Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 132(3): 555-570. **November 2026**
DOI: https://doi.org/10.54103/2039-4942/29903

CONODONT BIOSTRATIGRAPHY AND LITHOSTRATIGRAPHY OF THE LATE GIVETIAN–EARLY FRASNIAN INTERVAL IN THE ARPI SECTION (CENTRAL ARMENIA)

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Associate Editor: Yichun Zhang.

To cite this article: Serobyan V., Hairapetian V., Tsatryan M., Danelian T., Boulvain F., Avagyan N. & Grigoryan A. (2026) - Conodont biostratigraphy and lithostratigraphy of the late Givetian–early Frasnian interval in the Arpi section (Central Armenia). *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 132(3): 555-570.

Keywords: Ancyrodella; conodonts; Givetian; Frasnian; Gondwana; Lesser Caucasus.

Abstract. The Givetian–Frasnian (G–F) transition marks a time of significant palaeoenvironmental perturbations and biotic turnover, yet its stratigraphic record in the southern Caucasus remains poorly constrained. This study presents the first integrated examination of conodont biostratigraphy and lithofacies across the G–F transitional interval in Armenia, based on material from the Arpi section. The section yielded a relatively diverse and abundant conodont assemblage, with taxonomic assessment allowing to identify eleven species and subspecies assigned to genera *Polygnathus*, *Icriodus*, and *Ancyrodella*. The first occurrences of *Ancyrodella rotundiloba* s.s., *A. pristina*, and *A. binodosa* in the upper part of the section enable correlation with the upper FZ1–FZ2 zones of the Frasnian conodont zonation, constraining this interval to the lowermost Frasnian. The absence of *Ancyrodella* in the underlying strata, coupled with the presence of species such as *Polygnathus dubius*, *Icriodus cedarensis*, and *I. excavatus*, suggests that the lower to middle part of the section corresponds to the upper Givetian. This interval is further correlated with the Upper *hermanni* to *norrisi* zones. Lithostratigraphic observations and microfacies analyses indicate that the sedimentary sequence of the section accumulated in a ramp setting. Moreover, a shallowing trend is observed, from relatively deeper, low-energy black shale facies in the late Givetian to more oxygenated, proximal carbonate facies in the early Frasnian.

Received: October 12, 2025; accepted: August 05, 2026

Introduction

The Givetian–Frasnian (G–F) transition was marked by a succession of global eustatic fluctuations and hypoxic oceanic events, evidenced by pronounced perturbations in both the sedimentary and fossil records. More specifically, the Frasnes Event, occurred near the G–F boundary, triggering substantial biodiversity declines among major marine invertebrates, including mollusks, echinoderms, arthropods, brachiopods, corals, and stromatoporoids (House 2002; McGhee et al. 2013). This interval correlates with rapid sea-level transgressions in Euramerican sections (e.g., Ebert 1993; Walliser 1996; House 2002; McGhee et al. 2013), widespread hypoxic phases (House 1985, 2002; Aboussalam & Becker 2007), and major perturbations of the marine carbon cycle, documented in central and southern Europe (Montagne Noire and Carnia; Buggisch & Joachimski 2006) and in South China (Qie et al. 2019). Nevertheless, the causal links between the biotic crisis and these environmental disruptions remain poorly constrained. The key obstacles to resolve this relationship include (1) insufficient high-resolution palaeontological and biostratigraphic data, (2) discrepancies in defining the G–F boundary (see discussion in Liao & Valenzuela-Ríos 2008), and (3) taxonomic disputes among conodont specialists regarding the index species used to recognize the G–F boundary. Despite extensive research on the G–F boundary in regions such as Morocco (Aboussalam & Becker 2007; Gouwy et al. 2007), France (Feist & Klapper 1985; Klapper et al. 1987), Poland (Racki 1993; Narkiewicz & Bultynck 2007), Canada (Braun et al. 1988), South China (Hua et al. 2009), Belgium (Casier & Préat 2009; Devleeschouwer et al. 2010), Germany (Stichling et al. 2022), Iran (e.g., Ashouri 2004, 2006; Gholamalian et al. 2013, 2022), and Turkey (Özkan et al. 2019), the Lesser Caucasus (Armenia and Nakhichevan; Fig. 1) remains critically understudied. The earlier studies by Ovnatanova & Aristov (1984) and Aristov (1994), although examining several localities in Nakhichevan, recovered only sparse index ancyrodellid conodonts. Moreover, the use of non-systematic (sporadic) sampling methods made it difficult to determine the first and last occurrences of these species, hindering precise recognition of the G–F boundary. Additionally, neither study provides section-specific biostratigraphic detail; instead, they present generalized biochronostratigraphic charts, leaving it unclear whether these apply to all sections, a specific one, or only a subset. Consequently, the Givetian–Frasnian boundary remains poorly constrained in Nakhichevan, while in Armenia it has yet to be investigated within the framework of conodont biostratigraphy.

The primary objective of this study is to provide the first conodont-based biostratigraphic characterization of the G–F transitional interval in Armenia, with the Arpi section designated as the reference locality. Additionally, this study compares the biostratigraphic peculiarities of the examined section with the Global Stratotype Section for the base of Frasnian at Col du Puech de la Suque E in the Montagne Noire, southern France, as well as with contemporaneous sections from other northern Gondwanan terranes, including those in Morocco, Turkey, and Iran. In addition, carbonate facies analyses, supported by detailed field observations, are applied to refine the lithostratigraphic framework of the Arpi section and to reconstruct changes in depositional environments across the G–F transition.

Devonian stratigraphy and palaeogeography of Armenia

From southwest to northeast, the Lesser Caucasus consists of three main structural units: the South Armenian Block (SAB), the Sevan-Akera ophiolites, and the Somkheto-Karabagh arc (Milanovsky 1968). The SAB, a continental block of Gondwanan origin, was initially situated to the north, facing the Palaeotethys ocean. Sosson et al. (2010) proposed that it was detached from Gondwana during the Triassic and migrated northward during the Jurassic following the opening of the Neotethys to the south. More recent evidence suggests that rift initiation of the SAB may have started earlier, during the Late Permian–Early Triassic interval (Nikoghosian et al. 2023). Mid-Palaeozoic sedimentary sequences of the SAB are exposed primarily in southwestern Armenia and extend westward into Nakhichevan (Fig. 1). These sequences consist of mixed carbonate-siliciclastic deposits, forming an approximately 1500 m-thick Lower Devonian–Lower Carboniferous succession (Abrahamyan 1964; Arakelyan 1964). Arakelyan (1964) subdivided the Lower–Upper Devonian sedimentary succes-

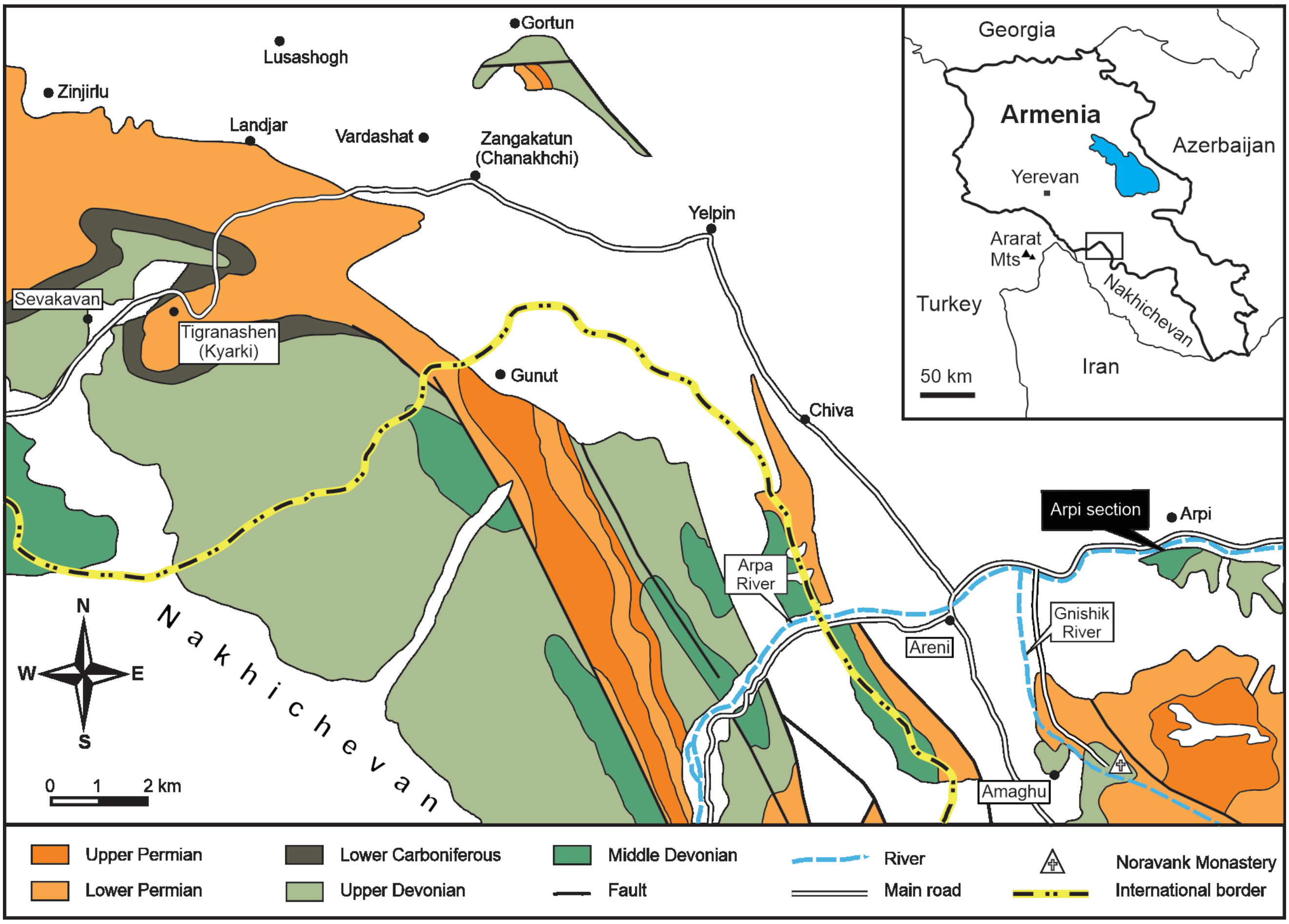


Fig. 1 - Schematic geological map and distribution of the middle–upper Palaeozoic successions in the Lesser Caucasus (Central Armenia and Nakhichevan), including the location of the Arpi section (modified from Ginter et al. 2011).

sion of the Lesser Caucasus into twelve fossil-based "formations" (e.g., Danzik, Chrakhana; Fig. 2). However, these units were differentiated primarily by their fossil content rather than on lithological criteria. In practice, most exhibit nearly identical lithological characteristics, making field discrimination challenging without knowledge of their brachiopod assemblages. Consequently, as argued by Serobyan et al. (2019), these units hold mainly biostratigraphic than lithostratigraphic significance and it is more appropriate to classify as horizons rather than formations. To date, Lower Devonian strata have been documented only in Nakhichevan, with no confirmed occurrences in Armenia (Fig. 1). Additionally, while Nakhichevan hosts several outcrops of Middle Devonian (Eifelian–Givetian) strata, these successions appear to be very restricted in Armenia, where they are seemingly represented solely by Givetian-aged deposits. Prior to this study, the presence of Middle Devonian deposits in Armenia was only inferred based on lithostratigraphic correlations, and was thought to be genuinely exposed only along the boundary with Nakhichevan (Arakelyan 1964; Abrahamyan 1973). Among the limited contributions to the Middle–Upper Devonian biostratigraphy, notable works include Grechishnikova et al. (1983) on brachiopods, and Ovnatanova & Aristov (1984) and Aristov (1994) on regional conodont assemblages. The latter studies established local conodont zones and correlated with the standard zonations of Klapper (1985) and Klapper & Ziegler (1979). Figure 2 summarizes the tentative correlations between these brachiopod and conodont zonations in the region, correlating with the global conodont frameworks.

Material and methods

The study material was collected during systematic field works conducted between 2023 and 2024 at the Arpi section. The section is located in

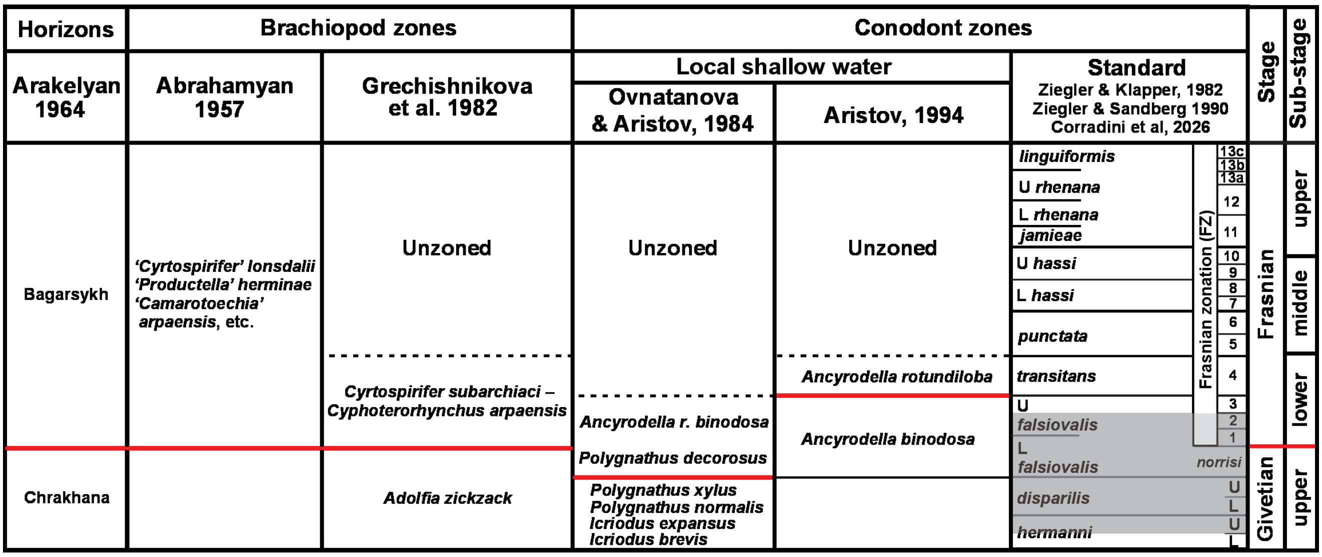


Fig. 2 - Stratigraphic scheme of the upper Givetian–Frasnian strata and the major lithostratigraphic units (Arakelyan 1964) correlated with local brachiopod biozones (Abrahamyan 1957 in Central Armenia; Grechishnikova et al. 1982 in Nakhichevan), local conodont biozones (Ovnatanova & Aristov, 1984; Aristov, 1994), as well as the global standard conodont zones of Ziegler & Klapper 1982; Ziegler & Sandberg 1990; Klapper & Johnson 1990; Corradini et al. 2026) in the southern Caucasus. The gray zone represents time interval of the Arpi section. As defined in Ovnatanova & Aristov (1984) and Aristov (1994), the G–F boundary (red bar) is based on correlating old and recent conodont biozonation schemes.

western Vayots Dzor Province, approximately 7 km northeast of the Areni Municipality, near the village of Arpi. The sedimentary sequence is well-exposed along the left bank of the Arpa River, adjacent to the road leading to Mozrov village (Fig. 3.1). Eight conodont samples (Ar23/5, Ar23/10, Ar23/14, Ar23/15, Ar23/16, Ar23/17, Ar24/12, and Ar24/13), each weighing 4–6 kg, were collected from limestone beds. Carbonate dissolution was performed using a buffered 5–9% formic acid solution in 10-L plastic buckets, with sieves (63–500 µm mesh) immersed to retain insoluble residues. The process was repeated iteratively until complete sample dissolution was achieved. Residues were dry-sieved, and the 125–500 µm fractions were subjected to density separation using bromoform. Subsequently, conodont elements were manually extracted from the heavy fraction under a Leica EZ4 E stereomicroscope. A total of 470 conodont specimens were recovered, with all samples yielding faunal remains, albeit in variable abundances (Table 1). It must be worth noting that the conodont color alteration index (CAI) values range between 3.5 and 4, suggesting that the fossils were subjected to elevated thermal maturity. Approximately 24% of the material consists of fragmented or incomplete

Conodont biozones	Upper *hermanni - norrisi*			Upper FZ1 – FZ2				
Taxa / Samples	Ar23/5	Ar23/10	Ar24/12	Ar24/13	Ar23/14	Ar23/15	Ar23/16	Ar23/17
Ancyrodella binodosa	-	-	-	10	-	3	3	-
Ancyrodella pristina	-	-	-	-	4	4	2	1
Ancyrodella rotundiloba s.s.	-	-	-	-	3	4	1	-
Polygnathus praepolitus		-	-	2	3	6	5	-
Polygnathus alatus	-	-	-		3	4	-	-
Polygnathus dubius	10	4	1	3	8	8	7	-
Polygnathus webbi	-	-	-		3	1	-	-
Polygnathus cf. *webbi*	-	-	-		1	-	-	-
Icriodus cedarensis	13	3	6	3	17	12	2	-
Icriodus excavatus	9	-	-		2	-	-	-
Icriodus cf. *excavatus*	6	-	-		-	-	1	-
Total	38	7	7	18	44	42	21	1
Ancyrodella % (tibe)	-	-	-	-	22.8 (16)	12.8 (10)	13.6 (9)	25
Polygnathus % (tibe)	24.2 (16)	54.5 (6)	25 (3)	68.6 (24)	42.9 (30)	56.4 (44)	65.2 (43)	75 (3)
Icriodus % (tibe)	75.8 (50)	45.5 (5)	75 (9)	31.4 (11)	34.3 (24)	30.8 (24)	21.2 (14)	-
Unassigned elements	6	-	12	-	30	44	23	-

Tab. 1 - Distribution chart and conodont biozones in the Arpi section. Tibe: total including broken elements.

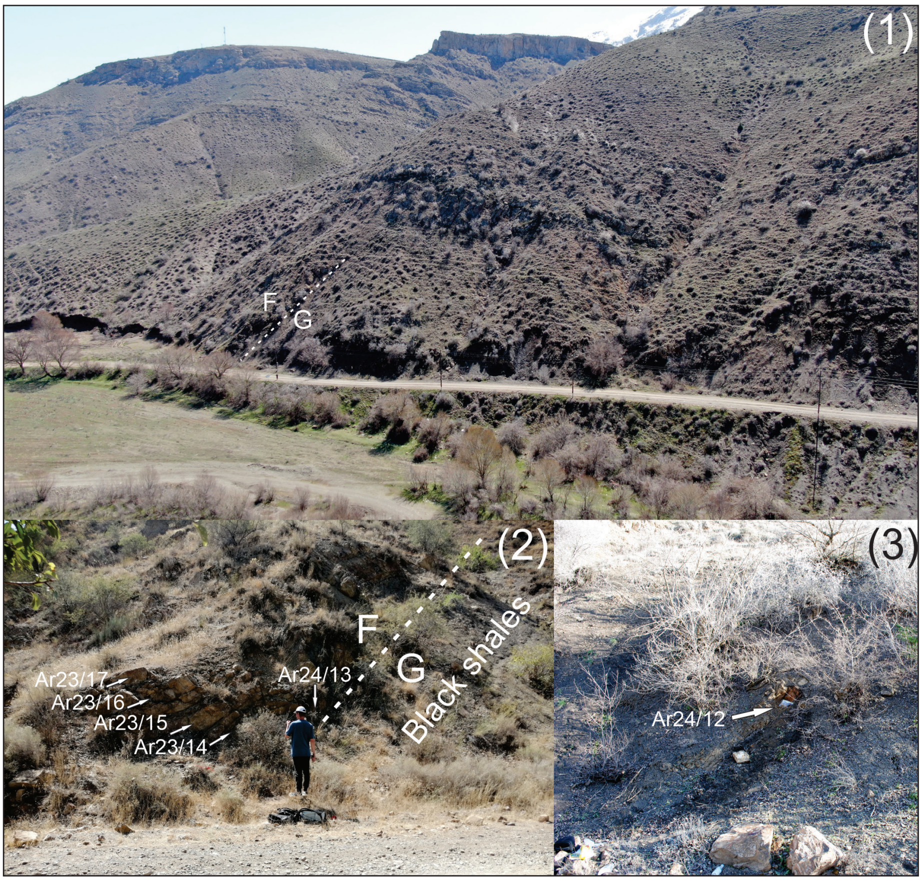


Fig. 3 - 1) General view of the middle–upper part of the Arpi section, showing the Givetian–Frasnian (G–F) transitional interval; 2) Close-up of the upper part of the section, showing Frasnian carbonate rocks with sample locations and the underlying Givetian black shale interval; 3) Close-up of the last limestone bed (Ar24/12) in the upper Givetian part of the section.

ramiform elements that could not be confidently assigned to a genus or species and are therefore categorized as unassigned elements (Table 1). Representative specimens selected for scanning electron microscopy (SEM) were mounted on aluminum stubs, gold-coated (45 s, 15 mA), and imaged using a Thermo Scientific Prisma E SEM at the A.B. Nalbandyan Institute of Chemical Physics, National Academy of Sciences of the Republic of Armenia (NAS RA). All recovered specimens are stored at the Geological Museum of the Institute of Geological Sciences, NAS RA, under the catalog numbers prefixed as IGS/PS. The 'PS' designation refers to the Laboratory of Palaeontology and Stratigraphy. The prefix 'Ar' (e.g., Ar23/5) used in the manuscript specifies the samples collected from the Arpi section. The following abbreviations are used: An. = *Ancyrodella*, I. = *Icriodus*, P. = *Polygnathus*.

Lithofacies and depositional environments of the Arpi section

The Arpi section, consisting predominantly of black shales with intercalations of limestone, sandstone and siltstone beds, along with multiple intrusive sills, fits well with the description of lower–middle Chrakhana Horizon of Arakelyan (1964). The presence of magmatic intrusions within these Devonian strata was first documented by Arakelyan (1952), who noted their significantly younger age relative to the host sedimentary rocks. Recent geochronological work by Nikoghosian et al. (2023) confirmed a Middle Triassic age for the basaltic sills and an Early Cretaceous age for the cross-cutting andesitic dykes.

The basal portion of the section features two distinct basaltic sills intruding into black shales (Fig. 4). The upper part of this black shale interval contains fragmented plant remains measuring 10 to 20 mm in length, representing an as yet unidentified species. This interval is overlain by the first conodont-bearing bed in the section, a 15 cm thick carbonate bed, designated as Ar23/5. This bed includes several marly and sandy nodules, measuring up to 70 cm in diameter. Microfacies analysis of this bed reveals a composition dominated by fragmented crinoid stem segments, with broken brachiopod shells and spines as the second most common component, all embedded in a micritic matrix

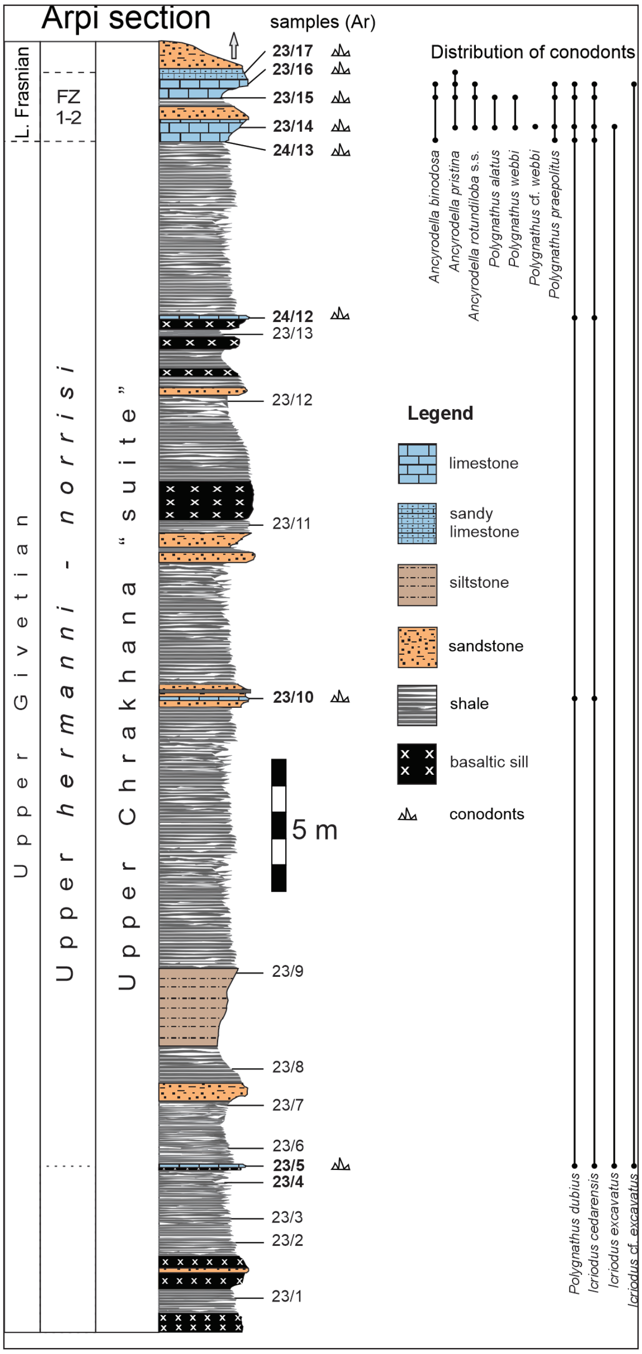


Fig. 4 - Lithostratigraphic column of the studied Arpi section, displaying the stratigraphic positions of the sampled beds and occurrences of conodonts.

(Fig. 5.1-3). Additional bioclasts present include ostracods, tentaculitids, mollusks, algae, phosphatic fish bones, and bryozoans, indicating a complex assemblage (Fig. 5.1-3). Fine-sized quartz grains are also observed. Consequently, Ar23/5 is classified as a crinoidal bioclastic packstone. Furthermore, the extensive fragmentation of fossils suggests deposition under storm-induced processes (tempestite facies). The Ar23/5 bed is succeeded by another black shale interval, containing a middle bed of fine-grained sandstone (Fig. 4), with its upper portion transitioning into siltstones. The subsequent limestone bed, designated as Ar23/10, crops out in the middle part of the section and is approximately 25 cm thick (Fig. 4). Microfacies analysis of this bed reveals that it is primarily composed of abundant fragmented crinoid debris, with minor components including bivalves, brachiopods, and, more rarely, sea urchins, fish remains, and a barnacle (Fig. 5.4). Some of these bioclasts display micritic rims (cortoids). A few quartz grains are also present. Based on these characteristics and the general textural features, this bed is a bioclastic crinoidal grainstone. The Ar23/10 bed is bounded both above and below by fine-grained sandstone horizons (Fig. 4). The upper portion of the section contains at least four additional basaltic sills interbedded with thin sandstone and black shale beds. The next carbonate bed (Ar24/12; Fig. 3.3), approximately 15 cm thick, exhibits a crinoidal packstone facies similar to that of the underlying beds (Ar23/5, Ar23/10). It is primarily composed of coarse crinoid fragments, with a lesser proportion of fragmented mollusks, both embedded in a micritic matrix (Fig. 5.5-6). Subordinate bioclasts include ostracods, tentaculitids, brachiopods, and phosphatic fish bones. Fine-grained quartz particles are moderately abundant. Compared to beds Ar23/5 and Ar23/10, it appears slightly different in assemblage composition due to the higher abundance of mollusks and likely reflects a shallower depositional setting. The uppermost portion of the section is characterized by a predominantly carbonate interval with a 3-4 m thickness (Fig. 3.2; 4). Microfacies analysis shows that the bed designated as Ar23/14 apparently exhibits pressure solution seams and contains fine-grained bioclasts of crinoids, mollusks, gastropods, ostracods and some peloids (Fig. 5.7). Some burrows are also observed in the thin section. Consequently, this bed is classified as a bioclastic packstone (or micropackstone). Microfacies analysis of the overlying beds (Ar23/15–Ar23/17) reveals that they are more matrix-supported, yet still reflect shallow depositional patterns. These beds contain scattered small bioclasts, including ostracod and brachiopod shells. They also show pressure solution seams, burrows, and bioturbation (Fig. 5.8). Based on their texture and composition, they are classified as wackestone. Field observations indicate that

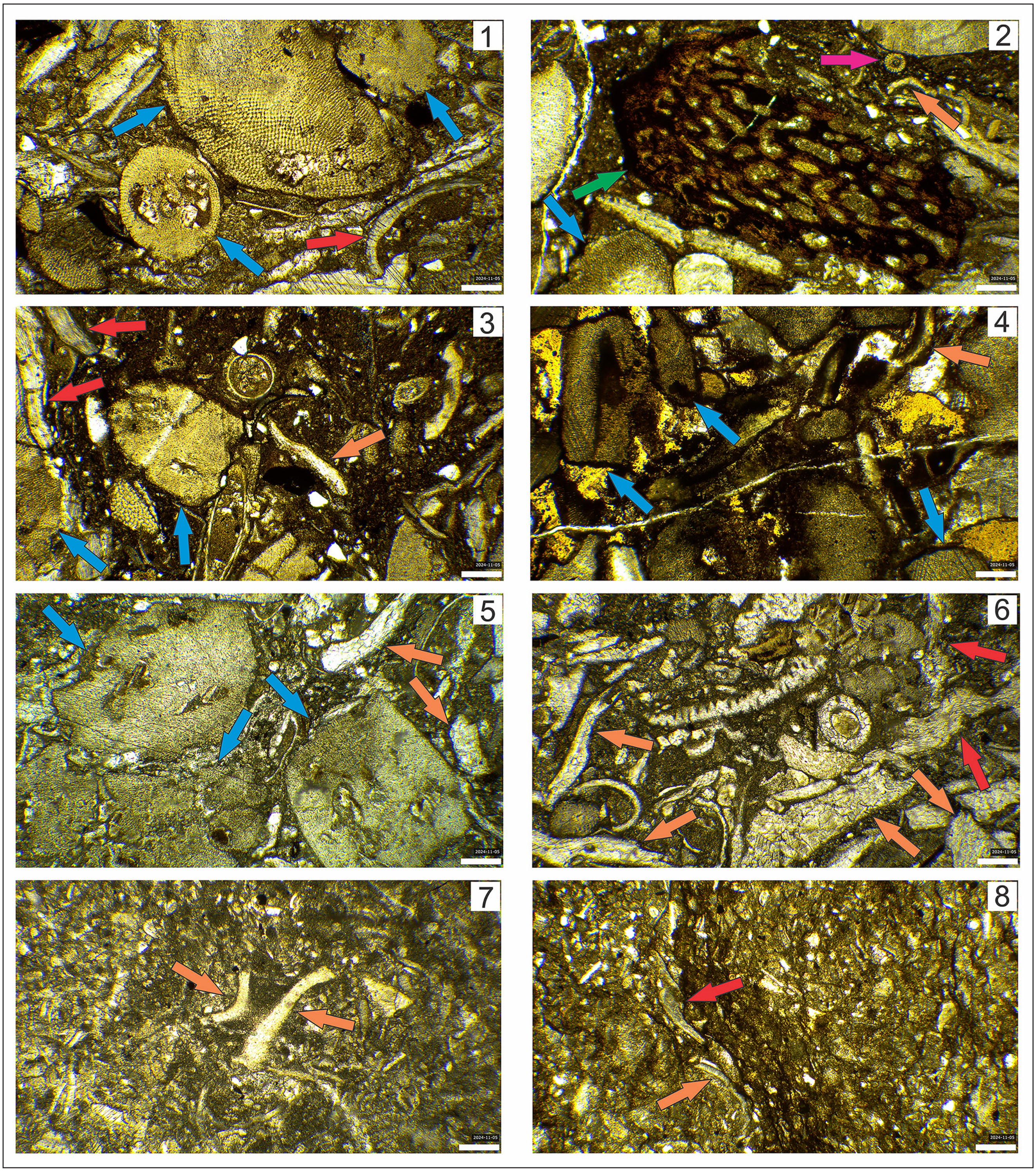


Fig. 5 - Microfacies aspects of thin sections from the Arpi section. (1–3) Sample Ar23/5: crinoidal bioclastic packstone with broken brachiopod shells and spines as the second most common components, all embedded in a micritic matrix. (4) Sample Ar23/10: crinoidal bioclastic grainstone with components including bivalves, brachiopods, and, more rarely, sea urchins, fish remains, and a barnacle. Some fragments display micritic rims (cortoids). (5–6) Sample Ar24/12: bioclastic crinoidal packstone; in addition to echinoderms, it contains a lesser amount of fragmented brachiopod shells, all embedded in a micritic matrix. (7) Sample Ar23/14: bioclastic packstone with fine-grained bioclasts of crinoids, bivalves, brachiopods, and ostracods, all embedded in a micritic matrix. Fine- to relatively coarse-sized quartz grains are comparably abundant. (8) Sample Ar23/17: bioturbated microbioclastic wackestone. Scale bars equal 0.2 mm. Arrows indicate bioclasts: blue – crinoid; red – brachiopod; green – bryozoan; orange – mollusk; purple – sea urchin.

these beds are particularly rich in atrypid brachiopods, including *Atrypa (Planatrypa) ertichensis* (Abrahamyan, 1959) and *Spinatrypa* sp., both of which have been previously reported from the Frasnian strata of the Ertych section (Serobyan et al. 2023). The Ar23/17 bed is overlain by fine-grained sandstone beds that are devoid of any fauna (Fig. 4). The whole section is primarily composed of black shale intervals but also includes a few beds of limestone, sandstone, and siltstone, as well as a few intrusions of sills. Furthermore, the section consists of a single lithostratigraphic unit, which, based on its composition, can be correlated with the lower–middle part of the Chrakhana Horizon of Arakelyan (1964).

Conodont biostratigraphy and biofacies

The taxonomic assessment of the conodonts from the Arpi section revealed the presence of eleven species, including five species of *Polygnathus*, three of *Icriodus*, and three of *Ancyrodella*. Notably, *Polygnathus* dominates the assemblage in both diversity and abundance. The stratigraphic distribution of conodonts and specimen counts per sample are detailed in Table 1. The biostratigraphic interpretation follows the global upper Givetian–Frasnian conodont zonation of Klapper (1985, 1989), Klapper & Johnson (1990), and Klapper & Kirchgasser (2016). Throughout this paper, the Frasnian zones are designated using the FZ notation (e.g., FZ1 and FZ2) following Corradini et al. (2026). Taxonomic assignments follow recent revisions of *Ancyrodella* by Klapper (2021).

Upper *hermanni–norrisi* Zones

Sample Ar23/5, collected from the lower part of the section (Fig. 4), contains a conodont assemblage composed of *Polygnathus dubius*, *Icriodus cedarensis*, and *I. excavatus*. Notably, *P. dubius* and *I. cedarensis* are of particular biostratigraphic significance, with the former originating in the Lower *hermanni* Zone and the latter in the uppermost part of the Upper *hermanni* Zone (Narkiewicz & Bultynck 2010). Samples Ar23/10 and Ar24/12 contain depauperate faunas: Ar23/10 yields only *P. dubius* and *I. cedarensis*. Collectively, the assemblage, observed in the beds Ar23/5, Ar23/10, Ar24/12, define an interval spanning the Upper *hermanni* to *norrisi* Zones. The upper limit of this interval is marked by the lowest occurrence of *Ancyrodella binodosa* in the overlying strata.

Upper FZ1–FZ2 Zones

The upper part of the section comprises several carbonate beds, positioned between an underlying black shale interval and overlying sandstone beds. The base of this carbonate interval is marked by sample Ar24/13, which yielded *Ancyrodella binodosa* along with *Polygnathus dubius*, *P. praepolitus* and *Icriodus cedarensis*. The occurrence of *Ancyrodella* demonstrates that this level is already Frasnian in age, although the recovered assemblage does not permit an unequivocal assignment to a formal conodont biozone. Sample Ar23/14, taken from the top of the same carbonate bed, yielded a more diverse conodont assemblage comprising two biostratigraphically significant species, *Ancyrodella rotundiloba* sensu stricto and *A. pristina*, along with *P. dubius*, *P. webbi*, *P. alatus*, *P. praepolitus*, *I. cedarensis*, and *I. excavatus*. The first occurrence of *A. rotundiloba* s.s. formally defines the base of FZ2 in the Frasnian conodont zonation of Klapper & Kirchgasser (2016) and Corradini et al. (2026), thereby assigning sample Ar23/14 to this biozone. Representatives of *Ancyrodella* continue throughout the overlying carbonate succession, with *A. rotundiloba* s.s. and *A. binodosa* recorded up to sample Ar23/16 and *A. pristina* persisting to the uppermost sampled bed, Ar23/17 (Table 1). The occurrence of *A. rotundiloba* s.s. throughout the interval, together with the presence of *A. pristina*, whose range extends into FZ2 (Klapper 1985; Narkiewicz & Bultynck 2010), indicates that the interval between samples Ar23/14 and Ar23/17 belongs to FZ2. Since sample Ar24/13 immediately underlies the first occurrence of *Ancyrodella rotundiloba* s.s., it is most plausibly interpreted as representing the upper part of FZ1. This interpretation is based primarily on the stratigraphic position of the sample rather than on the presence of taxa diagnostic of FZ1 and should therefore be regarded as tentative. If correct, it would imply that the lower part of FZ1 is either preserved within the underlying conodont-barren black-shale interval or absent owing to a stratigraphic hiatus.

Fig. 6 - Scanning electron micrographs of selected conodont species from the Arpi section. 1-8 - *Ancyrodella pristina* Khalymbadzha and Chernysheva 1970. 1-2) IGS-C44, sample Ar23/15. 3-4) IGS-C45, sample Ar23/14. 5-6) IGS-C46, sample Ar23/15. 7-8) IGS-C47, sample Ar23/16. 9-22 - *Ancyrodella rotundiloba* sensu stricto Bryant, 1931; 9-10) IGS-C48, sample Ar23/14. 11-12) IGS-C49, sample Ar23/14. 13-14) IGS-C50, sample Ar 23/15. 15-16) IGS-C51, sample Ar23/14. 17-18) IGS-C52, sample Ar23/15. 19-20) IGS-C53, sample Ar23/15. 21-22) IGS-C54, sample Ar23/15.

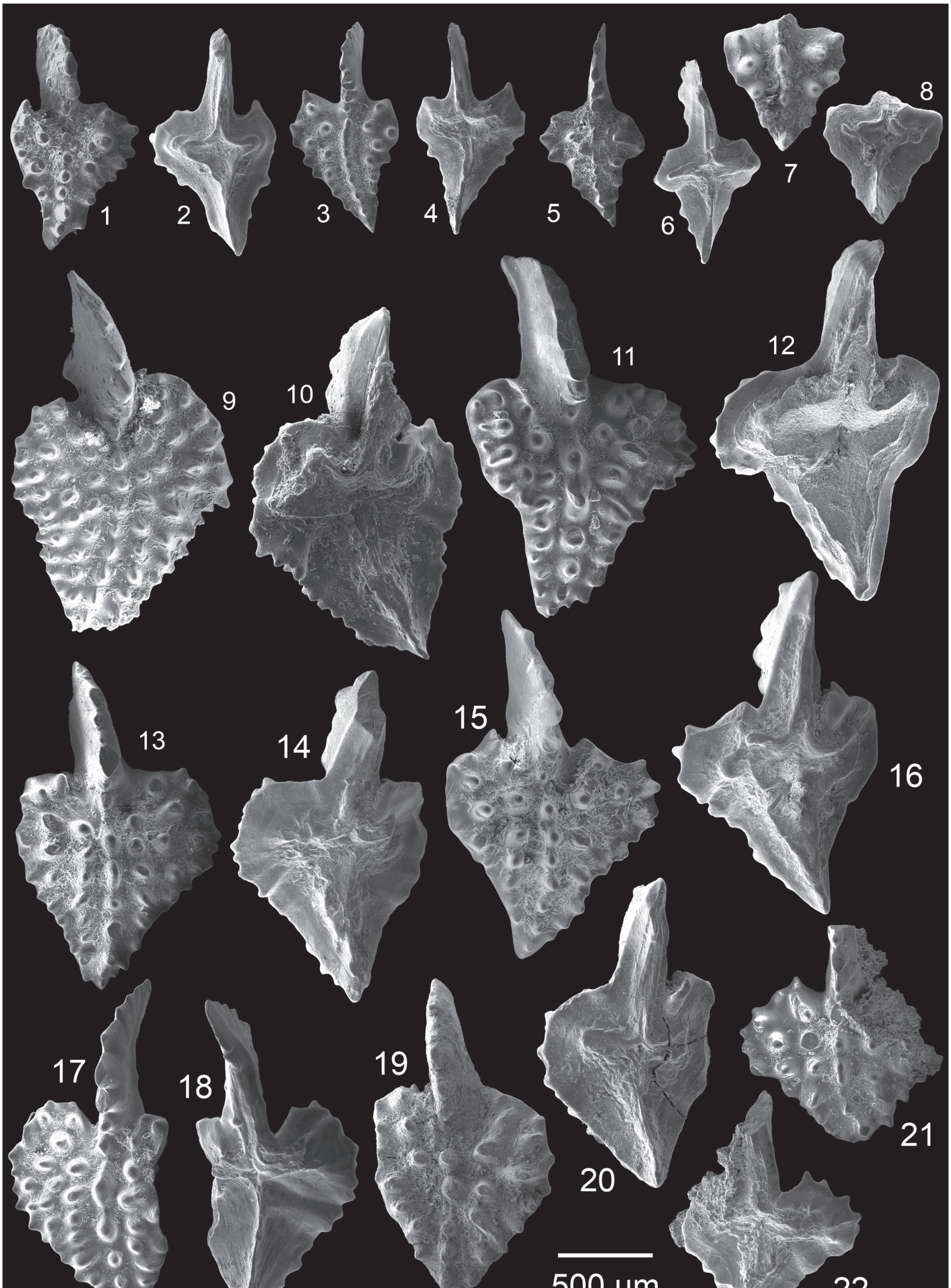


Fig. 6

Biofacies

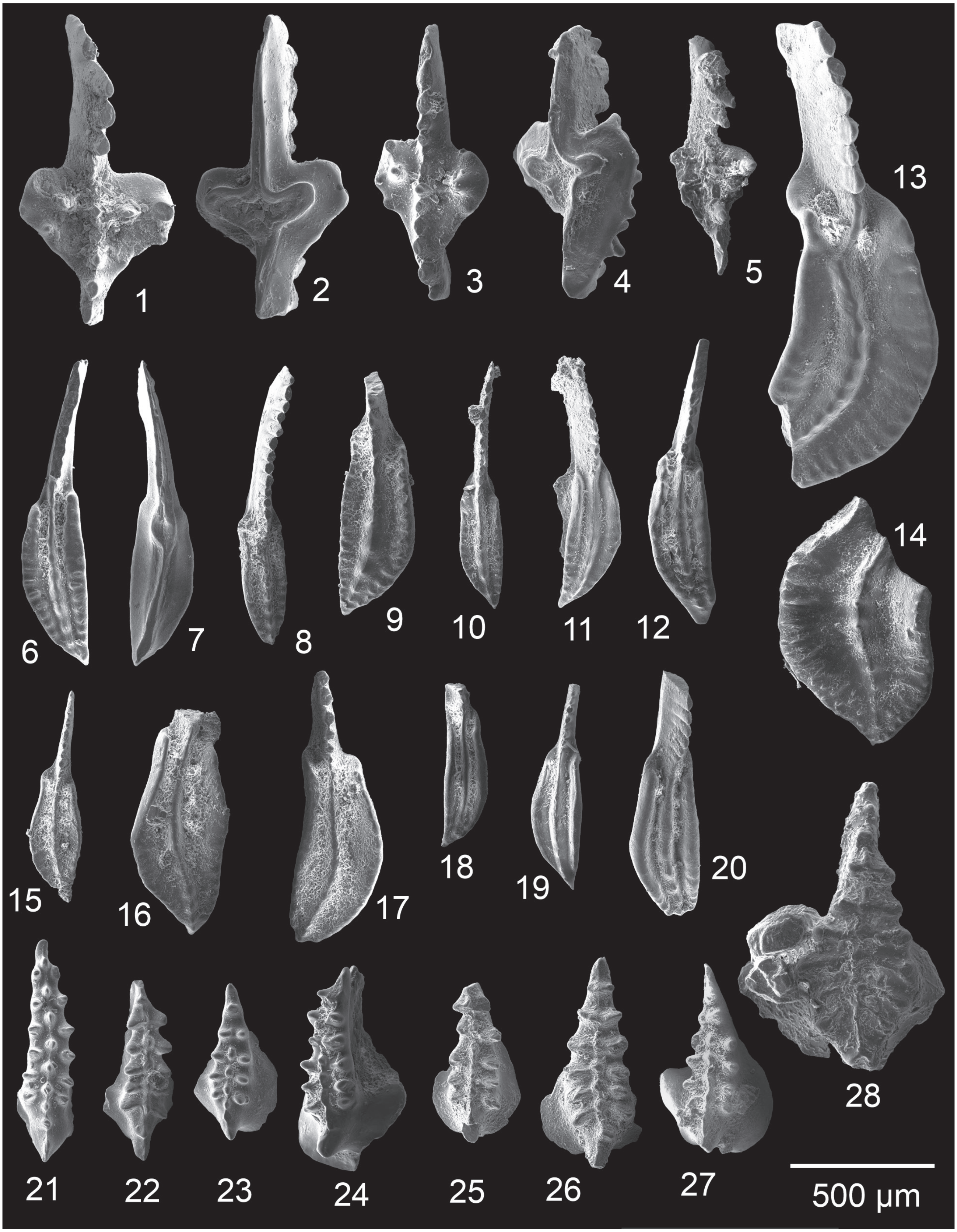
The conodont fauna in the upper Givetian is dominated by icriodids (ranging from 45.5% to 75.8%), whereas in the lower Frasnian, polygnathids and later ancyrodellids become dominant (Table 1). The conodont assemblages from the Arpi section indicate a relatively shallow marine environment, characterized by an icriodid-polygnathid to polygnathid-icriodid-ancyrodellid biofacies. According to Sandberg et al. (1989), the presence of *Ancyrodella* suggests a neritic setting away from the outer pelagic belt.

Discussion

GSSP Definition and Current Consensus on the Givetian–Frasnian Boundary. The Global Stratotype Section and Point (GSSP) defining the base of Frasnian boundary was established at the "Col du Puech de la Suque E" section, in southeastern Montagne Noire, France (Feist & Klapper 1985); it was subsequently ratified by the International Union of Geological Sciences (Klapper et al. 1987). The exact position of the boundary was chosen to coincide with the base of the Lower *asymmetricus* Zone of Klapper & Ziegler (1979) and is defined by the first appearance of *Ancyrodella rotundiloba* (early form), or A. pristina in current terminology (see Klapper, 2021). This level corresponds to the base of MN Zone 1 of Klapper (1989) (= FZ1 in current terminology) and falls within the middle part of the Lower *falsiovalis* Zone of Sandberg et al. (1989). Sandberg et al. (1989) challenged the GSSP marker, citing *A. rotundiloba*'s shallow-water affinity and uncertain phylogeny. Subsequent studies, such as Ziegler & Sandberg (1996, 2000), proposed alternative conodont markers, including *A. pristina* or *A. soluta*. Klapper (2000) later suggested relocating the boundary to the first occurrence of *Ancyrodella rotundiloba rotundiloba* s.s. The situation was further complicated by the findings of Liao et al. (2019), who documented an earlier occurrence of *A. pristina* below the current GSSP. They suggested that, before considering any stratigraphical revisions to the GSSP, the potential for selecting a different taxon should be thoroughly evaluated. This supports Klapper's (2000) proposal that a more appropriate level for the base of Frasnian might be the base of Bed 46, marked by the first occurrence of *A. rotundiloba rotundiloba* s.s. Despite numerous studies and reports, including those by e.g. Ziegler et al. (1976), Ziegler & Klapper (1982), Racki & Wrzolek (1989), Aboussalam & Becker (2007), Liao & Valenzuela-Rìos (2008, 2012, 2013, 2017), and Casier et al. (2013), the definition of the G–F boundary remains a complex issue and continues to be a subject of ongoing investigation. Nevertheless, the *A. pristina* criterion currently remains the operational standard (Becker et al. 2020).

Reassessing Givetian–Frasnian biostratigraphy in the Lesser Caucasus. The broader challenge of accurately identifying the boundary is particularly pronounced in the Lesser Caucasus, where the conodont biostratigraphy of the G–F transition remains poorly constrained, with only two significant studies, those by Ovnatanova & Aristov (1984) and Aristov (1994), having examined stratigraphic sections in Nakhichevan. These works, while pioneering, contain several stratigraphic inconsistencies that require revision in the light of modern taxonomic concepts. More particularly, Ovnatanova & Aristov's (1984) study of the Bagarsykh Horizon described a lower Frasnian conodont assemblage dominated by *Ancyrodella rotundiloba binodosa* and *Polygnathus decorosus*, which they correlated with the lowermost *asymmetricus* Zone (Fig. 2). However, this correlation presents a fundamental chronological conflict, as modern biostratigraphic schemes (Klapper 2000; Becker et al.

Fig. 7 - Scanning electron micrographs of selected conodont species from the Arpi section. 1-5 - *Ancyrodella binodosa* Uyeno, 1967; 1-2) IGS-C55, sample Ar23/15; 3-4) IGS-C56, sample Ar23/15; 5) IGS-C57, sample Ar23/15. 6-12 - *Polygnathus dubius* Hinde, 1879; 6-7) IGS-C24, sample Ar23/5; 8) IGS-C25, sample Ar23/14; 9) IGS-C26, sample Ar23/5; 10) IGS-C26/1 sample Ar23/14; 11) IGS-C27, sample Ar23/14; 12) IGS-C28, sample Ar 23/14. 13 - *Polygnathus webbi* Stauffer, 1938; IGS-C29, sample Ar 23/15. 14 - *Polygnathus* cf. *webbi* Stauffer, 1938; IGS-C30, sample Ar23/14. 15-17 - *Polygnathus alatus* Huddle, 1934; 15) IGS-C31, sample Ar23/14; 16) IGS-C31, sample Ar23/14; 17) IGS-C32, sample Arpi 23/15. 18-20 - *Polygnathus praepolitus* Kononova et al., 1996; 18) IGS-C33, sample Ar 23/15; 19) IGS-C34, sample Ar23/14; 20) IGS-C35, sample Ar23/14. 21-24 - *Icriodus cedarensis* Narkiewicz & Bultynck, 2010; 21) IGS-C36, sample Ar23/15. 22) IGS-C37, sample Ar23/5. 23) IGS-C38, sample Ar23/5. 24) IGS-C39, sample Ar23/15. 25 - *Icriodus* cf. *excavatus* Weddige, 1984; IGS-C43, sample Ar23/5. 26-28 - *Icriodus excavatus* Weddige, 1984; 26) IGS-C40, sample Ar23/5. 27) IGS-C41, sample Ar23/5. 28) IGS-C42, sample Ar23/5.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2020) clearly show that the *asymmetricus* Zone corresponds to the uppermost Givetian strata, whereas *Ancyrodella* species, including *A. rotundiloba binodosa*, are diagnostic of the Frasnian. The underlying Chrakhana Horizon, containing *Polygnathus xylus*, *P. normalis*, *Icriodus expansus* and *I. brevis*, was correctly assigned to the upper Givetian (*hermanni–cristatus* Zone). However, the absence of illustrated sections or range charts in their publication makes it impossible to verify either the stratigraphic relationships or the taxonomic identifications. Aristov (1994) established two biozones within the Bagarsykh Horizon: the *Ancyrodella binodosa* Zone, erroneously correlated with the lowermost *asymmetricus* Zone, and the *A. rotundiloba* Zone, placed within the lower *asymmetricus* Zone. This correlation reiterates the same stratigraphic inconsistency noted in an earlier study, as Aristov, although not explicitly stating it, regarded the *A. binodosa* Zone as representative of upper Givetian strata. Given these considerations, our study of shallow-water sequences containing diagnostic ancyrodellid species offers crucial insights for refining the stratigraphy of the Givetian–Frasnian boundary in the Lesser Caucasus. These findings not only enhance our understanding of Devonian basin evolution, but also underscore the importance of re-examining historical sections using modern analytical approaches.

Regional implications. While the reason of the co-occurrence of these *Ancyrodella* species at the Arpi section rather than their successive appearance (as documented at the base Frasnian Global Stratotype Section and Point [GSSP] in Montagne Noire, southern France), is difficult to determine, it is noteworthy that similar patterns have been observed in other northern Gondwanan localities. Most notably, this is the case of the Bou Tchrafine section of the Tafilalt Platform in the eastern Anti-Atlas (SE Morocco), which was examined in the search for a Middle–Upper Devonian stratotype section. Bensaid et al. (1985) mentioned that at the base of a condensed bed just above the boundary, *Ancyrodella rotundiloba* s.s. occurs alongside *A. alata*, with *A. pramosica* first appearing slightly above this level. This suggests that the lower part of the Lower *asymmetricus* Zone, and thus the MN 1 Zone (= FZ1 in current terminology), is not represented in this section according to the sequence established in the Montagne Noire. Bultynck (1986) later examined a 6 cm thick styliolinid coquina bed across the G–F transition, sampling the latter five cm, and noted that the bed directly below belongs to the *disparilis* Zone, while the overlying bed correlates with the Middle *asymmetricus* Zone, indicating a clear sedimentary gap. Subsequently, Aboussalam & Becker (2007) resampled multiple sections within the Tafilalt Platform and noted that their re-sampling of the G–F interval confirms that the basalmost Frasnian is absent in all but the Bine Jebilet section. Additionally, it is worth noting that they documented *A. pristina* and *A. binodosa* appearing within the same bed, considering them as contemporaneous sister taxa; the presence of *A. rotundiloba* s.s. was not recorded. Interestingly, despite high-resolution biostratigraphic studies by Gholamalian et al. (2013, 2022) examining the G–F interval across multiple sections in Iran, including Sar-Ashk, Anarak, Baghin, Sardar, and Hojedk, this particular species has yet to be recorded in the country. The same applies to Turkey, as Özkan et al. (2019) conducted a detailed study of the Kocadere section in the eastern Taurides, revealing only the presence of *A. pristina*. Therefore, it can be stated that this is the first record of *A. rotundiloba* s.s. in the region. It is also worth emphasizing the lithostratigraphic peculiarities of the studied section, which is dominated by black shales in its lower to middle Givetian part, with carbonate rocks only at the top, whereas G–F sections in both Iran and Turkey mainly consist of carbonate beds.

Sedimentological model. Sedimentation in the studied section is interpreted to have taken place on a mixed siliciclastic–carbonate system with subordinate carbonate development, characterized by the following features: (1) a facies succession from deeper to shallower environments; (2) absence of barrier reefs; (3) lack of extensive lagoonal or restricted facies; (4) widespread storm-related deposits; and (5) absence of slope sediments such as slumps and turbidites. These characteristics are consistent with a ramp setting rather than a shelf (Read 1985; Burchette & Wright 1992; Herbig & Weber 1996). Accordingly, the facies may be interpreted as reflecting a carbonate ramp model in the sense of Burchette & Wright (1992). This model may represent either a homoclinal or a distally steepened ramp (Flügel 2004). Most carbonate facies observed in the section are fully open marine, as indicated by the abundance of crinoids and brachiopods (Mabille &

Boulvain 2007). However, detrital silt- to sand-sized quartz is locally present. The scarcity of lamination and other sedimentary structures likely reflects intense bioturbation (Sepkoski et al. 1991). Among the sampled microfacies, Ar23/5 represents the most distal carbonate facies, characterized by tempestite deposits that accumulated around the storm wave base, indicative of a mid-ramp depositional environment. Ar23/10 marks the transition toward the inner ramp and exhibits extensive micritization, reflecting proximal mid-ramp conditions approaching shallower environments. The subsequent bed, Ar24/12, differs slightly from Ar23/5 and 23/10 in assemblage composition due to a higher abundance of mollusks, which corresponds to the inner ramp, indicating a slightly shallower depositional setting. The upper part of the section shows an increased abundance of well-preserved brachiopods with delicate morphological features, such as the frills on atrypid shells, which, according to Copper (1967), are characteristic of low-energy settings. Together with the presence of bioturbation and burrows in thin sections, these features indicate that the Ar23/15–Ar23/17 interval was deposited in a quiet inner-ramp environment, partially protected by shoal complexes (Bertola et al., 2013). Consequently, the facies distribution suggests that the lower to middle parts of the section, dominated by black shales with occasional crinoidal packstone beds, represent a low-oxygen distal environment deposited in a mid-ramp setting. In contrast, the bioclastic wackstone and overlying sandstones at the top of the section likely indicate a more proximal setting, although the former still reflect relatively low-energy conditions. The abrupt contact between these facies associations, lacking intermediate deposits, implies a period of non-deposition or erosion, followed by a marked environmental shift to shallow-water deposition rather than a gradual regression.

It is worth noting that the G–F boundary is commonly associated with a global transgression, which followed a regressive phase during the Upper FZ1–FZ2 (see Walliser 1996; Becker et al. 2012). The lithostratigraphic peculiarities of the Arpi section correlate with this global record, as its shallowing trend from the upper Givetian to the lower Frasnian occurred within the same interval. Regionally, however, the Arpi section differs from most documented sections in both Iran and Turkey, where the G–F interval is predominantly represented by carbonate facies (Özkan 2019; Wehrmann et al. 2010; Gholamalian 2013, 2022). The only section with a very similar lithostratigraphic succession of black shales near the G–F boundary is the Kocadere section in the Eastern Taurides. In that section, this black shale interval, indicative of anoxic conditions, is interpreted as a facies expression of the Frasnes Event, though further biological evidence is required to confirm this (Wehrmann et al. 2010). A comparable interpretation may also apply to the black shale interval exposed between beds Ar24/12 and Ar23/14 in the Arpi section.

Conclusions

The integrated biostratigraphic and lithofacies analysis of the Arpi section provides the first robust framework for understanding the Givetian–Frasnian (G–F) transition in the Lesser Caucasus. The appearance of *Ancyrodella rotundiloba* s.s., *A. pristina*, and *A. binodosa* in the upper part of the section constrains this interval to the lowermost Frasnian. Notably, *A. pristina* does not precede either *A. rotundiloba* s.s. or *A. binodosa*, and this pattern suggests that the lower part of the FZ1 is either absent from the Arpi section or confined to the underlying black shale interval, which yielded no conodonts. Consequently, the limestone interval at the top correlates with the upper FZ1–FZ2. The absence of *Ancyrodella* in underlying beds, alongside species such as *Polygnathus dubius*, *Icriodus cedarensis*, and *I. excavatus*, indicates upper Givetian strata, specifically correlating with the Upper *hermanni–norrisi* Zones. Lithofacies analysis reveals an abrupt transition from distal facies in the lower to middle section to more proximal deposits in the lower Frasnian interval, indicating a shallowing trend across the G–F transition. The Givetian interval reflects an anoxic, low-energy and storm-influenced environment, whereas the Frasnian interval exhibits comparatively increased oxygenation, although conditions remained low-energy. Future work should focus on expanded sampling above the Givetian interval to ascertain whether the lower FZ1 is preserved or absent due to a hiatus, as documented in Moroccan sections. If a hiatus is confirmed, this pattern may reflect a broader regional phenomenon rather than a localized event. Additionally, subsequent research should incorporate geochemical proxies to differentiate between local and global environmental perturbations, complemented by comparative analyses of coeval sections from Armenia and Nakhichevan.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access.

Acknowledgements: This research was supported by the Higher Education and Science Committee of the Ministry of Education, Science, Culture, and Sports of the Republic of Armenia (Research project 22RL-016). Fieldwork was conducted with the logistic support of the Institute of Geological Sciences, National Academy of Sciences of the Republic of Armenia. VS and TD thank the Erasmus + Program for funding their 2025 staff mobility to Lille and Yerevan, respectively. We extend our sincere gratitude to Prof. Gilbert Klapper (University of Iowa) and Dr. Katarzyna Narkiewicz (Polish Geological Institute) for their invaluable taxonomic consultations. We are grateful to Karine Asatryan (Institute of Chemical Physics after A. B. Nalbandyan) for her expertise in SEM imaging of conodont specimens, and to Alexandre Allain (Lilliad, University of Lille) for providing essential literature on Givetian–Frasnian boundary definitions. Tamara Hambardzumyan, Aram Ghazaryan and Meri Eghiazaryan are gratefully acknowledged for their meticulous work in conodont extraction and processing. The manuscript benefited from the constructive reviews of Yichun Zhang, Jau-Chyn Liao and Andrey V. Zhuravlev to whom we are sincerely grateful.

References

Aboussalam Z.S. & Becker R.T. (2007) - New upper Givetian to basal Frasnian conodont fauna from the Tafilalt (Anti-Atlas, southern Morocco). *Geologica Quarterly*, 51: 345-374.

Abrahamyan M.S. (1959) - Novyye vidy brakhiopod iz verkhnego devona Armenii [New brachiopod species from the Upper Devonian of Armenia]. *Izvestiya Akademii Nauk Armyanskoy SSR*, 12: 4-10 [in Russian and in Armenian].

Abrahamyan M.S. (1964) - Karbon [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 SSR], 2: 96-118. Yerevan, Akademiya Nauk Armyanskoy SSR. [in Russian]

Abrahamyan M.S., Arakelyan R.A. & Azizbekov Sh. A. (1973) - Malyy Kavkaz (Yuzhnoe Zakavkaz'ya) [Lesser Caucasus (South Transcaucasia)]. In: Rzhonsnitskaya M.A. (Ed.) - Kavkazskaya Geosinklinal'naya Oblast i Predkavkaz'e [Caucasian geosynclinal region and Ciscaucasia]. In: Nalivkin D.V., Rzhonsnitskaya M.A. & Markovski B.P. (Eds) 1: 210-219. Stratigrafiya SSSR, Devonskaya Sistema Nedra, Moscow [in Russian].

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]. Yerevan, Akademiya Nauk Armyanskoy SSR, Institut Geologicheskikh Nauk, Yerevan, 142 pp. [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 SSR], 2: 46-96. Akademiya Nauk Armyanskoy SSR, Yerevan [in Russian].

Aristov V.A. (1994) - Konodonty devona-nizhnego karbona Evrazii: soobshhestva, zonalnoye raschleneniye, korrelyatsiya raznofatsialnykh otlozheniy [Conodonts from the Devonian and Lower Carboniferous of Eurasia: communities, zonation and correlation of heterofacial deposits]. *Trudy Geologicheskogo Instituta Rossiyskoy Akademii Nauk*, 484: 1-193 [in Russian].

Ashouri A.R. (2004) - Late Devonian and Middle–Late Devonian conodonts from eastern and northern Iran. *Revista Española de Micropaleontología*, 36: 355-365.

Ashouri A.R. (2006) - Middle Devonian–Early Carboniferous conodont faunas from the Khoshyeilagh Formation, Alborz Mountains, North Iran. *Journal of Sciences, Islamic Republic of Iran*, 17: 53-65.

Becker R.T., Gradstein F.M. & Hammer O. (2012) - The Devonian Period. In: Gradstein F.M., Ogg J.G., Schmitz M.D. & Ogg G.M. (Eds) - The Geologic Time Scale: 559-601, Elsevier, Amsterdam.

Becker R.T., Aboussalam Z.S., El Hassani A., Eichholt S. & Helling S. (2020) - The Devonian of the Oued Cherrat Zone (Western Meseta) – review and new data. *Frontiers in Science and Engineering, Earth, Water and Oceans, Environmental Sciences*, 10: 27-85.

Bensaid M., Bultynck P., Sartenaer P., Walliser O.H. & Ziegler W. (1985) - The Givetian–Frasnian boundary in pre-Sahara Morocco. *Courier Forschungsinstitut Senckenberg*, 75: 287-300.

Bertola C., Boulvain F., Da Silva A.-C. & Poty E. (2013) - Sedimentology and magnetic susceptibility of Mississippian (Tournaisian) carbonate sections in Belgium. *Bulletin of Geosciences*, 88: 69-82.

Braun W.K., Norris A.W. & Uyeno T.T. (1988) - Late Givetian to Early Frasnian biostratigraphy of western Canada: The Slave Point–Waterways boundary and related events. In: McMillan, N.J., Embry A.F. & Glass D. J. (Eds) - Devonian of the World. 3: Paleontology, Paleoecology, Biostratigraphy. Proceedings of the Second International Symposium on the Devonian System, Memoirs 14: 93-111. Canadian Society of Petroleum Geologists, Calgary.

Buggisch W. & Joachimski M.M. (2006) - Carbon isotope stratigraphy of the Devonian of Central and Southern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240: 68-88.

Bultynck P. (1986) - Accuracy and reliability of conodont zones: the *Polygnathus asymmetricus* "Zone" and the Givetian–Frasnian boundary. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 56: 269-280.

Burchette T.P. & Wright V.P. (1992) - Carbonate ramp depositional systems. *Sedimentary Geology*, 79: 3-57.

Casier J.G. & Préat A. (2009) - Late Givetian to Middle Frasnian ostracods from Nismes (Dinant Synclinorium, Belgium) and their lithological context. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 79: 87-115.

Casier J.G., Devleeschouwer X., Maillet S., Petitclerc E. & Préat A. (2013) - Ostracods and rock facies across the Givetian/Frasnian boundary interval in the Sourd d'Ave section at Ave-et-Auffe (Dinant Synclinorium, Ardenne, Belgium). *Bulletin of Geosciences*, 88: 241-264.

Copper P. (1967) - Adaptations and life habits of Devonian atrypid brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 3: 363-379.

Corradini C., Henderson C., Barrick J.E. & Ferretti A. (2026) - Conodonts in Biostratigraphy. A 300-million-years long journey through geologic time. *Newsletters on Stratigraphy*, 59: 77-116.

Devleeschouwer X., Petitclerc E., Spassov S. & Préat A. (2010) - The Givetian–Frasnian boundary at Nismes parastratotype (Belgium): The magnetic susceptibility signal controlled by ferromagnetic minerals. *Geologica Belgica*, 13: 351-366.

Ebert J. (1993) - Globale Events im Grenz-Bereich Mittel-/Ober-Devon. *Gottinger Arbeiten zur Geologie und Paläontologie* 59: 1-106. University of Göttingen, Göttingen.

Feist R. & Klapper G. (1985) - Stratigraphy and conodonts in pelagic sequences across the Middle–Upper Devonian boundary, Montagne Noire, France. *Palaeontographica Abteilung A*, 188: 1-18.

Flügel E. (2004) - Microfacies of carbonate rocks. Springer-Verlag, Berlin, 976 pp.

Gholamalian H., Hairapetian V., Barfehei N., Mangelian S. & Faridi P. (2013) - Givetian–Frasnian boundary conodonts from Kerman Province, Central Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, 119: 141-158.

Gholamalian H., Hairapetian V. & Poosti M. (2022) - Middle–Late Devonian boundary conodonts from Anarak and Sar-Ashk sections, Central Iran. *Turkish Journal of Earth Sciences*, 31: 71-84.

Gouwy S., Hayduckiewicz J. & Bultynck P. (2007) - Conodont-based graphic correlation of upper Givetian–Frasnian sections of the Eastern Anti-Atlas (Morocco). *Geologica Quarterly*, 51: 375-392.

Grechishnikova I.A., Levitskii E.S., Polozhikhina A.I. & Feliks V.P. (1983). - Kratkaya kharakteristika opornogo razreza srednego devona u sela Danzik (Nakhichevanskaya ASSR). [Brief characteristics of the reference section of the Middle Devonian near the village of Danzik (Nakhchivan ASSR)]. *Izvestiya Vysshikh Uchebnykh Zavedeniy, Geologiya i Razvedka*, 11: 98-105.

Herbig H.-G. & Weber H.M. (1996) - Facies and stromatoporoid biostromes in the Strunian (Latest Devonian) of the Aachen region, Germany. In: Reitner J., Neuweiler F. & Gunkel F. (Eds) - Global and regional controls on biogenic sedimentation. I. Reef evolution 2: 359-364. Göttinger Arbeiten zur Geologie und Paläontologie, Sonderband, Göttingen.

Hinde G.J. (1879) - On conodonts from the Chazy and Cincinnati Group of the Cambro–Silurian, and from the Hamilton and Genesse-Shale divisions of the Devonian, in Canada and the United States. *Quarterly Journal of the Geological Society of London*, 35: 351-369.

House M.R. (1985) - Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature*, 313: 17-22.

House M.R. (2002) - Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 181: 5-25.

Hua L., Ma X. & Wei L. (2009) - A Middle–Upper Devonian boundary section in the open-platform, platform-margin facies of Guilin, South China. *Acta Geologica Sinica*, 83: 524-534.

Khalymbadzha V.G. & Chernysheva N.G. (1970) - Konodonty rod *Ancyrodella* iz Devonskikh otlozheniy Volgo-Kamskogo kraya i ikh stratigraficheskoe znachenie [Conodonts of the genus Ancyrodella from the Devonian deposits of the Volga-Kama region and their stratigraphic significance]. In: Biostratigrafiya I Paleontologiya Paleozoyskikh otlozheniy vostoka Russkoy Platformy I zapadnogo priural'ya [Biostratigraphy and paleontology of the Palaeozoic deposits of the Eastern Russian Platform and the Western Urals]. 1: 81-103. Izdatel'stvo Kazanskogo Universiteta Vypusk [in Russian].

Klapper G. (1985) - Sequence in the conodont genus *Ancyrodella* in the Lower *asymmetricus* Zone (earliest Frasnian, Upper Devonian) of the Montagne Noire, France. *Palaeontographica, Abteilung A*, 188: 19-34.

Klapper G. (1989) - The Montaigne Noire Frasnian (Upper Devonian) Conodont Succession. In: McMillan N.J., Embry D.J. & Glass D.J. (Eds) - Devonian of the World, Proceedings of the Second International Symposium on the Devonian System, 14: 449-468. Canadian Society of Petroleum Geologists.

Klapper G. (2000) - Species of Spathognathodontidae and Polygnathidae (Conodonta) in the recognition of Upper Devonian stage boundaries. *Courier Forschungsinstitut Senckenberg*, 220: 153-159.

Klapper G. (2021) - Revision of the Frasnian Late Devonian conodont genus *Ancyrodella*. *Bulletin of Geosciences*, 96: 295-325.

Klapper G. & Johnson J.G. (1990) - Revisions of Middle Devonian conodont zones. In: Johnson J.G. (Ed.) - Lower and Middle Devonian brachiopod-dominated communities of Nevada, and their position in a biofacies-province-realm model. *Journal of Paleontology,* 64: 934–941.

Klapper G. & Kirchgasser W.T. (2016) - Frasnian Late Devonian conodont biostratigraphy in New York: Graphic correlation and taxonomy. *Journal of Paleontology*, 90: 525-554.

Klapper G. & Ziegler W. (1979) - Devonian conodont biostratigraphy. *Special Papers in Palaeontology*, 23: 199-224.

Klapper G., Feist R. & House M.R. (1987) - Decision on the boundary stratotype for the Middle/Upper Devonian Series boundary. *Episodes*, 10: 97-101.

Kononova L.I., Alekseev A.S., Barskov I.S & REIMERS A.N. (1996) - New species of Polygnathid assemblages from the Frasnian Stage of the Moscow Syneclise. *Paleontologicheskii Zhurnal* 3: 94-99.

Liao J.C. & Valenzuela-Ríos J.I. (2008) - Givetian and early Frasnian conodonts from the Compte section (Middle–Upper Devonian, Spanish Central Pyrenees). *Geologica Quarterly*, 52: 1-18.

Liao J.-C. & Valenzuela-Ríos J.I. (2012) - Upper Givetian and Frasnian (Middle and Upper Devonian) conodonts from Ampriú (Aragonian Pyrenees, Spain): Global correlations and palaeogeographic relations. *Palaeontology*, 55: 819-842.

Liao J.-C. & Valenzuela-Ríos J.I. (2013) - The Middle and Upper Devonian conodont sequence from La Guardia d'Ares sections (Spanish Central Pyrenees). *Bulletin of Geosciences*, 88: 339-368.

Liao J.-C. & Valenzuela-Ríos J.I. (2017) - Givetian (Middle Devonian) historical bio- and chronostratigraphical subdivision based on conodonts. *Lethaia*, 50: 440-446.

Liao J.C., Girard C., ValenzuelaRíos J.I. & Feist R. (2019) - New conodont data from the Middle–Upper Devonian boundary stratotype at Col du Puech de la Suque (Montagne Noire, France). *STRATI 2019, Third International Congress on Stratigraphy, Milano,* p. 188.

Mabille C. & Boulvain F. (2007) - Sedimentology and magnetic susceptibility of the Upper Eifelian –Lower Givetian (Middle Devonian) in southwestern Belgium: Insights into carbonate platform initiation. In Álvaro J.J., Aretz M., Boulvain F., Munnecke A., Vachard D. & Vennin E. (Eds) - Palaeozoic reefs and bioaccumulations. Climatic and evolutionary controls, 275: 109-124. Geological Society, Special Publications, London.

Milanovsky E.E. (1968) - Noveyshaya tektonika Kavkaza [Neotectonics of the Caucasus]. Nedra, Moscow, 483 pp. [in Russian].

McGhee G.R., Clapham M.E., Sheehan P.M., Bottjer D.J. & Droser M.L. (2013) - A new ecological-severity ranking of major Phanerozoic biodiversity crises. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 370: 260-270.

Narkiewicz K. & Bultynck P. (2007) - Conodont biostratigraphy of shallow marine Givetian deposits from the Radom-Lublin area, SE Poland. *Geological Quarterly*, 51: 419-442.

Narkiewicz K. & Bultynck P. (2010) - The Upper Givetian (Middle Devonian) subterminus conodont zone in North America, Europe, and North Africa. *Journal of Paleontology*, 84: 588-625.

Nikogosian I.K., Bracco Gartner A.J., Mason P.R., van Hinsbergen D.J.J., Kuiper K.F., Kirscher U., Matveev S., Grigoryan A., Grigoryan E., Israyelyan A., van Bergen M.J., Koornneef J.M., Wijbrans J.R., Davies G.R. & Meliksetian K. (2023) - The South Armenian Block: Gondwanan origin and Tethyan evolution in space and time. *Gondwana Research*, 121: 168-195.

Ovnatanova N.S. & Aristov V.A. (1984) - Biostratigrafiya verkhnedevonskikh otlozheniy Zakavkaz'ya po konodontam [Biostratigraphy of the Upper Devonian deposits of Transcaucasia based on conodonts]. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya,* 5: 61-68 [in Russian].

Özkan R., Nazik A., Munnecke A., Demiray D.G., Schindler E., Özbek T.A., Zor E.Ş., Yılmaz İ., Brocke R., Sancay R.H., Wilde V. & Yalçın M.N. (2019) - Givetian–Frasnian (Middle/Upper Devonian) transition in the eastern Taurides, Turkey. *Turkish Journal of Earth Sciences*, 28: 207-231.

Qie W., Liang K. & Königshof P. (2019) - Devonian palaeoecosystems and palaeoenvironments of South China. *Palaeobiodiversity and Palaeoenvironments*, 99: 1-5.

Racki G. (1993) - Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. *Acta Palaeontologica Polonica*, 37: 87-182.

Racki G. & Wrzolek T. (1989) - Middle–Upper Devonian boundary: Ambiguous reality of its stratotype. *Courier Forschungsinstitut Senckenberg*, 110: 231-236.

Read J.E. (1985) - Carbonate platform facies models. *Bulletin of the American Association of Petroleum Geologists*, 69: 1-21.

Sandberg C.A., Ziegler W. & Bultynck P. (1989) - New standard conodont zones and early *Ancyrodella* phylogeny across the Middle–Upper Devonian boundary. *Courier Forschungsinstitut Senckenberg*, 110: 195-230.

Sepkoski J.J. Jr., Bambach R.K. & Droser M.L. (1991) - Secular changes in Phanerozoic event bedding and biological overprint. In: Einsele G., Ricken W. & Seilacher A. (Eds) - Cycles and events in stratigraphy: 298-312. Berlin, Springer.

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 the National Academy of Sciences of the Republic of Armenia, Earth Sciences*, 72: 3-18.

Serobyan V., Danelian T., Hairapetian V., Grigoryan A., Crônier C., Randon C. & Mottequin B. (2023) - Frasnian (Upper Devonian) brachiopods from Armenia: Biostratigraphic and paleobiogeographic implications. *Rivista Italiana di Paleontologia e Stratigrafia*, 129: 373-409.

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: Sosson M., Kaymakci N., Stephenson E.A., Bergerat F. & Starostenko V. (Eds) - Sedimentary Basin Tectonics from the Black Sea and Caucasus to the Arabian Platform 340: 329-352. Geological Society, London.

Stauffer C.R. (1938) - Conodonts of the Olentangy Shale. *Journal of Paleontology*, 12: 411-443.

Stichling S., Becker R.T., Hartenfels S., Aboussalam Z.S. & May A. (2022) - Drowning, extinction, and subsequent facies development of the Devonian Hönne Valley Reef (northern Rhenish Massif, Germany). *Palaeobiodiversity and Palaeoenvironments*, 102: 629-696.

Uyeno T.T. (1967) - Conodont zonation, Waterways Formation (Upper Devonian), northeastern and central Alberta. *Geological Survey of Canada Paper*, 67: 1-21.

Walliser O.H. (1996) - Global events in the Devonian and Carboniferous. In: Walliser O.H. (Ed.) - Global Events and Event Stratigraphy: 225-250. Springer-Verlag, Berlin.

Weddige K. (1984) - Zur Stratigraphie und paläogeographie des Devons und Karbons von NE Iran. *Senckenbergiana lethaea*, 65: 179-223.

Wehrmann A., Yılmaz I., Yalçın M.N., Wilde V., Schindler E., Weddige K., Saydam Demiray G., Özkan R., Nazik A. & Nalcıoğlu G. (2010) - Devonian shallow-water sequences from the north Gondwana coastal margin (central and eastern Taurides, Turkey). *Gondwana Research*, 17: 546-560.

Ziegler W. & Klapper G. (1982) - The *disparilis* conodont Zone, the proposed level for the Middle–Upper Devonian boundary. *Courier Forschungsinstitut Senckenberg*, 55: 463-492.

Ziegler W. & Sandberg C.A. (1996) - Reflexions on Frasnian and Famennian Stage boundary decisions as a guide to future deliberations. *Newsletters on Stratigraphy*, 33: 157-180.

Ziegler W. & Sandberg C.A. (2000) - Utility of palmatolepids and icriodontids in recognizing Upper Devonian series, stage, and possible substage boundaries. *Courier Forschungsinstitut Senckenberg*, 225: 335-347.

Ziegler W., Klapper G. & Johnson J.G. (1976) - Redefinition and subdivision of the *varcus*-Zone (Conodonts, Middle–?Upper Devonian) in Europe and North America. *Geologica et Palaeontologica*, 10: 109-140.