Acta Geologica Polonica, Vol. 59 (2009), No. 2, pp. 173–200

Famennian chondrichthyan remains from the Chahriseh section, central Iran

VACHIK HAIRAPETIAN[1] AND MICHAŁ GINTER[2]

[1]*Department of Geology, Islamic Azad University, Khorasgan branch, PO Box 81595-158, Esfahan, Iran.*
E-mail: vachik@khuisf.ac.ir
[2]*Institute of Geology, University of Warsaw, Żwirki i Wigury 93, 02-089 Warsaw, Poland.*
E-mail: m.ginter@uw.edu.pl

ABSTRACT:

Hairapetian, V. and Ginter, M. 2009. Famennian chondrichthyan remains from the Chahriseh section, central Iran. *Acta Geologica Polonica*, **59** (2), 173–200. Warszawa.

A diverse shallow water assemblage of chondrichthyan microremains is described from the Famennian of the Chahriseh section, central Iran. Twenty-two taxa are identified; of these two new taxa viz. *Roongodus phijani* gen. et sp. nov. (Hybodontoidea) and *Arduodens flammeus* gen. et sp. nov. (Ctenacanthiformes) have been erected. Two morphoecological subtypes of *Ph. gothicus* dentition, characteristic of deeper and shallower shelves, are proposed.

Key words: Chondrichthyes; Teeth; Scales; Palaeoecology; Devonian; Famennian; Iran.

INTRODUCTION

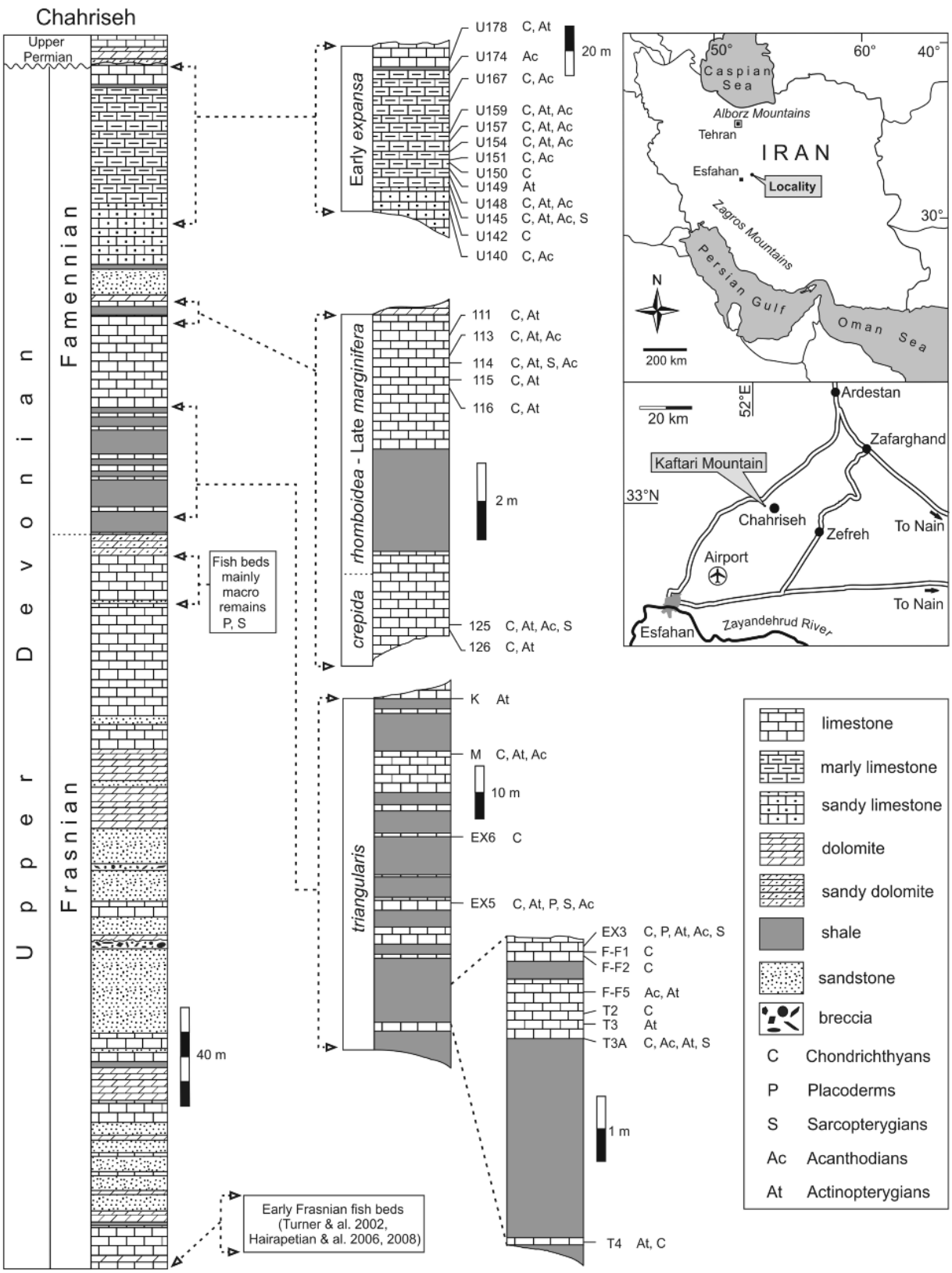
Fish remains were first reported from the Upper Devonian sedimentary sequence from the Chahriseh region (c. 55 km northeast of Esfahan; N 32º 59', E 52º 3'; Text-fig. 1; see Hairapetian *et al*. 2006; Gholamalian 2007 for general information), by Hairapetian and Gholamalian (1998). Turner *et al*. (2002) described a thelodont and acanthodian assemblage of early Frasnian age from the basal part of the section. Further investigations have provided additional, more diverse vertebrate material from these basal beds, revealing rich collections of acanthodians and chondrichthyans (Hairapetian *et al*. 2006, 2008).

Here we describe a rich chondrichthyan fauna, mainly microremains, collected by detailed sampling of twenty-seven horizons in the Famennian of Chahriseh (Text-fig. 1). The fauna from the lower part of the Famennian is associated with numerous macroremains of placoderms (*Bothriolepis* sp., dinichthyids and ptyctodontids; identified by John Long, 1998-1999, and Philippe Janvier, 2004), sarcopterygians (probably a megalichthyid, several dipnoan and coelacanth species; identified by Gaël Clément and Per Ahlberg, 2006), and acanthodians (an ischnacanthid similar to *Atopacanthus dentatus*; identified by Carole Burrow, February 2005). No macroremains (except a holocephalian tooth from the upper Famennian) were found in the upper part of the section. An updated faunal list of all identified fish taxa from Chahriseh is given in Appendix 1. We consider this paper as complementary to our earlier study on Famennian chondrichthyans from central Iran in Ginter *et al*. (2002).

AGE AND PALAEOENVIRONMENTS

Lower Famennian

Shallow water and/or nearshore conodonts, belonging to the icriodid-polygnathid biofacies were recovered from samples T3A, T3, T2, F-F5, F-F2, F-F1, EX3, EX5, EX6 and M of the Chahriseh section (Gho-



Text-fig. 1. Simplified stratigraphic column of the Chahriseh section (after Hairapetian *et al*. 2006 and Gholamalian 2007) with magnifications of fish-bearing horizons. Maps of Iran show location of the section.

lamalian 2007). Characteristic conodont species are *Icriodus cornutus, I. deformatus deformatus, I. deformatus asymmetricus, I. multicostatus multicostatus*, *I. alternatus alternatus, I. alternatus helmsi, Pelekysgnathus serradentatus* and *Polygnathus brevilaminus*, indicating an age of Middle to Late *triangularis* Zones (Gholamalian 2007). The icriodid species occur in much greater abundance than the polygnathids here, also indicative of very shallow water. These thin- to medium-bedded limestones, alternating with dark grey shales, are dominated by brachiopods, mostly rhynchonellids and, to a lesser degree, by fish macroremains and ostracods. The microfacies of these beds can be interpreted as bioclastic packstones to grainstones.

In the overlying levels, samples 126 and 125, from mollusc-brachiopod grainstones, yielded *Icriodus alternatus alternatus, I. cornutus, Pelekysgnathus inclinatus, Polygnathus communis communis* and *Mehlina* sp. The co-occurrence of these polygnathid and icriodid species in both levels indicates an age not older than the Middle *crepida* Zone and not younger than the Late *crepida* Zone. Thus, the most probable age range lies within the Middle through Late *crepida* Zones (Gholamalian 2007). The lower Famennian succession of the Chahriseh section is inferred to have been deposited on an inner shelf basement (Gholamalian 2007; Safari and Kangazian 2003).

Middle Famennian

From samples 116, 115, 114, 113 and 111 *Icriodus cornutus*, *Pelekysgnathus inclinatus, Polygnathus bouckaerti, P. communis communis*, *P. lanceolus, P. semicostatus* and *Mehlina* sp. were collected. The most important species, *Polygnathus bouckaerti* and *Icriodus cornutus*, suggest a time span from the *rhomboidea* through to Late *marginifera* Zones. Sample 114 is particularly significant in containing numerous shark teeth (Appendix 2). As the samples were recrystallised, detailed microfacies analysis could not be carried out, although some levels (e.g., 113) could be assigned to a brachiopod grainstone. Abundance of *Polygnathus* and *Icriodus* species, with the absence of Famennian deep water forms (e.g., *Palmatolepis* and *Ancyrognathus*), are characteristic of shallow shelf conodont palaeocommunities.

Upper Famennian

Several conodont species were retrieved from samples U140, U142, U145, U148, U150, U151, U154, U157, U159, U167, and U178. They include *Clydagnathus ormistoni*, *Polygnathus delicatulus*, *P. communis communis*, *P. communis collinsoni*, *P. semicostatus, Bispathodus bispathodus, Mehlina strigosa* and *Branmehla inornata,* indicative of the Early *expansa* Zone (see also Gholamalian 2003; Yazdi *et al*. 2000). The lithology of this unit commences with sandy limestones and grades into marly limestones. Rich assemblages of brachiopods (mostly spiriferids and strophomenids, Djafarian and Brice 1973), crinoid ossicles and bryozoans can be found embedded in the wackestone/packstone matrix. There are rare occurrences of the trilobite *Phacops* (*Omegops*) *cornelius* and large shell fragments of cyrtoclymeniid ammonoids (R. Feist, Yazdi and Ghobadipour in Mistiaen *et al*. 2000; Becker *et al*. 2004). The unit was deposited in a nearshore, shallow marine environment (Mistiaen *et al*. 2000; Safari and Kangazian 2003).

MATERIAL AND METHODS

Calcareous samples were dissolved in a buffered solution of 10% acetic acid and the residues sieved (0.177 mm). Specimens were picked from the residues by a wet brush under a Nikon SMZ-1 stereo microscope, and stored in cavity slides. For the SEM photography the specimens were mounted on one side of a carbon conductive tape (PELCO Tabs™, 12 mm in diameter); the other side was already attached to a pin aluminum stub. Photomicrographs were taken in Esfahan and in the Institute of Palaeobiology, Polish Academy of Sciences (Warsaw, Poland), using a Leica 360 and a Philips XL 20 Scanning Electron Microscopes, respectively.

The chondrichthyan microremains are generally grey or very dark grey. Some specimens (particularly those from sample 114, Chahriseh) are extensively covered with adhering clay, sand grains or calcite blades. The specimens are deposited in the Department of Geology, Azad University, Esfahan (AEU).

SYSTEMATIC PALAEONTOLOGY

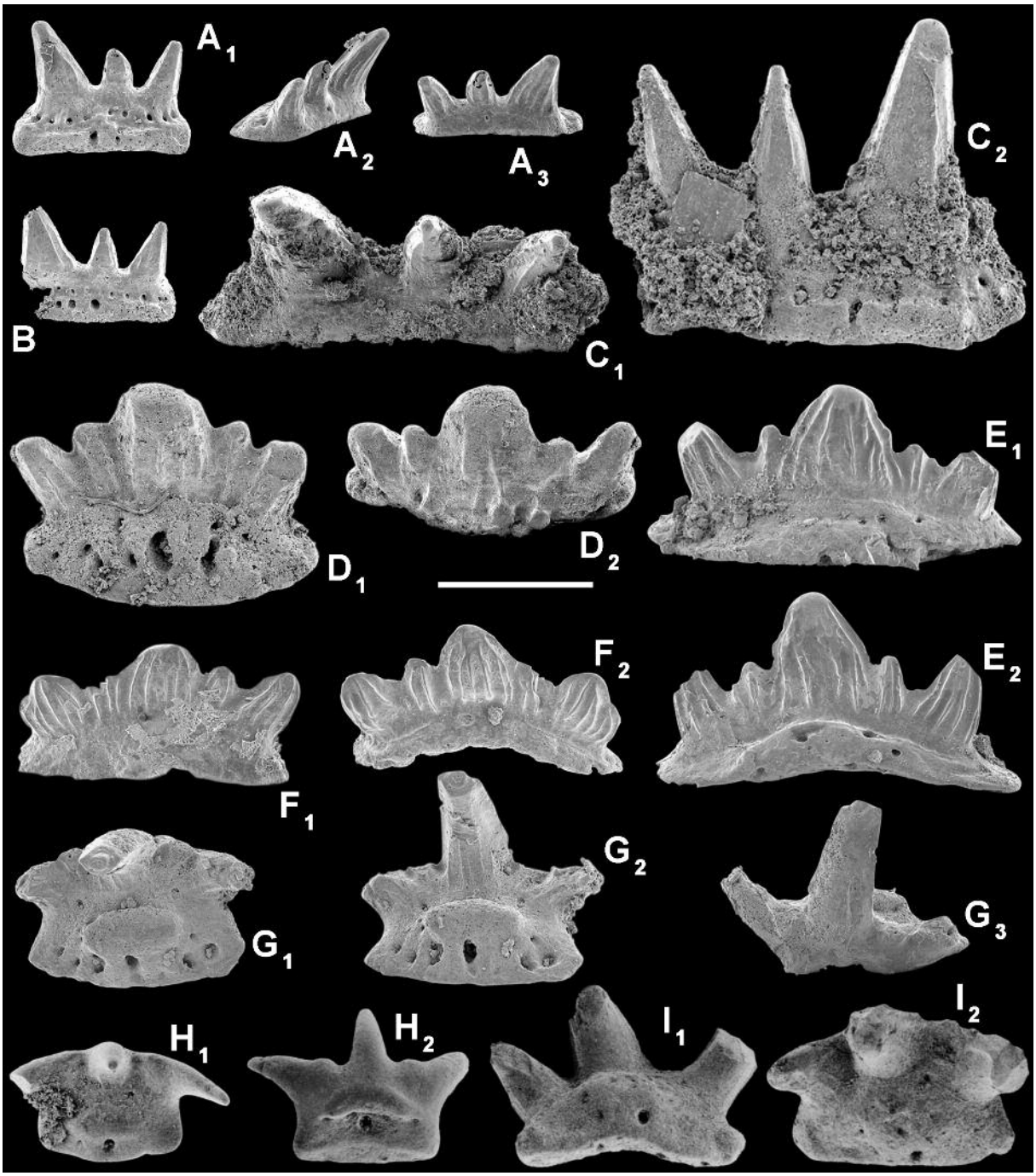
Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Omalodontiformes Turner, 1997
Family *incertae sedis*

Genus *Siberiodus mirabilis* Ivanov and Rodina, 2004 (Text-fig. 2A–C)

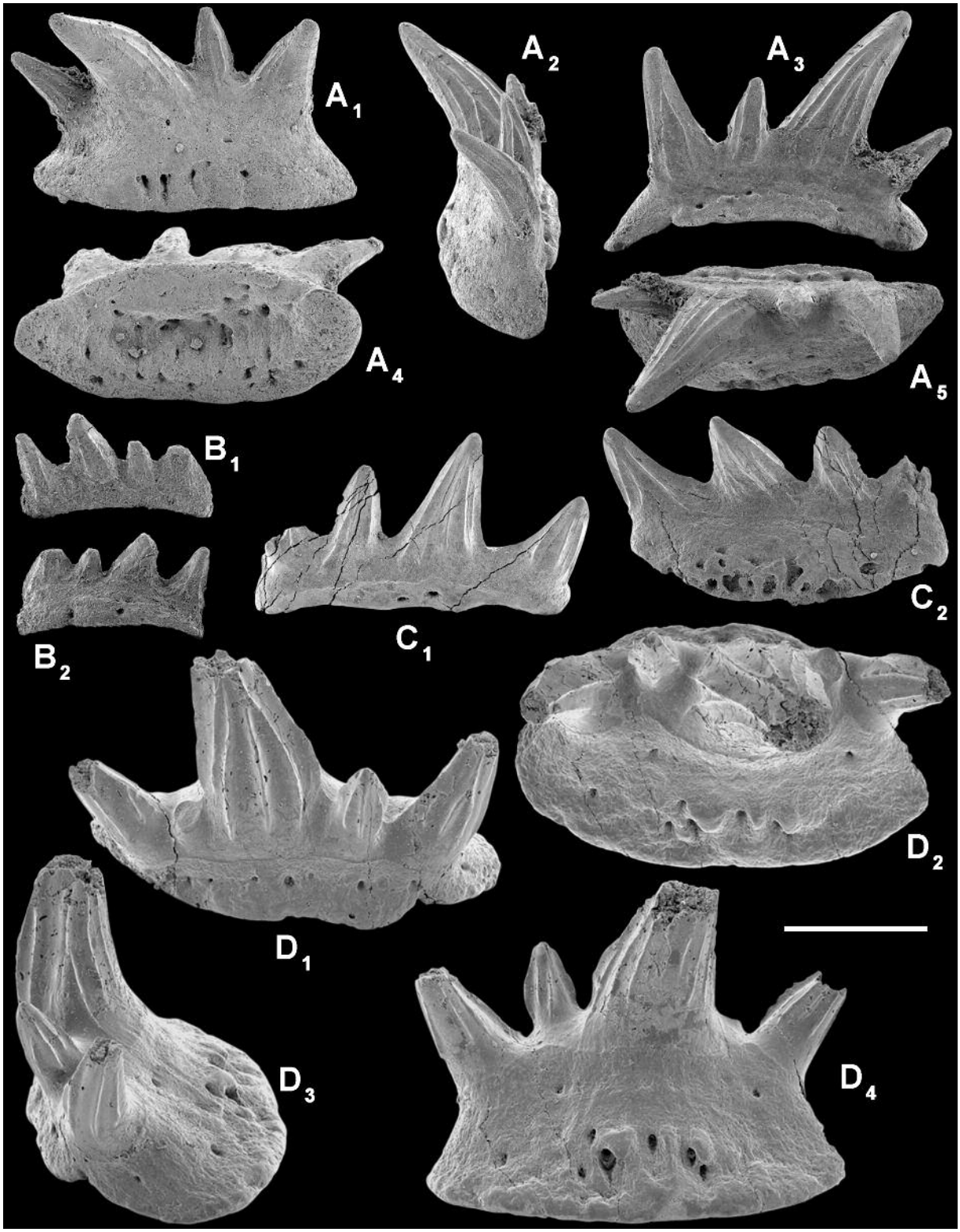
1977. ?*Cladodus* sp. Janvier, p. 282, fig. 3F [only].
1981. "*Cladodus*" sp. Janvier, p. 161–162, pl. 2, figs A, C, F, H.
2004. *Siberiodus mirabilis* gen. et sp. nov.; Ivanov and Rodina, pp. 85–90, figs 3A–L, figs 4A–F, figs. 5A–B.

MATERIAL: Six specimens from sample T3A (Early *triangularis* Zone), Chahriseh.

DESCRIPTION: The teeth are characterised by a tricuspid asymmetric crown. The cusps are well-sepa-



Text-fig. 2. Early Famennian chondrichthyan teeth from Chahriseh. **A-C** – *Siberiodus mirabilis* Ivanov and Rodina, 2004 from sample T3A; **A** – AEU 607 in labial (A_1), lingual/lateral (A_2) and lingual (A_3) views; **B** – AEU 608 in labial view; **C** – AEU 609 in labial (C_1) and lingual (C_2) views. **D** – *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; **D** – AEU 613 from sample EX3, in lingual (D_1) and labial (D_2) views. **E-F** – Elasmobranchii gen. et sp. indet. C; **E** – AEU 614 from sample F-F2, in lingual (E_1) and labial (E_2) views; **F** – AEU 615 from sample T2, in lingual (F_1) and labial (F_2) views. **G** – Cladodont indet.; **G** – AEU 616 from sample M in occlusal (G_1), lingual (G_2) and labial (G_3) views. **H-I** – *Phoebodus typicus* Ginter and Ivanov, 1995; **H** – AEU 617 from sample EX5, in occlusal (H_1) and labial/basal (H_2) views; **I** – AEU 618 from sample 114, in lingual (I_1) and occlusal (I_2) views. Scale bar equals 0.5 mm



Text-fig. 3. Teeth of *Arduodens flammeus* gen. et sp. nov. (type series) from central Iran; **A** – AEU 610 from sample EX3, Chahriseh in lingual (A_1), lateral (A_2), labial (A_3), basal (A_4) and occlusal (A_5) views; **B** – AEU 611 from sample K_5, Kale Sardar, in labial (B_1) and lingual (B_2) views; **C** – AEU 612 from sample K_5, Kale Sardar, in labial (C_1) and lingual (C_2) views; **D** – AEU 697 from sample N, Kale Sardar in labial (D_1), occlusal (D_2), lateral (D_3), and lingual (D_4) views. Scale bar equals 0.5 mm

rated, slender, and unequal in size, ornamented with distinct straight cristae. The cristae are more gentle and numerous on the lingual side. In cross-section the cusps are circular or subcircular in shape. The right (e.g., Text-fig. $2C_2$) and left-hand morphotypes (e.g., Text-fig. $2A_1$) are easily recognized, on the basis of the largest cusp position in labial views. The base is lingually shortened and developed labially, without any articulation button. Two rows of vascular canal openings penetrate the labial face of the base and a single row of openings is located on the lingual side (e.g. Text-fig. $2A_1$, B, C).

REMARKS: The teeth from Chahriseh are identical to that described as the holotype of *Siberiodus mirabilis* from the Famennian of the Kuznetsk Basin, Russia (Ivanov and Rodina 2004). Multicuspid teeth of *Siberiodus* have never been found in the samples from Chahriseh. In Iran, the teeth illustrated from the ?middle Frasnian of the Chanaruh (= Bidou 1) section in Kerman (Janvier 1977, 1981), the lower Famennian of Hodjedk (Hairapetian 2008), the lower Famennian of Dalmeh and Bashi (undescribed collections) and the probable middle Famennian (older than *expansa* Zone) horizon of the Khush-Yeilagh Formation in the Mighan section, eastern Alborz Range show tricuspid crowns only.

STRATIGRAPHIC RANGE: ?Middle Frasnian (Janvier 1977, 1981); Early *triangularis-expansa* Zones (Ivanov and Rodina 2004, this study).

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 gothicus Ginter, 1990
(Text-figs 6A–E, 7A–G)

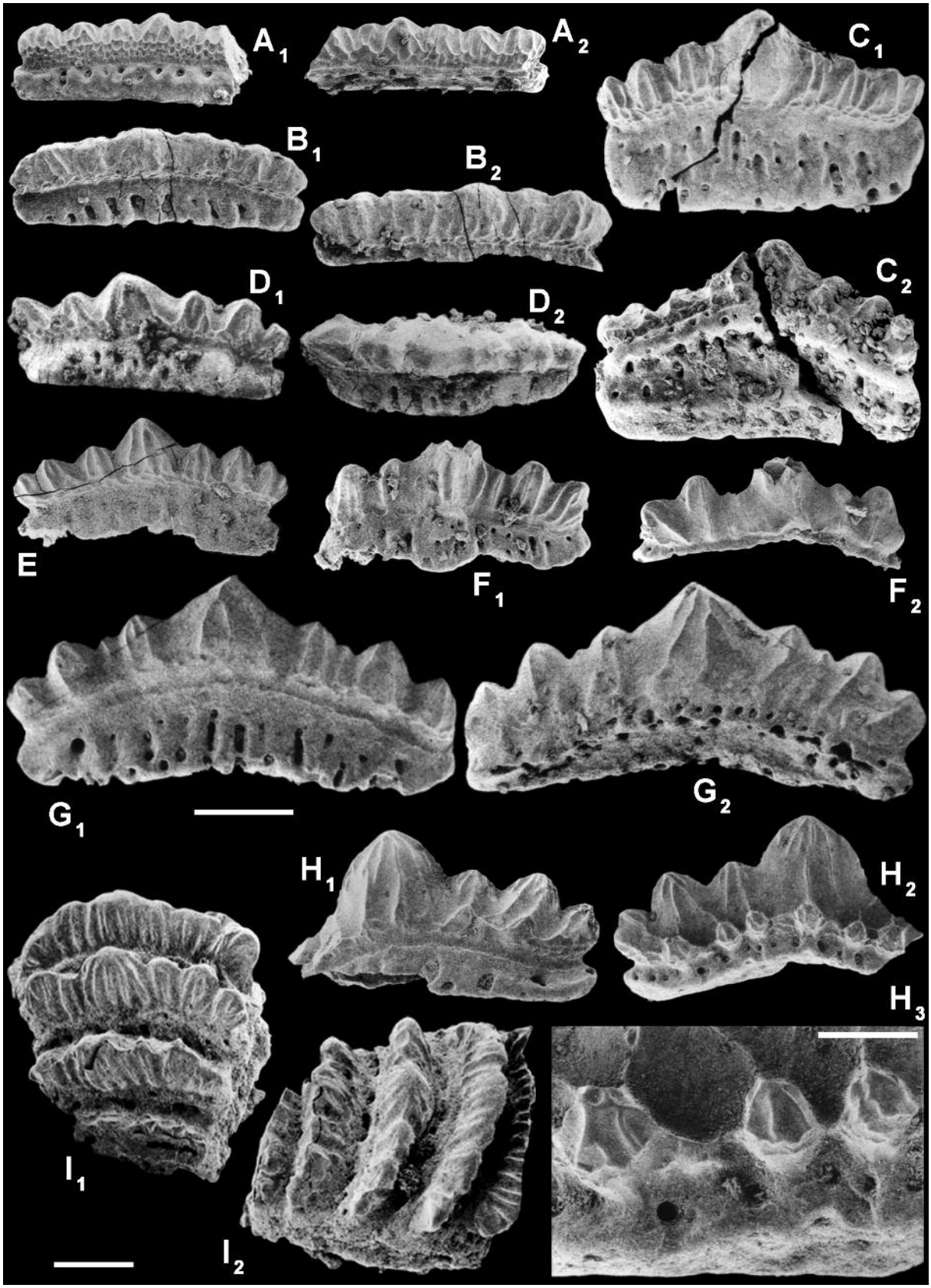
2000. *Phoebodus gothicus* Ginter; Ginter and Ivanov, p. 327, pl. 2, fig. C. [see for older synonymy].
2000. *Phoebodus gothicus* Ginter; Ginter, p. 371, figs 2G, M, 5E–G.
2000. *Phoebodus gothicus* Ginter; Hampe, p. 358–360, fig. 2A–E, pl. 1, figs 1–9.
2000. *Phoebodus gothicus* Ginter; Long and Hairapetian, p. 211–212, figs 4a–d, f, h, j.
cf. 2001. *Phoebodus* cf. *gothicus* Ginter; Ginter, p. 716, fig. 3A-B.
2002. *Phoebodus gothicus* Ginter; Ginter *et al*., text-fig. 6D-E, pl. 1, figs E–N; pl. 2, fig. G; pl. 3, figs A–C; pl. 8, figs K–N; pl. 8, figs J–L.
2004. *Phoebodus gothicus* Ginter; Hampe and Schindler, p. 273–274, pl. 2, figs 1–2 [only].

MATERIAL: From Chahriseh: five specimens from sample 125 (*crepida* Zone), one specimen from sample 116 (*rhomboidea*-Late *marginifera* Zones), one specimen from sample 115 (*rhomboidea*-Late *marginifera* Zones), 63 specimens from sample 114 (*rhomboidea*-Late *marginifera* Zones), eight specimens from sample 113 (*rhomboidea*-Late *marginifera* Zones), two specimens from sample U140 (Early *expansa* Zone).

DESCRIPTION: Tooth bases of the species show a high morphological variation. The base of first morphotype is characterised by a "gothic" outline (e.g., Text-fig. 6E), resembling that of the type material from the Holy Cross Mountains (Poland, Ginter 1990), and other localities around the world (e.g. Iowa, USA, Gross 1973; South Urals, Russia, Ginter and Ivanov 1992; Iran and Morocco, Ginter *et al*. 2002).

In the second morphotype, the abrupt narrowing of the base does not begin from the area near the crown, but from the area near the lingual end and sometimes the lingual half of the base is even wider than its region near the crown (e.g., Text-fig. 7D, F–G). The form of the lingual end varies from pointed to rounded, to almost straight. Thus, several forms of the base outline can be distinguished: a pear-shape with rounded lingual end (e.g., Text-fig. 7B) and a high trapezoid with or without rounded angles (e.g., Text-fig. 7E-F). The teeth referred here to the second morphotype are usually smaller in size than those of the first morphotype, although some exceptions of huge dimension were also found (e.g., Text-fig. 7D). There are a few teeth of small sizes with three upright cusps (Text-fig. 6A),

Text-fig. 4. Early–middle Famennian protacrodonts from Chahriseh. A-H from sample 114, I from sample T3A. **A-B** – *Dalmehodus turnerae* Long and Hairapetian, 2000; **A** – AEU 619 in lingual (A_1) and labial (A_2) views; **B** – AEU 620 in lingual (B_1) and labial (B_2) views. **C-G** – *Protacrodus* spp.; **C** – AEU 621 in lingual (C_1) and labial/basal (C_2) views; **D** – AEU 622 in lingual (D_1) and occlusal (D_2) views; **E** – AEU 623 in lingual view; **F** – AEU 624 in lingual (F_1) and labial (F_2) views; **G** – AEU 625 in lingual (G_1) and labial (G_2) views. **H** – *Deihim mansureae* Ginter, Hairapetian and Klug, 2002; **H** – AEU 626 in lingual (H_1), labial (H_2, H_3: magnified view of labial cusplets) views. **I** – Protacrodont tooth-whorl; **I** – AEU 627 in occlusal (I_1) and lateral (I_2) views. Scale bar equals 0.5 mm (for figs I, H_3 = 0.2 mm).


A1
A2
C1
B1
B2
D1
D2
C2
E
F1
F2
G1
G2
H1
H2
H3
I1
I2

possibly representing a juvenile stage or a specific position (?parasymphysial) in the dentition.

REMARKS: This species is the most abundant in Famennian samples from central Iran. The second morphotype is a typical form in the Iranian collections (Ginter *et al*. 2002; this work), but almost unknown from elsewhere. In the richest Famennian sample (sample 114 of Chahriseh), approximately three times as many teeth of the second morphotype were recovered, compared to teeth of the first morphotype and the "gothic" forms are always lower in frequency in other Iranian samples. From the upper Famennian of Ostrówka Quarry in the western Holy Cross Mountains, only a few teeth resembling the second morphotype were found in a sample rich in *Ph. gothicus* teeth (Ginter 1994). Ginter *et al*. (2002) suggested that the forms representing the second morphotype (pear-like forms particularly) most probably represent intraspecific variation or heterodonty in *Ph. gothicus* dentition, although the hypothesis that they could belong to another species, was not precluded.

High frequencies of teeth representing the first morphotype almost always come from moderately deeper shelf environments that are relatively rich in palmatolepid conodonts and ammonoids (e.g., Ginter 1990; Ginter *et al*. 2002), whereas the Iranian horizons are characterised by the presence of icriodids and polygnathids on a shallower shelf. Taking the strong heterodonty in *Ph. gothicus* dentition and these palaeoenvironmental differences into consideration, there were probably two morphoecological subtypes of *Ph. gothicus* dentition, each characterised by a larger proportion of one of the morphotypes.

STRATIGRAPHIC RANGE: *Ph. gothicus* is known from the Early *marginifera* through the Early/Middle *praesulcata* Zones in Europe. It seems that the Iranian specimens appeared earlier (*crepida* Zone, lower Famennian) on the shallower shelves (Dalmeh *et al*. 2000; Ginter *et al*. 2002; this work).

Phoebodus gothicus cf. *transitans* Ginter, Hairapetian and Klug, 2002
(Text-fig. 7J–K)

MATERIAL: Two specimens from sample 114, *rhomboidea*-Late *marginifera* Zones, Chahriseh.

DESCRIPTION AND REMARKS: These two specimens from sample 114 were differentiated from the symmetrical teeth referred to *Ph. gothicus gothicus* by a slightly rotated crown and an asymmetric base. The first tooth (Text-fig. 7J) seems to have only its tricuspid crown rotated to the left and the basolabial projection twisted, but no lateral lobe of the lingual torus can be recognised. The base in the other tooth (Text-fig. 7K) shows a lateral lobe and the pentacuspid crown is slightly rotated to the right. Both teeth have a distinct oval button, situated at a distance from the lingual rim, closer to the central cusp. However, the rotation of crown and also the extension of the lateral lobe in both seem to be less pronounced than those present in the *Phoebodus gothicus transitans* material from Algeria (Ginter *et al*. 2002).

STRATIGRAPHIC RANGE: Lower or middle Famennian (Ginter *et al*. 2002); *rhomboidea*-Late *marginifera* Zones (this work)

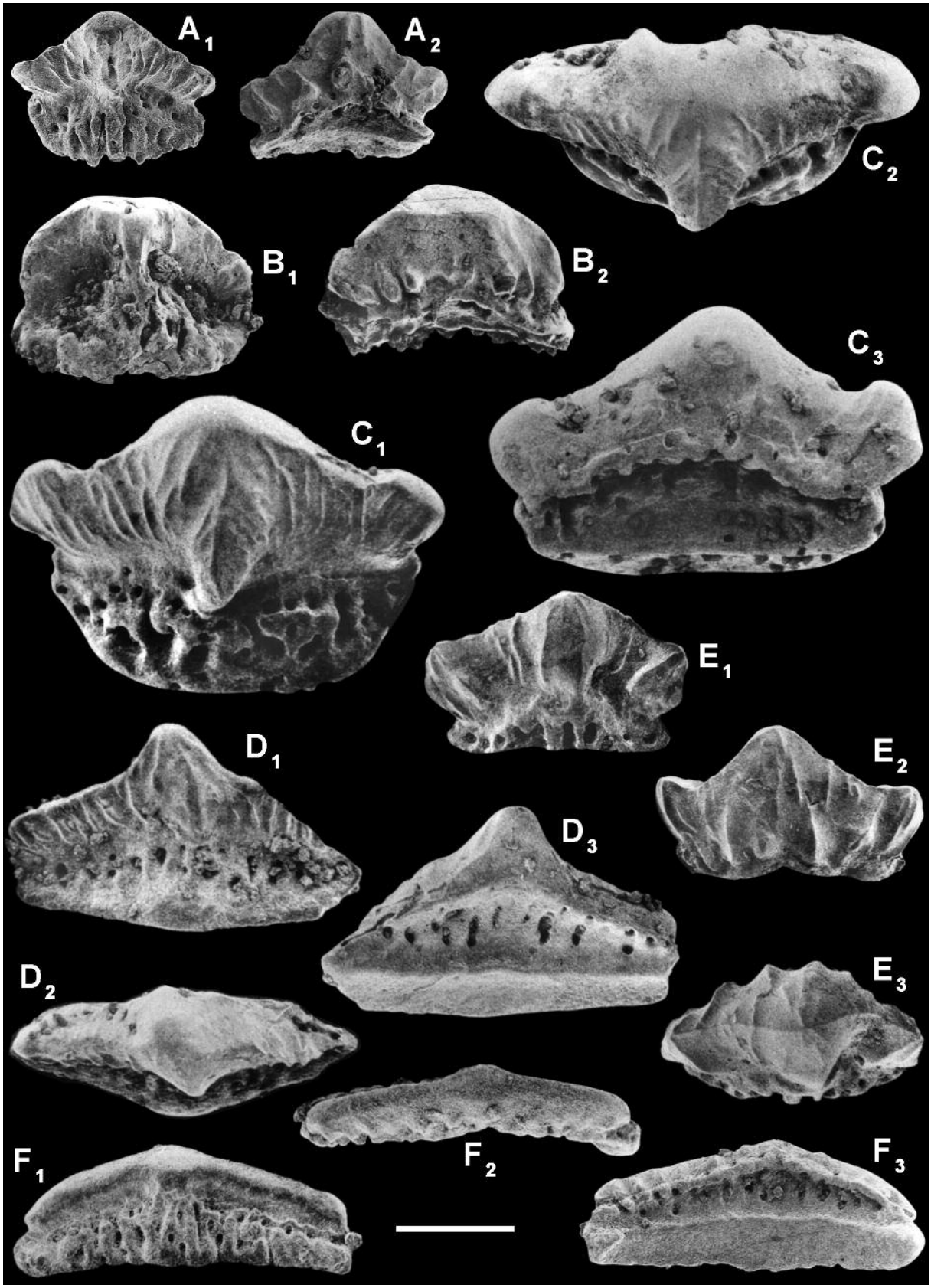
Phoebodus turnerae Ginter and Ivanov, 1992
(Text-fig. 6F–H)

1992. *Phoebodus turnerae* sp. nov.; Ginter and Ivanov, p. 68–70, figs 6B–C, 8A–H.
1995. *Phoebodus turnerae* Ginter and Ivanov; Ginter, fig. 4C.
1999. *Phoebodus turnerae* Ginter and Ivanov; Ginter and Turner, fig. 3H–I.
2000. *Phoebodus turnerae* Ginter and Ivanov; Ginter and Ivanov, p. 328, pl. 2, fig. A.
2002. *Phoebodus turnerae* Ginter and Ivanov; Ginter *et al*., text-fig. 6A–C.
2005. *Phoebodus turnerae* Ginter and Ivanov; Derycke, p. 63–64, pl. V, figs 1–2.

MATERIAL: Three specimens from sample 114, *rhomboidea*-Late *marginifera* Zones, Chahriseh.

DESCRIPTION AND REMARKS: The specimens from Chahriseh are of different sizes and show a wide base with a large oval button close to the lingual rim (compare Ginter and Ivanov 1992, fig. 8E). Several openings are present between the lingual rim and the button. *Phoebodus turnerae* was already recorded from the lower Famennian of the Dalmeh section, central Iran (Ginter *et al*. 2002).

Text-fig. 5. Teeth of Famennian hybodont, *Roongodus phijani* gen. et sp. nov. from Chahriseh. A-D, F from sample 114, E from sample 113. **A** – AEU 628 in lingual (A_1) and labial/basal (A_2) views; **B** – AEU 629 in lingual (B_1) and labial (B_2) views; **C** – AEU 630, holotype in lingual (C_1), occlusal (C_2) and labial/basal (C_3) views; **D** – AEU 631 in lingual (D_1), occlusal (D_2) and basal/labial (D_3) views; **E** – AEU 632 in lingual (E_1), labial (E_2) and occlusal (E_3) views; **F** – AEU 633 in lingual (F_1), occlusal (F_2) and basal (F_3) views. Scale bar equals 0.5 mm


A1
A2
C2
B1
B2
C3
C1
E1
D1
E2
D3
D2
E3
F2
F1
F3

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

Phoebodus aff. *turnerae* Ginter and Ivanov, 1992
(Text-fig. 6I–K)

MATERIAL: Five specimens from sample 114, *rhomboidea*-Late *marginifera* Zones, Chahriseh.

DESCRIPTION AND REMARKS: Tooth-bases of these specimens from Chahriseh are lingually narrowing, with a semicircular outline (Text-fig. 6I–K). The button is oval, mesio-distally elongated, and almost centrally situated. The lingual canal opening is situated medially below the button or slightly to one side in rare cases. The specimens have three or five cusps in the crown, including intermediate cusplets. The labial side of the cusps is coarsely spirally cristate. The lingual side is ornamented with a dense set of faint striations. The forms with similar morphological aspects were suggested to have an affinity to *Ph. turnerae* (Ginter 1994; Ginter and Ivanov 1992; Ginter *et al*. 2002).

STRATIGRAPHIC RANGE: Lower to upper Famennian.

Phoebodus cf. *depressus* Ginter, Hairapetian and Klug, 2002
(Text-fig. 7H–I)

MATERIAL: One specimen from sample 125, *crepida* Zone; three specimens from sample 114, *rhomboidea*-Late *marginifera* Zones, Chahriseh.

DESCRIPTION AND REMARKS: Three and five-cuspid teeth with long, lingually extended tooth-bases. The base is narrowed lingually in its medial part. Further lingually, the base becomes wider, but possesses neither linguo-lateral horn-like ends, nor the lingual tip. The button is minute, circular in outline. The lingual face of cusps is ornamented by subparallel cristae and separated from the smooth labial face by a lateral carina.

It should be noted that such forms could also well belong to a *Ph. gothicus gothicus* dentition.

STRATIGRAPHIC RANGE: Lower or middle Famennian.

Phoebodus typicus Ginter and Ivanov, 1995
(Text-fig. 2H–I)

1995. *Phoebodus typicus* sp. nov.; Ginter and Ivanov, p. 19, fig. 2.
1999. *Phoebodus typicus* Ginter and Ivanov; Ginter and Turner, fig. 3A–D.
2000. *Phoebodus typicus* Ginter and Ivanov; Ginter and Ivanov, p. 328–329, pl. 2, fig. B [see for older synonymy].
2002. *Phoebodus typicus* Ginter and Ivanov; Ginter *et al*., p. 186, text-fig. 6F, pl. 6, figs A–C.

MATERIAL: Two specimens from Chahriseh: one from sample EX5, Middle-Late *triangularis* Zone, and one from sample 114, *rhomboidea*-Late *marginifera* Zones.

DESCRIPTION AND REMARKS: The specimens from Chahriseh are characterised by a crown with three to five cusps and a subrectangular base. The cusps are smooth or covered with a few gentle cristae. The central cusp of the specimen AEU 618 (Text-fig. 2I) is inclined to one side; this could be a matter of preservation. The buttons of both teeth are prominent and slightly elongated mesio-distally. There are rather large nutritive foramina, just beneath the button.

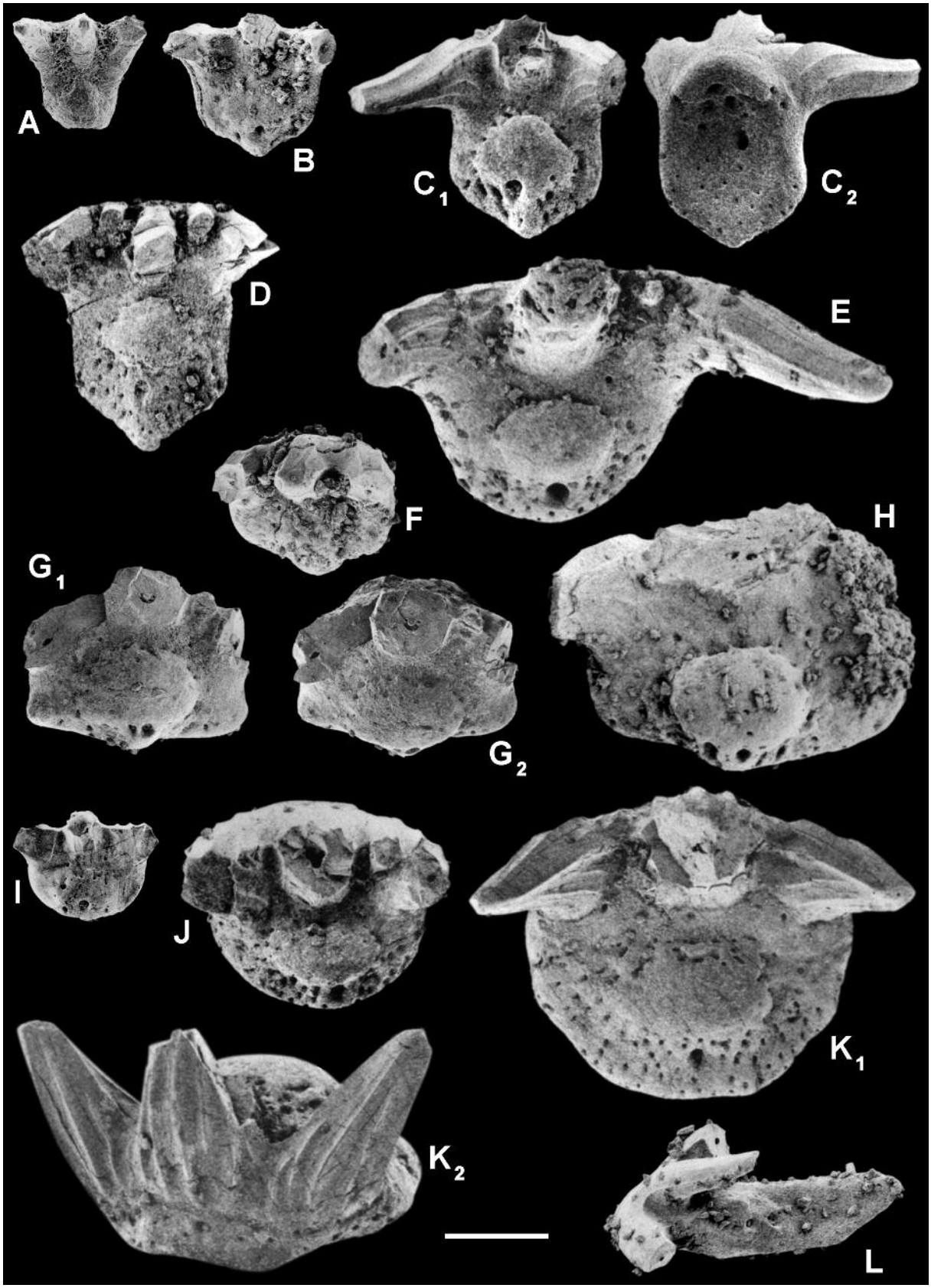
The Chahriseh teeth resemble those from the *crepida* Zone of the Hodjedk section, Iran (Ginter *et al*. 2002) and the Early *marginifera* Zone of north Queensland, Australia (Ginter and Turner 1999), in overall appearance.

STRATIGRAPHIC RANGE: Late *triangularis*-Late *marginifera* Zones, Famennian.

Genus *Thrinacodus* St. John and Worthen, 1875

TYPE SPECIES: *Thrinacodus nanus* St. John and Worthen, 1875.

Text-fig. 6. Famennian phoebodontiformes from Chahriseh. A-B, D-L from sample 114, C from sample 115. **A** – *Phoebodus* ?*gothicus* Ginter, 1990; **A** – AEU 634 in occlusal view. **B-E** – *Phoebodus gothicus gothicus* Ginter, 1990 morphotype I; **B** – AEU 635 in occlusal view; **C** – AEU 636 in occlusal (C_1) and basal (C_2) views; **D** – AEU 637 in occlusal view; **E** – AEU 638 in occlusal view. **F-H** – *Phoebodus turnerae* Ginter and Ivanov, 1992. **F** – AEU 639 in occlusal view; **G** – AEU 640 in occlusal (G_1) and occlusal/labial (G_2) views; **H** – AEU 641 in occlusal view. **I-K** – *Phoebodus* aff. *turnerae* Ginter and Ivanov, 1992; **I** – AEU 642 in occlusal view; **J** – AEU 643 in occlusal view; **K** – AEU 644 in occlusal (K_1) and oblique labial (K_2) views. **L** – *Thrinacodus tranquillus* Ginter, 2000; **L** – AEU 645 in oblique occlusal view. Scale bar equals 0.5 mm


A
B
C1
C2
D
E
F
G1
G2
H
I
J
K1
K2
L

Thrinacodus tranquillus Ginter, 2000
(Text-figs 6L, 9C–D)

2000. *Thrinacodus tranquillus* sp. nov.; Ginter, p. 374–377, figs 2A–C, 3A–F, 4A–C, 5H–K [see for older synonymy].
2000. *Thrinacodus* cf. *ferox* (Turner); Long and Hairapetian, p. 214–216, fig. 4n.
2002. *Thrinacodus tranquillus* Ginter; Ginter *et al*., p. 186–188, text-fig. 9F–H, pl. 2, fig. H, pl. 3, fig. H, pl. 11, figs H–I.

MATERIAL: Eleven specimens from Chahriseh: two from sample 114, *rhomboidea*-Late *marginifera* Zones, one from sample U151, four from sample U154, four from sample U157, Early *expansa* Zone.

DESCRIPTION AND REMARKS: All specimens have symmetrical crowns, horizontally twisted on a lingually elongated base. The crown consists of three subequal cusps without any intermediate cusplets. The cusps are cristate and circular in cross-section. The base is usually long with a lingual depression and devoid of a button. An opening penetrates the lingual side of the base (Text-fig. 9C–D). On the base of tooth AEU 645 (Text-fig. 6L), there occurs a very small rounded button, surrounded by at least three foramina. The existence of a button in *Thrinacodus* has never been noted before. This is a very rare phylogenetic character, and direct evidence indicating that the tooth can be certainly placed somewhere between *Th. tranquillus* and its probable phoebodont ancestor, *Phoebodus gothicus transitans*, just before the complete reduction of locking devices in the early evolution of *Thrinacodus* in the lower or lower middle Famennian.

STRATIGRAPHIC RANGE: *Th. tranquillus* is a common species in shallow to moderately deep water palaeoenvironments of the upper middle – upper Famennian (Late *trachytera*-Early/Middle *praesulcata* Zones), elsewhere (Ginter and Ivanov 2000). An occurrence has also been reported from the *marginifera* Zone of Hunan Province, China by Lelièvre and Derycke (1998). Discovery of *Th. tranquillus* in sample 114 of Chahriseh within the time interval from the *rhomboidea* to Late *marginifera* Zones, makes it one of the two oldest records of the species.

Order Bransonelliformes Hampe and Ivanov, 2007
Family indet.
Genus *Bransonella* Harlton, 1933

TYPE SPECIES: *Bransonella tridentata* Harlton, 1933.

Bransonella? sp.
(Text-fig. 9F)

MATERIAL: One specimen from sample U154, Chahriseh, Early *expansa* Zone.

DESCRIPTION AND REMARKS: The crown consists of three non-sigmoidal cusps of equal size. Only traces of coarse cristation are preserved on their labial and lingual sides. The angle between the central and either of the lateral cusps is less than 30°. The base is rather short lingually, but remarkably arched. The labio-basal projection is an elongated narrow ridge. The button is distinct, and situated on the highest point of the lingual surface; its margins are well-emerged as in *Bransonella*. The Chahriseh specimen can be discriminated from *Jalodus* by the different type of ornamentation and the smaller angle between the cusps. To date, several forms, some of which may belong to *Jalodus*, some to the early form of *Bransonella*, were recorded elsewhere from the upper Famennian through the lower Tournaisian. The arched base with the distinct button, and the form of the cusps, strongly resemble those of teeth from the upper Famennian of Dalmeh, Iran, referred to as *Bransonella*? sp. by Ginter *et al*. (2002; pl. 2, figs E–F). The other similar tooth, from the upper Famennian of Utah, USA (Ginter 2001; fig. 4D), unfortunately has its lingual side eroded and several features on the base, including the form of button, cannot be determined. The specimens from the Middle *praesulcata* Zone of Guilin, South China (Ji and Ziegler 1992, pl. VI, figs 1–2) differ from the Iranian representatives in having an irregular stacked lanceolate sculpture, instead of longitudinal ridges. Other Chinese teeth from the middle Famennian of Xinjiang, North China are again very poorly-preserved, and only show a trace of lanceolate sculpture, possibly representing that of *Jalodus* (Xia 1997; pl. 27, figs 5–6, 9).

Bransonella sp. from the Devonian-Carboniferous boundary beds of Timan, Russia (Ivanov 1999, pl. 4,

Text-fig. 7. Famennian phoebodontiformes from Chahriseh. A-G, I-N from sample 114, H from sample 125. **A-G** – *Phoebodus gothicus gothicus* Ginter, 1990 morphotype II; **A** – AEU 646 in occlusal view; **B** – AEU 647 in occlusal view; **C** – AEU 648 in occlusal view; **D** – AEU 649 in occlusal (D_1) and basal (D_2) views; **E** – AEU 650 in occlusal view; **F** – AEU 651 in occlusal view; **G** – AEU 652 in occlusal view. **H-I** – *Phoebodus* cf. *depressus* Ginter, Hairapetian and Klug, 2002; **H** – AEU 653 in occlusal view; **I** – AEU 654 in occlusal view. **J-K** – *Phoebodus gothicus* cf. *transitans* Ginter, Hairapetian and Klug, 2002; **J** – AEU 655 in occlusal (J_1) and basal (J_2) views; **K** – AEU 656 in occlusal view. **L-N** – Chondrichthyan scales; **L** – AEU 657 in crown view; **M** – AEU 658 in crown view; **N** – AEU 659 in crown view. Scale bar for figs A-K equals 0.2 mm (for figs L-N = 0.5 mm)

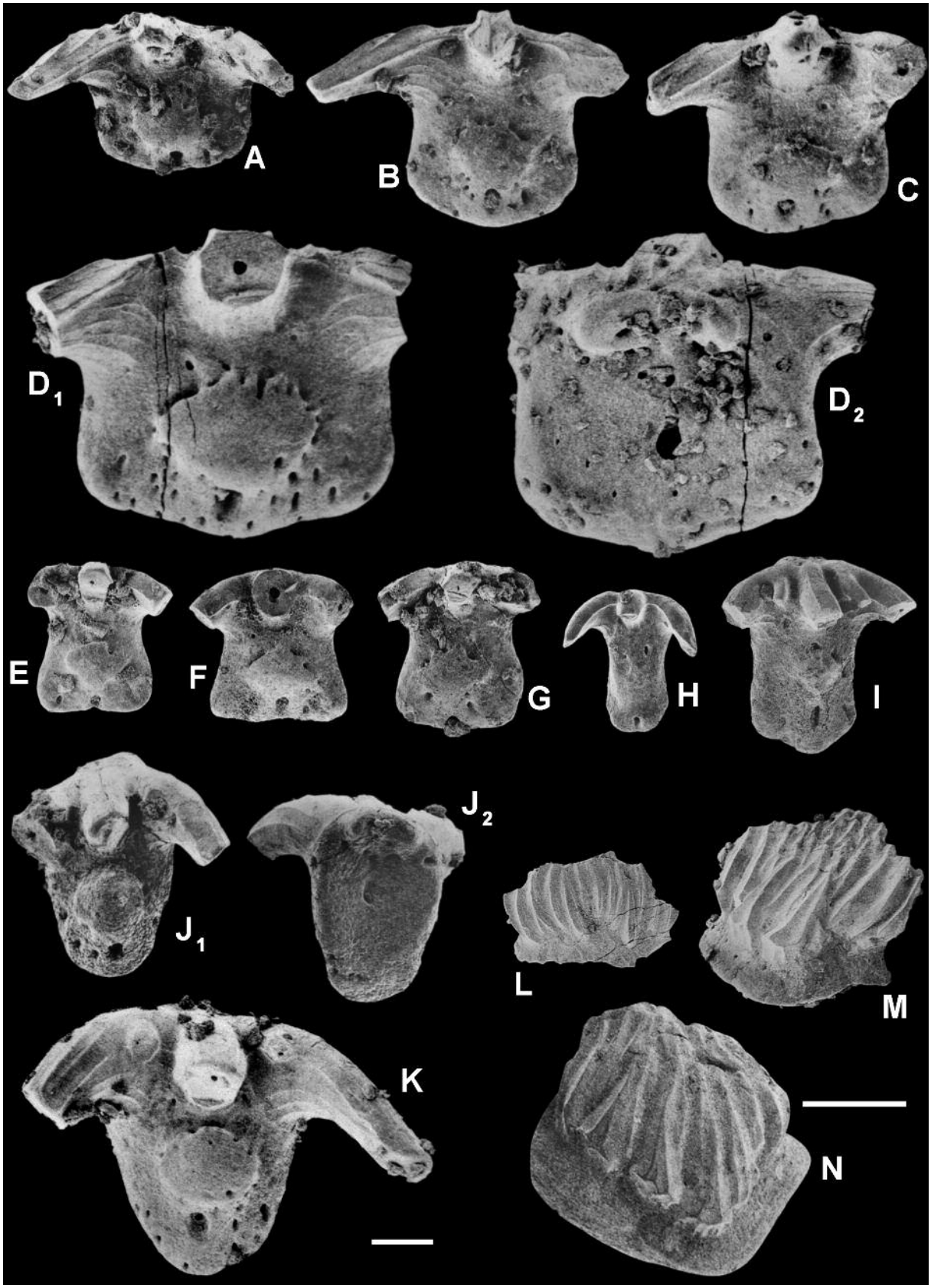

A
B
C
D1
D2
E
F
G
H
I
J2
J1
L
M
K
N

fig. 1) and "*Phoebodus*" sp. from the upper Famennian of Belgium (Derycke 2005; pl. V, figs 3–4) differ from the above-mentioned specimens in possessing a lingually extended base and a wide indistinct button. Further material in a better state of preservation will assist in determination.

Order Ctenacanthiformes Glikman, 1964
Family Ctenacanthidae Dean, 1909
Genus *Cladodoides* Maisey, 2001

TYPE SPECIES: *Cladodus wildungensis* Jaekel, 1921.

Cladodoides sp.
(Text-fig. 8A–E)

MATERIAL: 132 specimens from lower – middle Famennian of Chahriseh: one from sample F-F1, three from sample EX3, four from sample EX5, one from sample EX6, two from sample M, one from sample 126, one from sample 125, one from sample 116, three from sample 115, 102 from sample 114, six from sample 113 and seven from sample 111.

DESCRIPTION AND REMARKS: These teeth are characterised by a crown composed of three main cusps and two intermediate cusplets (e.g., Text-fig. 8B). The central cusp is high, and prominent. The outer lateral cusps are considerably laterally divergent. Both labial and lingual sides of the cusps are ornamented by a few strong cristae. The base is mesio-distally elongated and has a lenticular or subtriangular outline. The button and the labio-basal projection are distinct and mesio-distally elongated. A few tricuspid forms of small size with similar characters were also found and are tentatively included here (Text-fig. 8A). Numerous identical teeth from the Frasnian-Famennian boundary beds from many localities around the world were referred to *Stethacanthus* cf. *thomasi* (Turner 1982) and *S. resistens* Ginter, 2002. However, Ginter (2002) based on his observations, proposed that the *S.* cf. *thomasi* teeth and those of *Cladodoides wildungensis* Jaekel, 1921 were closely related. Further study is necessary to confirm that both can be considered as conspecific forms. Taking this morphological information into account, we provisionally refer these specimens to *Cladodoides*.

STRATIGRAPHIC RANGE: Upper Frasnian-middle Famennian.

Genus *Arduodens* gen. nov.

TYPE SPECIES: *Arduodens flammeus* sp. nov.

ETYMOLOGY: Latin *Arduus* = steep, *dens* = tooth.

DIAGNOSIS: Cladodont teeth with a low labio-lingual/mesio-distal ratio and an asymmetric crown consisting of four slender cusps. The crown is characterised by a high central main cusp, two laterals (outermost) of different sizes and an intermediate cusplet on one side; all the cusps are inclined laterally. The cusps and the cusplet are gently striated on both sides. The tooth base is lenticular in outline, and is devoid of a button.

Arduodens flammeus gen. et sp. nov.
(Text-fig. 3A–D)

ETYMOLOGY: Latin *flammeus* = flaming.

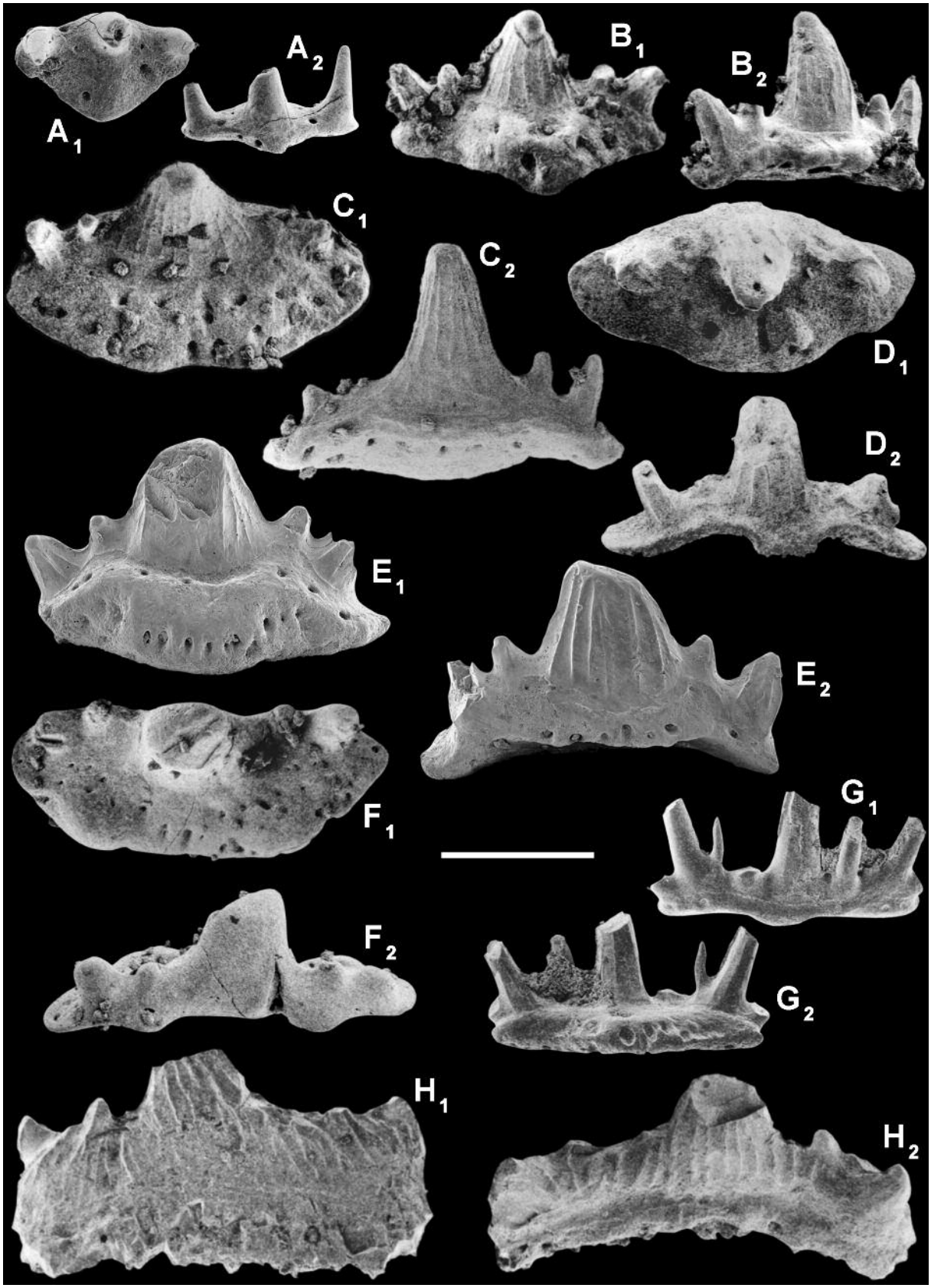
TYPE SERIES: Specimen AEU 610 from sample EX3, Chahriseh and two specimens AEU 611 and 612 from sample K5, Kale Sardar (Text-fig. 3A–D).

DIAGNOSIS: As for genus.

MATERIAL: Three specimens from sample K5 (Late *rhenana* to *linguiformis* Zones), and one specimen from sample N (Late *rhenana* Zone), Kale Sardar; one specimen from sample EX3 (Early *triangularis* Zone), Chahriseh.

DESCRIPTION: The asymmetric tooth-crown consists of four slender cusps of different sizes. The largest and also the highest cusp has a central position; the larger lateral cusp and the intermediate

Text-fig. 8. Famennian cladodontomorphes from Chahriseh. A-C, F from sample 114, D-E from sample 125, G from sample EX5, H from sample M. **A-E** – *Cladodoides* sp.; **A** – AEU 660 in occlusal (A_1) and labial (A_2) views; **B** – AEU 661 in lingual (B_1) and oblique labial (B_2) views; **C** – AEU 662 in occlusal (C_1) and labial/basal (C_2) views; **D** – AEU 663 in occlusal (D_1) and labial (D_2) views; **E** – AEU 664 in lingual (E_1) and labial (E_2) views. **F** – *Squatinactis glabrum* (Ginter, 1999); **F** – AEU 665 in occlusal (F_1) and labial (F_2) views. **G** – Elasmobranchii gen. et sp. indet. A; **G** – AEU 666 in labial (G_1) and lingual (G_2) views. **H** – Elasmobranchii gen. et sp. indet. B; **H** – AEU 667 in lingual (H_1) and labial/occlusal (H_2) views. Scale bar equals 0.5 mm


A1
A2
B1
B2
C1
C2
D1
D2
E1
E2
F1
F2
G1
G2
H1
H2

cusplet occur on one side and the smaller lateral is the only one on the other side. The smaller lateral cusp and the intermediate cusplet are subequal in size. All these are laterally inclined (probably distally) and the angle between the central and larger lateral cusps reaches about 55° on the larger specimen and about 45° on the others. The central and larger lateral cusps are also lingually directed, but the two cusps are not (Text-fig. $3A_2$, C_2). In smaller specimens, the size difference between the central and the lateral cusps is less obvious (e.g., Text-fig. 3B). The cusps and the cusplet are rounded in cross-section and ornamented with numerous subparallel cristae. The cristae are usually more prominent on the labial side and can make inverted Y-shaped junctions (Text-fig. $3A_2$, A_3).

The tooth-base is lenticular in outline and lacks any button (mesio-distal width 0.7–1.1 mm). The labial part of the base is arched and produces a prominent, arcuate labio-basal projection. The base on its lingual side remained undeveloped. The aboral side of the base is penetrated by numerous foramina and a few occur at the lingual end (Text-fig. $3A_1$, A_4). The labio-lingual/mesio-distal dimension ratio is remarkably low.

There is a large tooth in the collection from the Kale Sardar section (Text-fig. 3D) which is tentatively referred to *A. flammeus* gen. et sp. nov. The asymmetrical tooth-crown possesses one main central and two lateral cusps, plus two intermediate cusplets of unequal sizes. All the cusps are relatively thick. The base is slightly extended lingually, more than in the typical *Arduodens* teeth.

REMARKS: The only comparable specimen is from the lower Frasnian Gogo Formation, Western Australia (Long 2007, p. 289). This hitherto undescribed species has symmetrical tricuspid and asymmetrical tetra- to pentacuspid tooth-crowns. The latter asymmetrical form (particularly those with four cusps) resembles *Arduodens flammeus* in having a distally inclined cusp, and unequal numbers of intermediate cusplets. The Australian tooth differs from *A. flammeus* in having several accessory labial cusplets or blades, a thick higher central cusp, and a base with a lingual extension. A similar corroded tooth from the Frasnian of Iran, referred to as *"Cladodus"* sp. by Janvier (1981, pl. II, fig. E), cannot be taken into synonymy here as only its labial side was illustrated.

STRATIGRAPHIC RANGE: Upper Frasnian (Late *rhenana* to *linguiformis* Zones) – lower Famennian (Early *triangularis* Zone).

Cladodont indet.
(Text-fig. 2G)

MATERIAL: One specimen from sample M (Middle *triangularis – crepida* Zones), Chahriseh.

DESCRIPTION: The specimen AEU 616 (Text-fig. 2G) is characterised by a tricuspid crown with a high central cusp and two smaller lateral cusps; they are ornamented by subparallel cristae. The base is lingually developed and has a trapezoid outline, similar to that in *Phoebodus*. The elliptical button is prominent and clearly defined. It is mesio-distally elongated and surrounded by several large foramina. The shape of the labio-basal projection is arcuate.

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. 8F)

2000. "*Symmorium*" *glabrum* Ginter; Ginter, p. 377–378, fig. 7A [see for older synonymy].
2002. *Symmorium* sp.; Riemann *et al*., p. 17–18, pl. 5, figs 15, 18 (not figs 10, 11).
2002. "*Symmorium*" *glabrum* Ginter; Ginter *et al*., p. 190, pl. 9; pl. 11, fig. D.
2007. "*Symmorium*" *glabrum* Ginter; Randon *et al*., p. 819–821, fig. 4(7).

MATERIAL: One specimen from sample 114 (*rhomboidea*-Late *marginifera* Zones), Chahriseh.

DESCRIPTION AND REMARKS: The examined tooth is strongly abraded. The crown is composed of a high median cusp and two pairs of much smaller lateral cusps. The base bears widely spaced buttons, and remnants of two labio-basal projections of probably triangular shape. There is a median concavity in the labio-basal area, beneath the central cusp.

Teeth with comparable morphology were originally labelled as "*Symmorium*" *glabrum* from the upper Famennian of Thuringia, Germany (Ginter, 1999, pl. 4, figs 6–11) and reported from deep marine environments of the lower Famennian (Riemann *et al*.

2002) to the upper Famennian (e.g., Ginter 2000; Ginter *et al*. 2002). Debate as to the generic assignment of this species has continued until recently; Ginter *et al*. (in press) transferred it to *Squatinactis*.

Elasmobranchii gen. et sp. indet. A
(Text-fig. 8G)

MATERIAL: Three specimens from Chahriseh: one from sample EX5 (Middle *triangularis – crepida* Zones), two from sample 113 (*rhomboidea* – Late *marginifera* Zones).

DESCRIPTION: Teeth with multicuspid crowns of cladodont design; a high central cusp and three pairs of lateral cusps. The second or third pair of lateral cusps is the highest. The cusps are generally smooth; a very few cristae occur on both sides of the central cusp. The base has a lenticular outline (Text-fig. 8G) and may or may not have a shallow labio-basal rim. No button is developed.

Elasmobranchii gen. et sp. indet. B
(Text-fig. 8H)

MATERIAL: One specimen from sample M (Middle *triangularis – crepida* Zones), Chahriseh.

DESCRIPTION: This specimen is characterised by a crown with laterally fused cusps. The central cusp is prominent and the tips of two other lateral cusps are elevated. Both sides have strong cristae; the cristae are spirally grown on the lingual side. The crown is labially concave. The base is not preserved.

Elasmobranchii gen. et sp. indet. C
(Text-fig. 2E–F)

MATERIAL: Two specimens from Chahriseh: one from sample T2, one from sample F-F2 (Early *triangularis* Zone).

DESCRIPTION AND REMARKS: The specimens are characterised by a pentacuspid crown with a high central cusp, one pair of lateral cusps, and one pair of intermediate cusplets; all compressed labio-lingually. The lower parts of the cusps are fused laterally. Both lingual and labial sides are ornamented by strong cristae, joining at the tips. The base is short lingually, and lacks any button. The labio-basal thickening is concave. The base is penetrated by numerous foramina.

These teeth share several morphological features in the crown and base with cladodonts and protacrodonts. They generally resemble protacrodonts in having crowns with laterally fused, labio-lingually compressed cusps and a similar sculpture. On the other hand, the material also shows similarities with the tooth-crowns of cladodont design, and with those of some protacrodonts, in having at least one pair of small intermediate cusplets. In the basal structure, such teeth certainly share the distinct labio-basal thickening with the cladodonts, although similarities to the protacrodonts, including the remarkable short lingual side and the absence of button should not be overlooked.

STRATIGRAPHIC RANGE: Lower Famennian (Early *triangularis* Zone).

Cohort Euselachii Hay, 1902
Superfamily Protacrodontoidea Zangerl, 1981
Family Protacrodontidae Cappetta, Duffin and Zidek, 1993
Genus *Dalmehodus* Long and Hairapetian, 2000

TYPE SPECIES: *Dalmehodus turnerae* Long and Hairapetian, 2000

Dalmehodus turnerae Long and Hairapetian, 2000
(Text-figs 4A–B, 9A–B)

2000. *Dalmehodus turnerae* gen. et sp. nov.; Long and Hairapetian, p. 216–217, figs 6d, f, g.

MATERIAL: Seven specimens from Chahriseh: four from sample 114 (*rhomboidea*-Late *marginifera* Zones), two from sample U145, one from sample U151 (Early *expansa* Zone).

DESCRIPTION AND REMARKS: Long and Hairapetian (2000) proposed a new protacrodontid, *Dalmehodus turnerae*, based on three specimens from the Famennian of Dalmeh. The reticulate network sculpture cannot be longer considered unique for *Dalmehodus* as similar patterns were seen in other Famennian protacrodontids and orodontids, and may have resulted from an intersection between the vertical cristae and the growth lines of the crown (Ginter *et al*. 2002). The most important character to discriminate this species from other protacrodonts seems to be the absence of a prominent central cusp (Ginter *et al*. 2002).

In contrast to the original material, the specimens from Chahriseh are well-preserved and therefore the morphological features can be re-examined and their description slightly modified. The number of cusps in the original material was four (in broken teeth) to eight of nearly equal size. However, some complete teeth from the upper Famennian of Chahriseh (e.g., Text-fig. 9B) show even more, as many as eleven short cusps on a mesio-distally elongated base. All the cusps are ornamented with a few vertical cristae on their lingual and labial sides, joining at the tips. The base itself is lingually short with several, relatively large canal openings, mostly ordered in a row.

STRATIGRAPHIC RANGE: Famennian, *crepida* through Early *expansa* Zones.

Genus *Deihim* Ginter, Hairapetian and Klug, 2002

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

Deihim mansureae Ginter, Hairapetian and Klug, 2002
(Text-figs 2D, 4H)

2000. ?*Protacrodus* sp.; Long and Hairapetian, p. 217–218, fig. 4o.
2000. *Protacrodus* sp. cf. "*P. aequalis*" sensu Ginter and Turner; Yazdi and Turner, p. 226, fig 3.4-7, 4.4 [non fig 3.8-10 = *Protacrodus* sp.]
2002. *Deihim mansureae* gen. et sp. nov; Ginter *et al*., p. 191–193, text-fig. 10; pl. 1, fig. R; pl. 2, fig. K; pl. 4, figs F–G, J–M; pl. 5, figs A–M.
2005. Polyacrodontidae *insertae sedis*; Derycke, p. 76, pl. VII, figs 7–10.
2005. *Bobbodus* sp.; Derycke, p. 95–96, pl. XII, figs 1–2.

MATERIAL: Nine specimens from Chahriseh: one from sample EX3 (Early *triangularis* Zone), one from sample EX5 and one from sample M (Middle *triangularis – crepida* Zones), one from sample 116 and four from sample 114 (*rhomboidea* – Late *marginifera* Zones), one from sample U145 and one from sample U157 (Early *expansa* Zone).

DESCRIPTION AND REMARKS: Ginter *et al*. (2002) assigned some clutching-crushing teeth of a specific design to a new genus and species, *Deihim mansureae*, based on the presence of certain characteristic features. This species was known to have some smaller teeth with a high central cusp (as morphotype 4), probably positioned at the symphyseal region, and more elongated forms of symmetric and asymmetric teeth with laterally fused cusps (as morphotypes 1–3) in antero- and postero-laterals, suggesting a remarkable monognathic heterodonty (Ginter *et al*. 2002).

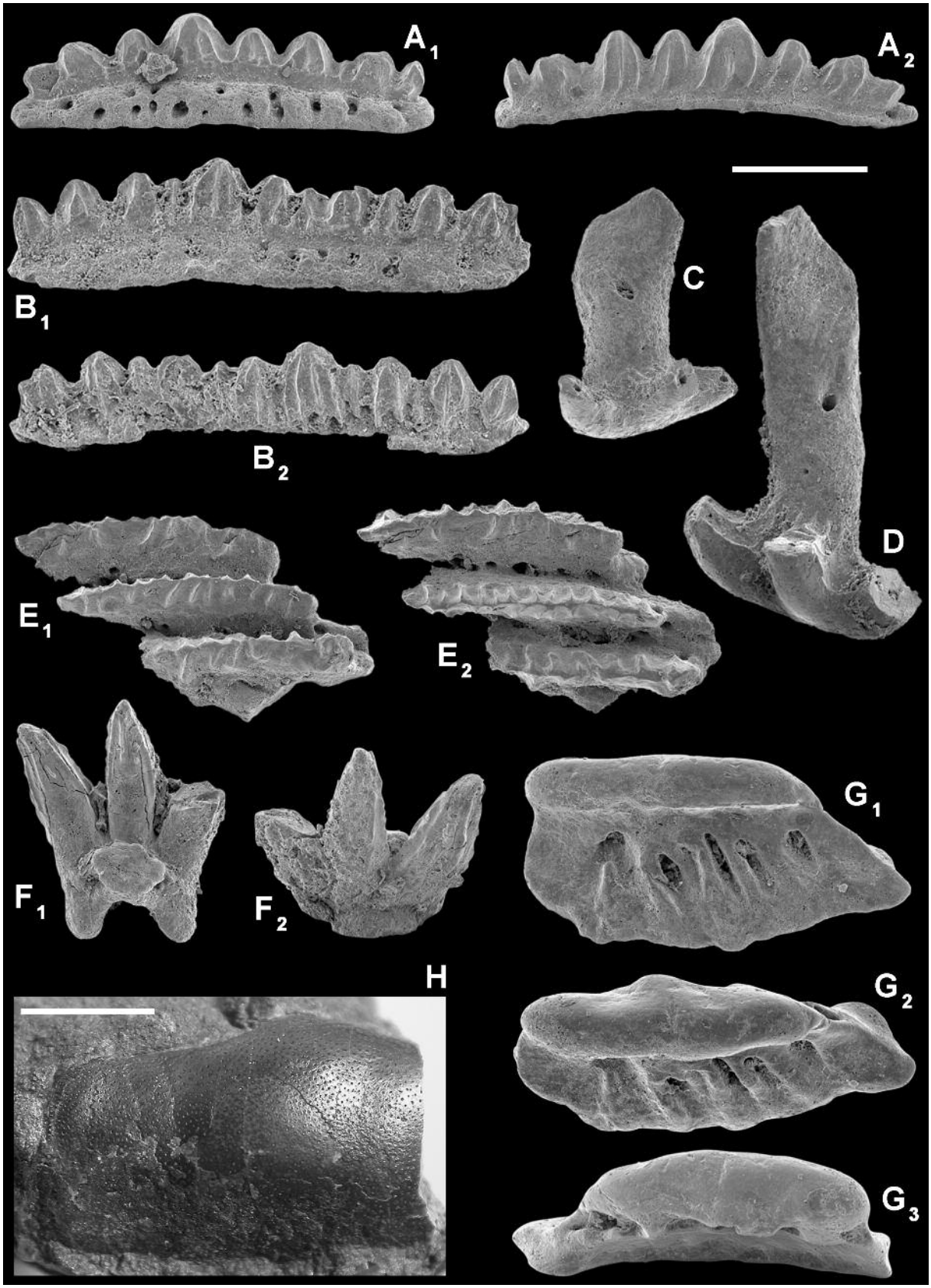
The teeth considered here fall within the morphological range of these morphotypes. Teeth of the first morphotype (Text-fig. 2D) are characterised by an arched crown with a high central cusp and two others on each side. The base of these is short mesio-distally. The second morphotype (Text-fig. 4H) is represented by teeth with three pairs of lateral cusps. In contrast to the material of Ginter *et al*. (2002), the central cusp can be as prominent as in the first morphotype. The labial cusplets of specimen AEU 626 (Text-fig. 4H) are well-preserved and ornamented with distinct cristae and it seems that the cusps of the second lateral pair (the other side is missing) are higher than the others.

Protacrodus orientalis Li, (1988) from the Carboniferous of Jiangsu Province in China resembles an abraded tooth of *D. mansureae* (Ginter *et al*. 2002; text-fig. 10G-I) in having a crown with fused lateral cusps and a similar base. However, in *P. orientalis*, the size difference between the lateral and the central cusps is much greater than that seen in the original material of *D. mansureae* and it also lacks a groove along the crown/base interface and probably the labial cusplets. Some poorly-preserved material referred to as *P. orientalis* from the uppermost Famennian of the Menggongao Formation, south China, resemble *D. mansureae* in overall appearance, but these also lack the labial cusplets (Lelièvre and Derycke 1998, fig. 7; Hervé Lelièvre, personal communication, September 2002).

STRATIGRAPHIC RANGE: Early *triangularis* through Early *expansa* Zones, Famennian (Ginter *et al*. 2002, this work).

Genus *Protacrodus* Jaekel, 1921

Text-fig. 9. Upper Famennian chondrichthyan teeth from Chahriseh. A-B from sample U145, C-G from sample U154. **A-B** – *Dalmehodus turnerae* Long and Hairapetian, 2000; **A** – AEU 668 in lingual (A_1) and labial (A_2) views; **B** – AEU 669 in lingual (B_1) and labial (B_2) views. **C-D** – *Thrinacodus tranquillus* Ginter, 2000 ; **C** – AEU 670 in occlusal view; **D** – AEU 671 in occlusal view. **E** – ?Chondrichthyan scale; **E** – AEU 672 in crown/lateral (E_1) and crown (E_2) views. **F** – *Bransonella*? sp.; **F** – AEU 673 in lingual (F_1) and labial (F_2) views. **G** – *Lissodus* sp.; **G** – AEU 674 in lingual (G_1), occlusal (G_2) and occlusal/labial (G_3) views. **H** – Holocephali gen. et sp. indet.; **H** – AEU 776 in occlusal view. Scale bar for figs A-G equals 0.5 mm (for fig. H = 4mm)


A1
A2
B1
B2
C
D
E1
E2
F1
F2
G1
G2
G3
H

TYPE SPECIES: *Protacrodus vetustus* Jaekel, 1921

Protacrodus spp.
(Text-fig. 4C–G, I)

MATERIAL: Seventy two specimens from the Famennian of Chahriseh (samples T3A, M, 126, 125, 116, 114, 113, 111, U140, U142, U148, U150, U151, U157, U159, U167, U167 and U178).

DESCRIPTION: Protacrodont teeth with a high morphological variability in crowns and bases are considered here. The specimens are characterised by crowns with a prominent pyramidal central cusp and three to four pairs of lateral cusps, all compressed labio-lingually. The height of the lateral cusps either reduces gradually towards the mesial and the distal ends (e.g., Text-fig. 4C, F) or the cusps of the second or third lateral pair are slightly larger than the others (Text-fig. 4E, G). The lower parts of the cusps are largely fused, giving some teeth the appearance of having a cutting edge (Text-fig. 4C). The base varies from a lingually extended form (Text-fig. 5C) to those with a short extension (Text-fig. 4D). It bears several foramina, ordered in one or several horizontal rows. In some specimens (e.g., Text-fig. $4G_1$), a mesio-distal groove occurs along the lingual crown/base boundary, resembling those of *Deihim mansureae*.

There are a few protacrodont tooth-whorls in the collections studied. The specimens consist of three to five teeth, of different sizes with fused bases (e.g., Text-fig. 4I). Each tooth has a tilted position in relation to the other. The cusps are ornamented by vertical strong cristae.

Superfamily Hybodontoidea Zangerl, 1981
Family Polyacrodontidae Glikman, 1964
Genus *Roongodus* gen. nov.

TYPE SPECIES: *Roongodus phijani* sp. nov.

ETYMOLOGY: Armenian *Roong* = nose, and Greek *odous* = tooth.

DIAGNOSIS: Crushing type tooth-crowns with a central, swelling cusp and a diagnostic median lingual projection. The cusps are fused, only two lateral ends are elevated. A few strong cristae run irregularly on the lingual side of the crown; the labial side possesses fewer cristae, or is almost smooth. A row of labial cusplets may or may not occur at the crown/base interface.

The base is extended lingually and perforated with numerous canals or grooves. The linguo-aboral side of the base lacks foramina.

Roongodus phijani sp. nov.
(Text-fig. 5A–F)

ETYMOLOGY: After Philippe Janvier (Paris), in recognition of his pioneer contributions to the knowledge of Middle Palaeozoic vertebrates from the Middle East.

HOLOTYPE: Specimen AEU 630 (Text-fig. 5C) from Chahriseh, sample 114, *rhomboidea*-Late *marginifera* Zones, Famennian.

DIAGNOSIS: As for genus.

MATERIAL: Thirteen specimens from Chahriseh: 12 from sample 114 and one from sample 113, *rhomboidea*-Late *marginifera* Zones.

DESCRIPTION: The monolithic tooth-crowns (mesio-distal width 0.8–2.0 mm) have a central, prominent cusp and two downward lateral sides which are labio-lingually compressed. All the lateral cusps are completely fused. Some teeth have elevated lateral ends, functioning as the outermost cusps. A median lingual projection, diagnostic of the taxon, extends from the central cusp. It may take the form of a pronounced beak in the larger specimens (Text-fig. 5C) or of a moderately developed ridge in the smaller ones (Text-fig. 5A-E). The lingual projection always connects the central cusp to the upper part of the lingual face of the base. The lingual side of the crown, including the projection, is ornamented by a few strong cristae; the labial side bears fewer cristae (Text-fig. 5A), or is almost smooth (Text-fig. 5C-D); the latter may be a result of abrasion. A tooth with a better preserved occlusal surface, showed a lateral carina separating the lingual and the labial sides; occasionally two cristae meet each other at a point on the carina (Text-fig. $5E_3$). A mesio-distal row of labial cusplets may occur in the labial crown/base interface. A shallow median depression can occur on the labial side of the crown, corresponding to a well-developed lingual projection (Text-fig. 5A–C), suggesting that teeth in each tooth file were closely arranged by their overlapping bases.

The lingually extended base is characterised by numerous canals or grooves. The lower lingual part of the base lacks foramina (e.g., Text-fig. 5D). A specimen with an unusual form of a low crown is ascribed to

Roongodus phijani because of the presence of the lingual projection (Text-fig. 5E). Such more elongated and lower teeth were probably positioned postero-laterally.

REMARKS: Among the taxa recently described from Northern Gondwana, *R. phijani* shares several general features with a strongly heterodont protacrodont, *Deihim mansureae* Ginter, Hairapetian and Klug, 2002 from the Famennian of central Iran, such as labial cusplets and a similar base. However, it differs in possessing a crown with fused cusps and a lingual projection. A considerable variability in the tooth-crowns of *Roongodus* suggests a strong heterodonty, although a tooth with a high central cusp, similar to that in the presumed symphyseal region of *Deihim* (morphotype 4), was not found.

Several teeth of Late Palaeozoic – Mesozoic hybodonts were known to have the lingual projection. A few *Lissodus* species, such as *L. zideki* (Johnson, 1981; figs 9, 14), *L. hasleensis* (Rees, 1998, fig. 4) and *L. pattersoni* (Duffin, 1985; text-fig. 22, figs 1a–i), have developed lingual projections of various forms, all distinctly protruded but restricted to the crown. Additionally, *Lissodus pectinatus* (Lebedev, 1996; fig. 2) is characterised by rows of very strong labial and lingual nodes near the crown/base junction. However, all *Lissodus* species differ from *Roongodus* in having a larger labial projection (= peg) on their monolithic crowns.

The specimens from the Lower Triassic of Spitsbergen known as *Hybodus microdus* Stensiö, 1921 (Birkenmajer and Jerzmanska 1979, text-figs $9B_2$, 10–11, pl. 2, figs 1–6; Błażejowski 2004, fig. 9c) differ from those of *Roongodus phijani* in having a labio-lingually shorter base and node- and tear-like projections on the labial and the lingual sides respectively; the latter does not connect to the base. The crown itself consists of regularly ornamented cusps with fused bases and lacks the labial cusplets.

Two Triassic species, *Polyacrodus contrarius* from the Ladinian and Carnian of British Columbia, Canada, and the Anisian/Carnian of Guizhou Province, southwestern China (Johns *et al*. 1997; Chen *et al*. 2007) and *Polyacrodus bucheri* from the Anisian of Nevada, USA (Cuny *et al*. 2001) differ from *Roongodus phijani* in having crowns with a lower central cusp, flanked by separated fused lateral cusps on labio-lingually shorter bases in their presumed posterior teeth. Although lateral cusps are fused in the antero-lateral teeth of *Polyacrodus contrarius*, they possess labial and lingual nodes near the crown/base interface and a labio-lingually short base.

Despite the presence of lingual projections of various shapes in Mesozoic and Cenozoic neoselachian taxa such as squaliformes (*Squalogaleus* Maisey, 1976), squatiniformes (*Squatina* Duméril, 1806), orectolobiformes (*Cretorectolobus* Case, 1978; *Orectoloboides* Cappetta, 1977; *Paraginglymostoma* Herman, 1982) and rajiformes (*Archingeayia* Vullo, Cappetta and Néraudeau, 2007; *Engolismaia* Vullo, Cappetta and Néraudeau, 2007), they differ greatly from *Roongodus* in the crown and the base structures.

A tooth with a lingual projection from the *expansa* Zone of northern Iran (Ginter *et al*. 2002; pl. 4, fig. C), similar to that from Chahriseh (Text-fig. 6E), was erroneously referred to *Lissodus* sp. The discovery of *Roongodus phijani* in the *rhomboidea*-Late *marginifera* Zones of Chahriseh, makes this the earliest record of hybodontiform teeth.

STRATIGRAPHIC RANGE: Famennian, *rhomboidea*-Late *marginifera* Zones.

Genus *Lissodus* Brough, 1935

TYPE SPECIES: *Hybodus africanus* Broom, 1909

Lissodus sp.
(Text-fig. 9G)

MATERIAL: One specimen from sample U154 (Early *expansa* Zone), Chahriseh.

DESCRIPTION AND REMARKS: The tooth from Chahriseh, attributed here to *Lissodus* sp., is characterised by a low monolithic crown with a small, weakly developed labial peg. The crown is smooth and narrow labio-lingually. The central cusp is not present in this specimen; the lingual margins are straight. The base is lingually developed, and perforated by foramina and grooves.

None of these teeth can be attributed to any of the *Lissodus* species listed by Duffin (2001). Teeth of *Lissodus* from the upper Famennian of central and northern Iran (Ginter *et al*. 2002, text-fig. 12. pl. 4, figs A–C) differ from the specimens from Chahriseh in having a crown with a well-developed labial peg, a high central cusp and a few smaller cusplets.

Several species of *Lissodus* were recently reported from the upper Famennian of Belgium (Derycke *et al*. 1995; Derycke 2005). It appears that the figured *L.* sp. cf. *L. zideki* does not have a labial peg (Derycke 2005; pl. VI, figs 1–2) and *L. tursusae* and *L. brousclaudiae* have been characterised by strongly crenulated crowns. These two species seem to be closely related and are most probably conspecific, as they have certain fea-

tures in common (Derycke 2005; compare pl. VI, figs 7–8 with pl. VII, figs 3–4).

Superorder Holocephali Bonaparte, 1831
Holocephali gen. et sp. indet.
(Text-fig. 9H)

MATERIAL: One specimen from samples U178 (Early *expansa* Zone), Chahriseh.

DESCRIPTION AND REMARKS: The incomplete specimen AEU 776 (Text-fig. 9H) is characterised by a labio-lingually convex crown, and its edges do not possess vertically oriented crenulations or nodes. The central crown area is flat-topped and its margin protrudes distinctly labially. The crown is composed of tubular dentine, giving a finely punctated pattern to the superficially smooth surface.

Holocephalians are rarely seen prior to the Lower Carboniferous (Stahl 1999). Ginter and Piechota (2004) recently recorded an unambiguous occurrence; *Psephodus* cf. *magnus* in the middle Famennian (*trachytera* Zone) of the Holy Cross Mountains, Poland. The Chahriseh specimen is the first illustrated holocephalian tooth from the upper Famennian of Iran and North Gondwana.

Chondrichthyan scales
(Text-figs 7L–N, 9E)

A few growing chondrichthyan scales of protacrodont-type (Text-figs 7N) are characterised by a flattened crown composed of several closely packed odontodes. The crown is developed anteriorly, and the base is of diamond shape, resembling those assigned to *Protacrodus vetustus* Jaekel (1925), from the Frasnian of Bad Wildungen, Germany (Gross 1938).

The ctenacanth-type scales *sensu* Reif (1978) have a small rounded or elliptical base with a flat or concave lower surface (Text-figs 7L–M). The crown in these scales has an irregular pattern of parallel or subparallel odontodes. These scales were usually found together with the ctenacanthiform "*Ctenacanthus*" *costellatus* Traquair, 1884 (Reif 1978), and also with *Phoebodus rayi* (Ginter and Turner 1999) and *Phoebodus fastigatus* (Liao *et al*. 2007)

The specimen (Text-fig. 9E) is composed of three probable scales with an oak-leaf crown, fused by their vertical bases. It also resembles the cranial denticles recently found from the head region of an articulated thrinacodont, *Thrinacoselache gracia* (Grogan and Lund 2008, figs 7A, B). A similar specimen was also figured by Ginter (2001, fig. 4E–G).

DISCUSSION

Rich collections of lower and upper Famennian chondrichthyan microremains have been known to date from central Iran (Dalmeh and Mighan sections) and the Tafilalt Platform in Morocco, North Gondwana (Ginter *et al*. 2002). The composite list from the lower Famennian samples of Chahriseh now includes *Phoebodus*, *Deihim*, *Protacrodus*, *Cladodoides*, *Siberiodus* and *Arduodens*; this is more diverse at generic level than the lower Famennian assemblages previously recorded from these regions. The rich sample 114 from Chahriseh, representative of a shallow water environment characteristic of the lower middle Famennian of central Iran (*rhomboidea*-Late *marginifera* Zones), yielded a chondrichthyan assemblage that is very different from the low diversity faunas already known from North Gondwana (Ginter *et al*. 2002). It consists of at least eight genera, including *Phoebodus* (33%), *Thrinacodus* (1%), *Deihim* (2%), *Dalmehodus* (2%), *Protacrodus* (19%), *Cladodoides* (39%), *Squatinactis* (less than 1%) and the hitherto unknown hybodont, *Roongodus phijani* (4%), whereas in a contemporaneous fauna from the deeper shelf environment of Kale Sardar (east central Iran) the number of genera does not exceed three (*Phoebodus*, *Protacrodus* and *Jalodus*; Hairapetian 2008). Although some lower to middle Famennian assemblages from Iran and Morocco were also tentatively analysed by Ginter *et al*. (2002), any environmental interpretation on samples from earlier than

Locality/Age	Chahriseh		
	rhomboidea - Late *marginifera*		
samples / species	114	%	ci (95%)
Phoebodus spp.*	86	33	±6
Thrinacodus tranquillus	2	1	±1
subtotal	88	34	±6
Deihim mansureae	4	2	±2
Dalmehodus turnerae	4	2	±2
Protacrodus spp. ♦	49	19	±5
Roongodus phijani	12	4	±3
subtotal	69	27	±5
Cladodoides sp.	102	39	±6
Squatinactis glabrum	1	~ 0	-
subtotal	103	39	±6
Total specimens number	260		

Table 1. Relative abundances of chondrichthyans in the sample 114, Chahriseh. ci – confidence interval; * – including *Ph. gothicus*, *Ph. g.* cf. *transitans*, *Ph.* cf. *depressus*, *Ph. turnerae*, *Ph.* aff. *turnerae*, *Ph. typicus*, and unassigned phoebodonts; ♦ – including tooth-whorls

the upper Famennian is problematic for several reasons, such as the absence of any equivalent taxon for the deep-water *Jalodus* and a generally higher phoebodontid / protacrodontid ratio. As was suggested by Ginter *et al*. (2002), the lower to middle Famennian phoebodonts probably occupied shallower environments than in the upper Famennian. This is confirmed by the assemblage in sample 114 from Chahriseh (Table 1). The proportions of phoebodontids (34%) and protacrodontids plus hybodonts (27%) are very high. The subequal proportions of these morphoecological groups do not necessarily mean any particular palaeoenvironmental conditions, although they might show that both assemblages are in between the shallow and intermediate biofacies. The rest of the fauna in sample 114 is represented by cladodonts (39%) whose ecological preferences still remain unresolved.

It was proposed in the systematic section that there were two morphoecological subtypes of *Ph. gothicus* dentition in deeper and shallower shelf environments respectively; the subtype in the latter environment is composed of a larger proportion of the second morphotype. The much higher frequency of teeth representing the second morphotype in sample 114 could be an indicator of the shallower-shelf environment, as this horizon is characterised by the presence of icriodid and polygnathid conodonts and the absence of groups indicative of the deeper shelf, such as palmatolepid conodonts and ammonoids.

Although there are not enough shark teeth from the upper Famennian (≤ 9 teeth per sample) to present any meaningful analysis of the assemblages, a composite picture on selected samples (U140, U145, U154 and U157) from Chahriseh can be drawn. From these samples, at least seven genera (*Phoebodus*, *Thrinacodus*, *Deihim*, *Dalmehodus*, *Protacrodus*, *Lissodus* and probably *Bransonella*) have been collected. A more diverse fauna consisting of nine genera, evidently indicating the *Protacrodus* biofacies, has previously been recorded from the Dalmeh section in central Iran by (Ginter *et al*. 2002).

Acknowledgments

This work benefited from the assistance of Dr. Carole Burrow (Queensland Museum, Australia) in identification of acanthodians, Dr. Gaël Clément (Muséum national d'Histoire naturelle, Paris, France), Prof. Per Eric Ahlberg (University of Uppsala, Sweden), Dr. Philippe Janvier (Muséum national d'Histoire naturelle, Paris, France), and Dr. John Long (Victoria Museum, Melbourne, Australia) in identification of placoderm and sarcopterygian macroremains.

We are very grateful to Drs Mansoureh Ghobadi Pour (University of Gorgan, Gorgan, Iran), and Hossein Gholamalian (University of Hormozgan, Bandar Abas) for assistance with fieldwork and laboratory preparation. VH received much help from Arsine Gharibian (Esfahan) in the preparation of digital plates. Thanks are due to Dr. Cyprian Kulicki (Institute of Palaeobiology, Warsaw) for help with SEM photography. We are grateful to Dr. Kate Trinajstic (Perth) and an anonymous reviewer for their helpful comments and corrections.

REFERENCES

Becker, R.T., Ashouri, A.R. and Yazdi, M. 2004. The Upper Devonian *Annulata* Event in the Shotori Range (eastern Iran). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **231**, 119–143.

Birkenmajer, K. and Jerzmańska, A. 1979. Lower Triassic shark and other fish teeth from Hornsund, south Spitsbergen. *Studia Geologica Polonica*, **40**, 7–37.

Błażejowski, B. 2004. Shark teeth from the Lower Triassic of Spitsbergen and their histology. *Polish Polar Research*, **25**, 153–167.

Bonaparte, C. 1838. Introduzione alla Classie IV. Pesci. Iconografia della Fauna Italica per le quattro Classi degli Animali Vertebrati. Vol. 3, 16 pp. Salviucci, Rome.

Broom, R. 1909. Fossil fishes of the Upper Karoo Beds of South Africa. *Annals of the South African Museum*, **7**, 251–269.

Brough, J. 1935. On the Structure and Relationships of the Hybodont sharks. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, **79**, 35–49.

Cappetta, H. 1977. Sélaciens nouveaux de l'Albien supérieur de Wissant (Pas-de-Calais). *Geobios*, **10**, 967–973.

Cappetta, H., Duffin, C. and Zidek, J. 1993. Chondrichthyes. In: Benton, M.J. (Ed.), The Fossil Record 2, pp. 593-609. Chapman and Hall; London.

Case, G.R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica A*, **160**, 176–205.

Chen, L., Cuny, G., and Wang, X. 2007. The chondrichthyan fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China). *Historical Biology*, **19**, 291–300.

Cuny, G., Rieppel, O. and Sander, P.M. 2001. The shark fauna from the middle Triassic (Anisian) of North-Western Nevada. *Zoological Journal of the Linnean Society*, **133**, 285–301.

Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoirs of the American Museum of Natural History*, Part V, **9**, 211–287.

Derycke-Khatir, C. 2005. Microrestes de Vertébrés du Paléozoïque supérieur de la Manche au Rhin. *Société géologique du Nord, Publication*, **33,** 1–261.

Derycke, C., Cloutier, R. and Candilier, A-M. 1995. Palaeozoic vertebrates of northern France and Belgium: part II - Chondrichthyes, Acanthodii, Actinopterygii (uppermost Silurian to Carboniferous). *Geobios, Memoire Special*, **19**, 343-350.

Djafarian, M.A. and Brice, D. 1973. Biostratigraphie des brachiopodes dans le Famennien supérieur de la région d'Ispahan (Iran central). *Comptes Rendus de l'Academie des Sciences*, **276**, 2125–2128.

Duffin, C.J. 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935). *Palaeontographica A*, **188**, 105–152.

Duffin, C.J. 2001. Synopsis of the selachian genus *Lissodus* Brough, 1935. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **221,** 145–218.

Duméril, A.M.C. 1806. Zoologie analytique ou méthode naturelle de classification des animaux, Paris. *Zoologie Analytique*. i-xxxiii + 1–344.

Gholamalian, H. 2003. Age-implications of Late Devonian conodonts from the Chah-Riseh area, northeast of Esfahan, central Iran. *Courier Forschungsinstitut Senckenberg*, **245**, 201–207.

Gholamalian, H. 2007. Conodont biostratigraphy of the Frasnian–Famennian boundary in the Esfahan and Tabas areas, Central Iran. *Geological Quarterly*, **51**, 453–476.

Ginter, M. 1990. Late Famennian shark teeth from the Holy Cross Mts, Central Poland. *Acta Geologica Polonica*, **40**, 69–81.

Ginter, M. 1994. Ichtiolity dewońskie z Polski i Uralu oraz ich znaczenie stratygraficzne [Devonian ichthyoliths from Poland and the Urals, and their application in stratigraphy]. *Unpublished Ph.D. thesis*. University of Warsaw; Warszawa.

Ginter, M. 1995. Ichthyoliths and Late Devonian events in Poland and Germany. *Ichthyolith Issues, Special Publication,* **1**, 23–30.

Ginter, M. 1999. Famennian – Tournaisian chondrichthyan microremains from the eastern Thuringian Slate Mountains. *Abhandlungen und Berichte für Naturkunde*, **21**, 25–47.

Ginter, M. 2000. Late Famennian pelagic shark assemblages. *Acta Geologica Polonica*, **50**, 369–386.

Ginter, M. 2001. Chondrichthyan biofacies in the late Famennian of Utah and Nevada. *Journal of Vertebrate Paleontology*, **21**, 714–729.

Ginter, M. 2002. Chondrichthyan fauna of the Frasnian-Famennian boundary beds in Poland. *Acta Palaeontologica Polonica*, **47**, 329–338.

Ginter, M. and Ivanov, A. 1992. Devonian phoebodont shark teeth. *Acta Palaeontologica Polonica*, **37**, 55–75.

Ginter, M. and Ivanov, A. 1996. Relationships of *Phoebodus*. *Modern Geology*, **20**, 263–274.

Ginter, M. and Ivanov, A. 2000. Stratigraphic distribution of chondrichthyans in the Devonian on the East European Platform margin. *Courier Forschungsinstitut Senckenberg*, **223**, 325–339.

Ginter, M. and Piechota, A. 2004. The first Devonian holocephalian tooth from Poland. *Acta Palaeontologica Polonica*, **49**, 409–415.

Ginter, M. and Turner, S. 1999. The early Famennian recovery of phoebodont sharks. *Acta Geologica Polonica*, **49**, 105–117.

Ginter, M., Hairapetian, V. and Klug, C. 2002. Famennian chondrichthyans from the shelves of North Gondwana. *Acta Geologica Polonica*, **52**, 169–215.

Ginter, M., Duffin, C. and Hampe, O. in press. Chondrichthyes (Paleozoic Elasmobranchii: teeth). In: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology, vol. 3D. Friedrich Pfeil, München.

Glikman L.S. 1964. Podklas Elasmobranchii. Akulovye [Subclass Elasmobranchii. Sharks; in Russian]. *In*: Obruchev, D.W. (Ed.), Osnovy paleontologii, 196-237. Nauka; Moscow.

Grogan, E.D. and Lund, R. 2008. A basal elasmobranch, *Thrinacoselache gracia* n. gen. & sp. (Thrinacodontidae, new family) from the Bear Gulch limestone, Serpukhovian of Montana, USA. *Journal of Vertebrate Paleontology*, **28**, 970–988.

Gross, W. 1938. Das Kopfskelett von *Cladodus wildungensis* Jaekel. 2. Teil: Der Kieferbogen. Anhang: *Protacrodus vetustus* Jaekel. *Senckenbergiana*, **20**, 123–145.

Gross, W. 1973. Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen Bonebeds des Devons. *Palaeontographica A*, **142**, 51–155.

Hairapetian, V. 2008. Late Devonian – Early Carboniferous fish micro-remains from central Iran. *Unpublished Ph.D. thesis*. University of Esfahan, Esfahan. 244 pp.

Hairapetian, V. and Gholamalian, H. 1998. First report of the Late Devonian fish remains and microvertebrate fragments in the Chahriseh area, North East of Esfahan. In: Mawson, R., Talent, J., Wilson, G. and Cockle, P. (Eds), North Gondwanan mid-Palaeozoic bioevent/biogeography patterns in relation to crustal dynamics. IGCP 421, Esfahan meeting, 5-20 December. Abstracts, 15. University of Esfahan.

Hairapetian, V., Ginter, M. and Yazdi, M. 2008. Early Frasnian sharks from central Iran. *Acta Geologica Polonica,* **58**, 173–179.

Hairapetian, V., Valiukevičius, J. and Burrow, C. 2006. Early Frasnian acanthodians from central Iran. *Acta Palaeontologica Polonica*, **51**, 499–520.

Hairapetian, V., Yazdi, M. and Long J. A. 2000. Devonian vertebrate biostratigraphy of central Iran. *Records of the Western Australian Museum, Supplement* **58**, 241–247.

Hampe, O. 2000. Occurrence of *Phoebodus gothicus* (Chondrichthyes: Elasmobranchii) in the middle Famennian of

northwestern Iran (Province East Azarbaijan). *Acta Geologica Polonica*, **50**, 355–367.

Hampe, O. and Ivanov, A. 2007. Bransonelliformes - a new order of the Xenacanthimorpha (Chondrichthyes, Elasmobranchii). *Fossil Record*, **10**, 190–194.

Hampe, O. and Schindler, T. 2004. Late Famennian fish remains from the Refrath 1 Borehole (Bergisch Gladbach-Paffrath Syncline; Ardennes-Rhenish Massif, Germany). *Courier Forschungsinstitut Senckenberg*, **251**, 267–289.

Harlton, B.H. 1933. Micropaleontology of the Pennsylvanian Johns Valley Shale of the Ouachita Mountains, Oklahoma, and its relationship to the Mississippian Caney Shale. *Journal of Paleontology*, **7**, 3–29.

Hay, O.P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *US Geological Survey Bulletin*, **179**, 1–868.

Herman, J. 1982. Die Selachier-Zähne aus der Maastricht Stufe von Hemmoor, Niederelbe (NW-Deuschland). *Geologisches Jahrbuch*, **61**, 129–159.

Huxley, T.H. 1880. A manual of the anatomy of vertebrated animals. D. Appleton, New York, NY, 431 pp.

Ivanov, A. 1999. Late Devonian – Early Permian chondrichthyans of the Russian Arctic. *Acta Geologica Polonica*, **49**, 267–285.

Ivanov, A. and Ginter, M. 1996. Early Carboniferous xenacanthids (chondrichthyes) from eastern Europe. *Bulletin de la Société Géologique de France*, **167**, 651–656.

Ivanov, A. and Rodina, O. 2004. A new omalodontid-like shark from the Late Devonian (Famennian) of western Siberia, Russia. *Fossils and Strata*, **50**, 82–91.

Jaekel, O. 1921. Die Stellung der Paläontologie zu einigen Problemen der Biologie und Phylogenie. 2. Schädelprobleme. *Paläontologische Zeitschrift*, **3**, 213–239.

Jaekel, O. 1925. Das Mundskelett der Wirbeltiere. *Gegenbaurs Morphologishes Jahrbuch*, **55**, 402-409.

Janvier, P. 1977. Les poissons dévoniens de l'Iran central et de l'Afghanistan. *Mémoires de la Société Géologique de France*, **8**, 277–289.

Janvier, P. 1981. Late Devonian fishes from central Iran. Part I: Dipnoi and Elasmobranchi. *Geological Survey of Iran*, *Report*, **49**, 155–166.

Ji, Q. and Ziegler, W. 1992. Introduction to some Late Devonian sequences in the Guilin area of Guangxi, South China. *Courier Forschungsinstitut Senckenberg*, **154**, 149–177.

Johns, M.J., Barnes, C.R. and Orchard, M.J. 1997. Taxonomy and biostratigraphy of Middle and Late Triassic elasmobranch ichthyoliths from northeastern British Columbia. *Geological Survey of Canada, Bulletin*, **502**, 1–235.

Johnson, G.D. 1981. Hybodontoidei (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas. *Journal of Vertebrate Paleontology*, **1**, 1–41.

Lebedev, O.A. 1996. Fish Assemblages in the Tournaisian-Viséan environments of the East European Platform. In: Strogen, P., Somerville, I.D. and Jones, G.L.L. (Eds), Recent Advances in Lower Carboniferous Geology. *Geological Society, Special Publication,* **107**, 387–415. London

Lelièvre, H. and Derycke, C. 1998. Microremains of vertebrates near the Devonian-Carboniferous boundary of southern China (Hunan Province) and their biostratigraphical significance. *Revue de Micropaléontologie*, **41**, 297–320.

Li, G. 1988. A new species of *Protacrodus* from north Jiangsu. *Vertebrata Palasiatica*, **26**, 101–106.

Liao, J.-C., Ginter, M. and Valenzuela-Ríos, J.I. 2007. Chondrichthyan microremains from the Givetian of the Aragonian Pyrenees (Spain). *Bulletin de la Société Géologique de France*, **178**, 171–178.

Long, J.A. 2007. Swimming in Stone: the amazing Gogo fossils of the Kimberley. Fremantle Arts Centre Press, 320 pp.

Long, J.A. and Hairapetian, V. 2000. Famennian microvertebrates from the Dalmeh area, central Iran. *Records of the Western Australian Museum, Supplement*, **58**, 211–221.

Lund, R. and Zangerl, R. 1974. *Squatinactis caudispinatus*, a new elasmobranch from the Upper Mississippian of Montana. *Annals of Carnegie Museum*, **45**, 43–54.

Maisey, J.G. 1976. The Jurassic selachian fish *Protospinax* Woodward. *Palaeontology*, **19**, 733–747.

Maisey, J.G. 2001. CT-scan reveals new cranial features in Devonian chondrichthyan "*Cladodus*" *wildungensis*. *Journal of Vertebrate Palaeontology*, **21**, 807–810.

Mistiaen, B., Gholamalian, H., Gourvennec, R., Plusquellec, Y., Bigey, F., Brice, D., Feist, M., Feist, R., Ghobadi Pour, M., Kebria−ee, M., Milhau, B., Nicollin, J.P., Rohart, J.C., Vachard, D. and Yazdi, M. 2000. Preliminary data on the Upper Devonian (Frasnian, Famennian) and Permian fauna and flora from the Chahriseh area Esfahan Province, Central Iran). *Annales de la Société Géologique du Nord*, **8** (2éme série), 93–102.

Randon, C., Derycke, C., Blieck, A., Perri, M.C. and Spalletta, C. 2007. Late Devonian – Early Carboniferous vertebrate microremains from the Carnic Alps, northern Italy. *Geobios*, **40**, 809–826.

Rees, J. 1998. Early Jurassic selachians from the Hasle Formation on Bornholm, Denmark. *Acta Palaeontologica Polonica*, **43**, 439–452.

Reif, W.-E. 1978. Types of morphogenesis of the dermal skeleton in fossil sharks. (Konstruktionsmorphologie, Nr. 89). *Paläontologische Zeitschrift*, **52**, 110–128.

Riemann, F., Schülke, I. and Thies, D. 2002. Mikrovertebratenreste aus dem basalen Famennium (*triangularis*-bis *crepida* Zone) der Montagne Noire (Frankreich). *Geologica et Palaeontologica*, **36**, 1–43.

Safari, A. and Kangazian, A. 2003. Microfacies and sedimentary environment of Upper Devonian sedimentary rocks in

Chahriseh area [in Persian with English abstract]. *Research Bulletin of Esfahan University (Science)*, **18**, 117–144.

St. John, O. and Worthen, A.H. 1875. Description of fossil fishes. *Geological Survey of Illinois, Paleontology,* **6,** 245–488.

Stahl, B.J. 1999. Chondrichthyes III. Holocephali. In: H.-P. Schultze (ed.), Handbook of Paleoichthyology, vol. 4. pp. 1–164. Friedrich Pfeil, München.

Traquair, R.H. 1884. Description of a fossil shark (*Ctenacanthus costellatus*). *Geological Magazine* (3rd ser.), **3**, 3–8.

Turner, S. 1982. Middle Palaeozoic elasmobranch remains from Australia. *Journal of Vertebrate Paleontology*, **2**, 117–131.

Turner, S. 1997. "*Dittodus*" species of Eastman 1899 and Hussakof and Bryant 1918 (Mid to Late Devonian). *Modern Geology*, **21**, 87–119.

Turner, S., Burrow, C.J., Gholamalian, H. and Yazdi, M. 2002. Late Devonian (early Frasnian) microvertebrates and conodonts from the Chahriseh area near Esfahan, Iran. *Memoirs of the Association of Australasian Palaeontologists*, **27**, 149–159.

Vullo, R., Cappetta, H., and Néraudeau, D. 2007. New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Palaeontologica Polonica*, **52**, 99–116.

Xia, F.-S. 1997. Marine microfaunas (bryozoans, conodonts and microvertebrate remains) from the Frasnian-Famennian interval in Northwestern Junggar Basin of Xinjiang in China. *Beiträge zur Paläontologie*, **22**, 97–207.

Yazdi, M. and Turner, S. 2000. Late Devonian and Carboniferous vertebrates from the Shishtu and Sardar Formations of the Shotori Range, Iran. *Records of the Western Australian Museum, Supplement,* **58**, 223–240.

Yazdi, M., Ghobadi Pour, M. and Mawson, R. 2000. Late Devonian conodonts from the Chahriseh area, central Iran. *Records of the Western Australian Museum*, **58**, 179–189.

Zangerl, R. 1981. Paleozoic Elasmobranchii. In: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology 3A, pp. 1-115. Gustav-Fischer; Stuttgart – New York.

Manuscript submitted: 31th July 2008
Revised version accepted: 31th March 2009

Appendix 1. Upper Devonian fish fauna from the Chahriseh section (*; macroremains)

Thelodonti (Turner *et al*. 2002, Hairapetian 2008)
- *Turinia hutkensis* Blieck and Goujet, 1978
- *Australolepis* cf. *seddoni* Turner and Dring, 1981

Acanthodii (Hairapetian *et al*. 2006, Hairapetian 2008)
- *Iranolepis ginteri* Hairapetian, Valiukevičius and Burrow, 2006
- *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, 1998
- *Milesacanthus* sp. aff. *M. antarctica* Young and Burrow, 2004
- Diplacanthid gen. et sp. indet.
- Ischnacanthiform gen. et sp. indet.
- cf. *Atopacanthus dentatus* *
- "*Acanthodes*" sp.

Placodermi (Hairapetian *et al*. 2000, Hairapetian 2008)
- *Holonema* sp.
- ?Euantiarcha gen. et sp. indet.
- Bothriolepididae gen. et sp. indet.
- *Bothriolepis* sp.*
- Ptyctodontidae gen. et sp. indet.*
- Dinichthyidae gen. et sp. indet.*

Chondrichthyes (Hairapetian *et al*. 2008, this work)
- *Manberodus fortis* Hairapetian and Ginter, 2008 (in Hairapetian *et al*. 2008)
- *Siberiodus mirabilis* Ivanov and Rodina, 2004
- *Phoebodus* cf. *latus* Ginter and Ivanov, 1995
- *Phoebodus* cf. *depressus* Ginter, Hairapetian and Klug, 2002
- *Phoebodus gothicus gothicus* Ginter, 1990
- *Phoebodus gothicus* cf. *transitans* Ginter, Hairapetian and Klug, 2002
- *Phoebodus turnerae* Ginter and Ivanov, 1992
- *Phoebodus* aff. *turnerae* Ginter and Ivanov, 1992
- *Phoebodus typicus* Ginter and Ivanov, 1995
- *Thrinacodus tranquillus* Ginter, 2000
- *Deihim mansureae* Ginter, Hairapetian and Klug, 2002
- *Dalmehodus turnerae* Long and Hairapetian, 2000
- *Protacrodus* spp.
- *Roongodus phijani* gen. et sp. nov.
- *Lissodus* sp.
- *Arduodens flammeus* gen. et sp. nov.
- *Cladodoides* sp.
- Elasmobranchii gen. et sp. indet. A
- Elasmobranchii gen. et sp. indet. B
- Elasmobranchii gen. et sp. indet. C
- *Squatinactis glabrum* (Ginter, 1999)
- *Bransonella*? sp.
- Holocephali gen et sp. indet.

Sarcopterygii (Hairapetian *et al*. 2000, Hairapetian 2008)
- Megalichthyidae gen. et sp. indet.*
- Onychodontidae gen. et sp. indet.
- Sarcopterygii gen. et sp. indet.*
- *Chirodipterus* sp.*
- *Adololopas* sp. *
- *Rinodipterus* sp.*
- Dipnoi gen. et sp. indet.*
- Dipnoi gen. et sp. indet.

Actinopterygii (Hairapetian 2008)
- *Moythomasia durgaringa* Gardiner and Bartram, 1977
- *Orvikuina* sp.
- Palaeonisciformes gen. et sp. indet.

Appendix 2. Distribution of chondrichthyan teeth in the Famennian of the Chahriseh section, central Iran

Age (Famennian)	Lower									Middle			Upper								
species \ samples	T4	T3A	T2	F-F2	F-F1	EX3	EX5	EX6	M	126	125	116	115	114	113	111	U140	U142	U145	U148	U150	U151	U154	U157	U159	U167	U178
Siberiodus mirabilis	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoebodus cf. *depressus*	-	-	-	-	-	-	-	-	-	-	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Ph. gothicus gothicus morphotype I	-	-	-	-	-	-	-	-	-	-	2	-	1	17	-	-	-	-	-	-	-	-	-	-	-	-	-
Ph. gothicus gothicus morphotype II	-	-	-	-	-	-	-	-	-	-	3	1	-	46	8	-	2	-	-	-	-	-	-	-	-	-	-
Ph. gothicus cf. *transitans*	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Ph. turnerae	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Ph. aff. *turnerae*	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Ph. typicus	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Thrinacodus tranquillus	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	4	4	-	-	-
Deihim mansureae	-	-	-	-	-	1	1	-	1	-	-	1	-	4	-	-	-	-	1	-	-	-	-	1	-	-	-
Dalmehodus turnerae	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	2	-	-	1	-	-	-	-	-
Protacrodus spp.	-	1	-	-	-	-	-	-	1	1	5	2	-	45	2	1	1	2	-	1	1	3	-	4	1	1	1
Roongodus phijani gen. et sp. nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	12	1	-	-	-	-	-	-	-	-	-	-	-	-
Lissodus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Arduodens flammeus gen. et sp. nov.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladodoides sp.	-	-	-	-	1	3	4	1	2	1	1	1	3	102	6	7	-	-	-	-	-	-	-	-	-	-	-
Elasmobranchii gen. et sp. indet. A	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Elasmobranchii gen. et sp. indet. B	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elasmobranchii gen. et sp. indet. C	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladodont indet.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Squatinactis glabrum	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Bransonella? sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Holocephali gen et sp. indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
unassigned phoebodonts	-	-	-	-	-	-	-	-	-	-	6	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-
protacrodont tooth-whorls	-	1	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	1	-	-	-	-
unassigned chondrichthyans	1	1	-	-	-	1	1	-	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Total	1	9	1	1	1	6	8	1	7	3	18	5	4	260	19	8	4	2	3	1	1	5	7	9	1	1	2