

Pelagic chondrichthyan microremains from the Upper Devonian of the Kale Sardar section, eastern Iran

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ABSTRACT:

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An assemblage of fifteen taxa of chondrichthyan microremains from late Frasnian through late Famennian pelagic deposits of the Kale Sardar section, eastern Iran, is described. Several taxa (*Phoebodus bifurcatus*, *Phoebodus sophiae* and *Protacrodus vetustus*) are reported for the first time from Iran. The presence of *Deihim mansureae* and *Ph. sophiae* in the Late *rhenana* to *linguiformis* Zones and *Phoebodus rayi* in the Early *triangularis* Zone of the Kale Sardar section, provides new biostratigraphic information. The late Frasnian part of the assemblage corresponds to the faunas from the intrashelf basins of Central Europe, and the middle–late Famennian part is comparable to that from the Tafilalt Platform of Morocco.

Key words: Chondrichthyes; Teeth; Scales; Devonian; Frasnian; Famennian; Eastern Iran.

INTRODUCTION

In eastern Iran, Upper Devonian strata are well exposed in the Shotori Range (c. 100 km long), Derenjaj and Ozbak Kuh Mountains. On the western flank of the Shotori Range, there is a chaotic set of scattered hills (numbered as Hills I to V in Becker *et al.* 2004) composed of the Upper Devonian Shishtu Formation. This formation comprises the famous “cephalopod beds”, exposed on the northern bank of the Sardar River. As noted by Becker *et al.* (2004) and Wendt *et al.* (2005), the “cephalopod beds” are composed of several horizons ranging from the middle Frasnian to the late Famennian, variable in lithology. The lower boundary of the “cephalopod beds” is diachronous, as its age is late Frasnian in the Kale Sardar and early Famennian farther south in the Shotori Range (e.g., Wendt *et al.* 1997, 2005; Yazdi 1999). The sampled

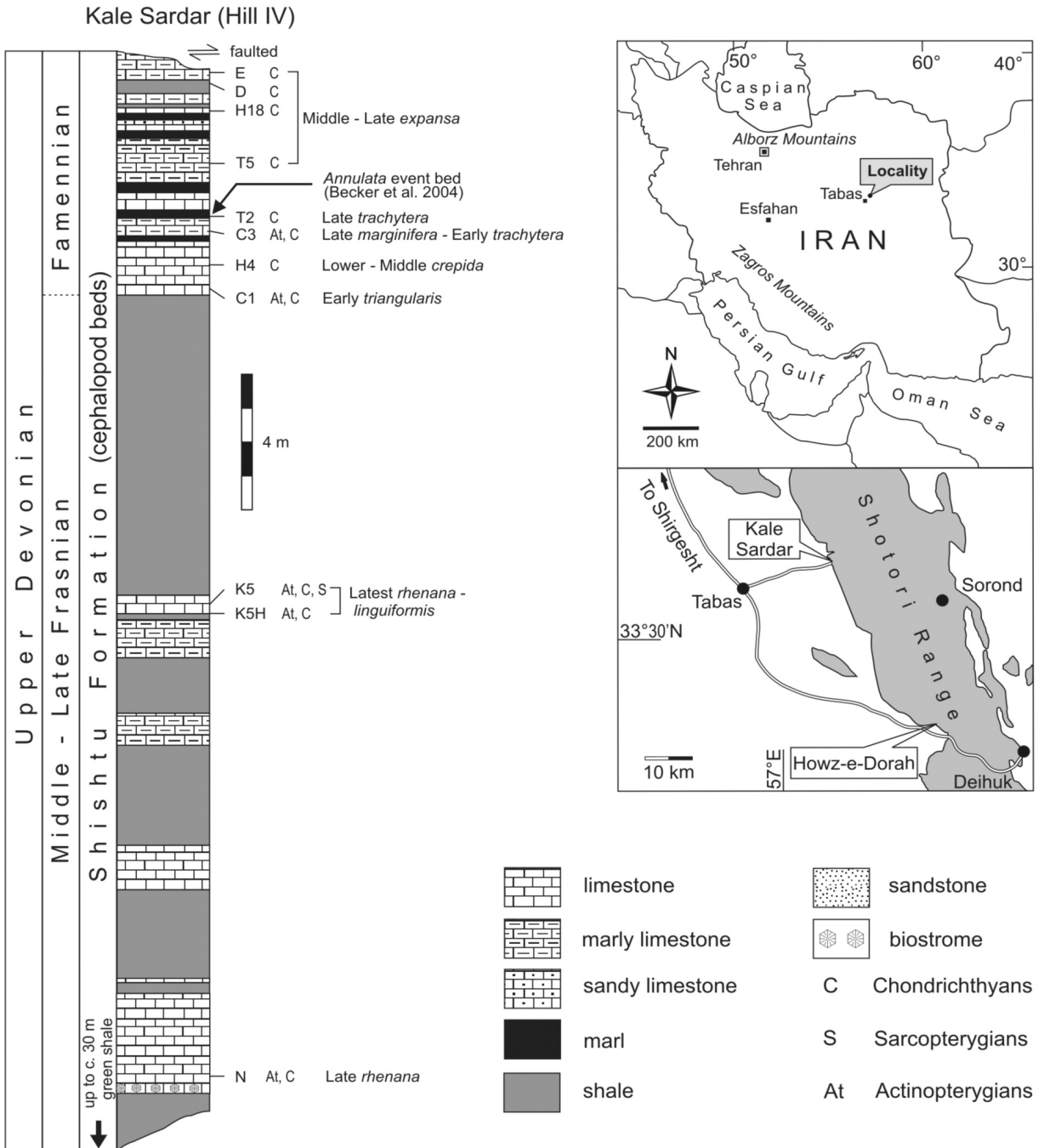
section (= Hill IV in Becker *et al.* 2004) is located c. 22 km east of Tabas (N 33°39'26"; E 57°8'38"; Text-fig. 1). The succession begins with a series of oolitic limestones alternating with green shale grading upwards into a thin complex of condensed marls, marly limestones and shales.

As recently stated by Yazdi (1999), Ashouri (2002) and Wendt *et al.* (2005), these hills probably represent a tectonic mélange, rather than olistolites as proposed by Becker *et al.* (2004). Following an early report by Clapp (1940), the outcrops in Kale Sardar were studied by Stöcklin *et al.* (1965). The horizons at Kale Sardar are much more fossiliferous than those in the southern sections of the Shotori Range (e.g., Howz-e-Dorah and Ghale-Kalaghu). To date, several works have documented the very rich Upper Devonian faunas, including ammonoids (Walliser 1966; Becker *et al.* 2004), brachiopods (Sartenaer 1966; Legrand-Blain 1999), con-

odonts (Yazdi 1999; Ashouri 2002, 2004; Gholamalian 2007; Gholamalian *et al.* 2009), crinoids (Webster *et al.* 2007), receptaculitids (Flügel 1961) and trilobites (Haas and Mensink 1970; Haas 1994; Morzadec 2002; Feist *et al.* 2003). As yet unconfirmed occurrences of rugose corals and stromatoporoids were reported from the vestiges of possible Middle Devonian blocks in an overthrust zone at Kale Sardar (Mistiaen 2001). Schultze (1973) described large brachythoracid placoderms,

Eastmanosteus sp., *Aspidichthys* cf. *ingens*, *Holonema* sp. cf. *H. rugosum* and a few indeterminable arthrodire fragments, all from late Frasnian limestones.

The present paper describes microremains of pelagic chondrichthyans, collected from eleven horizons in the Upper Frasnian and Famennian of Kale Sardar (Text-fig. 1, Table 1); an additional sample was collected from the base of the Niaz section in the Kale Sardar area (Yazdi 1999, pp. 170–171). The numer-



Text-fig. 1. Simplified stratigraphic column of the Kale Sardar section. Maps of Iran show location of the section

ous associated microremains are scales and bone fragments of sarcopterygians and actinopterygians. The faunal list of all identified fish taxa from Kale Sardar is given in Appendix 1.

AGE OF SAMPLES

Late Frasnian

The lowermost of the studied samples (N, Table 1) contains *Icriodus alternatus alternatus*, *I. alternatus mawsonae*, *Palmatolepis bogartensis*, *Ancyrodella curvata*, *Ad. buckeyensis*, *Anyrognathus triangularis*, *Polygnathus evidens*, *P. politus* and *P. webbi*, suggesting a late Frasnian (Late *rhenana* Zone) age (Gholamalian 2007, table 2). From the underlying white oolitic limestone, Yazdi (1999) reported the ammonoid *Beloceras tenuistriatum*, the index of the Late *hassi* Zone of the middle Frasnian. The oolitic limestone changes laterally to a coeval red ferruginous ammonoid-bearing bed, lacking *B. tenuistriatum*. Walliser (1966) probably found *Manticoceras ammon* at this horizon.

Samples K5H and K5 yielded very rich conodont assemblages (Gholamalian 2007, table 2, and Table 1 herein). Their characteristic species are: *Icriodus alternatus alternatus*, *I. alternatus helmsi*, *I. alternatus mawsonae*, *Ancyrodella buckeyensis*, *Anyrognathus triangularis*, *Palmatolepis gigas gigas*, *Pa. winchelli*, *Polygnathus aequalis*, *P. evidens*, *P. politus*, *P. procerus*, *P. webbi*, and *P. vachiki*. These species indicate an interval from the Late *rhenana* to the *linguiformis* Zones (Gholamalian 2007) and are entirely consistent

with an earlier conodont dating (Yazdi 1999). The dominance of polygnathid biofacies species in these samples suggests a distal shelf or slope palaeoenvironment (Gholamalian 2007).

The thick black and barren shale member between fossiliferous late Frasnian and earliest Famennian beds possibly represents the uppermost Frasnian.

Early Famennian

In sample C1 (= sample Cly1 in Gholamalian 2007, table 2, and Table 1 herein) several conodonts species, including *Palmatolepis* aff. *perlobata*, *Icriodus alternatus alternatus*, *I. alternatus mawsonae*, *I. alternatus helmsi* and *Polygnathus tenellus* suggest the Early *triangularis* zone of early Famennian age. The conodont assemblage from sample H4, represented by *Icriodus alternatus alternatus*, *I. alternatus mawsonae*, *Palmatolepis clarki*, *Pa. minuta loba*, *Pa. minuta minuta*, *Pa. quadrantinodosalobata*, *Pa. subperlobata*, *Polygnathus brevilaminus*, *P. nodocostatus*, *P. pseudobrevilaminus* and *P. sardarensis* indicates the Early to Middle *crepida* Zones of the early Famennian (Gholamalian *et al.* 2009).

Middle Famennian

The conodont assemblage of sample C3 includes (Table 1) *Palmatolepis perlobata schindewolfi*, *Clydagnathus* sp., *Polygnathus glaber bilobatus*, *Bispathodus* sp. and *Mehlina* sp., suggesting the Late *marginifera*–Early *trachytera* Zones. Sample T2 is taken from the marly bed which yielded *Bispathodus stabilis*, *Palmatolepis gracilis gracilis*, *Pa. gracilis sigmoidalis*,

taxa	samples												N1	
	N	K5H	K5	C1	H4	C3	T2	T5	H18	D	E			
<i>Phoebodus bifurcatus</i>	-	1	1	-	-	-	-	-	-	-	-	-	-	2
<i>Ph. gothicus gothicus</i>	-	-	-	-	-	1	1	2	2	-	-	-	2	8
<i>Ph. rayi</i>	-	-	-	2	-	-	-	-	-	-	-	-	-	2
<i>Ph. sophiae</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Ph. turnerae</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Phoebodus</i> spp.	-	-	-	-	-	-	-	-	-	?1	2	-	-	3
<i>Jalodus australiensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Cladodoides</i> sp.	1	27	32	14	2	-	4	-	1	-	-	-	-	81
<i>Squatina glabrum</i>	-	-	-	-	-	1	2	-	-	-	-	-	-	3
Ctenacanthiformes gen. et sp. indet.	-	-	-	-	1	-	-	-	-	-	-	-	-	1
<i>Arduodens flammeus</i>	1	-	3	-	-	-	-	-	-	-	-	-	-	4
<i>Protacrodus vetustus</i>	-	3	19	-	-	-	-	-	-	-	-	-	-	22
<i>Protacrodus</i> spp.	-	-	-	-	-	-	-	1	-	-	-	-	3	4
<i>Deihim mansureae</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Protacrodontidae gen. et sp. nov.	-	-	-	3	1	-	-	-	-	-	-	-	1	5
Total (teeth)	2	31	57	19	4	2	7	3	3	1	2	8	139	
Chondrichthyan scales	-	16	93	19	-	-	-	-	-	-	-	-	-	

Table 1. Distribution of chondrichthyan teeth in the Upper Devonian of the Kale Sardar section, central Iran

Pa. rugosa cf. *ampla*, *Pa. perlobata schindewolfi*, *Polygnathus communis* group, *P. nodocostatus*, *P. nodoundatus*, *P. semicostatus*, *P. subirregularis*, *Alternognathus beulensis* and *Icriodus cornutus*, suggesting the Late *trachytera* Zone. Becker *et al.* (2004) detected the *Annulata* event of the uppermost Late *trachytera* Zone in this marly horizon (Text-fig. 1).

The conodonts of the latest *marginifera* Zone of sample N1 (= sample 1 in Yazdi 1999, fig. 6), taken 4.5 metres above the base of the Niaz section, are composed of *Pelekysgnathus inclinatus*, *Mehlina* sp., *Scaphignathus velifer velifer*, *S. velifer leptus*, *Polygnathus communis communis*, *P. nodocostatus*, *P. semicostatus*, *Palmatolepis glabra glabra*, *Pa. klapperi*, *Pa. minuta minuta*, *Pa. perlobata schindewolfi*, *Pa. perlobata sigmoida* and *Pa. wolskae*.

Late Famennian

Samples T5, H18, D and E (Table 1), all occur within an interval of the Middle–Late *expansa* Zones, in which a rich conodont fauna including *Bispathodus aculeatus aculeatus*, *Bi. costatus*, *Bi. stabilis*, *Polygnathus semicostatus*, *P. delicatulus*, *P. communis* group, *P. nodocostatus*, *P. nodoundatus*, *P. perplexus*, *Palmatolepis gracilis gracilis*, *Pa. gracilis sigmoidalis*, *Pa. perlobata schindewolfi*, *Pa. rugosa ampla*, *Pseudopolygnathus primus*, *Ps. brevipennatus*, *Clydagnathus* sp., *Mehlina* sp., *Branmehla inornata* and *Pelekysgnathus inclinatus* was identified by Gholamaljan *et al.* (2009, table 1).

MATERIAL AND METHODS

Calcareous samples were dissolved in a buffered solution of 10% acetic acid and the residues were prepared by sieves. SEM photographs were taken at the Institute of Palaeobiology, Polish Academy of Sciences (Warsaw, Poland) using a Philips XL 20. The chondrichthyan microremains are of grey or very dark grey colour and are generally well preserved. All of the specimens described are deposited in the Department of Geology, Azad University, Esfahan (AEU).

SYSTEMATIC PALAEOONTOLOGY

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Phoebodontiformes Ginter, Hairapetian and Klug, 2002
 Family Phoebodontidae Williams in Zangerl, 1981
 Genus *Phoebodus* St. John and Worthen, 1875

TYPE SPECIES: *Phoebodus sophiae* St. John and Worthen, 1875

Phoebodus sophiae St. John and Worthen, 1875
 (Text-fig. 2A)

MATERIAL: One specimen from sample K5, Late *rhenana* to *linguiformis* Zones.

DESCRIPTION AND REMARKS: This is a large tooth (base width c. 3 mm) with a thick and trapezoidal base. Its typically phoebodont crown is composed of five cusps, probably smoothed by abrasion; only a lateral carina separates the labial and lingual faces (Text-fig. 2A₃). The aboral side of the base is perforated by a few large foramina.

The labio/basal projection is almost split in two by a median depression (Text-fig. 2A₅). The button looks almost bilobed (Text-fig. 2A₃₋₄). A tendency for splitting of the button, albeit much weaker, can be observed in the holotype of *Ph. sophiae* (NMNH 13192, MG personal observation; the original drawing in St. John and Worthen 1875 does not show it) and also in the material from the Givetian of the Holy Cross Mountains, Poland (Liszkowski and Racki 1993; figs 3C, D particularly) and Aragonian Pyrenees (Ginter *et al.* 2008, fig. 2K, M). The presence of a bilobed button has occasionally been noted from other phoebodonts, such as *Ph. politus* (Newberry 1889, pl. 27, figs 27, 28), *Ph. bifurcatus* (Ivanov 1999, pl. 1, fig. 10a) and *Ph. rayi* (Ginter and Turner 1999, fig. 4J, K).

The tooth of *Ph. sophiae* from the late Frasnian of Kale Sardar is stratigraphically the latest known occurrence of this species. So late a presence in Iran of this generally Givetian–early Frasnian form supports the earlier idea that it was a species of the *Ph. sophiae* group which gave rise to Famennian phoebodonts, rather than any widespread late Frasnian species, such as *Ph. latus* or *Ph. bifurcatus*.

STRATIGRAPHIC RANGE: Givetian (Middle *varcus* Zone) – late Frasnian (Late *rhenana* to *linguiformis* Zones).

Phoebodus bifurcatus Ginter and Ivanov, 1992
 (Text-figs 2B, 2C)

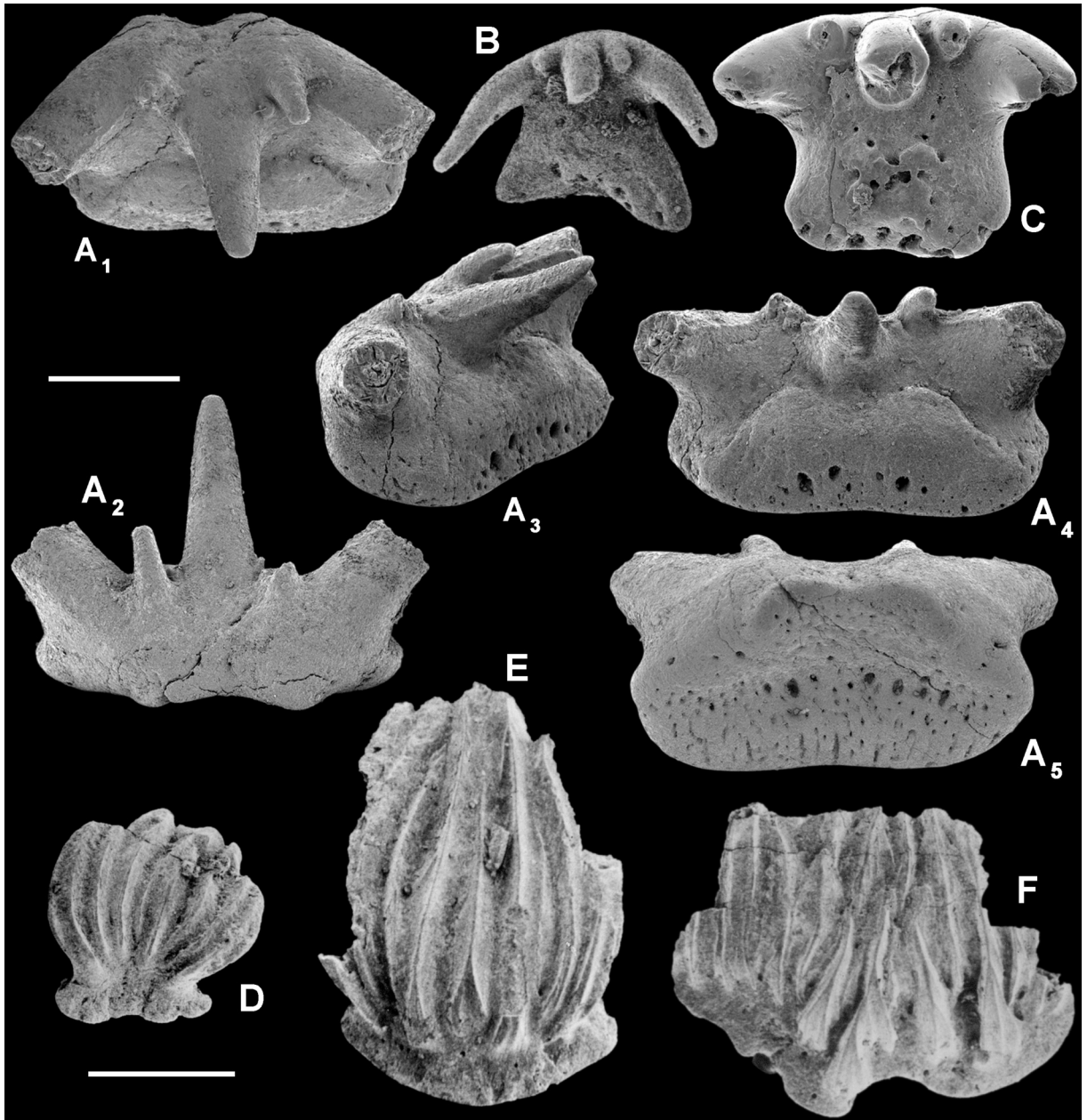
MATERIAL: One specimen from sample K5H and one specimen from sample K5, Late *rhenana* to *linguiformis* Zones.

DESCRIPTION AND REMARKS: AEU 678 (Text-fig. 2B) has horn-like linguo-lateral ends on the base. In AEU 679 (Text-fig. 2C), a very abraded tooth, the linguo-lateral corners of a long base appear to have originally been more expanded than its median part. The crown is composed of five smooth cusps. If the smoothness of the cusp surfaces is not only the result of abrasion, the teeth could represent a juvenile stage of development (compare Ginter and Ivanov 1992,

figs 5G, H). These are the first illustrated teeth referable to *Ph. bifurcatus* from North Gondwana.

STRATIGRAPHIC RANGE: Frasnian, *rhenana*–lower part of *linguiformis* Zones.

Phoebodus gothicus gothicus Ginter, 1990
(Text-figs 4G–J)

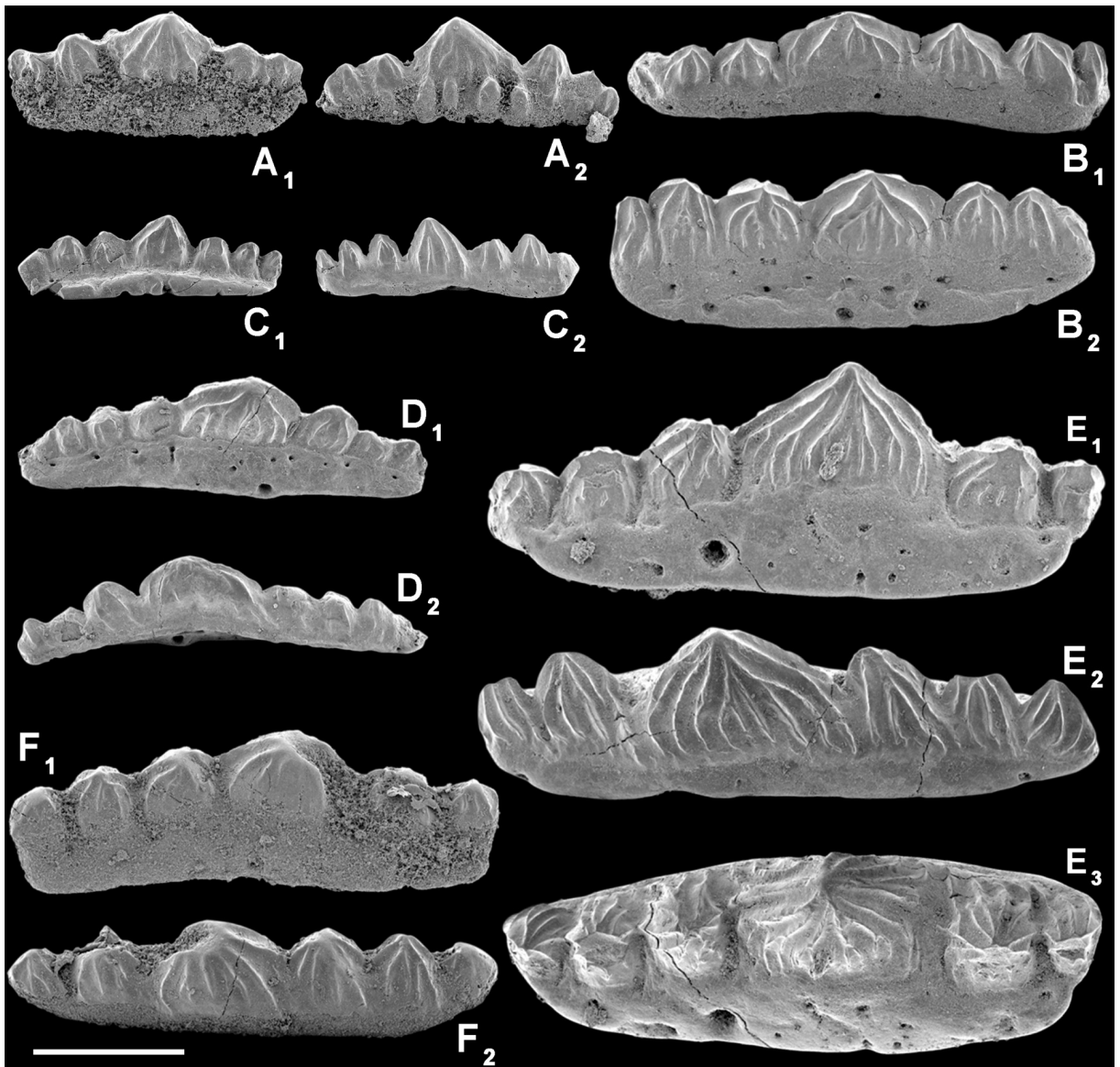


Text-fig. 2. Late Frasnian chondrichthyan teeth and scales from Kale Sardar. A, C–F from sample K5; B from sample K5H. A – *Phoebodus sophiae* St. John and Worthen, 1875, AEU 680, in occlusal (A₁), labial (A₂), lateral (A₃), lingual (A₄) and basal/labial (A₅) views. B, C – *Phoebodus bifurcatus* Ginter and Ivanov, 1992; B – AEU 678 in occlusal view; C – AEU 679 in occlusal view. D–F – Chondrichthyan scales; D – AEU 681 in crown view; E – AEU 682 in crown view; F – AEU 683 in crown view. Scale bar for figs B–F equals 0.5 mm (for figs A₁–A₅ = 1 mm)

MATERIAL: One specimen from sample C3 (Late *marginifer*–Early *trachytera* Zones), one specimen from sample T2 (Late *trachytera* Zone), two specimens from sample T5 (Middle–Late *expansa* Zones), two specimens from sample H18 (Middle–Late *expansa* Zones) and two specimens from sample N1 (Latest *marginifera* Zone).

REMARKS: Most of the specimens studied from Kale Sardar have a tooth base of the “gothic” outline (e.g., Text-fig. 4G), resembling the type material from the Holy Cross Mountains (Poland, Ginter

1990). Two specimens illustrated (Text-figs 4H, I) are characterized by a very long and narrow base, resembling specimens from Ostrówka, Poland (Ginter and Ivanov 1996, fig. 2E) and the Ardennes-Rhenish Massif, Germany (Hampe and Schindler 2004, pl. 2, figs 1, 2). A single isolated crown is characterised by very long intermediate cusplets (Text-fig. 4J). As was observed by Hairapetian and Ginter (2009), the predominance of the gothic morphotype of *Ph. g. gothicus* over the second morphotype, with rounded lingual part, almost always indicates a deeper shelf environment.



Text-fig. 3. Late Frasnian protacrodonts from Kale Sardar. A–E, G from sample K5; F from sample K5H. A – *Deihim mansureae* Ginter, Hairapetian and Klug, 2002, AEU 685, in lingual (A₁) and labial (A₂) views. B–F – *Protacrodus vetustus* Jaekel, 1921; B – AEU 677 in labial (B₁) and lingual (B₂) views; C – AEU 675 in lingual (C₁) and labial (C₂) views. D – AEU 686 in lingual (D₁) and labial (D₂) views; E – AEU 687 in lingual (E₁), labial (E₂) and occlusal (E₃) views; F – AEU 676 in lingual (F₁) and labial (F₂) views. Scale bar equals 0.5 mm

STRATIGRAPHIC RANGE: From the *crepida* through the Early/Middle *praesulcata* Zones (Ginter *et al.* 2002; Hairapetian and Ginter 2009).

Phoebodus rayi Ginter and Turner, 1999
(Text-fig. 4D)

MATERIAL: Two specimens from sample C1, Early *triangularis* Zone.

DESCRIPTION AND REMARKS: The figured specimen has a pentagonal base and a five-cuspid crown. The rounded button is located near the lingual rim of the base and surrounded by a few foramina.

It resembles the original teeth of *Ph. rayi* from the *crepida* Zone of the Canadian Arctic (Ginter and Turner 1999) in the base shape and the position of the button.

STRATIGRAPHIC RANGE: The discovery of this tooth in the Early *triangularis* Zone of Kale Sardar extends the lower range of the species. Its last appearance is recorded in the Early or Middle *crepida* Zone (Ginter and Turner 1999).

Phoebodus turnerae Ginter and Ivanov, 1992
(Text-fig. 4F)

MATERIAL: One specimen from sample N1, Latest *marginifera* Zone.

DESCRIPTION AND REMARKS: The tooth (Text-fig. 4F) resembles the type specimens from the South Urals (e.g., Ginter and Ivanov 1992, fig. 8B). The base is a wide, lingually narrowing pentagon, with a prominent button close to the lingual rim. There is a large canal opening, just below the button. Although these features fit well to the species diagnosis, the considerable labio-lingual length of the base makes the tooth also slightly similar to those of *Ph. gothicus*.

STRATIGRAPHIC RANGE: Early to middle Famennian (Early *crepida* – Late *marginifera* Zones).

Family Jalodontidae Ginter, Hairapetian and Klug, 2002

Genus *Jalodus* Ginter, 1999

TYPE SPECIES: *Phoebodus australiensis* Long, 1990.

Jalodus australiensis (Long, 1990)
(Text-fig. 4E)

MATERIAL: One specimen from sample N1, Latest *marginifera* Zone.

DESCRIPTION: It is characterised by a crown with three cusps; the central one is smaller (Text-fig. 4E₂). The labial side of one of the lateral cusps is ornamented with a specific “semilanceolate” pattern; only half of the cusp has the characteristic lanceolate sculpture and a distinct crista runs upward on the other half. The central cusp itself seems to have a stacked lanceolate ornament. A small, rounded button lies on the weakly developed base (Text-fig. 4E₁). The oral and lateral surfaces of the base are perforated with several foramina. The labio-basal projection is short and very prominent.

STRATIGRAPHIC RANGE: Middle Famennian (Early *marginifera* Zone) through late Tournaisian (*anchoralis/latus* Zone).

Order Ctenacanthiformes Glikman, 1964
Ctenacanthiformes gen. et sp. indet.
(Text-fig. 5E)

MATERIAL: One specimen from sample H4 (Early to Middle *crepida* Zones).

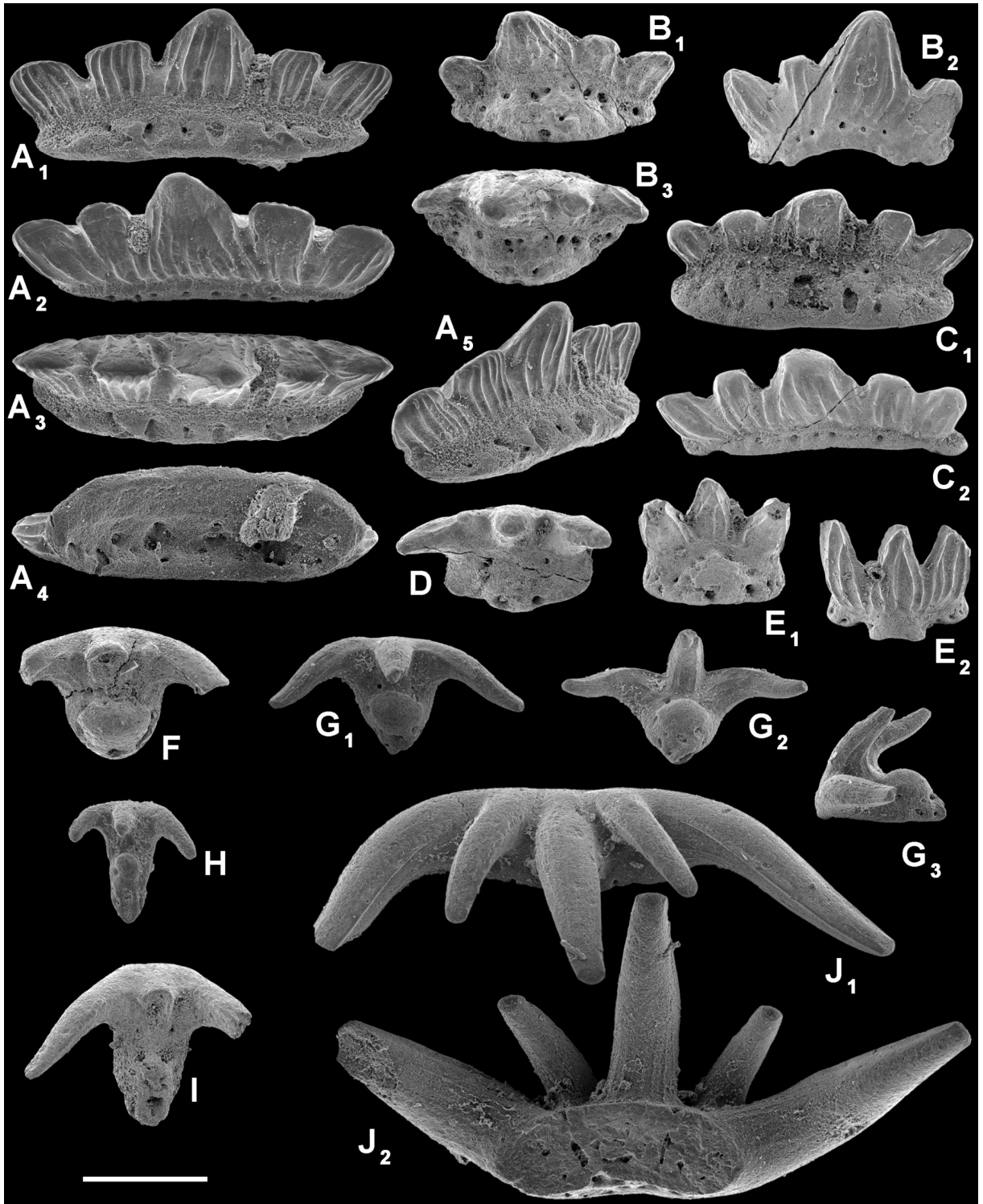
DESCRIPTION AND REMARKS: The crown of the specimen (AEU 781, Text-fig. 5E) is of cladodont design, with a high prominent central and four lateral cusps on one side; the other side is incompletely preserved, with only two lateral cusps remaining. The cusps are ornamented by subparallel strong cristae. The central cusp becomes very wide at the base and is elliptical in cross-section. The base is mesio-distally elongated and seems to be lingually developed, although a large part of the lingual part is missing. The labio-basal projection is arcuate, and perforated by two large foramina.

Family Ctenacanthidae Dean, 1909

Genus *Cladodoides* Maisey, 2001

TYPE SPECIES: *Cladodus wildungensis* Jaekel, 1921

Cladodoides sp.
(Text-figs 5A–E)



Text-fig. 4. Famennian chondrichthyan teeth from Kale Sardar. **A** from sample H4; **B–D** from sample C1; **E, F, I** from sample N1; **G, H** from sample H18; **J** from sample T5. **A–C** – Protacrodontidae gen. et sp. nov.; **A** – AEU 777 in lingual (A₁), labial (A₂), occlusal (A₃) and basal (A₄) and lateral (A₂) views; **B** – AEU 699 in lingual (B₁), labial (B₂) and occlusal (B₃) views; **C** – AEU 701 in lingual (C₁) and labial (C₂) views. **D** – *Phoebodus rayi* Ginter and Turner, 1999, AEU 704, in occlusal view. **E** – *Jalodus australiensis* (Long, 1990), AEU 705, in lingual (E₁) and labial (E₂) views. **F** – *Phoebodus turnerae* Ginter and Ivanov, 1992, AEU 703, in occlusal view. **G–J** – *Phoebodus gothicus gothicus* Ginter, 1990; **G** – AEU 778 in occlusal (G₁), lingual (G₂) and lateral (G₃) views; **H** – AEU 779 in occlusal view; **I** – AEU 702 in occlusal view. **J** – AEU 780, large, well preserved crown, in occlusal (J₁) and lingual (J₂) views. Scale bar equals 0.5 mm

MATERIAL: Eighty-one specimens from Kale Sardar: one from sample N (Late *rhenana* Zone), 27 from sample K5H and 32 from sample K5 (Late *rhenana* to *linguiformis* Zones), 14 from sample C1 (Early *triangularis* Zone), 2 from sample H4 (Early to Middle *crepida* Zones), 4 from sample T2 (Late *trachytera* Zone) and one from sample H18 (Middle–Late *expansa* Zones).

DESCRIPTION: The tooth crowns have three main cusps (central high and two laterally divergent ones) and two intermediate cusplets ornamented by a few strong cristae. The mesio-distally elongated base has a lenticular or subtriangular outline, a distinct and mesio-distally elongated button and an arcuate labio-basal projection. A few tricuspid teeth with similar characters were also found (Text-fig. 5A).

STRATIGRAPHIC RANGE: Late Frasnian – Middle Famennian.

Genus *Arduodens* Hairapetian and Ginter, 2009

TYPE SPECIES: *Arduodens flammeus* Hairapetian and Ginter, 2009

Arduodens flammeus Hairapetian and Ginter, 2009
(Text-fig. 5G)

MATERIAL: Three specimens from sample K5 (Late *rhenana* to *linguiformis* Zones), and one specimen from sample N (Late *rhenana* Zone).

DESCRIPTION AND REMARKS: The asymmetrical tooth crown is composed of four, laterally inclined slender cusps, including a high central main cusp, two laterals and an intermediate cusplet. The tooth base is characterized by having a lenticular outline and by lacking a button.

The teeth of *Arduodens flammeus* from Kale Sardar have recently been described, together with the type material of this species from the Chahriseh section in central Iran, by Hairapetian and Ginter (2009, text-figs 3B–D). One of these teeth is reillustrated here (AEU 612, Text-fig. 5G).

STRATIGRAPHIC RANGE: Late Frasnian (Late *rhenana* to *linguiformis* Zones) – early Famennian (Early *triangularis* Zone) (Hairapetian and Ginter 2009, this work).

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

Genus *Squatinactis* Lund and Zangerl, 1974

TYPE SPECIES: *Squatinactis caudispinatus* Lund and Zangerl, 1974

Squatinactis glabrum (Ginter, 1999)
(Text-fig. 5F)

MATERIAL: One specimen from sample C3 (Late *marginifera*–Early *trachytera* Zones) and two specimens from sample T2 (Late *trachytera* Zone).

DESCRIPTION: The tooth crown is composed of a high median cusp and two pairs of much smaller lateral cusps. There are remnants of two labio-basal projections, corresponding to widely spaced buttons on the base. In the labio-basal area there is a median concavity beneath the central cusp.

STRATIGRAPHIC RANGE: Middle to late Famennian.

Cohort Euselachii Hay, 1902
Superfamily Protacrodontoidea Zangerl, 1981
Family Protacrodontidae Cappetta, Duffin and Zidek, 1993

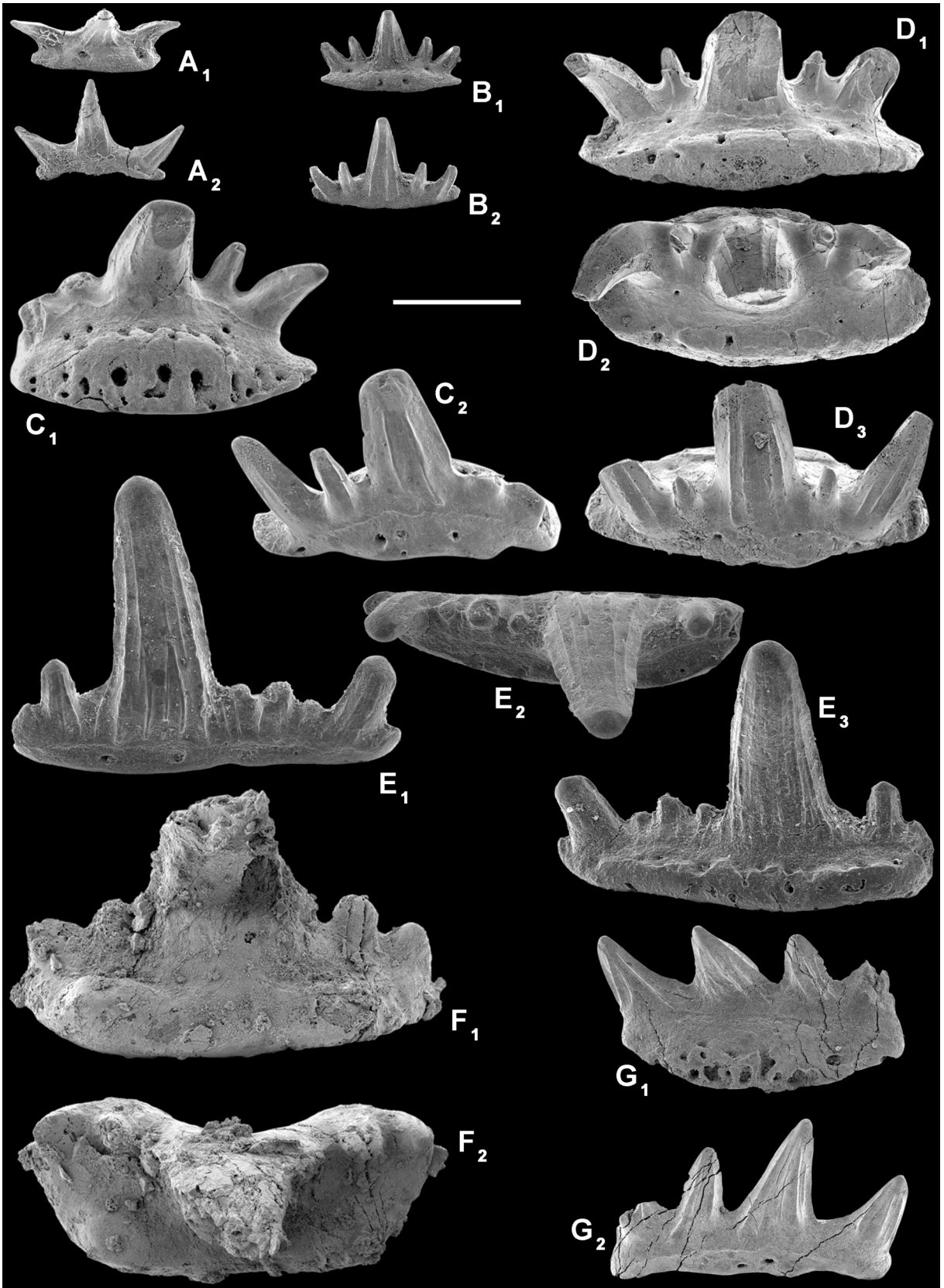
Genus *Deihim* Ginter, Hairapetian and Klug, 2002

TYPE SPECIES: *Deihim mansureae* Ginter, Hairapetian and Klug, 2002

Deihim mansureae Ginter, Hairapetian and Klug, 2002
(Text-fig. 3A)

MATERIAL: One specimen from sample K5, Late *rhenana* to *linguiformis* Zones.

STRATIGRAPHIC RANGE: The specimen from Kale Sardar is the first definitive occurrence of this species in the late Frasnian (Late *rhenana* to *linguiformis* Zones), thereby extending the known age range from late Frasnian, Late *rhenana* – *linguiformis* Zones through late Famennian, Early *expansa* Zone. It seems to have successfully survived the Frasnian/Fa-



mennian boundary events, and then dispersed on the Famennian shallow shelves of Iran.

Genus *Protacrodus* Jaekel, 1921

TYPE SPECIES: *Protacrodus vetustus* Jaekel, 1921

Protacrodus vetustus Jaekel, 1921
(Text-figs 3C–F)

MATERIAL: Twenty-two specimens (Late *rhenana* to *linguiformis* Zones): three from sample K5H and nineteen from sample K5.

DESCRIPTION AND REMARKS: The crown has a pyramidal to bulbous median cusp and usually three lateral cusps on each side (e.g., Text-fig. 3C). The lower parts of the cusps are fused. The central cusp is prominent, may be oriented ?distally; all cusps are ornamented by distinct wavy cristae on both the lingual and labial sides. The base has a short but laterally elongated lingual extension and is perforated with canal openings. This is the first record of this species from Iran.

STRATIGRAPHIC RANGE: *Protacrodus vetustus* is a common species in the Frasnian–Famennian boundary beds of the areas between Laurussia and NW Gondwana (e.g., Germany, Gross 1938; Moravia, Ginter in Hladil *et al.* 1991; South Urals, Ginter and Ivanov 2000; Poland, Ginter 2002; Morocco, Ginter *et al.* 2002).

Protacrodontidae gen. et sp. nov.
(Text-figs 4A–C)

MATERIAL: Five specimens: three from sample C1 (Early *triangularis* Zone), one from H4 (Early to Middle *crepida* Zones) and one from N1 (Latest *marginifera* Zone).

DESCRIPTION AND REMARKS: Several specimens possess a pentacuspoid tooth crown with laterally fused, labio-lingually compressed cusps and intermediate

cusplets, ornamented by strong cristae on the lingual and labial sides (e.g., Text-fig. 4A). All the cusps are slightly lingually inclined (Text-fig. 4A₅). The base is short lingually, and buttonless. The labio-basal thickening is concave and distinct, bearing a row of foramina. The base is penetrated by numerous foramina.

Similar teeth which share several morphological features in crown and base with cladodonts and protacrodonts are also recorded from the Chahrisheh section, central Iran (Hairapetian and Ginter 2009, text-figs 2e, f).

There are also some rare teeth in the collections in which the asymmetrical tooth crown possesses four cusps only (Text-fig. 4B). The base has an elevated lingual extension and several foramina ordered in a row, on both sides of the crown-base interface.

We temporarily refrain from naming this probably new protacrodontid taxon, due to paucity of material. It is difficult to ascertain whether the differences between the individual teeth are due to heterodonty (which we presume) or whether the specimens described herein represent different species.

STRATIGRAPHIC RANGE: Early–middle Famennian (Early *triangularis*–Latest *marginifera* Zones) (Hairapetian and Ginter 2009, this work).

Chondrichthyan scales
(Text-figs 2D–F)

The ctenacanth-type scales *sensu* Reif (1978) are characterised by an elliptical or irregular base with flat or concave lower surface (Text-figs 2D–F). The scale crowns have parallel or subparallel odontodes. These were usually found together with the ctenacanthiform “*Ctenacanthus*” *costellatus* Traquair, 1884 (Reif 1978), also with *Phoebodus rayi* (Ginter and Turner 1999) and *Phoebodus fastigatus* (Liao *et al.* 2007).

PALAEOECOLOGICAL REMARKS

Former records of Upper Devonian chondrichthyans from Iran considered only shallow water

Text-fig. 5. Late Frasnian and early Famennian cladodont teeth from Kale Sardar. A, B from sample K5H; C, D, G from sample K5; E from sample H4; F from sample C3. A–D – *Cladodoides* sp.; A – AEU 692 in occlusal (A₁) and labial (A₂) views; B – AEU 693 in lingual (B₁) and labial (B₂) views; C – AEU 694 in lingual (C₁) and labial (C₂) views, D – AEU 695 in lingual (D₁), occlusal (D₂) and labial (D₃) views. E – Ctenacanthiformes gen. et sp. indet., AEU 781, in labial (E₁), occlusal (E₂) and lingual (E₃) views. F – *Squatina glabrum* (Ginter, 1999), AEU 706, in lingual (F₁) and occlusal (F₂) views. G – *Arduodens flammeus* Hairapetian and Ginter, 2009 (reillustrated), AEU 612 in lingual (C₁) and labial (C₂) views. Scale bar equals 0.5 mm

faunas (e.g., Ginter *et al.* 2002; Hairapetian *et al.* 2008; Hairapetian and Ginter 2009). Yazdi and Turner (2000) presented Upper Devonian fish microremains (chondrichthyans exclusively from Famennian and younger strata) from the Howz-e-Dorah section in the Shotori Range (c. 42 km SE of Kale Sardar; Text-fig. 1). The conodont biofacies data from Howz-e-Dorah revealed a rather shallow palaeoenvironment, whereas the conodont fauna from Kale Sardar indicated palmartolepid-polygnathid and polygnathid-bispathodid biofacies, characteristic of outer shelf to middle slope realms (Gholamalian 2007; Gholamalian *et al.* 2009). These palaeoenvironmental differences between Kale Sardar and Howz-e-Dorah were attributed to a considerably diversified palaeorelief of the depositional area, formed in a graben system by the activity of N–S-trending faults (Gholamalian *et al.* 2009).

Indeed, the late Frasnian chondrichthyan palaeo-community from Kale Sardar indicates conditions of a relatively deeper shelf setting rather than a deep marine, far offshore environment. It is composed of five genera (samples N, K5 and K5H counted together): *Protacrodus* (32%), *Deihim* (2%), *Phoebodus* (4%), *Cladodoidea* (54%) and *Arduodens* (5%). Protacrodonts, with their crushing teeth, are generally considered to have been inhabitants of submerged platforms, full of shelly benthic fauna (see, e.g., Ginter 2001). Such an abundance of protacrodont teeth precludes really great depths and long distances from shallow-water areas. The true far offshore late Frasnian facies would probably have yielded more phoebodontids and fewer protacrodontids (compare the late Frasnian fauna from the Pilot Shale in Confusion Range, Utah, USA, Turner and Youngquist 1995, Ginter 2008; see also Sandberg *et al.* 1988).

The high proportion of protacrodonts and cladodonts (and, in particular, *Protacrodus vetustus* and *Cladodoidea wildungensis*) is very similar to the situation observed in the upper Frasnian of Poland and Germany. In fact, these two sharks are the only species found thus far in the classic Kellwasserkalk locality at Bad Wildungen (Rhenish Slate Mountains; Gross 1938), Kowala and Plucki (Holy Cross Mountains), and Dębniak (Cracow Upland) (see Ginter 2002). All the listed Polish localities are considered to represent intrashelf basinal facies.

The middle–late Famennian part of the Kale Sardar section yielded too few shark teeth for any statistical analysis, which renders the application of the chondrichthyan biofacies model developed by Ginter (2000, 2001) impossible. Nevertheless, just the mere faunal list shows that the assemblage must be similar

to that of the Tafilalt Platform in the Anti-Atlas (Morocco, Ginter *et al.* 2002). It is less diverse than those from central Iran (e.g., Dalmeh section, Ginter *et al.* 2002; Chahriseh section, Hairapetian and Ginter 2009), apparently with a strong phoebodont component, fewer protacrodonts, no orodonts and crushing teeth of hybodonts and with the presence of such deeper-water forms as *Squatina glabrum* and *Jalodus australiensis*. Slightly confusing is the total absence of *Thrinacodus tranquillus*, the common late Famennian phoebodontid occurring both in Tafilalt and central Iran, but this is perhaps the result of the low number of specimens collected. While comparing assemblages from the two North Gondwanan regions, Ginter *et al.* (2002, p. 212) concluded that there were “close connections between the Tafilalt Platform and the open intercontinental sea”, but “large distance between central Iran and deeper marine areas”. Apparently, the same can be said when the two Iranian sections, Kale Sardar and Dalmeh, are compared. The former probably represents deeper environments with better connections to the ocean, and the latter belongs to the typical proximal shelf.

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Appendix 1.

Upper Devonian fish fauna from the Kale Sardar section (*; macro-remains).

Placodermi (Schultze 1973)

Aspidichthys cf. *ingens* Koenen, 1883 *

Holonema cf. *H. rugosum* Claypole, 1883 *

Eastmanosteus sp. *

Chondrichthyes (Hairapetian and Ginter 2009; this work)

Protacrodus vetustus Jaekel, 1921

Protacrodus spp.

Deihim mansureae Ginter, Hairapetian and Klug, 2002

Phoebodus sophiae St. John and Worthen, 1875

Phoebodus bifurcatus Ginter and Ivanov, 1992

Phoebodus gothicus gothicus Ginter, 1990

Phoebodus turnerae Ginter and Ivanov, 1992

Phoebodus rayi Ginter and Turner, 1999

Phoebodus spp. indet.

Jalodus australiensis (Long, 1990)

Cladodooides sp.

Squatinactis glabrum (Ginter, 1999)

Ctenacanthiformes gen. et sp. indet.

Arduodens flammeus Hairapetian and Ginter, 2009

Protacrodontidae gen. et sp. nov.

Actinopterygii (Hairapetian 2008)

Moythomasia durgaringa Gardiner and Bartram, 1977

Palaeonisciformes gen. et sp. indet.

Sarcopterygii (Hairapetian 2008)

Sarcopterygii gen. et sp. indet.