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Chondrichthyan microfossils from the Famennian and Tournaisian of Armenia

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ABSTRACT:

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The assemblages of chondrichthyan microremains from the Famennian of Armenia show great resemblances to those from central Iran. Particularly, the very rich sample (almost 200 teeth) from the lower Famennian of Ertych contains a fauna similar to that from the Iranian section of Hutk, and the sample from the upper Famennian of Khor Virap has its counterpart in the sample from Dalmeh, Iran. Only one chondrichthyan taxon definitely unknown from Iran, *Ertychius intermedius* gen. et sp. nov., was recorded. The other newly described species, *Lissodus lusavorichi* sp. nov., was noted earlier from Dalmeh, but at that time was left unnamed. It appears that the same type of relatively shallow marine environment predominated in the central and north-western parts of the Iranian Platform during the Famennian and that in a given time-interval the same type of ichthyofauna was distributed throughout the area. The single lower Tournaisian sample from the Sevakavan section yielded a peculiar form of thrinacodont teeth, possibly intermediate between *Thrinacodus tranquillus* and *Th. ferox*.

Key words: Chondrichthyes; Teeth; Devonian; Carboniferous; Transcaucasus.

INTRODUCTION

Hitherto, only a few reports on the occurrence of fish remains in the Devonian and Lower Carboniferous of Armenia and Nakhichevan (a nearby autonomous territory in the southern Transcaucasus) were published. A Late Devonian (probably Frasnian) placoderm *Bothriolepis* cf. *prima* and crossopterygians were recorded from Armenia by Garkusha *et al.* (1971). Krupina (1979) described an endemic lungfish, *Ganorhynchus caucasius* from the upper Famennian of the Danzik section in Nakhichevan. Zakharenko (2000) reported on the occurrence of *Holonema* and a coccosteid placoderm from the Eifelian of the Janaam-Deresi section. Famennian–Tournaisian fish microremains were also recently recovered from the Gerankalasy section, Nakhichevan (Lebedev 2005).

In the Middle Palaeozoic, the South Armenian Block formed the north-western extension of the North Gondwanan/Peri-Gondwanan Iranian Platform. Studies of Upper Devonian chondrichthyans from Iran were started by Janvier (1977, 1981), but large-scale investigations were not undertaken until the last years of the 20th century, when one of us (VH) began systematic collecting and processing samples from several outcrops in central Iran. The subsequent cooperation of VH and MG, based on that material and new collections, led to a larger work (Ginter *et al.* 2002), as well as several shorter publications presenting fossil fish microfossils from the study area (Hairapetian *et al.* 2008; Hairapetian and Ginter 2009, 2010). In the meantime (2003), we (together with AG) organised a short expedition to the Devonian of central Armenia, hoping to find faunas different from the shallow-water assemblages that characterize of the central part of the Platform.

However, it turned out that the lithology of the Armenian Upper Devonian is similar to that known from Iran, and so is the chondrichthyan fauna, despite the long distance. We found almost no taxa unreported from Iran. Also the relative abundances of taxa in the samples (where statistical methods were applicable) coincided with those in Iranian samples of an equivalent age. Additional collecting in the next years did not change this picture. Thus far, the results of our studies were presented twice, during the conferences in Yerevan, Armenia (Hairapetian *et al.* 2005) and at Żarki, Poland (Ginter and Hairapetian 2010). We consider that, despite the resemblances to the earlier described Iranian microfossils, the material from Armenia deserves systematic, formal publication, because of its high quality. We also hope that the stratigraphic columns of the most important fish-bearing localities, provided here, will be a useful update to the stratigraphy of the Palaeozoic of Armenia.

Institutional abbreviations: MWGUW, Museum of the Faculty of Geology, University of Warsaw, Poland.

GEOLOGICAL SETTING

Upper Devonian and Lower Carboniferous of Armenia

Mid-Palaeozoic deposits occur mainly in the southern part of central Armenia within the South Armenian Block of Gondwanan origin (Sosson *et al*. 2010). They are composed everywhere of shallow marine deposits, developed in neritic facies, such as Devonian and Permian carbonates, and Upper Devonian–Lower Carboniferous mixed carbonate-siliciclastic sequences. Mid-Palaeozoic fossiliferous deposits crop out on both sides of the border between south-western Armenia and the area of Nakhichevan (Text-figs 1, 2). Biostratigraphy is based mostly on monographic studies of individual faunal groups, such as nautiloids (actinoceratids), brachiopods, corals, foraminifers, ostracods, crinoids, algae, and conodonts; several composite works are also available.

The Devonian outcrops in the area were first examined by Abich (1858), and then several papers were published between 1900 and 1950 (e.g. Frech and Arthaber, 1900; Bonnet, 1947). In Armenia, the Upper Devonian to Lower Carboniferous biostratigraphy was studied systematically by Arakelyan (1964) and Abramyan (1957, 1964). They also introduced local Upper Devonian lithostratigraphical units. The first Devonian biostratigraphical zonal scheme based on brachiopods was established by Rzhonsnitskaya (1948). Subsequently it was revised and correlated with local conodont assemblages and the standard conodont biozones by Mamedov and Rzhonsnitskaya (1985), and recently updated (Rzhonsnitskaya and Mamedov 2000, see Text-fig. 3).

Most of the authors frequently used a term “suite” for the Russian word “svita” in their stratigraphic publications on the area. Here we tentatively use the term “Formation” instead.

The Givetian/Frasnian boundary is placed within the lowermost part of the Bagarsykh Formation, which comprises mainly yellowish sandstones and quartzites with some units of dark grey limestones interbedded with black shales. Its type section is situated in the gorge of the Bagarsykh river, Nakhichevan area. The overlying Yaidzhi Formation (middle to upper Frasnian) consists of non-marine quartzites and sandstones.

The Famennian has a wider distribution than the Frasnian in Armenia. It is characterised by the absence of corals and by the abundance of brachiopods. The lower Famennian (*triangularis–crepida* Conodont Zone) is subdivided onto two lithostratigraphical units (Noravank and Ertych formations), whereas the middle Famennian includes three formations (Kadrlu, Shamamidzor, and Gortun Formations). The Noravank Formation comprises dark grey brachiopod and algal limestones, black shales, and quartzites. The Ertych Formation consists of quartzites, black shales and limestones. The middle Famennian (*rhomboidea–marginifera* Conodont Zone) Kadrlu Formation consists mainly of alternating quartzites, sandstones, shales and some beds of limestones. In the type section, at the village of Kadrlu, this formation is conformably overlain by the Lower Carboniferous deposits. The Shamamidzor Formation is well exposed throughout the area. It consists of intercalating limestones, quartzites and shales with a few units of sandstones (Upper *marginifera–trachytera* Conodont Zone). The Gortun Formation (*postera*–Lower *expansa* Conodont Zone) is also widely distributed. It comprises ferruginous-sandy limestones, sandstones and black shales. The Arshakiakhpur Formation (*sensu stricto*) consists of intercalating quartzites, dark clayey shales, dark grey limestones and shales. It contains conodonts characteristic of the Middle *expansa*–Middle *praesulcata* Conodont Zone.

The Lower Carboniferous consists of siliciclastic and carbonate rocks rich in corals and brachiopods. In the upper part of the sequence, corals predominate in the carbonates, whereas brachiopods are only locally abundant. Three Lower Carboniferous formations (Gerankalasy, Armash and Saripap) are presently recognised within the Tournaisian to Viséan stages.

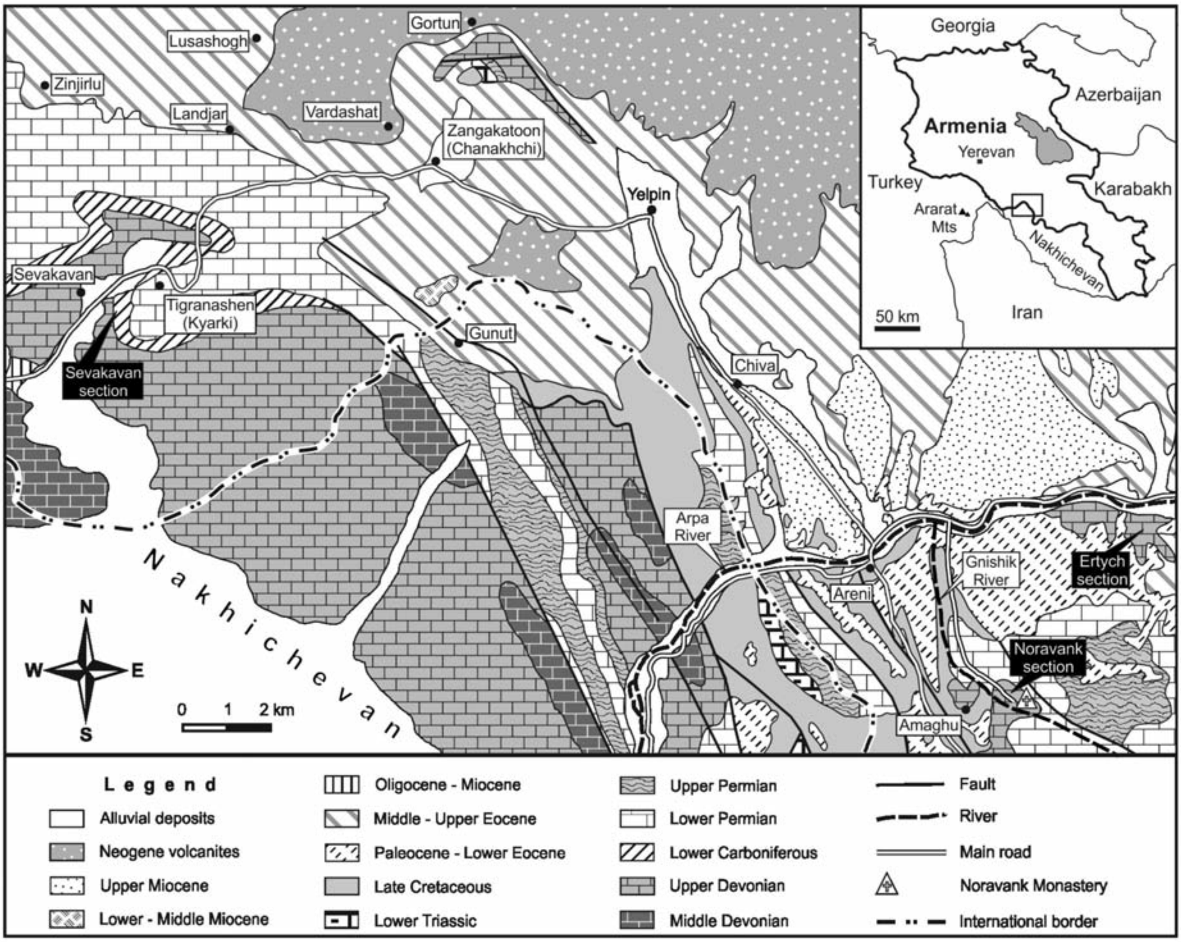
The Devonian/Carboniferous boundary is tentatively placed at the base of the Kyarki beds, which represent a basal unit of the Gerankalasy Formation (*sulcata* Conodont Zone), comprising shale units interbedded with sandy limestone rich in brachiopods. These beds are presently considered as the lowermost Tournaisian, but they are poor in diagnostic conodonts and may include the uppermost part of the *praesulcata* Conodont Zone. The Gerankalasy Formation consists in general of limestones, sandstones and shales with rich coral and brachiopod faunas.

The carbonates of the overlaying upper Tournaisian Armash Formation contain an abundant fauna of corals, brachiopods and foraminifers. The Viséan deposits, several hundred metres thick, referred to the Saripap Formation have a limited distribution, with the best exposures within the Saripap anticline. They are composed of interbedded calcareous sandstones and sandy to argillaceous, bituminous, bioclastic limestones, with abundant corals and foraminifers.

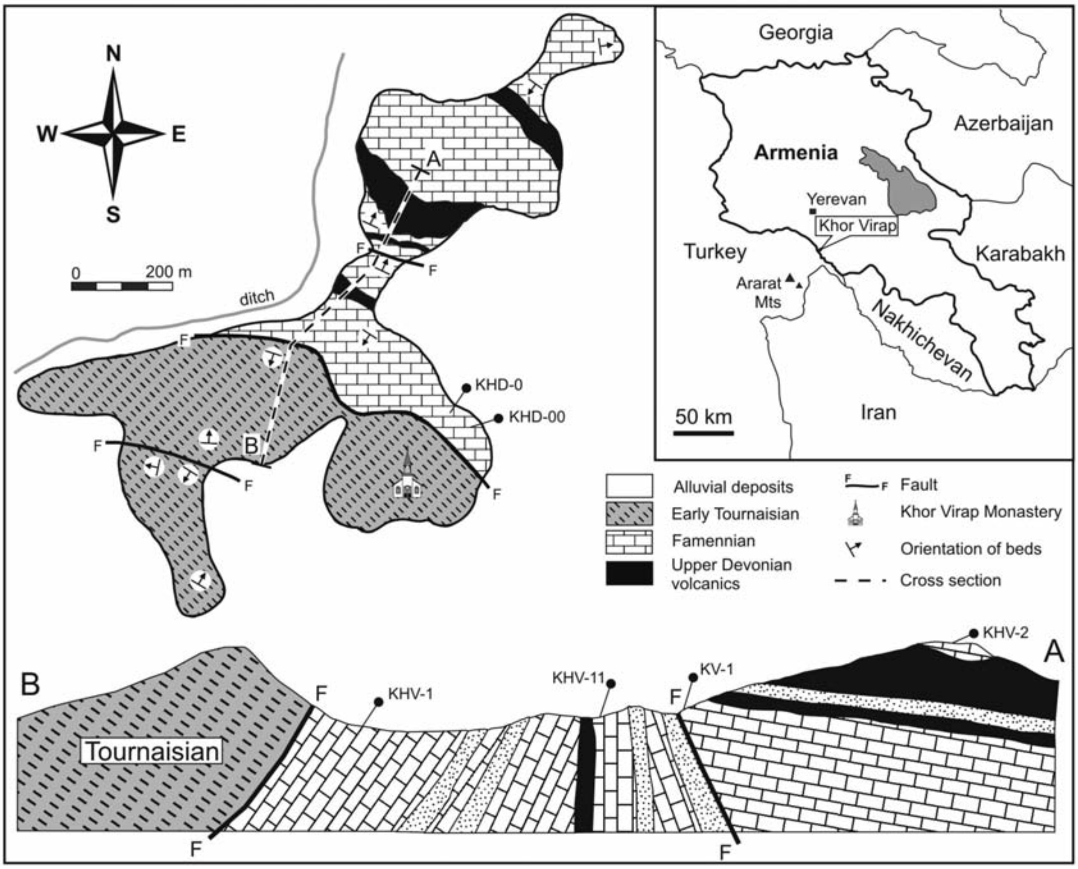
The Lower Carboniferous and, locally, Devonian sediments are overlain unconformably by Permian carbonates. This major unconformity is also traceable in northern and central Iran and neighbouring countries.

Studied sections

We studied chondrichthyan microfossils from the Famennian of four sections: Khor Virap, Sevakavan (also Tournaisian), Noravank and Ertych (see Table 1). These sections are briefly described below.



Text-fig. 1. Simplified geological map of the south-western part of Armenia and the north-eastern part of the Nakhichevan area showing the Sevakavan, Noravank and Ertych sections



Text-fig. 2. Geological map and the schematic cross-section through the Middle Palaeozoic of Khor Virap

Series	Stage	Standard conodont zonation		Formation	Local brachiopod zones	Local conodont zones (Aristov, 1994)
L. Carb.	Tn	*sulcata*		Gerankalasy *Kyarki beds*	*Unispirifer praeulbanensis*	*Polygnathus inornatus* *Siphonodella* sp.
Upper Devonian	Famennian	*praesulcata*	U	↓	↓	↓
			M	Arshakiakhpur (*s. str.*)	*Spinocarinifera niger* *Hamlingella georgesi* *Sphenospira julii*	*Pelekysgnathus superstes* *Polygnathus inornatus*
			L			
		expansa	U			*Pelekysgnathus superstes* *Icriodus costatus*
			M			
			L			*Pelekysgnathus inclinatus*
		postera	U	Gortun	*Paragastroderhynchus nalivkini*	*Polygnathus semicostatus* *Pelekysgnathus inclinatus*
			L			
		trachytera	U	Shamamidzor	*Enchondrospirifer ghorensis*	*Polygnathus semicostatus* *Scaphignathus velifer*
			L			
		marginifera	U	Kadrlu	*Dmitria seminoi*	*Polygnathus semicostatus* *Icriodus cornutus*
			M			
			L			
		rhomboidea	U			
			L			
		crepida	Um	Ertych	*Cyrtiopsis orbelianus* *Cyrtiposis armenicus*	*Polygnathus brevilaminus* *Icriodus cornutus*
			U			
			M			
			L			
		triangularis	U	Noravank	*Mesoplica meisteri* *Cyrtospirifer asiaticus*	*Polygnathus brevilaminus*
			M			
			L			

Text-fig. 3. Biostratigraphic scheme of the Famennian and lower Tournaisian of the southern Transcaucasus and the major lithostratigraphic units (after Rzhonsnitskaya and Mamedov 2000, modified)

Khor Virap

Tectonised Upper Devonian–Lower Carboniferous rocks exposed in the section on a few hills near the Khor-Virap Monastery (Text-figs 2, 5A) comprise shallow marine carbonates and siliciclastics. Several thick diabase or altered basalt sills are present in the area. Absolute age dating of these volcanics is unavailable, but they can most probably be attributed to Upper Devonian volcanic activity in the region that also affected north-western and northern Iran. The spot samples taken from a unit of bioclastic limestones near the tectonic boundary between the Devonian and Carboniferous prove a middle to late Famennian age whereas some other samples suggest early to middle Famennian. A single sample, KHV-11, contains identifiable fish microremains. Because of the lack of index conodonts, the dating of this sample (late Famennian, probably *expansa* CZ) is based on the chondrichthyan assemblage, which is very similar to that of sample 64 from Dalmeh, Iran. Samples taken from slightly metamorphosed coral limestones are extremely poor in conodonts and fish remains but contain invertebrates characteristic of the Tournaisian.

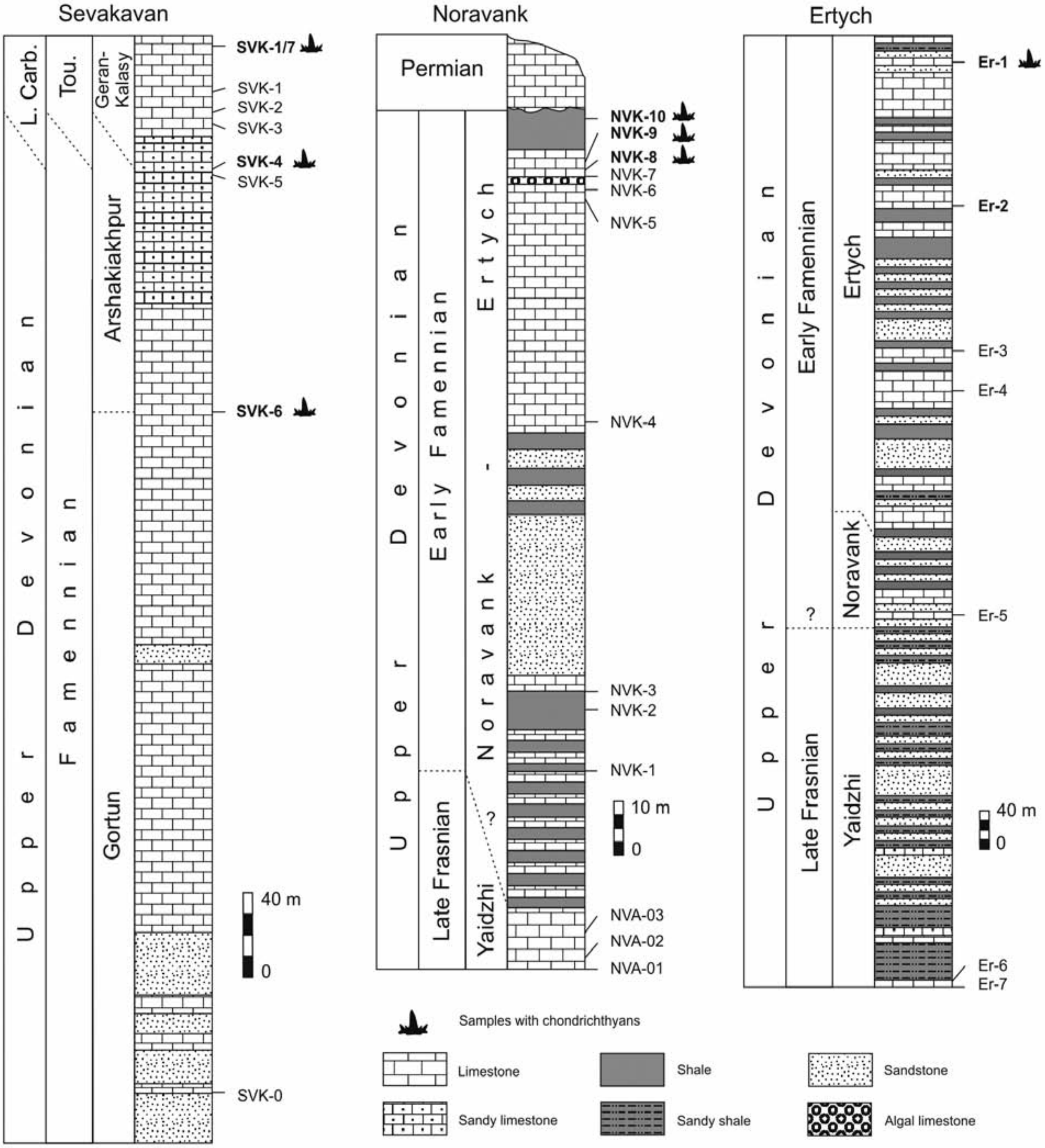
Sevakavan

The section shows a thick Upper Devonian to Lower Carboniferous sequence situated about 2 km east of the village of Sevakavan (= Paruyr Sevak). The upper part of the section comprises dark grey sandy limestones and dark argillaceous shales referred to the Arshakiakhpur and Gerankalasy Formations (Text-figs 4, 5C). The Famennian part contains conodonts of the Middle *expansa–praesulcata* Conodont Zone. Samples SVK-4 (undetermined position within the Middle *expansa–praesulcata* interval) and SVK-6 (Middle-Late *expansa*) from the limestone

Taxa / samples	Er-1	NVK-8	NVK-9	NVK-10	KHV-11	SVK-6	SVK-4	SVK-1/7	Total
Siberiodus mirabilis		1	1						2
Phoebodus gothicus	82				3				85
Phoebodus turnerae	4?								4
Phoebodus cf. *typicus*	2?								2
Thrinacodus spp.					4	3		6	13
Symmoriiformes indet.					1				1
Squatinactis glabrum	1?								1
Cladodoides cf. *wildungensis*	18								18
Ertychius intermedius gen. et sp. nov.	41								41
Ctenacanthiformes indet.		1	1				1		3
Protacrodus serra					3				3
Deihim mansureae	45			1?			3		49
Dalmehodus turnerae					1				1
Lissodus lusavorichi sp. nov.					3				3
Hybodontiformes indet.					6		4		10
holocephalian tooth						1			1
Total chondrichthyan teeth	193	2	2	1	21	4	8	6	**237**
chondrichthyan scales					+			+	
ischnacanthiform acanthodian tooth-whorls	+		+						
actinopterygian teeth and bone fragments			+		+	+		+	
dipnoan tooth-plates	+								

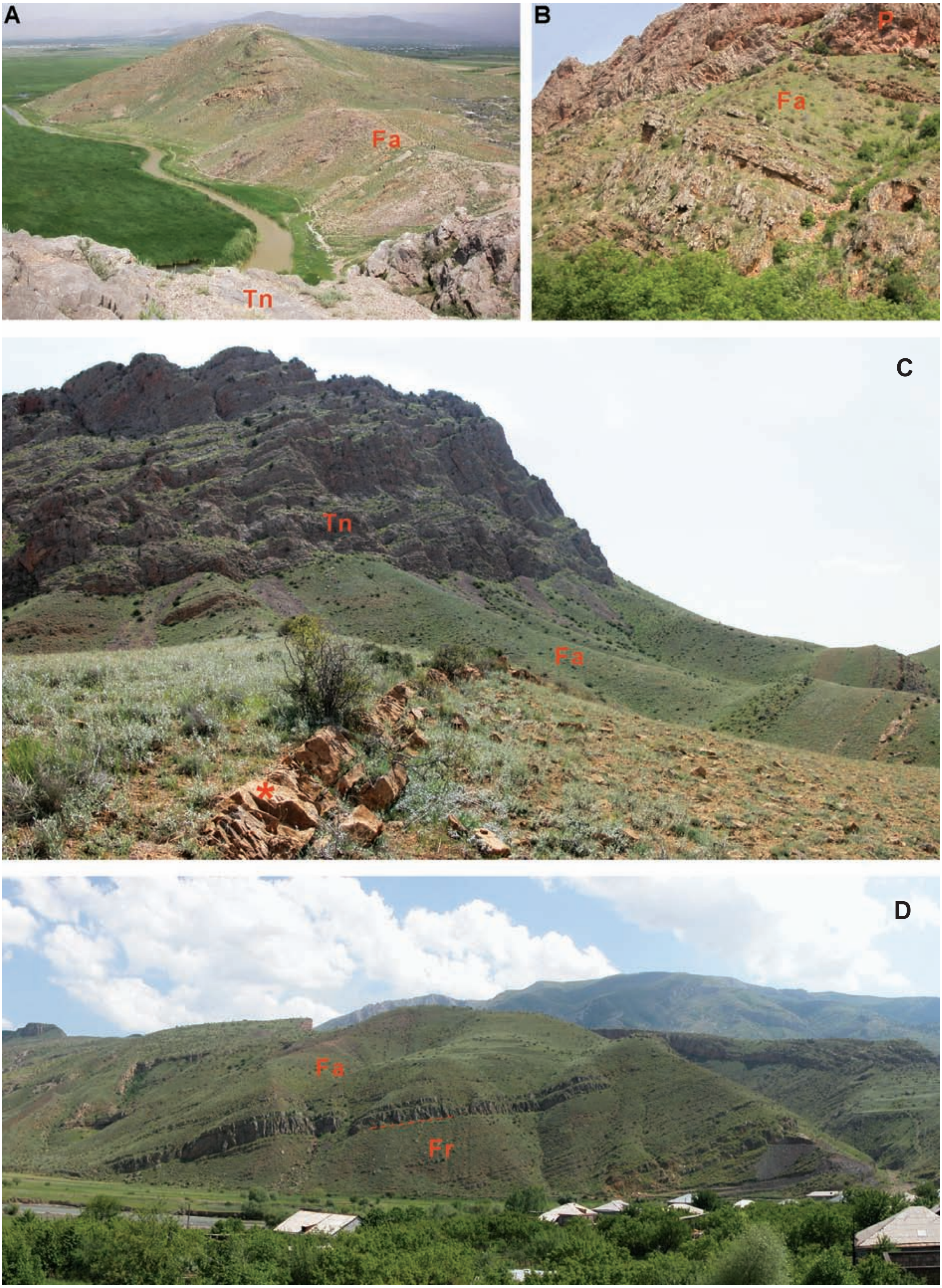
Table 1. Distribution of fish microfossils in the chondrichthyan-bearing samples from the lower Famennian (Er-1 – NVK-10), upper Famennian (KHV-11 – SVK-4), and lower Tournaisian (SVK-1/7) of Armenia

units yielded fish microremains of chondrichthyan, acanthodian and actinopterygian origin. The overlying lower Tournaisian Gerankalasy Formation includes a distinctive horizon with abundant brachiopods and corals of an age not younger than the *crenulata* Conodont Zone. The sample SVK-1/7 from this horizon contains shark teeth and acanthodian scales.



Text-fig. 4. Stratigraphic columns of the Upper Devonian–Lower Carboniferous at the Sevakavan, Noravank and Ertych sections in south-western Armenia

Text-fig. 5. A – The northeastward view of the Khor Virap outcrop showing tectonised Famennian beds (Fa) and Tournaisian coral limestones (Tn). B – Upper part of the Noravank section (northward view) showing Early Famennian deposits and cliff-forming Permian (P) massive limestones. C – Upper part of the Sevakavan section with late Famennian levels (Fa), overlain by Tournaisian (Tn) strata. Lowermost chondrichthyan-bearing level (sample SVK-6) is indicated in the foreground by an asterisk. D – Northern flank of the Upper Devonian Ertych monocline showing late Frasnian (Fr) and early Famennian (Fa) deposits. Dashed line indicates the probable Frasnian-Famennian boundary


A
Fa
Tn
B
P
Fa
C
Tn
Fa
*
D
Fa
Fr

Noravank

Late Frasnian–early Famennian siliciclastic and carbonate deposits including some units of algal limestones are perfectly exposed in a deep valley, on a slope of the Gnishik River, below the Noravank Monastery, 6 km to the south-east of Areni (Text-figs 4, 5B). They contain several horizons rich in brachiopods. Most of the conodont samples from the section represent the *rhenana–crepida* Conodont Zone and indicate the polygnathid–icriodid shallow water biofacies. From the Famennian part (samples NVK-8, -9, and -10, *crepida* Conodont Zone), chondrichthyan teeth, acanthodian tooth-whorls (Text-fig. 11E) and antiarch placoderm bone fragments (unpublished material) were recovered.

Ertych

This is the easternmost site studied by us. The outcrop is situated on the southern bank of the Arpa River (ca. 8.5 km east of Areni), near the ruins of the village of Ertych (Text-figs 4, 5D). The entire section is dated as late Frasnian to early Famennian (*rhenana–crepida* Conodont Zone) by conodonts. The main lithologies are quartzites, black shales and limestones. Unlike the other sections, palmatolepid and ancyrognathid taxa occur here in the early Famennian (*triangularis–crepida* Conodont Zone), which may suggest a deeper environment than those of the sequences in the western part of the region. One of the uppermost limestone units (sample Er-1, *crepida* Conodont Zone) contains a considerable number of fish microremains, including chondrichthyan teeth, acanthodian tooth-whorls, dipnoan tooth-plates (Text-fig. 9) and antiarch placoderm bone fragments.

SYSTEMATIC DESCRIPTION OF THE ICHTHYOFAUNA

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Omalodontiformes Turner, 1997
Family indet.

Genus *Siberiodus* Ivanov and Rodina, 2004
Siberiodus mirabilis Ivanov and Rodina, 2004
(Text-fig. 11D)

MATERIAL: Two teeth from the lower Famennian of Noravank, samples NVK-8 and NVK-9.

REMARKS: Both teeth are greatly damaged, but the labial direction of the base, typical of omalodontiforms, and the shape of the only fairly well preserved cusp on the illustrated specimen (Text-fig. 11D) leave no doubt as to their assignment. The teeth of *S. mirabilis* were reported from the lower to middle Famennian of several sections in Iran (see the review in Hairapetian and Ginter 2009). The putative middle Frasnian age of the material from the Chanaruh (= Bidou 1) section of the Kerman region (Janvier 1977, fig. 3F; 1981, pl. 2, figs A, C, F, H) is unconfirmed.

Janvier (1981) suggested that the teeth of *Siberiodus* (called by him "*Cladodus*" sp.) are in fact branchial denticles of a cladodont shark whose teeth co-occurred with them in the samples. Similar ideas were independently discussed (but never expressed in print) in connection with some other omalodontiforms, because of their unusual shape and direction of bases. For instance, Givetian–Frasnian *Omalodus* was supposed to be a denticle of *Phoebodus fastigatus*, because these two forms very often occur together (e.g. Hampe *et al.* 2004) and their crowns (but not the bases) show many common features. The studies on the dentition of Lower Devonian *Doliodus* (Turner 2004; Maisey *et al.* 2009) revealed that elements with the omalodont type of bases can indeed be dentition teeth. However, this does not necessarily mean that all forms currently included in the Omalodontiformes are true teeth and it seems quite possible to us that, at least as far as *Siberiodus* is concerned, Janvier's (1981) suggestion may be vindicated in future.

DISTRIBUTION: Lower to upper Famennian of Kuznetsk Basin (Russia); Middle Frasnian? to middle Famennian of the Iranian Platform.

Order Phoebodontiformes Ginter, Hairapetian and Klug, 2002
Family Phoebodontidae Williams in Zangerl 1981

Genus *Phoebodus* St. John and Worthen, 1875
Phoebodus gothicus Ginter, 1990
(Text-figs 6A–I, 10A, B)

MATERIAL: 82 teeth from the lower Famennian of Ertych, sample Er-1; 3 teeth from the upper Famennian of Khor Virap, sample KHV-11.

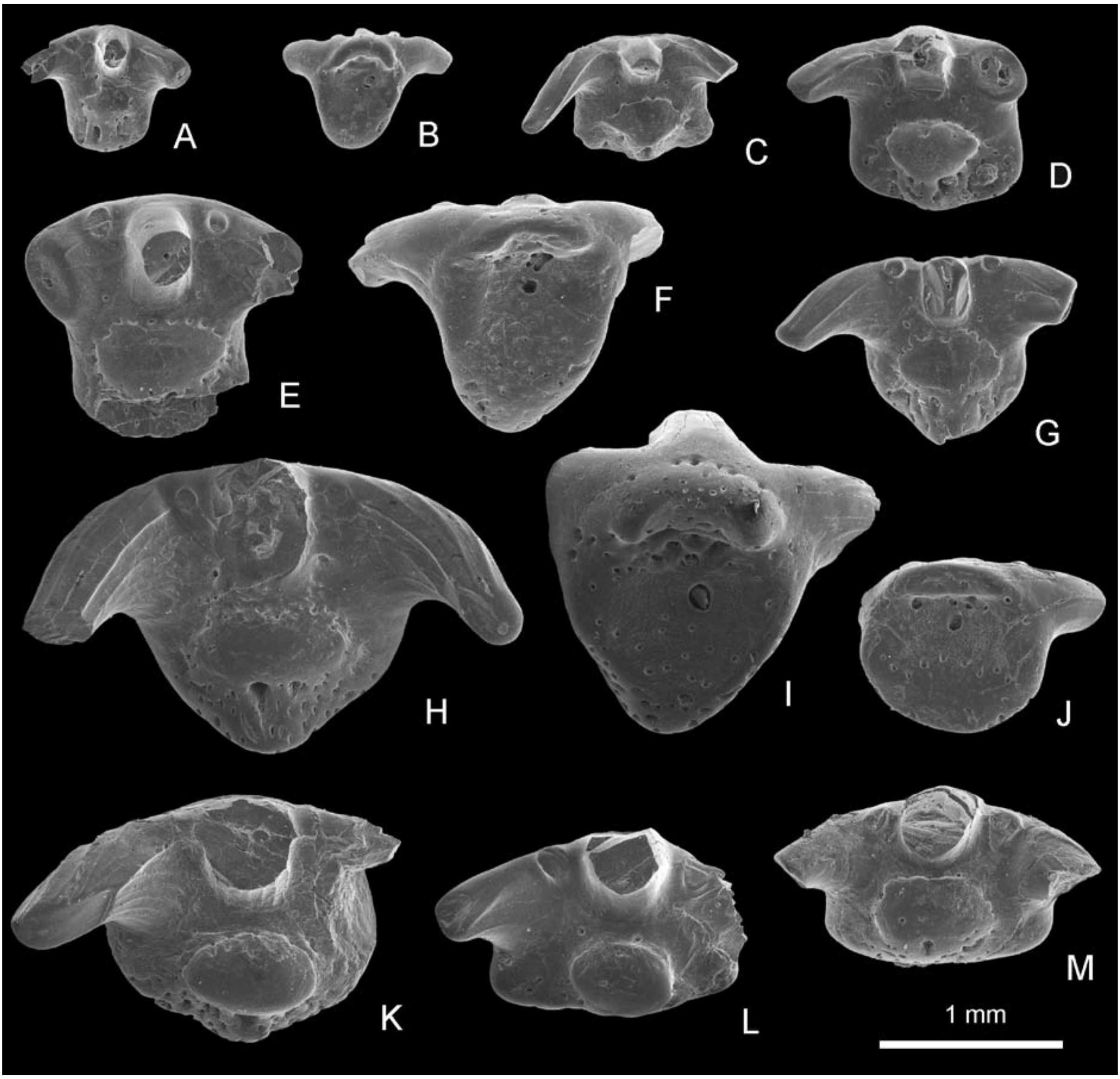
REMARKS: The diversity of basal outlines in *Ph. gothicus* from Ertych (Text-fig. 6A–I) is considerable. However, all of the morphotypes fit in the list of forms from central Iran (Ginter *et al.* 2002, pp. 199–200), and particularly resemble those from the lower Famennian of Hutk (Ginter *et al.* 2002, pl. 1, figs G–M). On the other hand, one of the specimens from Khor Virap (Text-fig. 10A), with its long, lingually-rounded base and relatively short cusps, is similar to the specimen from the upper Famennian of Dalmeh (Ginter *et al.* 2002, pl. 2, fig. G). The other tooth from Khor Virap (Text-fig. 10B) seems either curiously abraded or pathological.

DISTRIBUTION: Cosmopolitan in the Famennian of Laurussia and northern Gondwana.

Phoebodus turnerae Ginter and Ivanov, 1992
(Text-fig. 6J, K)

MATERIAL: Four teeth from the lower Famennian of Ertych, sample Er-1.

REMARKS: There are only four teeth among the rich phoebodont assemblage from Ertych which can be attributed to this species. In such cases, the suspicion arises whether they really belong in *Ph. turnerae* or are simply slightly differently formed teeth of *Ph. gothicus*. However, the relatively short and wide bases and lingually-positioned large button (unlike the centrally-placed button in *Ph. gothicus*) are arguments in favour of the former identification.



Text-fig. 6. Teeth of *Phoebodus* from the lower Famennian of Ertych, sample Er-1. A-I, *Phoebodus gothicus* Ginter, 1990. A – MWGUW/Ps/10/1; B - MWGUW/Ps/10/2; C – MWGUW/Ps/10/3; D – MWGUW/Ps/10/4; E – MWGUW/Ps/10/5; F – MWGUW/Ps/10/6; G – MWGUW/Ps/10/7; H – MWGUW/Ps/10/8; I – MWGUW/Ps/10/9. J, K, *Ph. turnerae* Ginter and Ivanov, 1992. J – MWGUW/Ps/10/10; K – MWGUW/Ps/10/12. L, M, *Ph.* cf. *typicus* Ginter and Turner, 1999. L – MWGUW/Ps/10/13; M – MWGUW/Ps/10/14. All in oral views, except F, I, J in aboral views. Scale bar

DISTRIBUTION: Together with the forms named "*Ph.* aff. *turnerae*", cosmopolitan but relatively rare in the lower and middle Famennian of eastern Laurussia and northern Gondwana.

Phoebodus cf. *typicus* Ginter and Turner, 1999
(Text-fig. 6L, M)

MATERIAL: Two teeth from the lower Famennian of Ertych, sample Er-1.

REMARKS: These phoebodont teeth, with very short bases, could be attributed either to *Ph. typicus* Ginter and Ivanov, 1995, or to *Ph. rayi*. The difference between these two species lies in the shape of the base (pentagonal in *Ph. rayi* and rectangular in *Ph. typicus*) and the position of the button (close to the lingual rim in *Ph. rayi* and centrally in *Ph. typicus*). The tooth bases of the specimens from Ertych look squarish, as in *Ph. typicus*, but the button is large and appears to be situated lingually, as in *Ph. rayi*. The determination of these teeth as *Phoebodus* cf. *typicus* is therefore only tentative and they are best kept in open nomenclature.

DISTRIBUTION: Lower to middle Famennian of south Urals, Morocco, Armenia, Iran, and Australia.

Genus *Thrinacodus* St. John and Worthen, 1875
Thrinacodus spp. Ginter, 2000
(Text-figs 10C, 11H-J)

MATERIAL: Four teeth from the upper Famennian of Khor Virap, sample KHV-11; three teeth from the upper Famennian of Sevakavan, sample SVK-6; six teeth from the lower Tournaisian of Sevakavan, sample SVK-1/7.

REMARKS: The specimens from Khor Virap (Text-fig. 10C) are poorly preserved, but they generally look like typical teeth of *Th. tranquillus*, having three slender, almost equal cusps. The specimens from SVK-7/1 (Text-fig. 11H–J) also resemble *Th. tranquillus*, but they have a special form of the median cusp which looks as if it was moved from its normal position and displaced slightly lingually. Its basal/labial part bears a distinct canal opening, unknown from other teeth of this species. Such a shape of the median cusp, even more strongly compressed from the labial side, can be observed on certain teeth of *Th. ferox* Turner, 1982, e.g. those from the upper Tournaisian of Kilbride, Ireland (Duncan 2003, fig. 5B). Thus, it is possible that the teeth from SVK-1/7 are intermediate forms between *Th. tranquillus* and *Th. ferox*.

There is a great difference in size between the smallest (Text-fig. 11H, I) and the largest (Text-fig. 11J) teeth of *Thrinacodus* from SVK-1/7, but it is difficult to say whether they belong to small and large individuals respectively, or can exist in the same jaw. Nevertheless, there is no doubt that they represent the same variety of form (which we can call here *Th.* aff. *tranquillus*), despite some minor differences in the base shape.

The specimens from SVK-6 are too damaged to be identified at species level, so they are only tentatively included here. One of the loose cusps looks like the distal (largest) cusp of the asymmetrical tooth of *Th. ferox*, but there is no way to confirm this impression.

DISTRIBUTION: *Thrinacodus tranquillus* – Middle to upper Famennian of Laurussian margins, northern Gondwana and northern China; *Th. ferox* – cosmopolitan in the upper Famennian to Tournaisian.

Order Symmoriiformes Zangerl 1981
Symmoriiformes gen. et sp. indet.
(Text-fig. 10D)

MATERIAL: One tooth from the upper Famennian of Khor Virap, sample KHV-11.

REMARKS: Although the tooth has only two cusps and a fragment of the base preserved, the typical symmoriiform features can easily be discerned. The cusps are rounded in cross-section, the delicate cristae covering both faces of the cusps reach from the base to the tip, the lateral carina is absent, and the cusps are histologically separate, i.e., unconnected with the enameloid/orthodentine layer. The base is thin, but nothing can be said about the articulation devices. Before the damage, the tooth was probably tricuspid and looked similar to the teeth of Pennsylvanian *Cobelodus* from the North American mid-continent (Zangerl and Case 1976, fig. 16; see also Ginter *et al.* 2010, fig. 57).

The presence of such a tooth in the upper Famennian of Armenia is rather unexpected, since thus far true symmoriiforms were rarely found from the Devonian of Gondwana and elsewhere (not counting several misidentifications made in previous works, including ours). Slightly similar teeth of *Stethacanthus* were reported from the late Famennian Cleveland Shale of Ohio (Ginter *et al.* 2010, fig. 58E, F), but unlike the tooth from Khor Virap, they are pentacuspid, the size difference between the main lateral cusps and the median cusp is greater, and all the cusps are virtually parallel to each other.

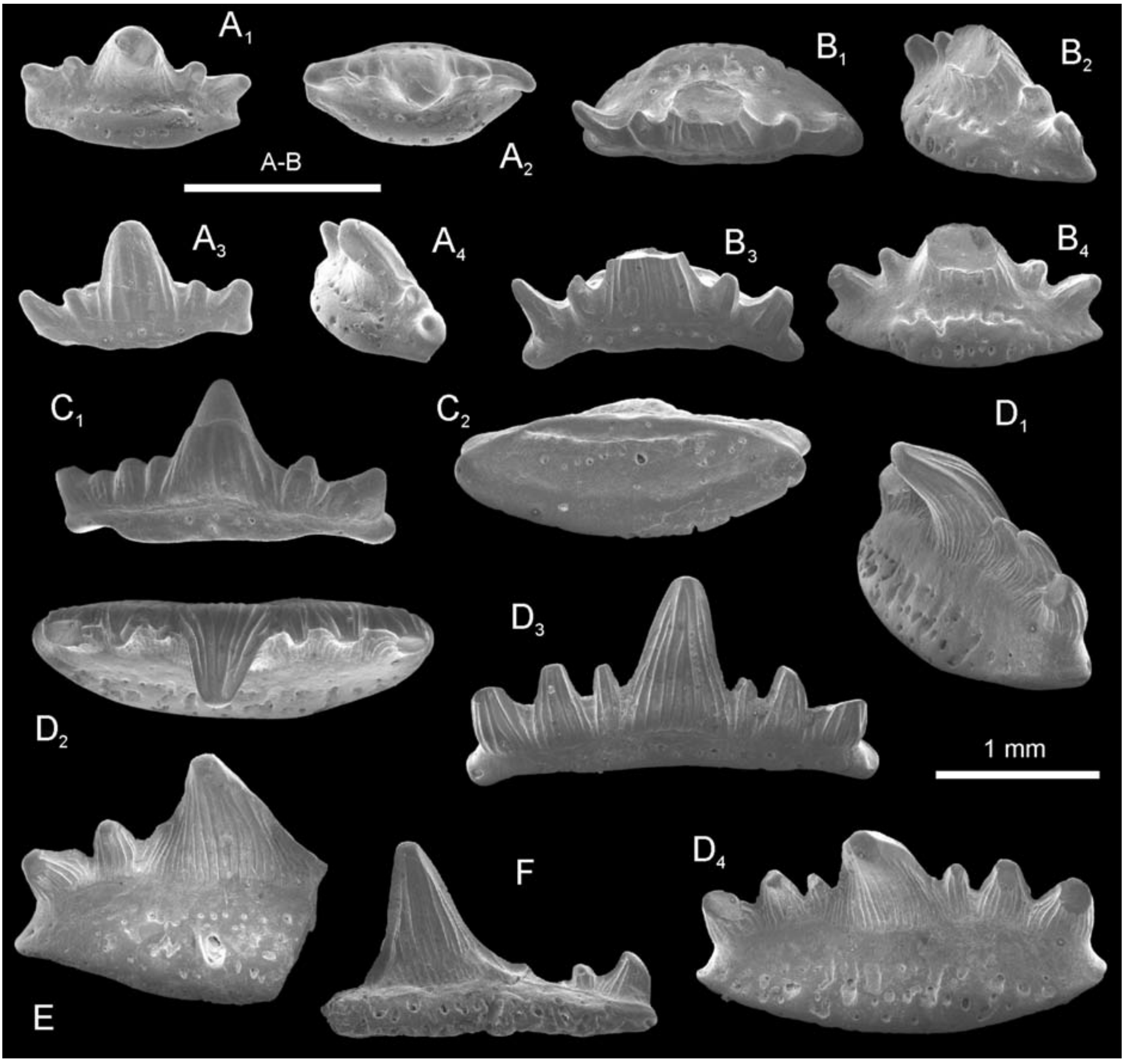
Order Squatinactiformes Zangerl 1981
Family Squatinactidae Cappetta, Duffin and Zidek 1993

Genus *Squatinactis* Lund and Zangerl 1974
Squatinactis glabrum (Ginter, 1999)

MATERIAL: One tooth from the lower Famennian of Ertych, sample Er-1.

REMARKS: There was a fragment of a tooth probably belonging to this species, with only the base and basal parts of the cusps preserved, displaying the typical labio-basal depression and two separate orolingual buttons. It had been documented after preparation with a low-resolution digital photograph, but afterwards it was probably lost before SEM photography. Although *S. glabrum* is common in the Famennian of southern Laurussia and Morocco, it is extremely rare in Iran (Hairapetian and Ginter 2009, 2010) and so it is in Armenia.

DISTRIBUTION: Famennian of Laurussian margins, North Africa, Iran, Armenia, and Thailand.



Text-fig. 7. Cladodont teeth from the lower Famennian of Ertych, sample Er-1. A, B, *Cladodoides* cf. *wildungensis* (Jaekel, 1921). A – MWGUW/Ps/10/15 in lingual, oral, labial and lateral views; B – MWGUW/Ps/10/16 in oral, lateral, labial and lingual views. C-F, *Ertychius intermedius* gen. et sp. nov. C – MWGUW/Ps/10/17 in labial and aboral views; D – MWGUW/Ps/10/18, holotype, in lateral, oral, labial and lingual views; E – MWGUW/Ps/10/19, broken tooth in lingual view; F – MWGUW/Ps/10/20, broken tooth in lingual view. Scale bars 1 mm

Order Ctenacanthiformes Glikman, 1964
Family Ctenacanthidae Dean, 1909
Genus *Cladodoides* Maisey, 2001
Cladodoides cf. *wildungensis* Jaekel, 1921
(Text-fig. 7A, B)

MATERIAL: 18 teeth from the lower Famennian of Ertych, sample Er-1.

DESCRIPTION: The teeth referred here to this genus are relatively small, compared to other shark teeth from sample Er-1. The base width usually does not exceed 1 mm. The crown is pentacuspid, with a prominent median cusp, oval in cross-section, ornamented on labial and lingual sides with a few (6–10) strong, subparallel cristae. It is unknown whether the cristae rich the tip of the cusp, because it is broken in all cases. The lateral main cusps are much shorter and thinner than the median cusp. They are rounded in cross-section, strongly inclined laterally and curved linguad. They are also covered with coarse cristae. The intermediate cusplets are of the same shape as the lateral cusps, but only about half their size. All of the cusps are connected by a distinct lateral carina. The base is lenticular to semilenticular with an oval, mesio-distally elongated orolingual button and a straight basolabial projection, slightly wider than the base of the median cusp.

REMARKS: The teeth generally look like those attributed by Ginter *et al.* (2010, see especially fig. 66A–D) to *Cladodoides wildungensis* (Jaekel, 1921). However, because none of the specimens from Ertych is complete and larger teeth, typical of the holotype of *C. wildungensis*, are absent, we prefer to use open taxonomy here. Similar teeth were found in the upper Frasnian of the Kale Sardar section (Hairapetian and Ginter 2010, fig. 5B–D), the lower Famennian of the Chahriseh section (Hairapetian and Ginter 2009, fig. 8B–E) and also in younger Famennian strata of central Iran, but it is unknown whether all such ctenacanthiform teeth really represent *Cladodoides*.

DISTRIBUTION: Teeth similar to these (also referred to as *Stethacanthus* cf. *thomasi* or *S. resistens*) are common in the upper Frasnian and lower to middle Famennian of the margins of Laurussia, northern Gondwana, and the Kuznetsk Basin (Russia). The only articulated specimen of *C. wildungensis* (skull with teeth) came from the uppermost Frasnian of Germany.

Family indet.
Genus *Ertychius* gen. nov.

ETYMOLOGY: From the geological section near the ruined village of Ertych.

TYPE SPECIES: *Ertychius intermedius* sp. nov.

DIAGNOSIS: Mesio-distally elongated teeth with symmetrical to asymmetrical crowns. The median cusp prominent but relatively short, triangular, slightly labio-lingually compressed. Up to three pairs of lateral cusps in symmetrical forms, the outermost pair the largest. In asymmetrical forms four cusps on the mesial side and only two on the distal side. The cusps recurved and covered with densely packed but distinct subparallel cristae reaching the tips; lateral carina connecting all the cusps. The base oval, provided with a short lingual extension and a well developed, straight basolabial shelf extending mesio-distally almost to the bases of the most lateral cusps. The presence of the orolingual ridge uncertain.

Ertychius intermedius sp. nov.

ETYMOLOGY: Latin *intermedius* = intermediate, from the morphology of teeth intermediate between typical ctenacanthiforms and euselachians.

HOLOTYPE: Specimen MWGUW/Ps/10/18 from the lower Famennian of Ertych, sample Er-1, undefined position within the *crepida* conodont Zone.

DIAGNOSIS: As for genus.

MATERIAL: 41 teeth from the lower Famennian of Ertych, sample Er-1.

DESCRIPTION: Although in the studied collection from Ertych there are many teeth which can be identified as *Ertychius intermedius* sp. nov., only a few of them are complete enough to help in the detailed description of the species. Particularly, the apparent abrasion of the bases precludes a definite statement as to the shape of the orolingual button or ridge. The presence of the straight basolabial shelf (Fig. 7C) suggests, by analogy with the other Palaeozoic shark teeth, that there should be a long, straight orolingual ridge, and indeed, faint traces of such a structure were observed on a few specimens. Otherwise, the lingual side of the base looks as if it was devoid of any button and perforated by numerous canals (Fig. 7D4, E) which is probably mostly the result of postmortem destruction of the base surface.

There are two specific features of the crown: the angular, relatively broad-based and low median cusp; and the asymmetrical number of lateral cusps in certain specimens (Text-fig. 7C). Unfortunately, most specimens are broken (e.g. Text-fig. 7E, F) and it is impossible to say if they were originally symmetrical or not, and what the relative abundance of each of these morphotypes is.

The ornamentation of the median cusp consists of subparallel cristae which are more distinct but fewer on the labial face (about 10 in the holotype, Text-fig. 7D3) and numerous but more delicate on the lingual face (about 15 in the holotype, Text-fig. $7D_4$, and 20 in the specimen with the broadest cusp, Text-fig. 7E). The cristae on the labial face run parallel to the lateral edges of the cusp, and so the cristae in the middle join together and then wedge away. On the lingual side the cristae are vertical and so the lateral ones quickly join the edge and only those near the midline continue to the tip of the cusp. The lateral carina is rather distinct (see especially Text-fig. 7F), and it continues between all the cusps.

REMARKS: The morphology of the teeth of *E. intermedius* sp. nov. places it in the as yet poorly understood area between the cladodontomorph Ctenacanthidae and the basal euselachian Protacrodontidae. For a long time such Upper Devonian teeth, mesio-distally elongated, with multicuspid low crowns (protacrodont features), but with the cusps clearly separate and the basal articulation devices still present (cladodont features), were called by us "cladodont-protacrodonts", without formal identification. However, recently Ginter (2008) described *Lesnilomia sandbergi* from the uppermost Frasnian of Laurussia and *E. intermedius* is the second species of this type to receive a formal name. *Lesnilomia*, although similar at first sight, differs clearly from *Ertychius* in its stronger labio-lingual compression of the crown, usually greater number of cusps (up to 11; in *Ertychius* no more than seven), the occurrence of lateral accessory cusplets and a shallow basolabial depression. Also, the size difference between the median cusp and the main lateral cusps is greater in *Ertychius*. Interestingly, in both species symmetrical and asymmetrical teeth occur, probably reflecting the different (anterio-mesial and postero-lateral, respectively) positions in the jaw.

Somewhat similar to *Ertychius* is the tooth from the Tournaisian of Muhua, southern China (Ginter and Sun 2007, fig. 6D) designated as Euselachii gen. et sp. indet. However, its cusps are more protacrodont than cladodont in their shape and ornamentation (pyramidal median cusp, coarse cristae on both faces), and the base lacks any traces of articulation devices. Thus, we consider that that tooth is closer to the euselachians, whereas *Ertychius intermedius* belongs to the ctenacanthiforms.

DISTRIBUTION: Lower Famennian of Armenia.

Ctenacanthiformes gen. et sp. indet.
(Text-fig. 11A, B)

MATERIAL: Two teeth from the lower Famennian of Noravank, samples NVK-9 and NVK-10; one tooth from the upper Famennian of Sevakavan, sample SVK-4.

REMARKS: Here we place the cladodont teeth whose cusps are connected by a lateral carina (and thus do not belong in the Symmoriiformes) and possess a single, straight basolabial projection (which excludes them from the Squatinactiformes), but we are unable to identify them more closely at the moment.

Cohort Euselachii Hay, 1902
Order indet.
Family Protacrodontidae Zangerl, 1981

Genus *Protacrodus* Jaekel, 1925
Protacrodus serra Ginter, Hairapetian and Klug, 2002
(Text-fig. 10I, J)

MATERIAL: Three specimens from the upper Famennian of Khor Virap, sample KHV-11.

REMARKS: As in the material from Iran and Morocco (Ginter *et al.* 2002, fig. 11), there are two tooth morphotypes of *P. serra* at Khor Virap. The first, presumably from the postero-lateral part of the jaw, is low-crowned, asymmetrical, four-cuspid, with an intermediate cusplet on the mesial side of the median cusp (Text-fig. 10I). The second, more symmetrical, probably anterior tooth morphotype, has a prominent, triangular median cusp with distinct lateral carinae and only one cusp on each side (Text-fig. 10J). In sample 64 from Dalmeh, Iran, there exists an intermediate form (Ginter *et al.* 2002, pl. 2, figs L–N) with the median cusp prominent, but inclined distally. Despite these differences, all these morphotypes share the labio-lingual compression of the crown, coarse cristation on the cusps, and shallow bases with only a few labio-lingual canals. The anterior teeth in *P. serra* were probably adjusted to grasp and even cut prey (an unusual function in Devonian sharks), and the low-crowned to clutch and crush.

DISTRIBUTION: Upper Famennian of northern Gondwana and southern Laurussia; similar forms were found in the Tournaisian of southern China (Ginter and Sun 2007, fig. 4C).

Genus *Dalmehodus* Long and Hairapetian, 2000
Dalmehodus turnerae Long and Hairapetian, 2000
(Text-fig. 10H)

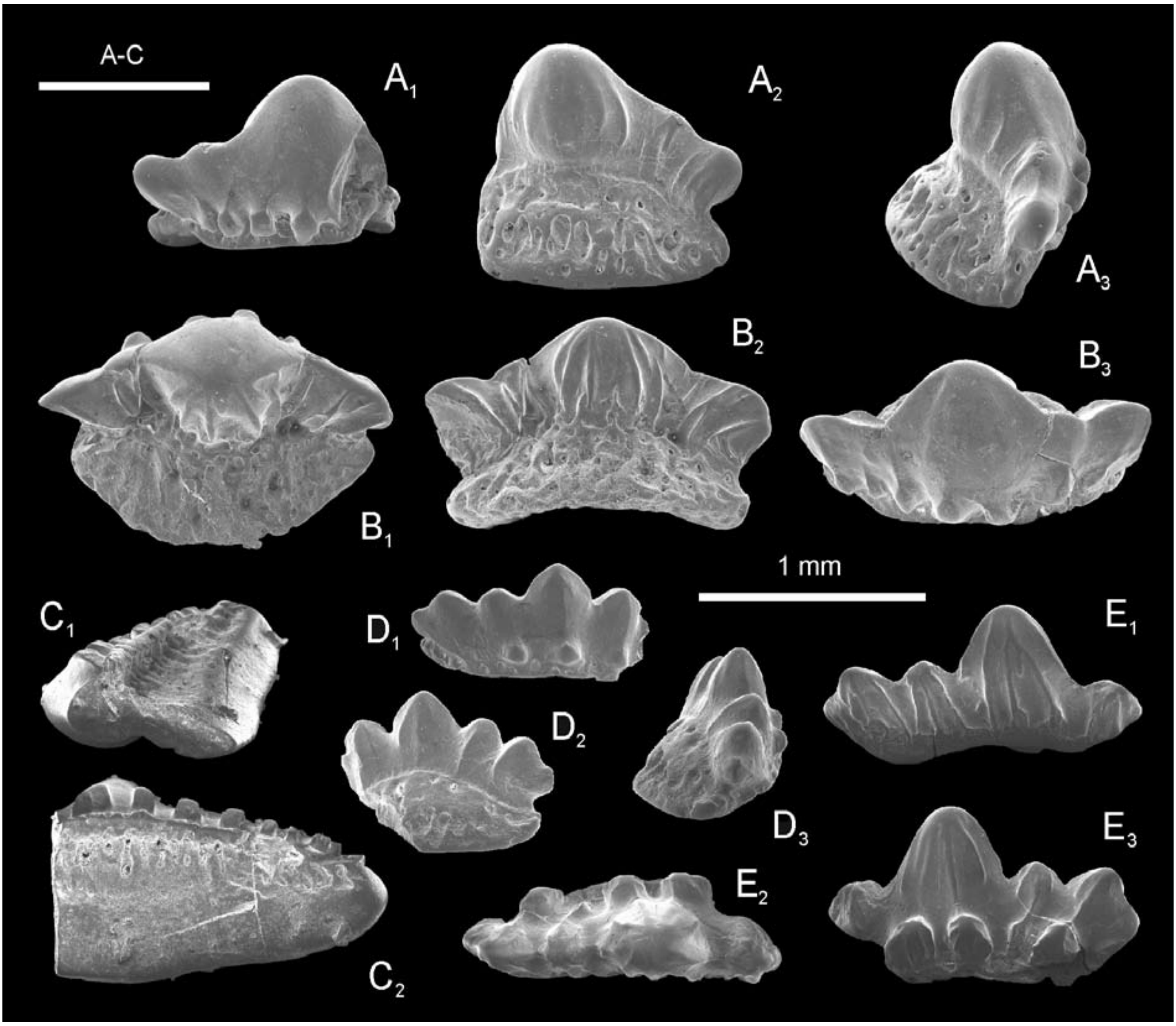
MATERIAL: Two attached teeth of a tooth-family from the upper Famennian of Khor Virap, sample KHV-11.

REMARKS: The teeth look like typical protacrodonts, laterally elongated, with seven low pyramidal cusps and a euselachian base with a short overlap area. However, unlike in *Protacrodus vetustus* or *P. serra*, almost all the cusps are of the same size, only the median cusp is insignificantly higher and thicker. Such an evenness of cusps sizes was considered a crucial feature of *D. turnerae* by Ginter *et al.* (2002) in their revision of the species (see also Hairapetian and Ginter 2009, pp. 189–190).

DISTRIBUTION: Lower to upper Famennian of Iran and Armenia.

Genus *Deihim* Ginter, Hairapetian and Klug, 2002
Deihim mansureae Ginter, Hairapetian and Klug, 2002
(Text-figs 8A–E, 11C)

MATERIAL: 45 specimens from the lower Famennian of Ertych, sample Er-1; possibly one specimen from the



Text-fig. 8. Teeth of *Deihim mansureae* Ginter, Hairapetian and Klug, 2002 from the lower Famennian of Ertych, sample Er-1. A – MWGUW/Ps/10/21 in labial, lingual and lateral views; B – MWGUW/Ps/7/7 in oral, lingual and labial views; C – MWGUW/Ps/7/8, broken tooth i aboral and oblique aboral views, showing internal structure of the base; D – MWGUW/Ps/10/22, small tooth very similar to the holotype, in labial, lingual and lateral views; E – MWGUW/Ps/10/23, broken crown of a tooth with extremely developed labial tubercles, in labial, lingual and oral views. Scale bars 1 mm lower Famennian of Noravank, sample NVK-10; 3 specimens from the upper Famennian of Sevakavan, sample SVK-4.

REMARKS: The specimens from Ertych correspond to the type material from Hutk in Iran (Ginter *et al.* 2002, fig. 10A–F), but they are much better preserved and show certain characters previously poorly known, such as the shape and ornamentation of the cusps. One of the elongated, broken specimens (Text-fig. 8C) reveals the internal distribution of basal canals. There is also a piece of a crown with extremely large labial tubercles, covered with coarse cristae (Text-fig. 8E). The specimen from Noravank (Text-fig. 11C), although generally similar, differs from the typical forms of *D. mansureae* in its relatively high, largely separate cusps. It is morphologically close to the specimen from the lower Famennian of Dalmeh (Iran; Ginter *et al.* 2002, pl. 4, figs L, M).

DISTRIBUTION: Upper Frasnian to upper Famennian of Iran and the Famennian of Armenia.

Order Hybodontiformes Maisey, 1975
Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1935

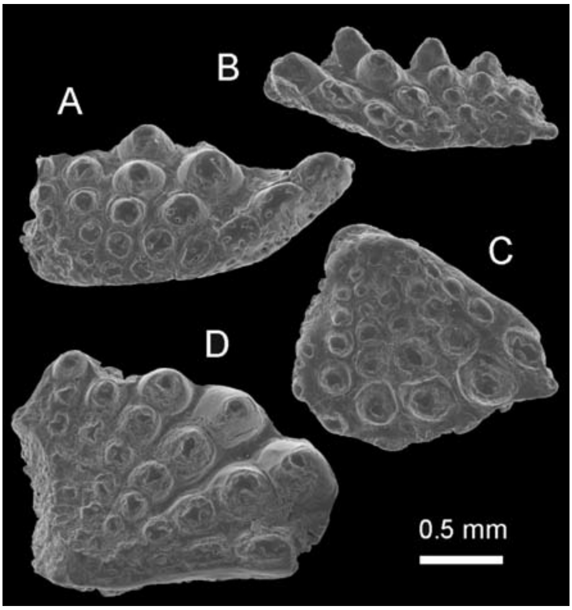
TYPE SPECIES: *Hybodus africanus* Broom, 1909.

Lissodus lusavorichi sp. nov.
(Text-fig. 10E, F)

ETYMOLOGY: From Grigor Lusavorich (Gregory the Illuminator), the apostle of Armenia, who spent 13 years imprisoned at Khor Virap.

HOLOTYPE: specimen MWGUW/Ps/10/32 from the upper Famennian of Khor Virap, sample KHV-11, probable *expansa* Conodont Zone.

DIAGNOSIS: Teeth of *Lissodus* with a well developed occlusal crest, smooth or rarely gently crenulated, and a prominent median cusp, directed labially. Crown smooth or with delicate, short vertical striations, moderate labial peg bearing up to two tubercles; lingual margin virtually straight in lingual view and straight to convex in oral view; horizontal longitudinal crest on both sides of the crown shoulder. Base of euselachian type, rather deep, vertical or slightly directed lingually, with a concave labial side.



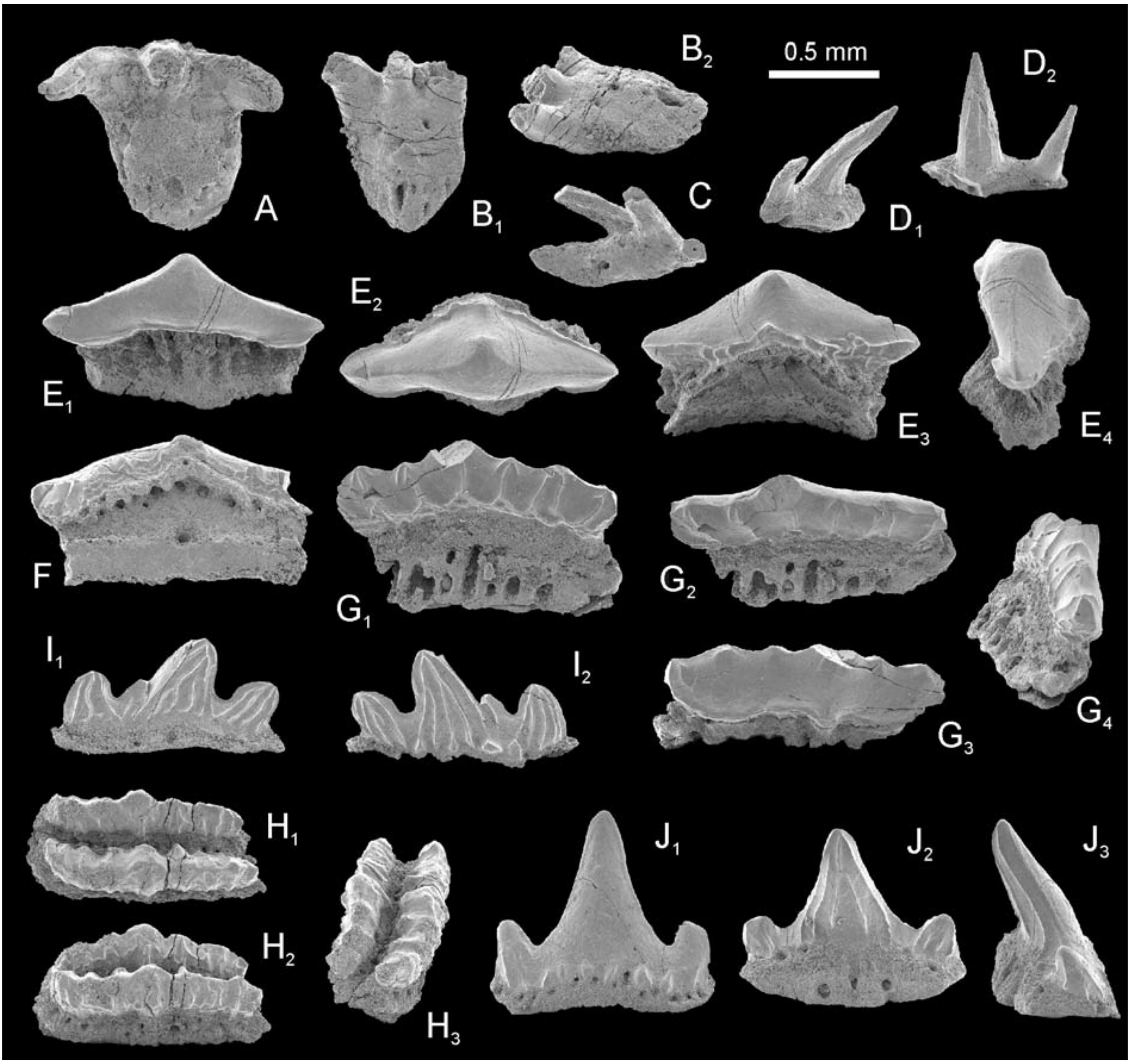
Text-fig. 9. A–D, MWGUW/Ps/10/24-27, dipnoan tooth-plates from the lower Famennian of Ertych, sample Er-1. Scale bar 0.5 mm

MATERIAL: Three specimens from the upper Famennian of Khor Virap, sample KHV-11; comparative material: nine specimens from the upper Famennian of Dalmeh (Iran), sample 64 (*Lissodus* sp., Ginter *et al.* 2002, fig. 12).

DESCRIPTION: The teeth vary from about 1 to 2 mm in mesio-distal width. In the narrowest specimens the labio-lingual and mesio-distal dimensions are almost identical (Ginter *et al.* 2002, fig. 12A, B) and the crown is dome-shaped. In wider specimens, such as the holotype (Text-fig. 10E) the crown looks like a low and broad triangle in lingual and labial views. In most specimens, including the type, the occlusal crest is smooth, but in the largest tooth from Dalmeh (Ginter *et al.* 2002, fig. 12F–I) there are a few minute cusplets or tubercles on the lateral parts. Usually the labial peg is at least partly broken, but where preserved, it also bears tubercles. The middle part of the crown forms a broad cusp whose tip is directed labially.

The lingual side of the base is vertical, numerous canal openings and grooves give it a spongeous look, typical of the euselachian-type bases (Text-fig. $10E_1$). The labial side is concave (Text-fig. $10E_3$), its lower, rectangular part is smooth and its upper part bears a row of large foramina (Text-fig. 10F).

REMARKS: The teeth of *L. lusavorichi* sp. nov. generally resemble the species attributed to *Lissodus* by Ginter *et al.* (2010), but do not seem to belong to any of them. The tooth of *L. lacustris* Gebhardt, 1988 (see also



Text-fig. 10. Chondrichthyan teeth from the upper Famennian of Khor Virap, sample KHV-11. A-B, *Phoebodus gothicus* Ginter, 1990. A – MWGUW/Ps/10/28 in oral view; B – MWGUW/Ps/10/29 in oral and lateral views. C, *Thrinacodus tranquillus* Ginter, 2000, MWGUW/Ps/10/30 in oblique lingual view. D, broken tooth of a *Cobelodus*-like symmoriiform, MWGUW/Ps/10/31 in oblique lingual and labial views. E, F, *Lissodus lusavorichi* sp. nov. E – MWGUW/Ps/10/32, holotype, in lingual, oral, labial and lateral views; F – MWGUW/Ps/10/33 in aboral/labial view. G, Hybodontiformes gen. et sp. indet., MWGUW/Ps/10/34 in lingual, oral, oral/labial, and lateral views. H, *Dalmehodus turnerae* Long and Hairapetian, 2000, two attached teeth, MWGUW/Ps/10/35, in oral, labial and lateral views. I, J, *Protacrodus serra* Ginter, Hairapetian and Klug, 2002. I – MWGUW/Ps/10/36, lateral tooth in lingual and labial views; J – MWGUW/Ps/10/37, anterior tooth in labial, lingual and lateral views. Scale bar 0.5 mm

Ginter *et al*. 2010, fig. 86A–C) from the Upper Pennsylvanian of Germany shows the closest morphology. It has a compact crown with a smooth occlusal crest and a remnant of a principal cusp; a vertical, labially concave base; and it even has something like a broad tubercle on the labial peg. The differences may be due to the preservation of the tooth and incorrect drawing. However, the large stratigraphic distance between the two rather suggests that they represent different, albeit similar, species.

The presence of *Lissodus* in the Palaeozoic was questioned in the past (e.g. Rees and Underwood 2002) and other generic names were proposed. Here we follow Duffin (in Ginter *et al*. 2010, p. 93) who did not accept those new genera, considering their erection as premature. Nevertheless, we acknowledge that further work is needed to clarify the relationships between Palaeozoic and Mesozoic *Lissodus*-like sharks and it is quite possible that *L.*

lusavorichi will be transferred into another genus in future.

DISTRIBUTION: Upper Famennian of Iran and Armenia.

Hybodontiformes gen. et sp. indet.
(Text-fig. 10G)

MATERIAL: Six teeth from the upper Famennian of Khor Virap, sample KHV-11; four teeth from the upper Famennian of Sevakavan, sample SVK-4.

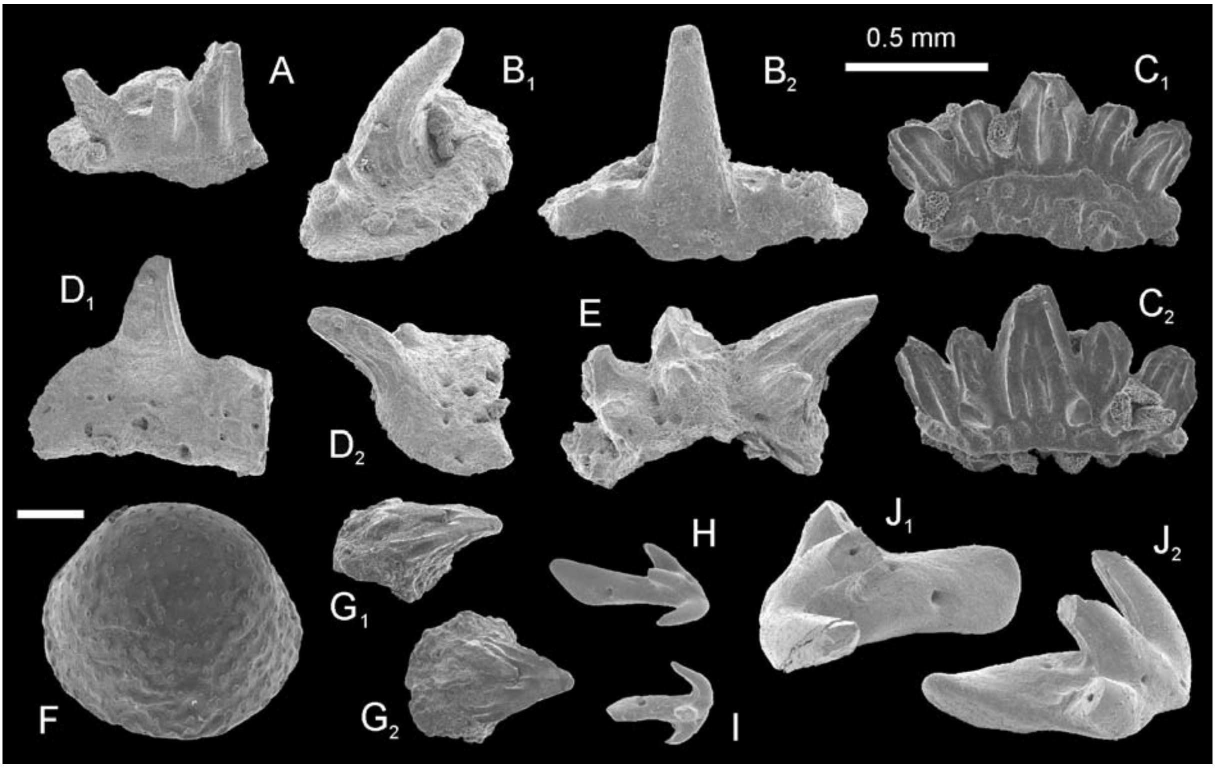
REMARKS: There are a few teeth in the upper Famennian of Armenia which perhaps represent early hybodontiforms. Among them the most interesting is a tooth which possesses a deep euselachian-type base and a crown similar to that of *Lissodus*, but with the cusps incompletely fused, the loose tips of the cusps pyramidal, and coarse vertical cristae ornamenting both faces of the crown. There occurs a minute labial peg (Text-fig. $10G_3$). Such teeth are somewhat similar to *Gansuselache* (Wang *et al*. 2009, fig. 10) from the Upper Permian of northwestern China, but more material is needed to make a detailed comparison.

Subclass Euchondrocephali Lund and Grogan, 1997
Superorder Holocephali Bonaparte, 1832-41

Holocephali gen. et. sp. indet.
(Text-fig. 11F)

MATERIAL: One tip of a crown from the upper Famennian of Sevakavan sample SVK-6.

REMARKS: The dome-shaped element with a porous surface (suggesting the presence of tubular dentine) is

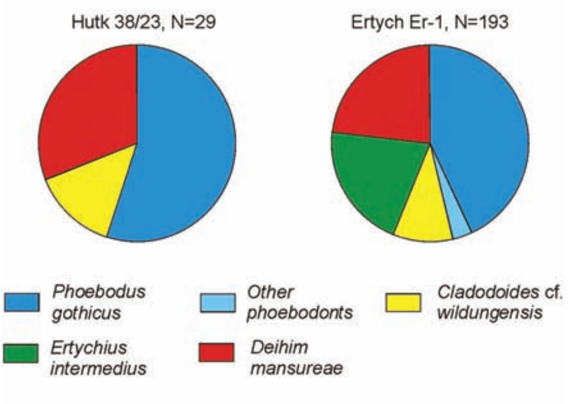


Text-fig. 11. Fish microfossils from the lower Famennian of Noravank (A–E) and the upper Famennian of Sevakavan (F–J). A, broken tooth of a ctenacanthiform, MWGUW/Ps/10/38, sample NVK-9, in labial view. B, unidentified cladodont, MWGUW/Ps/10/39, sample NVK-8, in oblique lingual and labial views. C, euselachian tooth cf. *Deihim mansureae*, MWGUW/Ps/10/40, sample NVK-10, in lingual and labial views. D, *Siberiodus mirabilis* Ivanov and Rodina, 2004, broken tooth with only one cusp preserved, MWGUW/Ps/10/41, sample NVK-8, in labial and lateral views. E, ischnacanthiform acanthodian tooth-whorl, MWGUW/Ps/10/42, sample NVK-9, in lateral view. F, tip of a helodontid holocephalian tooth, MWGUW/Ps/10/43, sample SVK-6. G, chondrichthyan scale or branchial denticle, MWGUW/Ps/10/44, sample SVK-1/7, in lateral and coronal views. H–J, *Thrinacodus* aff. *tranquillus* Ginter, 2000, sample SVK-1/7. H – MWGUW/Ps/10/45, in oral/lateral view; I – MWGUW/Ps/10/46, in oral view; J – MWGUW/Ps/10/47, in oral and lateral views. Scale bars 0.5 mm probably a piece of the highest, median portion of the crown of a “bradyodont” holocephalian tooth. The tooth may represent the Helodontiformes, but similar teeth with high, rounded median parts also belong to the dentitions of certain Cochliodontiformes, e.g., *Psephodus* (see Stahl 1999, fig. 58A, H) and thus separation of these two orders based on dental elements seems artificial.

CHONDRICHTHYAN ASSEMBLAGES

Of all the samples from the Famennian of Armenia, the sample Er-1 from the *crepida* Zone of Ertych is the most interesting. It yielded a large number of chondrichthyan teeth (almost 200), almost the largest of all the samples processed from the Iranian Platform. The abundance of *Phoebodus gothicus* finally confirms the earlier suggestion (Ginter *et al.* 2002) that at least in this area it appeared already in the lower Famennian. Some time in the *crepida* Zone (the dating is not precise enough, but probably near the end of it) and in the middle Famennian this relatively large phoebodont shark predominated in the Irano-Armenian seas. We have records of it from Hutk in the Kerman region (more than 50%, Ginter *et al.* 2002), to Chahriseh near Esfahan (26% in a very diverse sample 114, Hairapetian and Ginter 2009), to Zonuz in the East Azerbaijan province in northwestern Iran (almost only *Ph. gothicus*, but a small sample, Hampe 2000), and finally to Ertych (42 %, this paper). In Hutk and Ertych it is associated mainly with the crushing teeth of *Deihim mansureae* and the clutching teeth of ctenacanthiforms.

The only important difference between the samples from the latter two sections is the occurrence of *Ertychius intermedius* sp. nov. in Er-1. It would be interesting to discover if this new species is endemic to Armenia or distributed all over the Iranian Platform, but simply so rare that it could only be found coincidentally in this very rich sample. When one looks at the diagrams comparing the taxonomic compositions of the samples from Ertych and Hutk (Text-fig. 12), it is evident that if *E. intermedius* were absent from Er-1, both diagrams would look almost identical.



Text-fig. 12. Comparison of taxonomic compositions of chondrichthyan faunas from the lower Famennian of Hutk, central Iran (sample 38/23), and Ertych, Armenia (sample Er-1)

The sample KHV-11 from Khor Virap is too small to be used for any statistical comparison (only 21 shark teeth), but the taxa represented there are generally the same as in the upper Famennian of Dalmeh (central Iran, Yazd region; sample 64, Early/Middle *expansa* Conodont Zone). It is likely that these samples represent the same transgression at the beginning of the *expansa* Zone noted in other regions (e.g., Anti-Atlas in Morocco, Ginter *et al*. 2002). The relative abundance of protacrodont and hybodont crushing teeth shows that, despite the probable transgression, the basin remained relatively shallow and the water was oxygenated from the surface to the bottom.

Although Late Devonian rock successions on the Iranian terranes form thick, perfectly accessible sections, the record of chondrichthyans is extremely patchy. This is due to generally shallow water conditions on the platform and frequent emersions or at least extreme shallowing, marked by the layers of coarse siliciclastic sediments. Therefore, in spite of the richness of particular samples, the evolution of Famennian chondrichthyan fauna can be observed only in snapshots, separated from each other by intervals of several conodont zones with no information at all. We can only hope that further investigations in the other parts (e.g., the Tabas block of the Central East Iran Microplate) with deeper-water deposits (Hairapetian and Ginter 2010) will connect the isolated assemblages in order to form a continuous picture.

Acknowledgment

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