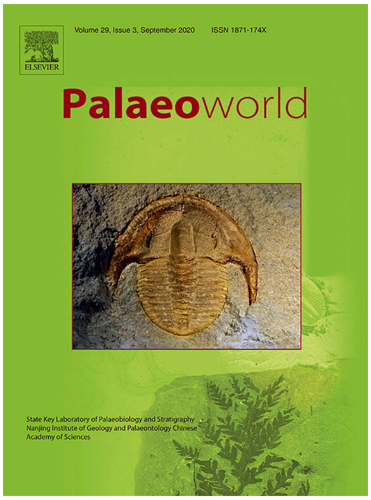

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# First palynological evidence from the Upper Devonian of Armenia (northern Gondwanan margin): biostratigraphic implications

Sirush Khachatryan [a,b,c], Borja Cascales-Miñana [d], Taniel Danelian [b] *, Pierre Breuer [e], Philippe Steemans [e], Araik Grigoryan [a], Ivan Gabrielyan [c], Vachik Hairapetian [f], Sylvie Regnier [b], David Marius Kroeck [g], Vahram Serobyan [a]

[a] Institute of Geological Sciences, National Academy of Sciences of the Republic of Armenia, 24A Marshal Baghramyan Avenue, Yerevan 0019, Republic of Armenia

[b] Univ. Lille, CNRS, UMR 8198, Evo-Eco-Paleo, F-59000 Lille, France

[c] Takhtajian Institute of Botany, National Academy of Sciences of the Republic of Armenia, Yerevan 0063, Republic of Armenia

[d] CNRS, Univ. Lille, UMR 8198, Evo-Eco-Paleo, F-59000 Lille, France

[e] EDDY Lab/Palaeopalynology, Department of Geology, University of Liège, Allée du 6 Août, B18 Sart Tilman, B4000 Liège, Belgium

[f] Department of Geology, Isfahan (Khorasgan) Branch, Islamic Azad University, Isfahan, Iran

[g] School of Ecology/State Key Laboratory of Biocontrol, Shenzhen Campus of Sun Yat-sen University, Shenzhen 518107, China

* Corresponding author.

*E-mail addresses*: sirush_xachatryan@mail.ru (S. Khachatryan), borja.cascales-minana@cnrs.fr (B. Cascales-Miñana), taniel.danelian@univ-lille.fr (T. Danelian), piet79@yahoo.fr (P. Breuer), p.steemans@uliege.be (P. Steemans), aragrigoryan@yandex.ru (A. Grigoryan), ivangabrielyan100@gmail.com (I. Gabrielyan), vhairap@gmail.com (V. Hairapetian), sylvie.regnier@univ-lille.fr (S. Regnier), kroeck@mail.sysu.edu.cn (D.M. Kroeck), vahramserobyan@gmail.com (V. Serobyan)

## Abstract

Diverse and abundant terrestrial palynomorphs are recovered from the shales in the Frasnian–Famennian succession of the Ertych section situated in central Armenia. They represent the first discovery of spores from the Upper Devonian shallow marine sedimentary sequences of the South Armenian Block, which at that time was part of the northern Gondwanan continental margin. Their taxonomic assessment recognizes

37 spore taxa assigned to 22 genera. Notably, the presence of *Teichertospora torquata* allows us to assign the entire studied succession to the *torquata–gracilis* zone, indicating a late Frasnian to early Famennian age. In addition, the occurrence of *Acinosporites lindlarensis*, which corresponds to the spores of the herbaceous lycophyte *Leclercqia*, suggests that the age of the studied succession should be further restricted to the late Frasnian. The presence of chitinozoans (i.e., *Angochitina mourai*) in the studied interval argues for marine deposition. Our biostratigraphic results provide a more coherent picture for the sedimentary evolution of this Frasnian–Famennian sequence arguing for a rather uninterrupted sedimentation close to the critical boundary interval. The identified spore assemblage highlights the close affinity of the Frasnian vegetation preserved in Armenia with other parts of the Northern Gondwana and southern Laurentia. We provide the first evidence of the occurrence of *Kraeuselisporites ollii* outside Canada and extend its known age range to late Frasnian.

**Keywords:** Palynoflora; Miospores; Upper Devonian; Palaeogeography; Biostratigraphy; Armenia

## 1. Introduction

The Devonian Period marked a critical interval in Earth's history, characterized by numerous significant geological and biological events, among which one of the most astounding is the evolution of plants in terrestrial environments, with far-reaching consequences for Earth system dynamics (Becker et al., 2016). More specifically, during this time, plants underwent a major radiation; they increased in size, they diversified and enhanced propagule dispersion (Cascales-Miñana et al., 2019). Therefore, the study of their spores is a good proxy to trace the spatial and temporal distribution of early land plants (Steemans et al., 2012). The Upper Devonian strata crop out in a limited geographical area in the country, primarily within the southern part of central Armenia, but they also continue westwards into Nakhichevan (Fig. 1). Their presence has been known since the middle of the 19th century (Abich, 1858), but detailed lithostratigraphic and biostratigraphic data are still lacking (see Serobyan et al., 2023, for a recent update). Biostratigraphic subdivision of these sequences has been based essentially on brachiopods, only occasionally on conodonts, both of which are mainly recovered from the limestone parts of these sequences. More particularly, the important stratigraphic and mapping efforts conducted during the 1960s and 1970s by the Institute of Geological Sciences (National Academy of Sciences of the Republic of Armenia) revealed the fossil richness of these sequences in terms of brachiopods (Abrahamyan, 1954, 1957, 1959, 1974; Arakelyan, 1964). This initial stratigraphic framework was much later supplemented with data on conodonts (Aristov, 1994; Grigoryan et al., 2019), as well as occasional chondrichthyan microremains (Ginter et al., 2011). However, despite the numerous studies and recent taxonomic and biostratigraphic revisions on brachiopods (Serobyan et al., 2019, 2021, 2022a, 2022b, 2023; Serobyan and Mottequin, 2022) and bryozoans (Ernst et al., 2024), the question related to the stratigraphic completeness or possible presence of stratigraphic gaps, is still a major challenge in understanding the Upper Devonian sequences. It is noteworthy that this challenge persists predominantly due to the facies-dependent nature of various fossils. More particularly, several sections in Armenia featuring Upper Devonian strata comprise lithostratigraphic intervals that are dominated by terrigenous facies, such as sandstones and shales. Remarkably, these intervals still remain unzoned as neither brachiopods nor conodonts have been recovered from them. Palynology has obviously the potential to offer crucial biostratigraphic constraints for these terrigenous intervals and to provide evidence for the reconstruction of the Late Devonian vegetation that once thrived in this region. This paper constitutes the first palynological study of Upper Devonian sequences in the Lesser Caucasus. Its main objective is to document the miospore assemblages discovered in a Frasnian–lower Famennian succession of Armenia and discuss their biostratigraphic significance in relation to the existing knowledge derived from the brachiopod and conodont record. Additionally, correlations are drawn with the spore record from neighbouring sequences in Iran and elsewhere in the world.

## 2. Stratigraphic and palaeogeographic settings

The recognition of the Devonian stages and the boundaries of the internationally recognized chronostratigraphic units is still problematic in the Lesser Caucasus. This issue stems from the paucity of modern and comprehensive palaeontological and biostratigraphic investigations. Additionally, previous biostratigraphic studies have primarily targeted limestone sequences, overlooking intervals dominated by terrigenous facies that remain largely unsampled. The Upper Devonian sedimentary sequences of Armenia are represented by a succession of mixed carbonate-siliciclastic deposits. They consist mainly of marly and sandy biogenic limestones and intercalations of quartzose sandstones (arenites), fine-grained sandstones and shales (Serobyan et al., 2023). Only a few sections exposing the Frasnian–lower Famennian interval are known in the Armenian sector. They consist mainly of two distinct nodular limestone sequences separated by an interval of black shales, siltstones and fine sandstones that are overlain by well-sorted quartzitic sandstones, as is the case in the Ertych section studied here (Fig. 2). The lower limestone interval of the sequence corresponds to the *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* brachiopod zone established by Serobyan et al. (2023) and correlates with the latest early to late Frasnian time interval, based on extracted conodonts that are characteristic of the *transitans* to late *rhenana* conodont zones. The upper limestone interval of the sequence is assigned to the *Aramazdospirifer orbelianus–Tornatospirifer armenicus* brachiopod zone introduced by Serobyan et al. (2022b). Conodonts studied by Ginter et al. (2011) suggest that these limestones belong to the lower Famennian *Palmatolepis crepida* zone of Ziegler and Sandberg (1990).

Serobyan et al. (2023) correlated these recently established brachiopod zones in Armenia with the ones established by Grechishnikova et al. (1982), Rzhonsnitskaya and Mamedov (2000) and Mirieva (2010) in Nakhichevan, as well as with the local conodont zones introduced by Aristov (1994), also in Nakhichevan (Fig. 3). It is noteworthy that the unzoned interval in all these biozonations corresponds to the terrigenous intervals intercalated between the two limestone sequences, which are the main focus of the present study.

## 3. Material and methods

The palynological material was collected from the Ertych section during several field seasons organized during the years 2017 to 2019. The section crops out on the southern bank of the Arpa River (Fig. 1), along a quarry situated ca. 8.5 km east of the famous wine-producing village of Areni (39°43.850'N, 45°16.300'E). Samples Er18/P1–Er18/P13 were collected in 2018. Abundant and well-preserved miospore taxa were recovered from two lithostratigraphic units in the Ertych section (Fig. 2). The miospore bearing samples studied here come from a lower interval characterized by black shales, with intercalations of fine grain sandstones and from the shaly intercalations of an overlying lithological interval characterized mainly by quartzose sandstones (arenites). Two additional samples (ER-17.01 and ER-18.02) were collected from a level bearing unidentified plant remains (just below sample Er18/P7). The palynomorphs were extracted only from shales using standard palynological laboratory methods. Each sample was crushed and 25–30 g were disaggregated and subsequently immersed in hydrochloric acid (36%) to dissolve the carbonates. The silicates were removed with hot hydrofluoric acid (40%). Subsequently, a hot bath in hydrochloric acid (25%) eliminated the remaining fine neoformed fluoride particles. The remaining organic residues were oxidized with fuming Schulze solution for a time interval varying from 1 to 5 minutes. Organic residues were then sieved through 10–20 μm nylon meshes to eliminate the finer debris and facilitate palynological analyses. The final residue was mounted on palynological slides for their examination under a light microscope. Three to five slides were prepared for each productive sample. Each palynological slide was observed in detail with a Zeiss Axio Imager A2 optical microscope hosted by the Palaeontology Team of the University of Lille (UMR 8198, Evo-Eco-Paleo) and a Leica DM2700 P optical microscope at the Laboratory of Palaeontology and Stratigraphy of the Institute of Geological Sciences. Images were obtained using a Zeiss AxioCam ERc5s and Flexacam c5. All images were further processed with Adobe Photoshop CS6. All material illustrated and investigated herein is deposited at the Geological Museum of the Institute of Geological Sciences of the National Academy of Sciences of the Republic of Armenia, Yerevan (prefixed IGS/PS/P). The prefixes PS and P indicate the Laboratory of Palaeontology and Stratigraphy, and Palynology, respectively. The prefixe Er designates the Ertych section.

## 4. Results

### *4.1. Identified taxa*

Amongst the 15 studied samples (46 palynological slides), spores were retrieved from only nine of them, but in varying quantities. The occurrence and number of identified specimens in the studied samples are given in Table 1. The morphographic system of suprageneric categories (anteturmae and turmae) adopted herein follows Potonié (1956), with the subsequent modifications by Dettmann (1963) and Potonié (1970).

The following spore taxa were identified; genera and species are arranged in alphabetical order for ease of use.

*Acinosporites lindlarensis* Riegel, 1968 (Fig. 4A)

*Ancyrospora ancyrea* Richardson, 1962 (Fig. 4B, C)

*Ancyrospora longispinosa* Richardson, 1962 (Fig. 4D–F)

*Ancyrospora* sp.; poorly preserved specimens displaying a two-layered exine with grapnel-tipped spines.

*Aneurospora greggsii* (McGregor) Streel in Becker et al., 1974 (Fig. 4G, H)

*Anueurospora* cf. *greggsii* (McGregor) Streel in Becker et al., 1974; it displays all the features of *A. greggsii* with the exception of a cingulum and a thickening of exine.

*Aneurospora* sp. (Fig. 4I); poorly preserved specimens displaying coni and crassitude, a sculptural element and an outer proximo- equatorial thickening.

*Apiculiretusispora brandtii* Streel, 1964 (Fig. 4J)

?*Apiculiretusispora plicata* (Allen) Streel, 1967 (Fig. 4K); a single poorly preserved specimen assigned tentatively to *A. plicata* based on the presence of the regular ornamentation of small cones (less than one micron) and a thin exine layer.

*Apiculiretusispora* sp. (Fig. 4L); poorly preserved specimens displaying distinctive curvaturae and sculptural elements on the exine layer.

*Chelinospora concinna* Allen, 1965 (Fig. 4M, N)

*Camarozonotriletes parvus* Owens, 1971 (Fig. 4W)

*Cristatisporites* sp. (Fig. 4O); poorly preserved specimens with equatorial amb and ornamentation of cristae characteristic of this genus.

*Cymbosporites catilius* Allen, 1965 (Fig. 4P, Q)

*Cymbosporites cyathus* Allen, 1965 (Fig. 4R)

*Cymbosporites* sp.; includes specimens with very thick patinate exine.

*Densosporites* sp. (Fig. 4S–V); our material displays the camerate zonal structure typical of this genus, but the differences between sculptural elements and indistinguishable light and dark parts of the zona make their determination difficult at the species level.

*Dibolisporites* sp. (Fig. 4X); genus assignment is based on the elongate, densely ornamented biform spines of the distal region present in our material.

*Emphanisporites rotatus* McGregor, 1973 (Fig. 4Y, Z)

*Geminospora lemurata* Balme emend. Playford, 1983 (Fig. 4AA, BB)

*Geminospora* cf. *lemurata* Balme emend. Playford, 1983 (Figs. 4CC, 5A); a morphotype distinguished by the absence of coarse or sculptured elements on the contact area.

*Geminospora* sp. (Fig. 5B, C); poorly preserved specimens displaying scabrate or granulate sculptural elements and a thicker outer layer in distal view.

*Grandispora* sp. (Fig. 5D, E); typical, two layered structure of exine; exoexine extends equatorially as a zona and sculpture of spines observed in our material.

*Hystricosporites multifurcatus* Winslow, 1962 (Fig. 5F, G)

*Hystricosporites* sp.; a single poorly preserved specimen of large size, bearing long spines on the distal surface.

*Kraeuselisporites ollii* McGregor and Camfield, 1982 (Fig. 5H–J)

*Punctatisporites* sp. (Fig. 5K); assignment is based on the thin, smooth exine devoid of a distinct internal structure and the punctate or infragranulose internal structure of the exine observed on our material.

*Retusosporites triangulatus* Streel, 1967 (Fig. 5L)

*Retusosporites* sp. (Fig. 5M); our material displays discernible curvaturae or an apical differentiation of the exine at the proximal pole.

*Rugospora bricei* Loboziak and Streel, 1989 (Fig. 5N)

*Rugospora* cf. *flexuosa* (Jushko) Streel in Becker et al., 1974 (Fig. 5O); a single, poorly preserved specimen displaying a thick and sinuous type rugulae as ornamentation and a three layered exine.

*Rugospora* sp. (Fig. 5P); two specimens, with rugulae type of ornamentation and a three layered exine.

*Samarisporites triangulatus* Allen, 1965 (Fig. 5Q, R)

*Teichertospora torquata* (Higgs) McGregor and Playford, 1990 (Fig. 5S–U)

*Verrucosisporites bulliferus* Richardson and McGregor, 1986 (Fig. 5V, W)

*Verrucosisporites* cf. *mesogrumosus* (Kedo) Byvscheva, 1985 (Fig. 5X); a single specimen with no ornamentation in contact areas, only partially visible in the single observed specimen.

*Vallatisporites* sp. (Fig. 5Y, Z); assignment is based on the camerate zona and sculptural elements.

In addition to the above-mentioned spores we have also encountered several chitinozoans and acritarchs in most of the studied samples; we were able to identify the chitinozoan species *Angochitina mourai* Lange, 1952 (Fig. 5AA, BB). However, further examination of chitinozoans and acritarchs is beyond the scope of our current investigation and will be the focus of a separate paper on marine palynomorphs.

### *4.2. Relative abundance and diversity of miospore morphogroups*

Taxonomic assessment of the recovered palynomorph material allows us to recognize the presence of at least 37 trilete spore taxa belonging to 22 genera. The abundance of the spore taxa for each morphological group is listed in the supplementary table. The assemblages are dominated by zonate camerate spores, which constitute the most diverse and abundant group, composed of seven taxa assigned to six genera accounting for 54% of the identified spore specimens in our material. The group of crassitate apiculate spores, represented by only one genus (*Aneurospora*), is the second largest in terms of abundance, constituting 13.3% of the total material. Murornate zonate spores appear to exhibit low diversity and are represented only by *Kraeuselisporites ollii*, yet they account for 6.3% of the entire studied material. The groups, such as apiculate retusoid, ancyrate, and zonate acamerate, are each represented by 6% of the total abundance. Among them, both the apiculate retusoid and ancyrate groups are characterized by relatively high diversity, with the former including six taxa belonging to three genera and the latter including six taxa belonging to two genera. Whereas, the group of zonate acamerate spores consists of two species assigned to two genera. The group of retusoid spores consists of three taxa assigned to two genera and makes up 3.3% of the total identified specimens. The crassitate patinate and crassitate laevigate groups each account for 2% of the total number of identified specimens. However, the former is more diverse, comprising four species belonging to two genera, while the latter is represented by only a single species (*Punctatispotisporites* sp.). The group of camerate spores includes three species of the same genus and appears to be the least abundant, with only 1.1% of the total abundance.

## 5. Discussion

The presence of the miospore species *Teichertospora torquata* in most of our studied samples collected from the Ertych section is significant, as this index species suggests that the entire studied succession should be assigned to the "*torquata–gracilis*" biozone of Richardson and McGregor (1986); the latter is correlated with the late Frasnian–early Famennian time interval. Moreover, the presence in our material of several species that are not known in strata younger than the Frasnian (i.e., *Acinosporites lindlarensis*, *Ancyrospora longispinosa*, *Aneurospora greggsii*, *Chellinospora concinna*) suggests that the studied succession should be restricted to the upper Frasnian. Indeed, *Acinosporites lindlarensis* is known to cover the middle Emsian to lower Frasnian interval (Breuer and Steemans, 2013), *Ancyrospora longispinosa* is known from middle to upper Frasnian strata of Iran (Ghavidel-Syooki, 1995), *Aneurospora greggsii* is last known from the upper Frasnian (Mayr, 1980; Stempien-Salek, 2002), while *Chelinospora concinna* is last known from the lower Frasnian (Brice et al., 1979; Loboziak and Streel, 1980, 1988; Marshall et al., 1996). The most important argument for a late Frasnian age is based on the miospore species

*Acinosporites lindlarensis*, as its parent plant (*Leclercqia*), and the stratigraphic distribution of this plant, is known with certainty (Richardson et al., 1993). Xu et al. (2020) recently reviewed the extensive stratigraphic and palaeobiogeographic evidence of both the *Leclercqia* plant remains and the miospore *Acinosporites lindlarensis*. They clearly demonstrated that this herbaceous lycophyte, with a wide geographic distribution during the Middle and Late Devonian in Laurentia, Gondwana, Siberia and Kazakhstan, went extinct at the end of the Frasnian. Additionally, the presence of the chitinozoan species *Angochitina mourai*, known from the Frasnian and earliest Famennian (Grahn et al., 2006), is consistent with this age. The presence of chitinozoans in nearly all of our palynomorph-bearing samples suggests that the entire studied interval was accumulated in marine environments to which spores were transported. The Devonian sedimentary sequences that crop out in the Lesser Caucasus were deposited on a carbonate shelf environment of the northern margin of Gondwana (Fig. 4), which was later defined as the South Armenian Block, following its northward migration and opening of the Neotethys further to the South (Sosson et al., 2010; Nikogosian et al., 2023). Thus, during the Late Devonian, this realm was part of a considerable carbonate platform that was positioned within the tropical zone of the southern hemisphere (Brock and Yazdi, 2000; Scotese, 2014). It is therefore interesting to compare the spore assemblages recovered from the Ertych section with the ones documented from Iran. Based on the presence of *T. torquata*, our material may be assigned to the assemblage zone IV of Ghavidel-Syooki and Owens (2007) established in the Alborz Range, which was correlated with the upper Frasnian part of the Kuh-e-Ozum section. Taherian et al. (2022) studied the miospores from an Upper Devonian section in northeastern Alborz; our material may be assigned to their *bulliferous–torquata* biozone, which was correlated with the late Frasnian. Finally, several miospore species recovered by Rouzegar and Ozvart (2022) from the Frasnian-Famennian interval of the northwestern Kerman region (southeast Iran) are also present in our material, including *Geminospora lemurata*, *Samarisporites triangulatus*, *Apiculiretusispora plicata*, *Emphanisporites rotatus* and *Teichertospora torquata*. Although *E. rotatus* and *T. torquata* are not recorded before the transition between assemblage zones IV and V in the study of Rouzegar and Ozvart (2022), the co-occurrence of *G. lemurata*, *S. triangulatus* and *A. plicata* points to a higher affinity with assemblage zones II–IV. As assemblage zones III and IV contain clear indicator taxa for the middle–uppermost Famennian, which are absent in our material, the assemblage from the studied interval of the Ertych section is most comparable to assemblage zone II of Rouzegar and Ozvart (2022), which has been assigned a late Frasnian–early Famennian age. In summary, it is reasonable to infer that the entire interval between samples Er-18/P1 and Er-18/P13 corresponds to the lower part (late Frasnian) of the *torquata–gracilis* biozone. Thus, the biochronostratigraphic significance of the miospores identified in the present study suggest that the previously unzoned interval of the regional biozonations established on brachiopods (e.g., Grechishnikova et al., 1982; Rzhonsnitskaya and Mamedov, 2000) and conodont (Aristov, 1994) corresponds to the upper Frasnian (Fig. 4). This new evidence suggests that the Ertych section preserves a relatively continuous sedimentary record. Consequently, the Frasnian–Famennian boundary should be investigated in the future between the uppermost beds of the upper Frasnian terrigenous interval and the base of the overlying Famennian limestones.

Palaeogeographically, it is noteworthy that the miospores identified in the present study have already been reported from other Upper Devonian sedimentary sequences worldwide, including Iran, Saudi Arabia, and western Asia, North Africa, Portugal, Western and Central Europe, South and North America. This widespread distribution spans vast areas across Laurentia and Gondwana (Richardson and McGregor, 1986; Streel et al., 1987; Loboziak and Streel, 1988; McGregor and Playford, 1992; Breuer and Steemans, 2013; Taherian et al., 2022). However, the presence of *Kraeuselisporites ollii* is noteworthy, as this species was previously known with certainty only from Eifelian to early Frasnian strata of Canada (McGregor and Camfield, 1982; McGregor and Playford, 1992). Although its possible presence was reported tentatively from Australia (Grey, 1991), our results establish for the first time with certainty the presence of this species in Northern Gondwana; which also extends its known age range up to the late Frasnian. This evidence highlights the close relationship of the vegetation flourishing on the emerged parts of the South Armenian Block with other parts of the northern margin of Gondwana and the southern Laurentian domain during the late Frasnian (see also Steemans et al., 2007 for Devonian palaeophytogeographical considerations around the Rheic Ocean).

## 6. Conclusions

The taxonomic assessment of the miospores recovered from the terrigenous intervals of the Ertych section in central Armenia allows us to identify 37 miospore taxa assigned to 22 genera. The co-occurrence of the species *Teichertospora torquata* and *Acinosporites lindlarensis* assigns the entire studied interval to the lower *torquata–gracilis* zone and correlate it with the upper Frasnian. The presence of chitinozoans in the studied interval argues for a marine depositional environment for the entire section. The obtained results provide a more coherent picture for the sedimentary evolution of the Frasnian–lower Famennian sequences preserved in Armenia and call for more detailed paleontological and biostratigraphic studies throughout the critical Frasnian–Famennian boundary. The examined assemblages are dominated by zonate camerate spores, which constitute the most diverse and abundant group, whereas the group of crassitate apiculate, despite of its low diversity, ranks second in abundance. The assemblage is comparable with coeval spore assemblages recorded worldwide and this highlights the close affinity of the late Frasnian vegetation developed on the emerged parts of the South Armenian Block with other parts of northern Gondwana and southern Laurentia. We here document for the first time the occurrence of *Kraeuselisporites ollii* outside Canada and extend its known age range to the late Frasnian.

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## Figure captions

Fig. 1. Schematic geological map and distribution of the Upper Palaeozoic sequences in the Lesser Caucasus (Central Armenia and Nakhichevan), including the location of the Ertych section (modified after Serobyan et al., 2019).

Fig. 2. Lithostratigraphic column of the studied Ertych section and levels of the 15 studied samples, including the 11 samples with palynological remains.

Fig. 3. Biochonostratigraphic framework of the Frasnian–lower Famennian sedimentary sequences in the Lesser Caucasus, including lithostratigraphic units, the correlation of the brachiopod assemblage biozones of Abrahamyan (1957) and Serobyan et al. (2022b, 2023) in Central Armenia, and Rzhonsnitskaya and Mamedov (2000) in Nakhichevan. The figure also includes the regional conodont zonation established by Aristov (1994) in Nakhichevan, standard conodont zones of Ziegler and Sandberg (1990) and the miospore biozonation of Richardson and McGregor (1986). Abbreviations: Giv., Givetian; Up., Upper.

Fig. 4. Miospores from the Upper Devonian Ertych section (Armenia). Taxon name followed by sample/slide number and England Finder co-ordinates. Scale bar = 20 µm. (A) *Acinosporites lindlarensis* Riegel, 1968 (Sample Er18/P7, G14/4). (B, C) *Ancyrospora ancyrea* Richardson, 1962 (Sample Er18/P2, R6, V14). (D–F) *Ancyrospora longispinosa* Richardson, 1962 (Sample Er18/P12, Q15/1, R18, Q16). (G, H) *Aneurospora greggsii* (McGregor) Streel in Becker et al., 1974 (Sample Er18/P7, E5/3, K25/4). (I) *Aneurospora* sp. (Sample Er18/P8, J5). (J) *Apiculiretusispora brandtii* Streel, 1964 (Sample Er18.02, Q14/3). (K) ?*Apiculiretusispora plicata* (Allen) Streel, 1967 (Sample Er18/P7, P5/1). (L) *Apiculiretusispora* sp. (Sample Er18/P7, U 21/1). (M, N) *Chelinospora concinna* Allen, 1965 (Sample Er18/P12, C11, R3). (O) *Cristatisporites* sp. (Sample Er18.02, L26). (P, Q) *Cymbosporites catillus* Allen, 1965; (P) Sample Er18/P8, V5/3; (Q) Sample Er18/P7, E10/4. (R) *Cymbosporites cyathus* Allen, 1965 (Sample Er18/P7, F17/1). (S–V) *Densosporites* sp.; (S, T) Sample Er18/P13, E18, U28.1; (U, V) Sample Er17.1, R29.4, U28.1. (W) *Camarozonotriletes parvus* Owens, 1971 (Sample Er18/P7, M20/4). (X) *Dibolisporites* sp. (Sample Er17.1, C17/2). (Y, Z) *Emphanisporites rotatus* McGregor, 1973; (Y) Sample Er18/P7, F2/4; (Z) Sample Er18/P8, L11. (AA, BB) *Geminospora lemurata* Balme emend. Playford, 1983 (Sample Er18/P7, H28/5, W24). (CC) *Geminospora* cf. *lemurata* Balme emend. Playford, 1983 (Sample Er18/P7, Q6).

Fig. 5. Miospores (A–Z) and Chitinozoans (AA, BB) from the Upper Devonian Ertych section (Armenia). Taxon name followed by sample/slide number and England Finder co-ordinates. Scale bar = 20 µm. (A) *Geminospora* cf. *lemurata* Balme emend. Playford, 1983 (Sample Er18/P8, B17/3). (B, C) *Geminospora* sp.; (B) Sample Er18/P13, V14; (C) Sample Er18/P7, M12/1. (D, E) *Grandispora* sp. (Sample Er18/P7, S7, K12/1). (F, G) *Hystricosporites multifurcatus* Winslow, 1962 (Sample

Er18/P12, Q16, Q16/3). (H–J) *Kraeuselisporites ollii* McGregor and Camfield, 1982; (H) Sample Er18/P12, C10/4; (I, J) Sample Er18/P2, K1, X11/2. (K) *Punctatisporites* sp. (Sample Er18/P13, N17/1). (L) *Retusosporites triangulatus* Streel, 1967 (Sample Er17.1, F24/4). (M) *Retusosporites* sp. (Sample Er18/P7, C6/2). (N) *Rugospora bricei* Loboziak and Streel, 1989 (Sample Er18.02, F21/2). (O) *Rugospora* cf. *flexuosa* (Jushko) Streel in Becker et al., 1974 (Sample Er18.02, L27/2). (P) *Rugospora* sp. (Sample Er18/P4, M71/4). (Q, R) *Samarisporites triangulatus* Allen, 1965; (Q) Sample Er18/P13, L11/3; (R) Sample Er18/P8, S16). (S–U) *Teichertospora torquata* (Higgs) McGregor and Playford, 1990; (S, T) Sample Er18/P12, Q23/1, R6; (U) Sample Er18/P13, Q68/2. (V, W) *Verrucosisporites bulliferus* Richardson and McGregor, 1986; (V) Sample Er18/P13, M3/2; (W) Sample Er18.02, L48/4. (X) *Verrucosisporites* cf. *megrosumosus* (Kedo) Byvscheva, 1985 (Sample Er18/P13, E48/2). (Y, Z) *Vallatisporites* sp. (Sample Er18/P11, R56/3, P50). (AA, BB) *Angochitina mourai* Lange, 1952 (Sample Er18/P2, D50, T72).

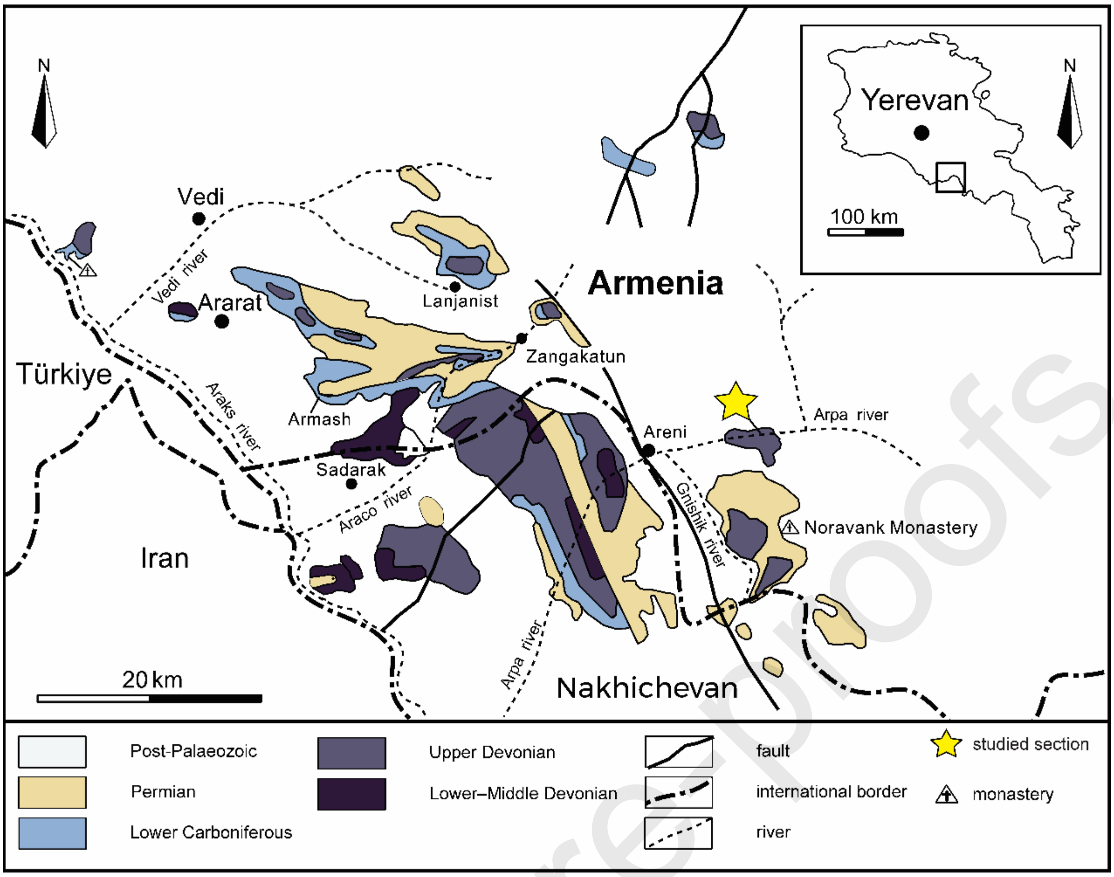
Fig. 6. Late Devonian paleogeographic map including the position of the South Armenian Block along the northern margin of Gondwana megacontinent (redrawn and modified after Denayer and Hoşgör, 2014, based on the maps of Stampfli et al., 2002).

Table 1. Species occurrence and number of identified miospore specimens in the studied samples from the Ertych section.

| | **Er18/P1** | **Er18/P2** | **Er18/P4** | **Er18/P5** | **ER-17.1** | **ER-18-02** | **Er18/P7** | **Er18/P8** | **Er18/P11** | **Er18/P12** | **Er18/P13** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acinosporites lindlarensis* | _ | 1 | _ | _ | _ | _ | 3 | _ | 1 | _ | _ |
| *Ancyrospora ancyrea* | _ | 3 | _ | _ | _ | _ | _ | _ | _ | 3 | _ |
| *Ancyrospora longispinosa* | _ | 3 | _ | _ | _ | _ | _ | _ | _ | 3 | _ |
| *Ancyrospora* sp. | 1 | 1 | _ | 1 | _ | _ | _ | _ | 1 | 10 | 3 |
| *Aneurospora greggsii* | _ | 4 | 2 | _ | 3 | 5 | 7 | 5 | 3 | _ | 5 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aneurospora* cf. *greggsii* | 1 | _ | _ | _ | 2 | _ | 5 | 4 | 3 | _ | _ |
| *Aneurospora* sp. | _ | 1 | _ | _ | 2 | _ | 2 | 1 | 1 | _ | 3 |
| *Apiculiretusispora brandtii* | _ | _ | _ | _ | _ | 2 | _ | _ | _ | _ | _ |
| ?*Apiculiretusispora plicata* | _ | _ | _ | _ | _ | _ | 1 | _ | _ | _ | _ |
| *Apiculiretusispora* sp. | 1 | 1 | _ | _ | 2 | 7 | 4 | 2 | _ | _ | _ |
| *Chelinospora concinna* | _ | _ | _ | _ | _ | _ | _ | _ | _ | 2 | _ |
| *Camarozonotriletes parvus* | _ | _ | _ | _ | _ | _ | 1 | _ | _ | _ | _ |
| *Cristatisporites* sp. | _ | _ | _ | _ | _ | 1 | _ | _ | _ | _ | _ |
| *Cymbosporites catillus* | _ | _ | _ | _ | _ | _ | 3 | 1 | _ | _ | _ |
| *Cymbosporites cyathus* | _ | _ | _ | _ | _ | _ | 3 | _ | _ | _ | _ |
| *Cymbosporites* sp. | 1 | _ | _ | _ | _ | _ | _ | 1 | _ | _ | _ |
| *Densosporites* sp. | _ | 7 | 1 | _ | 3 | _ | 1 | 1 | 5 | 4 | 3 |
| *Dibolisporites* sp. | _ | 1 | _ | _ | 2 | _ | _ | 1 | 5 | _ | _ |
| *Emphanisporites rotatus* | _ | _ | _ | _ | _ | _ | 2 | 2 | _ | _ | 1 |
| *Geminospora lemurata* | 3 | 7 | _ | _ | 4 | 3 | 6 | 45 | 25 | 6 | 34 |
| *Geminospora* cf. *lemurata* | _ | _ | 1 | _ | _ | _ | 1 | 1 | _ | _ | _ |
| *Geminospora* sp. | 2 | _ | _ | _ | _ | _ | 4 | 2 | _ | _ | 1 |
| *Grandispora* sp. | _ | _ | _ | _ | 2 | _ | 3 | _ | _ | _ | 2 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hystricosporites multifurcatus* | _ | _ | _ | _ | _ | _ | _ | _ | _ | 2 | _ |
| *Hystricosporites* sp. | _ | _ | _ | _ | _ | _ | _ | _ | _ | 1 | _ |
| *Kraeuselisporites ollii* | 1 | 23 | 1 | _ | _ | _ | _ | _ | 1 | 7 | 3 |
| *Punctatisporites* sp. | 1 | 2 | _ | _ | _ | _ | 1 | 1 | 1 | _ | 2 |
| *Retusotriletes triangulatus* | _ | _ | _ | _ | 2 | _ | _ | _ | _ | _ | _ |
| *Retusotriletes* sp. | 1 | _ | _ | _ | 1 | 1 | 2 | 1 | _ | _ | _ |
| *Rugospora bricei* | _ | _ | _ | _ | _ | 1 | _ | _ | _ | _ | _ |
| *Rugospora* cf. *flexuosa* | _ | _ | _ | _ | _ | 1 | _ | _ | _ | _ | _ |
| *Rugospora* sp. | _ | _ | _ | _ | _ | _ | 1 | _ | _ | _ | 1 |
| *Samarisporites triangulatus* | 3 | 1 | 1 | _ | _ | 4 | _ | 2 | 2 | _ | 13 |
| *Teichertospora torquata* | 1 | 1 | 1 | 2 | _ | _ | 2 | _ | 10 | 48 | 2 |
| *Verrucosisporites bulliferus* | _ | _ | _ | _ | _ | _ | _ | 1 | _ | _ | 1 |
| *Verrucosisporites* cf. *megrosumosus* | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | 1 |
| *Vallatisporites* sp. | _ | _ | _ | _ | 1 | _ | _ | _ | 2 | _ | _ |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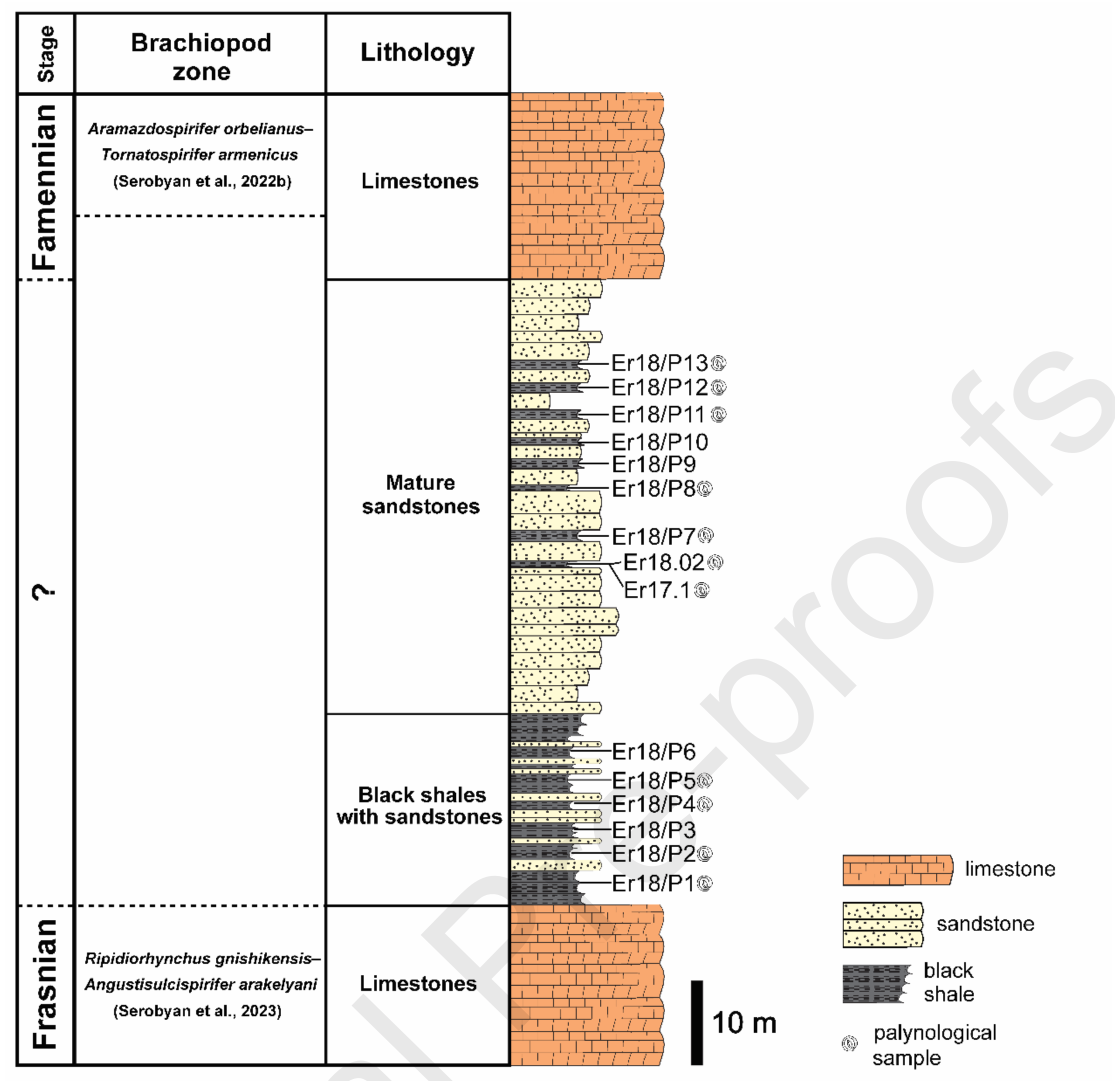
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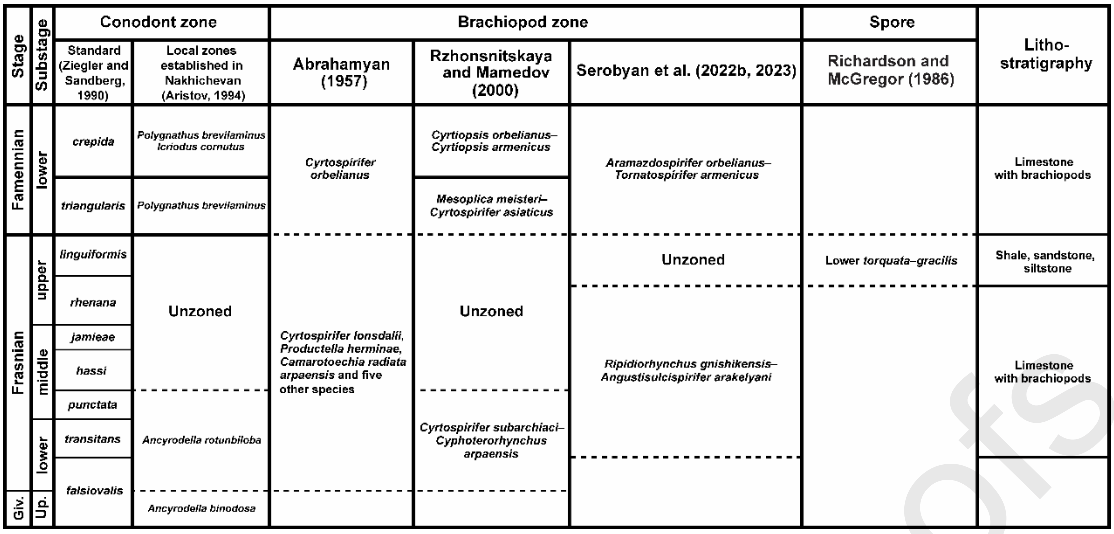
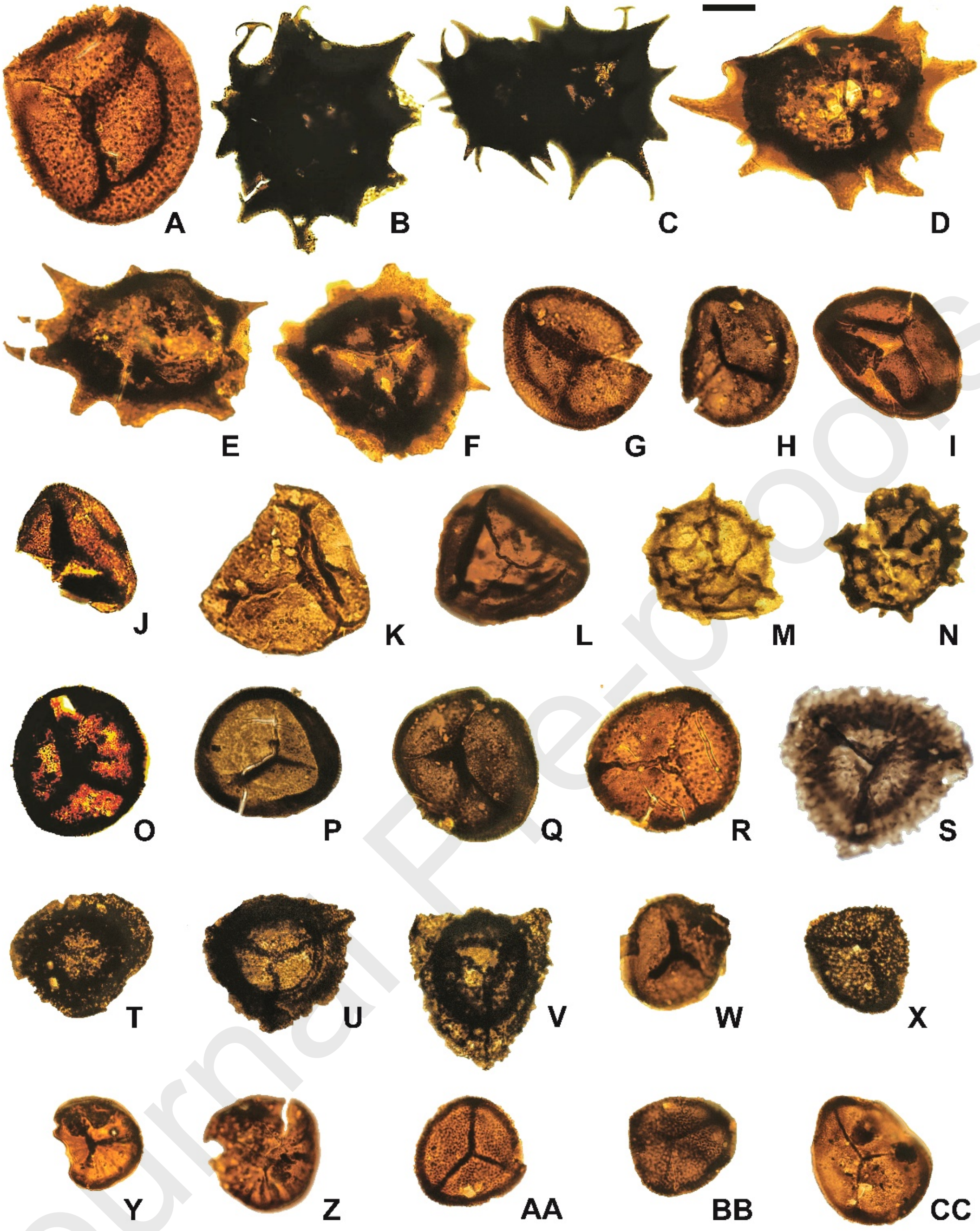
Black shales with sandstones
Frasnian
Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani (Serobyan et al., 2023)
Limestones
Er18/P13
Er18/P12
Er18/P11
Er18/P10
Er18/P9
Er18/P8
Er18/P7
Er18.02
Er17.1
Er18/P6
Er18/P5
Er18/P4
Er18/P3
Er18/P2
Er18/P1
10 m
limestone
sandstone
black shale
palynological sample



| Stage | Substage | Conodont zone | | Brachiopod zone | | | Spore | Litho-stratigraphy |
|---|---|---|---|---|---|---|---|---|
| | | Standard (Ziegler and Sandberg, 1990) | Local zones established in Nakhichevan (Aristov, 1994) | Abrahamyan (1957) | Rzhonsnitskaya and Mamedov (2000) | Serobyan et al. (2022b, 2023) | Richardson and McGregor (1986) | |
| Famennian | lower | *crepida* | *Polygnathus brevilaminus*<br>*Icriodus cornutus* | *Cyrtospirifer orbelianus* | *Cyrtiopsis orbelianus–Cyrtiopsis armenicus* | *Aramazdospirifer orbelianus–Tornatospirifer armenicus* | | Limestone with brachiopods |
| | | *triangularis* | *Polygnathus brevilaminus* | | *Mesoplica meisteri–Cyrtospirifer asiaticus* | | | |
| Frasnian | upper | *linguiformis* | Unzoned | *Cyrtospirifer lonsdalii*, *Productella herminae*, *Camarotoechia radiata arpaensis* and five other species | Unzoned | Unzoned | Lower *torquata–gracilis* | Shale, sandstone, siltstone |
| | | *rhenana* | | | | *Ripidiorhynchus gnishikensis–Angustisulcispirifer arakelyani* | | Limestone with brachiopods |
| | middle | *jamieae* | | | | | | |
| | | *hassi* | | | | | | |
| | | *punctata* | *Ancyrodella rotunbiloba* | | *Cyrtospirifer subarchiaci–Cyphoterorhynchus arpaensis* | | | |
| | lower | *transitans* | | | | | | |
| | | *falsiovalis* | | | | | | |
| Giv. | Up. | | *Ancyrodella binodosa* | | | | | |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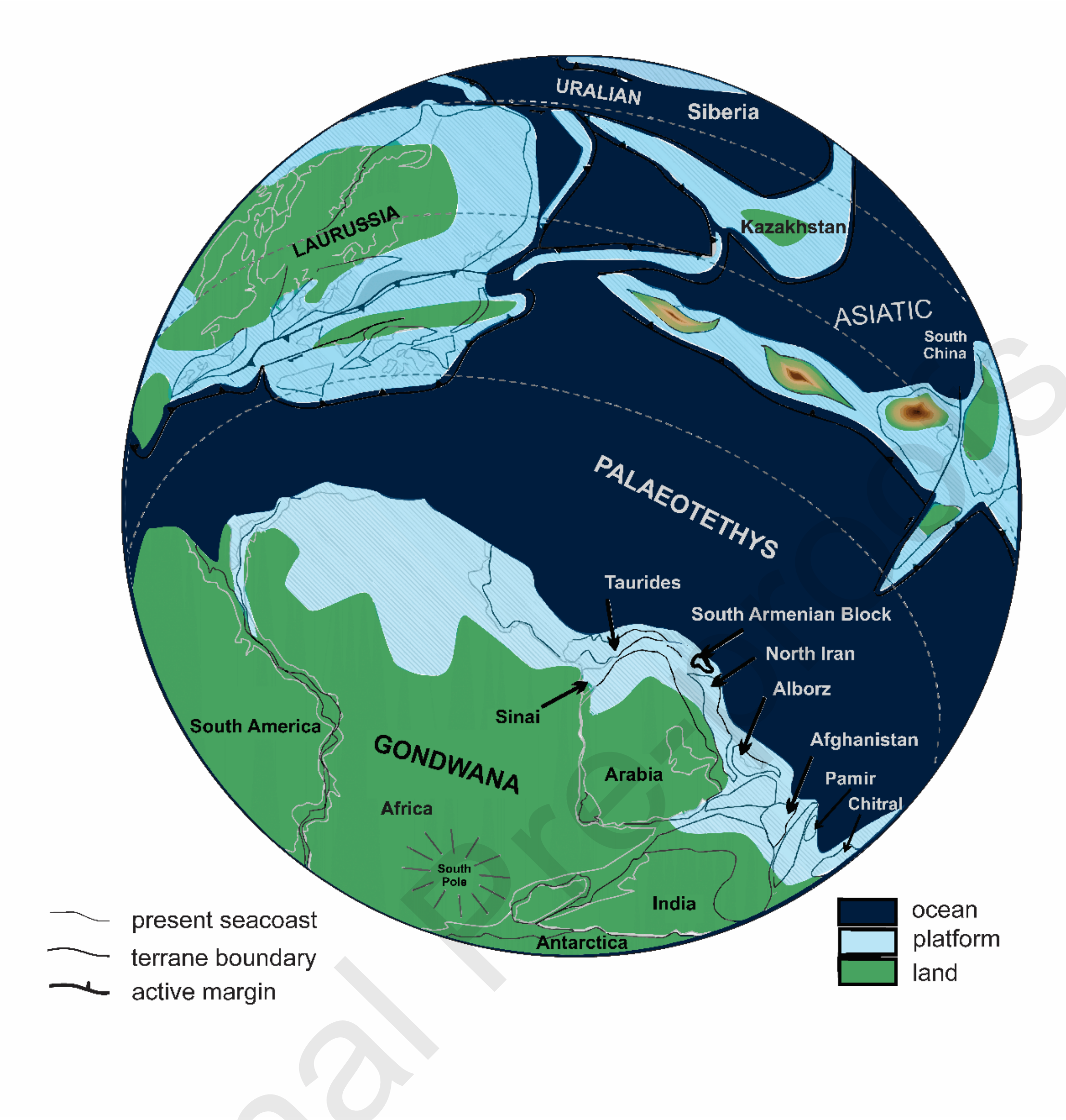
URALIAN
Siberia
LAURUSSIA
Kazakhstan
ASIATIC
South China
PALAEOTETHYS
Taurides
South Armenian Block
North Iran
Alborz
Afghanistan
Pamir
Chitral
Sinai
South America
GONDWANA
Arabia
Africa
South Pole
India
Antarctica
present seacoast
terrane boundary
active margin
ocean
platform
land