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Early Carboniferous chondrichthyans from the Mobarak Formation, Central Alborz Mountains, Iran

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ABSTRACT:

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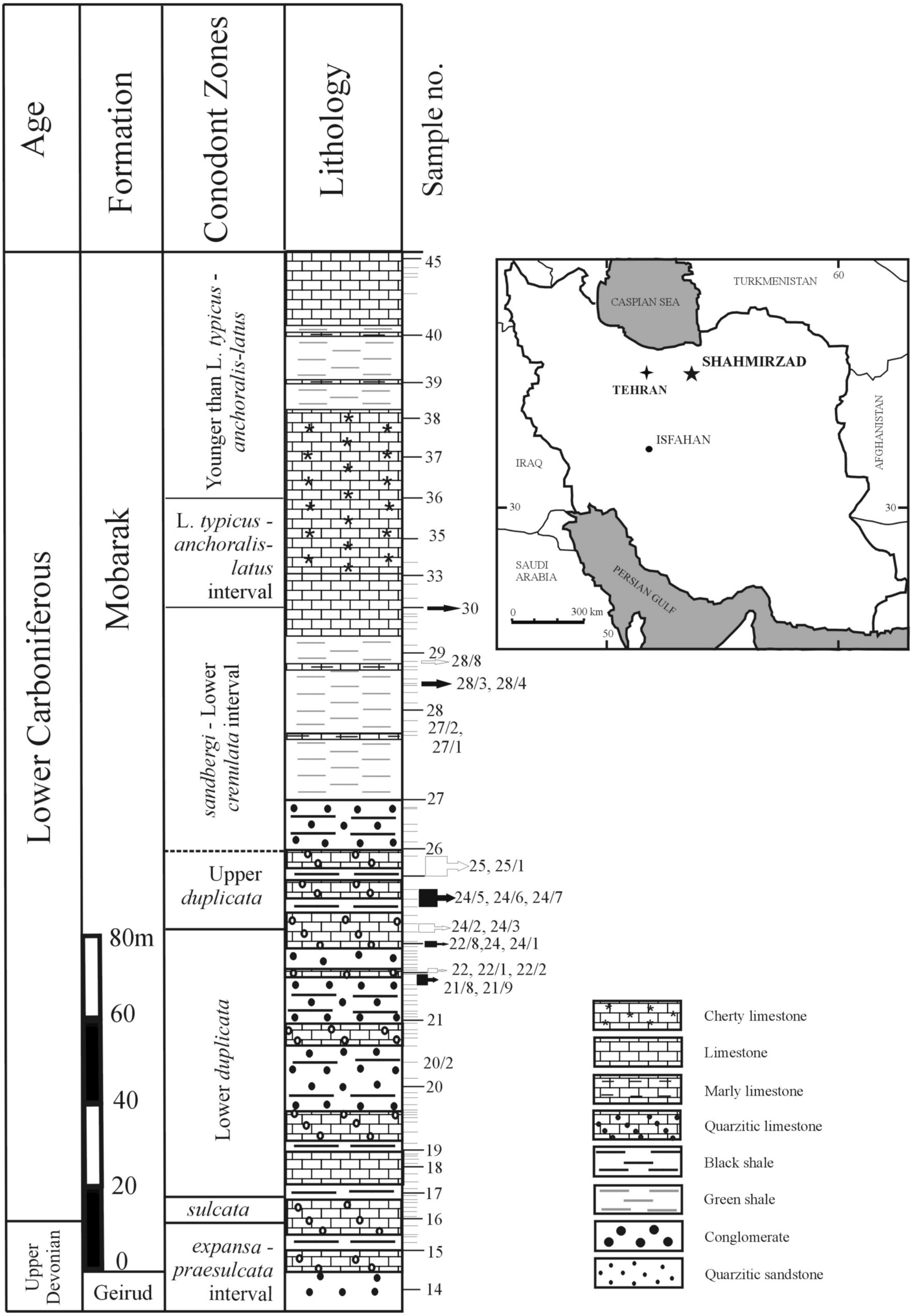
Well exposed Tournaisian, mainly carbonate, rocks of the Mobarak Formation in the area of Shahmirzad village, Central Alborz, Iran, yielded almost 200 chondrichthyan teeth and scales, associated with numerous actinopterygian microremains. Ten different taxa were recognised among the chondrichthyan teeth, of which the most abundant are those representing Euselachii (*Protacrodus* and *Lissodus*), Symmoriiformes (*Denaea*), and Phoebodontiformes (*Thrinacodus*). The high relative abundance of protacrodont crushing teeth, but lack of holocephalian dental elements suggest that the sediments forming the Shahmirzad section were deposited in a shallow shelf environment, but probably not on a carbonate platform.

Key words: Chondrichthyes; Tournaisian; Mobarak Formation; Alborz; Iran.

INTRODUCTION

In the history of studies on Palaeozoic chondrichthyans from the Iranian Platform, several papers were published, but almost none of them dealt with Carboniferous faunas. Most of the publications dealt with Upper Devonian assemblages from the central and northern parts of Iran, e.g., Hairapetian *et al.* (2000), Ginter *et al.* (2002), and Hairapetian and Ginter (2009). Even in the articles which provided some information on Carboniferous chondrichthyan remains, it was limited either to a list of represented groups, with no illustrations (e.g., Cladoselachier, Bradyodonten, Hybodonten, W. Gross' identification in Huckriede *et al.* 1962), or to a description of a few teeth (orodonts from the Kerman area, Yazdi and Turner 2000), or a single tooth-plate (holocephalian from Central Alborz, Dashtban 1996). Thus, the present paper, in which we describe chondrichthyan microfossils from the Mobarak Formation of the Shahmirzad section, Central Alborz Mountains, northern Iran, is the first to present a larger collection of Lower Carboniferous sharks from Iran.

Habibi (2008) and Habibi *et al.* (2008) studied the biostratigraphy and biofacies of Famennian–Tournaisian rocks in that section, a sequence about 450 m of terrigenous and carbonate sediments of the Geirud and Mobarak Formations. All samples from the Geirud Formation were barren of fish microremains, but some levels of the well exposed Tournaisian, mainly carbonate, sediments of the Mobarak Formation in the area of Shahmirzad village yielded microvertebrate remains as a by-product of acid-leaching for conodonts (Habibi, 2008). They are associated with diverse assemblages of conodonts, dating the fish-bearing part of the section as the Lower *duplicata* Zone through to the *sandbergi*-Lower *crenulata* interval (Text-fig. 1).



Text-fig. 1. Stratigraphic column of the Shahmirzad section showing fish-bearing horizons. Samples 21-30 produced vertebrate microfossils (Table 1). Map of Iran shows location of the section

CONODONT ZONES	Lower *S. duplicata*										Upper *S. duplicata*						*S. sandbergi* - Lower *crenulata*				
Samples	21/8	21/9	22	22/1	22/2	22/5	22/8	24	24/1	24/2	24/3	24/5	24/6	24/7	25	25/1	28/3	28/4	28/8	30	
Thrinacodus ferox		1	1			1								2		2				1	8
Thrinacodus bicuspidatus			1																		1
Bransonella cf. *nebraskensis*														1							1
Denaea sp.		1	6											2		1		1			11
"*Cladodus*" *thomasi*						1									1						2
Squatinactis sp.			1										1								2
Protacrodus sp.		8	24		2	9	2	3	4		1			2		1					56
Lissodus wirksworthensis			1			1			1				1	1							5
Vallisia sp.			1																		1
Euselachii indet.						1															1
Ctenoptychius ?			1																		1
Protacrodont-type scales		7			2	8	3	1	9	2	1	5	3	3		8			1	7	60
Ctenacanth-type scales						3			1			1	1	2	1	2				1	12
Stemmatias bicristatus			1													1					2
Actinopterygian scales			16		3	6	1	8	8	2	4	3		15		3		3	3		75
Actinopt. teeth and fragments	2	7	8	1	20	20	6	14	24	8	7	25	18	16	5	44	1	6	12	10	254
unassigned		2			5	4	3	2	8	1		6	3	2	2	3			1		42
TOTAL	2	26	61	1	32	54	15	28	55	13	13	40	27	46	9	65	1	10	17	19	534

Table 1. Distribution of chondrichthyan teeth and associated vertebrate microremains in the Shahmirzad section

The collection from Shahmirzad consists of 89 chondrichthyan teeth and 74 scales (of protacrodont and ctenacanth design) and branchial denticles ("*Stemmatias*"), associated with numerous (above 350) scales, teeth and bone fragments of actinopterygians, and other unassigned vertebrate microremains (Table 1; Pl. 4, Figs C–H). Most of the shark teeth are broken or abraded, but in spite of that, we were able to recognise ten different taxa. Unfortunately, most of these taxa (except protacrodonts) are represented in the samples only by one or two teeth, so it was impossible for us to investigate their diversity, possible heterodonty, or vertical changes in relative abundance. This being the case, we can only document their presence in the studied Tournaisian section of Alborz, but without extensive conclusions.

Specimens of chondrichthyan microfossils illustrated herein are housed in the Geology Department of Isfahan University (EUIC).

SYSTEMATIC PALAEONTOLOGY

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

Thrinacodus ferox (Turner, 1982)
(Pl. 1, Figs A, B)

MATERIAL: Eight teeth from six samples (see Table 1).

REMARKS: The characteristic asymmetrical tricuspid teeth of *Th. ferox* were occasionally noted from the late Famennian (Ginter 2001), but they are much more common in the Tournaisian (e.g. Turner 1982; Duncan 2003). In certain areas (e.g., Muhua section in China), in the upper parts of the Tournaisian, this species is replaced by its probably more derived relative, *Th. bicuspidatus* Ginter and Sun, 2007. The latter species is known from its bicuspid teeth, but it also might have retained tricuspid teeth in some parts of the dentition. Therefore, when we deal with only a few tricuspid thrinacodont teeth in a sample, it is difficult to decide, whether they belong to *Th. ferox* or to *Th. bicuspidatus*. Here, we attribute all tricuspid teeth to *Th. ferox* and only bicuspid forms are identified as *Th. bicuspidatus*. As usual in the collections of *Th. ferox* teeth (e.g., Turner 1982; Duncan 2003), there occur two types of forms here: one, with a short base and a more symmetrical crown, considered to represent the anterior area of the jaw (Pl. 1, Fig. A), and the other, with a longer base and extremely asymmetrical crown, attributed to the lateral and posterolateral positions in a jaw (Pl. 1, Fig. B).

Thrinacodus bicuspidatus Ginter and Sun, 2007
(Pl. 1, Fig. C)

MATERIAL: One tooth from sample 22.

REMARKS: Thus far all the well-dated records of *Th. bicuspidatus* (southern China, western USA) have indicated a very short stratigraphic range for this species (only *crenulata* Zone). The occurrence of bicuspid thrinacodont teeth in sample 22 of the Shahmirzad section extends the lower range of this species down to the *duplicata* Zone.

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

Bransonella cf. *nebraskensis* (Johnson, 1984)
(Pl. 1, Fig. D)

MATERIAL: One tooth from sample 24/7.

REMARKS: *Bransonella*, known from the Carboniferous all over the world (central USA, Poland, Russia, China, possibly Brazil), is the open marine relative of xenacanthiforms. It was mostly recorded from the higher parts of Mississippian (Viséan, Serpukhovian, Ivanov and Ginter 1996) and from the Pennsylvanian (Johnson 1984), but similar teeth also were found in the Famennian (e.g., Turner in Xia 1997, pl. 27, figs 5, 6, 9). This is, however, the first probable record of *B. nebraskensis* from the Tournaisian. Unfortunately, the damaged base and partly broken cusps preclude the definite identification of the tooth.

Superorder Cladodontomorphi Ginter, Hampe and Duffin, 2010
Order Symmoriiformes Zangerl, 1981
Family Falcatidae Zangerl, 1990
Denaea Pruvost, 1922

Denaea sp.
(Pl. 1, Fig. E)

MATERIAL: Eleven teeth from five samples (see Table 1).

REMARKS: These tri- to pentacuspid cladodont teeth with delicate, slender cusps and thin bases are only tentatively referred here to *Denaea*, which is generally known from the Upper Mississippian. It is difficult to distinguish teeth of *Denaea* from those of small *Stethacanthus* teeth in such incomplete and abraded material. Only the labio-lingual dimension of the base, usually longer in the former and shorter in the latter, suggests that of these two possibilities, the teeth from Shahmirzad are closer to those of *Denaea*.

Order Squatinactiformes Zangerl, 1981
Family Squatinactidae Cappetta, Duffin and Zidek, 1993
Squatinactis Lund and Zangerl, 1974

Squatinactis sp.
(Pl. 2, Fig. A)

MATERIAL: Two teeth; one from sample 22 and one from sample 24/6.

REMARKS: The teeth of *Squatinactis* are characterised by a wide base provided with two widely spaced orolingual buttons and two triangular, hook-like basolabial projections, framing the depression at the base of the median cusp. These projections do not form isolated thickenings, but constitute parts of a specifically profiled labial rim. The crown consists of delicate cusps. The Famennian species known thus far as "*Symmorium*" *glabrum* Ginter, 1999 can probably be included in this genus. The structure of the base in "*S.*" *glabrum* is almost identical to that of *S. caudispinatus* Lund and Zangerl, 1974, whereas the crown differs in the number and distribution of the cusps. In the majority of "*S.*" *glabrum* specimens, there are no more than two cusps developed on either side of the median cusp. However, in some specimens an outermost accessory cusplet is present.

A rich collection of *Squatinactis* teeth from the Tournaisian of the South Urals (Bashkiria, Russia), has been described by Ivanov (1996, fig. 5, as *Symmorium* sp.). In this group of specimens it is possible to observe the full range of morphologies, from wide multicuspid teeth, to narrow ones, similar to *Squatinactis glabrum*. The specimens from Shahmirzad, with their relatively shorter, broader and labially flattened median cusps, are the closest to the teeth illustrated by Ivanov (1996) in his figures 5A, C, D, from the *Siphonodella sulcata* and *S. duplicata* conodont zones. They also have similar, slightly coarser cristae on the labial side.

Cladodontomorphi incertae sedis

„*Cladodus*" *thomasi* Turner, 1982
(Pl. 1, Figs F, G)

MATERIAL: One tooth from sample 22/5 and one from 25.

REMARKS: Turner (1982) illustrated a seven-cuspid cladodont tooth from the Tournaisian of Broken River embayment, North Queensland, and referred to it as *Cladodus thomasi*. Later (Turner 1984), she transferred it to *Stethacanthus*. It is certain that the tooth belongs neither to *Cladodus* nor *Stethacanthus*, but its correct generic name, and even its ordinal assignment, remain unknown. Some features make it similar to *Denaea* (Symmoriiformes; e.g., the orolingual button almost split in two by two canal openings), but its overall appearance resembles smaller teeth of *Cladodoides wildungensis* Jaekel, 1921 (Ctenacanthiformes; Ginter *et al.* 2010), characteristic of the Frasnian-Famennian boundary beds. The teeth from Shahmirzad are generally similar to "*Cladodus*" *thomasi*, but possess only five cusps and a more pronounced carina connecting them.

Cohort Euselachii Hay, 1902
Superfamily Protacrodontoidea Zangerl, 1981
Family Protacrodontidae Cappetta, Duffin and Zidek, 1993
Protacrodus Jaekel, 1925

Protacrodus sp.
(Pl. 2, Figs B-E)

MATERIAL: Fifty-six teeth from ten samples (see Table 1).

REMARKS: Based on the dentition alone, it is impossible to distinguish protacrodonts from the hybodonts, amongst which some genera occur with protacrodont-like, crushing teeth (*Tristychius*, *Sphenacanthus*, *Polyacrodus*). It is therefore impossible to draw a boundary between these two groups. Certainly, *Protacrodus vetustus* Jaekel, 1925, whose jaws and scales are known, differs from all Carboniferous and later hybodonts described from articulated skeletons. However, the rank of these differences is not easy to estimate. This being the case, the assignment of the protacrodont-like teeth found in the Tournaisian of Shahmirzad section to *Protacrodus* is only provisional.

Among such teeth, quite abundant in the samples, a few different crown morphologies can be distinguished (the base is of a common euselachian type, see Ginter *et al.* 2010). There are teeth with a relatively small median cusp and three lateral cusps on each side (Pl. 2, Fig. B). These are possibly from the lateral parts of the jaw. The others are characterised with a higher and broader median cusp, labio-lingual compression of the crown, and only two cusps on each side (Pl. 2, Fig. C). Such teeth are similar to *Protacrodus orientalis* Li, 1988 from the Carboniferous of Jiangsu Province in China. Yet another type of crown is similar to the above mentioned teeth, but the median cusp is narrower and relatively higher (Pl. 2, Fig. D), and the last crown type has a large median cusp, but three cusps on each side (Pl. 2, Fig. E). Despite these differences, it is possible that all of them belong to the same species, their specific features depending on the position in the jaw, upper or lower jaw, or on the age of an individual or its sex.

Order Hybodontiformes Maisey, 1975
Superfamily Hybodontoidea Owen, 1846
Family Lonchidiidae Herman, 1977
Lissodus Brough, 1935

Lissodus wirksworthensis Duffin, 1985
(Pl. 3, Figs A-C)

MATERIAL: Five teeth from five samples (see Table 1).

REMARKS: The teeth of *Lissodus* from Shahmirzad display the same features as the original material of *L. wirksworthensis* from the Viséan of England (Duffin 1985). They are elongated mesio-distally, with relatively low crowns and incompletely fused lateral cusps, visible in the single well preserved specimen (Pl. 2, Fig. A; compare Duffin 1985, text-fig. 21d, e). The other four specimens of *Lissodus* are only tentatively assigned to this species, because the surface of their crowns is abraded.

Euselachii incertae sedis
Vallisia? Duffin, 1982

Vallisia? sp.
(Pl. 3, Fig. D)

MATERIAL: One tooth from sample 22.

REMARKS: The tooth attributed here to the genus *Vallisia* consists of an asymmetrical, labio-lingually compressed crown and an almost vertical, slightly basolabially concave base of the euselachian type. The prominent main cusp is ornamented with a few coarse cristae and gently inclined laterally (probably distally). On its distal side there occurs a single, large lateral cusp, but on the mesial side there are three similar cusps, decreasing outwards in size, with fused bases. Between the main cusp and the nearest lateral one there is a small intermediate cusplet. The whole mesial side of the crown forms a kind of a saw.

The genus *Vallisia* was originally based upon rare isolated teeth from the Upper Triassic of Europe (Duffin 1982), but two specimens tentatively assigned to this genus have been described from the Upper Fammenian of Belgium as *Vallisia*? sp. by Derycke-Khatir (2005). Duffin (in Ginter *et al.* 2010) pointed out several differences between the Triassic and Famennian forms suggesting that the latter belong to a new genus. The tooth from Shahmirzad is generally similar to the Belgian teeth, but the latter have more fused and compressed lateral cusps.

Euselachii gen. et sp. indet.
(Pl. 4, Fig. A)

REMARKS: There are several unidentifiable fragments of euselachian teeth in the material from Shahmirzad and they will not be described here. However, one of them (SUIC 8917 from sample 22/5) deserves closer attention. It is a broken tooth with five cusps of almost equal size. The tooth slightly resembles *Protacrodus*, but the cusps are higher and more separate (less fused together) than in the latter. At present, the cusps are smooth, but this is perhaps only the result of abrasion.

Subclass Euchondrocephali Lund and Grogan 1997
Order Petalodontiformes Zangerl, 1981
Family Belantseidae Lund, 1989
Ctenoptychius? Agassiz, 1838

Ctenoptychius? sp.
(Pl. 4, Fig. B)

MATERIAL: One specimen from sample 22.

REMARKS: In this rich sample, particularly abundant in protacrodont crushing teeth, an unusual tooth was found. Its crown consists only of a mesio-distal, narrow, serrated ridge. The base is of the euselachian type, with a horizontal row of large foramina, but, although broken, it is evident that it was labio-lingually compressed and directed vertically. Along the crown-base interface extends a horizontal ridge or shelf. The vertical attitude of the base combined with the horizontal ridge suggests that the tooth represents a petalodont. The serrated vertical ridge of the crown most resembles that of belantseids, such as *Ctenoptychius*. However, the size of the tooth and weakly developed features suggest that it could have belonged to a juvenile individual. A similar tiny petalodont tooth, but with the non-serrated crown, was found in the Tournaisian of Muhua, southern China, and attributed to *Chomatodus* (Ginter and Sun 2007). Unfortunately, the poor state of preservation of the tooth from Shahmirzad precludes any further comparisons.

PALAEOECOLOGICAL REMARKS

As mentioned above, the chondrichthyan taxa found in the Shahmirzad section are scattered among the samples and none of the individual samples (except, perhaps, sample 22) is rich enough to serve for statistical purposes. However, if all the specimens from the middle Tournasian (*duplicata – crenulata* Zones) are counted together, the picture of relative abundances of taxa becomes more clear. Definitely, the largest number of teeth (69%) belongs to euselachians with crushing dentitions: *Protacrodus* and *Lissodus*. Cladodont teeth, usually belonging to fast-swimming surface hunters (in this case *Denaea* and "*Cladodus*" *thomasi*), form the second group (15%). *Thrinacodus*, a specialised eel-like shark with narrow jaws (Grogan and Lund 2008), probably slowly searching for soft prey above the bottom, is also relatively abundant (9%). Of the less abundant genera, *Bransonella*, which can be considered a Carboniferous equivalent of Famennian *Jalodus*, preferred the open marine environment (see Ginter 2000). It is difficult to interpret the mode of life of *Squatinactis* sp. The body structure of *S. caudispinatus*, known from the Serpukhovian Bear Gulch beds of Montana (Lund and Zangerl 1974), and especially the broad, batoid-like pectoral fins, suggests a benthic mode of life. However, the dentition of delicate, clutching cladodont teeth, together with data concerning the distribution of *S. glabrum* in Famennian seas (deeper water environments possessing an anoxic bottom water layer), suggests that it inhabited a position higher in the water column.

The predominance of crushing teeth suggests a similarity of the Tournaisian assemblage from Shahmirzad to the shallow-water *Protacrodus* biofacies of the palaeoecological model proposed by Ginter (2000) for the late Famennian pelagic environments and later applied to the Famennian of the Iranian Platform by Ginter *et al.* (2002). Based on this feature, the collection under study considerably differs from that described by Ivanov (1996) from the slightly older strata (*sulcata – duplicata* Zones) of the Sikaza River in the South Urals. There, *Squatinactis* sp. absolutely predominates, together with *Thrinacodus*, and crushing teeth are subordinate. On the other hand, holocephalian teeth and tooth-plates are completely absent from Shahmirzad, which is in contrast to the coeval (*crenulata* Zone), definitely shallow water assemblage from Muhua, southern China, in which the holocephalian remains form one of the major components (Ginter and Sun 2007). Thus, it seems that the three assemblages represent three different marine environments: far offshore (Sikaza); shallow shelf (Shahmirzad); and very shallow carbonate platform (Muhua).

Interestingly, the conodont assemblage recovered from the fish-bearing strata and adjacent horizons mainly consists of polygnathid biofacies (Habibi 2008). *Polygnathus communis communis* and *P. inornatus inornatus* are by far the most abundant. *P. c. communis* is interpreted to have lived at shallow depth in the photic zone (Lane *et al.* 1980). The absence of deep water conodont elements such as gnathodids and siphonodellids confirms the presence of a shallow shelf environment in the middle Tournaisian at Shahmirzad.

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PLATES 1–4

PLATE 1

A – *Thrinacodus ferox* (Turner, 1982), SUIC 8901, distal cusp missing, oral and lingual views; sample 30.
B – *Th. ferox*, SUIC 8902, oral view; sample 24/7
C – *Th*. *bicuspidatus* Ginter and Sun, 2007, SUIC 8903, oral view; sample 22.
D – *Bransonella* cf. *nebraskensis* (Johnson, 1984), SUIC 8904, lingual and oral views; sample 24/7.
E – *Denaea* sp. SUIC 8905, labial, oral and lingual views; sample 22.
F – „*Cladodus*“ *thomasi* Turner, 1982, SUIC 8906, labial, lingual and oral views; sample 25.
G – „*C.*“ *thomasi*, SUIC 8907, labial, oral and lingual views; sample 22/5.

Scale bar 0.2 mm

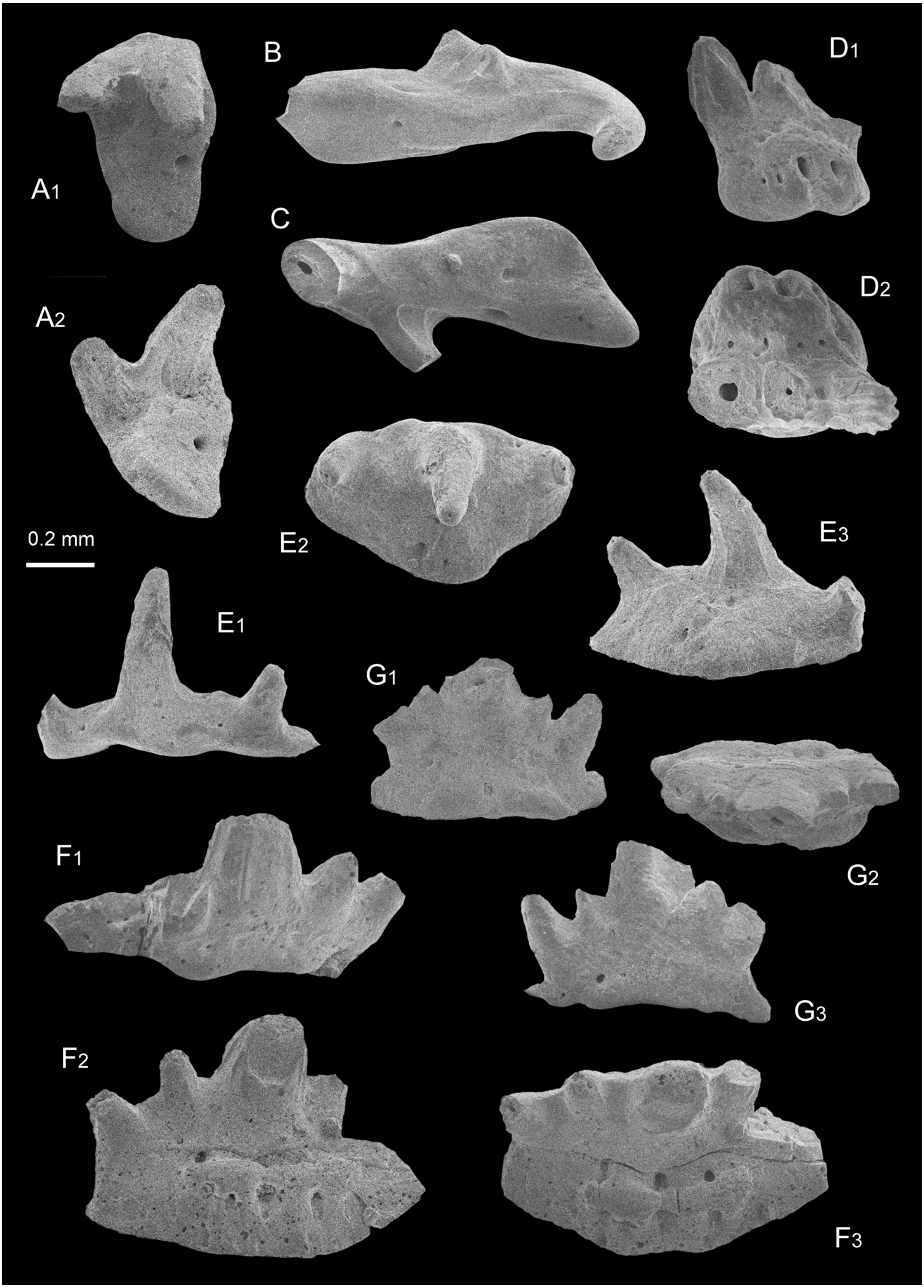
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PLATE 2

A – *Squatinactis* sp., SUIC 8908, oral, lingual and labial views; sample 28/3.
B-E – *Protacrodus* sp., sample 22; B – SUIC 8909, lingual, oral and labial views; C – SUIC 8910, lingual, oral and labial views; D – SUIC 8911, lingual, oral and labial views; E – SUIC 8912, lingual, oral and labial views.

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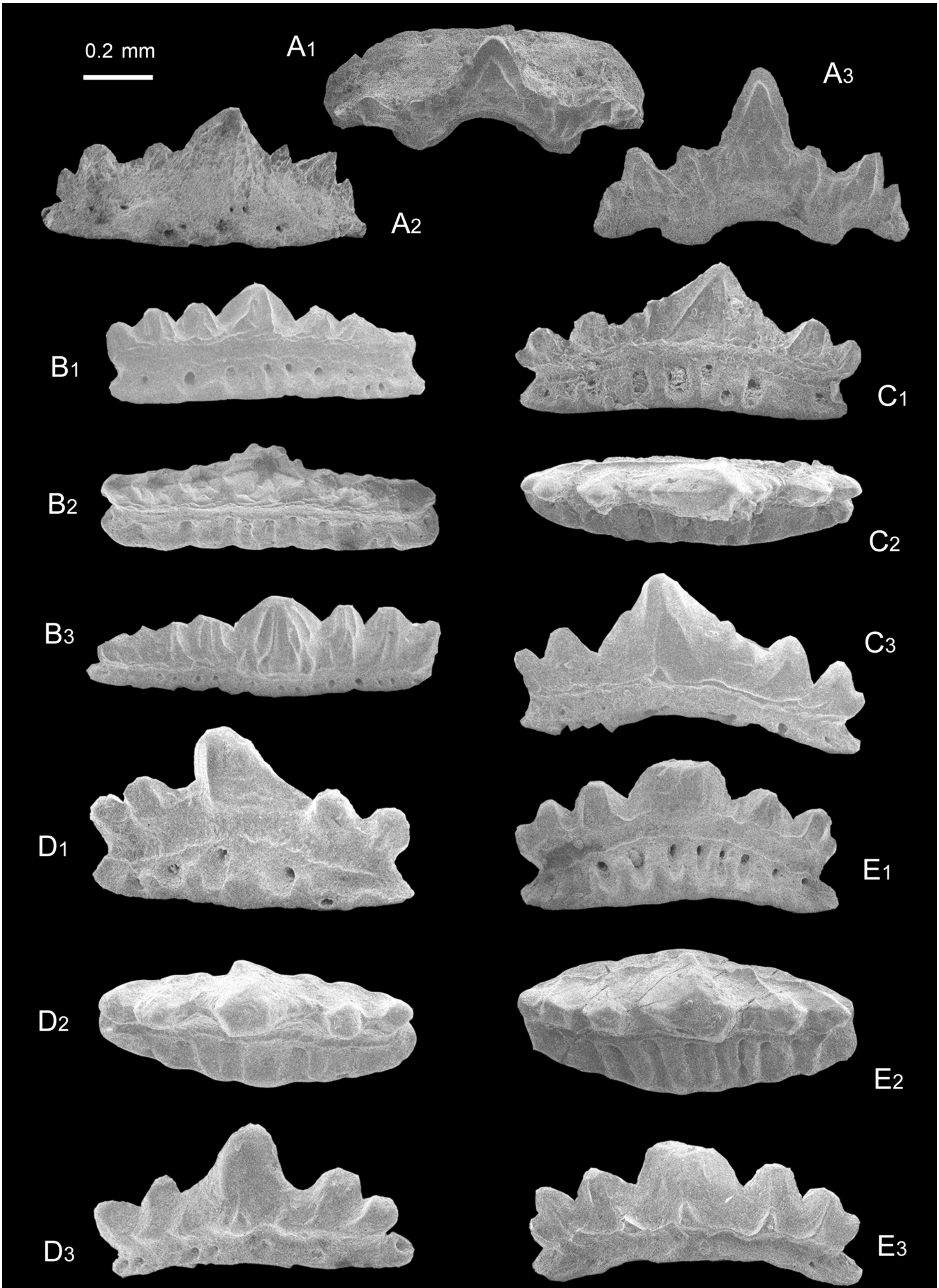
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PLATE 3

A-C – *Lissodus wirksworthensis* Duffin, 1985. A – SUIC 8913, lingual, oral and labial views; sample 24/6; B – SUIC 8914, lingual, oral and labial views; sample 22; C – SUIC 8915, labial, oral and lingual; sample 24/7.

D – *Vallisia*? sp. SUIC 8916, labial, oral and oblique lingual views; sample 22.

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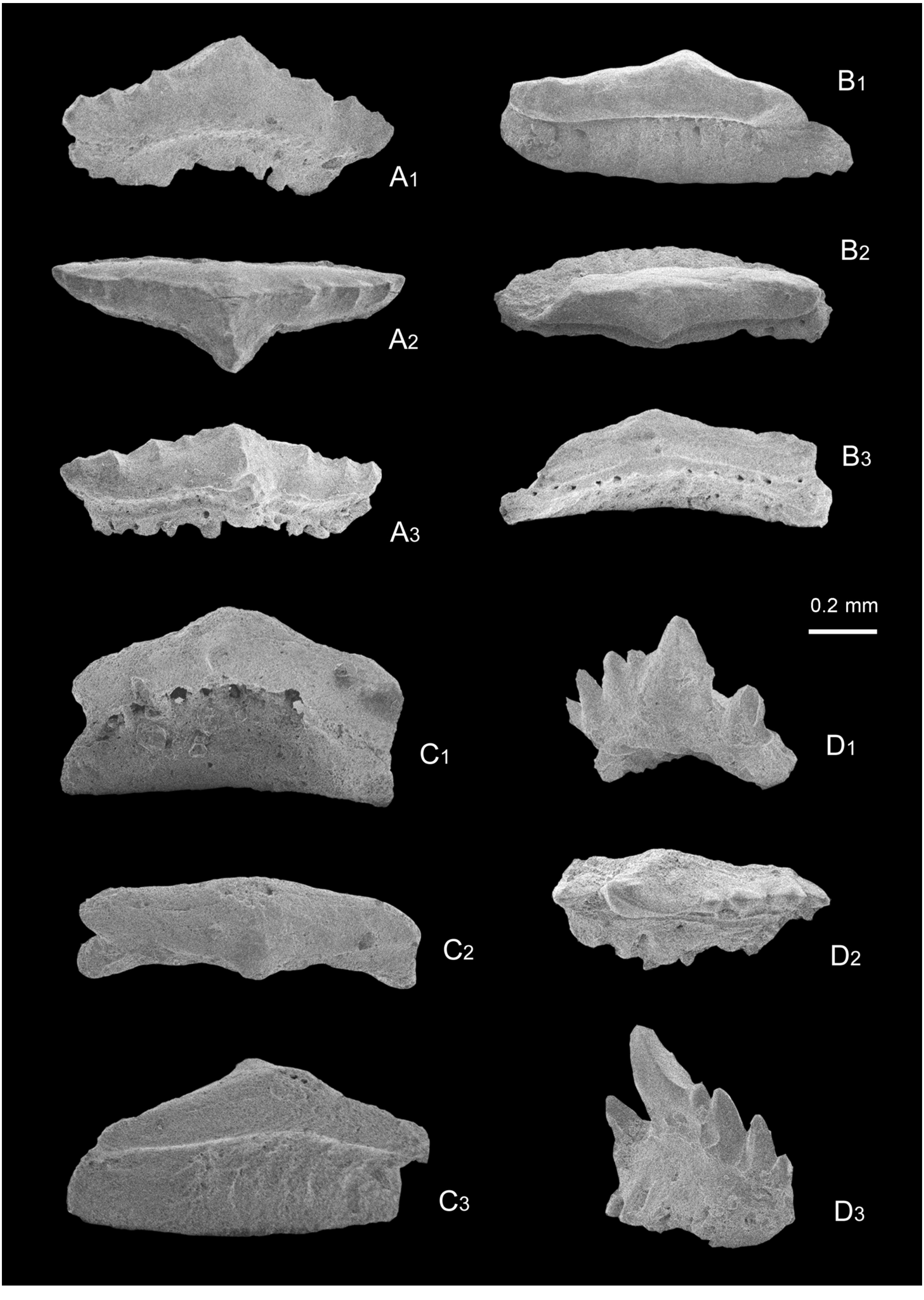
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PLATE 4

A – Euselachii gen. et sp. indet. SUIC 8917, labial, oral and lingual views; sample 22/5.
B – Petalodontiformes gen et sp. indet. (?*Ctenoptychius* sp.), SUIC 8918, labial, oral and lingual views; sample 22.
C – Protacrodont-type scale, SUIC 8919, basal view; sample 22.
D – Ctenacanth-type scale SUIC 8920, anterior view; sample 22.
E – Undefined chondrichthyan(?) scale, SUIC 8921, external view; sample 22.
F – Actinopterygian scale, SUIC 8922, external view; sample 22/5.
G – *Stemmatias bicristatus*-type chondrichthyan branchial denticle, SUIC 8923, lateral view; sample 25/1.
H – Actinopterygian palatal denticles, SUIC 8924, oral and lateral views; sample 22/8.

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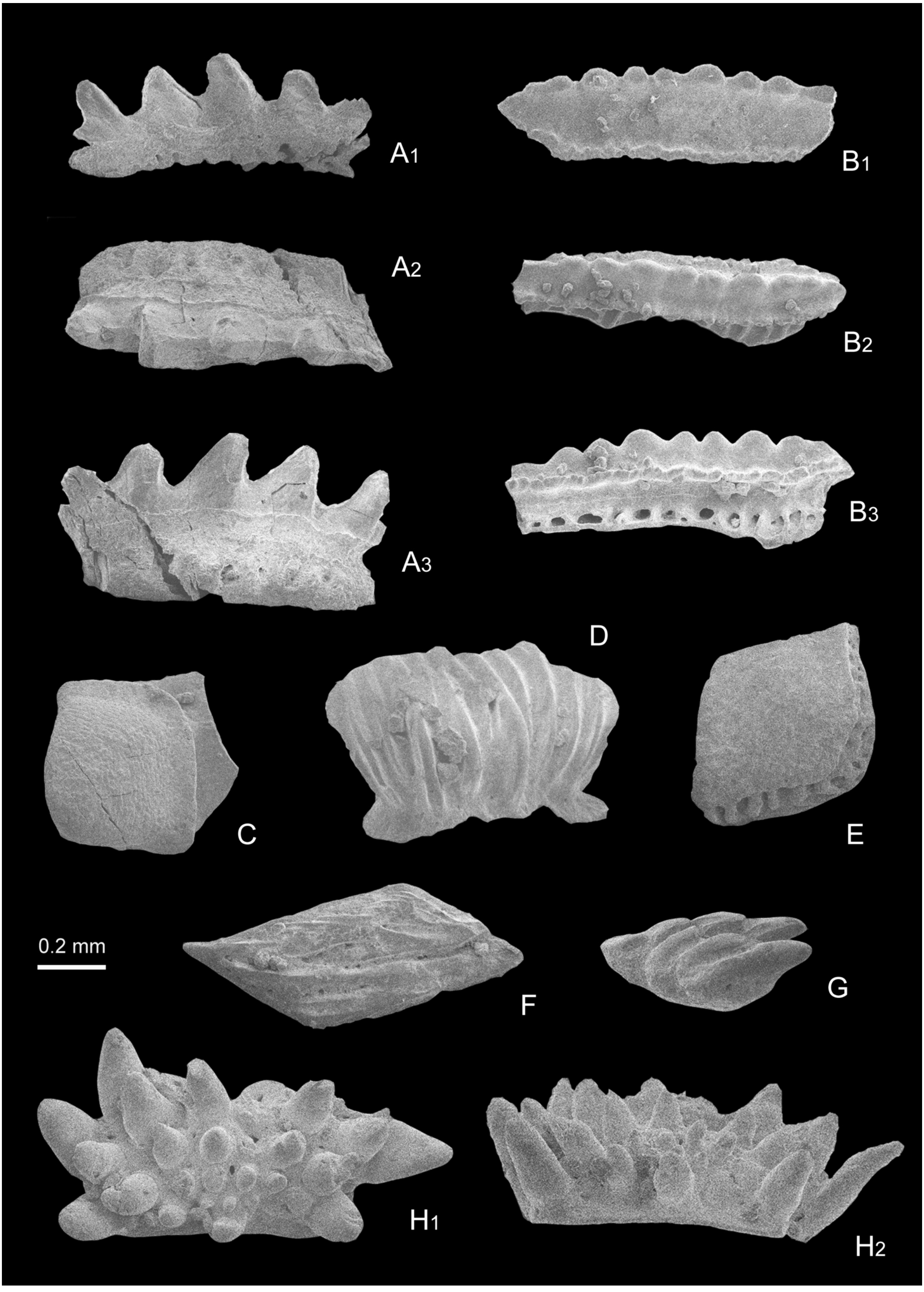
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