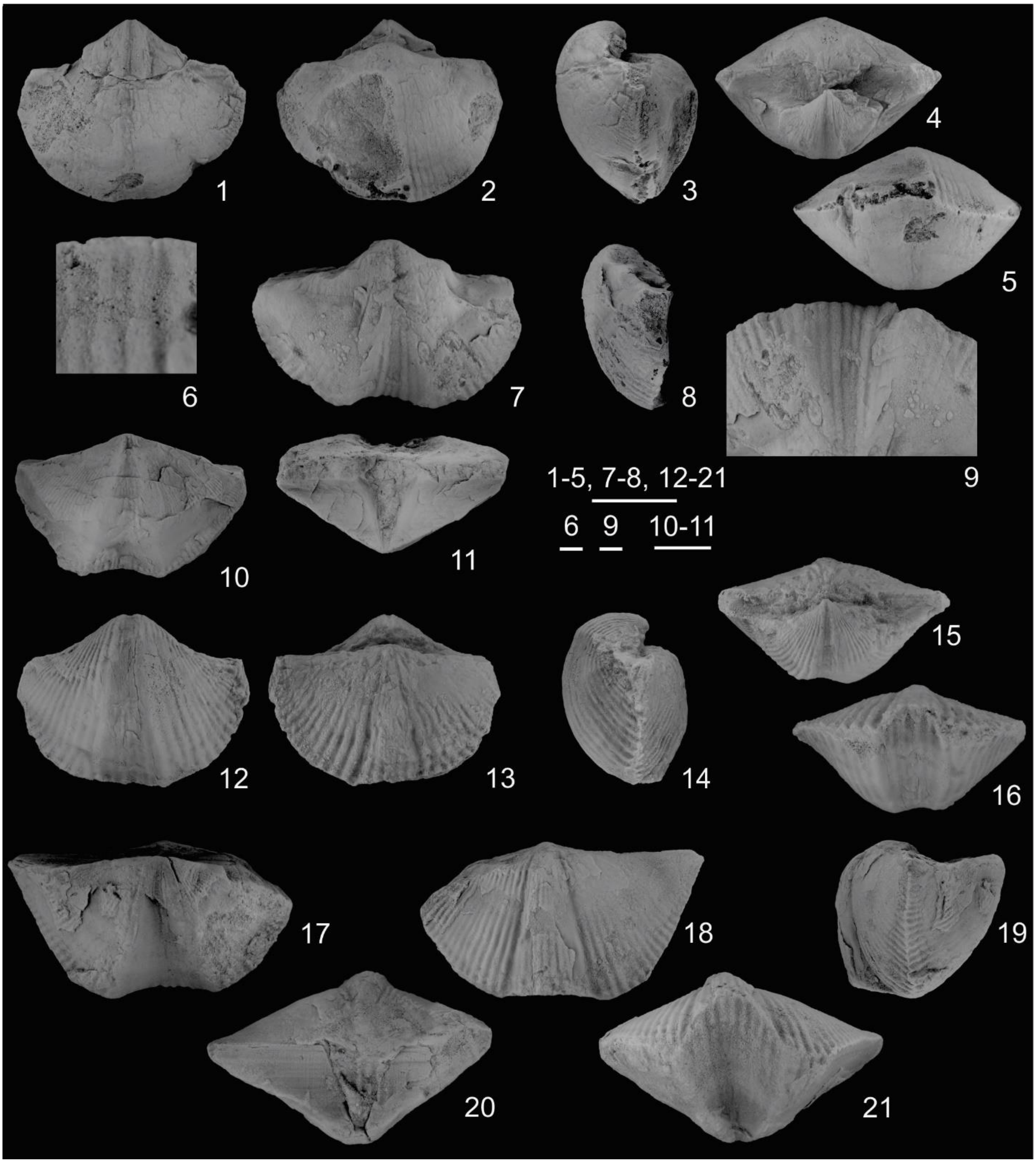


Plate 6

Cyrtospirifer pseudoasiaticus n. sp. from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957) in Armenia.

(**1–5**, **17**). IGSNASRAGM 3950/PS 3056 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (**1–5**), and close-up of the micro-ornament (capillae developed both on ribs and in interspaces).

(**6–10**, **18**). IGSNASRAGM 3951/PS 3057 (Djravank section), corroded specimen in ventral, dorsal, lateral, posterior and anterior views (**6–10**), and oblique anterior view showing a partially preserved cornulitid tubeworm on the ventral valve (**18**).

(**11–16**). IGSNASRAGM 3952/PS 3058 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (**11–15**), and close-up of the sulcus displaying the bifurcation of ribs (**16**).

(**19–21**). IGSNASRAGM 3953/PS 3059 (Ertych section), poorly preserved articulated specimen in posterior view (**19**) and close-up close-up of the ventral interarea showing the pseudodeltidium in posterior and oblique lateral views (**20–21**). Scal bars: 10 mm (1–15, 19), 5 mm (18), 2 mm (20–21), 1 mm (16), 0.5 mm (17).

Plate 6

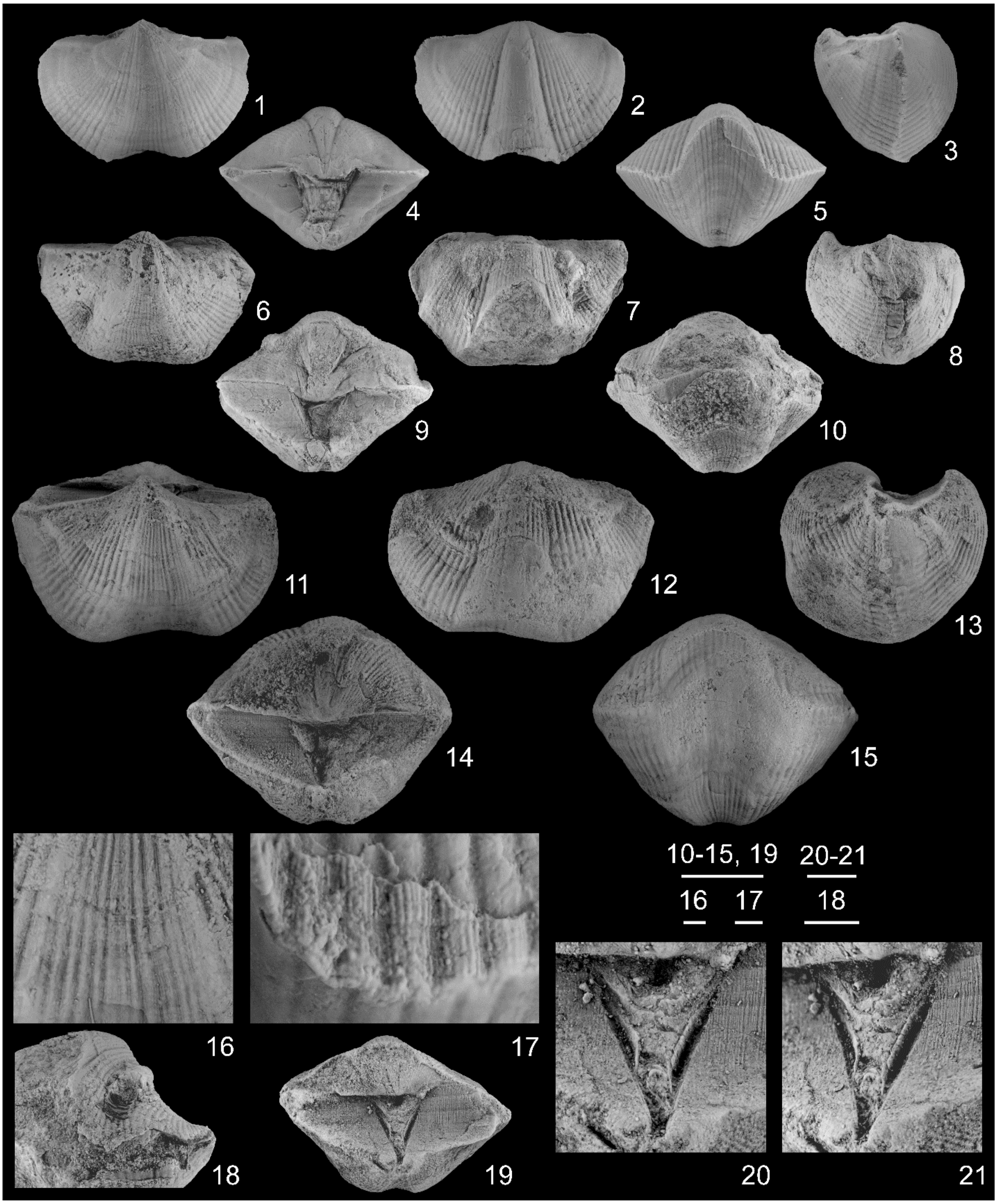


Plate 7

Sinospirifer sp. 1 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000).

(**1–6**). IGSNASRAGM 3955/PS 3061 (Ertych section), corroded specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views.

(**7–13**). IGSNASRAGM 3956/PS 3062 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior, posterolateral and anterior views (**7–12**), and close-up of the ventral interarea showing the partly preserved central foramen (**13**).

Sinospirifer sp. 2 from the Frasnian *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000).

(**14–18**). IGSNASRAGM 3958/PS 3064 (Ertych section), corroded specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bars: 10 mm (1–12, 14–18), 0.5 mm (13).

Plate 7

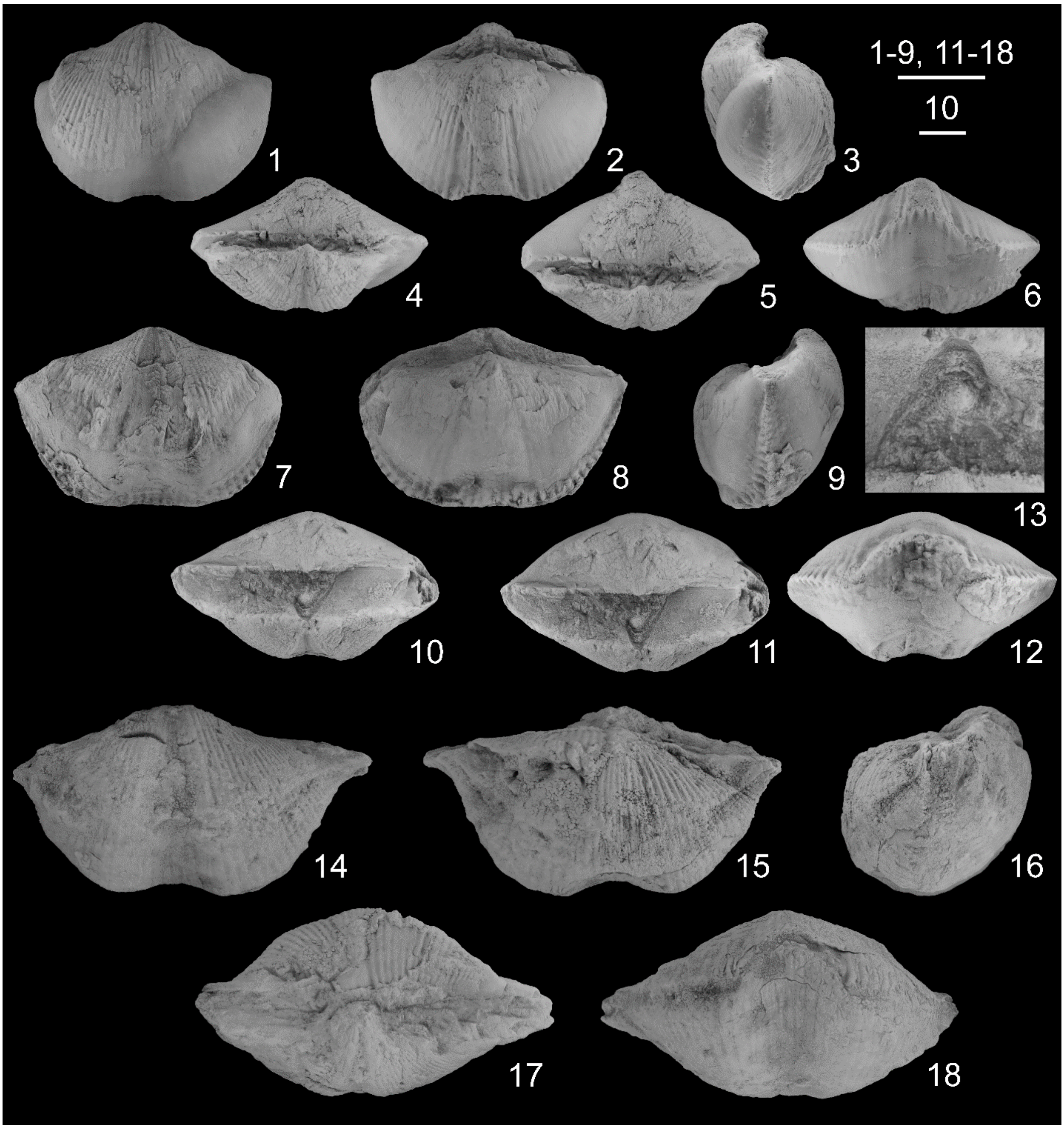


Plate 8

Pseudocyrtiopsis areniensis n. sp. from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957).

(**1–9**). IGSNASRAGM 3960/PS 3066 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views (**1–6**), and close-up of the ventral interior showing the pseudodeltidium (**7–8**) as well as close-up of the micro-ornament displaying capillae and tubercles deeloped both on ribs and in interspaces (**9**).

(**9–14**). IGSNASRAGM 3961/PS 3067 (Djravank section), corroded specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views.

(**15–20**). IGSNASRAGM 3962/PS 3068 (Ertych section), corroded specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views.

(**21–26**). IGSNASRAGM 3963/PS 3069 (holotype, Djravank section),corroded specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. Scal bars: 10 mm (1–6, 10–27), 2 mm (7–8), 1 mm (9).

Plate 8

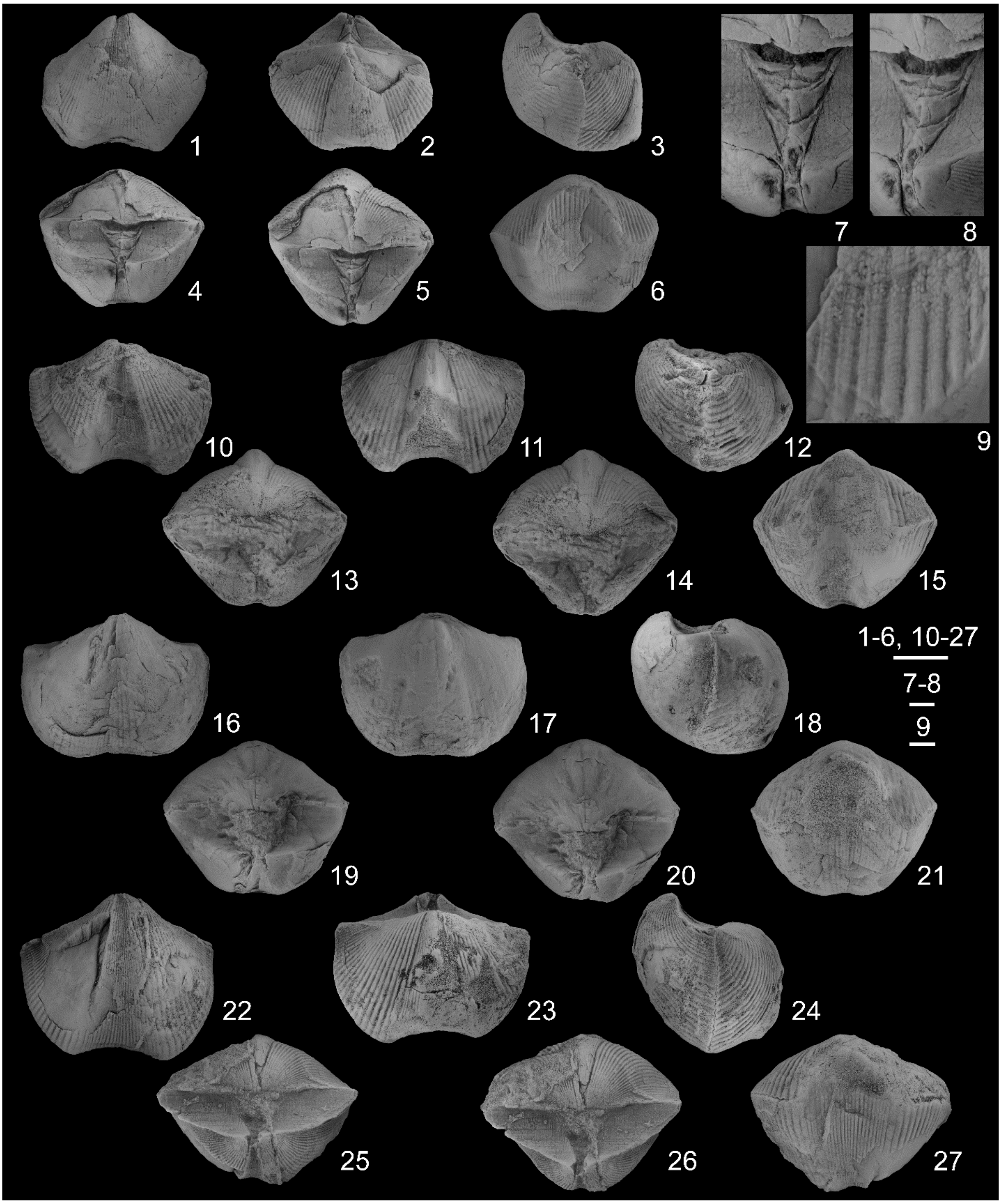

1
2
3
7
8
4
5
6
9
10
11
12
13
14
15
16
17
18
1-6, 10-27
7-8
9
19
20
21
22
23
24
25
26
27

Plate 9

Pentagonospirifer abrahamyanae n. gen., n. sp. from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957), Central Armenia. The arrows indicate the anterior margin.

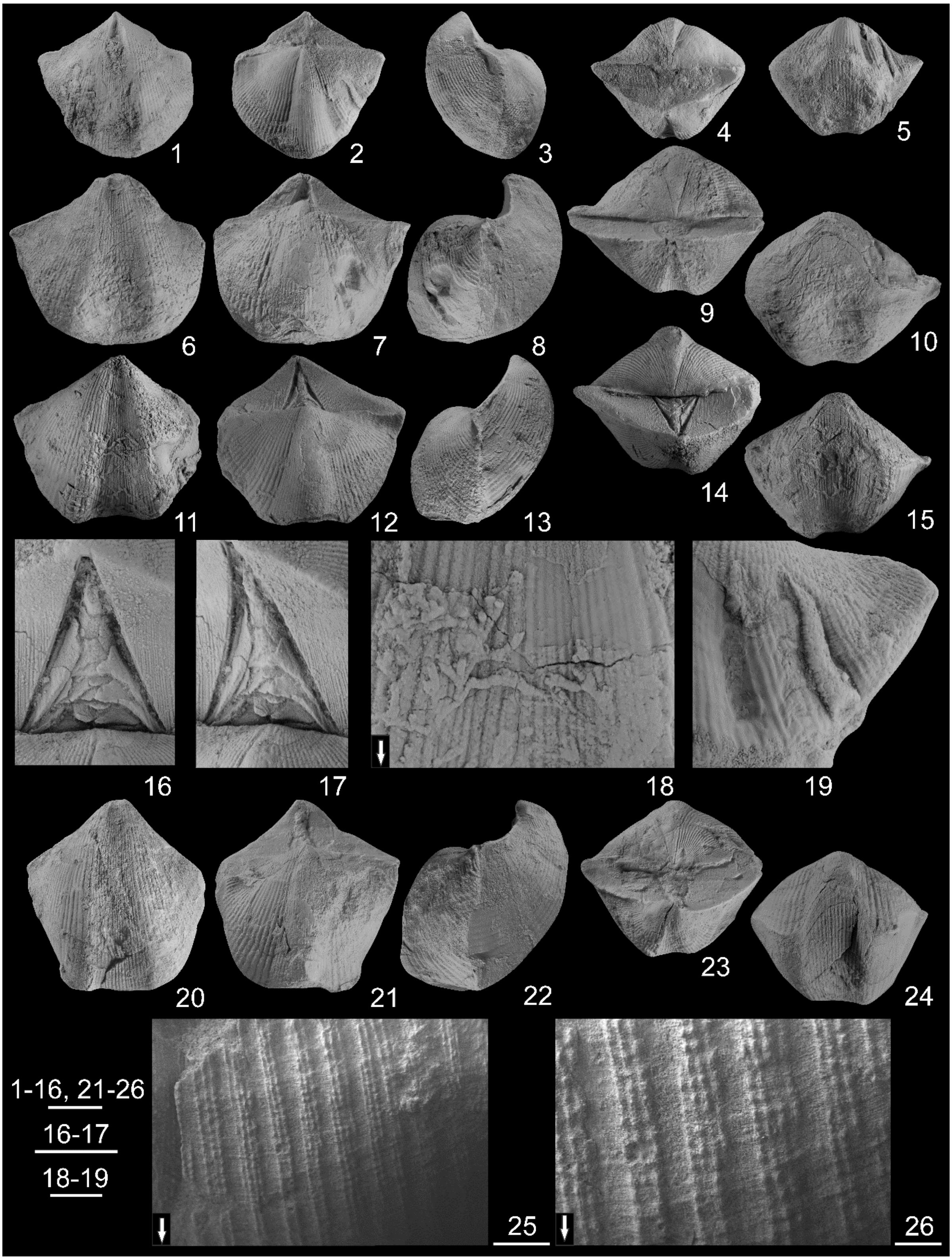
(**1–5**, **19**). IGSNASRAGM 3965/PS 3071 (Djravank section), almost complete juvenile specimen in ventral, dorsal, lateral, posterior and anterior views (**1**–**5**), and close-up of cornulitid tubeworm (**19**).

(**6–10**). IGSNASRAGM 3966/PS 3072 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views.

(**11–18**). IGSNASRAGM 3967/PS 3073 (holotype, Djravank section), almost compete 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 plates 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).

Plate 9



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
1-16, 21-26
16-17
18-19
25
26

Plate 10

Angustisulcispirifer arakelyani n. gen., n. sp. from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), Armenia. The arrows indicate the anterior margin.

(**1–6**). IGSNASRAGM 3970/PS 3076 (Djravank section), partly exfoliated juvenile specimen in ventral, oblique ventral, dorsal, lateral, posterior and anterior views.

(**7–12**). IGSNASRAGM 3971/PS 3077 (holotype, Noravank section), almost complete specimen in ventral, dorsal, lateral, posterior, posterdorsal and anterior views.

(**13–18**). IGSNASRAGM 3972/AR 3078 (Ertych section), partly exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views.

(**19–26**). IGSNASRAGM 3973/PS 3079, (Noravank section), almost complete specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views (**13–24**), and close-up of the ventral interarea showing the remnants of a delthyrial cover of unknown origin (**25–26**).

(**27**). IGSNASRAGM 3974/PS 3080 (Ertych section), incomplete specimen, close-up of the ventral interarea clearly displaying the delthyrial plate, though it is partly concealed by sediment. Scale bars: 10 mm (1–24), 2 mm (25, 27), 0.5 mm (26).

Plate 10

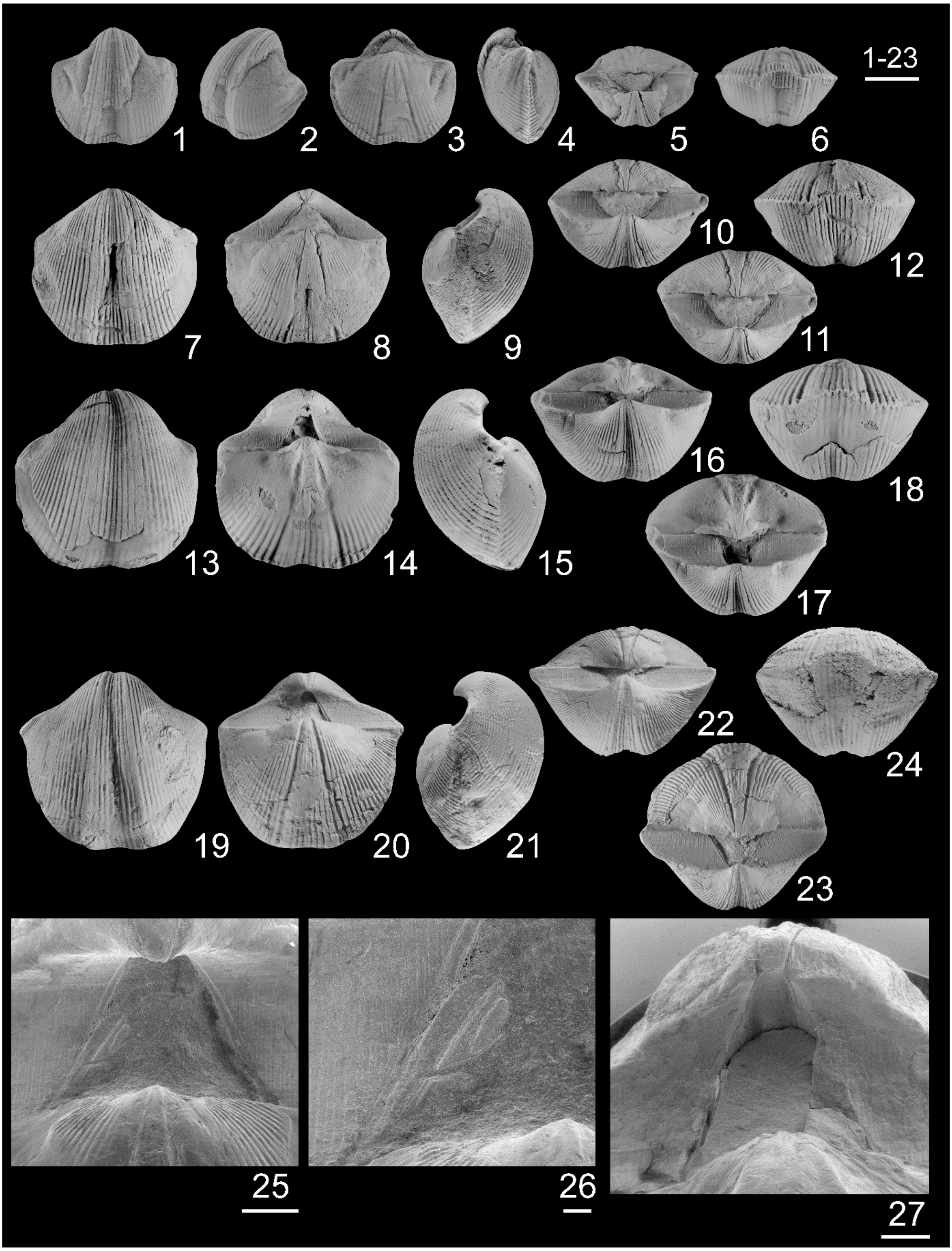


Plate 11

Angustisulcispirifer arakelyani n. gen., n. sp. from the Frasnian *Cyrtospirifer subarchiaci*–*Cyphoterorhynchus arpaensis* Zone of Rzhonsnitskaya and Mamedov (2000), Armenia. The arrows indicate the anterior margin.

(**1–3**). IGSNASRAGM 3975/PS 3081 (Ertych section), details of the micro-ornament from the lateral oblique view (**1–2**) and close to the anterior margin (**3**) showing only the growth lines that are still visible in more internal layers of the shell.

(**4**). IGSNASRAGM 3976/PS 3082, close-up of the ornament displaying the faint ribs in the sulcus.

Scale bars: 1 mm (1), 0.5 mm (2), 400 μm (3–4).

Plate 11

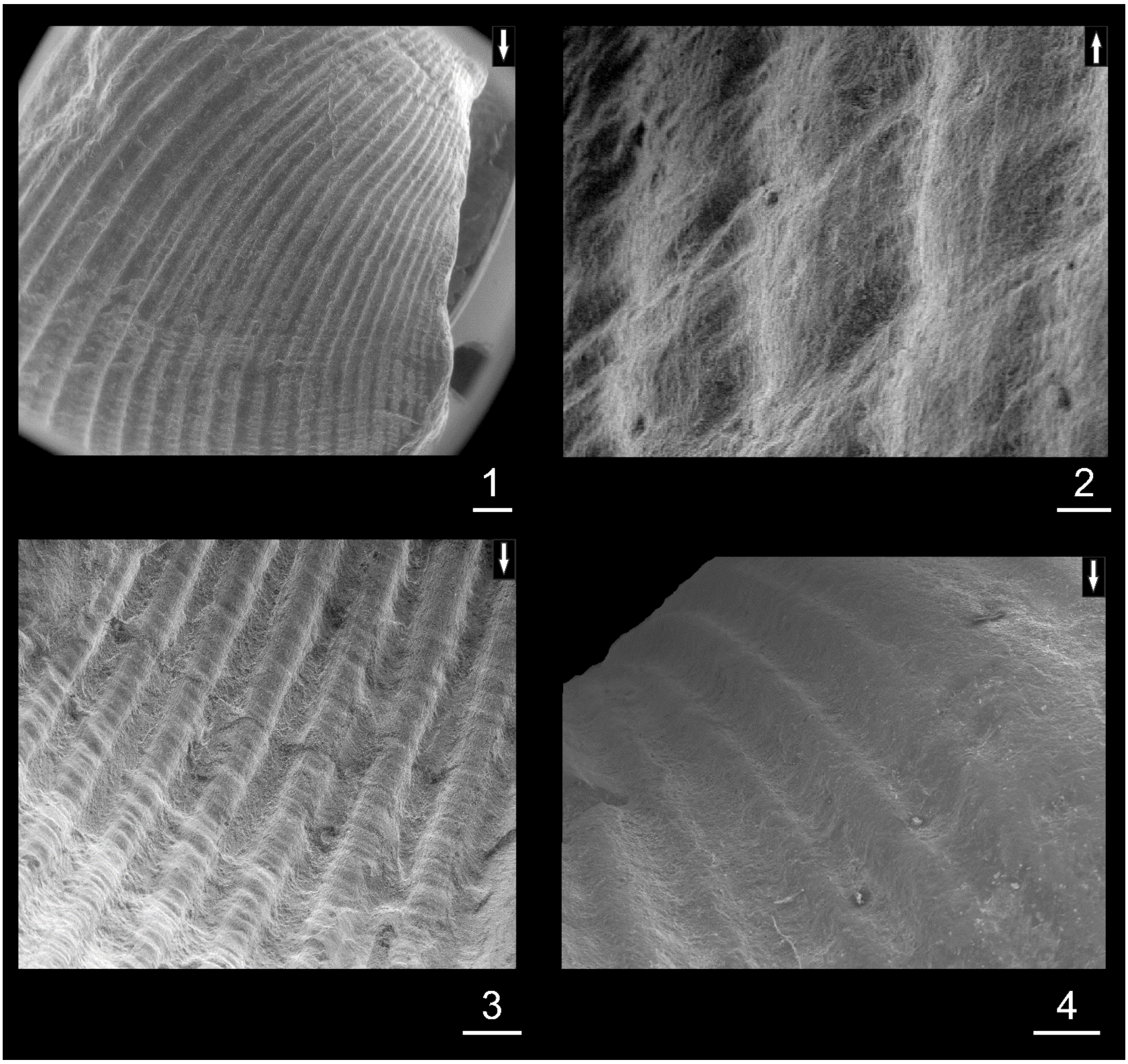


Plate 12

Tornatospirifer armenicus (Abrahamyan, 1974) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957), Central Armenia.

(**1–6**). IGSNASRAGM 3978/PS 3084 (Djravank 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 (Djravank), partly exfoliated specimen in ventral, dorsal, lateral, posterior, posterodorsal and anterior views. Scale bar: 10 mm (1–18).

Plate 12

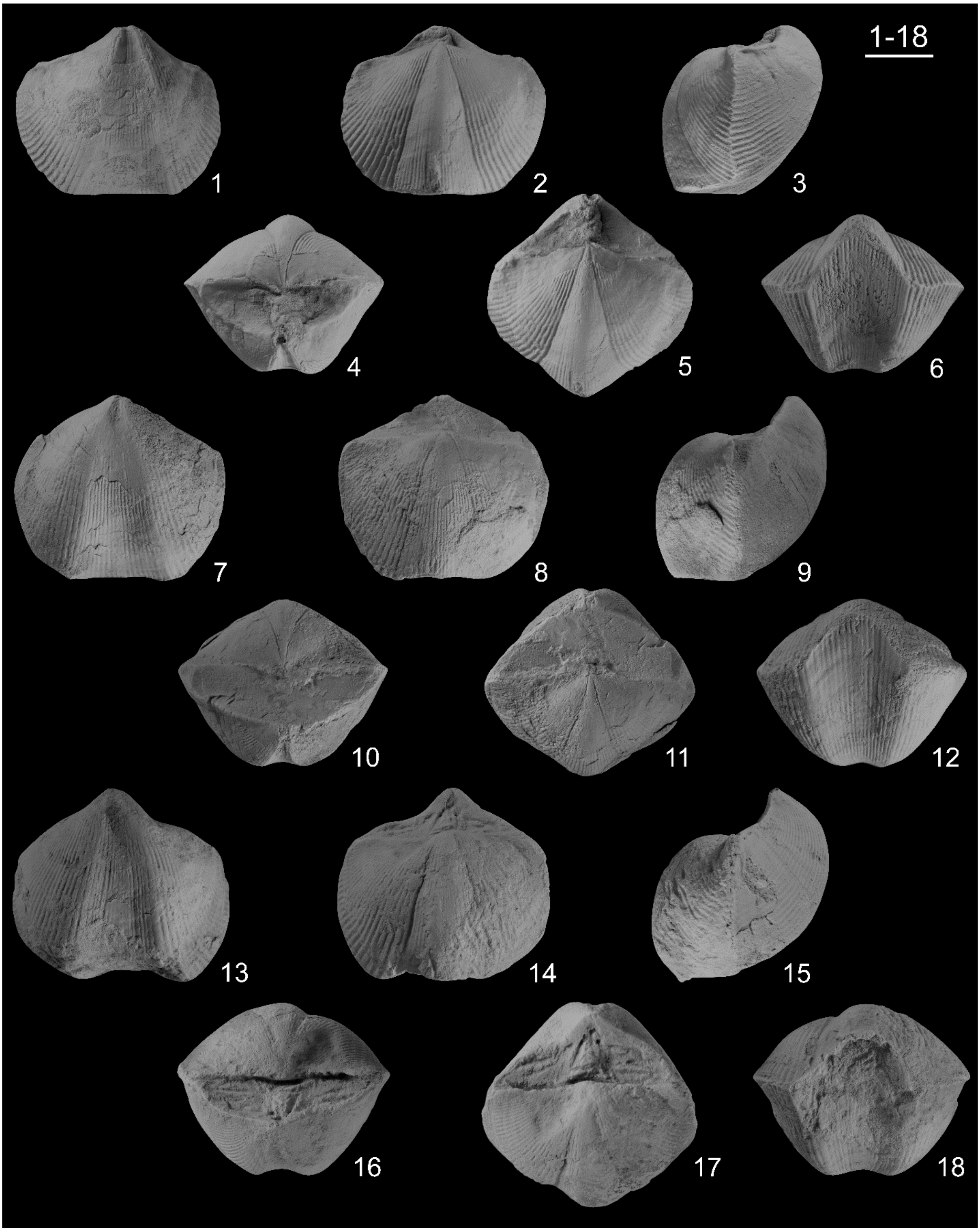


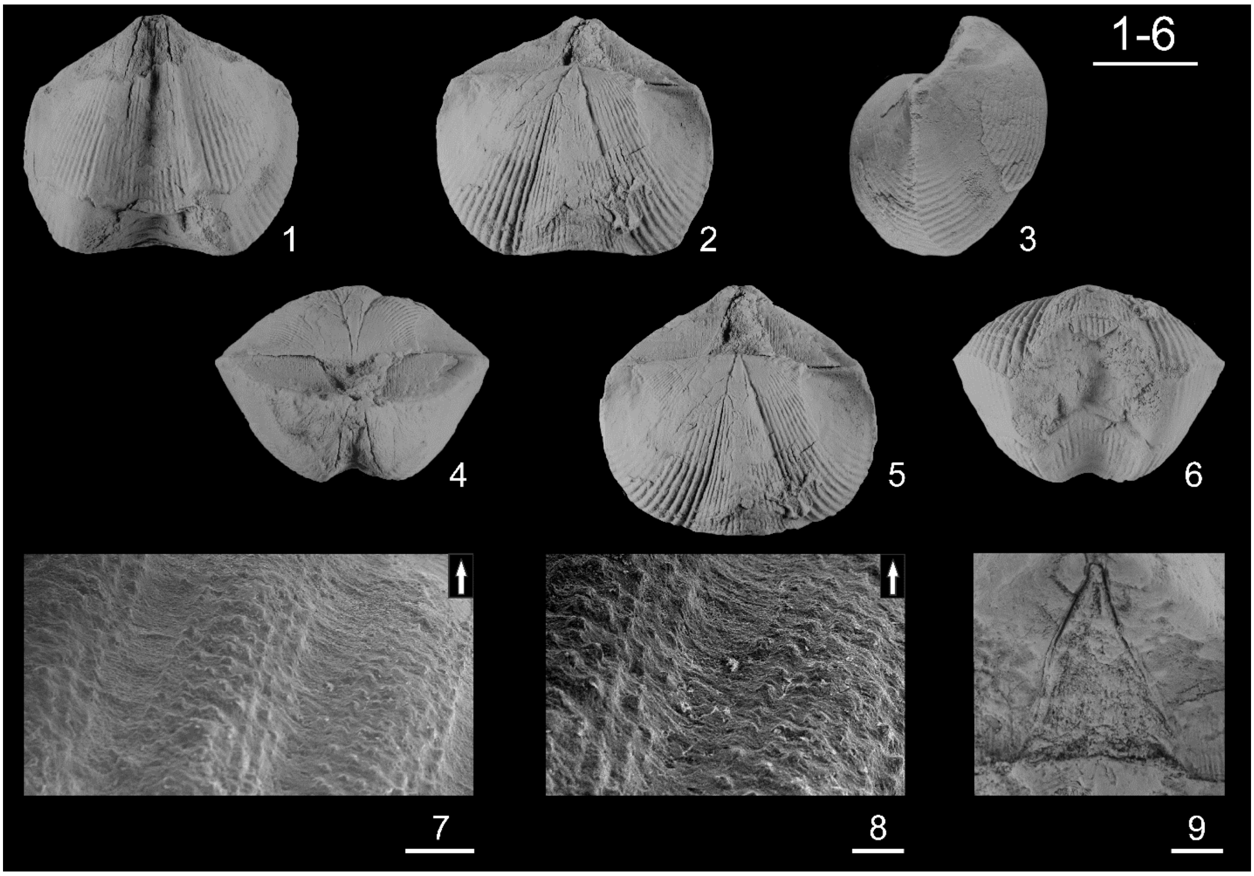
Plate 13

Tornatospirifer armenicus (Abrahamyan, 1974) from the lower Famennian *Cyrtospirifer orbelianus* Zone of Abrahamyan (1957), Central 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 (Djravank 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 µm (7), 200 µm (8).

Plate 13



Appendix 1

Vahram Serobyan, Taniel Danelian, Catherine Crônier,

Araik Grigoryan and Bernard Mottequin (2021)

Lower Famennian (Upper Devonian) rhynchonellide and athyride brachiopods from the South Armenian Block

Journal of Paleontology 95 (3), p. 527 - 552

Lower Famennian (Upper Devonian) athyridide and rhynchonellide brachiopods from the South–Armenian Block

Vahram Serobyan [1, 2,*], Taniel Danelian [2], Catherine Crônier [2], Araik Grigoryan [1] and Bernard Mottequin [3]

[1] Institute of Geological Sciences of the National Academy of Sciences of the Republic of Armenia-Yerevan, Armenia, 24A, Marshal Baghramyan Avenue, Yerevan 0019, Republic of Armenia <vahramserobyan@gmail.com> <aragrigoryan@yandex.ru>

[2] Univ. Lille, CNRS, UMR 8198- Evo-Eco-Paleo, F-59000 Lille, France <vahram.serobyan@univ-lille.fr> <taniel.danelian@univ-lille.fr> <catherine.cronier@univ-lille.fr>

[3] O.D. Earth and History of Life, Royal Belgian Institute of Natural Sciences, rue Vautier 29, B 1000 Brussels, Belgium <bmottequin@naturalsciences.be>

Running Header: Lower Famennian brachiopods from Armenia

Abstract.—The lower Famennian *orbelianus* brachiopod Zone established in Armenia by Abrahamyan (1957) (coeval to the *crepida* conodont Zone) contains an abundant and diverse brachiopod fauna that still remains poorly studied. In an effort to revise and update its systematic classification and to assess the brachiopod diversity after the Kellwasser extinction event in this area, our attention is here focused on rhynchonellides and athyridides. Six rhynchonellide species are described belonging to five genera as well as a single athyridide species (*Crinisarina* *pseudoglobularis* sp. nov.), which is new to science. The genus *Crinisarina* is reported for the first time in the South–Armenian Block (SAB), which was then part of the northern margin of Gondwana. Some of the rhynchonellide species identified were previously recognized in this area but they required modern documentation and taxonomic reassessment. More particularly, it is the first time that the internal structure of *Sartenaerus baitalensis* (Reed, 1922) is here illustrated, taking into account that it is the type species of a biostratigraphically significant Famennian genus. One of the oldest punctate rhynchonellide species *Greira transcaucasica* Erlanger, 1993 is described and its intraspecific variability is documented quantitatively. From the paleogeographic viewpoint, the studied brachiopod fauna clearly shares affinities with contemporaneous ones from other regions of the Gondwanan northern margin that extends eastwards of the SAB to Afghanistan and Pamir, although there are also some endemic elements.

Introduction

The Upper Devonian sequences of the Lesser Caucasus (or Transcaucasia, Fig. 1) are remarkable in terms of their completeness and richness in fossil remains (Abrahamyan, 1957, 1964; Arakelyan, 1964; Alekseeva et al., 2018a, b). They have attracted the interest of pioneer geologists such as the famous German geologist Hermann Abich, who first described in 1858 Devonian outcrops and a new spiriferide species from Armenia, ‘*Spirifer*’ *orbelianus*. In Armenia, Upper Devonian–Lower Carboniferous brachiopods were systematically studied by Abrahamyan during the years 1949 to 1974. One of her most important publications dates back to 1957 in which she described and illustrated 36 brachiopod species (including eight new ones) from the Famennian–Tournaisian interval. These species belong to the orders Athyridida, Orthida, Orthotetida, Productida, Rhynchonellida and Spiriferida. In the same publication she also presented a biostratigraphic scheme based on brachiopods wherein part of the lower Famennian was characterized by the *orbelianus* taxon–range Zone (Fig. 2). The latter brachiopods were partly revised by Abrahamyan (1974) in addition to newly studied Frasnian species. However, despite the extensive taxonomic studies led by Abrahamyan (1957, 1974) and more recently by Alekseeva et al. (2018a, b), who mainly focused on brachiopods from Nakhichevan (Azerbaijan), lower Famennian brachiopod assemblages from Armenia still remain poorly understood from the taxonomical and biostratigraphical points of view. This is especially true for the athyridide and rhynchonellide brachiopods, which are very common in the Upper Devonian–Lower Carboniferous sequences of this area, and their study can provide valuable insights into Late Devonian changes in brachiopod diversity and palaeobiogeographic distribution. Thus, the purpose of this paper is to re–investigate and to describe those present in the lower Famennian *orbelianus* Zone on the basis of newly collected material from three distinct localities in central Armenia (Fig. 1). Furthermore, their biostratigraphic and paleobiogeographic significance are also discussed.

Geological setting

The Upper Devonian sequences of Armenia are composed of mixed carbonate–siliciclastic sediments that accumulated on a shallow water platform. They consist essentially of marly and sandy biogenic limestones, rich in brachiopods, and intercalations of quartzites and shales. Geodynamically speaking, they are part of the South–Armenian Block, a Gondwana–derived microcontinent that was detached and individualized during the Triassic and Jurassic (Sosson et al., 2010). The ca. 1500 m–thick Upper Devonian–Lower Carboniferous sedimentary sequences in Armenia were subdivided by Abrahamyan (1964) and Arakelyan (1964) into a number of horizons (e.g. Baghrsagh, Noravank, Ertych, Fig. 2) that are difficult to be recognized exclusively on the basis of their facies as they are partly defined on their brachiopod content. Consequently, they have a biostratigraphic rather than lithostratigraphic significance (see Serobyan et al., 2019). Thus, because of their abundance in these sequences, brachiopods were recognized to be useful for stratigraphic correlations and used to support the extensive mapping effort planned for the area after the World War II. At the time, Armenia and Nakhichevan (Azerbaijan) were part of the USSR. Rzhonsnitskaya (1948) first established a Devonian biostratigraphical scheme based on brachiopods. This was a rudimentary zonal scheme that was much improved by Abrahamyan (1957), who introduced a continuous biozonation characterized by marker species or species assemblages (Fig. 2). The *'Cyrtospirifer' orbelianus* Zone of Abrahamyan (1957) is a taxon–range biozone covering part of the Lower Famennian. Grechishnikova et al. (1982) and Rzhonsnitskaya and Mamedov (2000) applied Abrahamyan's zonal scheme in Nakhichevan, by improving and complementing it for some intervals. A subsequent step forward was achieved by the integration of this brachiopod zonation with the conodont study carried out by Aristov (1994) in Nakhichevan. Figure 2 correlates the above mentioned brachiopod zones with the regional conodont zonation of Aristov (1994) established in Nakhichevan and the standard conodont zonation of Ziegler and Sandberg (1990).

Materials and Methods

The bulk of specimens illustrated and investigated herein was collected during several field seasons organized in 2018 and 2019. The material was collected from the *'Cyrtospirifer' orbelianus* Zone of Abrahamyan (1957) as the latter crops out well in three distinct sections of central Armenia (Ertych, Djravank and Noravank; Fig. 1). It can be correlated with the *'Cyrtiopsis' orbelianus–'Cyrtiopsis' armenicus* Zone of Rzhonsnitskaya and Mamedov (2000) and considered as coeval to the *crepida* standard conodont Zone of Ziegler & Sandberg (1990). The material sampled by our care in the field was complemented by specimens that were collected during the 1940s to 1980s by Abrahamyan and Arakelyan, both from Armenia and Nakhichevan.

All ground specimens were selected among recently collected material as historical specimens cannot be sectioned; thus, the latter have been used only for measurements. The internal morphology of specimens was investigated by using the standard technique of serial sections and acetate peels. Almost complete articulated specimens were coated with magnesium oxide before being photographed with a Canon EOS 700D camera. Afterwards, all images were further processed using Adobe Photoshop CS6. Specimens selected for scanning electron microscopy were coated with gold and digitization of their micro–ornament was performed by the use of a ZEISS EVO Scanning Electron Microscope.

Repositories and institutional abbreviations.—All illustrated material is housed 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. Part of the studied material is housed at the public paleontological collection of the University of Lille (USTL). The prefix RBINS is used for some specimens deposited at the Royal Belgian Institute of natural Sciences, Brussels. Specimens cited in Brice (1967) are stored at the Laboratoire de Paléontologie de la Faculté Libre des Sciences des Lille (Collection De Lapparent, Brice). The material studied by Erlanger (1993) is housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow and is calatogued under the prefix PIN and collection № 3744.

Systematic paleontology

The supraspecific classification follows Savage et al. (2002) and Savage (2007) for the Order Rhynchonellida instead of the one adopted by Sartenaer (2001, 2003) wherein the Subfamily Ripidiorhynchinae Savage, 1996 is elevated to the family level with *Ripidiorhynchus* Sartenaer, 1966 as its only representative, except otherwise stated, and the one suggested by Alvarez and Rong (2002) for the Order Athyridida.

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonirhynchiidae Schmidt, 1965

Subfamily Trigonirhynchiinae Schmidt, 1965

Genus *Sartenaerus* Özdikmen, 2008

Type species.—*Camarotoechia baitalensis* Reed, 1922.

Remarks.—*Camarotoechia baitalensis* was selected by Sartenaer (1970) as the type species of his new genus *Centrorhynchus*. Although Savage et al. (2002) placed this genus in the subfamily Hemitoechiinae, Nicollin and Brice (2004: p. 440) noted that it should be reassigned to the subfamily Trigonyrhynchiinae because its septalium is posteriorly covered. Finally, as the name *Centrorhynchus* Luehe, 1911 was preoccupied for a genus of parasitic worms (Acanthocephala), Özdikmen (2008) introduced a new genus name *Sartenaerus* for *Centrorhynchus sensu* Sartenaer (1970). Mottequin et al. (2014) indicated that the genus *Centrorhynchus* (= *Sartenaerus*) first occurs in the middle Famennian, but the brachiopod record from Armenia establishes that it was already present in the lower part of this stage.

Sartenaerus baitalensis (Reed, 1922)

Figures 3–4, 16–18; Table 1

1922 *Camarotooechia baitalensis* Reed, p. 94, pl. 14, figs. 11–21.

1922 *Camarotooechia baitalensis comitata*, var. nov.; Reed, p. 97, pl. 14, figs. 24–25; pl. 15, figs. 1–3a.

1922 *Camarotooechia baitalensis transversalis*, var. nov.; Reed, p. 97, pl. 14, figs. 22–23.

2019 *Sartenaerus baitalensis*; Serobyan et al. p. 9, 14 (see for a complete synonymy).

Occurrence and age.—This species was first described by Reed (1922) from the Famennian (the lowest and uppermost parts excluded; Sartenaer, 1970) of Pamir (Tajikistan). In Armenia it was first reported by Abrahamyan (1957) in the lower Famennian ‘*Cyrtospirifer*’ *orbelianus* Zone. This is consistent with the record of this species in Nakhichevan (Mirieva 2010).

Description.—Shell medium–sized, wider than long, strongly dorsibiconvex, rounded subpentagonal to transversally ovate in outline; widest more anteriorly to midlength; highest slightly posteriorly to the front (in adults); anterior margin slightly emarginate to straight; anterior commissure highly zigzagged and strongly uniplicate.

Ventral valve inflated with convex flanks sloping steeply towards zigzagged lateral commissures; highest at anterior margin, then decreasing gently or maintained towards the posterior margin; umbo wide, inflated; beak large, prominent, suberect; foramen unobserved; palintropes low, concave; sulcus shallow to moderately deep, wide, inconspicuously originating at umbo, well–delimited by bounding ribs, flat to slightly round–bottomed at front; tongue high to very high, wide, with sharp borders, subtrapezoidal in outline, strongly bent dorsally.

Dorsal valve strongly inflated, strongly curved in posterior and lateral profile views with convex flanks sloping steeply towards lateral commissures; highest slightly posteriorly to the front then moderately to strongly decreasing towards the posterior margin; beak obtuse, covering the delthyrium; fold starting at umbo, moderately high, well–defined, becoming relatively higher anteriorly.

Ornamentation of coarse, strong, angular ribs with rounded apices arising from beaks; 3 ribs in sulcus with one median rib usually stronger and 4 ribs on fold with two opposed ribs usually stronger, 6–7 ribs per flank; ribs wider than interspaces.

Ventral valve interior (Fig. 4) with strong and relatively short dental plates, subparallel posteriorly then converging ventrally more anteriorly; teeth strong, crenulated; ventral muscle field flabellate anteriorly then becoming hastate or subtrapezoidal (Fig. 4(2.2–3)); lateral apical cavities strongly filled in by callosities. Dorsal valve interior with long and quite high septum, extending up to 15% of the valve length; septalium narrow, relatively short, without cover; dental sockets large; hinge plates long, divided immediately anteriorly to septalium; crural bases horizontal.

Material examined.—Thirty–four articulated specimens, six ventral and four dorsal valves; 12 articulated specimens, two ventral and three dorsal valves come from the Ertych section; 11 articulated specimens, two ventral and two dorsal valves from the Djravank section and 11 articulated specimens, two ventral valves from the Noravank section.

Ontogeny.—Juveniles display all external morphological characters that are typical for this species with the exception of their maximum height, which is at about midlength of the shell, while the maximum height of adults is situated close to the front. Our collections contain juvenile specimens which may be split in to two groups based on their width/thickness ratio; some of them (Fig. 3. 1–5) are more inflated than their relatively older representatives. The shell growth follows a linear model, as this is more particularly reflected by the rather high coefficient of determination obtained for the ratios of length/width and width of sulcus/width (Fig. 5; see also the measurements provided in Table 1).

Remarks.—Sartenaer (1970) erected the genus *Centrorhynchus* (= *Sartenaerus* Özdikmen, 2008) based on the illustrations of *Camarotoechia baitalensis* in Reed's (1922) publication, as well as his own appreciation of a few specimens of this species coming from upper Famennian (?) strata of Pamir, which were offered to him by Rzhonsnitskaya in January 1964 during his stay in St. Petersburg and they are stored now at the RBINS. It is pertinent to highlight here that the internal structure of the type material of *Sartenaerus baitalensis* was poorly known as neither Reed (1922), nor Sartenaer (1970), had provided any drawings of serial sections. Our material is externally undistinguishable from Reed's species. This is also true for the internal features, with the single exception that none of our eight ground specimens displayed the connectivum that was reported by Sartenaer (1970) for this species. However, as noted by Brice (1967, 1971) for *S. charakensis*, this delicate structure is not always preserved. Only the serial sectioning of topotypic material of *S. baitalensis* will shed light on the real development of its connectivum.

Sartenaerus charakensis (Brice, 1967)

Figures 5.1–10, 6, 16–18; Table 2

1963 *Camarotoechia* cf. *baitalensis* Reed; de Lapparent and Le Maître, p. 188.

1967 '*Ptychomaletoechia*' *charakensis,* Brice, p. 95–100, pl. 8, figs. 1–6; text–figs. 2–3.

1968 '*Ptychomaletoechia*' *charakensis*; Brice et al., p. 120.

1969 '*Ptychomaletoechia*' *charakensis*; Brice et al., p. 1596.

1970 *Centrorhynchus charakensis*; Sartenaer, p. 12, 13.

1971 *Ptychomaletoechia* (?) *charakensis*; Brice, p. 22, pl. 1, figs. 4a–e, 5a–d, 6a–e; text–fig. 9A.

1999 *Centrorhynchus charakensis*; Brice et al., table 6.

Not: 2000 *Centrorhynchus charakensis*; Jafarian, p. 226, table 1; pl. 2; fig. 3a–c.

2007 *Centrorhynchus charakensis*; Brice and Deville, p. 11–12.

2010 *Ptychomaletoechia charakensis*; Mirieva, p. 74–75, table. 1.

2011 *Centrorhynchus charakensis*; Grechishnikova and Levitskii, p. 22, 31, table 1.

2018a *Sartenaerus charakensis*, Pakhnevich in Alekseeva et al., p. 899, pl. 6, fig. 1; text–fig. 46.

Holotype.—An articulated specimen (AF 3GK 40) from the middle–upper Famennian of Ghor province, Afghanistan (Brice, 1967, pl. 8, fig. 3a–e).

Occurrence and age.—Although Brice (1967) considered initially that this species occurs in the upper Frasnian–lower Famennian strata of Afghanistan, she later specified (Brice 1971) that *Sartenaerus charakensis* is restricted in the lower to upper Famennian interval and that it appears to be rare above the *Dmitria seminoi* brachiopod Zone (see Fig. 2). Mirieva (2010) indicated the presence of *S. charakensis* in Nakhichevan within the '*Cyrtiopsis' orbelianus*–'*C.' armenicus* and *Dmitria seminoi* brachiopod zones of Rzhonsnitskaya & Mamedov (2000). Afterwards, Grechishnikova and Levitskii (2011) reported the latter species in the younger deposits of Nakhichevan, more precisely in the *Enchondrospirifer ghorensis*–*Cyrtospirifer pamiricus* Zone. This study establishes for the first time the presence of this species in older Famennian levels in the Lesser Caucasus, in the lower Famennian *'C.' orbelianus* Zone of Abrahamyan (1957).

Description.—Shell medium–sized, wider than long, sharply dorsibiconvex, transversally elliptic in outline; widest in the anterior third of the valve; highest slightly posteriorly to the front; anterior margin slightly emarginate to straight; anterior commissure strongly uniplicate.

Ventral valve regularly convex in posterior and lateral profile views, with flanks slopping gently towards the lateral commissures; highest in the posterior third of the valve, then decreasing gently towards the anterior margin; umbo slightly inflated; beak and foramen unobserved; sulcus wide, moderately deep, starting at midlength or slightly posteriorly, well–

delimited by bounding ribs, flat–bottomed at the front; tongue high, wide, subtrapezoidal in outline, perpendicular to the commissural plane or bent dorsally.

Dorsal valve markedly inflated, regularly curved in both the posterior and lateral profile views, with convex flanks sloping moderately to steeply towards the lateral commissures; highest more posteriorly to the front, then decreasing progressively towards the posterior margin; fold moderately high, inconspicuously originating at some distance from the umbo, round–topped at the front.

Ornamentation of coarse, angular ribs, originating at beaks and becoming fainter towards lateral cardinal extremities; 9–10 ribs on the flanks, 3 ribs in sulcus, 3–4 ribs on fold; ribs wider than interspaces.

Ventral valve interior (Fig. 6) with thin, relatively long dental plates converging ventrally; teeth stout; central apical cavity wide. Dorsal valve interior (Fig. 6) with long and high septum, extending up to ca. 20% of the valve's length; septalium narrow, relatively long, moderately deep, covered anteriorly by stout connectivum bearing a median crest; hinge plates long, connected; crural bases nearly horizontal.

Material examined.—Twenty–two articulated specimens and four ventral valves; eight articulated specimens and two ventral valves come from the Ertych section, five articulated specimens and two ventral valves from the Djravank section and nine articulated specimens from the Noravank section.

Remarks.—Jafarian (2000) reported *S. charakensis* from the upper Famennian of Iran, but his illustrated specimens appears to be closer to *Sinotectirostrum delicatacostatum* (Abrahamyan,

1957) rather than Brice's species as they clearly have a different shell shape, strongly emarginate anterior commissure and markedly inflated ventral umbo.

Our material differs slightly from the *S. charakensis* from Afghanistan (Brice 1967, 1971) by its Y–shaped, moderately deep and thin septalium.

Genus *Porthmorhynchus* Sartenaer, 2001

Type species.—*Rhynchonella ferquensis* Gosselet, 1887.

Porthmorhynchus? sp.

Figures 5.11–15, 7

Occurrence and age.—The specimens were collected from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) of the Noravank and Djravank sections (Fig. 1).

Description.—Shell small–sized (ca. 14.9 mm in width, 13.4 mm in length and 10 mm in thickness), dorsibiconvex, widest and highest more anteriorly to midlength, rounded subpentagonal in outline; anterior margin slightly rounded; anterior commissure uniplicate.

Ventral valve regularly convex in posterior and lateral profile views, with flanks slopping gently towards the lateral commissures; highest in the posterior third of the valve; umbo inflated, prominent; beak and foramen unobserved (due to poor preservation); sulcus relatively wide, shallow to moderately deep, originating at about midlength, flat–bottomed at the front; tongue moderately high, wide, subtrapezoidal in outline, perpendicular to commissural plane or slightly bent dorsally.

Dorsal valve inflated, strongly curved in posterior and lateral profile views, with convex flanks sloping steeply towards the lateral commissures; highest slightly posteriorly to the front, then progressively decreasing towards the posterior margin; fold starting at some distances from the umbo, low, wide, well–defined, becoming relatively higher anteriorly.

Ornamentation of coarse, angular, low to moderately high ribs, radiating at beaks, becoming fainter towards the lateral cardinal extremities; ribs in sulcus and on fold slightly wider than those present on the flanks; 2 ribs in sulcus, 3 ribs on fold, 6–7 ribs on flanks, parietal ribs unobserved; ribs wider than interspaces.

Ventral valve interior (Fig. 7) with relatively long and robust dental plates converging ventrally; teeth massive; central apical cavity wide; lateral apical cavities poorly infilled by callosities. Dorsal valve interior with relatively high and long septum (Fig. 7(1–2.7)); septalium wide, relatively deep; connectivum not observed; hinge plates divided; dental sockets large; crural bases stout.

Material examined.—Two partly exfoliated articulated specimens.

Remarks.—*Porthmorhynchus* Sartenaer is mainly known from middle–upper Frasnian strata of the Boulonnais region in Northern France (Brice in Brice and Meats, 1972; Sartenaer, 2001). Our material is doubtfully assigned to this genus as the development of its fold and sulcus (originating far from the beaks), as well as the orientation of its dental plates (converging ventrally) are in contradiction with the diagnosis of the genus. Furthermore, it is worth nothing that Sartenaer (2001) mentioned that the septalium of *Porthmorhynchus* representatives is covered by a connectivum, which was not observed in our ground specimen. However, it should be stressed that this delicate structure is not always preserved. Additional material is needed for reaching a more confident identification.

Subfamily Ripidiorhynchinae Savage, 1996

Genus *Gesoriacorostrum* Sartenaer, 2003

Type species.—*Atrypa boloniensis* d'Orbigny, 1850.

Gesoriacorostrum? sp.

Figures 8–9

Occurrence and age.—The specimens were collected from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) of the Djravank section (Fig. 1).

Description.—Shell small–sized (ca.19 mm in width, 16.5 mm in length, 8.3 mm in thickness), dorsibiconvex, wider than long, widest and highest at about midlength, transversally elliptic in outline; anterior margin slightly rounded; anterior commissure uniplicate.

Ventral valve regularly convex in posterior and lateral profile views, with flanks slopping gently towards lateral commissures; umbo small; beak and foramen unobserved (due to poor preservation); sulcus only perceptible close to anterior margin, very shallow, wide, round–

bottomed at front; tongue low, wide, subtrapezoidal in outline, not perpendicular to commissural plane.

Dorsal valve highest at midlength or slightly anteriorly to it, then decreasing regularly towards anterior margin; fold only developed close to anterior margin, very low, wide, round–topped at front.

Ornamentation of up to 13 low, flattened, simple ribs on each flank originating at beaks and becoming progressively fainter towards posterolateral margins; in sulcus and on fold, 7–8 ribs, infrequently increasing by bifurcation; ribs wider than interspaces on the entire shell.

Ventral valve interior (Fig. 9) with thin, long and subparallel dental plates; teeth strong; central apical cavity wide; lateral apical cavities poorly infilled by callosities.

Dorsal valve interior with relatively thick and low septum (Fig. 9(1.9–2.1)); septalium wide, relatively deep, covered anteriorly by stout connectivum bearing a median crest; dental sockets large.

Material examined.—Two partly exfoliated articulated specimens.

Remarks.—The external and internal features observed in the two studied specimens argue for its tentative assignment to genus *Gesoriacorostrum* Sartenaer, 2003, which presence in the SAB is recently documented by Pakhnevich in Alekseeva et al. (2018a). However, the fold and sulcus are perceptible only anteriorly on our specimens, while the original material from the Boulonnais region in France displays fold and sulcus that start from midlength; in addition, parietal ribs are absent on our specimens.

Superfamily Rhynchoporoidea Muir–Wood, 1955

Family Rhynchoporidae Muir–Wood, 1955

Subfamily Greirinae Erlanger, 1993

Genus *Greira* Erlanger, 1993

Type species.—*Greira transcaucasica* Erlanger, 1993.

Greira transcaucasica Erlanger, 1993

Figures 10–11, 16–18; Table 3

1993 *Greira transcaucasica* Erlanger, p. 120, text–figs. 1 and 2.

2002 *Greira transcaucasica*; Savage, p. 1233, fig. 840, 2a–o (copy of Erlanger 1993, fig.1, 2a–d; fig. 2).

2018a *Greira transcaucasica*; Pakhnevich in Alekseeva et al., p. 855, 916, pl. 8, fig. 4; text–fig. 58.

Holotype.—An articulated specimen (PIN 4127/1042) from the lower Famennian *'Mesoplica' meisteri* Zone of Grechishnikova et al. (1982), left bank of the Arpa River, between Geran–Kalasy and Kabakhal mountains, Nakhichevan (Erlanger, 1993: text–fig. 1a–d).

Occurrence and age.—This species is considered by Erlanger (1993) as one of the oldest punctate rhynchonellides which are particularly abundant and diverse with four species and subspecies (Abrahamyan, 1954, 1957; Sartenaer and Plodowski (2003) known from the middle–upper Famennian succession of the South–Armenian Block. Initially *G. transcaucasica* was described by Erlanger (1993) from the lower Famennian '*Mesoplica' meisteri* Zone of Grechishnikova et al. (1982), equivalent to the '*Mesoplica' meisteri–Cyrtospirifer asiaticus* Zone of Rzhonsnitskaya and Mamedov (2000) in Nakhichevan (Paknevich in Aleksseva et al. (2018a)). This is the first time that this species is recorded within the Armenian sections, where it occurs in slightly younger strata, in the lower Famennian '*Cyrtospirifer' orbelianus* Zone of Abrahamyan (1957).

Description.—Shell medium–sized, aequibiconvex to dorsibiconvex, wider than long, widest at about midlength, transversally elliptic in outline; anterior margin slightly emarginate to straight ; anterior commissure uniplicate and serrate.

Ventral valve regularly convex in posterior and lateral profile views, with flanks sloping gently towards the lateral commissures; umbo small but prominent; beak small, inclined to straight; foramen unobserved; sulcus wide, shallow to moderately deep, inconspicuously originating from midlength or more anteriorly, flat–to round–bottomed at front; tongue variable in its height, low to moderately high, not perpendicular to the commissural plane, subtrapezoidal in outline.

Dorsal valve slightly inflated with flanks sloping gently to moderately towards the lateral commissures; fold wide, generally low, inconspicuously originating from midlength or more anteriorly, becoming more or less prominent at the anterior margin, flat–topped at the front.

Ornamentation made of low, angular ribs, running from beak, becoming weaker towards the posterolateral margins; 9–13 ribs on each flank, 4–5 ribs in sulcus, 4–6 ribs on fold; 5–6 ribs per 5 mm at the anterior margin near the sulcus and fold; ribs in sulcus and on fold somewhat wider than those present on the flanks; ribs wider than interspaces.

Ventral valve interior (Fig. 11) with thin, long, short and divergent dental plates; lateral apical cavities poorly infilled by callus; teeth small, rounded in transverse section.

Dorsal valve interior (Fig. 11) with wide and Y–shaped septalium, covered anteriorly; sockets smooth; dorsal median septum low but long, extending one–quarter of valve's length, crural bases proximally triangle–shaped in section, dorsally convergent.

Material examined.—Twenty–six articulated specimens and two ventral valves; 14 articulated specimens and two ventral valves come from the Ertych section and 12 articulated specimens from the Noravank section.

Ontogeny.—The shell growth of *Greira transcaucasica* Erlanger follows a linear model, as this is reflected by the high coefficient of determination obtained for the ratios of length/width, thickness/width and width of sulcus/width (Fig. 13; see also the measurements provided in Table 2).

Remarks.—Our material slightly differs from the holotype of *Greira transcaucasica*; according to Erlanger (1993) the interspaces of this species are wider than ribs, but the specimens from Armenia display ribs that are wider than the interspaces. This is consistent with the description of

Pakhnevich in Alekseeva et al. (2018a) for this species found in the lower Famennian of Nakhichevan. Thus, these differences in the width of ribs and interspaces are considered as expression of the intraspecific variability.

Genus *Sharovaella* Pakhnevich, 2012

Type species.—*Sharovaella mirabilis* Pakhnevich, 2012

Sharovaella? sp.

Figures 12–13

Occurrence and age.—The specimens were collected from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) of the Ertych section (Fig. 1).

Description.—Shell small–sized (12.7 mm in width, 11 mm in length and 8.4 mm in thickness), wider than long, strongly dorsibiconvex, rounded subpentagonal in outline, widest at midlength, highest at midlength or slightly anteriorly; anterior margin slightly emarginate; anterior commissure uniplicate.

Ventral valve gently inflated in posterior and lateral profile views, with slightly convex flanks sloping gently towards the lateral commissures; highest at midlength, then progressively decreasing towards the anterior margin; umbo prominent, somewhat curved; beak small, straight to inclined; foramen unobserved; sulcus well–defined by bounding ribs, wide, deep, originating from midlength or slightly posteriorly, flat to round–bottomed at the front; tongue wider than high, perpendicular to the commissural plane or slightly bent dorsally, high, subtrapezoidal in outline.

Dorsal valve strongly inflated with markedly convex flanks sloping moderately to steeply towards the lateral commissures; highest at midlength or more anteriorly to it, then decreasing progressively towards the posterior margin; umbo flattened, not prominent; beak small, overhanging the hinge line; fold high, well–delimited, wide, originating at midlength or slightly posteriorly, then becoming higher anteriorly, round–topped at front.

Ornamentation of 3–4 coarse, strong ribs on flanks originating at midlength by intercalations, becoming shorter and weaker towards the posterolateral margins; in sulcus and on fold, 1–2 ribs originating near the umbo or more anteriorly to it; ribs wider than interspaces, having rounded apices and being triangular in cross section; growth lamellae densely crowded, relatively prominent (2–3 lamellae per 1 mm) and penetrated by irregularly arranged punctae situated near the umbo on ventral valve. Ventral valve interior (Fig. 15) with thin intrasinal and slightly divergent dental plates, central and lateral apical cavities poorly filled in by callosities.

Dorsal valve interior with low but long septum (Figs. 12.2, 12.4, 13(1.15)); septalium covered and narrow; hinge plates short; crural bases stout.

Material examined.—Three articulated specimens.

Remarks.—Pakhnevich (2012) examined several specimens collected by Grechishnikova from different sections of Armenia and Nakhichevan identified as *Eoparaphorhynchus triaequalis* (Gosselet, 1877); he noticed that this material differs from Gosselet's species by the presence of punctae on the shell walls. Consequently, he erected the new monospecific genus *Sharovaella* with its type species *Sharovaella mirabilis*. Although the external and internal morphology of our material is a reminiscent of *S. mirabilis* in terms of size, general shape, well–developed fold and sulcus, short dental plates, covered, narrow septalium and low septum, this limited material is tentatively assigned to *Sharovaella* as it lacks strong ribs running from the umbo on flanks and in sulcus and on fold, contrary to what it is observed in Pakhnevich's material. Moreover, Pakhnevich observed irregularly spaced punctae along the whole shell, whereas in our material puncta–like structures are displayed only near the umbo (Fig. 14.6–8), and it is highly questionable whether that is one of the typical morphological characteristics of our material or whether they are just the results of dissolution due to the action of meteoric waters.

Order Athyridida Boucot, Johnson, and Staton, 1964

Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Cleiothyridininae Alvarez, Rong, and Boucot, 1998

Genus *Crinisarina* Cooper and Dutro, 1982

Type species.—*Crinisarina stainbrooki* Mottequin, 2008 (pro *Cleiothyridina reticulata* Stainbrook, 1947).

Crinisarina pseudoglobularis new species

Figures 14–18; Table 4

1952 *Athyris globularis* Phill. Arakelyan, p. 32–33, 40, 41.

1957 *Athyris globularis*; Abrahamyan, p. 9, table 2.

1964 *Athyris globularis*; Arakelyan, p. 75, 82–83, 94.

1973 *Athyris globularis*; Abrahamyan et al., p. 218.

1974 *Athyris globularis*; Abrahamyan, p. 9.

2000 *Athyris* ex gr. *globularis*; Rzhonsnitskaya and Mamedov, p. 330.

Holotype.—An almost complete articulated specimen (IGSNASRAGM XX; Fig. 16.24–28) from the lower Famennian *orbelianus* Zone of Abrahamyan (1957) Ertych section which is correlated with the Ertych horizon (Fig. 2); Ertych section (6 km southeast from Areni, Vayots Dzor Province, central Armenia).

Diagnosis.—Shell medium–sized (up to 24 mm in width, 22.5 mm in length, 21.2 mm in thickness), aequibiconvex, relatively aequidimensional, rounded pentagonal in outline; anterior margin straight to poorly emarginate; anterior commissure strongly uniplicate; fold and sulcus very shallow, wide at the front, more developed anteriorly; tongue moderately high to high, subtrapezoidal to semioval in outline; micro–ornament of imbricate, densely crowded growth lines projecting anteriorly and anterolaterally as flattened, radially–aligned solid spines; dental plates thin, relatively long and arched supporting cyrtomatodont teeth, lateral apical cavities strongly filled in by callosities; dorsal interior with cardinal plate pierced apically by a dorsal foramen; inner hinge plates conjunct, weakly concave ventrally to nearly flat depending on specimens; outer hinge plates flat; myophragm very short.

Occurrence and age.—This species is only found in the South–Armenian Block. More particularly, according to Abrahamyan (1957) it is restricted to the lower Famennian *'Cyrtospirifer' orbelianus* Zone of Abrahamyan (1957) and according to Rzhonsnitskaya and Mamedov (2000) in the *'Cyrtiopsis' orbelianus*–'*Cyrtiopsis' armenicus* Zone of Nakhichevan.

Description.—Shell medium–sized, relatively equidimensional, rounded subpentagonal in outline, aequibiconvex, widest at about midlength or slightly posteriorly; highest in the posterior third of the valve; anterior margin straight to poorly emarginate; anterior commissure uniplicate.

Ventral valve inflated with flanks sloping moderately to strongly towards the lateral commissures; highest in the posterior third of the valve, then decreasing progressively towards the anterior margin; umbo strongly inflated, prominent; beak suberect to erect, pierced by a permesothyrid foramen; sulcus poorly defined posteriorly, more defined anteriorly, wide at the front, very shallow, flat– to round–bottomed at the front, subtrapezoidal to semioval in outline, perpendicular to the commissural plane with distal part sometimes bent dorsally.

Dorsal valve with upper surface dome–shaped (median part sometimes raised by the fold), regularly and strongly curved in posterior and lateral profile views with flanks sloping moderately towards the lateral commissures; highest in the anterior third of the valve (near umbo in juveniles) then progressively decreasing towards the anterior margin; umbo prominent; fold low, inconspicuously originating close to umbo, wide at the front, poorly defined, round–topped at the front.

Micro–ornament of imbricate, densely crowded growth lines projecting anteriorly and anterolaterally as flattened, radially–aligned solid spines (Fig. 14.16–18). Growth lines less densely crowded posteriorly.

Ventral valve interior (Fig. 15) with thin, relatively long and arched dental plates, supporting cyrtomatodont teeth that are subrectangular in transverse section (Fig. 17); thick lens of prismatic calcite is developed in the middle part of the valve below the well–developed umbonal cavity; lateral apical cavities moderately filled in by callosities.

Dorsal valve interior (Fig. 15) with conjunct, weakly concave ventrally to nearly flat inner hinge plates; outer hinge plates flat; myophragm low but long; spiral cones with at least 11 whorls laterally oriented.

Etymology.—In reference to the confusion made with the athyridide species *Composita globularis* (Phillips, 1836).

Additional material.—Fourty–three articulated specimens and five ventral valves; 15 articulated specimens and three ventral valves come from the Ertych section, 16 articulated specimens and two ventral valves from the Djravank section and 12 articulated specimens from the Noravank section.

Ontogeny.—Juveniles display a rectimarginate to slightly uniplicate anterior commissure, semi–elliptic tongue and sharp lateral commissures. Although not visible on juveniles, sulcus and fold develop with age. The beak inclination angle does not change with age, as juveniles also have a suberect to erect beak. The maximum height of the dorsal valve is near the umbo in juveniles then moves towards the anterior margin. The shell growth follows a linear model, as this is more particularly reflected by the rather high coefficient of determination obtained for the ratios of length/width and width of sulcus/width (Fig. 18; see also the measurements provided in Table 3).

Remarks.—Reported initially by Arakelyan (1952) as *Athyris globularis*, this species was found both in Armenia and Nakhichevan, but it was never described and illustrated. It was considered by Abrahamyan et al. (1973) and Arakelian (1975) as a biostratigraphically important species for the lower Famennian *orbelianus* Zone. Moreover, until now it was confused with *Spirifera globularis* Phillips, 1836, a poorly known species from the Viséan of Bolland (Yorkshire, UK) which is currently assigned to the genus *Composita* (see Brunton and Tilsley 1991). This species is assigned herein to *Crinisarina* Cooper and Dutro, 1982 rather than to *Cleiothyridina* Buckman, 1906 because of its markedly inflated shell, rounded pentagonal outline, strongly uniplicate anterior commissure and highly inflated umbones.

C. pseudoglobularis sp. nov. is very close to *C. stainbrooki* Mottequin, 2008, known from the lower Famennian of southern Belgium and the USA (Nevada, New Mexico) (see references in Mottequin, 2008); however, *C. pseudoglobularis* differs externally by its more inflated shell, aequibiconvex lateral profile and narrower tongue and internally, by the presence of thick lens of prismatic calcite in the middle part of the ventral valve and long myophragm.

C. pseudoglobularis sp. nov. displays strong similarities to *Crinisarina angelicoides* (Merriam, 1940), a species known from the lower Famennian to ?middle Famennian of Nevada, southern Belgium, Cracow area and Holy Cross Mountains (Poland) and doubtfully reported from Alberta (Canada) and the Harz Mountains (Germany) (see references in Baranov, Sokiran and Blodgett, 2016); however *C. pseudoglobularis* is nearly as wide as long and it thus displays a different outline. Moreover, *C. angelicoides* has a sharply parasulcate anterior commissure, a markedly higher tongue and more developed sulcus and fold. The most significant internal difference is the presence of strong callosities in lateral apical cavities of *C. angelicoides*, whereas the lateral apical cavities of *C. pseudoglobularis* sp. nov. are moderately filled in.

The new species may be distinguished from *C. reticulata* (Gosselet, 1877) as revised by Mottequin (2008), by its more inflated and less transverse shell, less developed sulcus and fold and subtrapezoidal to semioval tongue.

C. pseudoglobularis sp. nov. differs externally from *C. shashishanensis* Mottequin, 2008, from the middle Famennian of South Tianshan (China), by its larger and thicker shell, poorly emarginate to straight anterior margin, less developed fold and sulcus and relatively lower subtrapezoidal to semioval tongue. Internally, the new species is distinguished by the presence of a thick lens of prismatic calcite developed in the middle part of the ventral valve, well–developed umbonal callus and the absence of a stout dorsal myophragm.

C. pseudoglobularis sp. nov. differs superficially from *C. neutra* Modzalevskaya and Pushkin, 2012 occurring in the lower Famennian of Belarus by its shell size, general outline and poorly developed sulcus. Furthermore, our material is also distinguished internally by its relatively stout dental plates, the presence of a thick lens of prismatic calcite developed in the middle part of the ventral valve, a well–developed umbonal callus, a comparably long dorsal myophragm.

C. pseudoglobularis sp. nov. may be distinguished from *C. ligularis* Modzalevskaya and Pushkin, 2012, a middle Famennian species from Belarus, by its larger shell with width exceeding the length and more or less aequidimensional lateral profile. It is difficult to compare the internal morphologies of both as Modzalevskaya and Pushkin (2012) did not illustrate serial sections of their material.

C. pseudoglobularis sp. nov. seems to be similar to *C. reticulatiformis* Modzalevskaya and Pushkin, 2012 from the middle Famennian of Belarus, but the latter differs by its always longer than wide shell and by its more solid spines covering the shell. The most significant difference lies in the ventral internal morphology. In *C. reticulatiformis*, the umbonal callus is divided into two parts by the median groove and lateral apical cavities are strongly filled in, whereas the lateral apical cavities of our material are only moderately filled in and the umbonal callus is not divided, instead it is supported by a thick lens of prismatic calcite developed in the middle part of the valve.

Comparative quantitative analyses

The size distributions between four studied species have been compared and tested. Statistical analysis, i.e., ANCOVA (test for comparison of several models of simple linear regression) were performed in order to determine if the regression line slopes of our four samples are significantly different. Statistical analysis were performed under the free PAST software.

The scatter plot of Width/Length ratios and linear regression lines for all the four taxa are presented Figure 16. The shell growth for each species follows a linear model, as this is more particularly reflected by the significant coefficient of correlation (Fig. 16; $p<0.001$***). For the Width/Length ratios, if equal adjusted means (between–groups effect) in the four species can be rejected at $p<0.005$ ($p=1.06E{-}20$***), equality of slopes cannot be rejected ($p=0.9735$ *NS*). In addition, it is interesting to underline that *Sartenaerus baitalensis*, and *Greira transcaucasica* show similar Length/Width ratios with *Sartenaerus baitalensis* rather represented by larger individuals while *Greira transcaucasica* is represented by smaller individuals. Moreover, while

Crinisarina pseudoglobularis sp. nov. and *Sartenaerus baitalensis* show similar slope for their Width/Length ratios, *Crinisarina pseudoglobularis* sp. nov. exhibit longer length relative to its width than *Sartenaerus baitalensis*. In the same way*,* while *Sartenaerus charakensis* and *Sartenaerus baitalensis* show similar slope for their Width/Length ratios, *Sartenaerus baitalensis* exhibit longer length relative to its width than *Sartenaerus charakensis.*

The scatter plot of Width/Thickness ratios and linear regression lines for all the four species are presented Figure 17. The shell growth for each species follows a linear model, as this is more particularly reflected by the significant coefficient of correlation (Fig. 17; p*<0.001*** or p<0.01***). For the Width/Thickness ratios, if equal adjusted means (between–groups effect) in the four species taxa can be rejected at *p<0.005* (*p=8.34E–15****), equality of slopes can be rejected also (*p=0.00905****). Moreover, if equal adjusted means (between–groups effect) in *Sartenaerus baitalensis* and *Greira transcaucasica* can be rejected at *p<0.005* (*p=1.18E–08***),* equality of slopes cannot be rejected (*p=0.7051 NS*). In the same way, if equal adjusted means (between–groups effect) in *Sartenaerus baitalensis* and *Sartenaerus charakensis* can be rejected at *p<0.005* (*p=0.00028***),* equality of slopes cannot be rejected (*p=0.9728 NS*). *Sartenaerus baitalensis* exhibit more important thickness relative to its width than *Sartenaerus charakensis* and than *Greira transcaucasica*.

Finally, the scatter plot of Width/Width of Sulcus ratios and linear regression lines for all the four species are presented Figure 18. The shell growth for each species follows a linear model, as this is more particularly reflected by the significant coefficient of correlation (Fig. 18; p*<0.001****). For the Width/Width of Sulcus ratios, if equal adjusted means (between–groups effect) in the three taxa can be rejected at *p<0.005* (*p=3.59E–15****), equality of slopes cannot be rejected (*p=0.6946NS*). As for the Width/Length ratios, it is interesting to underline that

Sartenaerus baitalensis and *Greira transcaucasica* show similar Width//Width of Sulcus ratios with *Sartenaerus baitalensis* rather represented by larger individuals while *Greira transcaucasica* is represented by smaller individuals. Interestingly, *Sartanearus charakensis* seems to be represented as an intermediate form with rather similar Width//Width of Sulcus ratios. Moreover, while *Crinisarina pseudoglobularis* sp. nov. and *Sartenaerus baitalensis* show similar slope for their Width/Width of Sulcus ratios, *Sartenaerus baitalensis* exhibit more important Width of Sulcus relative to its Width than *Crinisarina pseudoglobularis* sp. nov.

Discussion

Although a precise paleolatitudinal evaluation of the Late Devonian position of the SAB is still hampered due to the remagnetization of Upper Paleozoic rocks following the Late Cretaceous obduction of ophiolites (Meijers et al. 2015), existing paleogeographic reconstructions place the SAB at the junction between the Iranian terranes (to the east) and the Anatolide–Tauride microplate (to the west). It was thus an integral part of the northern passive margin of Gondwana, facing the Paleotethys ocean to the north (Fig. 19). Thus, during the Late Devonian it was part of a huge platform that was positioned at the southern hemisphere tropical carbonate development zone (Brock and Yazdi 2000). The taxonomic assessment of brachiopods collected from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone of Abrahamyan (1957) cropping out in the Ertych, Djravank and Noravank sections of central Armenia allows us to recognize the presence of six rhynchonellide and one athyridide species. As rhynchonelliform brachiopods have a benthic mode of life and produce lecithotrophic larvae, their paleobiogeographic patterns have a potential to reveal past geographic boundaries and oceanographic connections, although cautious should be exercised on questions of taxonomic consistency, comparison of assemblages of similar age and biofacies (Brock and Yazdi 2000). In that respect the two species of the Famennian genus *Sartenaerus* found in the *orbelianus* Zone of Armenia (*S. baitalensis* and *S. charakensis*) are of particular paleobiogeographic significance as they point to a likely wide lower Famennian brachiopod bioprovince developed along the northern Gondwana margin, from the SAB to Afghanistan and Pamir (Fig. 19). However, it should be stressed that in spite of the well constrained age of the occurrence of *S. baitalensis* in the Lesser Caucasus (the species occurs only in the *orbelianus* Zone) this is not the case for the occurrence of *S. baitalensis* in Pamir (Reed 1922). Finally, the apparent absence of both species in other parts of the northern Gondwanan margin, especially in Morocco may be due to the presence of deeper (cephalopod–bearing) facies for this interval and therefore it may reflect a paleoenvironmental rather than paleobiogeographical signal. This is the first time that the genus *Porthmorhynchus* is recognized (although doubtfully) from the Armenian sections. It is also worth stressing that the genus is known so far only from the Frasnian, as its type species *P. ferquensis* is known from the middle–upper Frasnian of the Boulonnais region and Nakhichevan (Pakhnevich in Alekseeva et al. (2018a)). The other species assigned to this genus *P. elburzensis* is known from the upper Frasnian of the Alborz Mts (northern Iran). Thus, the doubtful presence of this genus in the lower Famennian *orbelianus* Zone of Armenia is significant, although it requires further study to confirm its presence.

Greira transcaucasica is one of the oldest punctate rhynchonellide species and, as it is only known from the SAB, this may represent an interesting case of endemicity.

The single athyridide species recognized (*Crinisarina pseudoglobularis* sp. nov.) represents also the first ever report of genus *Crinisarina* in the South–Armenian Block and indeed in the entire northern margin of Gondwana, even if it is not excluded that *Crinisarina* representatives are present in the Famennian of North Africa (Algeria and Morocco), where taxonomical studies have been mostly dedicated to the rhynchonellides, productidines and spiriferides, whereas the other elements of the brachiopod faunas received scant attention (see references in Mottequin et al., 2015). Alike other species of *Crinisarina* (see discussion in Mottequin, 2008), it is likely that *C. pseudoglobularis* sp. nov. had a preference for soft substrates, made of argillaceous sediments on which it was attached with a thin pedicle. This corresponds well to our own observations, as this species was found mainly in shaly intervals.

Conclusions

Taxonomic reassessment of the rhynchonellide brachiopods collected from the lower Famennian *'Cyrtospirifer' orbelianus* brachiopod Zone of Abrahamyan (1957) from three distinct localities of central Armenia confirm the presence of a number of species known previously (e.g. *Sartenaerus baitalensis*, *S. charakensis* and *Greira transcaucasica*). However, this is the first time that extensive documentation of the internal structure of *Sartenaerus baitalensis* is provided and this is of particular significance as it is the type species of a biostratigraphically important genus. Thus, the brachiopod record from Armenia establishes firmly the presence of the Famennian genus *Sartenaerus* since the lower Famennian and not since the middle Famennian as it was previously believed (Mottequin et al. 2014). It is also the first documentation of *S. charakensis* in the Armenian sections; moreover, its stratigraphic range is extended here down to the *orbelianus* Zone (it was previously known from the *ghorensis–pamiricus* Zone). The intraspecific variability of *Greira transcaucasica* is documented and its stratigraphic range revised to include its presence up to the *orbelianus* Zone. This is also the occasion to introduce a new athyridide species (*Crinisarina pseudoglobularis* sp. nov.) and, thus, to report the first occurrence of the genus *Crinisarina* in the SAB and the entire north Gondwanan realm. The paleobiogeographic distribution of the rhynchonellides and athyridides within the lower Famennian of Armenia suggests that the brachiopod communities thriving on the shallow water carbonate platform of the SAB contained some apparently endemic species (*G. transcaucasica* and *C. pseudoglobularis* sp. nov.), but also species that were in common with other parts of the Gondwanan northern margin extending eastwards to Afghanistan and Pamir.

Acknowledgments

V. Serobyan is grateful to the French Embassy in Armenia and the MOBLILEX International Mobility Grant Programme of the University of Lille for funding his studies in France. T. Danelian and A. Grigoryan acknowledge the financial support of the Erasmus + International Credit Mobility Programme for their staff mobility in 2018 and 2019, respectively. C. Crônier acknowledges the financial support of the Lille Institute on Environmental Sciences (IRePSE). Fieldwork was also facilitated by the logistic support of the Institute of Geological Sciences (Armenian Academy of Sciences). The authors thank the Région Hauts–de–France, and the Ministère de l'Enseignement Supérieur et de la Recherche (CPER Climibio), and the European Fund for Regional Economic Development for their financial support. Sylvie Régnier (UMR Evo–Evo–Paleo, ULille) is gratefully acknowledged for the high–quality SEM pictures obtained on specimens deposited at IGNASRAGM.

References

Abich, H., 1858, Vergleichende geologische Grundzüge der Kaukasischen, Armenischen und Nordpersischen Gebirge: Prodromus einer Geologie der Kaukasischen Länder: Mémoires de l'Académie impériale des Sciences de Saint–Pétersbourg, 6ème série, Sciences mathémathiques et physiques, v. 7, p. 359–534.

Abrahamyan, M.S., 1954, Novyye vidy brakhiopod iz famenskikh otlozheniy Armyanskoy SSR: Izvestiya Akademii Nauk Armyanskoy SSR, v. 7, p. 65–71 [in Russian].

Abrahamyan, M.S., 1957, Brakhiopody verkhnefamenskikh i etrenskikh otlozheniiyugo–zapadnoi Armenii: Yerevan, Izdatelstvo Akademii Nauk Armyanskoi SSR, 142 p. [in Russian].

Abrahamyan, M.S., 1964, Karbon, *in* Mkrtchian, S.S., Vardaniants, L.A., Gabrielian, A.A, Maghakian, I.G., and Paffenholz, C.N., eds., Geologiya Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, v. 2, p. 96–118 [in Russian].

Abrahamyan, M.S., 1974, Opisanie fauny, Devonskaya sistema, Tip Brachiopoda, Brakhiopody, *in* Akopian, V.T., ed., Atlas iskopaemoy fauny Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologyiceskih Nauk, p. 48–67 [in Russian].

Abrahamyan, M.S., Arakelyan, R.A., and Azizbekov, Sh.A., 1973, Malyy Kavkaz (Yuzhnoye Zakavkaz'ye), *in* Rzhonsnitskaya, M.A., ed., Kavkazkaya geolsinklinal'naya oblast'i Predkavkaz'e, *in* Nalivkin, D.V., Rzhonsnitskaya, M.A., Markovski, B.P., eds., Stratigrafiya SSSR, Devonskaya sistema: Moscow, Nedra 1, p. 210–219 [in Russian].

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., and Pakhnevich, A.V., 2018a, Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia: Paleontological Journal, v. 52, p. 829–967.

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., and Pakhnevich, A.V., 2018b, Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia (Ending): Paleontological Journal, v. 52, p. 969–1085.

Alvarez, F., Rong, J.Y., and Boucot, A.J., 1998, The classification of athyridid brachiopods: Journal of Paleontology, v. 72, p. 827–855.

Alvarez, F., and Rong, J.Y., 2002, Athyridida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda 4 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), H1475–H1601.

Arakelyan, R.A., 1952, Stratigrafiya paleozoyskikh otlozheniy yugo–zapadnoy Armenii i prilegayushchikh chastey Nakhichevanskoy ASSR: Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk., 142 p. [in Russian].

Arakelyan, R.A., 1964, Devon, *in* Mkrtchian, S.S., Vardaniants, L.A., Gabrielian, A.A, Maghakian, I.G., and Paffenholz, C.N., eds., Geologiya Armyanskoy SSR: Yerevan, Akademiya Nauk Armyanskoy SSR, v. 2, p. 46–96 [in Russian].

Aristov, V.A., 1994, Konodonty devona–nizhnego karbona Evrazii: soobshchestva, zonalnoye raschleneniye, korrelyatsiya raznofatsialnykh otlozheniy: Trudy Geologicheskogo instituta Rossiyskoy akademii nauk v. 484, 1–193 [in Russian].

Baranov, V.V., Sokiran, E., and Blodgett, R.B., 2016, Late Devonian (Famennian) brachiopods, conodonts, biogeography and sedimentary geology of Bel'kovsky island (Russian Arctic): Record 5: New Mexico Museum of Natural History and Science Bulletin, v. 74, p. 13–24.

Boucot, A.J., Johnson, J.G., and Staton, R.D., 1964, On some atrypoid, retzioid, and athyridoid Brachiopoda: Journal of Paleontology, v. 38, p. 805–822.

Brice, D., 1967, Deux nouvelles espèces de Rhynchonelloidea dans le Dévonien supérieur d'Afghanistan central: Annales Société Géologique du Nord, v. 87, p. 95–105.

Brice, D., 1971, Etude paléontologique et stratigraphique du Dévonien de l'Afghanistan: Notes et Mémoires du Moyen Orient, v. 11, p. 1–364.

Brice, D., and Lang, J., 1968, Sur un nouveau gisement du Dévonien supérieur à Iraq (Bamian, Afghanistan): Comptes Rendus de la Société Géologique de France, v. 4, p. 1–120.

Brice, D., Colleau, A., and Lapparent A.F. de, 1969, Sur la stratigraphie du Dévonien de Robat–e–Paï (Afghanistan occidental): Comptes Rendus de la Société Géologique de France, v. 268, p. 2856–2858.

Brice, D., and Meats, P., 1972, Le genre *Ripidiorhynchus* (Rhynchonellida–Brachiopodes) dans le Dévonien de Ferques (Boulonnais). Annales de la Société géologique du Nord, v. 91, p. 15–228.

Brice, D., Mistiaen, B., and Rohart, J.C., 1999, New data on distribution of brachiopods, rugose corals and stromatoporoids in the Upper Devonian of central and eastern Iran: Paleobiogeographic implications: Annales de la Société géologique du Nord v. 2, p. 21–32.

Brice, D., and Deville, P., 2007, Brachiopodes du Dévonien d'Afghanistan, types et figurés (A3.01–B14) du catalogue systématique des collections de l'Université Catholique de Lille: Annales Société Géologique du Nord, v. 14, p. 9–21.

Brock, G.A., and Yazdi, M., 2000, Palaeobiogeographic affinities of Late Devonian brachiopods from Iran: Records of the western Australian Museum, Supplement, p. 321–334.

Brunton, C.H.C., and Tisley, C.J.W., 1991, A check list of brachiopods from Treak Cliff, Derbyshire, with reference to other Dinantian (Lower Carboniferous) localities: Proceedings of the Yorkshire Geological Society, v. 48, p. 287–295.

Buckman, S.S., 1906, Brachiopod nomenclature: *Epithyris*, *Hypothyris*, *Cleiothyris* Phillips, 1841: Annals and Magazine of Natural History (series7), v. 18, p.321–327.

Cooper, G.A., and Dutro, J.T., 1982, Devonian brachiopods of New Mexico: Bulletins of American Paleontology, v. 82–83, p. 1–215.

Davidson, T., 1881, On genera and species of spiral–bearing Brachiopoda from specimens developed by Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire: Geological Magazine, v. 8, p. 1–13.

Denayer, J., Hoşgör, I., 2014, Lower Carboniferous rugose corals from the Arabian Plate: An insight from the Hakkari area (SE Turkey): Journal of Asian Earth Sciences, v. 79, p. 345–357.

d'Orbigny, A., 1850, Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnés Faisant Suite au Cours Elémentaire de Paléontologie et de Géologie Stratigraphiques: Paris, Victor Masson, v. 1, 394 p.

Erlanger, O.A., 1993, *Greira* gen. nov.– Drevneyshiy rod poristykh rinkhonellid: Paleontologicheskiy Zhurnal, v.1, p. 118–122 [in Russian].

Gosselet, J., 1877, Note (1ère) sur le Famennien: Quelques documents pour l'étude des schistes de Famenne: Annales de la Société géologique du Nord, v. 4, p. 303–320.

Gosselet, J, 1887, Note sur quelques rhynchonelles du terrain dévonique supérieur: Annales de la Société géologique du Nord, v. 14, p. 188–221.

Grechishnikova, I.A., Aristov, V.A., Reitlinger, E.A., and Chizhova, V.A., 1982, Biostratigrafiya pogranichnykh otlozhenii devona i karbona Zakavkaz'ya (opornye razrezy): Severo–Vostochnyy kompleksnyy nauchno–issledovatel'skiy institut Dal'nevostochnogo nauchnogo tsentra Akademii nauk SSSR, p. 1–38 [in Russian].

Grechishnikova, I.A., and Levitskii, E.S., 2011, The Famennian–Lower Carboniferous Reference Section Geran–Kalasi (Nakhichevan Autonomous Region, Azerbaijan): Stratigraphy and Geological Correlation, v. 19, p. 21–43.

Jafarian M.A., 2000, Late Devonian index brachiopoda of North–East Esfahan in correlation with other regions: Journal of Sciences Islamic Republic of Iran, v. 11, p. 221–231.

Kyhn, O.,1949, Lehrbuch der Paläozoologie: Stuttgart, E.Schweizerbart'sche Verlagbuchhandlung, 326 p.

Lapparent, A.F. de, and Le Maître, D., 1963, Sur le Dévonien du Koh–i–Baba en Afghanistan: Comptes Rendus de la Société Géologique de France, v. 6, p. 1–188.

Luehe, M., 1911, Acanthocephala: Register der Acanthocephalan und parasitischen Plattwürmer, geordnet nach ihren Wirten, *in* Susswasser–fauna Deutschlands (Brauer), Heft 16, p. 1–116.

Meijers, M.J.M., Smith, B., Kirscher, U., Mensink, M., Sosson, M., Rolland, Y., Grigoryan, A., Sahakyan, L., Avagyan, A., Langereis, C., and Müller, C., 2015, A paleolatitude reconstruction of the South Armenian Block (Lesser Caucasus) for the Late Cretaceous: Constraints on the Tethyan Realm: Tectonophysics v. 644–645, p. 197–219.

Merriam, C.W., 1940, Devonian stratigraphy and paleontology of the Roberts Mountains Region, Nevada: Geological Society of America, Special Papers, v. 25, p. 1–114.

Mirieva, G.T. 2010. Zonal'noye raschleneniye otlozheniy verkhnego Devona Yuzhnogo Zakavkaz'ye (Nakhchyvanskoy AR) po rinkhonellidam: Evolyutsiya organicheskogo mira i bioticheskiye krizisy: Materially 56 sessii Paleontologicheskogo obshchestvo pri RAN, Saint Petersburg Russia, p. 74–76 [in Russian].

Modzalevskaya, T.L., 2012, New Upper Devonian Species of the Suborder Athyrididina Boucot, Johnson et Staton from Belarus: Paleontological Journal, v. 46, p. 360–369.

Mottequin, B., 2008, Late middle Frasnian to early Famennian (Late Devonian) strophomenid, orthotetid and athyridid brachiopods from southern Belgium: Journal of Paleontology, v. 82, p. 1052–1073.

Mottequin, B., Brice, D., and Legrand–Blain, M., 2014, Biostratigraphic significance of brachiopods near the Devonian–Carboniferous boundary: Geological Magazine, v. 151, p. 216–228.

Mottequin, B., Malti, F.Z., Benyoucef, M., Crônier, C., Samar, L., Randon C., and Brice D., 2015, Famennian rhynchonellides (Brachiopoda) from deep–water facies of the Ougarta Basin (Saoura Valley, Algeria): Geological Magazine, v. 152, p. 1009–1024.

Muir–Wood, H.M., 1955, A history of the classification of the phylum Brachiopoda: London, British Museum (Natural History), 124 p.

Nicollin, J.P., and Brice, D., 2004, Biostratigraphical value of some Strunian (Devonian, uppermost Famennian) Productidina, Rhynchonellida, Spiriferida, Spiriferinida brachiopods.: Geobios, v. 37, p. 53–437.

Özdikmen, H., 2008, Nomenclatural changes for a family group name and twelve genus group names: Munis Entomology and Zoology, v. 3, p. 217–230.

Pakhnevich, A.V., 2012, New Devonian punctate rhynchonellids (Brachiopoda) from Transcaucasia: Paleontological Journal, v. 6, p. 560–567.

Phillips, J., 1836, Illustrations of the Geology of Yorkshire: Part 2, the Mountain Limestone District: London, John Murray, 253 p.

Reed, F.R.C., 1922, Devonian fossils from Chitral and the Pamirs. Memoirs of the Geological Survey of India: Palaeontologica Indica, New Series, v. 6, no. 2, p. 1–134.

Rzonsnitskaya, M.A., 1948, Devonskiye otlozheniya Zakavkaz'ye: Doklady Akademy Nauk

SSSR, v. 59, p. 1477–1480 [in Russian].

Rzhonsnitskaya, M.A., and Mamedov. A.B., 2000, Devonian stage boundaries in the southern Transcaucasus: Courier Forschungsinstitut Senckenberg, v. 225, p. 329–333.

Sartenaer, P., 1966, *Ripidiorhynchus*, nouveau genre de Brachiopode Rhynchonellide du Frasnien: Bulletin du Museum National d'Histoire Naturelle, v. 42, no., 30, p. 1–15.

Sartenaer, P., 1970, Nouveaux genres Rhynchonellides (Brachiopodes) du Paléozoïque: Bulletin de l'Institut royal des Sciences naturelles de Belgique, v. 46, no., 32, p. 1–32.

Sartenaer, P., 2001, Revision of the rhynchonellid brachiopod genus *Ripidiorhynchus* Sartenaer: Geologica Belgica, v. 3, p. 191–213.

Sartenaer, P., 2003, *Gesoriacorostrum*, a new Middle Frasnian rhynchonellid (brachiopod) genus from Boulonnais (N France): Geologica Belgica, v. 6, p. 181–192.

Sartenaer, P., and Plodowski, G., 2003, Reassessment of the Strunian Genus *Araratella* Abrahamian, Plodowski and Sartenaer 1975 in the Northern Gondwanaland (Rhynchonellida, Brachiopoda): Courier Forschungs–Institut Senckenberg, v. 242, p. 329–348.

Savage, N.M., 1996, Classification of Paleozoic rhynchonellid brachiopods, *in* P. Copper, P., and Jin, J., eds., Proceedings of the Third International Brachiopod Congress: A.A. Balkema, Rotterdam, p. 60–249.

Savage, N.M., 2007, Rhynchonellida (part), *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, 6 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H19–H2703.

Savage, N.M., Manceñido, M.O., Owen, E.F., Carlson, S.J., Grant, R.E., Dagys, A.S., and Sun.

D.L., 2002, Rhynchonellida, *in* Kaesler, R.L., ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, 4 (revised). Boulder, Lawrence, Geological Society of America (and University of Kansas Press), p. H376–H1027.

Serobyan, V., Grigoryan, A., Mottequin, B., Mayilyan, R., Crônier, C., and Danelian, T., 2019, Biostratigraphy of the Upper Devonian trigonirhynchiid brachiopods (rhynchonellida) from Armenia: Proceedings of National Academy of Sciences of the Republic of Armenia, Earth Sciences, v. 72, no. 2, p. 3–18.

Schmidt, H., 1965, Neue Gattungen Paläozoischer Rhynchonellacea (Brachiopoda): Senckenbergiana lethaea, v. 45, no. 6, p. 1–25.

Schuchert, C., 1913, Class 2: Brachiopoda, *in* Eastman, C.R., ed., Text–book of Paleontology, v. 1, Part 1, 2nd edition: London, MacMillan and Co., Ltd., p. 355–420.

Sosson, M., Rolland, Y., Müller, C., Danelian, T., Melkonyan, R., Kekelia, S., Adamia, S., Babazadeh, V., Kangarli, T., Avagyan, A., Galoyan, G., and Mosar, J., 2010, Subductions, obduction and collision in the Lesser Caucasus (Armenia, Azerbaijan, Georgia), new insights. *in* Sosson, M., Kaymakci, N., Stephenson, E.A., Bergerat, F., and Starostenko, V., eds., Sedimentary Basin Tectonics from the Black Sea and Caucasus to the Arabian Platform: London, Geological Society, Special Publication v. 340, p. 329–352.

Stainbrook, M.A., 1947, Brachiopoda of the Percha Shale of New Mexico and Arizona: Journal of Paleontology, v. 21, p. 297–328.

Stampfli, G., Von Raumer, J.F., and Borel, G.D., 2002, Paleozoic evolution of pre–Variscan terranes: From Gondwana to the Variscan collision, *in* Martinez–Catalan, J.R., Hatcher, R.D., Jr., Arenas, R., and Diaz Garcia, F., eds, Variscan–Appalachian dynamics: The buildings of the late Paleozoic basement: Boulder, Colorado, Geological Society of America, Special Paper, v. 364, p. 263–280.

Ziegler, W., Sandberg, C.A., 1990, The Late Devonian standard conodont zonation: Courier Forschungsinstitut Senckenberg, v. 121, p. 1–115.

Figure Captions

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

Figure 2. Biochronostratigraphic framework of the upper Frasnian–middle Famennian sedimentary sequences in the Lesser Caucasus , including the brachiopod biozones established by Abrahamyan (1957) in central Armenia and by Grechishnikova et al. (1982) 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. *Sartenaerus baitalensis* (Reed, 1922) from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia. 1–5. IGSNASRAGM 3900/PS 3006 (Ertych section), almost complete juvenile specimen in ventral, dorsal, lateral, posterior, and anterior views. 6–10. IGSNASRAGM 3901/PS 3007 (Ertych section), partly exfoliated juvenile specimen in ventral, dorsal, lateral, posterior and anterior views. 11–15. IGSNASRAGM 3902/PS 3008 (Djravank

section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. 16–20. IGSNASRAGM 3903/PS 3009 (Djravank section), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. 21–25. IGSNASRAGM 3904/PS 3010 (Noravank section), articulated specimen in ventral, dorsal, lateral, posterior and anterior views. 26–30. IGSNASRAGM 3905/PS 3011 (Noravank section), articulated specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bars: 5 mm (1–10), 10 mm (11–30).

Figure 4. Transverse serial sections of *Sartenaerus baitalensis* (Reed, 1922) from the '*Cyrtospirifer*' *orbelianus* Zone in Armenia. Numbers refer to distances in mm from the top of the ventral umbo. The ground specimen corresponds to the one illustrated on Fig. 3.11 – 15.

Figure 5. 1–10. *Sartenaerus charakensis* (Brice, 1967) from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia. 1–5. IGSNASRAGM 3906/PS 3012 (Ertych section), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. 6–10. IGSNASRAGM 3907/PS 3013 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. 11–15. *Porthmorhynchus*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone of the Noravank section. IGSNASRAGM 3908/PS 3014, almost complete specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bar: 5 mm (1–15).

Figure 6. Transverse serial sections of *Sartenaerus charakensis* (Brice, 1967) from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia, Ertych section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 7. Transverse serial sections of *Porthmorhynchus*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia, Noravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 8. *Gesoriacorostrum*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia, Djravank section. 1–5. IGSNASRAGM 3909/PS 3015, partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views.

Figure 9. Transverse serial sections of *Gesoriacorostrum*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia, Djravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 10. *Greira transcaucasica* Erlanger, 1993 from the lower Famennian '*Cyrtospirifer' orbelianus* Zone in Armenia. 1–5. IGSNASRAGM 3910/PS 3016 (Ertych section), almost complete specimen in ventral, dorsal, lateral, and anterior views. 6–10. IGSNASRAGM 3911/PS 3017 (Ertych section), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. 11–18. IGSNASRAGM 3912/PS 3018 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (11–15), and close–up of the ventral umbo (thin dental plates are exposed as the ventral beak is broken; 16), and close–up of the micro–ornament (drill hole in the sulcus perhaps of predatory origin (17) and punctae or shell damage (18)). Scale bars: 5 mm (1–15), 1 mm (16), 200 µm (17), 10 µm (18).

Figure 11. Transverse serial sections of *Greira transcaucasica* Erlanger, 1993 from the lower Famennian '*Cyrtospirifer' orbelianus* Zone in Armenia, Djravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 12. *Sharovaella*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone of Armenia, Ertych section. 1–8. IGSNASRAGM 3913/PS 3019, almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (1–5), and close–up of the micro–ornament (punctae on ventral valve, near umbo; 6–8). Scale bars: 5 mm (1–5), 100 µm (24), 10 µm (25), 2 µm (26).

Figure 13. Transverse serial sections of *Sharovaella*? sp. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone of Armenia, Ertych section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 14. *Crinisarina pseudoglobularis* sp. nov. from the lower Famennian '*Cyrtospirifer*' *orbelianus* Zone in Armenia. 1–5. IGSNASRAGM 3914/PS 3020 (Ertych section), almost complete juvenile specimen in ventral, dorsal, lateral, posterior and anterior views. 6–10. IGSNASRAGM 3915/PS 3021 (Noravank), partly exfoliated juvenile specimen in ventral, dorsal, lateral, posterior and anterior views. 11–18. IGSNASRAGM 3916/PS 3022 (Djravank section), almost complete specimen in ventral, dorsal, lateral, posterior and anterior views (11–15), and close–up of the micro–ornament (radially–aligned solid spines) on ventral valve, near the anterior margin (16–18). 19–23. IGSNASRAGM 3917/PS 3023 (Noravank section), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. 24–27.

IGSNASRAGM 3918/PS 3024 (Djravank section), partly exfoliated specimen in ventral, dorsal, lateral, posterior and anterior views. Scale bars: 5 mm (1–15, 19–28), 500 µm (16), 100 µm (17), 40 µm (18).

Figure 15. Transverse serial sections of *Crinisarina pseudoglobularis* sp. nov. from the lower Famennian '*Cyrtospirifer' orbelianus* Zone of Armenia, Noravank section. Numbers refer to distances in mm from the top of the ventral umbo.

Figure 16. Scatter diagrams exhibiting the relation between shell width and length (in mm) of *Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967), *Greira transcaucasica* Erlanger, 1993, and *Crinisarina pseudoglobularis* sp. nov. Abbreviations: n, number of specimens measured; $y=ax+b$, linear model; r, coefficient of correlation; p^{***}, significant probability value.

Figure 17. Scatter diagrams exhibiting the relation between shell width and thickness (in mm) of *Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967), *Greira transcaucasica* Erlanger, 1993, and *Crinisarina pseudoglobularis* sp. nov. Abbreviations: n, number of specimens measured; $y=ax+b$, linear model; r, coefficient of correlation; p^{***}, significant probability value.

Figure 18. Scatter diagram exhibiting the relation between shell width (in mm) and width of sulcus (in mm) of *Sartenaerus baitalensis* (Reed, 1922), *Sartenaerus charakensis* (Brice, 1967), *Greira transcaucasica* Erlanger, 1993, and *Crinisarina pseudoglobularis* sp. nov. Abbreviations:

n, number of specimens measured; *y=ax+b*, linear model; *r*, coefficient of correlation; *p****, significant probability value.

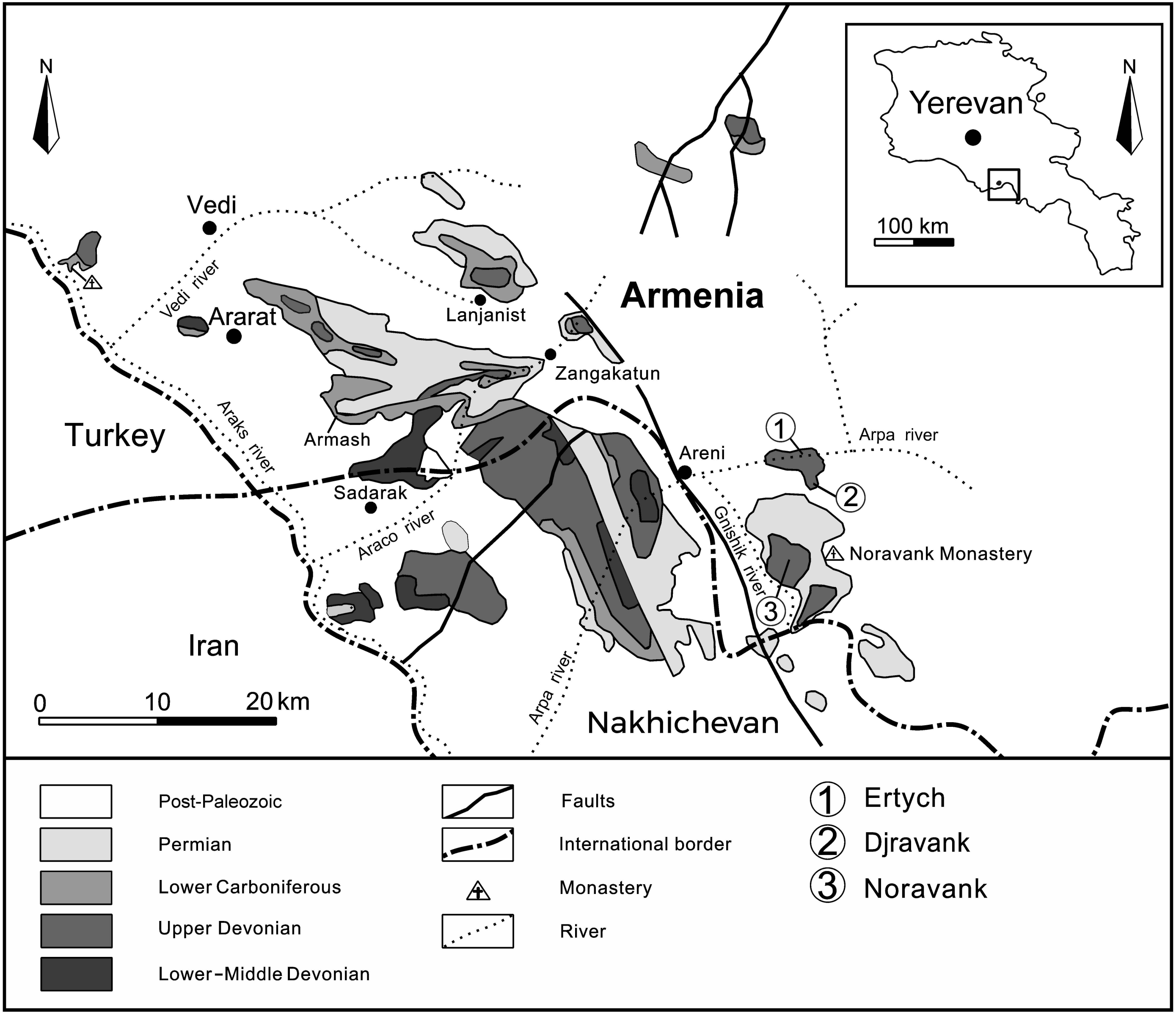
Figure 19. Late Devonian paleogeographic reconstruction of the Paleotethys ocean and its surrounding continents, including the position of the South Armenian Block along the northern margin of the Gondwana megacontinent (redrawn and modified after Denayer and Hoçgör 2014, based on the maps of Stampfli et al. 2002).

Table 1. Measurements in mm and ratios of *Sartenaerus baitalensis* (Reed, 1922). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

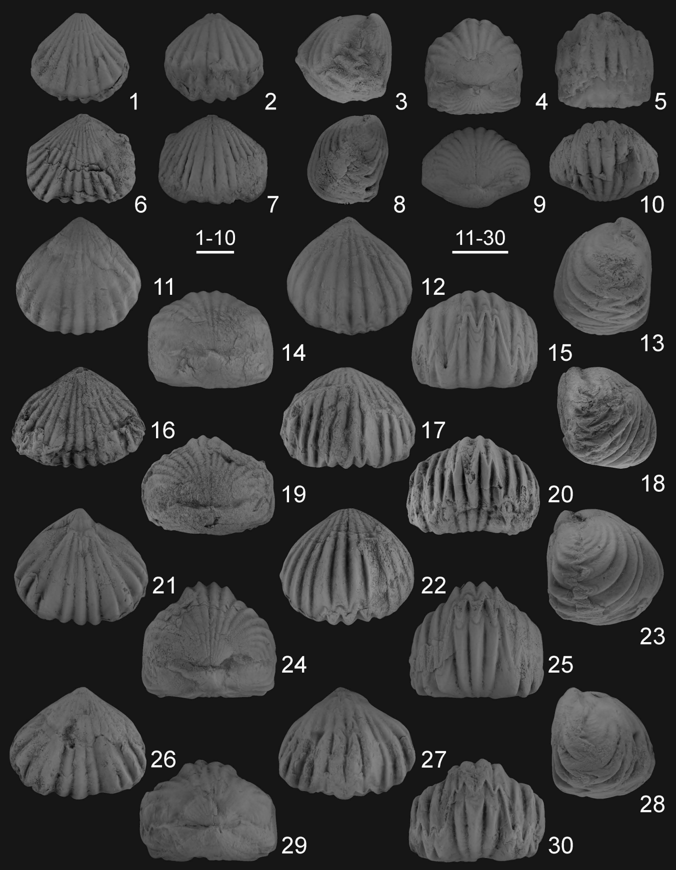
Table 2. Measurements in mm and ratios of *Sartenaerus charakensis* (Brice, 1967). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

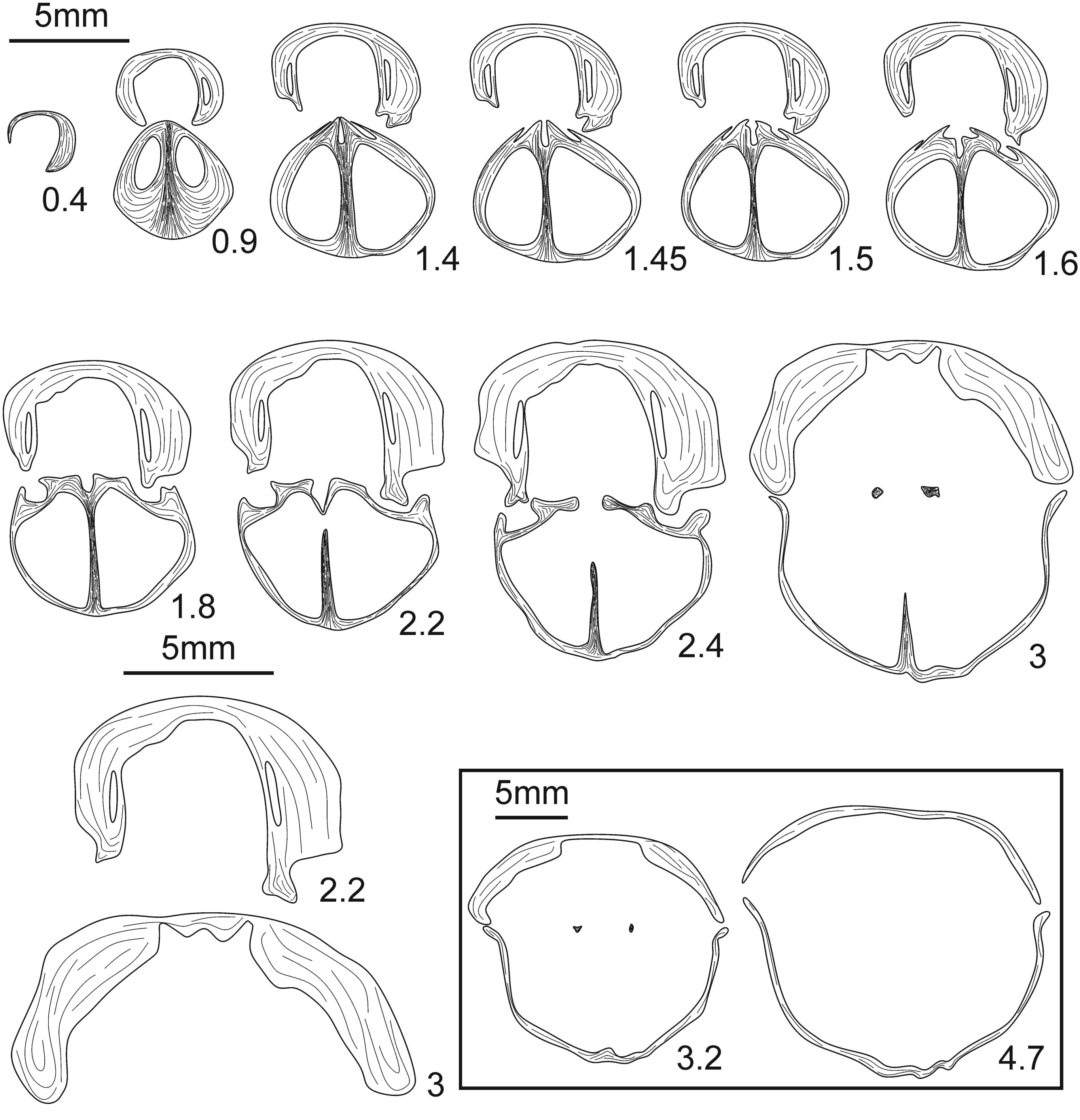
Table 3. Measurements in mm and ratios of *Greira transcaucasica* Erlanger, 1993 Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

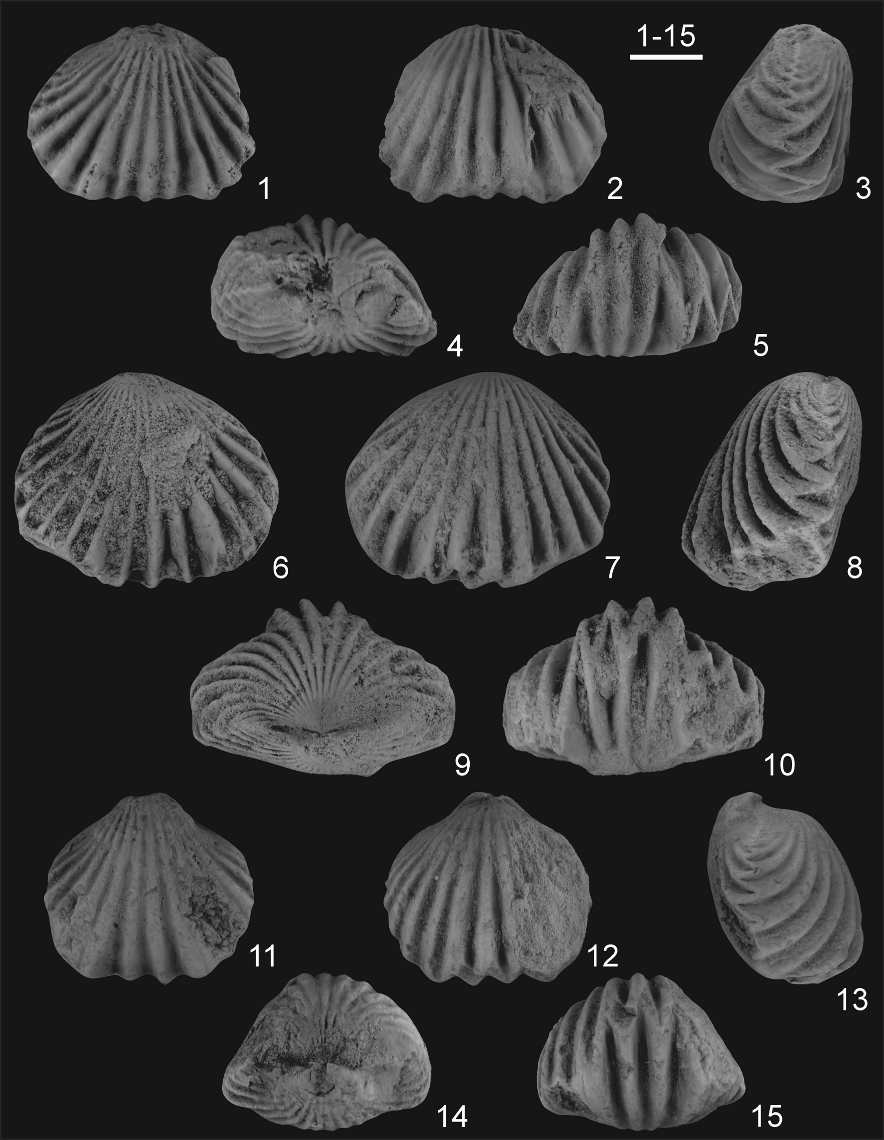
Table 4. Measurements in mm and ratios of *Crinisarina pseudoglobularis* sp. nov. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

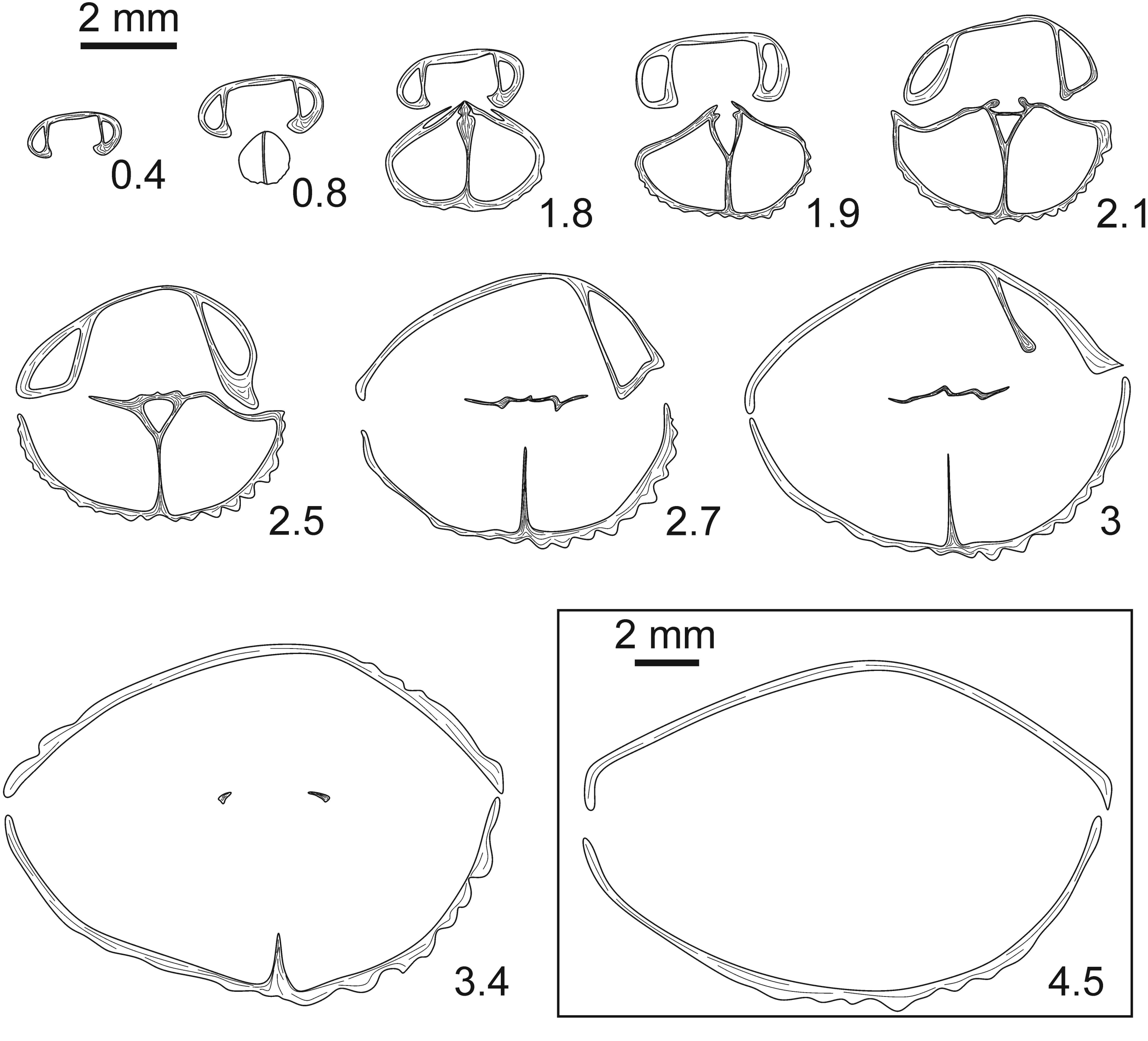

N
Yerevan
N
100 km
Vedi
Vedi river
Ararat
Lanjanist
Armenia
Zangakatun
Turkey
Araks river
Armash
Sadarak
Areni
Arpa river
Araco river
Gnishik river
Noravank Monastery
Iran
Arpa river
Nakhichevan
0
10
20 km
Post-Paleozoic
Permian
Lower Carboniferous
Upper Devonian
Lower–Middle Devonian
Faults
International border
Monastery
River
1 Ertych
2 Djravank
3 Noravank

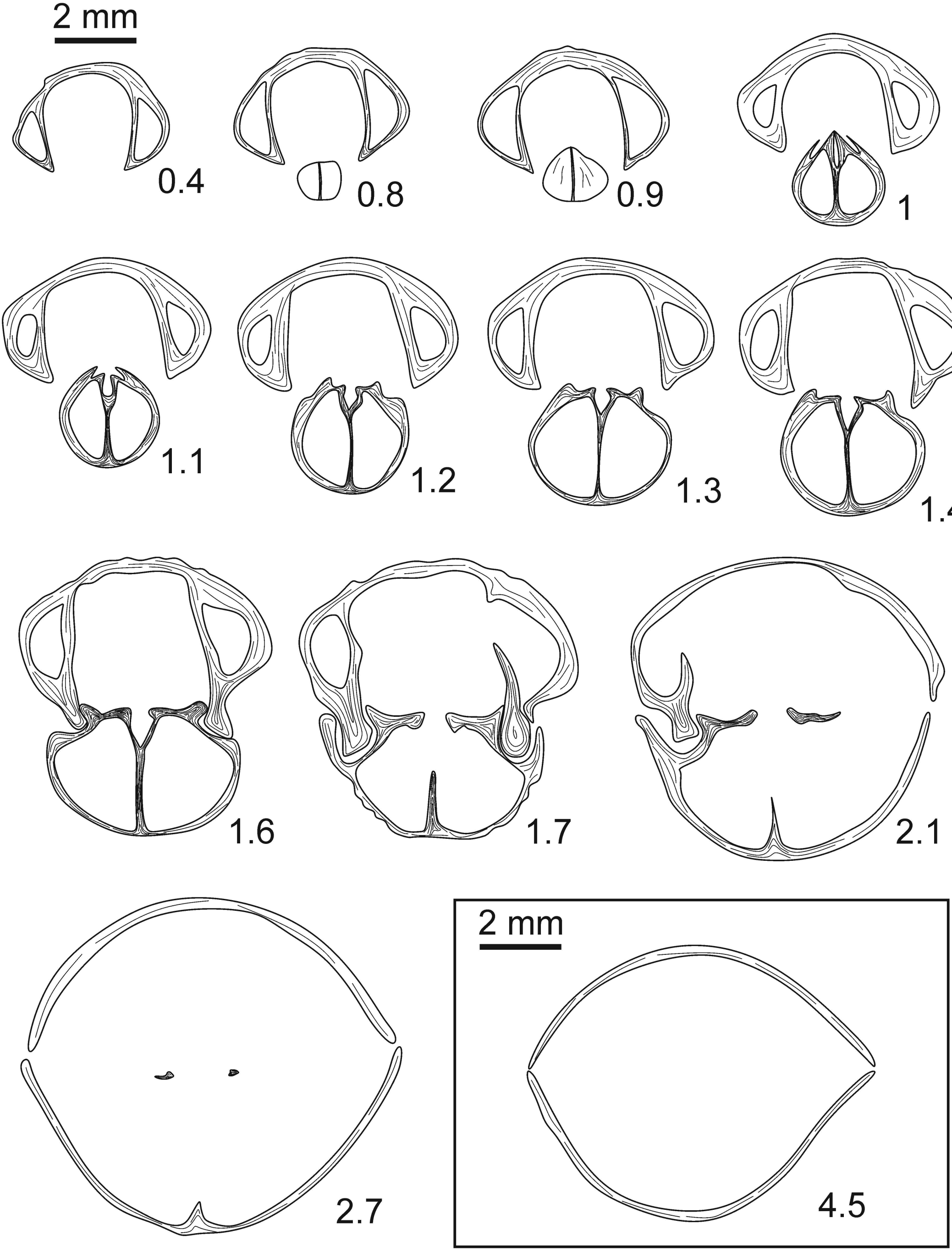
Stage	Sub-stage	Horizons: Arakelyan (1964)	Brachiopod zones: Abrahamyan (1957)	Brachiopod zones: Grechishnikova *et al.* (1982)	Brachiopod zones: Rzhonsnitskaya and Mamedov (2000)	Conodont zones: Standard (Ziegler & Sandberg, 1990)	Conodont zones: Local (Aristov, 1994)
Famennian	Middle	Shamamidzor	*Cyrtospirifer pamiricus*	*Enchondrospirifer ghorensis–Cyrtospirifer pamiricus*	*Enchondrospirifer ghorensis*	*trachytera* U, L	*Polygnathus semiocostatus Schaphignathus velifer*
		Kadrlu	*'Cyrtospirifer' seminoi*	*Dmitria seminoi*	*Dmitria seminoi*	*marginifera* U, M, L; *rhomboidea* U, L	*Polygnathus semicostatus Icriodus cornutus*
	Lower	Ertych	*'Cyrtospirifer' orbelianus*	*'Mesoplica' meisteri–Cyrtospirifer asiaticus*	*'Cyrtiopsis' orbelianus–'Cyrtiopsis' armenicus*	*crepida* Um, U, M, L	*Polygnathus brevilaminus Icriodus cornutus*
		Noravank	*'Cyrtospirifer' lonsdalii 'Productella' herminae 'Camarotoechia' arpaensis* etc.		*'Mesoplica' meisteri–Cyrtospirifer asiaticus*	*triangularis* U, M, L	*Polygnathus brevilaminus*
Frasnian	Upper	Baghrsagh		Unzoned	Unzoned	*unguiformis*	Unzoned
						rhenana U, L	
						jamieae	
						hassi U, L	
						punctata	
				'Cyrtospirifer' subarchiaci–Cyphoterorhynchus arpaensis	*'Cyrtospirifer' subarchiaci–Cyphoterorhynchus arpaensis*	*transitans*	*Ancyrodella rotunbiloba*
						falsiovalis U, L	*Ancyrodella binodosa*

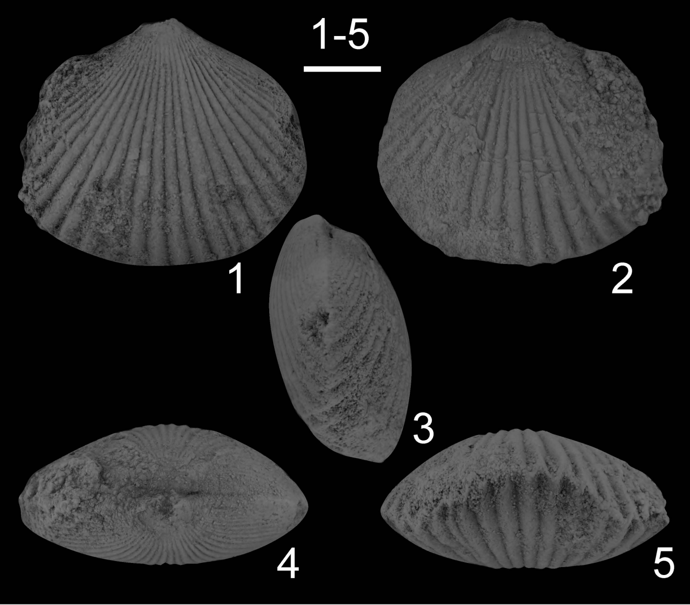

1-10
11-30
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

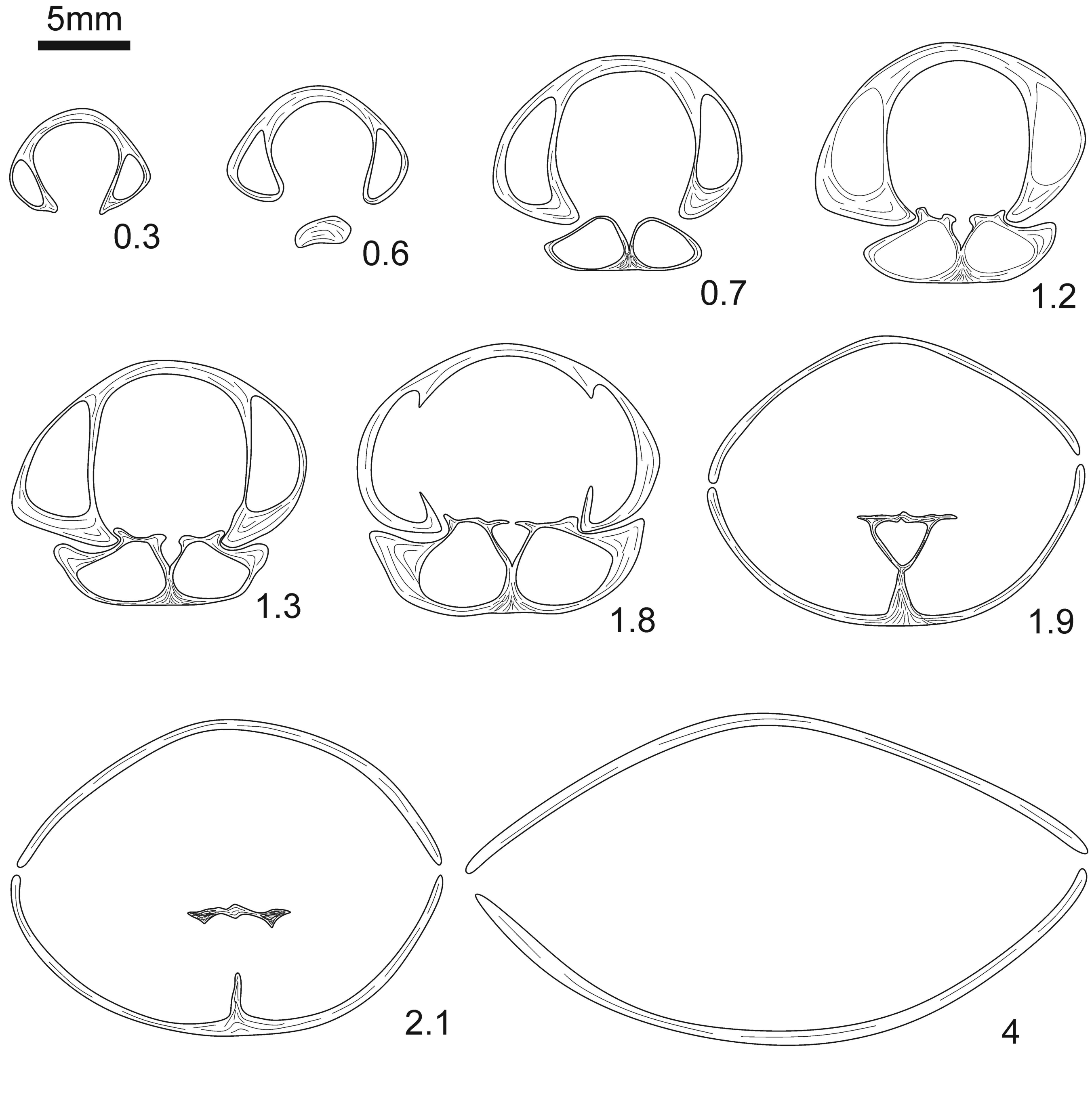

5mm
0.4
0.9
1.4
1.45
1.5
1.6
1.8
2.2
2.4
3
5mm
2.2
3
5mm
3.2
4.7

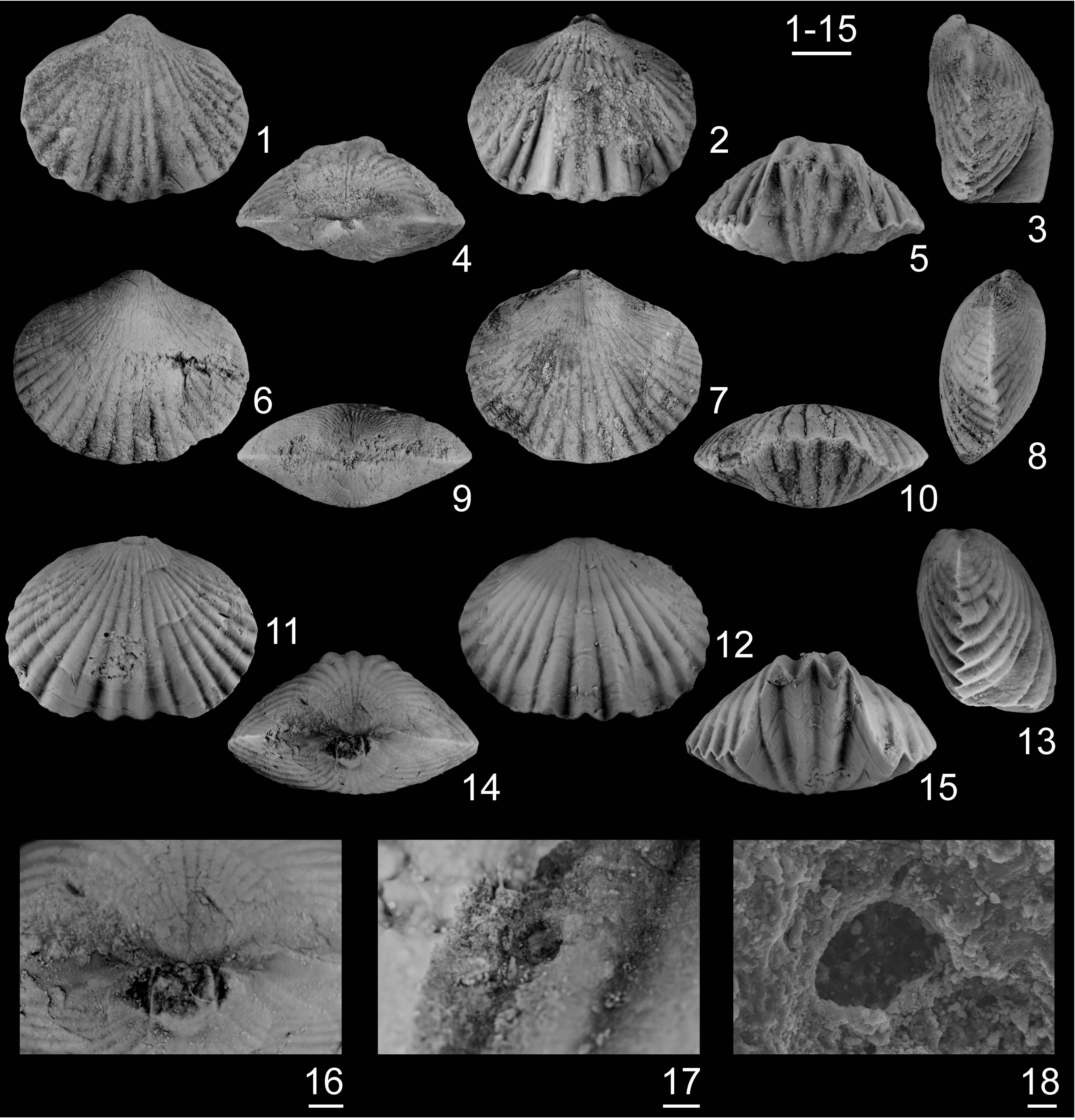

1-15
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

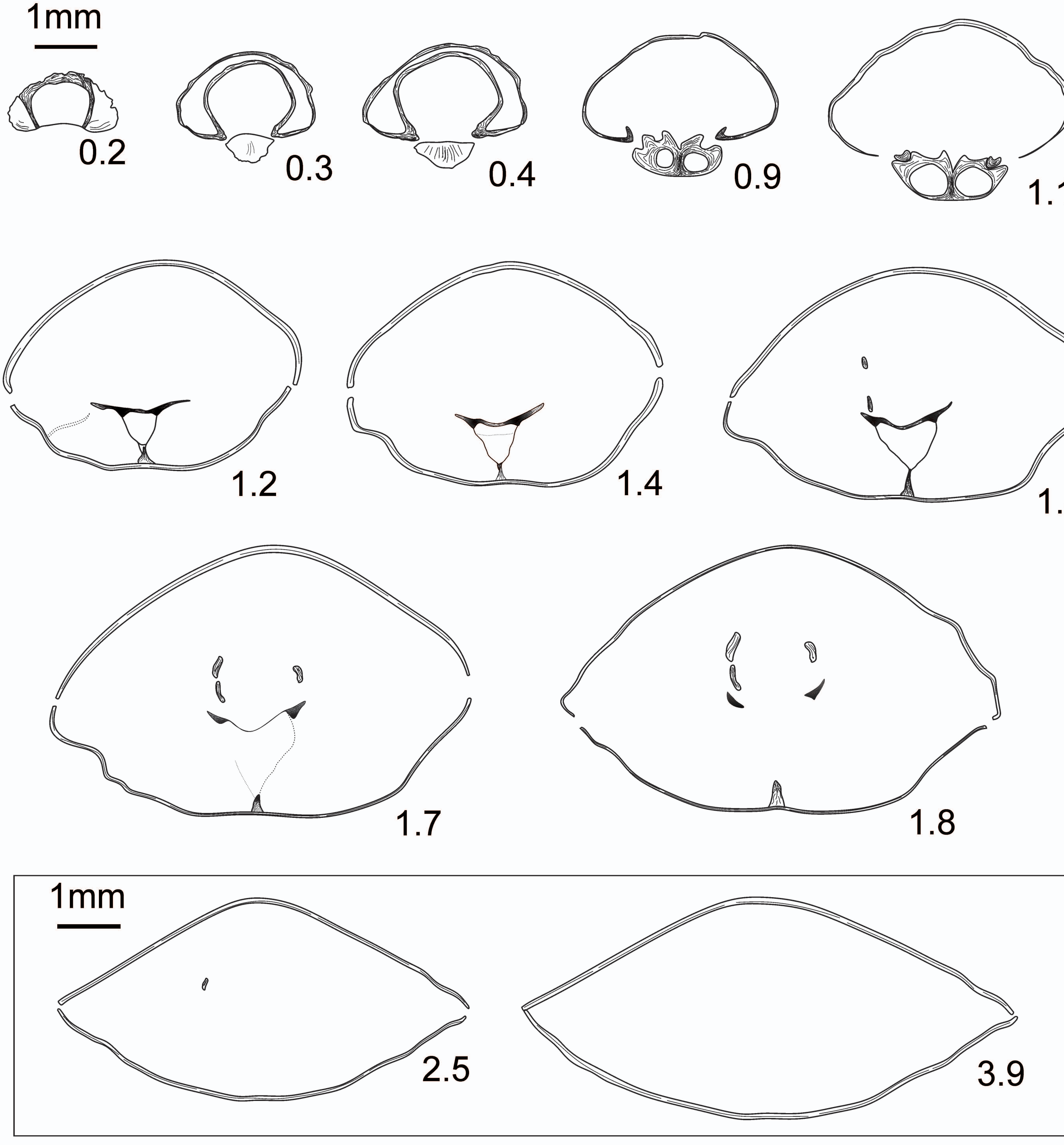

2 mm
0.4
0.8
1.8
1.9
2.1
2.5
2.7
3
3.4
2 mm
4.5


2 mm
0.4
0.8
0.9
1
1.1
1.2
1.3
1.4
1.6
1.7
2.1
2.7
2 mm
4.5

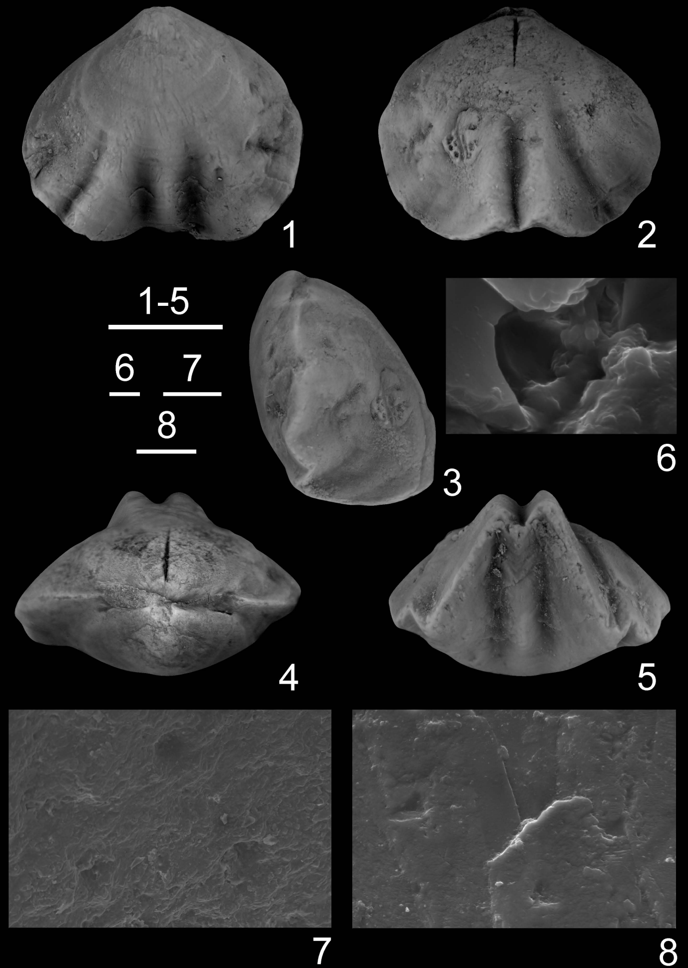

1-5
1
2
3
4
5

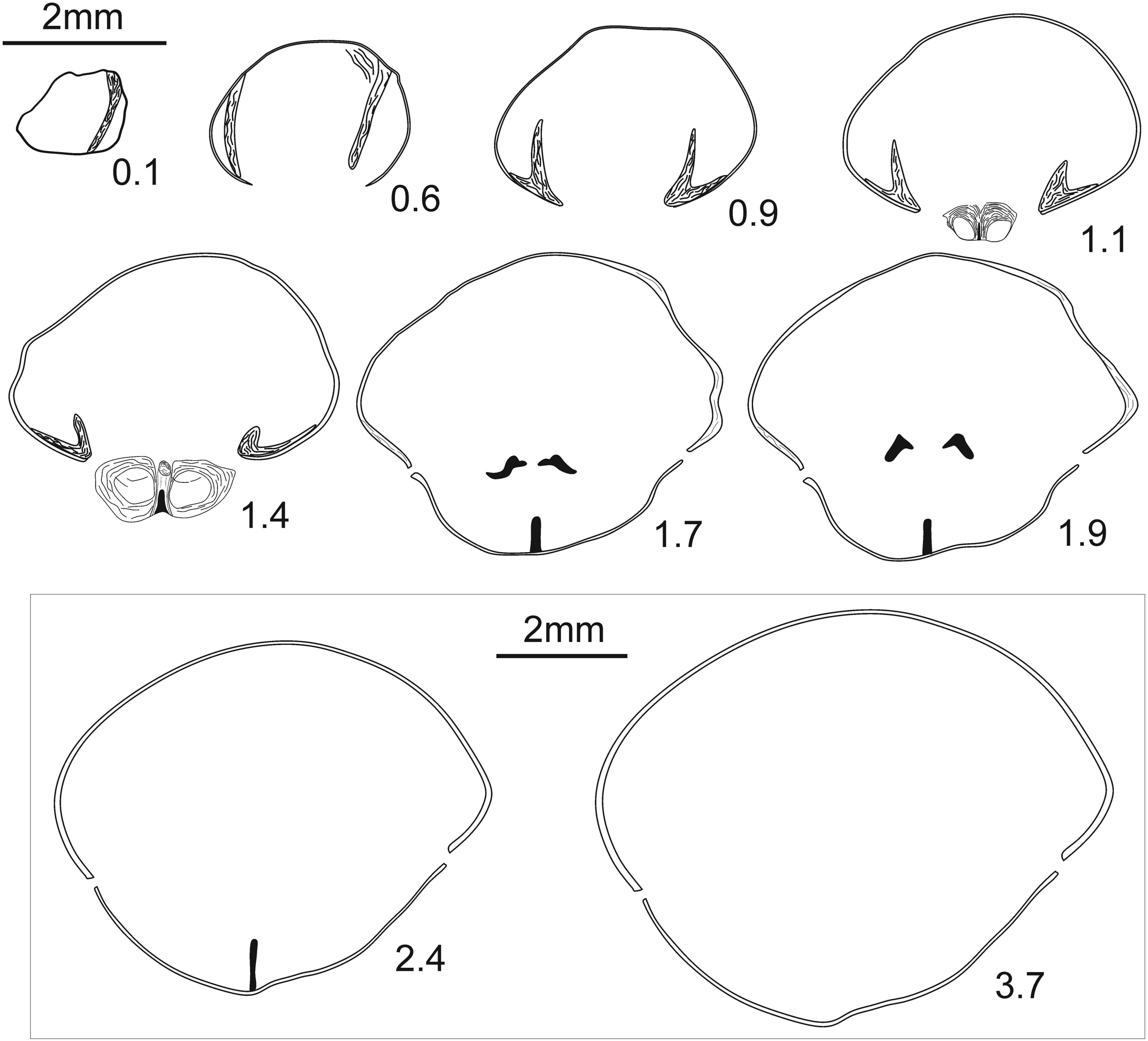

5mm
0.3
0.6
0.7
1.2
1.3
1.8
1.9
2.1
4

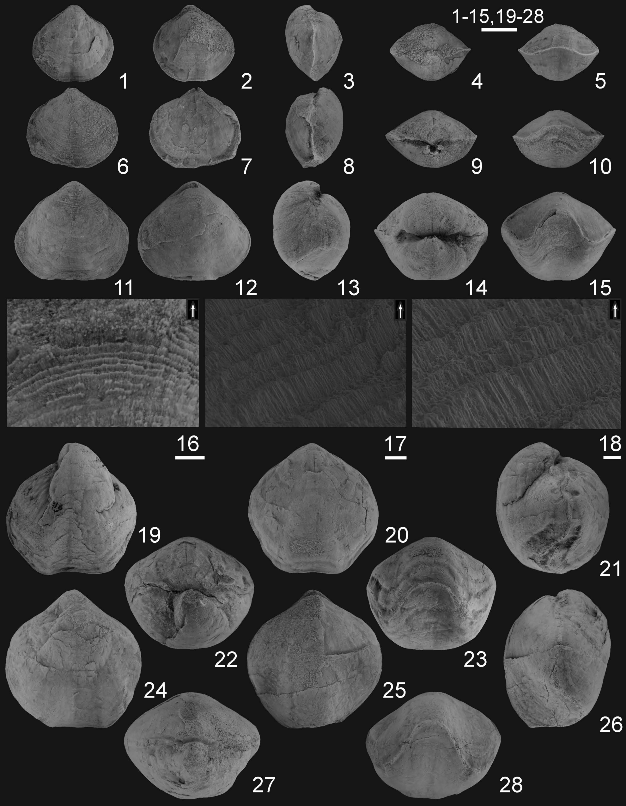

1-15
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

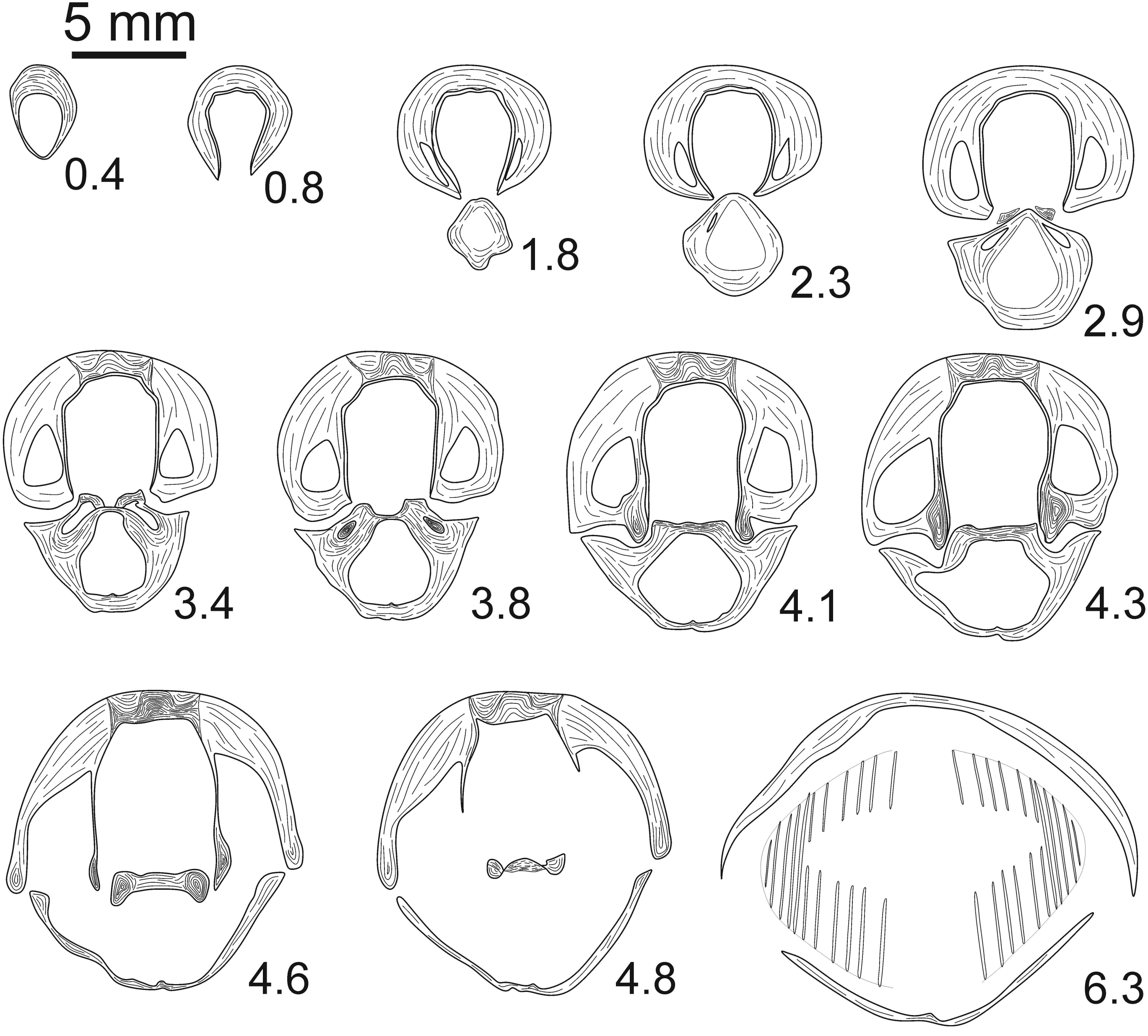


1mm
0.2
0.3
0.4
0.9
1.1
1.2
1.4
1.5
1.7
1.8
1mm
2.5
3.9

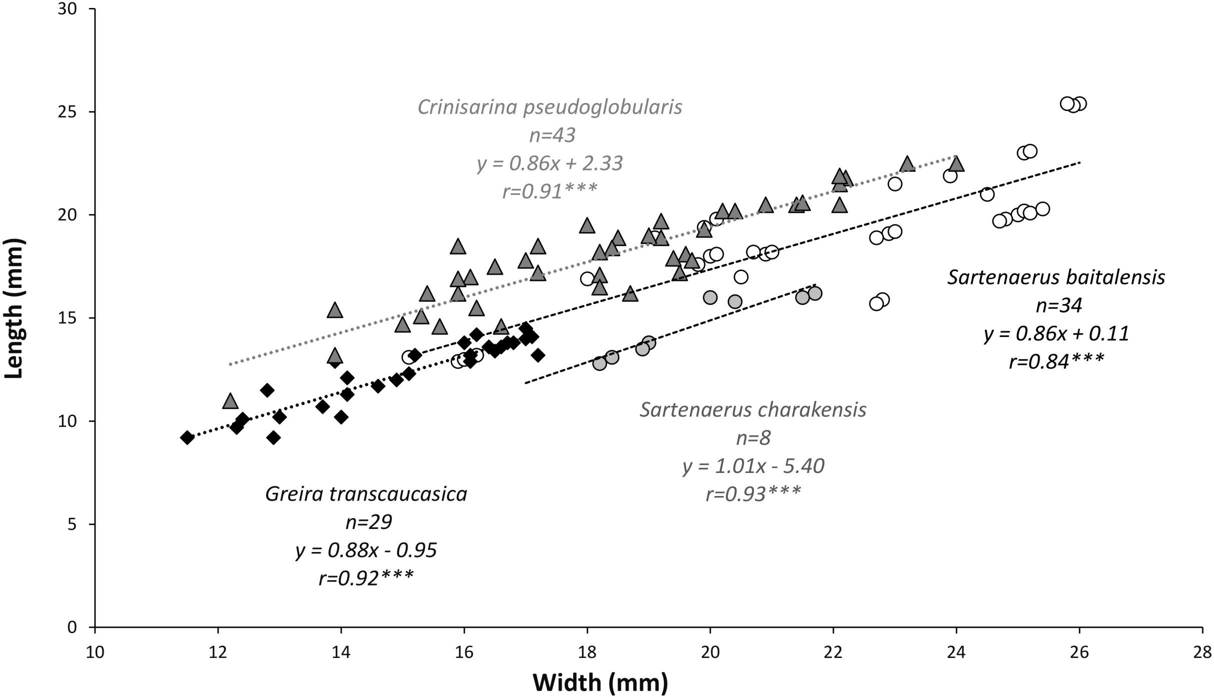

1
2
1-5
6
7
8
3
6
4
5
7
8


2mm
0.1
0.6
0.9
1.1
1.4
1.7
1.9
2mm
2.4
3.7

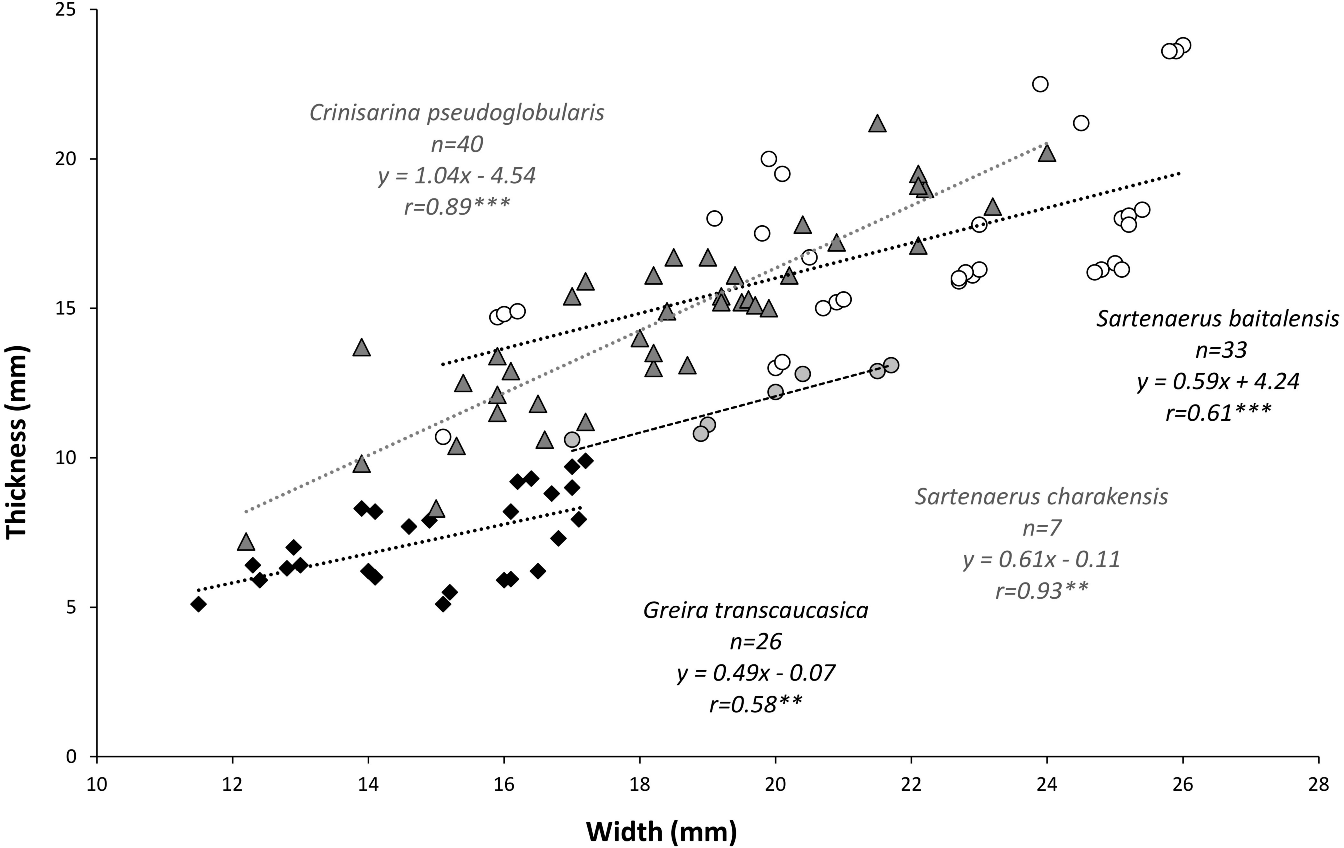

1-15,19-28
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28



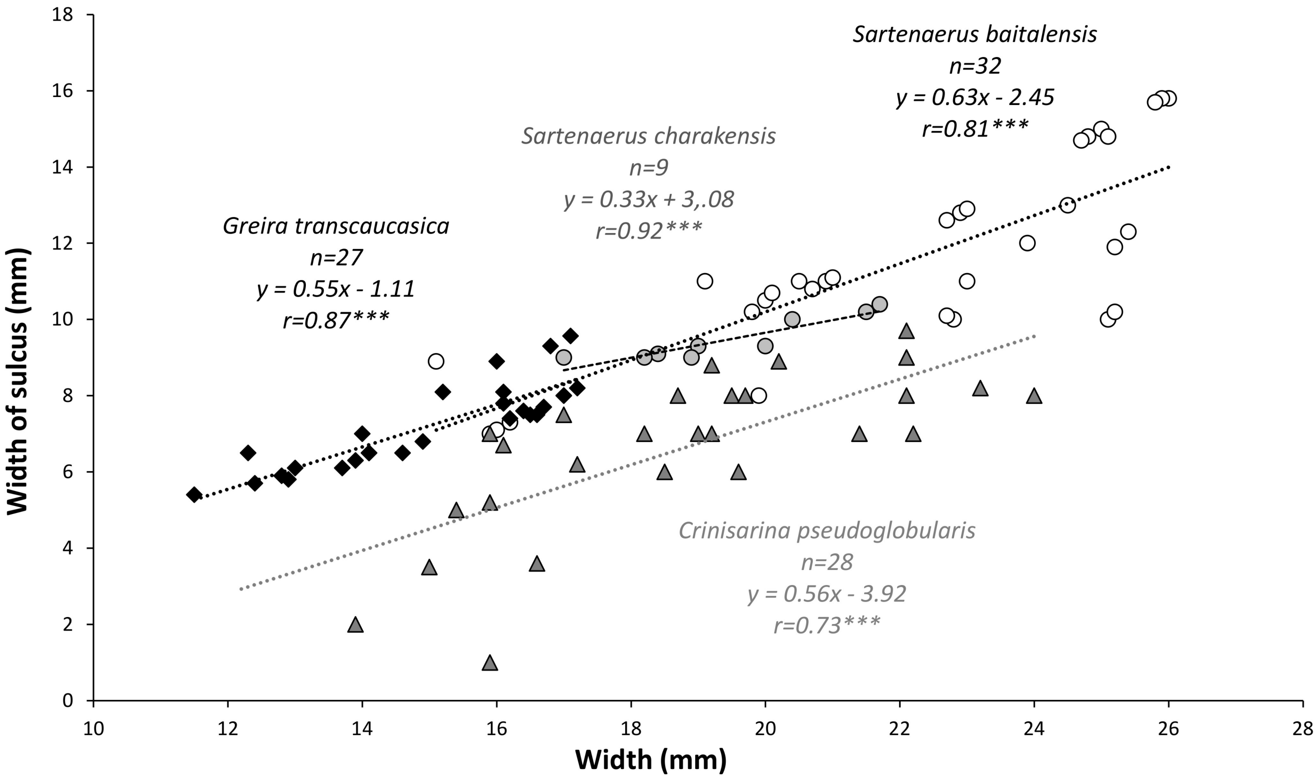
5 mm
0.4
0.8
1.8
2.3
2.9
3.4
3.8
4.1
4.3
4.6
4.8
6.3



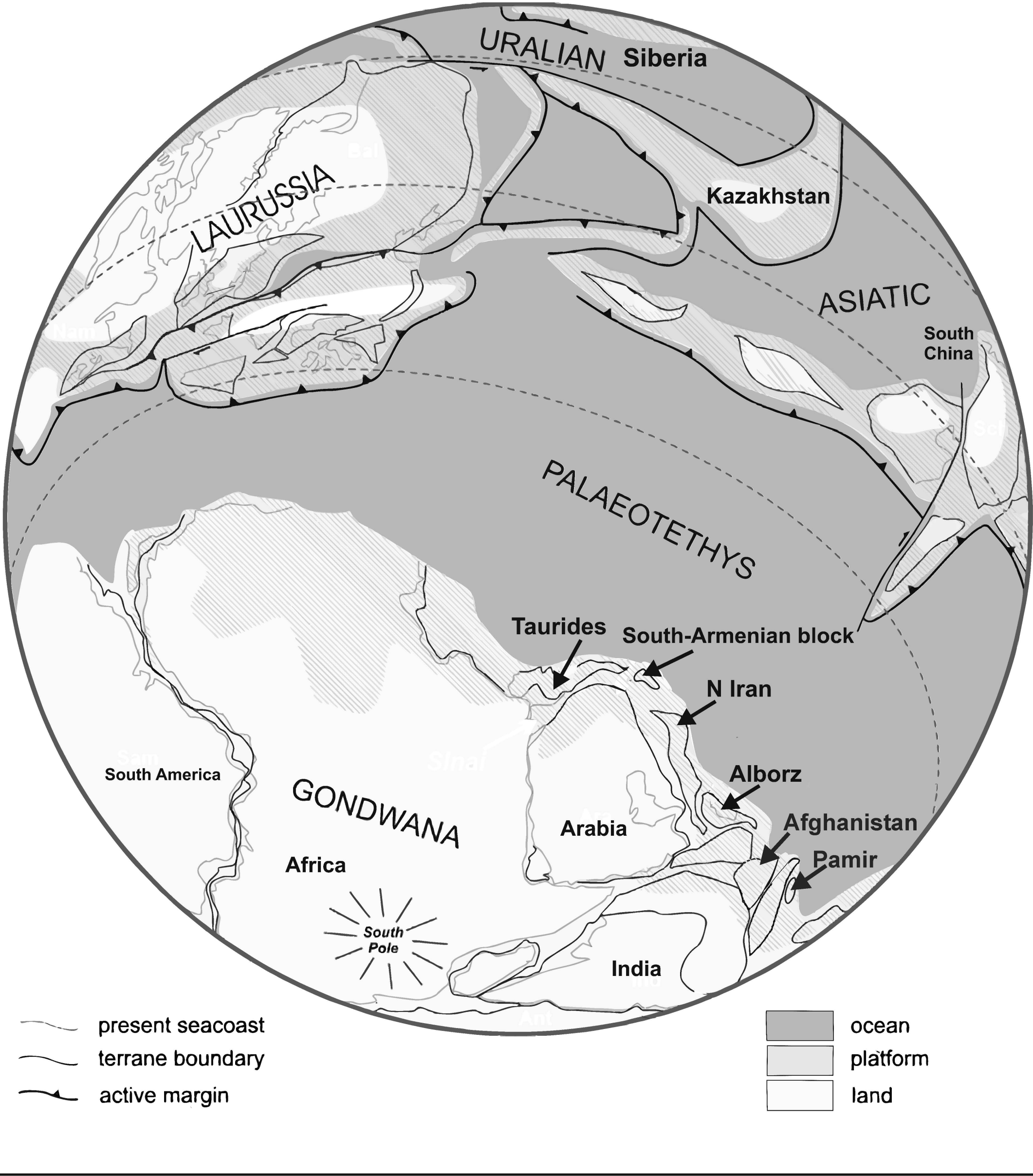
Crinisarina pseudoglobularis
n=43
y = 0.86x + 2.33
r=0.91***
Sartenaerus baitalensis
n=34
y = 0.86x + 0.11
r=0.84***
Sartenaerus charakensis
n=8
y = 1.01x - 5.40
r=0.93***
Greira transcaucasica
n=29
y = 0.88x - 0.95
r=0.92***
Length (mm)
Width (mm)
0
5
10
15
20
25
30
10
12
14
16
18
20
22
24
26
28



Crinisarina pseudoglobularis
n=40
y = 1.04x - 4.54
r=0.89***
Sartenaerus baitalensis
n=33
y = 0.59x + 4.24
r=0.61***
Sartenaerus charakensis
n=7
y = 0.61x - 0.11
r=0.93**
Greira transcaucasica
n=26
y = 0.49x - 0.07
r=0.58**
Thickness (mm)
Width (mm)
0
5
10
15
20
25
10
12
14
16
18
20
22
24
26
28



Sartenaerus baitalensis
n=32
y = 0.63x - 2.45
r=0.81***
Sartenaerus charakensis
n=9
y = 0.33x + 3,.08
r=0.92***
Greira transcaucasica
n=27
y = 0.55x - 1.11
r=0.87***
Crinisarina pseudoglobularis
n=28
y = 0.56x - 3.92
r=0.73***
Width of sulcus (mm)
Width (mm)
0
2
4
6
8
10
12
14
16
18
10
12
14
16
18
20
22
24
26
28


URALIAN
Siberia
LAURUSSIA
Kazakhstan
ASIATIC
South China
PALAEOTETHYS
Taurides
South-Armenian block
N Iran
Alborz
Afghanistan
Pamir
South America
GONDWANA
Arabia
Africa
South Pole
India
present seacoast
terrane boundary
active margin
ocean
platform
land

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	34	34	33	32	34	33	32
Mean value	21.97	19.1	17.24	11.56	0.87	0.78	0.52
Standard deviation	3.2136	3.2879	3.0715	2.5165	0.0776	0.1152	0.0663
Standard error±	±0.5511	±0.5639	±0.5347	±0.4449	±0.0133	±0.0201	±0.0117
Min	15.1	12.9	10.7	7	0.69	0.65	0.4
Max	26	25.4	23.8	15.8	0.99	1.01	0.61

Table 1. Measurements in mm and ratios of *Sartenaerus baitalensis* (Reed, 1922). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	9	8	7	9	8	7	9
Mean value	19.46	14.65	11.93	9.48	0.74	0.5	0.49
Standard deviation	1.567	1.4755	1.0704	0.563	0.0335	0.0201	0.0185
Standard error±	±0.5223	±0.5217	±0.4046	±0.1877	±0.0118	±0.076	±0.0062
Min	17	12.8	10.6	9	0.7	0.57	0.47
Max	21.7	16.2	13.1	10.4	0.8	0.63	0.53

Table 2. Measurements in mm and ratios of *Sartenaerus charakensis* (Brice, 1967). Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	29	28	26	27	28	26	27
Mean value	15.1	12.3	7.28	7.21	0.82	0.49	0.48
Standard deviation	1.719	1.6487	1.474	1.1151	0.0455	0.0773	0.0355
Standard error±	±0.3192	±0.3115	±0.289	±0.2146	±0.0086	±0.0172	±0.0068
Min	11.5	9.2	5.1	5.4	0.71	0.33	0.45
Max	14.5	34.1	9.9	9.57	0.93	0.6	0.56

Table 3. Measurements in mm and ratios of *Greira transcaucasica* Erlanger, 1993

Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

	W	L	T	Ws	L/W	T/W	Ws/W
Number of individuals	43	43	40	27	43	40	27
Mean value	18.36	18.03	14.69	6.64	0.98	0.79	0.35
Standard deviation	2.7128	2.5439	3.1965	2.1134	0.0641	0.0959	0.0938
Standard error±	±0.4137	±0.3879	±0.5054	±0.4067	±0.0098	±0.0152	±0.0181
Min	12.2	11	7.2	1	0.87	0.55	0.06
Max	24	22.5	21.2	9.7	1.16	0.99	0.46

Table 4. Measurements in mm and ratios of *Crinisarina pseudoglobularis* sp. nov. Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus.

Appendix 2

Vahram Serobyan, Taniel Danelian, Catherine Crônier,

Araik Grigoryan and Bernard Mottequin (in press)

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

Comptes Rendus Palevol

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

VAHRAM SEROBYAN [a, b,*], TANIEL DANELIAN [b], CATHERINE CRÔNIER [b], ARAIK GRIGORYAN [a], BERNARD MOTTEQUIN [c]

[a] Institute of Geological Sciences of the National Academy of Sciences of the Republic of Armenia–Yerevan, Armenia, 24A, Marshal Baghramyan Avenue, Yerevan 0019, Republic of Armenia

[b] Univ. Lille, CNRS, UMR 8198–Evo–Eco–Paleo, F–59000 Lille, France

[c] O.D. Earth and History of Life, Royal Belgian Institute of Natural Sciences, rue Vautier 29, B 1000 Brussels, Belgium

Abstract

The new genus *Aramazdospirifer* (Cyrtospiriferidae) is erected to include *Spirifer orbelianus* Abich, 1858 from the lower Famennian of Central Armenia as its type species and to resolve long standing issues related to the generic affinity 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) 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.

Keywords

Brachiopoda; Spiriferida; lower Famennian; Gondwana; Armenia.

* Corresponding author. vahram.serobyan@univ-lille.fr, vahramserobyan@gmail.com (V. Serobyan)

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

Le nouveau genre *Aramazdospirifer* (Cyrtospiriferidae) est ici érigé, afin d'inclure *Spirifer orbelianus* Abich, 1858 du Famennien inférieur d'Arménie centrale comme son espèce type et résoudre ainsi des discussions de longue date sur l'affinité générique 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) 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.

1. 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), which remain 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 spiriferide species *Spirifer orbelianus*. 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 an up–to–date 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* Abich, 1858 on the basis of recently collected material from the lower Famennian of Central Armenia, with implications for its palaeobiogeographic distribution.

2. Stratigraphic and palaeogeographic settings

In the southern part of Central Armenia crops out a ca. 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 individualized 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 Serobyan *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 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 and 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 and Mamedov (2000) and correlated with the international conodont biozonation based on the conodont study of Aristov (1994) carried out in Nakhichevan.

3. Material and methods

The examined material was collected from the Noravank, Ertych and Djravank 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 and 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 Institute of Geological Sciences of the National Academy of Sciences of Armenia, Yerevan (IGSNASRAGM). Some specimens are deposited at the Royal Belgian Institute of natural Sciences, Brussels (RBINS) and others at the University of Lille (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. The internal structure of the newly collected articulated specimens identified as *A. orbelianus* (Abich, 1858) 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.

4. Systematic palaeontology

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 and Termier, 1949

Family Cyrtospiriferidae Termier and Termier, 1949

Subfamily Cyrtospiriferinae Termier and Termier, 1949

Genus *Aramazdospirifer* gen. nov.

***Type species*:** *Spirifer orbelianus* Abich, 1858.

***Other species*:** It is currently difficult to assign other species to *Aramazdospirifer* gen. nov. with certainty in the absence of taxonomical revisions of the diverse cyrtospiriferide fauna from the Famenian 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, cubcircular tongue and lacks median and longitudinal elevations in sulcus and fold. It is worth nothing that the real *aperturatus* from Germany and the Franco–Belgian basin differs from

Nalivkin's species and does not belong to *Aramazdospirifer* gen. nov. (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* gen. nov. 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 *Aramadzospirifer*.

***Etymology*:** In honor of Aramazd, who was the chief god in pre–Christian Armenian mythology.

***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.

Remarks: *Aramazdospirifer* gen. nov. is included in the Superfamily Cyrtospiriferoidea 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 and Day (2000), is still pending, *Aramazdospirifer* gen. nov. 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* gen. nov. shares indeed several external and internal characters with *Uchtospirifer* Ljaschenko, 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 and triangular ventral interarea, divergent dental plates, and an unsupported ctenophoridium. However, *Aramazdospirifer* gen. nov. 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* gen. nov. 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* gen. nov. 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* gen. nov. 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 submesothyrid foramen. Additionally, *Aramazdospirifer* gen. nov. 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* gen. nov.

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* gen. nov. possesses an unsupported ctenophoridium, while the latter is supported by an apical callosity in many *Cyrtospirifer* representatives.

Aramazdospirifer gen. nov. is distinguished externally from *Lamarckispirifer* Gatinaud, 1949 *sensu* Ma and Day (2007), known from the lower Famennian of South China, 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* gen. nov. 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* gen. nov.

Aramazdospirifer gen. nov. can be distinguished from the genus *Pseudocyrtiopsis* Ma and 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* gen. nov. differs by its unsupported ctenophoridium.

Aramazdospirifer orbelianus (Abich, 1858)

Figures 3–7, Table 1

1858 *Spirifer Orbelianus*, nov. sp. Abich, p. 438, 440, 524–525, pl. 1, figs. 2–3; pl. 2, figs. 4–5.

1948 *Cyrtospirifer orbelianus* (Abich); Rzhonsnitskaya, p. 1480.

1952 *Cyrtospirifer orbelianus* (Abich); Arakelyan, p. 40, 42.

1957 *Cyrtospirifer orbelianus* (Abich, 1858); Abrahamyan, p. 70, pl. 8, fig. 3.

1964 *Cyrtospirifer orbelianus* (Abich, 1858); Arakelyan, p.75, 77, 82, 94.

1973 *Cyrtospirifer orbelianus* (Abich, 1858); Abrahamyan *et al*., p. 218.

1974 *Cyrtiopsis orbelianus* (Abich, 1858); Abrahamyan, p. 60, pl. 22, figs. 2–3.

1974 *Spirifer orbelianus* Abich, H., 1858; Sartenaer, p. 10 (only the Armenian specimens).

1975 *Cyrtiopsis orbelianus* (Abich, 1858); Arakelyan *et al*., p. 24.

2000 *Cyrtiopsis orbelianus* (Abich, 1858); Rzhonsnitskaya and Mamedov, p. 331, table 1.

2018a *Uchtospirifer orbelianus* (Abich, 1858); Afanasjeva in Alekseeva *et al*., pl. 30, fig. 4; text–fig. 103.

2018b *Uchtospirifer orbelianus* (Abich, 1858); Grechishnikova in Alekseeva *et al*., p. 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 3.9–14. 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 (1957), as well as the '*Cyrtiopsis*' *orbelianus*–'*Cyrtiopsis*' *armenicus* Zone of Rzhonsnitskaya and 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* is restricted to the lower Famennian (possibly corresponding to the equivalent of the *Palmatolepis crepida*–*P. glabra pectinata* conodont zones of Spalleta *et al.* (2017)). Previously this species has been observed in Armenia in the Argichi, Lanjanist (Kadrlu), 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* 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*. 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 Djravank (sixty articulated specimens and ten ventral valves), Noravank (type locality; twelve articulated specimens and four dorsal valves) and Ertych (eight articulated specimens and one 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 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* 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* are also presented in table 1 and figure 7. The length of the dorsal valve shows less dispersed values (Fig. 7).

5. Discussion

Aramazdospirifer orbelianus 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, p. 524) indicated that '*Sp. Orbelianus* ist bis jetzt nur in dem Baranco des Erhebungsthales 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 (e.g. 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, p. 32, p. 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 and 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* was reported extensively by Abrahamyan (1957, 1974), Abrahamyan *et al*. (1973) and Arakelyan (1952, 1964). Abrahamyan (1957) assumed that *A. orbelianus* could be a sister species of '*Cyrtiopsis*' *armenicus* as the latter appeared in aslightly 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* from Africa, the Franco–Belgian basin and Iran. He rightly concluded that none of them corresponds to Abich's species. In sum, *A.*

orbelianus is known only from the South–Armenian Block (Central Armenia and possibly Nakhichevan).

6. 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*. *A. orbelianus* (Abich, 1858) 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,* 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 and Brice, 2019).

Acknowledgments

The Ph.D. studies of V. Serobyan in France are funded by the French Embassy in Yerevan and the MOBLILEX International Mobility Grant Programme of the University of Lille. T. Danelian and A. Grigoryan are grateful to the Erasmus Programme for funding their staff mobility in 2018 and 2019, respectively. Fieldwork was also facilitated by the logistic support of the Institute of Geological Sciences (Armenian Academy of Sciences). The authors thank the Région Hauts–de–France, and the Ministère de l’Enseignement Supérieur et de la Recherche (CPER Climibio), and the European Fund for Regional Economic Development for their financial support. Sylvie Régnier (UMR Evo–Evo–Paleo, ULille) and Julien Cillis (RBINS, Brussels) are gratefully acknowledged for the high–quality SEM pictures obtained on specimens deposited at IGNASRAGM and at the RBINS, respectively. Daria Bezgodova is thanked for kindly providing information about Abich's collection. Constructive remarks by Jed Day, Elena Sokiran and an anonymous reviewer improved the initial manuscript. The authors are also grateful to E. Sokiran for her advice on literature related to brachiopod genera described from the ex–USSR.

References

Abich, H., 1858. Vergleichende geologische Grundzüge der Kaukasischen, Armenischen und Nordpersischen Gebirge. Prodromus einer Geologie der Kaukasischen Länder. Mémoires de l'Académie impériale des Sciences de Saint–Pétersbourg, 6ème série, Sciences mathémathiques et physiques, 7, 359–534.

Abrahamyan, M.S., 1957. Brakhiopody verkhnefamenskikh i etrenskikh otlozhenii yugozapadnoi Armenii (Brachiopods of the Upper Famennian and Etroeungt deposits of the South–Western Armenia). Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk, Yerevan, 142 p. (in Russian).

Abrahamyan, M.S., 1964. Karbon (The Carboniferous). In: Mkrtchian, S.S., Vardaniants, L.A., Gabrielian, A.A., Maghakian, I.G., Paffenholz, C.N (Eds.). Geologiya Armyanskoy SSR (Geology of the Armenian USSR). Akademiya Nauk Armyanskoy SSR, Yerevan, 2, pp. 96–118 (in Russian).

Abrahamyan, M.S., 1974. Opisanie fauny, Devonskaya sistema, Tip Brachiopoda, Brakhiopody (Description of fauna, Devonian System, Phylum Brachiopoda, brachiopods). In: Akopian, V.T. (Ed.), Atlas iskopaemoy fauny Armyanskoy SSR (Atlas of the fossil fauna of the Armenian SSR). Akademiya Nauk Armyanskot SSR, Institut Geologyiceskih Nauk, Yerevan, pp. 48–64 (in Russian).

Abrahamyan, M.S., Arakelyan R.A., Azizbekov Sh.A., 1973. Malyy Kavkaz (Yuzhnoye Zakavkaz'ye) (Lesser Caucasus (South Transcaucasia)). In: Rzhonsnitskaya, M.A. (Ed.), Kavkazkaya geolsinklinal'naya oblast'i Predkavkaz'e (Caucasus geosynclinal region and Ciscaucasia). In Nalivkin, D.V., Rzhonsnitskaya, M.A., Markovski, B.P. (eds.): Stratigrafiya SSSR, Devonskaya sistema (Stratigraphy of the USSR, the Devonian system). Nedra, Moscow, 1, pp. 210–219 (in Russian).

Abrahamyan, M.S., Arakelyan, R.A., Papoyan, A.S., 1975. Granitsa Devona i Nizhnego Karbona (The Devonian and Lower Carboniferous boundary). In: Stratigrafiya Karbona i Geologiya Uglenosnykh Formatsii SSSR (Stratigraphy of the Carboniferous and Geology of Coal–bearing Formations of the USSR). Nedra, Moscow, pp. 49–55 (in Russian).

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., Pakhnevich, A.V., 2018a. Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia (Ending). Paleontological Journal, 52/9, 969–1085, doi.org/10.1134/S0031030118090010

Alekseeva, R.E., Afanasjeva, G.A., Grechishnikova, I.A., Oleneva, N.V., Pakhnevich, A.V., 2018b. Devonian and Carboniferous Brachiopods and Biostratigraphy of Transcaucasia. Paleontological Journal, 52/8, 829–967, doi.org/10.1134/S0031030118080014

Arakelyan, R.A., 1952. Stratigrafiya paleozoyskikh otlozheniy yugo–zapadnoy Armenii i prilegayushchikh chastey Nakhichevanskoy ASSR (Stratigraphy of the Palaeozoic deposits of southwestern Armenia and the adjacent parts of the Nakhichevan ASSR). Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk, Yerevan, 142 p. (in Russian).

Arakelyan, R.A., 1964. Devon (The Devonian). In: Mkrtchian S.S., Vardaniants L.A., Gabrielian A.A., Maghakian I.G., Paffenholz C.N. (Eds.). Geologiya Armyanskoy SSR (Geology of the Armenian USSR). Akademiya Nauk Armyanskoy SSR, Yerevan, 2, pp. 46–96 (in Russian).

Arakelyan, R.A., Malxasyan, E.G., Mkrtchyan, C.C., Paffenholz, C.N., 1975. Geologicheskiy ocherk Armyanskoy CCP (Geological sketch of the Armenian SSR). Akademiya Nauk Armyanskoy SSR, Institut Geologyiceskih Nauk, Yerevan, 175 p. (in Russian).

Aristov, V.A., 1994. Konodonty devona–nizhnego karbona Evrazii: soobshchestva, zonalnoye raschleneniye, korrelyatsiya raznofatsialnykh otlozheniy (Conodonts from the Devonian and Lower Carboniferous of Eurasia: communities, zonation and correlation of heterofacial deposits). Proceedings of the Geological Institute of the Russian Academy of Sciences 484, 1–193 (in Russian).

Aristov, V.A., Gretschischnikova, I.A., Tschigova, V.A., Felix, V.P., 1979. Subdivision and correlation of the Famennian and the lower Tournaisian deposits of Transcaucasia (on brachiopods, conodonts and ostracods). Geological Survey of Belgium, Professional Paper 161, 91–95.

Bonnet, P., 1947. Description géologique de la Transcaucasie méridionale (chaînes de l’Araxe moyen). Mémoires de la Société géologique de France, nouvelle série 25/53, 1–62.

Carter, J.L., Johnson, J.G., Gourvennec, R., Hou, H.F., 2006. Spiriferida. In: Kaesler, R.L. (Ed.), Treatise on invertebrate paleontology: part H, Brachiopoda, revised, 5.Geological Society of America, and University of Kansas, Boulder, Colorado, and Lawrence, Kansas, pp. 1689–1870.

Feliks, V.P., Grechishnikova, I.A., Levitskii, E.S., Nagiev, V.N., 1980. Novyye dannyye o geologii rudnika Gyumyushlung (New data on the geology of the Gyumushlug mine). Izvestiya vysshikh uchebnykh zavedeniy. Geologiya i razvedka 2, 69–73 (in Russian).

Frederiks, G.N., 1924. O verkhnekamennougol’nykh spiriferidakh Urala (On the Upper Carboniferous spiriferids of the Urals. Izvestiya Geologicheskogo Komiteta 38 (1919), 295–324 (in Russian).

Gatinaud, G., 1949. Contribution à l’étude des Brachiopodes Spiriferidae. I.–Exposé d’une nouvelle méthode d’étude de la morphologie externe des Spiriferidae à sinus plissé. Bulletin du Museum National d’Histoire Naturelle, série 2/4, 487–492.

Gosselet, J., 1874. Carte géologique de la bande méridionale des calcaires dévoniens de l’Entre Sambre–et–Meuse. Bulletin de l’Académie royale des Sciences, des Lettres et des Beaux–Arts de Belgique, 2ème série 37, 81–114.

Gosselet, J., 1880. Esquisse géologique du Nord de la France et des contrées voisines. 1er fascicule. Terrains primaires, Imprimerie Six–Horemans, Lille, 167 p.

Gosselet, J., 1894. Étude sur les variations du *Spirifer Verneuili* et sur quelques espèces voisines. Mémoires de la Société géologique du Nord 4, 1–61.

Grechishnikova, I.A., 1986. Novyye devonskiye spiriferidy Zakavkaz’ye (New Devonian spiriferides of Transcaucasia). Zapiski Gornogo Instituta 107, 52–60 (in Russian).

Johnson, J.G., 2006. Cyrtospiriferoidea. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology: Part H, Brachiopoda, Revised, 5. Geological Society of America, and University of Kansas, Boulder, Colorado, and Lawrence, Kansas, pp. 1722–1732.

Liashenko, A. I., 1957. Novyi rod Devonskikh brakhiopod *Uchtospirifer* (A new genus of Devonian brachiopods: *Uchtospirifer*). Akademiia Nauk SSSR, Doklady 117/ 5, 885–888 (in Russian).

Ma, X. –P., Day, J., 1999. The late Devonian brachiopod *Cyrtiopsis davidsoni* Grabau 1923, and related forms from central Hunan of South China. Journal of Paleontology 73, 608–624, doi.org/10.1017/S0022336000032431

Ma, X. –P., Day, J., 2000. Revision of *Tenticospirifer* Tien, 1938, and morphologically similar spiriferid brachiopod genera from the Late Devonian (Frasnian) of Eurasia, North America, and Australia. Journal of Paleontology 74, 444–463, doi.org/10.1017/S0022336000031711

Ma, X. –P., Day, J., 2007. Morphology and revision of Late Devonian (Early Famennian) Cyrtospirifer (Brachiopoda) and related genera from South China and North America. Journal of Paleontology 81, 286–311, doi.org/10.1666/0022-3360(2007)81[286:MAROLD]2.0.CO;2

Mamedov, A.B., Rzhonsnitskaya, M.A., 1985. Devonian of the south Transcaucasus: Zonal subdivision, boundaries of series and stages, correlation. Courier Forschungsinstitut Senckenberg 75, 135–156.

Milanovsky, E.E., 2007. Hermann Abich (1806–1886): the “Father of Caucasian Geology” and his travels in the Caucasus and Armenian Highlands. Geological Society, London, Special Publications 287, 177–181, doi.org/10.1144/SP287.14

Mottequin, B., 2019. An annotated catalogue of types of Silurian–Devonian brachiopod species from southern Belgium and northern France in the Royal Belgian Institute of Natural Sciences (1870–1945), with notes on those curated in other Belgian and foreign institutions. Geologica Belgica 22 (1–2), 47–89, doi.org/10.20341/gb.2019.005

Mottequin, B., Brice, D., 2019. Reappraisal of some Upper Devonian (Famennian) spiriferide brachiopods from the Band–e Bayan Domain (Afghanistan). Geobios, 52, 47–65, doi.org/10.1016/j.geobios.2018.11.003

Nalivkin, D.V.,1930. Brakhiopody verkhnego i srednego devona Turkestana (Brachiopods from the Upper and Middle Devonian of Turkestan), Trudy Geologicheskogo Komiteta. Novaya seriya, 180, 1–221 (in Russian).

Oleneva, N.V., 2016. Devonian Brachiopods of the Orders Spiriferida and Spiriferinida of the European Russia and Transcaucasia: Systematics, Shell Microstructure. Paleontological Journal, 50 (11), 1207–1296, doi:10.1134/S0031030116110010

Reed, F.R.C., 1922. Devonian fossils from Chitral and the Pamirs. Memoirs of the Geological Survey of India. Palaeontologia Indica, 6/2, 1–134.

Rzonsnitskaya, M.A., 1948. Devonskiye otlozheniya Zakavkaz'ye (Devonian deposits of Transcaucasia). Doklady Akademy Nauk SSSR, 59/ 8, 1477–1480 (in Russian).

Rzhonsnitskaya, M.A., Mamedov, A.B., 2000. Devonian stage boundaries in the southern Transcaucasus. Courier Forschungsinstitut Senckenberg, 225, 329–333.

Sartenaer, P., 1974. Signification stratigraphique du 'niveau des monstres' du Frasnien franco–belge. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 50/7, 1–19.

Serobyan, V., Grigoryan, A., Mottequin, B., Mayilyan, R., Crônier, C., Danelian, T., 2019. Biostratigraphy of the Upper Devonian trigonirhynchiid brachiopods (Rhynchonellida) from Armenia. Proceedings of National Academy of Sciences of the Republic of Armenia. Earth Sciences, 72/2, 3–18.

Sidjachenko, A.I., 1962. Spiriferidy i stratigrafiya famenskikh otlozheniy tsentral'nogo i yugo–vostochnogo Karatau (Spiriferides and stratigraphy of the Famennian deposits of the Central and Southeasthern Kara–Tau). Akademiya Nauk SSSR, Sibirskoje otdelenie, Moskva, 147 p. (in Russian).

Sokiran, E. V., 2006. Early–Middle Frasnian cyrtospiriferid brachiopods from the East European Platform. Acta Palaeontologica Polonica, 51/4, 759–772.

Sosson, M., Rolland, Y., Müller, C., Danelian, T., Melkonyan, R., Kekelia, S., Adamia, S., Babazadeh, V., Kangarli, T., Avagyan, A., Galoyan, G., Mosar, J., 2010. Subductions, obduction and collision in the Lesser Caucasus (Armenia, Azerbaijan, Georgia), new insights. In: M. Sosson, N. Kaymakci, R. A. Stephenson, F. Bergerat, V. Starostenko, (Eds), Sedimentary Basin

Tectonics from the Black Sea and Caucasus to the Arabian Platform. Geological Society, London, Special Publications, 340, pp. 329–352, doi.org/10.1144/SP340.14

Spaletta, C., Perri, M.C., Over, D.J., Corradini, C., 2017. Famennian (Upper Devonian) conodont zonation: revised global standard. Bulletin of Geosciences, 92, 31–57.

Termier, H., Termier, G., 1949. Essai sur l'évolution des Spiriféridés. Notes et Mémoires, Service géologique, Division des Mines et de la Géologie (Maroc), 74, 85–112.

Waagen, W.H., 1883. Salt Range fossils, I. *Productus*–Limestone Fossils. Brachiopoda. Palaeontologia Indica, Series, 13–14, 391–546.

Figure 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).

Figure 1. Carte géologique schématique du Bloc Sud–Arménien; distribution des dépôts du Dévonien supérieur–Carbonifère inférieur avec localisation des coupes contenant *Aramazdospirifer orbelianus* (Abich, 1858).

Figure 2. Biostratigraphic scheme of the Lower Famennian of the Lesser Caucasus (Transcaucasus) correlated with the major lithostratigraphic units.

Figure 2. Schéma biostratigraphique du Famennien inférieur de la partie méridionale du Petit Caucase (Transcaucasie) corrélé avec les principales unités lithostratigraphiques.

Figure 3. *Aramazdospirifer orbelianus* (Abich, 1858). 1–6 and 18–20. Almost complete specimen (IGSNASRAGM 3895/PS 3001) from the Djravank section in ventral, dorsal, posterior, lateral, posterodorsal and anterior views (1–6), close–up of micro–ornament (capillae and growth lines) on dorsal valve (close to anterior margin; 18–20). 7–8. Incomplete specimen (IGSNASRAGM 3896/PS 3002) from the Noravank section, close–up of the ventral interarea (delthyrium; 7). 9–14. Almost complete specimen (IGSNASRAGM 3897/AB97/48; neotype, Noravank section) in ventral, dorsal, posterodorsal, posterior, anterior and lateral views. 15–22. Almost complete specimen (IGSNASRAGM 3898/PS 3004) from the Ertych section in ventral, dorsal, lateral, posterior and anterior views. 23–27. Almost complete juvenile specimen (IGSNASRAGM 3899/PS 3005) from the Djravank section in ventral, dorsal, posterior, anterior and lateral views. Scale bars: 10 mm (1– 6, 9–14, 15–17, 21–27), 2 mm (7), 5 mm (8), 200 µm (18), 400µm (19), 500 µm (20).

Figure 3. *Aramazdospirifer orbelianus* (Abich, 1858). 1–6 et 18–20. Spécimen quasi–complétement (IGSNASRAGM 3895/PS 3001) de la coupe de Djravank en vues ventrale, dorsale, postérieure, latérale, postérodorsale et antérieure (1–6), vue de détail de la micro–ornementation (capillae et lignes de croissance) sur la valve dorsale (proche de la marge antérieure 18–20). 7–8. Spécimen incomplet (IGSNASRAGM 3896/PS 3002) de la coupe de Noravank, vue de détail de l’interarea ventrale (delthyrium; 7). 9–14. Spécimen articulé quasi complet (IGSNASRAGM 3897/AB97/48; néotype, coupe de Noravank) en vues ventrale,

dorsale, postérodorsale, postérieure, antérieure et latérale. 15–22. Spécimen quasi complet (IGSNASRAGM 3898/PS 3004) de la coupe d'Ertych en vues ventrale, dorsale, latérale, postérieure et antérieure. 23– 27. Spécimen juvénile quasi complet (IGSNASRAGM 3899/PS 3005) de la coupe de Djravank en vues ventrale, dorsale, postérieure, antérieure et latérale. Echelles: 10 mm (1–6, 9–14, 15–17, 21–27), 2 mm (7), 5 mm (8), 200 µm (18), 400µm (19), 500 µm (20).

Figure 4. *Aramazdospirifer orbelianus* (Abich, 1858) the Ertych section. The arrows indicate the anterior margin. 1–7. 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. 8–11. 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. 12–13. Poorly preserved articulated specimen (RBINS a13461), view of the ventral area showing the pseudodeltidium and close–up of the latter. Scale bars: 10 mm (1–3, 8–9), 5 mm (4–5, 10, 13), 5 mm (12), 2 mm (11), 1 mm (6, 7).

Figure 4. *Aramazdospirifer orbelianus* (Abich, 1858) de la coupe d'Ertych. Les flèches indiquent le bord antérieure. 1–7. Spécimen quasi complet (RBINS a13459) en vue ventrale (les régions du muscle et des longues plaques dentaires intrabasinales sont visibles), vues dorsale et antérolatérale, vue de près du pseudodeltidium et détail de la micro–ornamentation capillate observée au niveau du sulcus près de la marge antérieure. 8–11. Spécimen incomplet (RBINS a13460) en vues ventrale (légèrement inclinée montrant les plaques dentaires intrasinales et le plissement médian au niveau du sulcus) et dorsale, vue de détail du myophragme, et détail de la micro–ornementation capillate observée sur le côté gauche de la valve dorsale. 12–13. Spécimen articulé mal préservé (RBINS a13461), vue de la région ventrale montrant le pseudodeltidium et vue de près de ce dernier. Echelles:10 mm (1–3, 8–9), 5 mm (4– 5, 10, 13), 5 mm (12), 2 mm (11), 1 mm (6, 7).

Figure 5. Transverse serial sections of *Aramazdospirifer orbelianus* (Abich, 1858) from the Djravank section. Numbers refer to distances in mm from the tip of the ventral umbo. Scale bars: 5 mm.

Figure 5. Coupes sériées transversales de *Aramazdospirifer orbelianus* (Abich, 1858) de la coupe de Djravank. Les chiffres se réfèrent à des distances en mm de l'extrémité de l'umbo ventral. Echelle: 5 mm.

Figure 6. Scatter diagrams of *Aramazdospirifer orbelianus* (Abich, 1858). Abbreviations: N, number of specimens measured; p: probability value; r: coefficient of correlation. 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.

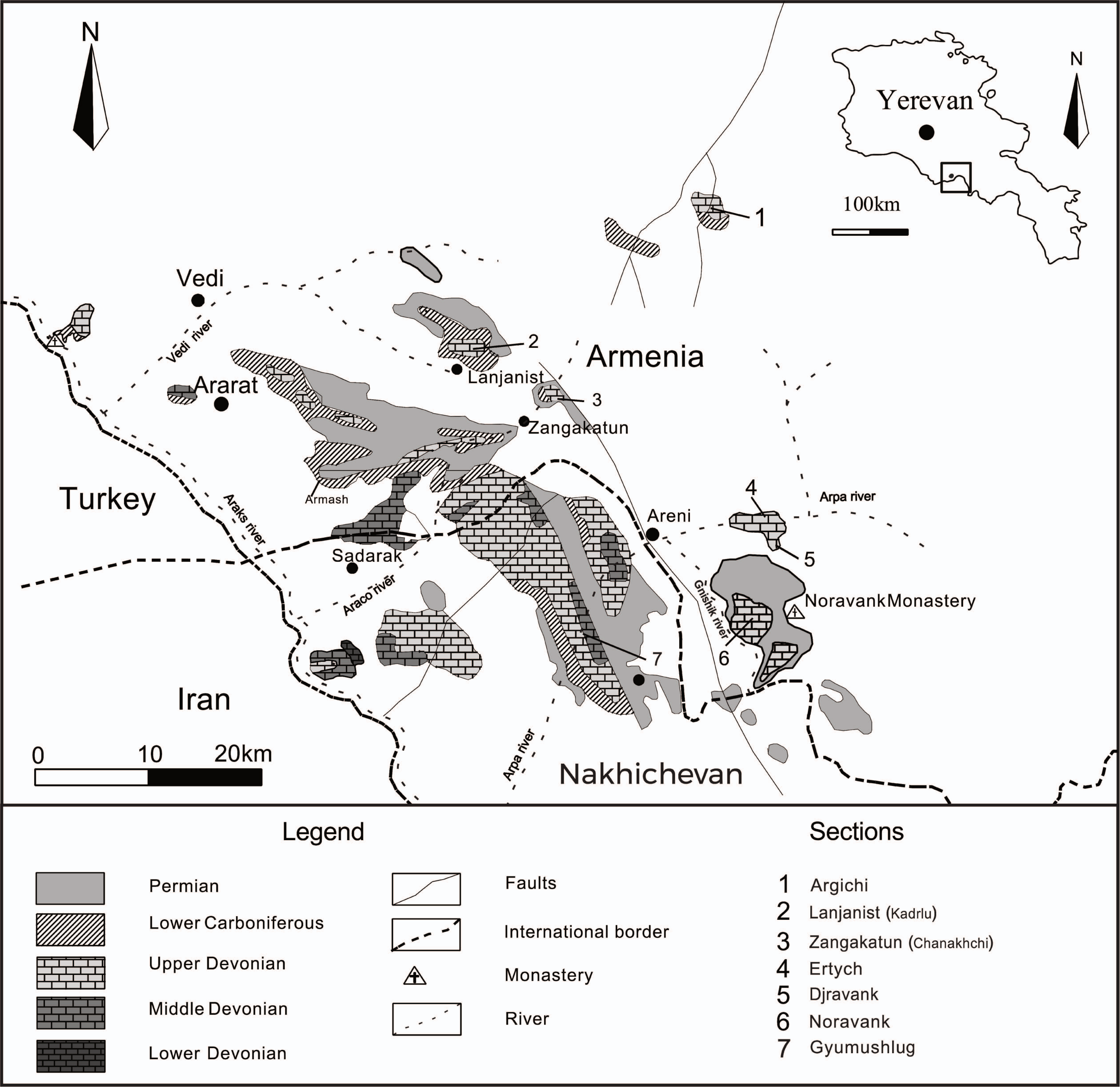
Figure 6. Diagrammes de dispersion d'*Aramazdospirifer orbelianus* (Abich, 1858). Abréviations: N, nombre de spécimens mesurés; p: valeur de probabilité; r: coefficient de corrélation. 1, Relation entre la largeur et la longueur de la coquille. 2, Relation entre la largeur et l'épaisseur de la coquille. 3, Relation entre la largeur de la coquille et la largeur du sulcus. 4, Relation entre la largeur et la longueur de la valve dorsale.

Figure 7. Measurements and ratios in mm of *Aramazdospirifer orbelianus* (Abich, 1858) 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.

Figure 7. Mesures et rapports en mm de *Aramazdospirifer orbelianus* (Abich, 1858) Abréviations: W–largeur de la coquille, L–longueur de la coquille, T–épaisseur de la coquille, Ws–largeur du sulcus, dL–longueur de la valve dorsale.

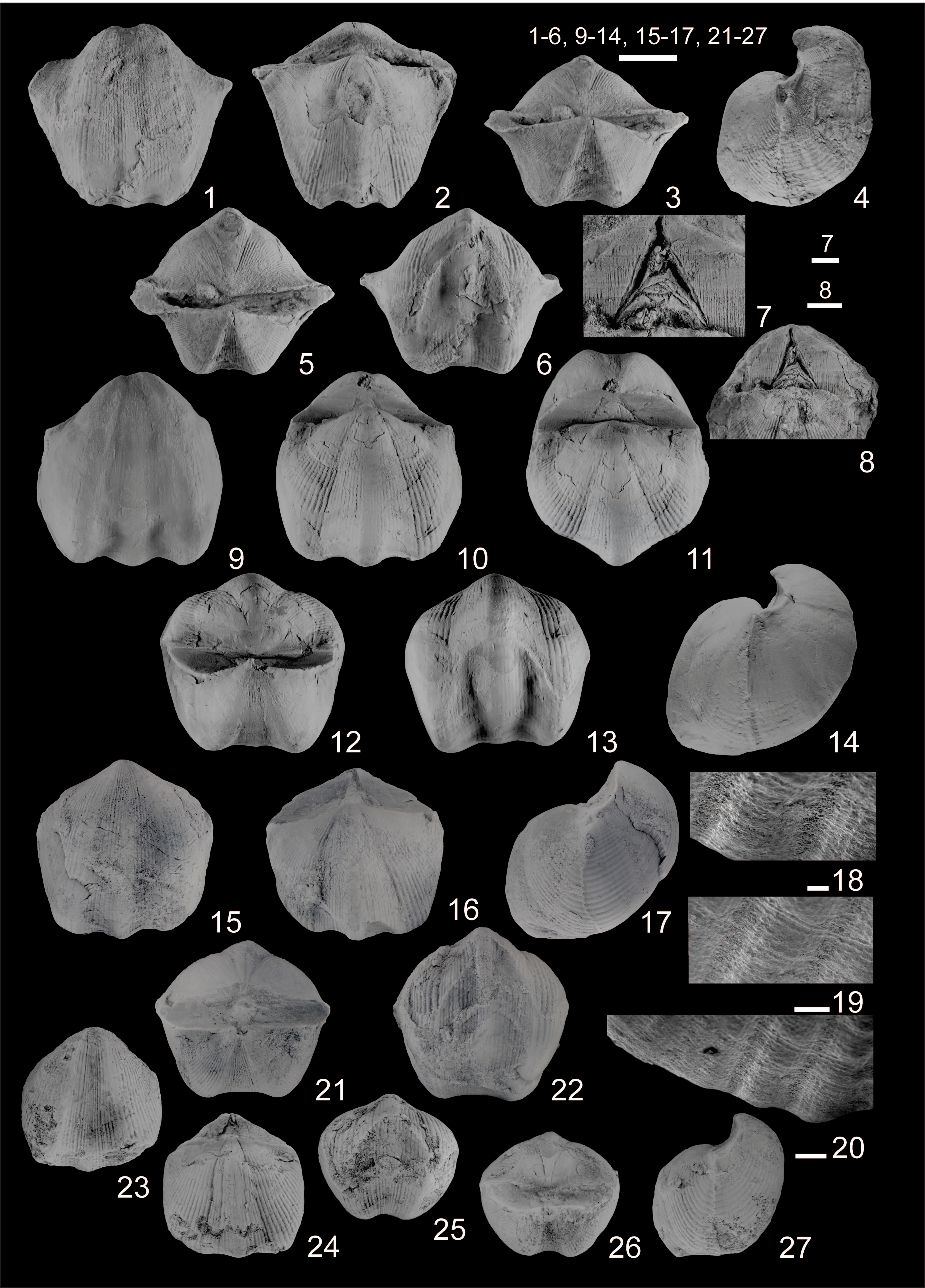
Table 1. Measurements and ratios in mm of *Aramazdospirifer orbelianus* (Abich, 1858) Abbreviations: W–width of the shell, L–length of the shell, T–thickness of the shell, Ws–width of the sulcus, dL–length of the dorsal valve.

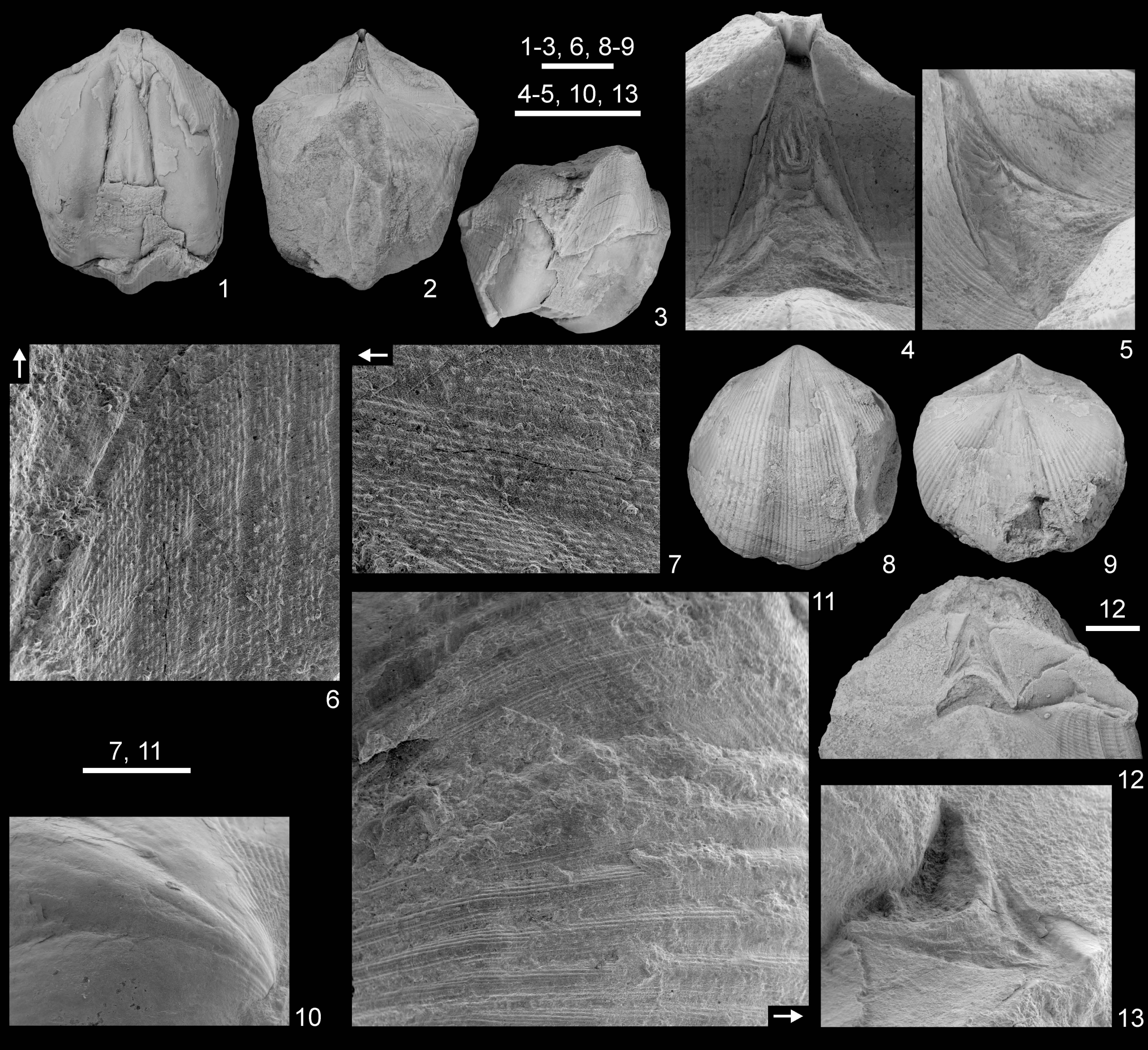
Tableau 1. Mesures et rapports en mm de *Aramazdospirifer orbelianus* (Abich, 1858) Abréviations: W–largeur de la coquille, L–longueur de la coquille, T–épaisseur de la coquille, Ws–largeur du sulcus, dL–longueur de la valve dorsale.

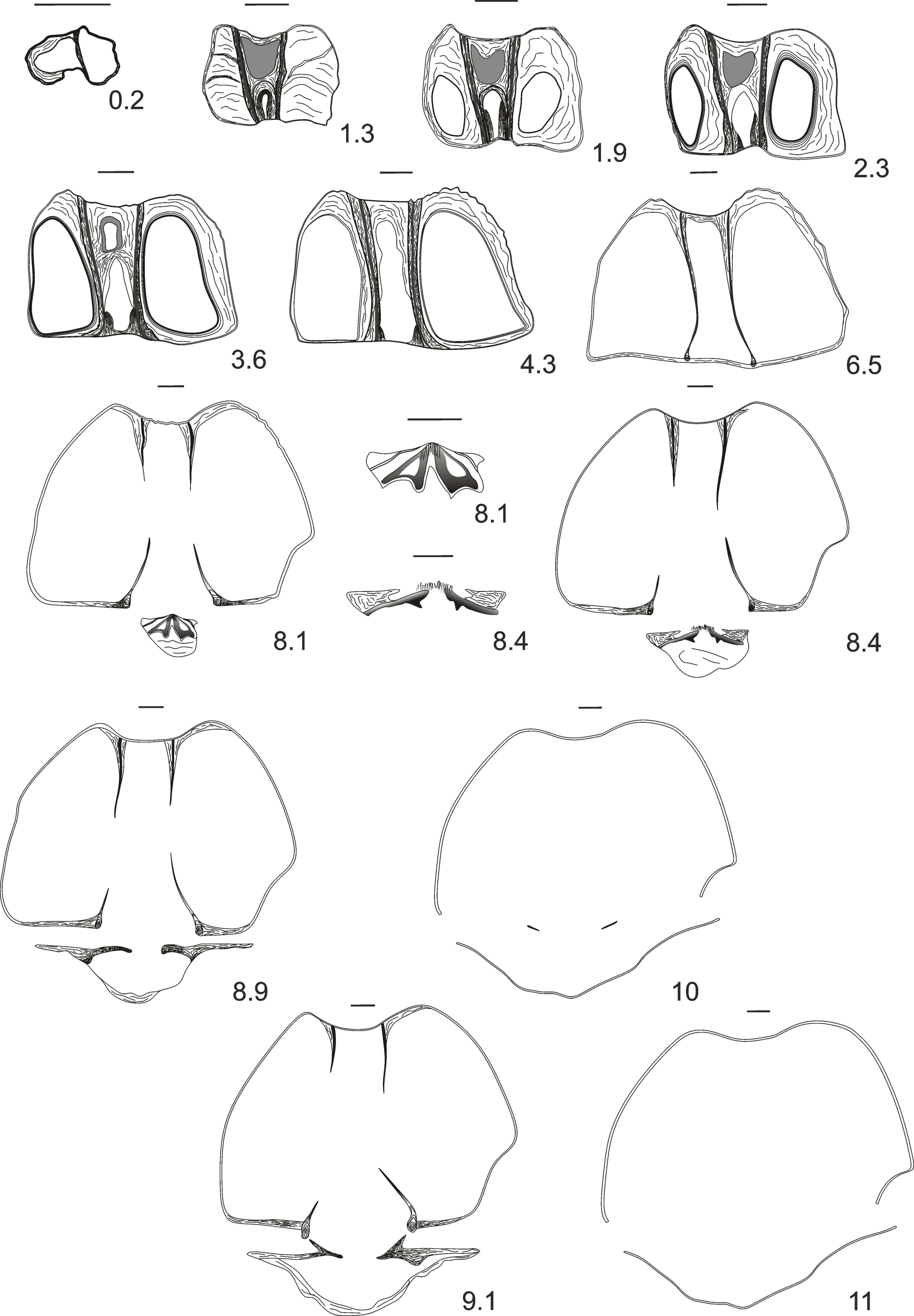


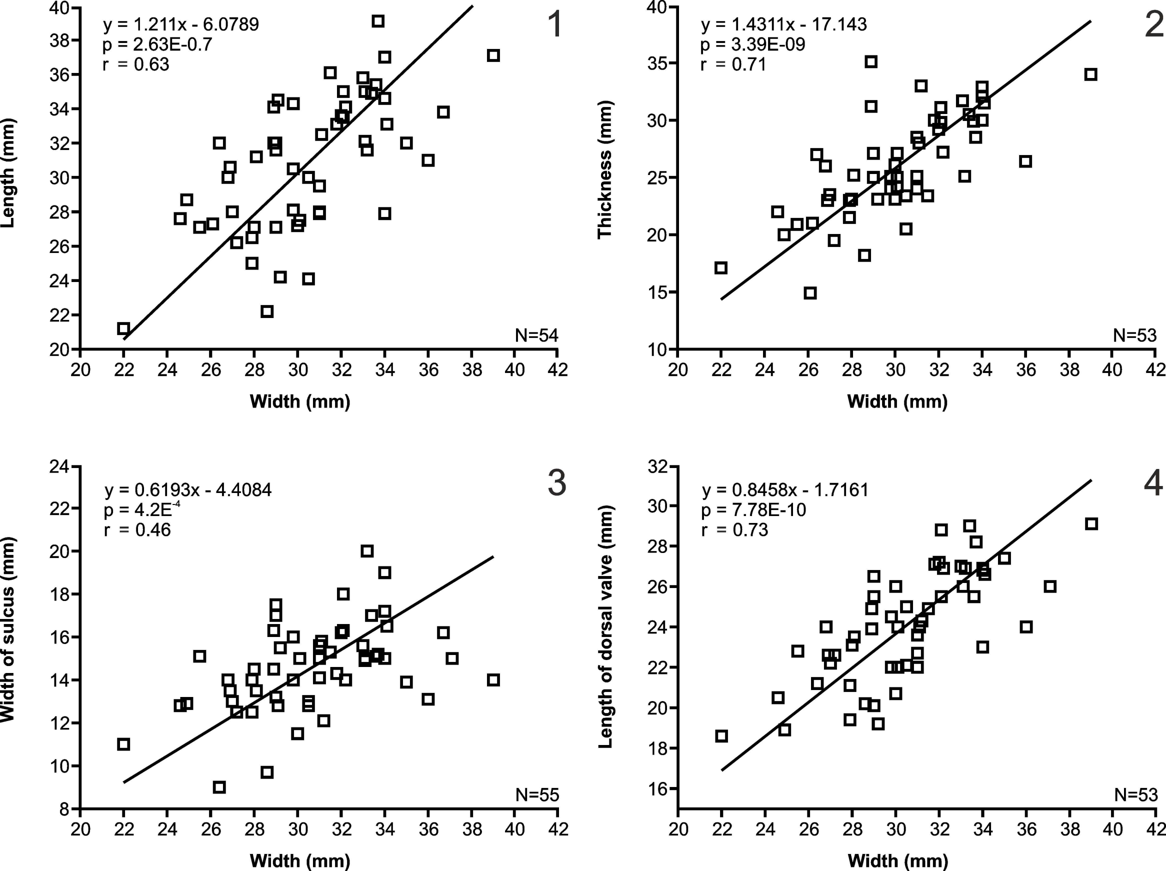
N
Yerevan
N
100km
1
Vedi
2
Vedi river
Armenia
Lanjanist
Ararat
3
Zangakatun
Armash
Turkey
Araks river
4
Arpa river
Areni
5
Sadarak
Araco river
Gnishik river
NoravankMonastery
6
7
Iran
Arpa river
0
10
20km
Nakhichevan
Legend
Permian
Lower Carboniferous
Upper Devonian
Middle Devonian
Lower Devonian
Faults
International border
Monastery
River
Sections
1 Argichi
2 Lanjanist (Kadrlu)
3 Zangakatun (Chanakhchi)
4 Ertych
5 Djravank
6 Noravank
7 Gyumushlug

<table>
<tr><th>Stage</th><th>Sub-stage</th><th>Arakelyan (1964)</th><th>Abrahamyan (1957)</th><th>Rzhonsnitskaya and Mamedov (2000)</th></tr>
<tr><td rowspan="2">Famennian</td><td rowspan="2">Lower</td><td>Ertych</td><td>Aramazdospirifer orbelianus</td><td>Aramazdospirifer orbelianus–
?Cyrtiopsis armenica</td></tr>
<tr><td>Noravank</td><td rowspan="2">Cyrtospirifer lonsdalii
Productella herminae
Camarotoechia arpaensis
etc.</td><td>Mesoplica meisteri–
Cyrtospirifer asiaticus</td></tr>
<tr><td>Frasnian</td><td>Upper</td><td>Baghrsagh</td><td>Uchtospirifer subarchiachi–
Cyphoterorhynchus arpaensis</td></tr>
</table>

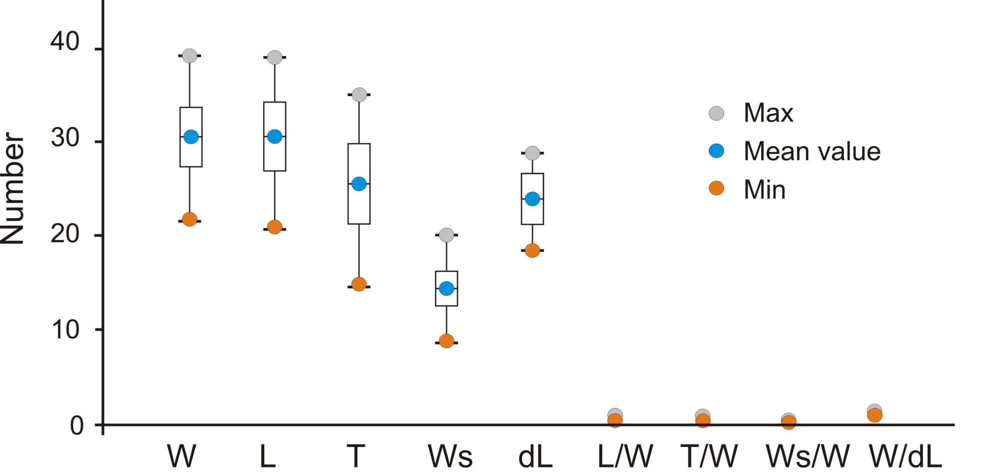

1-6, 9-14, 15-17, 21-27
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27


1-3, 6, 8-9
4-5, 10, 13
7, 11
12
1
2
3
4
5
6
7
8
9
10
11
12
13


0.2
1.3
1.9
2.3
3.6
4.3
6.5
8.1
8.1
8.4
8.4
8.9
10
9.1
11



1
y = 1.211x - 6.0789
p = 2.63E-0.7
r = 0.63
N=54
Length (mm)
Width (mm)
2
y = 1.4311x - 17.143
p = 3.39E-09
r = 0.71
N=53
Thickness (mm)
Width (mm)
3
y = 0.6193x - 4.4084
p = 4.2E-4
r = 0.46
N=55
Width of sulcus (mm)
Width (mm)
4
y = 0.8458x - 1.7161
p = 7.78E-10
r = 0.73
N=53
Length of dorsal valve (mm)
Width (mm)



Number
40
30
20
10
0
W
L
T
Ws
dL
L/W
T/W
Ws/W
W/dL
Max
Mean value
Min

	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	±0.5432	±0.6169	±0.2782	±0.3791	±0.0144	±0.015	±0.0084	±0.0148
MIN	22	21.2	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