A first Late Permian fish fauna from Baghuk Mountain (Neo-Tethyan shelf, central Iran)

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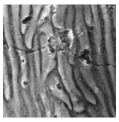

A diverse Late Permian assemblage of chondrichthyan and actinopterygian micro- and macroremains is presented from the central Iranian locality of Baghuk Mountain for the first time. The vertebrate remains were found in sediments containing mainly pelagic organisms such as nautiloids, ammonoids, and conodonts. Their habitat is interpreted as a deep shelf area with well-oxygenated bottom water conditions below the storm wave base. The chondrichthyans are represented by various dermal denticles, a fragment of a spine, and a low number of teeth from mostly durophagous hybodontiforms and eugeneodontiforms. A new eugeneodontid species is described as *Bobbodus xerxesi* sp. nov.; this genus was known only from the east coast of the former Panthalassic Ocean. The actinopterygian remains are represented by dermal bones, teeth, and scales. The bones are only fragmentarily preserved. The Baghuk Mountain vertebrate fauna shows closest similarities to remains known from the Russian Platform and from localities situated at the east coastal region of the Panthalassic Ocean (central United States). • Key words: chondrichthyans, actinopterygians, Wuchiapingian, Changxingian, palaeoenvironment.

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Up to now only a few occurrences of fish remains have been reported from the Middle to Late Permian successions of Iran. Douglas (1950) was the first to describe a specimen, which he referred to *Helicoprion* cf. *davisi*, from Artinskian (Early Permian) deposits at the Kuhgalu locality in the Zagros Mountains. There was an indication for the occurrence of a few Late Permian fish scales from the Ali Bashi Mountains near Julfa (NW Iran) by Stepanov *et al.* (1969). The only illustrated material was presented by Golshani & Janvier (1974), in which fragmentary teeth belonging to *Megactenopetalus* and *Petalorhynchus* were described from Late Permian strata of the Hambast Mountains, Abadeh region (central Iran).

The present paper describes diverse chondrichthyan and actinopterygian micro- and macroremains collected during several joint Iranian-German expeditions (2010, 2011) to the Baghuk Mountain (geographical coordinates, N 31° 33´ 49˝, E 52° 26´ 12.8˝), located about 45 km north-west of the town of Abadeh (Fig. 1). The material has been collected from five limestone horizons (samples SG2, SG9, SG34, H7/1 and H7/2) in the Hambast Formation (Fig. 2).

The Abadeh-Shahreza belt in the Sanandaj-Sirjan Terrane, as a part of the northern shelf of the Neo-Tethyan ocean (Stampfli & Borel 2002, Arfania & Shahriari 2009), is well known from its Permian-Triassic outcrops (Taraz *et al.* 1981).

Stratigraphic setting

The lithological units of the Permian rock formations in the Abadeh region were refined by Taraz *et al.* (1981), who separated three formations with a total of seven informal units, including the Surmaq Formation (units 1–3), the Abadeh Formation (units 4 and 5), and the Hambast Formation (units 6 and 7). Particular attention was paid to the Late Permian Hambast Formation with a special focus on conodont- and ammonoid-based biostratigraphy. The geochemistry of the Permian-Triassic boundary beds has been

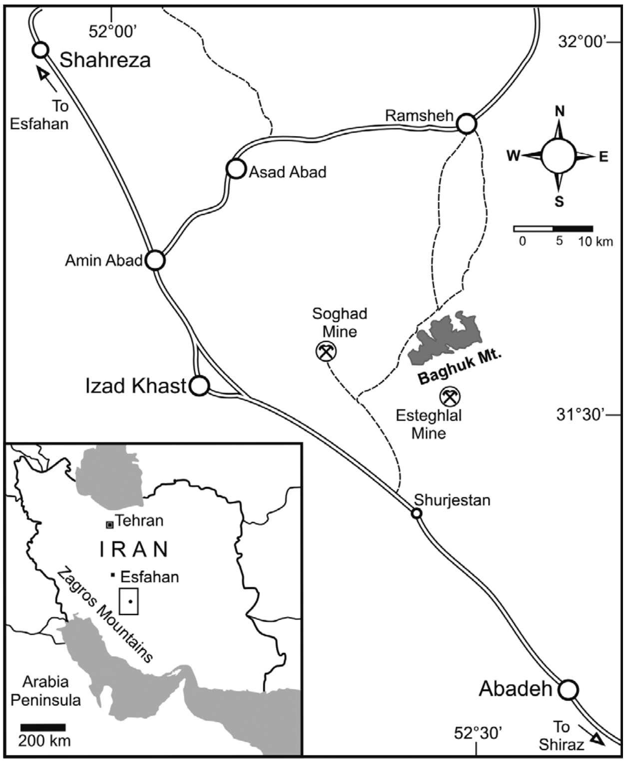


Figure 1. Map of the Shahreza-Abadeh area showing the newly discovered fish-bearing locality at Baghuk Mountain.

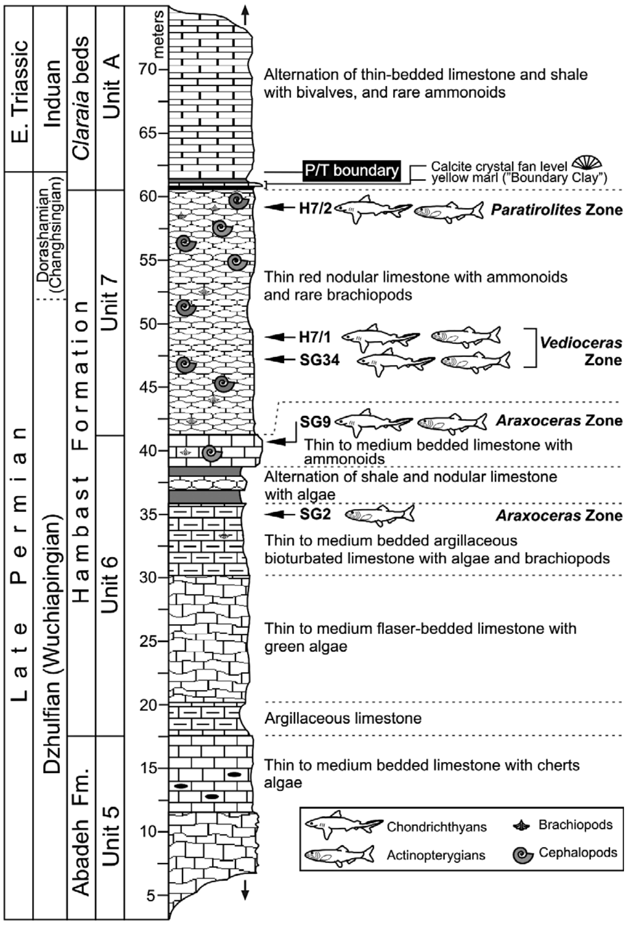


Figure 2. Lithological subdivisions of the Late Permian succession at Baghuk Mountain. Unit 6 of the Hambast Formation is dated as middle Dzhulfian based on conodonts and ammonoids (Bando 1979, Gallet *et al.* 2000). The succeeding unit 7, comprising thin-bedded brownish-red nodular limestone, was dated as late Dzhulfian to the top of Dorashamian (Kozur 2004, 2005; Richoz *et al.* 2010).

extensively studied (see Richoz *et al.* 2010 for a review of earlier works).

Unit 6 of the Hambast Formation is lithologically characterised by an alternation of shale and micritic grey limestone; it conformably overlays dark grey limestone beds of the Abadeh Formation. Based on conodonts and ammonoids, it was previously dated as middle Dzhulfian (Wuchiapingian) (Bando 1979, Taraz *et al.* 1981, Gallet *et al.* 2000).

Sample SG2, with a few actinopterygian scales, includes various ammonoids (*e.g.*, *Araxoceras* sp.) and nautiloids from the *Araxoceras* Zone. Sample SG9 from the same stratigraphic unit yielded chondrichthyan teeth and scales of small size, as well as an actinopterygian jaw fragment; ammonoids from the *Araxoceras* Zone include large representatives of *Prototoceras* sp. and *Pseudogastrioceras* sp. Both horizons can be dated as middle Dzhulfian (Wuchiapingian).

The succeeding unit 7 is composed of thin-bedded greyish red nodular limestone; it contains ammonoids, coiled and orthoconic nautiloids, rare brachiopods, rugose corals, and crinoid ossicles. Samples SG34 and H7/1 from the lower portion of unit 7 yielded various forms of chondrichthyan scales (some of large sizes), teeth, a spine fragment, and actinopterygian remains. The ammonoid *Vedioceras* sp. represents the *Vedioceras* Zone of the late Dzhulfian.

From the uppermost portion of unit 7, located within beds with *Paratirolites*, sample H7/2 (two metres below the top of unit) provided chondrichthyan teeth and scales as well as a large actinopterygian jaw with teeth. Associated ammonoids, including *Paratirolites* sp., indicate a Dorashamian (Changxingian) age, which is fully consistent with earlier studies of the upper part of Hambast Formation in the Abadeh district (*e.g.*, Taraz *et al.* 1981; Kozur 2004, 2005; Richoz *et al.* 2010; Shen & Mei 2010).

Material and methods

The fossil material was cleaned and partly mechanically prepared. Some of the rock samples were etched with 8% CH_2O_2 for 24 hours. The residue was sieved by 0.063 mm to extract especially the tiny chondrichthyan scales and teeth.

A selected number of the isolated fossil elements were coated with gold/palladium using a Polaron SC7640 Sputter Coater and analysed with a Zeiss Evo LS10 SEM. Other larger elements were investigated and photographed with a Z-stepper microscope (MZ9.5) with Application suite version 2.8.1., Leica Microsystems Ltd. The reconstructions were made with the aid of Auto-Montage Essentials version 5.03.0061 ES, Synoptics Ltd.

Institutional abbreviations. – AEU – Islamic Azad University, Esfahan; MB – Museum für Naturkunde, Berlin.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880a
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Maisey, 1975
Superfamily Hybodontoidea Owen, 1846

Family Acrodontidae Casier, 1959

Genus *Acrodus* Agassiz, 1838

?*Acrodus* sp.
Figure 3A, B

Material. – Two teeth from samples SG9 and H7/2 (*Araxoceras* and *Paratirolites* zones).

Description. – These teeth have a more or less triangular crown and a high levelled principal tumid cusp (Fig. 3A1, A2). The general tooth form is symmetric with a mesial and distal wing of nearly the same dimensions. The surface of the crown shows, on the coronal aspect, an unspecific pattern of strong branching ridges and folds, which divide especially on the lingual side into numerous smaller, more delicate ridges or cristae looking like miniature lightnings (Fig. 3B). The height of the crown is little lower than the height of the base.

The crown does not practically overhang the base. The base is situated directly below the crown and is perforated with multiple foramina and pores of different size, form, and diameter of irregular distribution (spongy appearance; Fig. 3B). The smallest foramina are located on the lower third of the base. The vascularisation type of the base is anaulacorhize.

The tooth from the *Paratirolites* Zone measures 10.69 mm in length and 6 mm in height (Fig. 3B). The broken tooth from the *Araxoceras* Zone (length of crown = 5.01 mm; Fig. 3A) shows interiorly a diffuse structure suggesting histologically the presence of trabecular dentine.

Remarks. – *Acrodus* is well represented in Mesozoic strata of Europe (Cappetta 1987) – there are only few remains documented for the Palaeozoic. A clear determination of the Baghuk teeth is not possible because the number of specimens is too low and there is to date only poor information about the base morphology. Late Pennsylvanian to Early Permian remains of *Acrodus* have been described by Johnson (1981) from the Waggoner Ranch area in Texas and the Peru local fauna of Nebraska. These might belong to three different species (?*Acrodus olsoni*, ?*A. sweetlacruzensis*, and ?*A.* sp.). All possess a straight and symmetric crown. A main difference to the North American teeth is that the Iranian ones do not show a clear longitudinal crest on the crown. However, abrasive damages and also ontogenetic changes cannot be excluded. Another difference is the presence of more delicate bifurcating ridges at the lateral (lingual/labial) aspects of the crown in the Baghuk teeth. Additionally, three *Acrodus* species were reported recently from Middle Permian strata of Arizona (Hodnett *et al.* 2011).

From Europe, another *Acrodus* tooth from the latest Permian *Bellerophon* Limestone was described by Mihály & Solt (1983) as *Acrodus gaillardoti*. This fragmentary tooth is quite different to the Iranian material. The ornamentation of the labial crown side containing fine and narrow spaced ridges is rather similar to the Iranian remains but the ornamentation in general, including the occlusal aspect reveals a higher number of very fine ridges as compared to the teeth from the Baghuk Mountain. Typical younger *Acrodus gaillardoti* teeth from the upper Muschelkalk (*e.g.*, Schultze & Kriwet 1999, fig. 1b) have a low crown and no distinct cusp but a relative similar ornamentation of irregular strong branching ridges and folds like that of the Baghuk teeth.

Family Polyacrodontidae Glikman, 1964

Genus *Polyacrodus* Jaekel, 1889

?*Polyacrodus* sp.
Figure 3C, D

Material. – Two teeth from samples SG9 and H7/2 (*Araxoceras* and *Paratirolites* zones).

Description. – There are only two teeth distinguishable as belonging to the morphological same type. The first tooth from the *Araxoceras* Zone (Fig. 3C) is long and slender and has a length of 12.13 mm. The width at the principal cusp is 3.28 mm. The tooth is arcuated inwards (lingually) in occlusal view with an angle of approximately 35° to 40° and decreases distally in width (Fig. 3C1). The distal wing slopes downward (Fig. 3C2, 3). The crown is asymmetric because of a short mesial wing. There is an extremely low median ridge on the crown. A principal cusp is situated behind the first quarter of the total length and is flanked lingually and labially by a short and very shallow ridge (Fig. 3C1, 3). The cusp itself is a small, very low cone and possesses a blunt tip. An ornamentation of short, radiating and branching ridges is weakly developed and restricted to the margins of the crown. The surface of the crown is somewhat punctuate, especially at the flanks of the cusp (Fig. 3C1). The lingual margin is characterised by smooth and rounded indentations (Fig. 3C1), the strongest of which are situated in the neighbourhood of the principal cusp. The labial margin is roughly wrinkled in a small scale. The base is perforated with many foramina. On the lingual side the diameter of the foramina is different and the outline is variable (Fig. 3C2), whereas the foramina on the labial side are all more or less rounded foramina and of an even size (Fig. 3C3).

A second tooth from the *Paratirolites* Zone exposes the coronal side of the crown. The crown has a shorter distal wing and in total five indentations lingually (Fig. 3D). The ornamentation of radiating and branching ridges is here a little rougher. It is significant that lingually the ridges are mainly oriented parallel to the crown margin, and labially perpendicularly to the margin. In occlusal view this shorter tooth arcuates lingually with a lesser angle of about 15°. The length of the crown is 9.32 mm.

Remarks. – Comparable teeth to the Baghuk Mountain specimens are not known from other Permian deposits; the known late Palaeozoic species are considerably different. Similarities are seen in *Polyacrodus lapalomensis*, of which more than 4,000 teeth have been collected from Early Permian strata of Baylor County in Texas (Johnson 1981). These teeth are usually also longitudinally asymmetrical, but not to that degree reached by the Baghuk teeth (Johnson 1981, figs 84–87) and with the same tendency concerning the arcuate crown shape in occlusal view. The principal cusp is poorly developed in *Polyacrodus lapalomensis*, and another difference in this species is the persistence of a longitudinal crest, which is missing in the teeth found at Baghuk. In addition, teeth of *Polyacrodus lapalomensis* measure only up to 3.5 mm in length and the ornamentation is partly less developed.

Polyacrodus is also known from the Late Permian deposits of the East European Platform, Vologda and Moscow Districts, Tataria, and the Pre-Urals Foredeep (Minikh & Minikh 1981). Ivanov (2000) considers *Polyacrodus* as a characteristic faunal element of these occurrences.

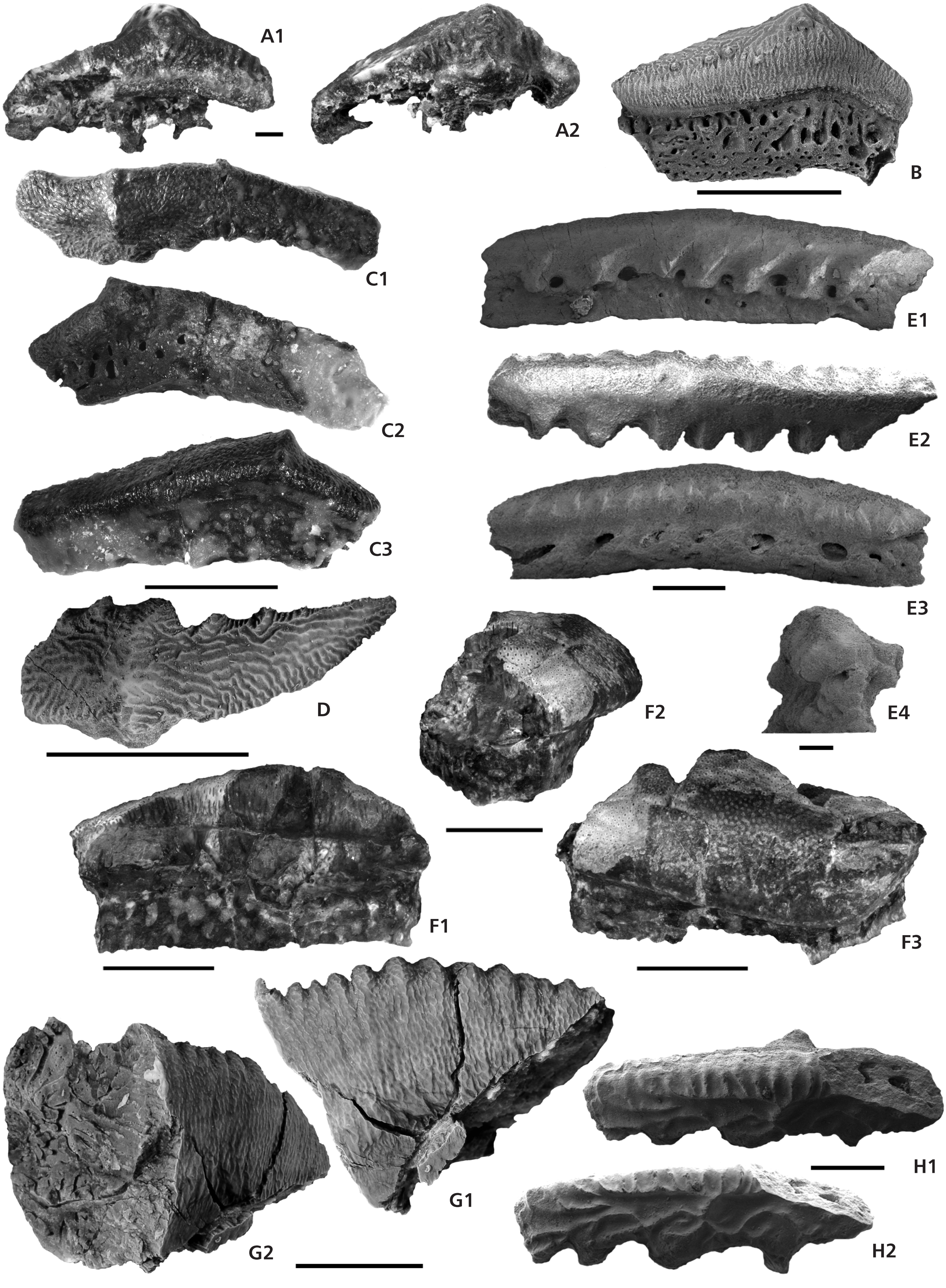
Polyacrodus was originally defined based on its tooth histology and a low coronal profile (Jaekel 1889). Later, Glikman (1964) restricted the genus only to histological orthodont forms while erecting the family Polyacrodontidae. Maisey (1987) mentioned that tooth histology alone is not a reliable character for subdividing higher leveled taxa. The difficulty recognizing *Polyacrodus* was also demonstrated by Rees & Underwoood (2002), who found no morphological synapomorphies to classify this genus. It is often a problem to distinguish isolated hybodont teeth and it cannot be excluded that the described teeth belong at least to ?*Acrodus* (heterodonty).

Despite the attribution to this hybodont taxon, there are teeth of Carboniferous to Middle Permian age that exhibit a rather similar morphology, for example, in the systematically artificial group of orodonts. Orodont-like teeth often have a low crown and a low principal cusp with a crown of partly recessive, partly strong surface sculpture (Ginter *et al.* 2010, figs 110–140). An elongated and asymmetric tooth shape is documented in the very tiny teeth of *Orodus minusculus* from the Mississippian Keokuk Limestone of Illinois (Newberry & Worthen 1866, pl. IV, fig. 11).

Other Mississippian forms referred to *Leiodus* with an asymmetrical arched tooth shape are known from deposits in USA and Belgium (Ginter *et al.* 2010, fig. 107). However, teeth of this taxon have a distinctly higher principal cusp.

Additionally, lateral teeth of the eugeneodontiform *Fadenia monscana* from Moscovian (Early Pennsylvanian) sediments of the Moscow region, Russia, are quite similar to the shape of the Baghuk teeth; these possess an asymmetric crown, marginal surface structure of short branching ridges (but only extremely weakly developed in the Russian teeth) and a single, moderately developed principal cusp (Ginter *et al.* 2010, fig. 113G–I). Lateral teeth of the younger Middle Permian *Fadenia crenulata* also shows kind of morphology with a low single cusp and asymmetric tooth shape, but less arcuated and almost no ornamentation (just punctate crown surface; Nielsen 1932, pl. 3, figs 1, 2).

Figure 3. Chondrichthyan teeth. • A – ?*Acrodus* sp., crown of MB.f. 19159 in lingual view (A1); same in labial view (A2), sample SG9. • B – AEU 801 in lingual view sample H7/2. • C, D – ?*Polyacrodus* sp., MB.f. 19173 in coronal view (C1); lingual view (C2); labial view (C3), sample SG9; AEU 802 in coronal view (D), sample H7/2. • E – *Bobbodus xerxesi* sp. nov., MB.f. 19201, in labial view (E1); coronal view (E2); lingual view (E3); mesial/distal view (E4), sample H7/1. • F – cf. *Asteracanthus* sp., MB.f. 19174 in lingual view with partly broken crown showing the vertically arranged vascular canals (F1); same in mesial view (F2); same in labial view (F3), sample SG34. • G – Chondrichthyes indet., AEU 803, element with an as yet equivocal orientation (G1); same in a 'parasagittal' view (G2), sample H7/2. • H – ?eugeneodontid indet., MB.f. 19196 in labiocoronal view (H1); in coronal view (H2), sample H7/1. Scale bars: A, E1–3, H = 500 μm; E4 = 200 μm; B–D, F, G = 5 mm.


A1
A2
B
C1
C2
C3
D
E1
E2
E3
E4
F1
F2
F3
G1
G2
H1
H2

Family incertae sedis

Genus *Asteracanthus* Agassiz, 1837

cf. *Asteracanthus* sp.
Figure 3F

Material. – One tooth from sample SG34 (*Vedioceras* Zone).

Description. – One isolated, robust tooth was found in the same facies as the miniature chondrichthyan scales described below. The tooth is relatively large and robust measuring 16.11 mm in crown length. The length of the base is 14.42 mm and the maximum width is 8.77 mm. The crown covers the base like the cap of a mushroom (Fig. 3F2). In occlusal view the crown is oval in outline and has a convex surface arching gently from the lingual to the labial side. Square-edged parts of the ?lingual side are broken away in that way that the coronal margin is not preserved (Fig. 3F1). The coronal margin of the opposite side is slightly inclined to the mesial or distal end of the tooth (Fig. 3F3). The surface of the crown is finely punctate with no evidence of striae or cristae or grooves (Fig. 3F3).

The base is relatively high and bears numerous nutrient foramina. The perforations do not describe a specific pattern and show various forms between rounded and slit-like openings.

The broken part gives an insight into the histology of the tooth (Fig. 3F1). It shows vertically arranged vascular canals opening into the crown surface, a pattern similar to the columnar trabecular ('osteo-') dentine according to Maisey (1987).

Remarks. – This is a provisional determination of a single tooth and even the systematic position of the genus *Asteracanthus* is still unclear. The dentitions presented by Peyer (1946) show similarities to the pattern known from living heterodontids, but *Asteracanthus* is usually grouped with the hybodonts (*e.g.*, Rieppel 1981). The stratigraphic distribution of *Asteracanthus* ranges from the Middle Triassic to the Late Cretaceous (Cappetta 1987).

Strong similarities are expressed with *Asteracanthus smithwoodwardi* from late Liassic strata of the canton Ticino (Peyer 1946, pl. 4) and other teeth from Switzerland. Kriwet (1995, pl. I, fig. 3) figured a broken tooth of *Asteracanthus biformatus* from the early Kimmeridgian sediments of Guimarota, Portugal; it shows a similar morphology and histological pattern consisting of columnar dentine in the peripheral regions of the crown like that in the Baghuk tooth.

Other, albeit minor, similarities occur with teeth of the holocephalian *Helodus*. Teeth with a comparable crown morphology often have a different shape of the base or the bases are oblique to the crown like the Tournaisian species *Helodus denticulatus* and *H. angulatus* from the Keokuk Limestone of Hancock County, Illinois (Newberry & Worthen 1866, pl. V, figs 6, 9). Similarities are also seen with respect to *Helodus coniculus* (Stahl 1999, fig. 52B; Ginter & Sun 2007, fig. 7B–E) from middle Tournaisian deposits of Illinois and Muhua, China. These teeth are characterised by a semi-spherical crown and a punctuated surface. However, the crowns of the American and Chinese teeth are distinctly bulbous in their centre and the vascularisation pattern of the base is different. The better preserved Muhua teeth reveal regularly arranged and more elongated foramina on the lingual side and tiny pores on the labial side of the base. Younger finds of "*Helodus*" (Bendix-Almgreen 1975, pl. 2G–S) from Artinskian deposits of NE Greenland partially show a quite different shape (probably varied jaw position). They have the thick and punctuate crown combined with a euselachian base type in common. It is important to mention that *Helodus* (Late Devonian to Early Permian; Stahl 1999) is also stratigraphically out of the range of the Baghuk Mountain specimen.

Euselachian indet.
Figure 4

Material. – One fragmentary spine from sample SG34 (*Vedioceras* Zone).

Description. – This heavily broken spine of a probable euselachian has a maximum length of 21.87 mm. There is practically no inclination visible, the spine is straight. The cross-section seems to be somewhat elliptical but the preservation does not reveal whether it is flattened laterally or anteroposteriorly. The surface of the exposed side shows an extremely weak ornamentation of fine striations in the distal half which become more distinct in the proximal half (Fig. 4). Here the striations are accompanied by delicate pores. The fragmentary spine reveals no denticulations.

Remarks. – An unequivocal determination of the spine found at Baghuk is not possible for this kind of preservation. Information about Late Permian chondrichthyan fin spines is generally low. The most important Late Permian euselachian spines are known from the German Kupferschiefer. *Wodnika striatula* also has here adenticulated spines (Schaumberg 1977, figs 6, 8) that are less inclined compared to the Iranian spine. The distal part of the *Wodnika* spine has strongly developed ribs, which is different to the spine from the Baghuk Mountain. Late Permian freshwater deposits in central Queensland, Australia uncovered the shark *Surcaudalus rostratus* that has finely ornamented fin spines consisting of a low number of vertical ribs. *Surcaudalus* spines are only gently inclined and show at the posterior side three pairs of closely spaced, barb-like denticles at the most distal portion (Leu 1989, figs 9, 10; pl. 34, figs 6, 7).

Subclass Euchondrocephali Lund & Grogan, 1997
Order Eugeneodontiformes Zangerl, 1981
Superfamily Caseodontoidea Zangerl, 1981
Family Eugeneodontidae Zangerl, 1981

Genus *Bobbodus* Zangerl, 1981

***Bobbodus xerxesi* sp. nov.**
Figure 3E

Etymology. – A tribute to famous Achaemenian king Xerxes I. who enforced the extension of Persepolis and constructed, among others, the Gate of all Nations and the Hall of a Hundred Columns, the largest and most imposing elements of the central palace there and which deeply impressed the first author.

Holotype. – MB.f. 19201, one tooth.

Type locality and horizon. – Baghuk Mountain, central Iran; sample H7/1 (*Vedioceras* Zone).

Diagnosis. – Elongated tooth morphology with regularly arranged, closely spaced, pronounced and thick triangular buttresses on the labial side; lingual side of crown with wavy margin resulting through presence of short vertical cristae that are ending at the margin; longitudinal crest probably recessive; trapezoid shape of base in mesial/distal view; large nutrient foramina alternating between the buttresses on the labial side.

Description. – The single tiny, elongated tooth with an overall length of 2.82 mm is the first evidence of the genus *Bobbodus* outside the USA. The tooth is low-crowned with seven pronounced triangular buttresses on the labial side (Fig. 3E1, 2). The buttress projections are quite regular. The tooth has a weakly preserved longitudinal crest due to abrasive processes (Fig. E2). The labial buttresses are thick in diameter. In mesial/distal view the crown shows its convex nature like a very gentle bow (Fig. E4). The lingual side has a wavy margin in occlusal view indicated by the presence of short vertical cristae (Fig. E3).

The form of the base of the tooth is trapezoidal in mesial/distal view (Fig. E4). The labial side shows large rounded nutrient foramina that alternate between the buttresses (Fig. E1). Three small apertures in a row are situated in the middle part of the base below the large foramina. The lingual side of the base has also seven large foramina in a row (Fig. E3).

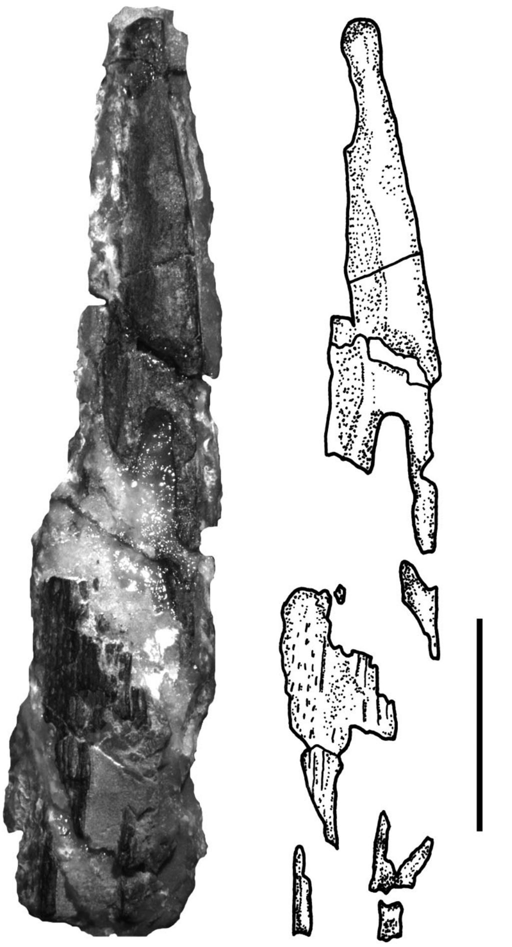


Figure 4. Euselachian indet., MB.f. 19172, fragmentary spine from sample SG34. Scale bar: 5 mm.

Remarks. – There are strong similarities to the teeth of the Late Pennsylvanian to Early Permian *Bobbodus schaefferi*, particularly in the morphology of the pavement teeth (Zangerl 1981, fig. 96; Schultze & West 1996, fig. 2). The buttresses are more pointed in *Bobbodus schaefferi* and the spaces between two buttresses appear to be larger. *Bobbodus schaefferi* is known from only three specimens (Kasimovian of Iowa, Gzhelian of Nebraska, Asselian of Kansas) consisting exclusively of jaw elements (Schultze & West 1996) and are characterised by the presence of about 12 symphyseal teeth in the lower jaw and probably over 200 pavement teeth in one quadrant.

There are also similarities to *Eugeneodus richardsoni* from the Early Pennsylvanian (Moscovian) of Indiana. However, the buttresses of *Bobbodus xerxesi* are more regularly arranged than in *E. richardsoni* (Ginter *et al.* 2010, fig. 115A).

The general bauplan of the pavement tooth is also present in *Caseodus*, known from Early Pennsylvanian (Moscovian) rocks of Illinois and Indiana and Early Triassic (?Induan) strata of British Columbia. However, *Caseodus* teeth possess distinct crenulations on both the lingual and labial sides of the crown, and a strong ornamentation of ridges (Mutter & Neuman 2008, fig. 6; Ginter *et al.* 2010, fig. 109).

?Eugeneodontid indet.
Figure 3H

Material. – One tooth from sample H7/1 (*Vedioceras* Zone).

Description. – There is a tooth (2.67 mm long) with a tumid crown and four buttress-like structures on one side of the crown which act as an indicator for eugeneodontid affiliation. The crown surface is ornamented with distinct but smooth wavy ridges (Fig. 3H2). There is one low elevation in the centre of the crown from which the ridges originate. Opposite to the side containing the buttresses, the crown margin has short vertical cristae, which branch off, tree-like, from the closest of the strong ridges (Fig. 3H1). The base shows a peg-like structure on the other side (Fig. 3H1). No foramina are positioned on that side of the base.

A sagittal breakage on one wing of the crown exhibits lacunae within the tooth, which probably represent a divided pulp cavity (Fig. 3H1).

Remarks. – No comparative elements are known so far. A naming and diagnosis of a new taxon is not useful at this stage, also because of the existence of only a single tooth.

Chondrichthyes indet.
Figure 3G

Material. – One tooth from sample H7/2 (*Paratirolites* Zone).

Description. – This element has a very unusual morphology such that its orientation cannot be determined with certainty. It has a high crown ornamented by numerous, mostly bifurcating, coarse vertical cristae. They form a network similar to a honeycomb pattern at the labial (?lingual) side (Fig. 3G1). There are 13 triangular, short cusps of subequal sizes; the largest cusps in the middle of the row. A lower part of the tooth is broken away. The break line is diagonal to the crown surface containing the cusps. The naturally preserved vertical section at the opposite side of the break reveals the shape of the crown (Fig. 3G2): there is a shallow, rather wide median groove at the top, flanked by the row(s) of blunt cusps standing at the probable mesiodistally elongated edges of the crown. However, the presumptive opposite side of the groove is not exposed but hidden in the rock. It is not known if there was a second row of small cusps adjacent to the groove. The structure of the section does not explain if there may be simply two teeth, coalesced together or if it is a single solid item. The length of this element is 11.92 mm; its maximum width reaches 12.7 mm.

Remarks. – Golshani & Janvier (1974, figs $4A_1$ and A_2) presented something similar from Late Permian strata of Abadeh, which they related to *Megactenopetalus.* However, the petalodontiform *Megactenopetalus* differs considerably from both the teeth of Abadeh and the Baghuk Mountain (Ossian 1976, pl. 1; Ginter *et al.* 2010, fig. 134). The tooth fragment from Abadeh is additionally quite different from the Baghuk element. It reveals a laterally compressed base. Such base-like structure cannot be identified for the Baghuk tooth. There is also no ornamentation documented at the crown of the Abadeh tooth. The serrated crest of the Abadeh tooth is reminiscent of that seen in Mississippian species of *Petalorynchus* (here *P. beargulchensis*, Lund 1989, fig. 14). Until now, comparative elements like the here described Baghuk tooth are unknown.

Dermal denticles

Chondrichthyan denticles have been collected from the samples SG34, SG9, and H7/1. Nearly all of them possess a crown that is long and comparatively thin. Denticles with fundamentally different proportions of the crown are very rare. Many specimens show a complex crown morphology. Spines are a common element of ornamentation and found on denticles of every sample. The samples contain different denticle types. Sample SG9 has yielded numerous denticles which show a high degree of variation concerning the crown morphology. All denticles show a concave base. Growth lines have been observed on the bottom surface of the base of some specimens. A low number of dermal denticles have been extracted from sample H7/1. They have dimensions similar to the denticles from sample SG9 and also a concave base. Denticles collected from SG34 are distinctly larger than any specimen from the samples of other horizons. Their base is convex or plane, but never as concave as in the specimens from the other samples.

The denticles are here attributed to morphotypes and the definition of the morphotypes is particularly based on crown morphology. Specimens that are not sufficiently preserved are not considered here. Histological characters are difficult to evaluate because most of the denticles are small and fragile, such that thin sections cannot be prepared. Denticles from SG34 were sectioned but did not preserve histological characters. The characters of the base do not influence the definition of the morphotypes because in many specimens the base is either incompletely preserved or covered with fine-grained sediment that makes it impossible to examine it in detail.

The number of specimens belonging to a given morphotype is presented by semi-quantitative categories. A morphotype is considered to be common if ten or more denticles occurred. Two to nine denticles of a morphotype are qualified as rare. A morphotype that is defined only by one denticle is labelled as a single specimen. One has to be aware that dermal denticles with a fragile crown might become more easily damaged and could thus be numerically underrepresented.

Morphotype I
Figure 5A–C

Material. – Common in sample SG9 (*Araxoceras* Zone).

Description. – The crown of this type of denticle is comparatively narrow, bends in a posterior direction and projects from the base considerably (Fig. 5A2). In some specimens there are a few unidentified openings in the lower subcrown. A kind of mesial platform is developed (*sensu* Johns 1996, text-fig. 1). It is prominent in most of the specimens in the anterior part of the upper crown and runs into one or two spine-bearing keels (Fig. 5A1, B1, C). Large spines are arranged along the crown margin. There is no distinct principal cusp developed. The subcrown does not show any kind of linear ornamentation, but some specimens have spines on the posterior part of the subcrown (Fig. 5B3).

Morphotype II
Figure 5D

Material. – Common in sample SG9 (*Araxoceras* Zone).

Description. – Type II denticles have a crown that bends in a posterior direction and projects from the base. The crown is usually broader compared to specimens of morphotype I and lacks any kind of prominent mesial structure. Spines are absent or extremely rare. The ornamentation consists of vertically oriented ridges, which furcate rarely (Fig. 5D1, 2). The apical half of the upper crown is smooth (Fig. 5D1). It is unclear whether this is an original character or a result of abrasion. The subcrown is smooth.

Morphotype III
Figure 5E

Material. – Rare in sample SG9 (*Araxoceras* Zone).

Description. – Dermal denticles of this type resembles specimens of morphotype II or morphotype I in their general morphology. There is no mesial platform developed. The ornamentation pattern is similar to specimens of morphotype II, except that the ridges cover the whole upper crown. Spines are absent or rare on the upper crown, but well-developed at the posterior crown margin. The subcrown is smooth.

Morphotype IV
Figure 5F

Material. – Single specimen from sample SG9 (*Araxoceras* Zone).

Description. – This specimen appears like two incompletely fused dermal denticles (Fig. 5F1, 2). The anterior part of the crown forms a broad and short cusp and a small and long cusp (Fig. 5F1). The latter is fused to the posterior part of the crown. The posterior part of the crown indicates a division into three cusps. The crown is ornamented with spine-bearing keels. The lower subcrown of both parts of the specimen shows many foramina.

Morphotype V
Figure 5G

Material. – Rare in sample SG9 (*Araxoceras* Zone).

Description. – Specimens which belong to this morphotype have a broad crown that bends in a posterior direction and projects from the base (Fig. 5G2, 4). The crown of the well-preserved specimen MB.f. 19181 is asymmetrically shaped because its lateral faces are unequally well developed (Fig. 5G1). A mesial platform bearing large keels is present. The size of the keels decreases posteriorly and they are hardly perceptible close to the posterior crown margin. Each keel is covered with a row of spines. Additional spines are situated along the crown margin (Fig. 5G1–3). One of them is distinctly larger and more prominent than the other spines. A single spine at the most basal part of the crown is very prominent.

Morphotype VI
Figure 5H

Material. – Rare in sample SG9 (*Araxoceras* Zone).

Description. – Denticles of this type have a nearly straight crown (Fig. 5H3). A mesial platform is developed. Platform and the lateral wings show keels that are equipped

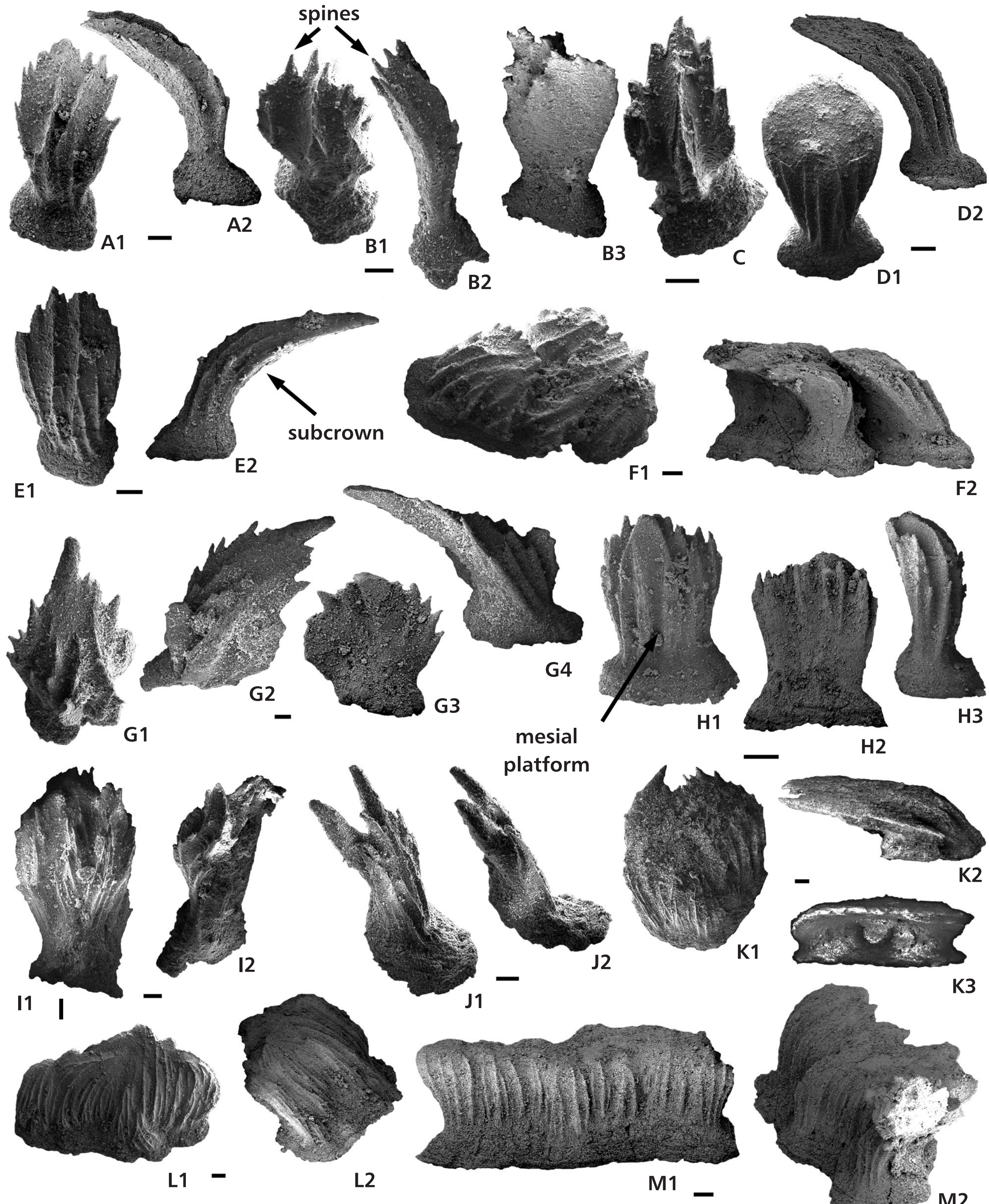
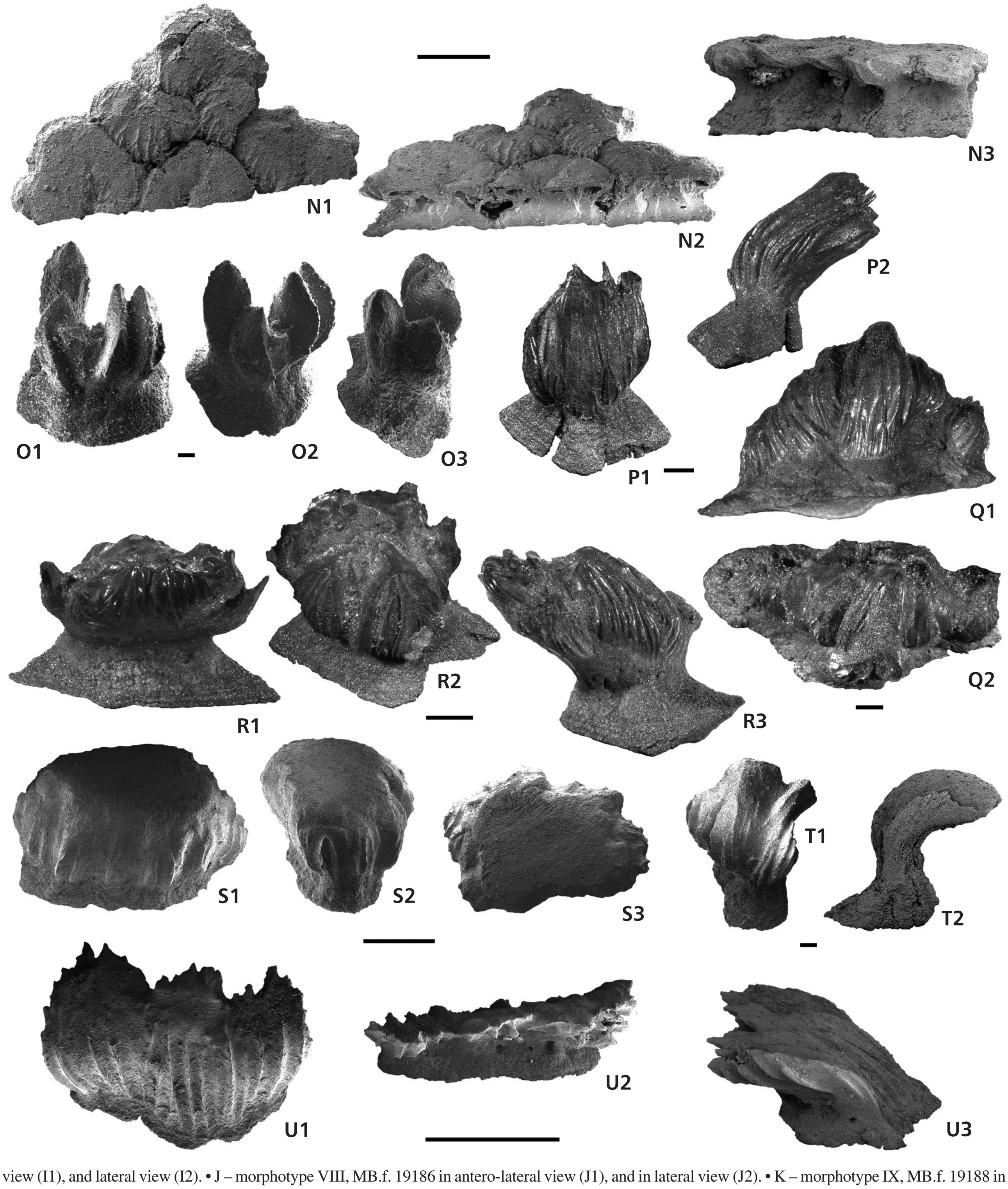


Figure 5. Chondrichthyan denticles. • A–C – morphotype I, MB.f. 19177 in anterior view (A1), same in lateral view (A2); MB.f. 19184 in anterior view (B1), same in lateral view (B2), and posterior view (B3); MB.f. 19183 in anterior view (C). • D – morphotype II, MB.f. 19214 in antero-apical view (D1), and lateral view (D2). • E – morphotype III, MB.f. 19176 in anterior view (E1), same in lateral view (E2). • F – morphotype IV, MB.f. 19190 in apical view (F1); same in lateral view (F2). • G – morphotype V, MB.f. 19181 in antero-apical view (G1), in an oblique view (G2), in posterior view (G3), and in lateral view (G4). • H – morphotype VI, MB.f. 19178, in anterior view (H1), in posterior view (H2), and lateral view (H3). • I – morphotype VII, MB.f. 19185 in anterior



view (I1), and lateral view (I2). • J – morphotype VIII, MB.f. 19186 in antero-lateral view (J1), and in lateral view (J2). • K – morphotype IX, MB.f. 19188 in apical view (K1), in lateral view (K2), and posterior view (K3). • L – morphotype X, MB.f. 19216 in anterior view (L1), and lateral view (L2). • M – morphotype XI, MB.f. 19215 in anterior view (M1), and antero-lateral view (M2). • N – morphotype XII, MB.f. 19189 in apical view (N1), in posterior view (N2), and in an oblique lateral view (N3). • O – morphotype XIII, MB.f. 19175 in anterior view (O1), in oblique view (O2), and apical view (O3). • P – morphotype XIV, MB.f. 19156 in antero-apical view (P1), and lateral view (P2). • Q – morphotype XV, MB.f. 19155 in anterior view (Q1), and apical view (Q2). • R – morphotype XVI, MB.f. 19158 in posterior view (R1), apical view (R2), and lateral view (R3). • S – morphotype XVII, MB.f. 19197 in ?anterior view (S1), in ?lateral view (S2), and apical view (S3). • T – morphotype XVIII, MB.f. 19203 in apical view (T1), and lateral view (T2). • U – morphotype XIX, MB.f. 19205 in apical view (U1), posterior view (U2), and lateral view (U3). Morphotypes I–XIII = sample SG9; morphotypes XIV–XVI = sample SG34; morphotypes XVII–XIX = sample H7/1. Scale bars: A–M, O, T = 100 μm; N, P–S, U = 500 μm.

with tiny spines (Fig. 5H1, 2). Spines at the posterior crown margin correspond to the pointed endings of keels, which originate on the crown and subcrown (Fig. 5H2).

Morphotype VII
Figure 5I

Material. – Rare in sample SG9 (*Araxoceras* Zone).

Description. – Specimen MB.f. 19185 is slightly damaged at the apical crown margin. The crown is roughly oriented vertically. The subcrown is concave. It is a distinct character of this morphotype that approximately one half of the upper crown forms a very prominent projection. The ornamentation consists of spine-bearing keels on the upper crown, the posterior part of the subcrown, and of spines at the posterior crown margin (Fig. 5I2). The keels on the projection show an orientation which differs slightly from that of the keels on the remaining part of the upper crown. The subcrown is concave. It is limited by a strong keel on one of its lateral faces.

Morphotype VIII
Figure 5J

Material. – Single specimen from sample SG9 (*Araxoceras* Zone).

Description. – The crown is thin and narrow. A substantial part of the crown is made up of two large spines (Fig. 5J1, 2). Further spines, being comparatively smaller, are situated at the posterior crown margin. The upper crown is ornamented with vertical ridges. The subcrown is smooth.

Morphotype IX
Figure 5K

Material. – Single specimen from sample SG9 (*Araxoceras* Zone).

Description. – The crown of this specimen is thin, strongly curved posteriorly and projects from the base considerably (Fig. 5K2). The posterior crown margin shows a convex incision (Fig. 5K1). Spines at the margin of the incision show that this structure is not the result of damage. A number of basally furcating vertical ridges is present on the anterior upper crown (Fig. 5K1). The central and the posterior upper crown are nearly plane and smooth, apparently because of abrasion. The subcrown does not show ornamentation. There is a large depression in the centre of the posterior base (Fig. 5K3). The subcrown contributes to the depression.

Morphotype X
Figure 5L

Material. – Rare in sample SG9 (*Araxoceras* Zone).

Description. – The crown of this morphotype resembles that of specimen MB.f. 19188 (morphotype IX) in its general shape, but is comparatively broader and lacks an incision at the crown margin. In some specimens the posterior crown margin is pointed, but a distinct spine is not developed. The ornamentation consists of furcating ridges (Fig. 5L1). The ridges are vertically oriented on the central part of the upper crown. In MB.f. 19216 they bend posteriorly in the direction of the central posterior crown margin (Fig. 5L1). The surface of the subcrown is smooth. The posterior denticle does not show a depression.

Morphotype XI
Figure 5M

Material. – Common in sample SG9 (*Araxoceras* Zone).

Description. – Denticles of this type are more elongate in comparison to representatives of other morphotypes described in this paper. The crown has a common shape and is thin and strongly curved posteriorly (Fig. 5M2). The anterior crown projects regularly as seen in specimen MB.f. 19215. The projections correspond to the posterior crown margin in a way such that the margin is incised between the projections. The anterior upper crown is ornamented with vertical ridges which furcate occasionally (Fig. 5M1). They are not distinct on the posterior part of the upper crown, probably because of abrasion (Fig. 5M1, 2). The subcrown is smooth.

Morphotype XII
Figure 5N

Material. – Single specimen from sample SG9 (*Araxoceras* Zone).

Description. – The fragmentarily preserved dermal denticle has a morphology which is unusual among other specimens described here. The specimen is flat and its outline is irregular in apical view (Fig. 5N1). The preserved part of the specimen appears as if it is composed of about five or six fused elements. The crowns of these elements are separated from each other by grooves (Fig. 5N1, 2). Their surface is smooth or covered with furcating ridges. The ridges of one element do not extend onto adjacent elements. Further ridges or keels are present on the crown margins and subcrowns (Fig. 5N3).

Morphotype XIII
Figure 5O

Material. – Single specimen from sample SG9 (*Araxoceras* Zone).

Description. – The crown of this specimen is damaged, but it is still obvious that it differs fundamentally from all of the other dermal denticles described here. It is slightly curved in posterior direction and overhangs the base moderately. The most conspicuous character of this specimen is that its crown is predominantly composed of five large and prominent projections (Fig. 5O1–3). One of the projections is seriously damaged and represented only by its basal part. Four projections are situated in a row. The fifth projection is situated posterior to the row. Morphotype XIII does not show ornamentation. The lower subcrown has a deep depression.

Morphotype XIV
Figure 5P

Material. – Common in sample SG34 (*Vedioceras* Zone).

Description. – The vast majority of dermal denticles from sample SG34 belong to this morphotype. The denticles have a thick, posteriorly curved crown (Fig. 5P2). The crown proportions vary, especially the ratio of length to height. The surface of the upper crown is divided into different portions which are covered with ridges (Fig. 5P1). The posterior crown margin shows many projections and spines of different size. The subcrown shows large foramina on its lower part. Ridges have rarely been observed here.

Morphotype XV
Figure 5Q

Material. – Rare in sample SG34 (*Vedioceras* Zone).

Description. – These denticles are distinctly broader than denticles of morphotype XIV. The crown ornamentation of morphotype XV corresponds to that of other denticles of this horizon. The upper crown is divided into vertically or roughly vertical-oriented portions which are covered with keels, ridges and lines (Fig. 5Q1). The posterior crown margin is very high in specimen MB.f. 19155 (Fig. 5Q2).

Morphotype XVI
Figure 5R

Material. – Single specimen from sample SG34 (*Vedioceras* Zone).

Description. – Specimen MB.f. 19158 is similar to other specimens from this sample. Its most distinctive character is the extremely deep posterior crown (Fig. 5R1). The posterior upper crown is incised and shows some spines (Fig. 5R3). Additional spines and many projections are located on the posterior crown margin and the subcrown. The lower subcrown shows vertical ridges that are comparatively stronger than in representatives of morphotype XIV. There are also large foramina present.

Morphotype XVII
Figure 5S

Material. – Single specimen from sample H7/1 (*Vedioceras* Zone).

Description. – This dermal denticle has a very distinctive shape (Fig. 5S2). The crown is bulbous and has an irregular outline in apical view (Fig. 5S3). The posteriormost portion of the crown is missing, probably because of abrasion. Weakly developed lobes are present. They are covered with ridges (Fig. 5S1, 3).

Morphotype XVIII
Figure 5T

Material. – Single specimen from sample H7/1 (*Vedioceras* Zone).

Description. – This morphotype has a broad, posteriorly curved crown that projects from the base considerably (Fig. 5T1, 2). The posterior area of the crown is damaged. A mesial platform is developed and bordered by lateral wings (Fig. 5T1). The ornamentation consists of vertical ridges. The subcrown shows a few ridges at the margin of a lateral wing.

Morphotype XIX
Figure 5U

Material. – Single specimen from sample H7/1 (*Vedioceras* Zone).

Description. – This specimen has a broad and thin crown (Fig. 5U2) which is strongly curved posteriorly (Fig. 5U3). The posterior crown margin is divided into three portions (Fig. 5U1). The upper crown is ornamented with keels, except for the posterior part which appears to be abraded (Fig. 5U1). Most of the keels are vertically oriented, but they are slightly oblique in that direction close to a lateral crown margin. Some of the ridges have fine lines on them. The subcrown shows keels which do not have any lines. Spines are present on the posterior crown margin (Fig. 5U1–3).

Remarks. – A comparison of the denticles described above shows that the samples yielded different denticle types. Denticles which are attributed to neoselachian sharks by some authors are not represented (*e.g.*, Ivanov 2005, fig. 4; Fischer *et al.* 2010, pp. 252, 253).

It is obvious that denticles from sample SG34 can be easily distinguished from denticles belonging to samples SG9 and H7/1. They have different dimensions and a differently shaped base that does not show growth lines. There are minor differences between the specimens from SG34 themselves so that it seems possible that they belong to a single species. Moreover, all of them are from the same slab and could even belong to the same individual. Denticles from sample SG9 show a high morphological variation. Some specimens exhibit growth lines; according to Reif (1978, pp. 112, 113, 117) the presence of growth lines distinguishes denticles of a ctenacanthid scale type from denticles of a hybodontid scale type. A closer identification is hindered by the general problem of assigning an isolated dermal denticle to a genus or even a particular body area. As a consequence, it is not possible to provide a meaningful statement on the taxonomical diversity represented by sample SG9. There are not enough specimens from sample H7/1 to discuss the diversity of dermal denticles from this horizon.

Dermal bone fragments of "Palaeonisciformes"

Although the term "Palaeonisciformes" does not refer to a natural grouping, but represents instead a paraphyletic assemblage of Palaeozoic and Mesozoic basal actinopterygians, it is used here as a descriptive standpoint. The following bone fragments are assigned to this group on the basis of the dermal sculpture and the presence of the tooth caps of acrodine where teeth are preserved.

Class Osteichthyes Huxley, 1880b
Subclass Actinopterygii Cope, 1871

"Palaeonisciformes" indet.
Figure 6A

Material. – Fragment of mandible from sample SG9 (*Araxoceras* Zone).

Description. – The specimen is an approximately 9 mm long fragment of a mandible. The bone is preserved in external (labial) view and slightly convex externally. Because most of the original bone surface was lost by horizontal splitting, the middle layer of the bone is exposed and a number of vascular canals are visible which run through the bone in a longitudinal direction. Near the ventral margin, a distinctly larger, longitudinal canal is visible that is filled with white calcite matrix. This canal can be interpreted as the mandibular line of the lateral line canal system. The original bone surface is partially preserved near the ventral margin of the bone; the dermal sculpture consists of rounded tubercles at least in this part of the bone. Five nearly complete, cone-like teeth are preserved, one of which bears a cap of acrodine. Apart from this, several broken teeth and tooth bases with large pulp cavities are visible. The dorsal margin is slightly concave at the posterior end of the bone (on the left in Fig. 6A), such that the bone increases slightly in depth.

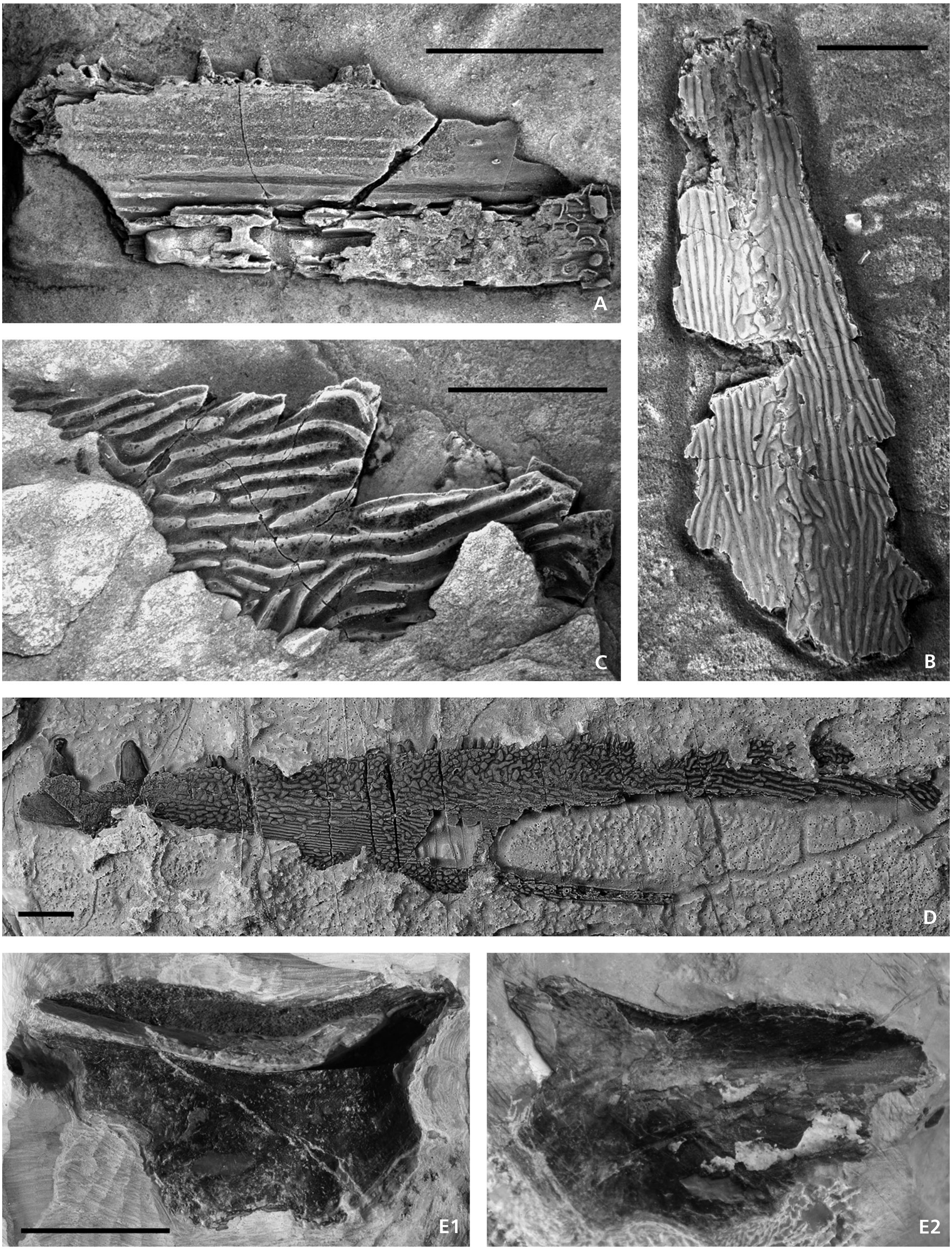
Remarks. – The lateral line canal within the bone fragment in question indicates that it belongs to a mandible and not to a maxilla. However, preservation is too poor to assign it to a genus or family.

"Palaeonisciformes" indet.
Figure 6B

Material. – Element of pectoral girdle, probably supracleithrum from sample SG34 (*Vedioceras* Zone).

Description. – This is a flattened, elongated bone fragment of approximately 18 mm in length, which is exposed in external view and bears pronounced dermal sculpture. The width of the bone narrows from approximately 6 mm near the one end to less than 3 mm at the other end, thus having the outline of a blunt cone. Although the margins of the

Figure 6. Dermal bone fragments of Osteichthyes. • A–D – "Palaeonisciformes" indet. • A – MB.f. 19161, fragment of dentary exposed in external labial view, with most of the original bone surface lost by horizontal splitting; it shows complete teeth with caps of acrodine and several tooth bases, sample SG9. • B – MB.f. 19164, flattened bone of the dermal pectoral girdle, probably a supracleithrum, showing dermal sculpture of broad, subparallel ridges that may bifurcate, sample SG34. • C – MB.f. 19163, dermal bone fragment with dermal ornament similar to B; poor preservation precludes determination of the bone, sample SG34. • D – AEU 805, almost complete left mandibular ramus in external (labial) view with strong dermal sculpture; two large anterior teeth are present, some of the posteriorly following small teeth display an acrodine cap, sample H7/2. • E – Osteichthyes indet., MB.f. 19160, plate-like bone of irregular outline that might represent a part of the palatoquadrate; on side (E1) bears a sharp, curved crest, whereas the other side (E2) is rather smooth, sample H7/1. Scale bars: 3 mm.


A
B
C
D
E1
E2

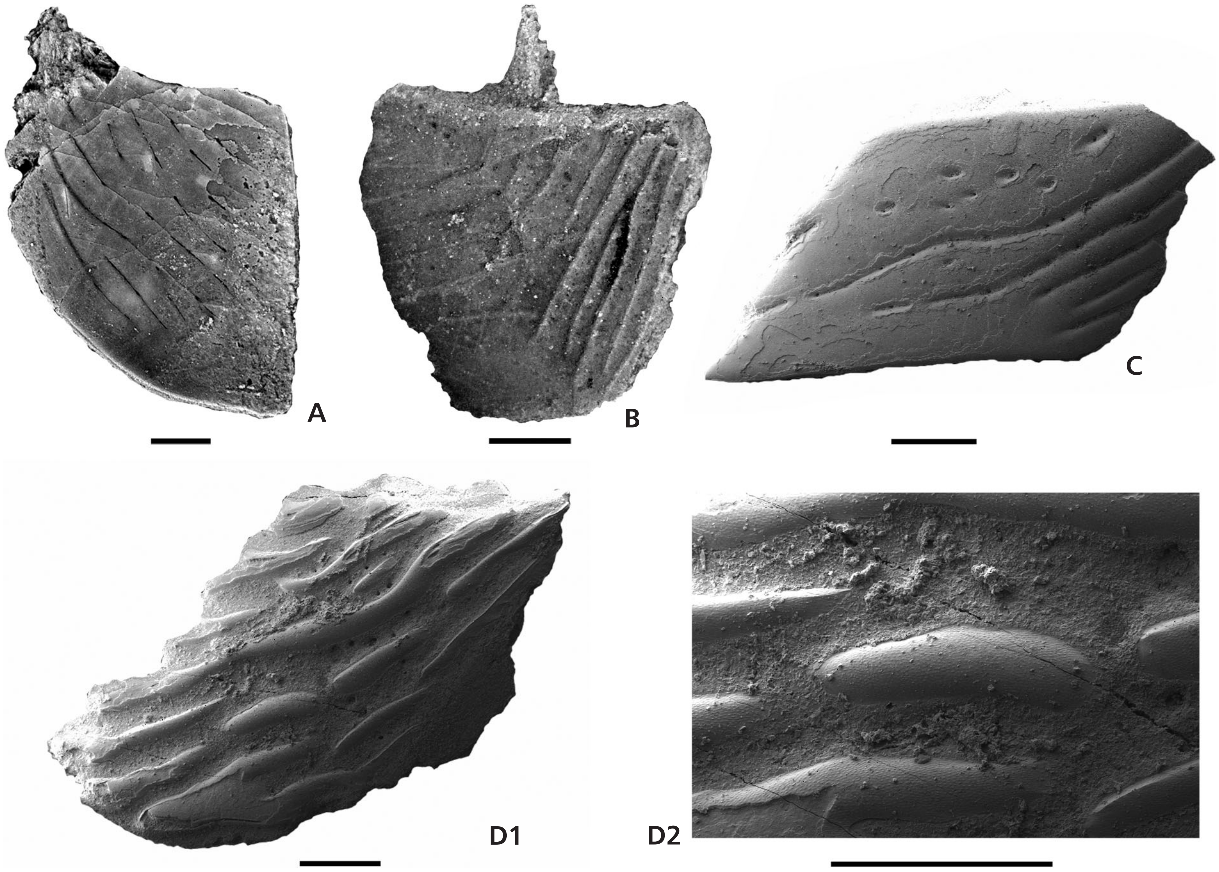


Figure 7. Rhomboid dermal scales of different "Palaeonisciformes" in external view. • A – morphotype I, MB.f. 19169, the dermal sculpture of the external surface resembles that of cheirolepiforms of the Russian Permian, sample SG34. • B – morphotype II, MB.f. 19168, sample SG34. • C – morphotype III, MB.f. 19198, the dermal sculpture of the external surface resembles that of Permian elonichthyiforms from Russia, sample H7/1. • D – morphotype IV, MB.f. 19199, the dermal sculpture of the external surface resembles that of Permian cheirolepiforms from Russia; complete scale (D1); close up (D2), showing the surface of the ridges that consists of numerous tiny tubercles, sample H7/1. Scale bars = 500 μm.

bone are broken, this outline approaches probably the original shape of the bone, since the sculptural ridges run parallel to the long margins of the specimen (Fig. 6B). The bone surface is externally slightly convex or roof-shaped and sculptured with broad, subparallel ridges that may bifurcate. In the midline of the bone, the sculptural ridges are conspicuously broader and discontinuous, thus forming irregular patches.

Remarks. – This bone is probably derived from the dermal pectoral girdle and most likely represents a supracleithrum. However, because of the absence of distinctive characters, assignment to a genus or family is not possible.

"Palaeonisciformes" indet.
Figure 6C

Material. – Fragment of sculptured dermal bone from sample SG34 (*Vedioceras* Zone).

Description. – This is a further dermal bone fragment bearing pronounced dermal sculpture of ridges and furrows, similar to the probable supracleithrum described above.

Remarks. – Poor preservation precludes determination of this bone fragment.

"Palaeonisciformes" indet.
Figure 6D

Material. – Almost complete left ramus of lower jaw from sample H7/2 (*Paratirolites* Zone).

Description. – This specimen is an almost complete left mandibular ramus in external (labial) view. The preserved part measures approximately 60 mm in length. It attains its greatest depth of slightly more than 10 mm in its posterior half and tapers distinctly towards the anterior end. The anterior portion bears two large, conical teeth with blunt peaks, whereas the teeth following posteriorly are distinctly smaller and more pointed (Fig. 6D). Some of them display an acrodine cap. Their number cannot be counted because of poor preservation, but there was space for more than 60 teeth present. The external bone surface bears strong dermal sculpture. Near the dorsal margin, the dermal sculpture is composed of tubercles that are irregular in outline and size. More ventrally, sculpture consists of longitudinally-oriented, parallel ridges and grooves (at least in the middle part of the bone, whereas large parts of original bone substance are missing in the anterior and especially posterior part). In the ventral part of the bone, the sculpture consists again of irregular tuberculation.

Remarks. – Assignment to a genus or family is not possible because of the absence of distinctive characters.

Rhombic scale morphotype I
Figure 7A

Material. – Single specimen from sample SG34 (*Vedioceras* Zone).

Description. – This scale has a straight ?posterior margin, whereas the ?anteroventral edge is clearly convex. The dorsal edge is straight and bears a broad-based dorsal peg in its ?anterior half. The scale is exposed in external view, showing a sculpture of narrow grooves on the otherwise smooth surface, extending from tiny pores towards the ?posterior margin (Fig. 7A).

Remarks. – The dermal sculpture of this scale resembles most closely that of the scales of cheirolepiforms *sensu* Minikh & Minikh (2009) from Permian strata in Russia, such as *Kazanichthys* (Minikh & Minikh 2009, pl. 3).

Rhombic scale morphotype II
Figure 7B

Material. – Single specimen from sample SG34 (*Vedioceras* Zone).

Description. – This nearly shovel-shaped scale has a slender dorsal peg in the middle part of its straight dorsal margin. The anterior and posterior margins converge towards each other in a ventral direction, such that the slightly convex ventral margin is distinctly shorter than the dorsal one. In the posterior half of the scale, the ornamentation of the external surface consists of narrow crests aligned parallel to the posterior margin, whereas the crests in the anterior half are aligned perpendicular to the anterior margin (Fig. 7B). The crests of the anterior and posterior portion of the scale intersect in the middle part of the scale.

Remarks. – In the absence of distinct characters, this scale is designated as "Palaeonisciformes" indet.

Rhombic scale morphotype III
Figure 7C

Material. – Single specimen from sample H7/1 (*Vedioceras* Zone).

Description. – This scale is longer than high, and a dorsal peg is not developed. The external surface is generally smooth, with scattered pores in the ?anterodorsal part and diagonally arranged, curved grooves in the ?posteroventral part, extending towards the slightly serrated ?posterior margin.

Remarks. – Dermal sculpture of this scale is quite similar to that of the scales of Permian elonichthyiforms *sensu* Minikh & Minikh (2009) from Russia such as *Alilepis* (Minikh & Minikh 2009, pl. 12). However, the scales of *Alilepis* often bear a distinct sculpture of rows of triangular tubercles at the anterior margin. These tubercles are not present in the Baghuk scale. A scale of similar outline and sculpture from Early Permian strata of Kansas, USA, was described and illustrated by Schultze (1985, fig. 7.1) and referred to as indetermined "palaeoniscoid".

Rhombic scale morphotype IV
Figure 7D

Material. – Single specimen from sample H7/1 (*Vedioceras* Zone).

Description. – The margins of this scale are partially broken off; however, the dorsal margin appears to be straight and the ventral margin convex. A dorsal peg is not developed. The dermal sculpture of the external surface consists of diagonally arranged, discontinuous broad ridges. Several pores are visible in the depressed areas between the ridges (Fig. 7D1). The surface of the ridges itself shows numerous tiny tubercles (Fig. 7D2).

Remarks. – The dermal sculpture resembles that of Permian cheirolepiforms *sensu* Minikh & Minikh (2009) from Russia such as *Samarichthys* (Minikh & Minikh 2009, pl. 7). Schultze (1985, fig. 7.8) described and illustrated a scale of an undetermined "palaeoniscoid" from Early Permian strata in Kansas, USA, having a similar dermal sculpture of discontinuous ridges and perforated depressed areas.

?Osteichthyes indet.
Figure 6E

Material. – Large, plate-like bone with conspicuous crest from sample H7/1 (*Vedioceras* Zone).

Description. – This is a comparatively large but very thin, plate-like bone of irregular outline, bearing a conspicuous crest (Fig. 6E1). The greatest length of the bone measures 45 mm, its greatest width is 26 mm. The sharp, curved crest divides the bone into two parts of unequal size. The larger part has more than three times the width of the smaller one and is concave in its central portion. The smaller part descends from the crest towards its outer margin. Together with the margin of the curved crest, the smaller part forms a continuous, concave lamina. The surface of the bone is generally smooth, but may be slightly roughened where the original bone surface is somewhat eroded.

Remarks. – The identity of this bone is not clear. The fact, however, that this plate-like bone is not sculptured but has instead a smooth surface indicates that it is not derived from the dermal skull roof, opercular apparatus or dermal pectoral girdle, but could rather represent a part of the palatoquadrate. In the absence of distinctive characters it cannot be assigned to either actinopterygians or sarcopterygians. It is best to designate it simply as Osteichthyes indet.

Concluding remarks

Late Permian chondrichthyan and actinopterygian assemblages from Baghuk Mountain (central Iran) represent a relatively deep shelf habitat, below the storm wave base. The lithology of the fish-bearing Hambast Formation consists of grey to red micritic limestone, which is widely exposed in the Shahreza-Abadeh belt. The fossil content is dominated by pelagic fossil organisms, such as nautiloids, ammonoids, and conodonts (Heydari *et al.* 2003, Richoz *et al.* 2010). Well-oxygenated bottom water conditions, without any signs of dramatic sea level change, is inferred from lithological characters (Heydari *et al.* 2003, Richoz *et al.* 2010) and confirmed by the occurrence of benthic ostracods (Kozur 2007).

Only a few chondrichthyan teeth could be extracted so far from the Baghuk Mountain. The assemblage consists mainly of hybodontiform and eugeneodontiform crushing teeth. There are only a handful of records of Middle and Late Permian chondrichthyan assemblages with a similar faunal content. A shark fauna comprising predominantly crushing teeth (*Polyacrodus* and *Lissodus*-type; not described in detail yet) is documented from the Wordian (Middle Permian) Khuff Formation of Oman (Tintori 1998). The Khuff Formation comprises shallow marine deposits with sandstones, marls and shell-beds and is interpreted as recording a major transgression of Neotethyan waters at a stage of full oceanisation (Angiolini *et al.* 2003). Older deposits around this area reveal a more diverse aquatic fauna like the Early Permian Gharif Formation of Oman, whose vertebrate fauna is not dominated by hard-shell feeders giving here a mixed signal for the palaeoenvironment. In agreement with the sedimentological data all collected vertebrate taxa are documented from both marine and freshwater deposits (Schultze *et al.* 2008). The faunal development was influenced by the increasing transgression respectively the extension of the Palaeo-Tethys Ocean. It can generally be observed that Middle and Late Permian chondrichthyans are less diverse than in the Early Permian (*e.g.*, Malysheva *et al.* 2000, Ivanov 2005). Hybodontoids strongly predominate in the shark assemblages of Middle and Late Permian age, of which several genera survived the Permo-Triassic biotic crisis and became distributed worldwide in the Mesozoic.

The eugeneodontid *Bobbodus* was known so far from the east coastal region of the Panthalassic Ocean (Nebraska, Iowa, Kansas) during the Late Pennsylvanian and Early Permian (Zangerl 1981, Schultze & West 1996), but spread out later to the area of the Palaeo-Tethys Ocean and to offshore environments of the southern hemisphere.

The scales of the Baghuk actinopterygians ("Palaeonisciformes" indet.) show close similarities to actinopterygian remains from Kansas (east coast of Panthalassic Ocean) and the Russian Platform (cheirolepiforms and elonichthyforms). Still, their taxonomic relationships are questionable since convergent development of similar sculptural patterns of dermal bones and scales cannot be excluded.

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