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Famennian chondrichthyans from the shelves of North Gondwana

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ABSTRACT:

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Ichthyoliths, mainly shark teeth, from the Famennian of Iran and Northwest Africa are described. Evolution of shallow-water chondrichthyan assemblages on the shelves of Central Iran and the Tafilalt Platform, Morocco, related to time and environmental changes, is discussed. Four new taxa, viz. *Deihim mansureae* gen. et sp. nov., *Protacrodus serra* sp. nov., *Phoebodus depressus* sp. nov., and *Ph. gothicus transitans* subsp. nov. are erected and provisional reconstructions of heterodonty in dentitions of several Famennian sharks are proposed.

Key words: Chondrichthyes, Famennian, Palaeoecology, Dentition, North Gondwana

INTRODUCTION (M.G.)

Rich and partially previously undescribed occurrences of Famennian chondrichthyan microremains from the Tafilalt Platform in Morocco, from several outcrops in Iran, and from a single sample collected in Algeria form the subject of this paper. Hitherto, the only paper dedicated to Late Devonian chondrichthyans from Morocco was published by DERYCKE (1992). A wide range of taxa was presented there, but since the specimens came from isolated, poorly dated samples from localities dispersed all over the Tafilalt region, no satisfactory biostratigraphical or palaeoecological analysis of assemblages could have been attempted. From Iran, the first reports of Late Devonian shark microremains were published by JANVIER (1977, 1981). In recent years, several other workers (HAIRAPETIAN & GHOLAMALIAN 1998, HAMPE 2000, LONG & HAIRAPETIAN 2000, YAZDI & TURNER 2000) have described further microvertebrates, predominantly shark teeth. Also, HAIRAPETIAN & *al.* (2000) presented a comprehensive review of the Devonian vertebrate faunas of central Iran with their age constraints.

Most of the Iranian samples used in our paper were collected from the Dalmeh section in central Iran by V.H. in 1998-2000 and by V.H. and M.G. in spring 2001; in addition, some specimens from J. WENDT's (Tübingen) collection (Hutk section, WENDT & *al.* 2002; Ali-Morad section, WENDT & *al.* 1997), as well as small assemblages from Mighan (collected by V.H. and L. KARIMI, Geological Survey of Iran, Tehran) and Hodjedk sections have been included in this study. The material from Dalmeh already described by LONG &

Hairapetian (2000) is partially reviewed. Specimens from North Africa were collected by C.K. and J. Wendt.

Our aim is to analyse the evolution of chondrichthyan assemblages in two, generally shallow water Famennian environments on the shelves of North Gondwana. The comparison of shark communities from Iran and Morocco shows substantial differences, in respect to the frequency and scale of environmental changes, between these two regions. The Iranian shelf was probably a relatively stable marine area, whereas the waters covering the Tafilalt Platform apparently provided rather variable conditions. The occurrence of an impoverished, low-diversity assemblage in the lower upper Famennian of one of the Moroccan sections (Oum El Jerane) and its absence from Iran, deserve special attention.

The presence of very rich upper Famennian samples from the Tizi Nersas and Oum El Jerane (Tafilalt) and Dalmeh (Iran) sections allowed us to interpret late Famennian faunas from the studied regions according to the chondrichthyan biofacies model, recently proposed by Ginter (2000, 2001) for that time interval. In that hypothesis, thus far, the definition of shallow water chondrichthyan biofacies was somewhat intuitive and based on small samples. The results of the present study support that subdivision, once again pointing out the predominance of sharks with crushing teeth (mainly early euselachians) in the communities from shallow, well oxygenated waters.

STRATIGRAPHICAL AND PALAEOGEOGRAPHIC CONTEXT

Geological setting of Iranian localities (V.H.)

During the Late Devonian, the Iranian platform was part of the northern Gondwana margin. According to palaeogeographic reconstructions (e.g. Scotese & McKerrow 1990), it was situated in a tropical realm, close to the southern tropic. Here, there was a vast, relatively stable Famennian marine shelf, characterised by thick shallow-water carbonates, locally interbedded with clastic sediments. These deposits now extend from northwestern Iran (Zonus area), along the northern (Djeirud and Mighan areas) to the southeastern part (Kerman province), and from the west of central Iran (Chahriseh area) to eastern central Iran, Howz-e-Dorah and Ali-Morad regions. In Text-fig. 1 we present a generalised palaeofacies map for the middle-late Famennian of Iran based on Weddige's (1984) series of lithofacies maps and new conodont and microvertebrate data. Moderate deepening of the depositional area takes place towards the east and northeast (Kopet Dagh zone).

The main areas yielding the chondrichthyan remains used in this study are: Mighan area (northern Iran); Dalmeh section (central Iran); Ali-Morad/Ozbak-Kuh region (eastern Iran); Hutk and Hodjedk sections (southeast of central Iran, Kerman province localities). Besides the localities mentioned above, the investigation by M.G. and V.H. of M. Yazdi's collection at the Department of Geology, Esfahan, revealed *Jalodus australiensis* and *Phoebodus gothicus* teeth from the middle-late Famennian palmatolepid-polygnathid biofacies of Howz-e-Dorah. Detailed stratigraphical columns of Dalmeh and Mighan sections, which were sampled bed-by-bed, are shown in Text-fig. 2.

The Dalmeh section is particularly significant because several samples whose age is well constrained by conodonts (especially samples 39, TP and 64) yielded a high number of shark teeth. In this section, the Late Devonian deposits are metamorphosed by regional tectonic activities and recrystalised samples did not permit more detailed lithostratigraphical studies. Conodonts associated with poorly preserved inverte-

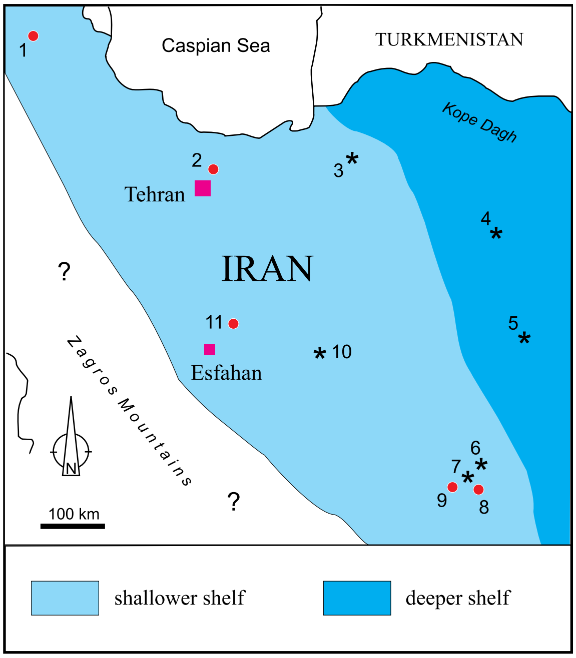


Fig. 1. Palaeofacies map of Iran during the middle-late Famennian. Numbers refer to localities which yielded chondrichthyans: 1 - Zonus, 2 - Djeirud, 3 - Mighan, 4 - Ali-Morad, 5 - Howz-e-Dorah, 6 - Hodjedk, 7 - Hutk, 8 - Kuh-e-Tizi, 9 - Shamsabad, 10 - Dalmeh, 11 - Chahriseh. Sections considered in this paper marked with asterisks

brate faunas (e.g. ostracods, gastropods and brachiopods) indicate a shallow water palaeoenvironment.

The Famennian portion of the Mighan section is composed of alternating fossiliferous limestones and shales, with brachiopods, ostracods, rare gastropods and crinoid stems, overlying a thick Givetian – Frasnian sequence with sandstones, dolomites, dolomitic limestones and limestones.

The lithology and stratigraphy of the Hutk section was presented by WENDT & *al.* (2002). Early or middle Famennian sample 38/23 of this section comes from dark skeletal, well bedded, highly fossiliferous limestones with abundant brachiopods and crinoid remains, just above a set of intertidal dolomites. According to WENDT & *al.* (1997), sample 61/8 from Ali-Morad, a locality situated in the northern part of Ozbak-Kuh, was taken from grey limestones some tens of meters above the tectonic boundary between the Sibzar and Bahram Formations (WENDT & *al.* 1997, p. 288, fig. 6B).

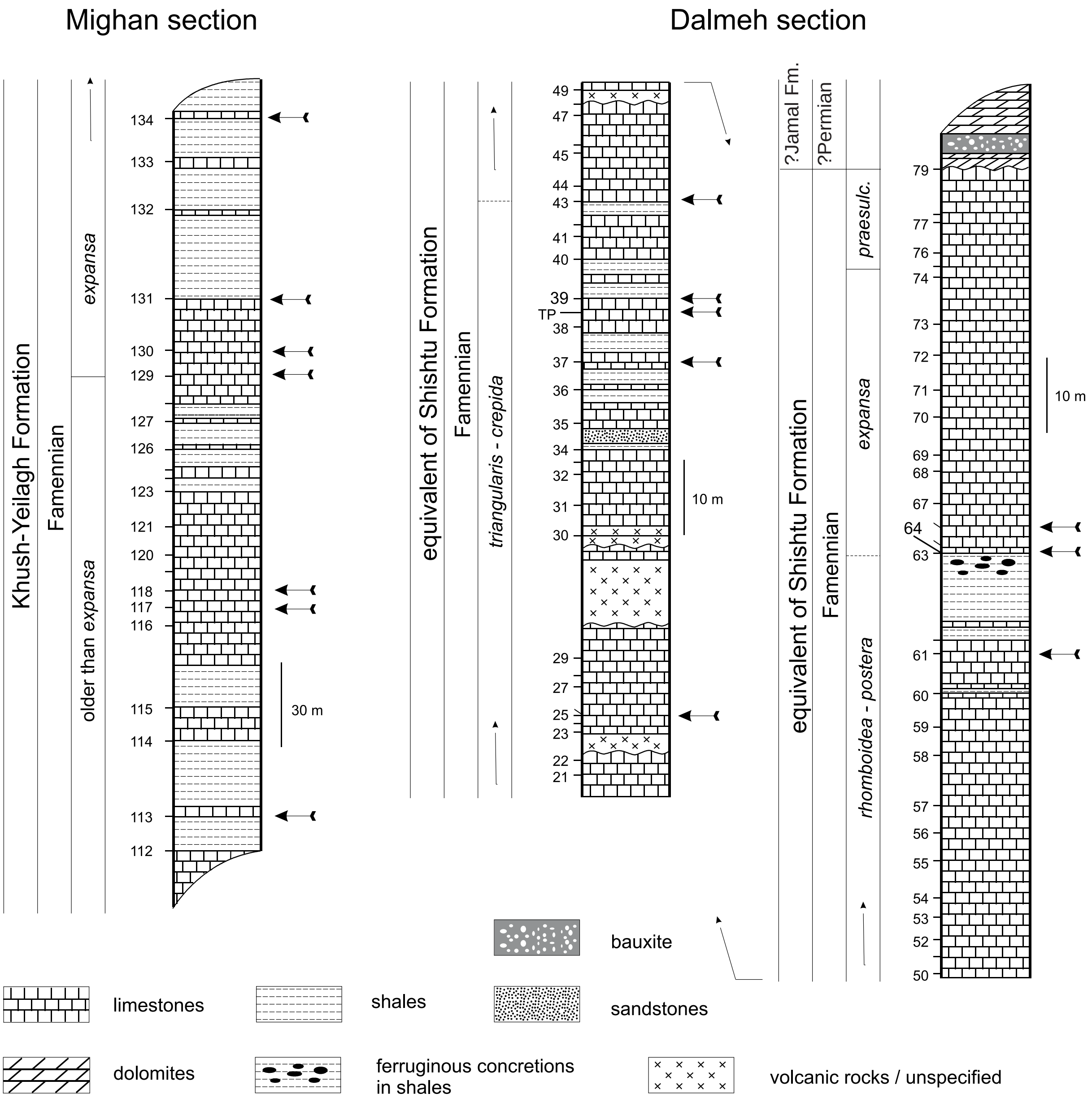


Fig. 2. Stratigraphical sections showing position of the samples, lithology and biozonal assignments in the Dalmeh and Mighan sections, Iran. Horizons which yielded chondrichthyan microremains indicated with arrows

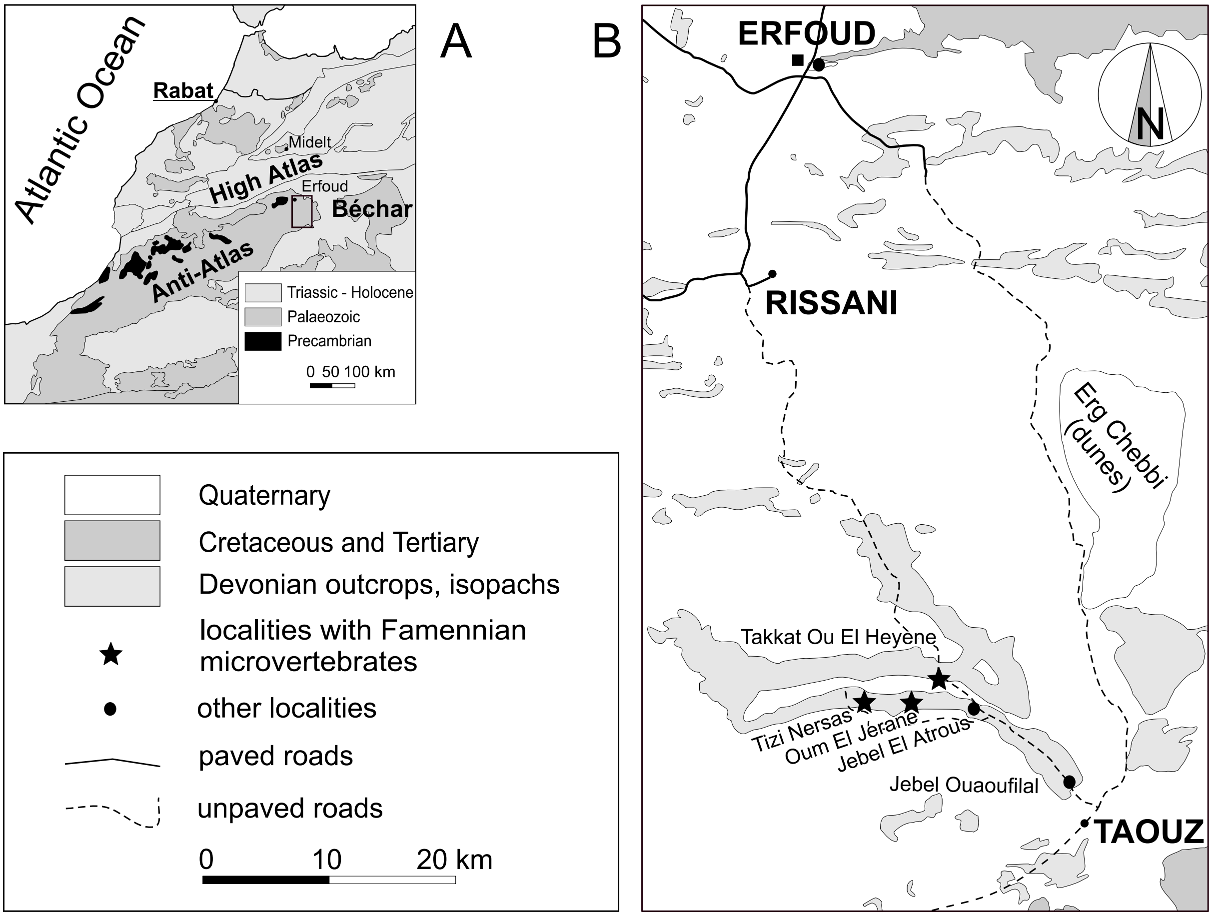


Fig. 3. Geologic map of the Tafilalt (eastern Anti-Atlas, Morocco) with the fossil localities

The lower Famennian of the Hodjedk section is represented by fossiliferous packstones/grainstones, mostly dominated by brachiopods. Sample R-3 which yielded a few interesting shark teeth, comes from the grey limestone with brachiopods and some ostracods.

Stratigraphy and palaeoecology of the Northwest-African localities (C.K.)

Vertebrate remains from samples of four Northwest-African outcrops of middle to late Famennian limestones were included in this study. Three sites are situated in the eastern Anti-Atlas of Morocco (Tizi Nersas, Oum El Jerane and Takkat Ou El Heyene) and one (Gour Bedda) in the Mouydir region East of InSalah in Algeria (near Amguid). The Moroccan localities are positioned in the Tafilalt in a large syncline west of Taouz (Text-fig. 3).

Localities

Tizi Nersas (c. 21 km west-northwest of Taouz; N 30°59’43”, 4°18’43”): Of the limestone beds described below, only the *Gonioclymenia* limestone (unit E in Text-fig. 4) is exposed here. It is embedded in thin layers of sandy limestones with brachiopods. Its thickness does not exceed 20 cm. However, this single bed yielded a rich vertebrate fauna. DERYCKE (1992) described microvertebrates of undetermined Famennian age (an orodont tooth and a ctenacanth fin spine) from a locality nearby (“Jebel Amessoui”), probably several kilometres to the west.

Oum El Jerane (c. 16 km west-northwest of Taouz; N 30°59’43”, E 4°08’26”): In the region of Oum El Jerane, the transition from an area in the west towards Tizi Nersas with a hiatus in the middle to upper Famennian to condensed sections towards the east (El Atrous, Jebel Ouaoufilal) is exposed. A section of intermediate thickness is shown in Text-fig. 4. This extremely

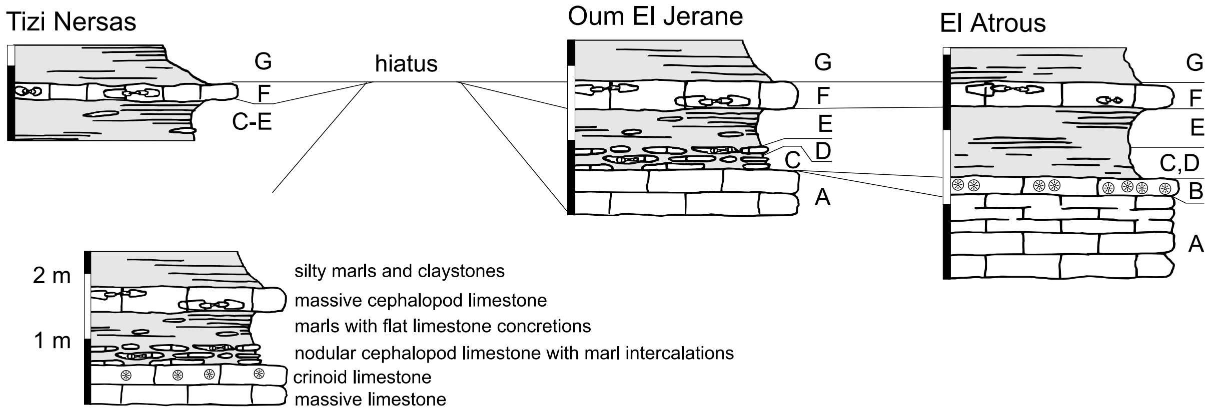


Fig. 4. Middle to upper Famennian sections of Tizi Nersas, Oum El Jerane, and El Atrous, Morocco (modified after KORN & *al.* 2000)

reduced section is discontinuous because of several sedimentary gaps, e.g. the horizon with *Platyclymenia annulata* is missing (compare KORN & *al.* 2000, text-fig. 3).

At the base of the section, thick-bedded layers of light grey limestones are exposed (unit A in Text-fig. 4). The content of siliciclastics and their grain-size increases westwards. Eastwards, the number of layers, their thickness, and the content of crinoid ossicles as well as cephalopods increases (unit B). These well-bedded, coarse-grained goniatite or crinoid packstones have an uneven upper surface (Text-fig. 4) which is mineralised by haematite. Numerous bones of arthrodire placoderms and one large cladodont shark tooth were extracted from this horizon. Above, two or three dark grey nodular limestone horizons are exposed (5 to 10 cm thickness each; units C and D), separated by thin clayey intercalations. They consist of ammonoid limestones (dominated by *Prionoceras*, *Erfoudites*, *Endosiphonites*, and other clymeniids, KORN & *al.* 2000) with few other faunal elements such as placoderm remains (probably *Dunkleosteus* and *Titanichthys*), crinoids, orthocone nautiloids, and bivalves (*Guerichia*).

Because of the exploitation of the *Gonioclymenia* limestone, the successive 10 to 50 cm of claystone, marl, and flat marly limestone nodules (unit E) could best be studied outside the fossil mines. These sediments contain flattened ammonoids, solitary rugose corals, heterocorals (WEYER 1995), brachiopods, and crinoids.

The *Gonioclymenia* limestone (unit F) is 10 to 30 cm thick and it is composed of an iron-rich yellow to red or grey cephalopod wacke- to packstone. Its fauna consists of *Gonioclymenia*, *Cyrtoclymenia*, orthocone nautiloids, trilobites, brachiopods, and crinoids. Only a few fossils were collected from the overlying clay- and marlstones. The content of quartz sand and silt increases noticeably in the succeeding claystones (unit G).

El Atrous (c. 14 km northwest of Taouz; N 30°55’46”, E 4°06’36”): Chondrichthyans from El Atrous were not studied, but it appears likely that several of the strata exposed at El Atrous contain microvertebrate remains and a few poorly preserved placoderm bones were seen in the field; it is mentioned here only as a comparative section. At this locality, the thickness is slightly greater than in Oum El Jerane. Below the part of the section shown in Text-fig. 4, 120 cm of massive cephalopod limestones with cheiloceratids are exposed. 60 cm of coarse-grained cephalopod limestones overlie these massive beds. The next horizon is 20 cm thick and consists of a light grey crinoid grainstone. A few kilometres towards the east, the facies of this unit changes towards a debrite which contains large pebbles (5 to 20 cm in diameter) in a crinoid limestone matrix (KORN & *al.* 2000, text-fig. 3). It is overlain by one metre of marls with flat limestone nodules and the *Gonioclymenia* limestone. MASSA & *al.* (1965) described some nearby sections, in the vicinity of the Jebel Ouaoufilal between El Atrous and Taouz.

Takkat Ou El Heyene (c. 16 km northwest of Taouz; N 31°00’49”, E 4°07’57”): At this locality, the middle Famennian facies resembles that of the deposits at Oum El Jerane of the same age. The top of the approximately 5 m thick massive cephalopod limestones is mineralised by haematite. One large cladodont chondrichthyan tooth was extracted from this crust. The massive limestones are overlain by c. 1 m of marls and limestone nodules. At the base of these marls, dark grey cephalopod limestone nodules with *Platyclymenia annulata* and other clymeniids were found (KORN & *al.* 2000). Above the marls, occasional remains of the *Gonioclymenia* limestone are preserved (because of the mining for fossils, most of it was excavated). The Famennian strata of this locality probably contain microvertebrate assemblages of a diversity and richness comparable to Oum El Jerane. This appears likely because the two localities are close and some of the layers display a similar microfacies and contain largely the same macrofauna.

Gour Bedda (c. 250 km east of In Salah; N 26°32'07", E 4°24'17"): Gour Bedda is the name of a broad and low hill in a large plain west of the sand field Kranguet El Hadid. It consists mainly of red to grey claystones with very thin-bedded nodular limestone intercalations. The flat packstone nodules, less than 3 cm in thickness, contain brachiopods in rock-forming number, conodonts, and sharks. On the geological map (1:200 000, Kranguet El Hadid), a middle to late Famennian age is indicated for this site.

Lithology

Massive limestones and sandstones (lower through middle Famennian; units A and B in Text-fig. 4)

The most conspicuous sedimentary feature at Oum El Jerane is a massive limestone unit of varying thickness (0 to 1 m). Near Taouz, this unit attains a thickness of up to 9 m. It consists mainly of moderately thick beds (usually up to 60 cm) of dark grey crinoid grainstone, with interbedded fine-grained limestones or debrites containing clasts of reworked crinoid limestone. At Oum El Jerane, sometimes small bodies of cephalopod grainstones are embedded in the massive crinoid grainstones. Towards the west, the facies changes gradually to coarse carbonate-rich sandstones and conglomerates with a carbonate matrix.

At localities east of Oum El Jerane, KORN & *al.* (2000) dated the upper, crinoid part of this unit using conodonts from the strata below (Early *marginifera* conodont Zone), by goniatites from the bed itself (*Maeneceras biferum* ammonoid Zone), and by poorly preserved specimens of *Platyclymenia* from its top (*Platyclymenia annulata* ammonoid Zone, i.e. Late *trachytera* conodont Zone). According to these authors, its reduced thickness can be explained by sedimentary gaps.

Like all the strata which are described in this chapter, the crinoid/cephalopod grainstones gradually wedge out at Oum El Jerane within a distance of about 500 m towards the west. Close to the last outcrop of this lithological unit, the siliciclastic content is very high. Remarkably, placoderms, shark remains, acanthodians, and conodonts become abundant at this site and the thickness is already reduced to 10 to 20 cm. This unit is not present at Tizi Nersas, but c. 5 km to the west at Jebel Amessoui, it occurs again and reaches a thickness of 6 m.

As indicated by a hardground with discoidal crinoid holdfasts and stromatolitic crusts at El Atrous (4 km east of Oum El Jerane) and Oum El Jerane, a gap follows in the succession that varies regionally in its extent. It often spans several ammonoid zones including the *P. annulata* Zone.

Dark nodular ammonoid packstone (lower part of the upper Famennian; units C and D in Text-fig. 4)

At Oum El Jerane, these one to three horizons of dark nodular ammonoid packstone contain an ammonoid fauna with *Endosiphonites muensteri* (KORN & *al.* 2000). They directly overlie the massive limestones described above. Besides numerous well preserved ammonoids, these beds yielded two samples quite rich in microvertebrates (palaeoniscoids, acanthodians, sharks), as well as bivalves, few gastropods, and crinoids. The packstones wedge out almost simultaneously with the underlying massive limestones. Further west, the ammonoid layer is absent because of facies changes and at least partially because of an hiatus.

At Takkat Ou El Heyene, an additional horizon of dark grey cephalopod limestone containing the *Platyclymenia annulata* fauna is preserved (KORN & *al.* 2000).

***Gonioclymenia* limestone** (upper Famennian; unit F in Text-fig. 4)

The *Gonioclymenia* limestone, 20 to 40 cm thick, is a massive bed of reddish-brown cephalopod packstone which is exposed virtually throughout the entire syncline (KORN & *al.* 2000). It is still of commercial interest for the local people and hence almost entirely trenched for exploitation. The *Gonioclymenia* limestone contains large specimens of *Gonioclymenia speciosa* as well as other ammonoids, orthocone cephalopods, crinoid remains, gastropods, heterocorals (WEYER 1995), and abundant microvertebrates. Throughout the syncline, this horizon displays a rather constant lithology. Between Tizi Nersas and Oum El Jerane, this horizon is missing over a distance of c. 3 km. Near Tizi Nersas, at the point where it occurs again, it is the only massive limestone bed in the middle to upper Famennian sedimentary succession. The other horizons described herein re-occur further to the west, i.e. the gaps in these stratigraphical levels are less extensive.

Sedimentary environment and palaeoecology

As described by WENDT (1985), facies patterns in the Devonian of the eastern Anti-Atlas reflect the gradual morphological differentiation of the initially rather uniform sedimentary basin. At the latest with the beginning of the Eifelian, thicknesses and facies vary considerably which can be explained by changes in regional palaeogeography. This process was probably caused by pre-Variscan tectonic movements and created the 'Mader

Basin', the 'Tafilalt Platform', and the 'Tafilalt Basin'. In the Late Devonian, this differentiation proceeded and an increasing number of synsedimentary tectonic structures developed at various scales. Simultaneously, the differences in thicknesses, litho-, and biofacies increased considerably.

In the middle to late Famennian, Oum El Jerane and Tizi Nersas were located on the 'Tafilalt Platform' which is recorded in the reduced thicknesses, hiatuses, cyanobacterial crusts, oolites, hardgrounds, and current-aligned cephalopod shells (WENDT 1995). This indicates a shallow water photic zone for the area.

During the deposition of the 'massive crinoid limestones', the water depth was probably already rather low (hardgrounds, crinoid holdfasts, cyanobacterial crusts, etc.) and the crinoids which occur in rock-forming number indicate at least fairly well oxygenated bottom water. In contrast to these strata, the 'dark nodular ammonoid packstones' contain only a few benthic faunal elements and in combination with their black colour, it appears likely that temporarily the sea-water near the sea-floor was poorly oxygenated or even anoxic. This change in oxygen content of the sea-water was reversed in the subsequent *Gonioclymenia* limestone which contains benthic organisms like trilobites, tabulate and rugose corals, brachiopods, and gastropods.

Age determination of samples and lithostratigraphical units (M.G., V.H. & C.K.)

Dating of rocks from the areas of North Gondwana is attended with considerable difficulties. The most important problem, concerning the majority of samples, is the absence of palmatolepid conodonts characterised by short stratigraphical ranges, due to the facies type. In Iran, we deal with the shallow water polygnathid-icriodid conodont biofacies of SANDBERG & DREESEN (1984). Polygnathids which occur here are often hard to identify and ranges of icriodids are long. In the upper Famennian of Morocco, the bispathodid fauna predominates, and only small admixtures of long-ranging palmatolepids, such as *Palmatolepis gracilis gracilis* or *Pa. perlobata schindewolfi* can be found.

Another difficulty results from the formal definition of the boundaries of the Early *praesulcata* conodont Zone. The lower boundary of that zone was established at the first appearance of *Siphonodella praesulcata*, unknown from the study area, and its upper boundary was defined by the extinction of a few rare species such as *Pa. gonioclymeniae* or *Polygnathus znepolensis*. The conodont fauna of the *Gonioclymenia* limestone in Morocco is composed only of species whose ranges cross those two boundaries, upwards and downwards. Therefore, although that fauna is abundant and diverse, direct age determination of samples cannot be precise.

The last, rather unexpected source of dating problems in Moroccan samples is an incongruence between the data obtained from conodonts and ammonoids. In at least two instances, dating based on ammonoids indicates an earlier age than that determined by conodonts, if we accept the correlation presented by BECKER & KORN (in WEDDIGE 1996, p. 282) between these two zonations as correct. That problem probably requires further discussion between specialists working on those two groups of fossils, and it has a considerable bearing on the comparison of chondrichthyan faunas from Morocco and the other parts of the world.

Samples from Iran

1. Conodonts recovered from samples 39 and TP of the Dalmeh section comprise *Icriodus iowaensis iowaensis*, "*I.*" *cornutus*, "*Polygnathus*" *brevilaminus, Pelekysgnathus* sp. and probably *I. alternatus alternatus*. Although the age of this assemblage can be determined directly as *triangularis* through Late *crepida* Zones, the occurrence of *Polygnathus semicostatus* in sample 34 (21.1 m below sample 39) indicates an age not older than the Middle *crepida* Zone (HAIRAPETIAN & YAZDI 2002, in press). Thus, the most probable age range of sample 39 lies within the Middle through Late *crepida* Zones.

2. About 559 m above the base of the Dalmeh section in sample 64, among other conodonts *Polygnathus delicatulus*, *P. communis collinsoni*, *P. communis communis*, *P. nodocostatus, P. perplexus, Clydagnathus ormistoni,* and *Bispathodus* cf. *aculeatus* occur, an assemblage which most probably indicates an Early *expansa* age (HAIRAPETIAN & YAZDI 2002, in press). The presence of *P. communis collinsoni* might indicate, according to JI & ZIEGLER (1993), also the Middle *expansa* Zone. However, several Russian authors (e.g. BARSKOV & *al.* 1991; VORONTSOVA 1996) presented records of this species as "*Neopolygnathus*" *collinsoni* from the base of the *postera* Zone. *Bispathodus aculeatus plumulus* was recovered from sample 69, collected some 14 m above sample 64. This indicates a Middle *expansa* age for sample 69 and consequently an older age for sample 64.

3. Sample R3 from Hodjedk yielded "*Icriodus*" *cornutus*, *I. iowaensis iowaensis*, "*Polygnathus*" *brevilaminus* and *P. semicostatus.* This small conodont assemblage indicates the Middle or Late *crepida* Zones.

4. Sample 38/23 from Hutk contains "*Icriodus*" *cornutus* and *Pelekysgnathus inclinatus* determining an early or middle Famennian age (Early *crepida* through Late *marginifera* Zones; WENDT & *al.* 2002).

5. Conodonts from sample 61/8 from Ali-Morad indicate the *rhomboidea* through Early *marginifera* Zones (Z. BELKA, pers. comm.).

6. Although conodonts from Famennian samples of the Mighan section were not always precise age determinants, sample 129 and higher samples can be considered as *expansa* Zone (L. KARIMI, pers. comm.). Other samples, with lower numbers, come from the middle Famennian (older than the *expansa* Zone).

Samples from Northwest Africa

Four samples from successive limestone layers at Oum El Jerane section (OEJ-1 to 4) and two samples from Tizi Nersas (TN-1 and 2) yielded conodonts and chondrichthyan remains.

1. Sample OEJ-1 comes from a "placoderm bonebed" layer, which represents the massive limestones complex (unit A in Text-fig. 4) at Oum El Jerane. The majority of almost 15 conodont species found in the sample, among them several palmatolepids, have rather long ranges, indicating an age of the Latest *crepida* through Late *marginifera* Zone (Z. BELKA, pers. comm.). However, the presence of *Palmatolepis loba* suggests an early rather than middle Famennian age for the sample (Latest *crepida* through Early *rhomboidea* Zones). This conforms with the maximum age of crinoid limestones (unit B) which overlie unit A to the east of Oum El Jerane (for instance in El Atrous), given by KORN & *al.* (2000; Early/Late *marginifera* through Late *trachytera* Zones). In Oum El Jerane, the crinoid limestones wedge out westwards.

2. Sample OEJ-2 represents the lower of two nodule layers (unit C in Text-fig. 4) of dark nodular ammonoid packstones. The conodont fauna (identified by VH and Z. BELKA) is composed mainly of bispathodids (more than 70%), among them *Bispathodus aculeatus aculeatus* and *B. costatus* which, together with *Polygnathus experplexus*, indicate the Middle *expansa* age. The presence of a few specimens of much older, shallow water species, such as *Scaphignathus velifer* or *S. subserratus* shows that some reworking took place at the base of this unit. The ammonoid fauna taken from unit C at Oum El Jerane is correlated with the *Franconiclymenia serpentina* Zone of the Rhenish Massif (KORN & *al.* 2000) which, in turn, according to BECKER & KORN (in WEDDIGE 1996, p. 282) is an equivalent of the basal part of the *expansa* conodont Zone. Since the ammonoid index species of *F. serpentina* Zone was not found in Morocco and the correlation made by KORN & *al.* (2000) is only tentative, the Middle *expansa* conodont Zone will be considered here as the most probable age of sample OEJ-2. It does not preclude the earlier age of the base of unit C in other more complete sections.

3. Sample OEJ-3 from unit D (the upper of two nodular layers; Text-fig. 4) unfortunately contains no conodonts useful for dating (Z. BELKA, pers. comm.). There are mainly specimens of *Bispathodus stabilis*, and a few elements of *Palmatolepis gracilis gracilis* and polygnathids. Only by superposition can the age of this sample be determined as Middle or Late *expansa* Zones (see dating of samples OEJ-2 and OEJ-4). As in the case of unit C, KORN & *al.* (2000) consider the age of unit D as not younger than the Early *expansa* Zone, which does not appear to be justified by the conodont fauna from the underlying bed.

4. Sample OEJ-4 was collected from the *Gonioclymenia* limestone (unit F in Text-fig. 4) and contains a very rich and diverse conodont fauna with polygnathids, palmatolepids and bispathodids, including *Bispathodus ziegleri*. However, a long interval, from the Late *expansa* through the Middle *praesulcata* Zone is indicated by these conodonts. Ammonoid dating (D. KORN, pers. comm.) indicates *Clymenia laevigata* or *Ornatoclymenia ornata* Zones, which are equivalent to or older than the Middle *expansa* conodont Zone. The reason for this contradiction is unknown, and we have decided to use the conodont ages as more reliable. However, since it seems impossible that the problem of correlation between conodont and ammonoid zonation could concern a difference of more than one conodont zone, the Late *expansa* Zone will be considered here as the most probable age of sample OEJ-4.

5. Samples TN-1 and TN-2 were collected from the *Gonioclymenia* Limestone layer (unit F in Text-fig. 4) at Tizi Nersas. The conodont assemblage obtained from these samples is virtually identical to that from OEJ-4, so their suggested age is also the Late *expansa* Zone.

6. A single cladodont tooth was extracted from the top of massive cephalopod limestones at Takkat Ou El Heyene, which may be correlated with units A or B of Oum El Jerane (early or middle Famennian).

7. Sample A-236 from Gour Bedda in Algeria yielded only one conodont species, "*Icriodus*" *cornutus*, the age range of which is very long and spans almost the entire early and middle Famennian which coincides with the information on the geological map.

DESCRIPTION OF CHONDRICHTHYAN MICROREMAINS (M.G., V.H. & C.K.)

With few modifications, we generally follow here the classification of chondrichthyans as compiled by CAPPETTA & *al.* (1993). Sections entitled "Stratigraphical range" concern the age of all hitherto published records of a given species, this paper included. Detailed information on the distribution of species in Iran and Northwest Africa only, is presented in the sections "Material" and in Tables 1 and 2. Note that only the most probable ages are shown; for discussion on the other possibilities see previous chapter. Iranian specimens are housed in the following institutions: Islamic Azad University (Khorasgan branch), Esfahan (abbreviated as AEU), Department of Geology, University of Esfahan (EUIV), and Institute of Geology, Warsaw University, Warsaw (IGPUW). All specimens from Northwest Africa are housed at the Institute of Geology, Warsaw University, Warsaw (IGPUW).

General information

Iran

Altogether 233 chondrichthyan teeth were recovered from Iranian samples.

Specimens from Dalmeh, the richest source of ichthyoliths in our material, are unfortunately often distorted due to tectonic deformation and metamorphism. Smaller specimens with separate cusps appeared particularly vulnerable to distortion. A lot of teeth are broken; hardly a single phoebodont or cladodont tooth with complete tips of cusps was found. Many euselachian teeth have crushed or removed bases, probably because of great porosity of the basal tissue, and consequently low resistance to abrasion and corrosion. The teeth are generally very dark, although a few light-brown or even amber elements were found. In spite of extensive washing most of specimens are covered with clay, which often makes identification difficult. A few larger teeth from the upper Famennian of Dalmeh were found on the rock surface.

Together with the shark teeth several chondrichthyan scales were found from Dalmeh. In addition, acanthodian ("*Acanthodes*" sp.) and palaeoniscoid (*Moythomasia*-type) scales were recovered from samples TP and 39 of that section, together with a dipnoan tooth plate referred to as ?*Rhinodipterus* sp. from the former and probably a fragment of pectoral fin of a bothriolepidid from the latter sample. Sample 64 yielded placoderms (undeterminable arthrodires) with dipnoan tooth plates and palaeoniscoid scales.

Preservation of teeth is clearly better in the material from Ali-Morad and Hutk, and particularly from Hodjedk and Mighan. Almost all specimens from the latter two sections are fairly complete, with only some traces of abrasion present.

Chondrichthyan, palaeoniscoid and acanthodian scales are abundant in the Mighan and Hodjedk samples.

Localities / Samples	Dalmeh			Hod.	Hutk	A-M	Mighan							
Species	TP	39	64	R3	38/23	61/8	113	117	118	129	130	131	134	Total
Jalodus australiensis	-	-	3	-	-	-	-	-	-	-	-	-	-	3
Thrinacodus tranquillus	-	-	35	-	-	-	-	-	-	-	-	-	1	36
Phoebodus gothicus	16	1	15	-	16	3	-	-	1	-	1	1	-	54
Phoebodus cf. *rayi*	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Phoebodus aff. *turnerae*	-	-	-	-	-	-	-	3	-	-	-	-	-	3
Phoebodus turnerae	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Phoebodus typicus	1	-	-	1	-	-	-	-	-	-	-	-	-	2
Protacrodus serra	-	-	12	-	-	-	-	-	-	-	-	-	-	12
Protacrodus spp.	-	-	23	-	-	1	-	1	-	-	-	3	-	28
Dalmehodus turnerae	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Deihim mansureae	1	3	7	3	9	-	-	-	1	-	-	-	-	24
Lissodus sp.	-	-	9	-	-	-	-	-	-	1	-	1	-	11
Orodus sp.	-	-	26	-	-	-	-	-	-	-	-	-	-	26
Stethacanthus spp.	1	2	16	-	4	1	2	-	-	-	-	2	-	28
Bransonella? sp.	-	-	3	-	-	-	-	-	-	-	-	-	-	3
Total	19	8	150	4	29	5	2	4	2	1	1	7	1	233

Table 1. Distribution and frequency of chondrichthyan teeth in the Famennian of Iran. Hod. – Hodjedk; A-M – Ali-Morad

Localities /	Oum El Jerane				Tizi Nersas		Gour Bedda	
Species Samples	OEJ-1	OEJ-2	OEJ-3	OEJ-4	TN-1	TN-2	A-236	Total
Jalodus australiensis	-	6	1	-	1	2	-	10
Thrinacodus tranquillus	-	6	1	1	3	3	-	14
Thrinacodus cf. *ferox*	-	2	-	1	1	-	-	4
Phoebodus depressus	-	-	-	-	-	-	4	4
Phoebodus g. gothicus	-	1	10	6	14	4	-	35
Phoebodus g. transitans	-	-	-	-	-	-	14	14
Phoebodus limpidus	-	-	-	-	2	-	-	2
Phoebodus aff. *turnerae*	-	-	-	-	-	-	7	7
Phoebodus typicus	5	-	-	-	-	-	-	5
Protacrodus serra	-	-	-	5	15	16	-	36
Protacrodus vetustus	4	-	-	-	-	-	-	4
Protacrodus sp.	1	-	-	-	-	-	-	1
cf. *Deihim mansureae*	3	-	-	-	-	-	-	3
"Symmorium" glabrum	-	78	5	1	5	1	-	90
"Symmorium" sp. A	-	-	-	-	-	-	2	2
"Symmorium" sp. B	8	-	-	-	-	-	-	8
Stethacanthus cf. *thomasi*	7	-	-	-	-	-	-	7
Stethacanthus sp.	-	22	2	8	19	17	1	69
cladodonts indet.	-	4	-	1	1	-	-	6
Clairina marocensis	-	-	-	-	-	1	-	1
Total	28	119	19	23	61	44	28	322

Table 2. Distribution and frequency of chondrichthyan teeth in the Famennian of Oum El Jerane and Tizi Nersas (Tafilalt Platform, Morocco) and Gour Bedda (Algeria)

Northwest Africa

The state of preservation, colour and diversity of ichthyoliths, and among them 295 chondrichthyan teeth from the Tafilalt Platform in Morocco, are strictly related to the litostratigraphic unit they come from. Most microremains, as well as macrofossils such as numerous placoderm bones from the sandy massive limestone of Oum El Jerane (sample OEJ-1) are rounded by abrasion, often devoid of ornamentation, and broken. Their colour usually varies from pale yellow to amber. Almost 30 shark teeth, several chondrichthyan and paleoniscoid scales (Pl. 6, Figs O-P), chondrichthyan branchial denticles (Pl. 6, Figs M-N), as well as hundreds of various acanthodian scales (Pl. 6, Figs. Q-R), were found together with pieces of placoderm armours. One well preserved acanthodian tooth-whorl was also recovered from that sample (Pl. 6, Fig. S). The residue was full of transparent, rounded quartz grains.

Specimens from dark nodular ammonoid packstones (samples OEJ-2 and 3) look completely different. They are often very well preserved, with even the tips of very long and delicate cusps present, but their colour is black, and they are almost always covered with an intransigent dark clay. Shark teeth are very abundant here (almost 140 specimens) and they are accompanied by ctenacanth-like chondrichthyan scales. However, palaeoniscoid remains, body scales, fulcral scales, conical teeth, jaw fragments and pieces of bones are even more numerous.

The *Gonioclymenia* limestone yielded the most beautiful chondrichthyan microremains from this region. The teeth (about 130 from this unit) are light brown (Tizi Nersas, TN-1 and 2) to dark brown (Oum El Jerane, OEJ-4), often broken but not worn by abrasion. They are associated with a few shark scales, a moderate number of palaeoniscoid remains, mainly teeth, and many benthic invertebrate fossils, such as crinoids, brachiopods, bivalves, gastropods, and bryozoans (?).

Algerian ichthyoliths, mainly phoebodont teeth, from Gour Bedda, sample A-236, are even better preserved.

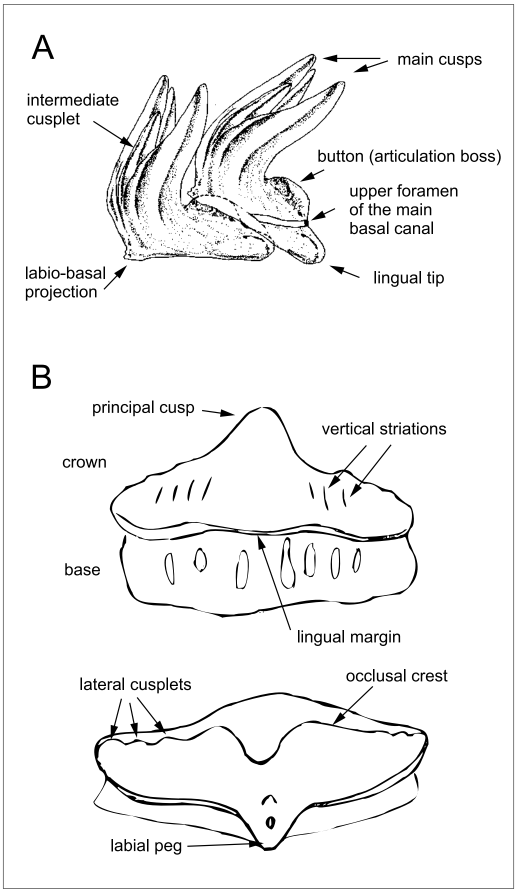


Fig. 5. Morphological terminology of Famennian shark teeth. A – Overlapping phoebodont teeth in lateral view. B – *Lissodus* sp. in lingual and occlusal/labial views

They are very colourful, from cream-orange to amber, to light brown, to (rarely) black, very clean and in some instances absolutely complete. Almost 30 shark teeth are associated with numerous palaeoniscoid scales (Pl. 7, Fig. O), teeth and bone fragments, and an extremely high number of acanthodian scales with smooth, diamond crowns (“*Acanthodes*”-type, Pl. 7, Figs L-M).

SYSTEMATIC ACCOUNT

Class Chondrichthyes
Subclass Elasmobranchii BONAPARTE, 1838
Order Phoebodontiformes nov.

REFERRED FAMILIES: Phoebodontidae WILLIAMS in ZANGERL, 1981; Jalodontidae nov.

REMARKS: Since the original description of *Phoebodus* by ST. JOHN & WORTHEN (1875), the knowledge of the diversity, stratigraphical range and relationships of this genus has increased considerably. Thus far, ten clearly defined phoebodont species were erected, which is a high number as far as Devonian sharks are concerned. More is also known about the phylogeny of *Jalodus* and *Thrinacodus*, presumed closest relatives of *Phoebodus*. It appears that the Phoebodontidae and Jalodontidae nov. (see below), two closely related families grouping sharks with phoebodont-like teeth, form together a characteristic unit which developed at least as early as in the Givetian. This unit is assigned here as a new order, Phoebodontiformes. Early representatives of this group share certain characters, such as the form of a tooth-base, with *Antarctilamna* (LONG & YOUNG 1995), *Wellerodus* (TURNER 1997), and the earliest symmoriiforms (see discussion in GINTER & IVANOV 1996). On the other hand, Famennian phoebodontiform teeth resemble those of Late Palaeozoic Xenacanthiformes which may indicate affinities of these two groups. Several forms which display intermediate phoebodontiform/xenacanthiform characters, such as *Bransonella* (IVANOV & GINTER 1996), were recorded.

STRATIGRAPHICAL RANGE: Devonian, (Eifelian?) Givetian – Carboniferous, Serpukhovian. If *Bransonella* (currently in the Xenacanthiformes) is treated as a phoebodontiform, the upper limit can be even in the Permian, based on SCHULTZE (1985). “*Phoebodus*” *brodiei* from the Triassic of England (WOODWARD 1893) has a phoebodont crown, but its relationship with the phoebodontiforms is uncertain.

Family Phoebodontidae WILLIAMS in ZANGERL, 1981

REFERRED GENERA: *Phoebodus* ST. JOHN & WORTHEN, 1875; *Thrinacodus* ST. JOHN & WORTHEN, 1875; ? *Bathycheilodus* ST. JOHN & WORTHEN, 1875.

Genus *Phoebodus* ST. JOHN & WORTHEN, 1875

TYPE SPECIES: *Phoebodus sophiae* ST. JOHN & WORTHEN, 1875

Phoebodus gothicus GINTER, 1990

REFERRED SUBSPECIES: *Ph. g. gothicus* GINTER, 1990; *Ph. g. transitans* subsp. nov.

REMARKS: Despite the high variability of *Ph. gothicus*, we presume that all of the teeth of this species, presented or referred to in this paper, belong to *Ph. g.*

gothicus, with exception of asymmetrical teeth from Algeria, described below as a new subspecies, possibly originally restricted to North Gondwana, *Ph. g. transitans* subsp. nov.

Phoebodus gothicus gothicus GINTER, 1990
(Text-fig. 6D-E; Pl. 1, Figs E-N; Pl. 2, Fig. G; Pl. 3, Figs A-C; Pl. 8, Figs K-N; Pl. 11, Figs J-L)

2000. *Phoebodus gothicus* GINTER; GINTER & 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 & HAIRAPETIAN, p. 211-212, figs 4a-d, f, h, j.
cf. 2001. *Phoebodus* cf. *gothicus* GINTER; GINTER, p. 716, fig. 3A-B.

MATERIAL: 54 specimens from Iran: 32 from Dalmeh, Middle or Late *crepida* and Early *expansa* Zones; 16 from Hutk, lower or middle Famennian; three specimens from Ali Morad, *rhomboidea* or Early *marginifera* Zones; and three specimens from Mighan, two from the *expansa* Zone and one from somewhat older Famennian rocks. 35 specimens from Morocco: 17 from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and 18 from Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: Two morphotypes of *Ph. g. gothicus* teeth are the most common in the Famennian of Iran. The first is characterised by moderately long, lingually narrowing bases, with a pointed lingual end (Pl. 1, Figs F, L; Pl. 3, Fig. C), resembling the type material from the Holy Cross Mountains (Poland; GINTER 1990), as well as specimens of this species from many other places of the world (e.g. Iowa, GROSS 1973; South Urals, GINTER & IVANOV 1992). The second morphotype is typical almost exclusively of Iran. Here, the lingual half of the base is wider than its region near the crown. The lingual margin may be pointed to rounded, to almost straight. Therefore, the base outline may resemble a pear (or a spoon), or a high trapezium with rounded angles (Text-fig. 6D-E; Pl. 1, Figs J, N, Pl. 3, Fig. A). There are intermediate forms between these two morphotypes, with subparallel lateral edges to the base (Pl. 1, Fig. E; Pl. 2, Fig. G; Pl. 3, Fig. B). The first, lingually narrowing morphotype is represented usually (but not always) by larger teeth, and the pear-like morphotype mainly by smaller specimens.

The largest phoebodont tooth from Iran (EUIV 99.5.209, LONG & HAIRAPETIAN 2000, fig. 4h), considered here as belonging to *Ph. gothicus*, comes from the Early *expansa* Zone of the Dalmeh section. Base length and width are almost equal (c. 5.5 mm), its button is laterally elongated, and the crown comprises only three cusps.

In contrast to collections from Iran, the variability of *Ph. g. gothicus* teeth from Morocco is rather low, related mainly to the tooth size and the length to width ratio of the base. Almost all specimens resemble the type material from the Holy Cross Mountains (GINTER 1990), with a “gothic” (lingually pointed) base outline and long, recurved, sigmoidal cusps.

REMARKS: The pear-like morphotype of *Ph. gothicus* is common in Iran from the lower through to the upper Famennian, but almost totally unknown from elsewhere. The only record of a few similar teeth comes from sample Ost-5 from the upper Famennian of Ostrówka Quarry in the western Holy Cross Mountains (GINTER 1994), very rich in *Ph. gothicus* teeth. The Polish teeth of that morphotype are generally smaller than those with lingually narrowing, pointed bases. It is not impossible that the pear-like teeth belong to some other phoebodont species, but because of the presence of intermediate forms, they more probably represent intraspecific variation or heterodonty.

The overall appearance of the large tooth, mentioned in the description, resembles that of *Ph. politus* from the Cleveland Shale in Ohio. However, the holotype of *Ph. politus* (NEWBERRY 1889, pl. 27, figs 27-28) has a bilobed button and the base forms a narrow parapet on the sides of the crown, which contrasts with the tooth from Dalmeh. On the other hand, knowing the large intraspecific variability of phoebodont teeth (compare *Ph. rayi* in GINTER & TURNER 1999), such differences might be considered minor. It is quite likely then that either the specimen from Dalmeh belongs to *Ph. politus*, or that *Ph. politus* and *Ph. gothicus* are conspecific. In any case, the similarities between very large teeth of *Ph. gothicus* and specimens of *Ph. politus* indicate that these two species are at least closely related.

STRATIGRAPHICAL RANGE: Outside Iran *Ph. g. gothicus* is known from the mid to upper Famennian, Early *marginifera* through the Early/Middle *praesulcata* Zones. However, in Iran, as has already been shown by LONG & HAIRAPETIAN (2000), typical specimens of *Ph. gothicus* are found in samples of alleged Middle or Late *crepida* age (Dalmeh, samples TP and 39). Co-occurrence of *Ph. gothicus* and early Famennian conodonts in the samples from Dalmeh shows that either *Ph. gothicus* appeared in Iran at least three conodont zones earlier than elsewhere or that the last occurrences of these conodonts may be higher here than in the other regions.

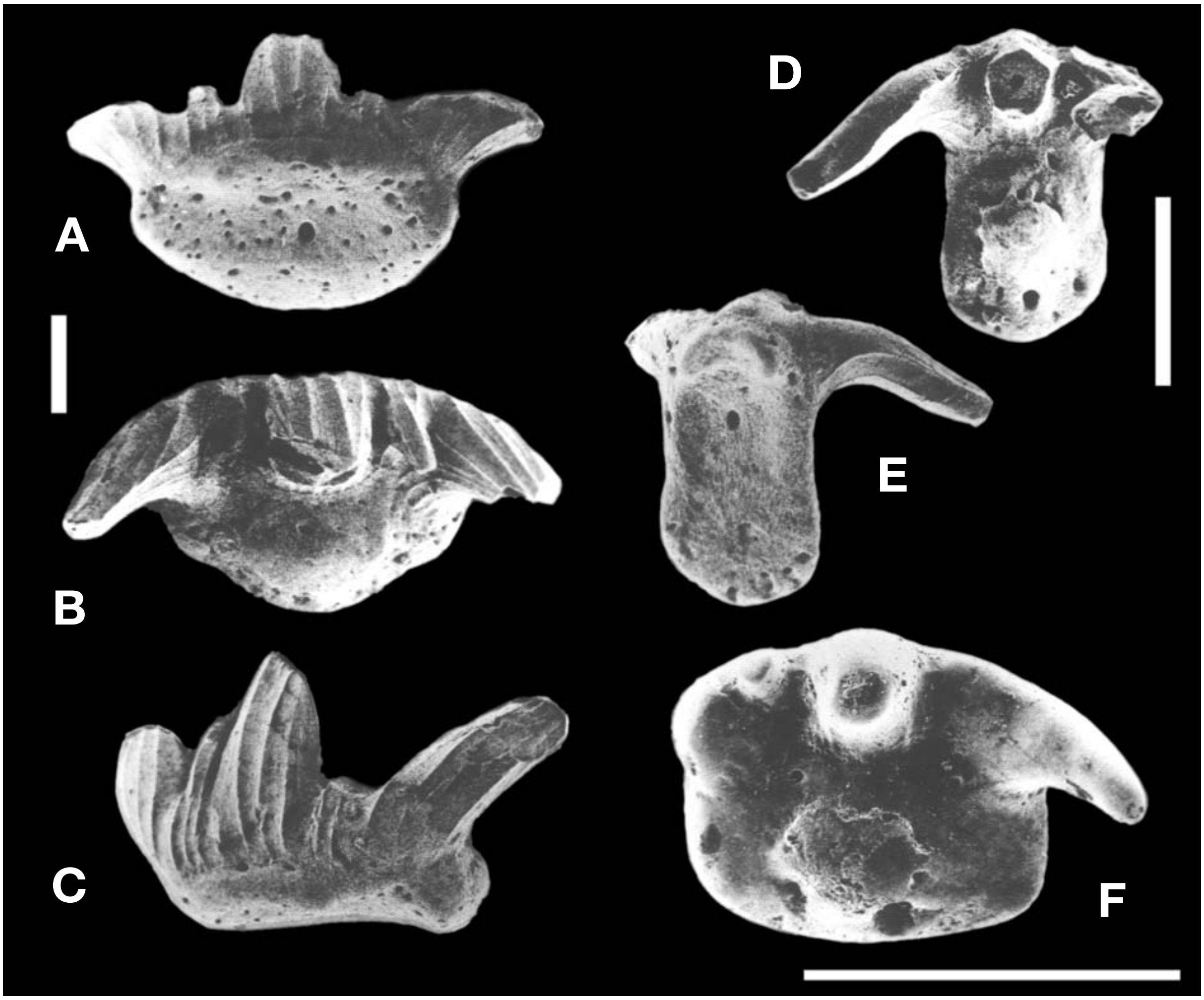


Fig. 6. Phoebodonts from the early Famennian of Iran. A-C – *Phoebodus turnerae*, specimen AEU 201, Dalmeh, sample 39, basal, occlusal, and oblique labial views, × 25. D-E – *Ph. gothicus*, specimen AEU 202, Dalmeh, sample 39, occlusal and basal views, × 50. F – *Ph. typicus*, specimen AEU 203, Hodjedk, sample R3, occlusal view, × 100. Scale bars = 0.5 mm

Phoebodus gothicus transitans subsp. nov.
(Text-fig. 7)

ETYMOLOGY: Latin *transitans* = changing, transitional.

HOLOTYPE: Specimen IGPUW/Ps/5/4 (Fig. 9A-C) from Gour Bedda, Algeria, sample A-236, early or middle Famennian.

MATERIAL: 14 specimens from Algeria, Gour Bedda, lower or middle Famennian.

DIAGNOSIS: A subspecies of *Ph. gothicus* with asymmetrical teeth. The crown is not transverse to the long axis of the base, but it is rotated at five to seven degrees to the right or left. The base is also asymmetrical, generally narrowing lingually, with a pointed lingual end and a small, flat lobe on one side of the lingual region. The button is situated well away from the lingual end of the base.

DESCRIPTION: Most features of the teeth of *Ph. g. transitans* subsp. nov. resemble those of typical specimens of *Ph. gothicus.* The crown has three long, slender, sigmoidal main cusps and one or two small, accessory, intermediate cusplets. The main cusps are ornamented with moderately distinct cristae, coarser on the labial and more delicate, but more dense on the lingual side. The accessory cusplets are virtually smooth. The base in the majority of specimens is long (labio-lingually) and narrow, with two main basal canal openings, one between the button and the lingual tip, and the other in

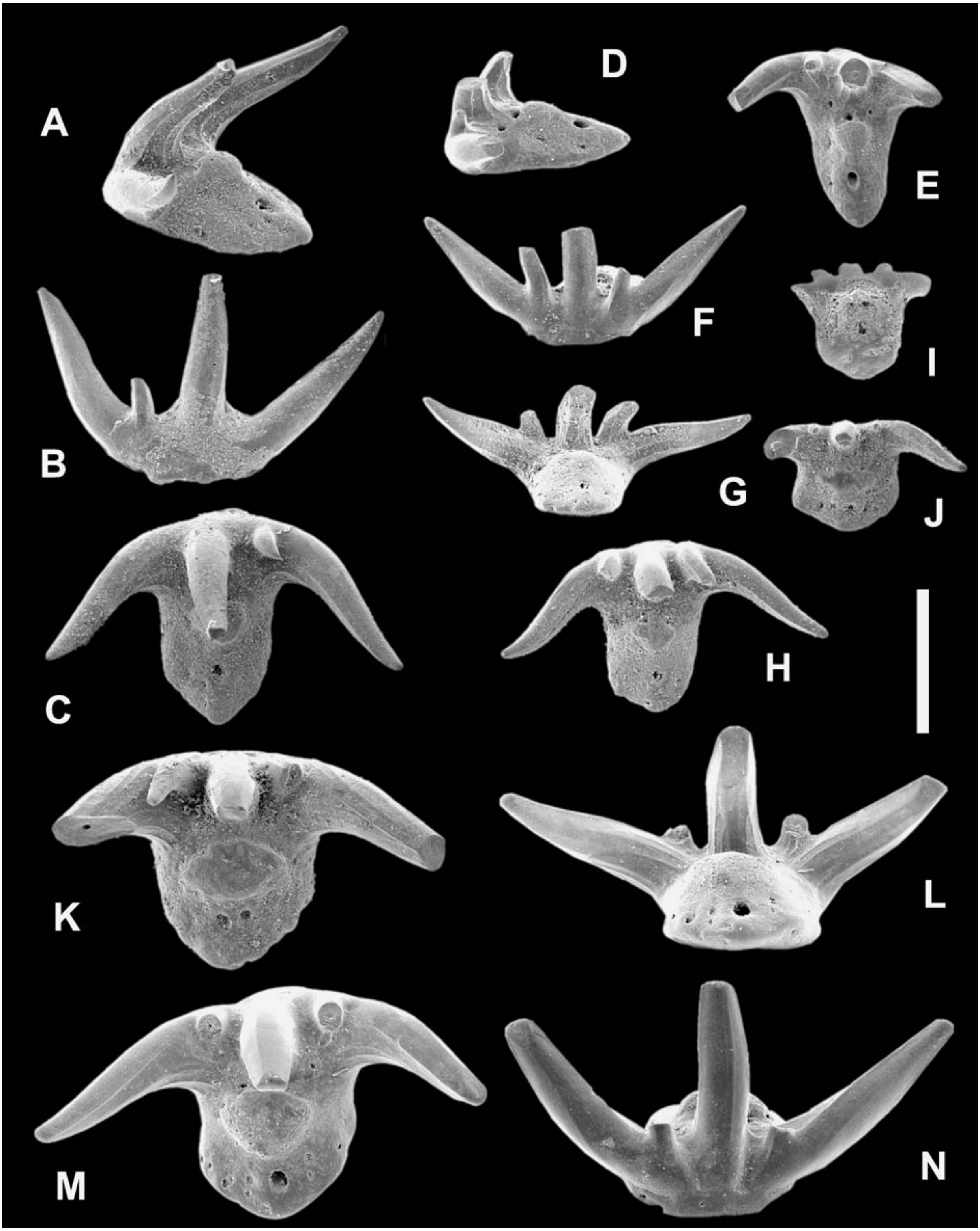


Fig. 7. *Phoebodus gothicus transitans* subsp. nov. from Algeria, Gour Bedda, sample A-236. A-C – IGPUW/Ps/5/4, **holotype**, lateral, labial, and occlusal views. D-E – IGPUW/Ps/5/5, lateral and occlusal views. F-H – IGPUW/Ps/5/6, labial, lingual, and occlusal views. I – IGPUW/Ps/5/7, basal view. J – IGPUW/Ps/5/8, occlusal view. K – IGPUW/Ps/5/9, occlusal view. L-N – IGPUW/Ps/5/10, lingual, occlusal and labial views. Scale bar = 0.5 mm

the centre of the basal depression. The button, subcircular or oval, is situated well away from the lingual rim, and slightly closer to the central cusp than to the lingual tip. However, a spectacular crown-base asymmetry and an asymmetry of the base itself distinguish these teeth from others of *Ph. gothicus*.

There are certain rules in the asymmetry of teeth in *Ph. g. transitans* subsp. nov. If the crown is rotated to the right, the lateral lobe occurs on the right side of the base as well (Text-fig. 7E), otherwise it is on the left (Text-fig. 7C, H, J, M). If only one accessory, intermediate cusplet is present, it is located on the opposite of the lobe (Text-fig. 7C, E). As usual for *Ph. gothicus* the base length to width ratio may vary from specimen to specimen. In longer and narrower specimens the lateral lobe is very narrow and the asymmetry of the base is hardly visible (Text-fig. 7E). In specimens with wider bases, the lobe is clearly distinguished (Text-fig. 7H). The asymmetry of the base is demonstrated in two more aspects, omitted from the diagnosis. The labio-basal projection is slightly twisted in the same direction as the crown, and in several specimens the lingual tip, the main lingual foramen, the button, and the base of the central cusp are not in line (Text-fig. 7M).

The size difference between the largest and smallest teeth of *Ph. g. transitans* from Algeria is not very high. The length of the base may reach from 0.3 to 0.8 mm.

REMARKS: The discovery of asymmetry in otherwise *Phoebodus*-looking teeth puts a new complexion on the evolution of the phoebodontid dentition (see discussion in the next chapter). According to the diagnosis of *Phoebodus* (and, therefore, of *Ph. gothicus*), its teeth are symmetrical. This is one of the characters that distinguish them from *Thrinacodus.* Therefore, the newly recovered asymmetrical teeth from Algeria should probably be treated as a new genus of the family Phoebodontidae. However, in the case of these teeth, the whole set of features shows that they closely resemble teeth of *Ph. gothicus*, and that the slight asymmetry is in fact the only difference between *Ph. g. gothicus* and *Ph. g. transitans* subsp. nov. It seems more prudent to retain the latter within the genus *Phoebodus*, as a specialised subspecies, than to create a new genus for a few teeth displaying transitional features.

STRATIGRAPHICAL RANGE: Early or middle Famennian.

Phoebodus depressus sp. nov.
(Text-fig. 8)

ETYMOLOGY: Latin *depressus* = depressed.

TYPE SERIES: Specimens IGPUW/Ps/5/11-14 (Text-fig. 8A-G) from Gour Bedda, Algeria, sample A-236, lower or middle Famennian.

MATERIAL: Four specimens from Algeria, Gour Bedda, lower or middle Famennian.

DIAGNOSIS: Phoebodont sharks with extremely long, lingually extended tooth-bases. Near the crown, the lateral rims of the base run parallel to each other. A minute, circular button, occupying no more than one third of the base width, occurs in this region. Further lingually, the base becomes wider and its lingual/lateral ends turn slightly upwards to form distinct horns. The lingual/median part of the base is depressed; a secondary swelling and a lingual tip may occur in the axial part of the depression. The upper main basal canal opening is located at the labial end of the depression, close to the button, or slightly more lingually. The basal opening is situated in the lingual part of an elongated basal concavity. The concavity is rimmed labially by a short and thin, arcuate labio-basal projection.

DESCRIPTION: There are two different tooth morphotypes within this new species. The first is smaller and narrower, with only three cusps in the crown, a long, narrow, undivided lingual depression and long lingual/lateral horns, rounded in cross section (Text-fig. 8A-B). The main upper foramen is located at the labial end of the lingual depression, very close to the button. The second morphotype is larger and wider, with accessory intermediate cusplets between the main cusps (Text-fig. 8C-G). It has an axial, secondary swelling in the lingual depression, ending as a lingual tip. The lingual/lateral horns are flattened, and the main upper foramen is situated on the axial swelling, not in the immediate proximity of the button. In both morphotypes the basal opening of the main basal canal is accompanied by a few smaller foramina (Text-fig. 8C-E). The base length in *Ph. depressus* ranges from 0.7 to 1.1 mm.

REMARKS: This is the most unusual phoebodont species of all those described hitherto, and the only one which has a lingual depression. It shares certain features with *Ph. gothicus*, such as the long lingual extension of the base and the relation between the button and the main upper foramen, but in *Ph. depressus* sp. nov. these features are exaggerated and transformed. On the other hand, lingual depressions may occur in the teeth of *Thrinacodus*, which, however, are asymmetrical and lack a clearly defined button or labio-basal projection. The position of *Ph. depressus* in the current ideas on the evolution of phoebodontid dentition will be discussed in the next chapter.

Quite recently, a new specimen of this species, resembling the second morphotype, was found in central Iran in a section which is currently under investigation (VH, personal observation). It will be described and figured in a future paper. Another tooth of similar morphology was figured from China (WANG & TURNER 1995, pl. 7, fig. 7) as *Ph. bifurcatus* GINTER & IVANOV, 1992. It has upturned lingual/lateral ends to the base, but no clear depression or axial lingual tip, and the base is evidently shorter than in the material from Algeria. Therefore, the Chinese specimen was probably identified correctly, although it might be a juvenile specimen.

STRATIGRAPHIC RANGE: Early or middle Famennian.

Phoebodus limpidus GINTER, 1990
(Pl. 8, Figs A-C)

2001. *Phoebodus limpidus* GINTER; GINTER, p. 716, fig. 2F-K. [see for older synonymy]

MATERIAL: Two specimens from Morocco, Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: The teeth of *Ph. limpidus*, the first two specimens found thus far from Gondwana, come from the same slab of *Gonioclymenia* limestone and have similar preservation: one lateral side of the base with two cusps is missing. However, the remaining parts of the specimens are diagnostic of *Ph. limpidus*: a semi-elliptical to triangular base, strongly diverging, gentle cusps and a rather vague button.

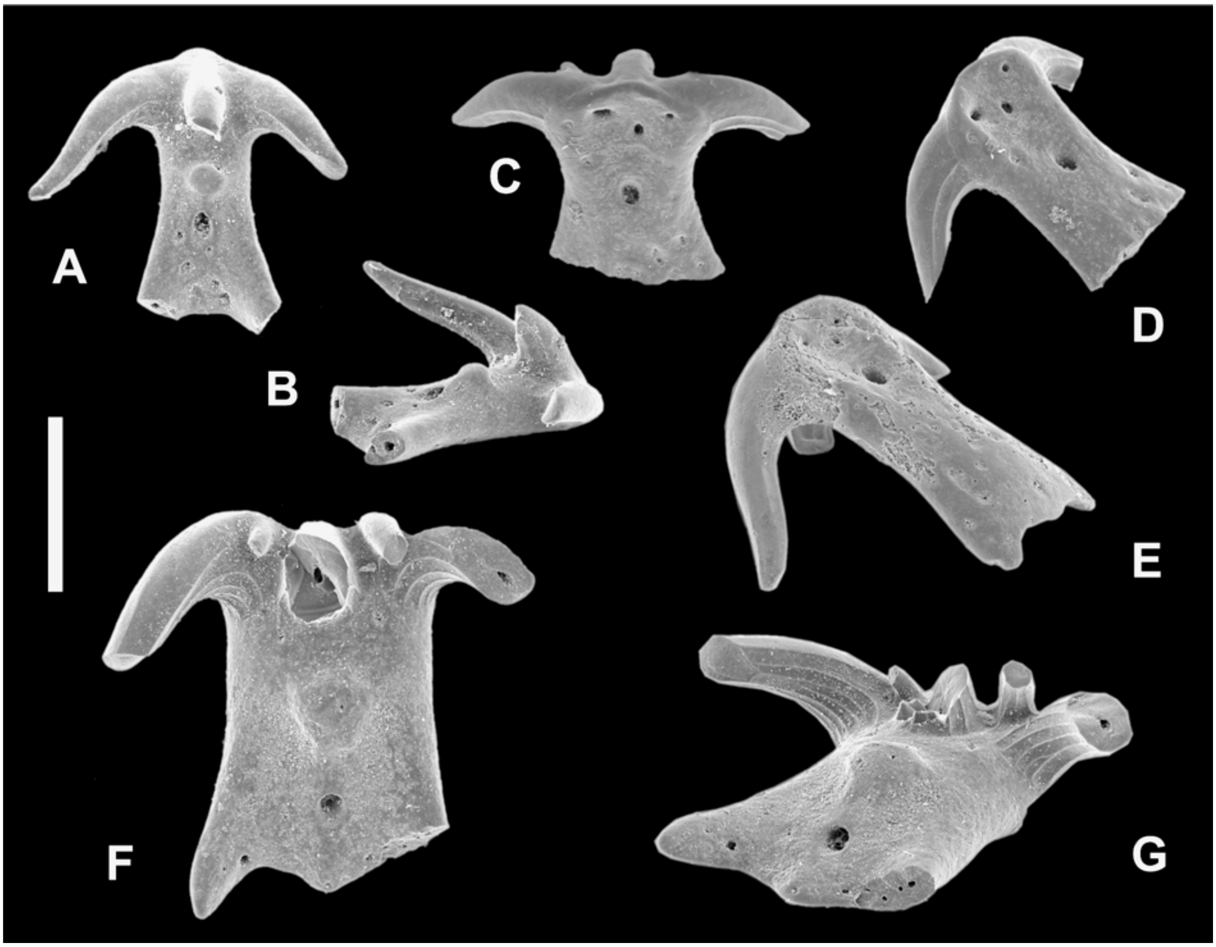


Fig. 8. *Phoebodus depressus* sp. nov., type series, from Algeria, Gour Bedda, sample A-236. A-B – IGPUW/Ps/5/11, occlusal and oblique lateral views. C-D – IGPUW/Ps/5/12, basal and oblique basal views. E – IGPUW/Ps/5/13, basal/lateral view. F-G – IGPUW/Ps/5/14, occlusal and oblique lingual views. Scale bar = 0.5 mm

REMARKS: It appears that *Ph. limpidus* was not a common visitor to the waters covering the Tafilalt Platform. This species, although already recorded from many places in the world, from China to Central Europe, to Western USA, is usually not abundant, even in very productive samples. The only exception is a sample from the upper Famennian of the Bactrian Mountains, Nevada, in which 19 specimens of 22 chondrichthyan teeth belong to *Ph. limpidus* (GINTER 2001). That sample probably represents a deep subtidal palaeoenvironment. Also in Thuringia, another relatively deep water area, *Ph. limpidus* is the only representative of late Famennian phoebodonts (GINTER 1999). This may indicate its more open marine preferences than, for instance, those of *Ph. gothicus*.

STRATIGRAPHICAL RANGE: Late Famennian, Early *expansa* through Early/Middle *praesulcata* Zones.

Phoebodus cf. *rayi* GINTER & TURNER, 1999

2000\. *Phoebodus* ?*gothicus* GINTER; LONG & HAIRAPETIAN, p. 212-214, fig. 4i [only].

MATERIAL: One specimen from Iran, Dalmeh, Middle or Late *crepida* Zone.

DESCRIPTION: The tooth is badly damaged, with only the basal parts of three closely spaced, equal cusps preserved. The base is broad, elongated mesio-distally, and pentagonal in outline, its lateral angles extending far beyond the foot of the crown. The lingual angle reaches almost 170º. The button is also laterally elongated, its labio-lingual to mesio-distal dimensions ratio is about 1:3. The lingual part of the button seems to be crushed, so it is difficult to judge whether or not it reached the lingual rim of the base. A large main basal canal opening was apparently located on the lingual rim or on the lingual face of the button.

REMARKS: The tooth was briefly described and figured by LONG & HAIRAPETIAN (2000, fig. 4i). They suggested an affinity to *Ph. gothicus*, which is incorrect, because tooth-bases of the latter species are usually long and not wide (see diagram in GINTER & IVANOV 1992, fig. 6A) and the button is more rounded. The tooth most probably belongs to *Ph. rayi* (compare especially the specimen from the possible lower- to mid-Famennian of New South Wales, JONES & TURNER 2000, fig. 8.1), however its state of preservation precludes complete certainty.

STRATIGRAPHICAL RANGE: *Ph. rayi*: Early or Middle *crepida* Zone (GINTER & TURNER 1999); *Ph.* cf. *rayi*: Middle or Late *crepida* Zone (this paper).

Phoebodus turnerae GINTER & IVANOV, 1992
(Text-fig. 6A-C)

1992\. *Phoebodus turnerae* sp. n.; GINTER & IVANOV, p. 68-70, figs 6B-C, 8A-H.

1995\. *Phoebodus turnerae* GINTER & IVANOV; GINTER, fig. 4C.

1999\. *Phoebodus turnerae* GINTER & IVANOV; GINTER & TURNER, fig. 3H-I.

2000\. *Phoebodus turnerae* GINTER & IVANOV; GINTER & IVANOV, p. 328, pl. 2, fig. A.

MATERIAL: One specimen from Iran, Dalmeh, Middle or Late *crepida* Zone.

DESCRIPTION: The single tooth of *Ph. turnerae* from Dalmeh is fairly complete, with at least the basal halves of each of the cusps preserved. The cusps are coarsely cristate on both sides, but the cristae are more gently developed and numerous on the lingual side. The base has a shape of a wide, lingually narrowing pentagon, typical of the species, with a prominent button almost reaching the lingual rim.

REMARKS: The specimen from Dalmeh strongly resembles teeth of *Ph. turnerae* from the *rhomboidea* and *marginifera* Zones of Ryauzyak, South Urals (GINTER & IVANOV 1992, fig. 8A-C and especially G), particularly in the shape of its base and button. The specimens from Ryauzyak lack coarse striations on the cusps, but this is probably only the matter of preservation.

STRATIGRAPHICAL RANGE: Early to middle Famennian, Early *crepida* through Late *marginifera* Zones.

Phoebodus aff. *turnerae* GINTER & IVANOV, 1992
(Pl. 3, Figs D-G; Pl. 7, Figs H-K)

cf. 1992. *Phoebodus turnerae* sp. n.; GINTER & IVANOV, fig. 8F.

MATERIAL: Three specimens from Iran, Mighan, Famennian, older than the *expansa* Zone. Seven specimens from Algeria, Gour Bedda, lower or middle Famennian.

DESCRIPTION: Tooth-bases of *Ph.* aff. *turnerae* from Mighan are pentagonal, narrowing lingually, with an obtuse angle at the lingual end. The basal length to width ratio is almost 1:1. The button is oval, elongated mesio-distally and situated centrally or near the lingual rim. The upper lingual opening of the main basal canal may be situated medially or slightly moved sidewards. Two specimens have only three main cusps in the crown (Pl. 3, Figs E-G); the third tooth has two accessory, intermediate cusplets (Pl. 3, Fig. D). Only parts of the cusps are preserved and in some places ornamentation is lost, but it is clear that the labial side of the main cusps was coarsely cristate and the striation of the lingual side was weaker and more dense.

As in the case of the teeth of *Ph.* aff. *turnerae* from Mighan section, specimens from Gour Bedda display intermediate characters between *Ph. turnerae* and *Ph. gothicus*. They have short, pointed or semi-elliptical bases, but with buttons situated centrally (Pl. 7, Figs H-I). However, in one very large specimen the button is placed very close to the lingual rim (Pl. 7, Fig. K), which is a typical feature of *Ph. turnerae* (see GINTER & IVANOV 1992, particularly fig. 8A-C).

REMARKS: Many characters of *Ph.* aff. *turnerae* suggest its close affinity to *Ph. turnerae*, especially the shape of the base, length to width ratio (compare GINTER & IVANOV 1992, Fig. 6A), and the structure of the crown. However, the central position of the button in several specimens indicates their probable intermediate position between *Ph. turnerae* and *Ph. gothicus*. A similar collection of features was noted in a few teeth from the Holy Cross Mountains, Poland: "*Ph. turnerae* transitional to *Ph. gothicus*" from Łagów (Early *marginifera* Zone; GINTER & IVANOV 1992, fig. 8F), and *Ph. gothicus* from Ostrówka (*expansa* Zone; GINTER 1994).

Phoebodus typicus GINTER & IVANOV, 1995
(Text-fig. 6F; Pl. 6, Figs A-C)

1999. *Phoebodus typicus* GINTER & IVANOV; GINTER & TURNER, fig. 3A-D.
2000. *Phoebodus typicus* GINTER & IVANOV; GINTER & IVANOV, p. 328-329, pl. 2, fig. B [see for older synonymy].

MATERIAL: Two specimens from Iran: one from Dalmeh, Middle or Late *crepida* Zone, and one from Hodjedk, *crepida* Zone. Five specimens from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: The specimen from Hodjedk is strongly abraded and lacks ornamentation on the cusps, but the subrectangular outline of the base, almost central position of the button and a phoebodont five-cuspid crown show that it belongs to *Ph. typicus*. The button is rather small and subcircular, surrounded by at least five quite large foramina. The specimen from Dalmeh also displays features typical of this species.

Only three teeth of *Ph. typicus* from Oum El Jerane display diagnostic features. Another two are preserved as fragments and only tentatively referred to this species. The more complete specimens differ in size, crown structure, and also slightly in the base shape. The mesio-distal dimension of the base of the largest tooth is almost 1.5 mm (Pl. 6, Fig. C). The outline of the base is rectangular to pentagonal. The median/lingual portion is missing, but the lingual rim was probably not straight, and the base ended lingually in a wide obtuse angle. The button is oval and situated centrally. The crown is typically phoebodont, composed of three main and two intermediate, slightly recurved cusps. The base of the second tooth (c. 0.8 mm) is absolutely rectangular, and the button is slightly less elongated laterally (Pl. 6, Fig. B). The smallest tooth (0.5 mm) has a trapezoid, lingually widening base, with an almost circular, indistinct button. There are no intermediate, accessory cusplets in the crown (Pl. 6, Fig. A).

REMARKS: From the form of the button, Iranian specimens of *Ph. typicus* resemble most closely those from Myrtlevale Formation of north Queensland (Australia, Early *marginifera* Zone), and particularly that figured by GINTER & TURNER (1999, fig. 3A-D); two other, more poorly preserved teeth of this type from the same locality and horizon were illustrated by TURNER (1982, figs 6A-B) under the name of *Phoebodus* cf. *P. politus*.

The teeth from Morocco apparently represent either an ontogenetic series or heterodonty in *Ph. typicus*. Notably, the smallest tooth has the weakest button and the lingually widening base, in a way similar to the "pear-like" smaller specimens of *Ph. gothicus* from Iran. The base of the largest specimen slightly resembles that of *Ph. rayi* which, however, is usually more clearly pentagonal, with the button situated closer to the lingual rim (GINTER & TURNER 1999). The problems encountered in distingushing the early forms of *Ph. typicus* and *Ph. rayi* were discussed by the latter authors.

STRATIGRAPHICAL RANGE: Early to middle Famennian, Late *triangularis* through Late *marginifera* Zones.

Genus *Thrinacodus* ST. JOHN & WORTHEN, 1875

TYPE SPECIES: *Diplodus incurvus* NEWBERRY & WORTHEN, 1866

Thrinacodus tranquillus GINTER, 2000
(Text-fig. 9F-H; Pl. 2, Fig. H; Pl. 3, Fig. H; Pl. 11, Figs H-I)

2000. *Thrinacodus tranquillus* sp. n.; GINTER, p. 374-377, figs 2A-C, 3A-F, 4A-C, 5H-K [see for older synonymy].
2000. *Thrinacodus* cf. *ferox* (TURNER); LONG & HAIRAPETIAN, p. 214-216, fig. 4n.

MATERIAL: 35 specimens from Iran: 35 from Dalmeh, Early *expansa* Zone, and one from Mighan, *expansa* Zone. 14 specimens from Morocco: eight from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and six from Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: Almost all specimens of *Th. tranquillus* from Dalmeh are small and delicate. Therefore, they were particularly vulnerable to destruction on the sea floor and distortions during the history of Dalmeh rocks. The specimens are rather uniform, with symmetrical crowns (sub-equal cusps), but strongly twisted in relation to bases. The bases are usually long and circular in cross section. Completely symmetrical, supposedly symphyseal teeth, such as that figured by GINTER (2000, figs 3A, 4A-C), were not found.

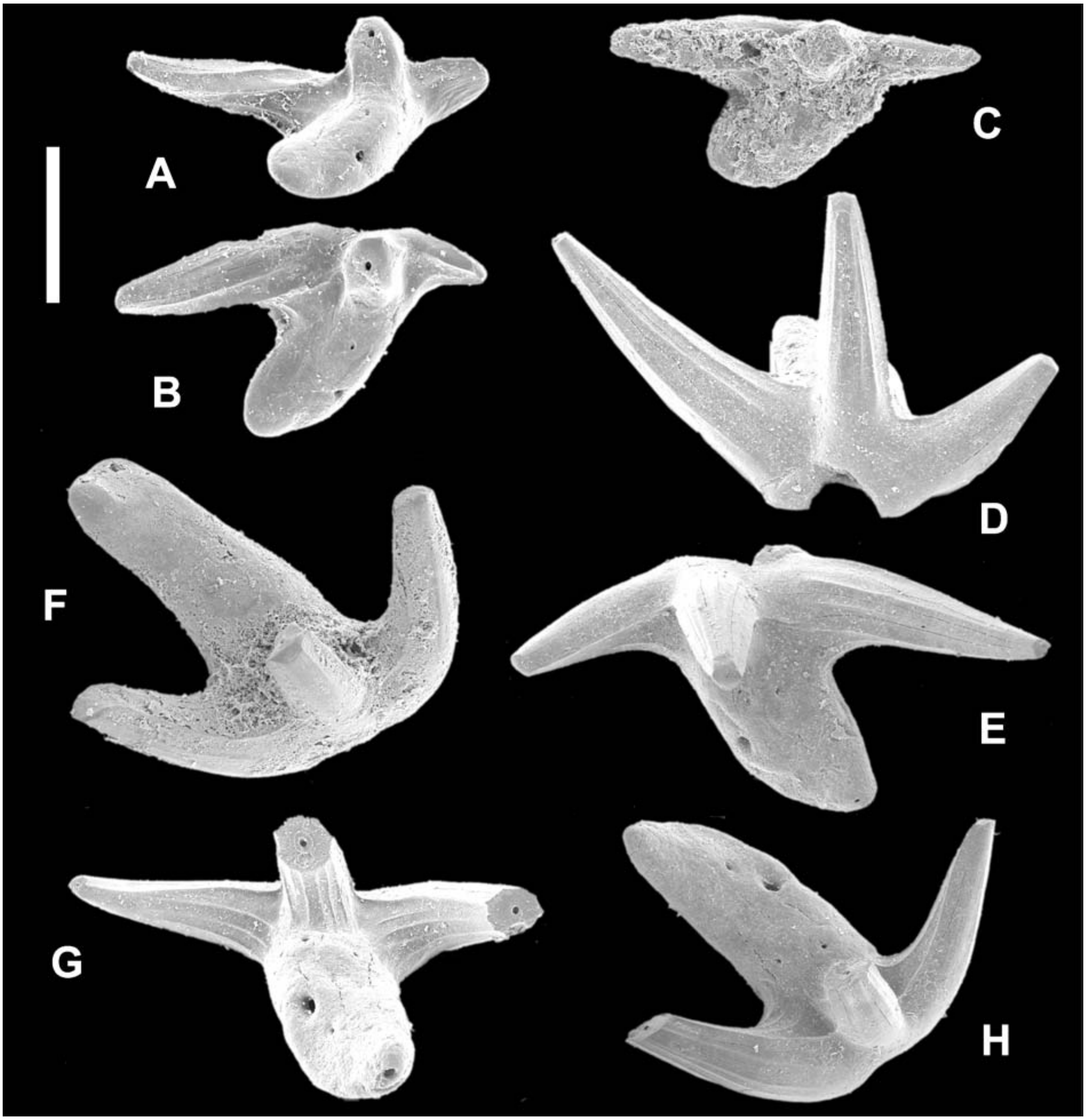


Fig. 9. A-E – *Thrinacodus* cf. *ferox* from Morocco; A-B – IGPUW/Ps/5/15, strongly asymmetrical, sample OEJ-4, lingual and occlusal views; C – IGPUW/Ps/5/16, sample OEJ-2, occlusal view; D-E – IGPUW/Ps/5/17, transitional to *Th. tranquillus*, sample TN-1, labial and occlusal views. F-H – *Th. tranquillus* from Morocco; F – IGPUW/Ps/5/18, sample OEJ-2, occlusal view; G-H – IGPUW/Ps/5/19, sample TN-1, lingual and oblique occlusal views. Scale bar = 0.5 mm

The diversity of *Th. tranquillus* teeth is also rather low in Moroccan material. Specimens with moderately long, lingually flattened bases, with only slightly marked depression, predominate in all studied samples. Such teeth are similar to the type specimen from the Holy Cross Mountains (GINTER 2000, fig. 2A-C) and the most common morphotype from Montagne Noire (GINTER 2000, fig. 3B-F). Their crowns are composed of three regularly cristate cusps, which are basically equal in length. However, some tendency to asymmetry can be observed. Specimens with strongly asymmetrical crowns are separated here from typical representatives of *Th. tranquillus* and described under the name of *Th.* cf. *ferox* (see below).

STRATIGRAPHICAL RANGE: The stratigraphical record of *Th. tranquillus* from most localities in the world falls within the interval from the Late *trachytera* through Early/Middle *praesulcata* Zones. However, data presented by LELIEVRE & DERYCKE (1998) from Hunan, China, indicate that *Th. tranquillus* might occur there in the *marginifera* Zone (see discussion in GINTER 2000, pp. 376 and 384).

Thrinacodus cf. *ferox* (TURNER, 1982)
(Text-fig. 9A-E)

MATERIAL: Four specimens from Morocco: three from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and one from Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: These teeth are characterised by three non-sigmoidal, almost straight and only slightly recurved cusps, covered with subparallel cristae. One of the lateral cusps is the largest, and the other is the smallest. However, the size difference between the cusps may be more or less extreme; there are specimens in which the length of the smallest cusp, very thin and almost unornamented, reaches no more than 1:3 of the length of the largest cusp (Text-fig. 9A-C), whereas in the other this ratio exceeds 1:2 (Text-fig. 9D-E). The base is rather short, turned and twisted. It always forms an acute angle with the largest cusp and an obtuse angle with the smallest. A single foramen opens in the middle part of the base, on the side of the smallest cusp. A kind of small labio-basal depression can be observed, although in most specimens this region is slightly damaged.

REMARKS: This *Thrinacodus* morphotype was first recorded by GINTER (2000, p. 377, fig. 2) from the upper Famennian of Montagne Noire. Then, because of the considerable difference in cusp length, it was named *Thrinacodus* cf. *Th. ferox* and this is followed here for the sake of consistency. However, there is clear evidence from the Moroccan material that there are intermediate forms between strongly asymmetrical specimens of *Th.* cf. *ferox* and typical teeth of *Th. tranquillus* with almost symmetrical crowns (Text-fig. 9G-H). Therefore, it appears likely that *Th.* cf. *ferox* teeth actually belong to the dentition of *Th. tranquillus* and could have been situated, for instance, in the lateralmost part of a jaw.

STRATIGRAPHICAL RANGE: Late Famennian, Early or Middle *expansa* through Late *expansa* Zones.

Family Jalodontidae nov.

REFERRED GENUS: *Jalodus* GINTER, 1999

DIAGNOSIS: Sharks whose teeth possess only three cusps, without intermediate cusplets; the cusps are triangular and compressed labio-lingually, straight or slightly recurved, but never sigmoidal; labial face of the cusps is covered with more or less regular stacked lanceolate ornament or, rarely, subparallel cristae; the median cusp is often much shorter than the lateral ones and may be uncompressed. The base is thick and directed lingually; the apical button is absent or weakly differentiated from the rest of the base; the form of the labio-basal projection is variable, from broad, sometimes arcuate, to tubercle-like.

Genus *Jalodus* GINTER, 1999

TYPE SPECIES: *Phoebodus australiensis* LONG, 1990

Jalodus australiensis (LONG, 1990)
(Pl. 2, Figs A-D; Pl. 8, Figs D-J)

1999. *Jalodus australiensis* (LONG); GINTER, p. 30, pl. 1, figs 1-11 [see for older synonymy].
2000. *Phoebodus? australiensis* LONG; GINTER & IVANOV, fig. 3E.
2000. *Jalodus australiensis* (LONG); GINTER, p. 371, figs 4D, 5A, 6D-E.

MATERIAL: Three specimens from Iran, Dalmeh, Early *expansa* Zone. Ten specimens from Morocco: seven from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and three from Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: The specimens from Dalmeh are abraded; they lack enameloid and therefore ornamentation on the cusps, and are partly covered with clay. However, the triangular outline and labio-lingual compression of the cusps, and the bulbous form of the base leave little doubt that these teeth belong to *Jalodus*.

All specimens of *Jalodus* from Morocco except for one belong to Morphotype 1 sensu GINTER (1990). In most specimens, the typical "lanceolate" ornamentation of the labial side of the cusps, composed of several enameloid layers is preserved. Only the assignment of one large tooth (Pl. 8, Figs H-J) is somewhat doubtful because of its unusually distinct button and the triangular outline of the base, which might indicate its phoebodont affinity. That specimen lost its ornamentation due to abrasion, but the triangular shape of the cusps and their relative length (the central cusp is evidently smaller) suggest that it belongs to *Jalodus*.

STRATIGRAPHICAL RANGE: From the Famennian Early *marginifera* Zone through the early Tournaisian.

Order Xenacanthiformes BERG, 1940
Family indet.
Genus *Bransonella* HARLTON, 1933

TYPE SPECIES: *Bransonella tridentata* HARLTON, 1933

Bransonella? sp.
(Pl. 2, Figs E-F)

MATERIAL: Three specimens from Iran, Dalmeh, Early *expansa* Zone.

DESCRIPTION: These damaged and/or distorted teeth are characterised by three subparallel, non-sigmoidal cusps almost equal in length, subcircular in cross section, with traces of coarse cristation at least on their labial side. None of the specimens has a well preserved base, but it probably was rather small, rounded and with a narrow, crescentic? labio-basal projection. The button is visible only in one specimen (Pl. 2, Fig. F). It is large in relation to the size of the base and its margins are apparently perforated with two or three foramina. It is possible that there was a single, large opening of a basal canal on the lingual rim of the base.

REMARKS: The shape and ornamentation of the cusps and the form of the labio-basal projection resemble those of *Bransonella*? sp. from the upper Famennian of the City Creek Canyon, Utah (GINTER 2001, fig. 4D). Also, *Bransonella* sp. from the Devonian-Carboniferous boundary beds of Timan (IVANOV 1999, pl. 4, fig. 1) and "*Phoebodus* sp. 1" from the Middle *praesulcata* Zone of Haiyang section in Guilin, South China (JI & ZIEGLER 1992, pl. VI, figs 1-2) display similar features. However, the teeth from Dalmeh are so badly destroyed that it is hard to decide if they belong to *Bransonella* or to *Jalodus*. From the latter, they differ only by smaller labio-lingual compression of the cusps and smaller angles between them, which could well be the result of ontogenetic differences or tectonic stress.

Order Symmoriiformes ZANGERL, 1981
Family Stethacanthidae LUND, 1974
Genus *Stethacanthus* NEWBERRY, 1899

TYPE SPECIES: *Physonemus altonensis* ST. JOHN & WORTHEN, 1875

Stethacanthus cf. *thomasi* (TURNER, 1982)
(Pl. 7, Figs A-C)

1991. *Stethacanthus* sp.; GINTER, p. 75, pl. 8, fig. 4, pl. 9, fig. 2-3.
1992. *Cladodus* cf. *C. thomasi* TURNER; IVANOV & *al.*, p. 89, pl. 36, figs 3-4.
1992. *Stethacanthus thomasii* TURNER [sic]; DERYCKE, p. 39-40, fig. 14, pl. 2, fig. 10-11.
1995. *Stethacanthus* cf. *thomasi* (TURNER); GINTER, fig. 2A.
1996. "symmoriid with button partially divided"; GINTER & IVANOV, fig. 4C.
1996. "stethacanthid?"; GINTER & IVANOV, fig. 5C-D.
2000. *Stethacanthus* cf. *thomasi* (TURNER); GINTER & IVANOV, p. 330-331, pl. 1, fig. J.

MATERIAL: Seven specimens from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: *Stethacanthus* cf. *thomasi* from Oum El Jerane has a five-cusped, cladodont crown with a large angle between the outer lateral cusps. The base is lenticular, elongated mesio-distally, with lateral tips extending beyond the foot of the crown. The button and the corresponding labio-basal projection are mesio-distally elongated and distinct.

REMARKS: This form is similar to Early Carboniferous *S. thomasi* (TURNER, 1982). The main difference is the number of lateral cusps; in *S.* cf. *thomasi* there are two cusps on each side, and the number of cusps in *S. thomasi* is usually larger, sometimes different on each side (TURNER 1982, fig. 6C, 8J).

STRATIGRAPHICAL RANGE: Late Frasnian *rhenana* Zone through early Famennian *rhomboidea* Zone.

Stethacanthus spp.
(Pl. 1, Figs C, D, O-Q; Pl. 3, Figs I-M; Pl. 10; Pl. 11, Figs F-G)

MATERIAL: 28 specimens from Iran: 19 from Dalmeh, Middle or Late *crepida* and Early *expansa* Zones; four from Hutk, lower or middle Famennian; one from Ali-Morad, *rhomboidea* or Early *marginifera* Zone; and four from Mighan, two from the Famennian older than the *expansa* Zone and two from the *expansa* Zone. 68 specimens from Morocco: 32 from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and 36 from Tizi Nersas, Late *expansa* Zone. One specimen from Algeria, Gour Bedda, lower or middle Famennian.

DESCRIPTION: Most stethacanthid teeth from Iran have five (rarely three) rather slender cusps, a short triangular lingual platform, a small, single button and a narrow labio-basal projection, rarely wider than the basal part of the central cusp. Such teeth are characteristic especially for Dalmeh (LONG & HAIRAPETIAN 2000, fig. 4e, g, k, l) and Ali-Morad sections (Pl. 1, Figs C-D). They resemble specimens from the upper Famennian of Montagne Noire (GINTER 2000, fig. 7B-G), but similar forms are ubiquitous in the mid to upper Famennian of other regions as well (e.g. Utah, GINTER 2001). A few stethacanthid teeth, especially those from Hutk, have slightly thicker and shorter cusps, almost like in protacrodonts (Pl. 1, Figs O-Q). There is also one unusual tooth from the *expansa* Zone of Mighan section (sample 131, Pl. 3, Fig. I) which has a nine-cusped crown, i.e. with four lateral cusps on each side of the central cusp. The tooth base is well developed and subtriangular. Such multicuspid elements have not been noted from the Famennian thus far, but they are common in the Lower Carboniferous (e.g. in the Viséan of the Ostrówka Quarry, Holy Cross Mountains, GINTER 1994).

All stethacanthids from the late Famennian of Morocco look rather similar. They are always five-cusped, with the lateral cusps much smaller than the central one, and with a well developed, usually triangular lingual extension of the base. However, the specimens may differ in the width of the base, as well as in the shape of the button and the labio-basal projection. Some teeth are elongated mesio-distally with the button forming a crescentic ridge. In such teeth, the labio-basal projection is distinct, its labial view is subrectangular and its basal outline is in the shape of a high and narrow letter "D" (Pl. 10, Figs E-F, H-J). The other specimens are narrower, their button is small, and their labio-basal projection is narrow and hook-like (Pl. 10, Figs C-D). There are also specimens with the lateral parts of the base formed in lingually curved sharp tips (Pl. 10, Fig. G). It is not certain whether all these stethacanthids belong to a single species or not, so they are left in open nomenclature.

Family Symmoriidae DEAN, 1909 ?
Genus *Symmorium* COPE, 1893 ?

REMARKS: For the explanation why inverted commas are used here with the generic name of "*Symmorium*" see discussion in GINTER (1999, p. 36; 2001, p. 721).

"*Symmorium*" *glabrum* GINTER, 1999
(Pl. 9; Pl. 11, Fig. D)

2000. "*Symmorium*" *glabrum* GINTER; GINTER, p. 377-378, fig. 7A [see for older synonymy].

MATERIAL: 90 specimens from Morocco: 84 from Oum El Jerane, Middle *expansa* through Late *expansa* Zones; and six from Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: The collection of "*Symmorium*" *glabrum* teeth from Oum El Jerane is thus far the richest in the world. The character variation is, however, not very high. It is expressed mainly in the presence or absence of intermediate cusplets, relative length of the central cusp, degree of asymmetry of the crown, and the size of the buttons. The most abundant form is that with rather short, symmetrical or only slightly diverging central cusps, with one pair of accessory cusplets, and widely spaced, medium sized buttons (e.g. Pl. 9, Figs A-D). Only a few teeth were found with narrow bases, very long central cusps, and lacking intermediate cusplets (Pl. 9, Fig. I). The highest number of cusps is five. Specimens with additional, outer lateral cusplets, characteristic of the holotype (GINTER 1999, pl. 4, figs 6-9) were not observed in Moroccan material.

STRATIGRAPHICAL RANGE: Middle to late Famennian, Early *marginifera* through Early/Middle *praesulcata* Zones.

"*Symmorium*" sp. A
(Pl. 7, Figs F-G)

MATERIAL: Two specimens from Algeria, Gour Bedda, lower or middle Famennian.

DESCRIPTION: Teeth of "*Symmorium*" sp. A from Algeria are heavily broken, but the main characters are visible. The crown is of cladodont design, composed of five cusps, and the central cusp is much wider and higher than the lateral ones. The base is kidney-shaped, with a labial depression and two triangular labio-basal projections. The buttons are relatively large, bulbous, and separated from one another only by a narrow groove leading labially to a foramen. It is possible that originally the groove was in fact a canal, covered by a narrow "bridge" between the buttons which could have been destroyed by abrasion.

REMARKS: "*Symmorium*" sp. A differs from "*Symmorium*" *glabrum* mainly by the close proximity of the buttons and the much more prominent central cusp. In "*S.*" *glabrum* it may be very long, but it is never so wide in relation to the lateral cusps.

"*Symmorium*" sp. B
(Pl. 7, Figs D-E)

MATERIAL: Eight specimens from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: These cladodont teeth have five-cusped crowns with the central cusp slightly labio-lingually compressed. The base is lenticular, with a labial depression. Two triangular labio-basal projections are present, but the button is undivided, forming a low, crescent-shaped ridge along the lingual margin of the base. The button is perforated by several (three or four) foramina from the lingual and labial sides.

REMARKS: With its morphology, "*Symmorium*" sp. B occupies an intermediate position between typical stethacanthids, such as *S.* cf. *thomasi* and forms with two buttons and two labio-basal projections, such as "*Symmorium*" sp. A or "*Symmorium*" *glabrum*. The best known Famennian shark, the teeth of which are morphologically close, characterised by a labial depression and a probably undivided button, is *Cladoselache* (WILLIAMS 2001; MG, pers. obs.). Later, in the Carboniferous, this combination of features is common in several different groups of cladodont sharks, as for instance in the holotype of true *Symmorium*, *S. reniforme* Cope, 1893.

Cohort Euselachii HAY, 1902
Superfamily Protacrodontoidea ZANGERL, 1981
Family Protacrodontidae CAPPETTA, DUFFIN & ZIDEK, 1993

Genus *Deihim* gen. nov.

TYPE SPECIES: *Deihim mansureae* sp. nov.

ETYMOLOGY: Ancient Persian *deihim* = diadem, crown.

DIAGNOSIS: Sharks with crushing teeth whose crowns are composed of a prominent, pyramidal central cusp and one to three pairs of lateral cusps. The size of the lateral cusps decreases mesially and distally, the basal parts (up to 2/3) of the cusps are fused together and the crown foot is convex which makes the crown resemble a fan or an oriental crown. Each cusp bears between one and four strong cristae at least on its lingual side. A row of additional small cusplets occurs just above the crown-base interface on the labial side. The base is extended lingually. The occlusal-lingual side of the base is perforated with numerous horizontal canals or grooves which continue into the crown and towards basal-labial openings; the basal-lingual part of the base is devoid of foramina. A narrow mesio-distal groove runs along the lingual crown-base interface.

Deihim mansureae sp. nov.
(Text-fig. 10; Pl. 1, Fig. R; Pl. 2, Fig. K; Pl. 4, Figs F-G, J- M; Pl. 5, Figs A-M)

2000. ? *Protacrodus* sp.; LONG & HAIRAPETIAN, p. 217-218, fig. 4o.

2000. *Protacrodus* sp. cf. "*P. aequalis*" sensu GINTER & TURNER; YAZDI & TURNER, p. 226, figs 3.4-7, 4.4 [non fig 3.8-10 = *Protacrodus* sp.].

ETYMOLOGY: In honour of Miss Mansooreh GHOBADI POUR, M.Sc., from the University of Esfahan, who helped us greatly during our investigation of the material from Dalmeh.

HOLOTYPE: Specimen IGPUW/Ps/5/1 (Text-fig. 10A-D) from Hutk, sample 38/23, Famennian, undetermined position within the interval from the Early *crepida* through Late *marginifera* conodont Zones (see WENDT & *al.* 2002, fig. XX).

DIAGNOSIS: As for genus.

MATERIAL: 24 specimens from Iran: 11 from Dalmeh, Middle or Late *crepida* and Early *expansa* Zones; nine from Hutk, lower or middle Famennian; three from Hodjedk, *crepida* Zone; and one from Mighan, Famennian, older than the *expansa* Zone.

DESCRIPTION: For convenience, the material is assigned to four tooth morphotypes based upon the number of cusps, labio-lingual/mesio-distal ratio, symmetry or asymmetry of the crown, the prominence of the central cusp in relation to the lateral cusps, the angle between the cusps, and the degree of convexity of the base in the crown region.

Morphotype 1 (M1; Text-fig. 10G-I; Pl. 4, Figs L-M; Pl. 5, Fig. J) has a rather narrow base (short mesio-distally), strongly arched below the crown. There are only two lateral cusps on each side, diverging at high angles. The central cusp is by far the largest in the crown, almost as in cladodonts. Morphotype 2 (M2; Text-fig. 10A-F; Pl. 1, Fig. R; Pl. 5, Figs A-C, G-I), represented by the type specimen, is more elongated mesio-distally. It is characterised by three pairs of lateral cusps diverging less strongly than in M1. The relative prominence of the central cusp cannot be determined with certainty because the tips of the cusps are worn. However, judging from the width of its basal part, that cusp was possibly relatively shorter than in M1. In Morphotype 3 (M3; Pl. 4, Figs F-G; Pl. 5, Figs K-M) the difference in size between the central and the lateral cusps is even less spectacular. The angle between the cusps, and the convexity of the base is similar to that in M2. The labio-lingual/mesio-distal dimension ratio is low and the crown may be asymmetrical. The most common crown asymmetry consists of the following features: the central cusp is inclined laterally (probably always distally); the cusps on the mesial side of a tooth, if our identification is correct, are almost equal to each other in size or

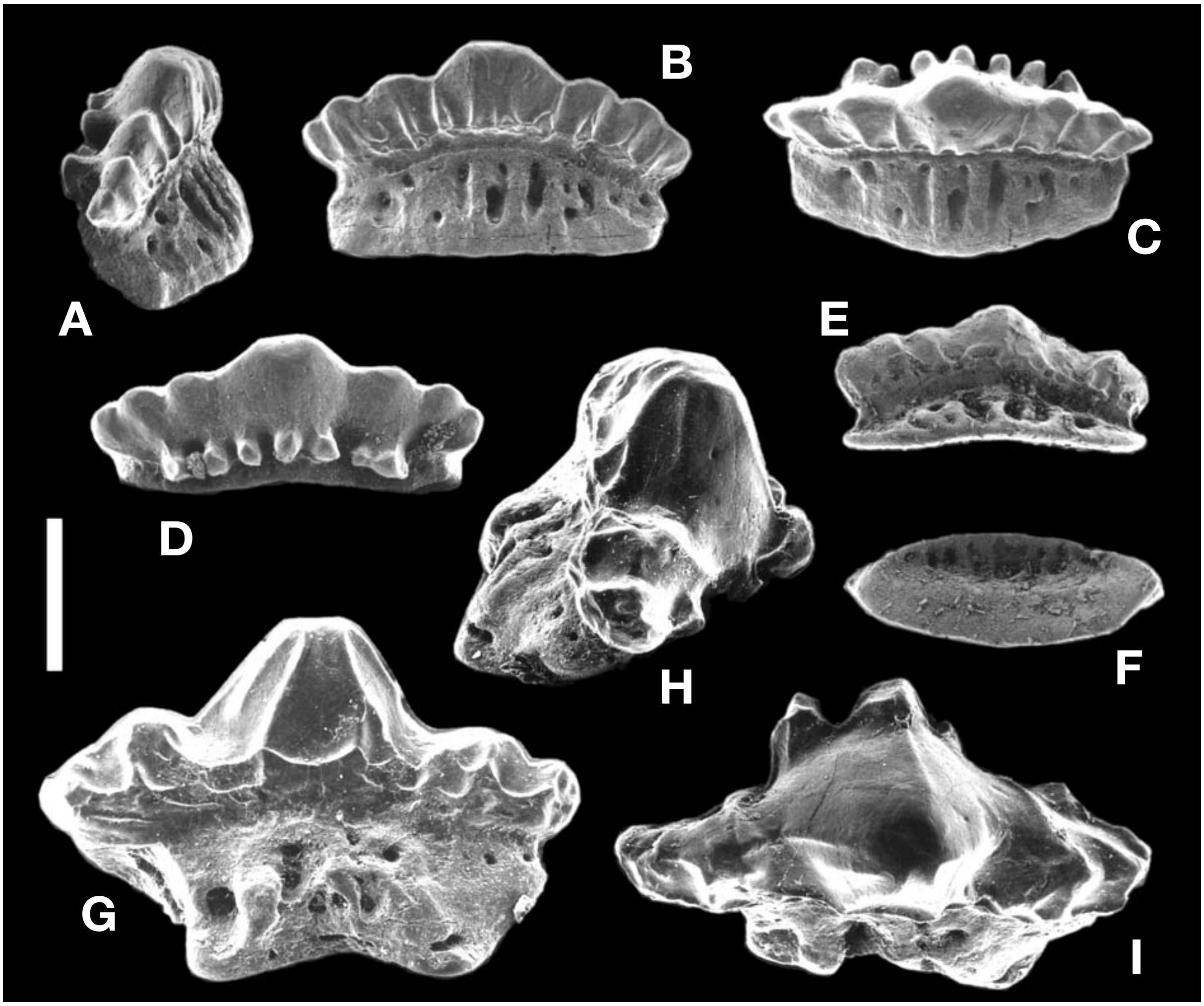


Fig. 10. *Deihim mansureae* gen. et sp. nov. from Iran. A-F – Morphotype 2; A-C – IGPUW/Ps/5/1, **holotype**, Hutk, sample 38/23, lateral, lingual, occlusal, and labial views; E – IGPUW/Ps/5/2, lingual view; F – IGPUW/Ps/5/3, basal view. G-I – Morphotype 1, specimen AEU 204, Dalmeh, sample 64, lingual, lateral and occlusal views. Scale bar = 0.5 mm

gradually lower laterally, whereas the second cusp on the distal side is much larger than the others which may be reduced to the size of tubercles. Generally, the teeth of M3 are very similar to the teeth of *Protacrodus*, from which they differ only in possessing a labial row of additional cusplets. There also occur two unusual tricuspid specimens, one from the *crepida* Zone of Hodjedk section (Pl. 5, Figs D-F) and another from the sample 64 (Early *expansa*) of the Dalmeh section, which can be tentatively ascribed to *D. mansureae* because of the presence of labial cusplets, and will be called here Morphotype 4 (M4). These teeth have a large but rather slender central cusp, almost twice as long as the lateral cusps. There is only one cusp on each side, diverging at about 45 degrees from the central cusp. Finally, there is one more tooth from Hodjedk, similar to M4, but devoid of labial cusplets. This specimen is only provisionally in the morphological range of *D. mansureae* (Pl. 4, Figs J-K).

REMARKS: We presume that all of these morphotypes can occur in one jaw, and that the differences between them is the result of their different positions and functions. Since we deal here only with isolated shark teeth, it is impossible to prove that statement directly. However, a reasonable model for a shark jaw possessing all of the described above tooth forms can be proposed, based on the dentition of the well known Recent shark *Heterodontus* (Cappetta 1987, fig. 24C). In the latter dentition there are two general dental types: seven rows (a symphyseal row and three rows on each side) of clutching teeth and 18 rows (nine on each side) of grinding teeth. Clutching teeth are relatively small and narrow, they have differentiated cusps, and serve to catch and hold prey. Grinding teeth, used to destroy shells, are elongated mesio-distally. Their crowns are covered with thick enameloid layers and are devoid of separate cusps; the size of such teeth increases posteriorly, but close to the angular part of the jaw, they become smaller again (the non-linear gradient monognathic heterodonty sensu Duffin & Ward 1983). Cappetta (1987) states that in the early ontogenetic stage the dentition of *Heterodontus* is essentially of clutching type throughout and the lateral grinding teeth gradually differentiate toward adulthood.

The dentition of *D. mansureae* cannot be called a clutching-grinding type, because none of the tooth morphotypes has completely fused cusps, but it possibly represents a clutching-crushing type, unknown from modern sharks. In the model proposed here, the M1 teeth, narrow and with high central cusps play a clutching role in a few anterior (mesial) tooth-families, together with M4 which, if they really belong to that species, could represent the symphyseal row. M2 occupy the intermediate position at the anterolateral parts of the jaw, and in the most posterolateral (distal) regions protacrodont-like crushing teeth of M3 occur. The extreme lateral position of the latter teeth probably implies their asymmetry. It is important to point out that, except perhaps for the symphysial M4, all of the teeth were capable not only of catching prey, but also crushing. In all of the morphotypes the central cusps are strong, coarsely cristate and their basal parts are broad and fused to the nearby lateral cusps. Very similar reconstructions of clutching-crushing dentitions were proposed for the Mesozoic palaeospinacid sharks *Synechodus* (Duffin & Ward 1993, text-fig. 4) and *Paraorthacodus* (Duffin 1993, text-fig. 3). However, according to the authors of the latter two reconstructions, in addition to clutching and crushing forms there occur typical grinding teeth, without cusps, in the posterolateral positions.

Although we consider the dentition model presented above as the most probable, it is also possible that differences in tooth shape are the result of sexual dimorphism in *Deihim*. In several Recent batoids, females have crushing dentitions and males are characterised by clutching teeth (Cappetta 1987). Unfortunately, the small number of specimens does not allow us to make any effective statistical analysis. We can only say that the number of strictly crushing teeth (M3) exceeds the number of teeth with the ability to clutch or pierce in our samples (M1, M4). This is inconclusive since the number of males and females in a shark community is not necessarily equal.

The teeth in each tooth family were probably closely spaced. Their bases were overlapping and blood vessels continued from one tooth to another, through the numerous large openings on the occlusal-lingual and basal-labial surfaces of the root. The precise function of the labial cusplets is unclear. They might have served, together with the basal parts of lingual cristae, as a kind of locking device, protecting the tooth family from separate mesio-distal motion of teeth during crushing. They might also have protected the soft tissue between the teeth against sharp particles of crushed shells. The presence of labial cusplets or nodes is not unique for *Deihim*. They are common in Mesozoic hybodont sharks, such as *Polyacrodus cloacinus* (Duffin & Delsate 1993, pl. 2, fig. 2), but they are rarely so numerous and distinct.

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

Protacrodontidae cf. *Deihim mansureae* sp. nov.
(Pl. 6, Figs F-K)

MATERIAL: Three specimens from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: The cusps in specimens from Oum El Jerane are weakly differentiated. However, the row of labial cusplets indicate that these teeth may belong to *Deihim* gen. nov. The labial view of a better preserved specimen (Pl. 6, Fig. F) indicates that it possessed seven cusps in a symmetrical crown, as in Morphotype 2 of *D. mansureae* (see Text-fig. 10A-E). The other tooth (Pl. 6, Figs I-K) appears to have completely fused cusps, which is not present in the original, Iranian material of that species.

Genus *Protacrodus* JAEKEL, 1921

TYPE SPECIES: *Protacrodus vetustus* JAEKEL, 1921

Protacrodus serra sp. nov.
(Text-fig. 11; Pl. 2, Figs L-N; Pl. 11, Figs A-C)

1990. "*Cladodus*" sp.; GINTER, p. 77, pl. 4, fig. 9.
2000. *Protacrodus* cf. *vetustus* JAEKEL; GINTER, p. 378-379, fig. 8.

ETYMOLOGY: Latin *serra* = saw.

HOLOTYPE: Specimen IGPUW/Ps/5/23 (Text-fig. 11H-J) from Tizi Nersas, Morocco, sample TN-1, upper Famennian, Late *expansa* conodont Zone.

MATERIAL: 12 specimens from Iran, Dalmeh, Early *expansa* Zone. 36 specimens from Morocco: five from Oum El Jerane, Late *expansa* Zone; and 31 from Tizi Nersas, Late *expansa* Zone.

DIAGNOSIS: Sharks with protacrodont teeth characterised by a labio-lingually compressed, slightly recurved crown, composed of three to seven cusps, connected by a distinct occlusal blade. The crown may be strongly asymmetrical with all the cusps inclined distally.

DESCRIPTION: Four basic morphotypes of *P. serra* sp. nov. teeth can be distinguished in the material from Morocco. Morphotype 1 (M1) has a symmetrical or almost symmetrical crown, composed of only three cusps (Text-fig. 11A-E, Pl. 11, Fig A). The central cusp is high and wide, and its foot occupies about 60% of the base width. It is more than twice the height of the lateral cusps, which are sometimes reduced to accessory cusplets. The base of M1 is narrow, but its lingual extension is rather long, in comparison with other morphotypes. The lingual side of the base is perforated by one to three large canals and a horizontal row of minute pores occurs on the labial side, at the crown-base interface.

Morphotype 2 (M2) is wider and its crown is composed of four to five cusps (Pl. 2, Figs L-N, Pl. 11, Fig. B). The size difference between the central and lateral cusps still may be considerable. The number of lateral cusps depends on the degree of asymmetry. In more symmetrical specimens two lateral cusps are well developed on each side, but when the central cusp is strongly inclined distally, the smaller lateral cusp on that side is usually lost.

Morphotype 3 (M3), represented by the holotype, has five to six cusps in the crown (Text-fig. 11H-J, Pl. 11, Fig. C). It is strongly asymmetrical and usually has two lateral cusps on each side of the central cusp, which is less prominent than in M1 and M2. Sometimes, a third lateral cusplet can be observed on the mesial side of the central cusp and the number of cusps on the distal side may or may not be reduced to one. The lingual extension of the base is very short, forming only a narrow shelf along the crown. M3 is the predominant morphotype in the material.

Morphotype 4 (M4) is symmetrical, with a short lingual extension, almost like in M3, and possesses three lateral cusps on each side (Text-fig. 11F-G).

All morphotypes have a few large openings on the lingual face of the base and a row of smaller pores in the labio-basal region, as in M1.

REMARKS: As in the case of *Deihim mansureae* the dentition of *P. serra* sp. nov. is of clutching-crushing type. However, the teeth of *P. serra* probably had yet another, cutting function, unique amongst Devonian sharks. Teeth of M1 and M2 were probably situated anteriorly in the dentition and their high and broad central cusps, provided with a blade, could not only have caught prey, but also initially cut its hard skin or carapace. The well developed lingual basal extension in M1 made considerable overlapping of the bases in parasymphyseal tooth rows possible, and consequently, it was probably a good protection against a single tooth being torn out by a struggling animal. M3, characterised by asymmetrical, low cusps apparently represent lateral tooth-families and served for further disintegration of food particles. It is unknown in what position symmetrical teeth of M4 could have functioned in this model, and it is possible that they actually belong to some other, more conservative species of *Protacrodus*.

STRATIGRAPHICAL RANGE: Late Famennian, Early through Late *expansa* (Middle *praesulcata*?) Zones.

Protacrodus vetustus JAEKEL, 1921
(Pl. 6, Fig. L)

1938. *Protacrodus vetustus* Jaekel; Gross, p. 131-141, figs 3-5, pl. 2.
1964. *Protacrodus vetustus* Jaekel; Glikman, fig. 20.
1981. *Protacrodus vetustus* Jaekel; Zangerl, p. 62, fig. 64, 65.
1991. *Protacrodus* cf. *vetustus* Jaekel; Ginter, p. 75, pl. 8, fig. 5.
1995. *Protacrodus* cf. *vetustus* Jaekel; Ginter, figs 2B [?], 4B.
2000. *Protacrodus* cf. *vetustus* Jaekel; Ginter & Ivanov, pl. 1, fig. F.

MATERIAL: Four specimens from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: Most specimens of *Protacrodus* are broken and abraded, but it is possible to observe pyramidal, uncompressed cusps, and a base with a very short lingual extension, perforated with horizontal, labio-lingual canals. The best preserved specimen shows a thick cen-

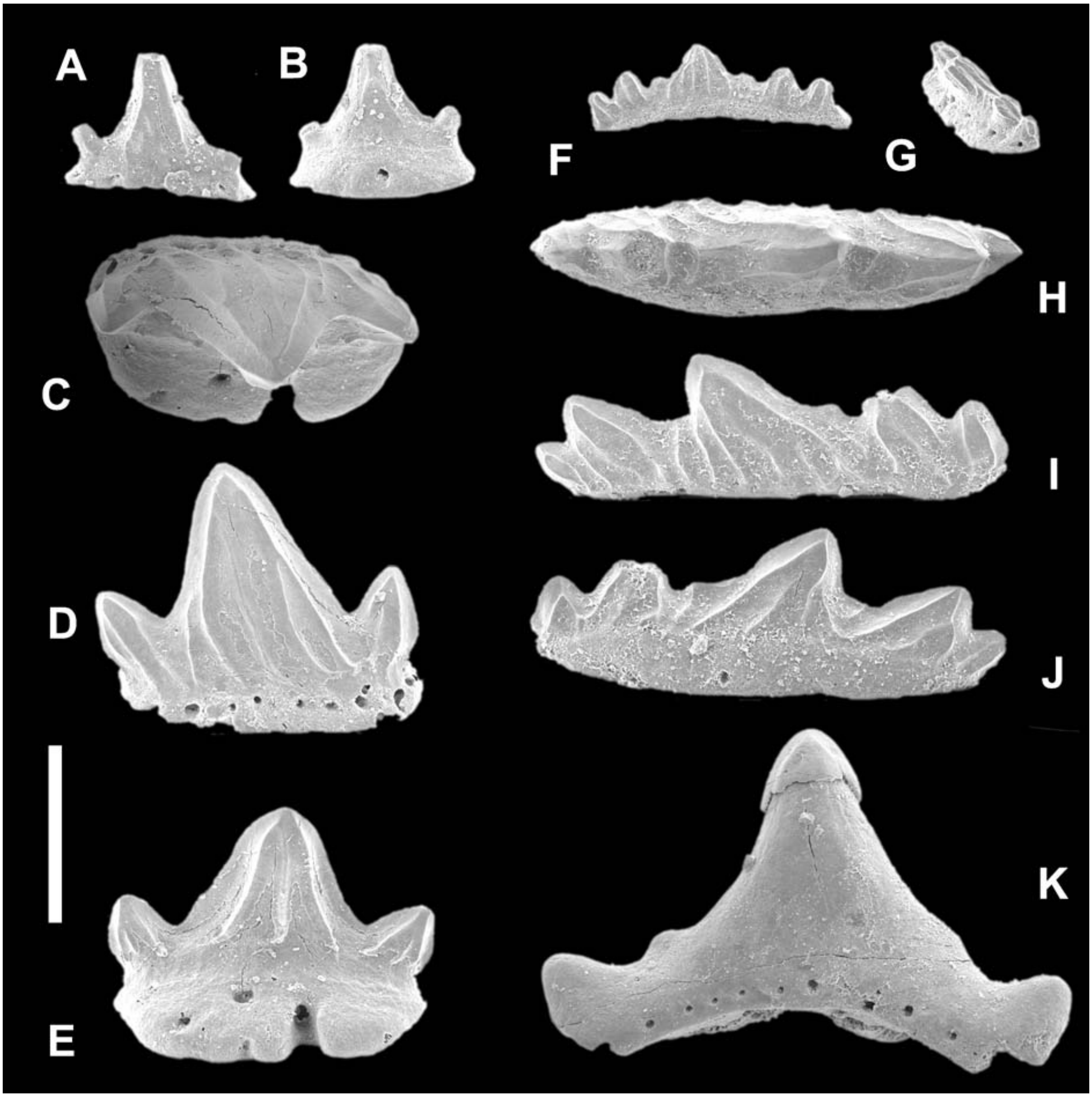


Fig. 11. *Protacrodus serra* sp. nov. from Morocco, sample TN-1. A-E – Morphotype 1; A-B – IGPUW/Ps/5/20, labial and lingual views; C-E – IGPUW/Ps/5/21, occlusal, labial and lingual views. F-G – Morphotype 4, IGPUW/Ps/5/22, labial and oblique lateral view. H-J – Morphotype 3, IGPUW/Ps/5/23, **holotype**, occlusal, labial, and lingual views. K – IGPUW/Ps/5/24, almost completely devoid of enameloid, labial? view. Scale bar = 0.5 mm

tral cusp and three slightly smaller lateral cusps, all ornamented with distinct cristae, joining at the tips (the other side of the tooth is missing). All these are typical features of *P. vetustus* (compare ZANGERL 1981, figs 64-65).

STRATIGRAPHICAL RANGE: Latest Frasnian – early Famennian.

Protacrodus spp.
(Pl. 1, Figs A-B; Pl. 4, Figs D-E, H-I, N; Pl. 6, Fig. D-E)

MATERIAL: 28 specimens from Iran: 23 from Dalmeh, Early *expansa* Zone; one from Ali Morad, *rhomboidea* or Early *marginifera* Zones; and four from Mighan, Famennian, *expansa* Zone and older. One specimen from Morocco, Oum El Jerane, Latest *crepida* or Early *rhomboidea* Zones.

DESCRIPTION: In addition to *P. serra*, a large variety of protacrodont teeth was recorded from Famennian rocks of Iran. Most of them are specimens resembling teeth of *P. vetustus*, elongated mesio-distally, with a prominent but not very high, pyramidal central cusp and several pairs (3-4) of similar lateral cusps gradually reducing in height mesially and distally (Pl. 1, Fig. A). However, the state of preservation usually does not allow such teeth to be properly identified.

In the specimen of *Protacrodus* sp. from Oum El Jerane (Pl. 6, Fig. D-E), a large part of the tooth-base and probably one lateral cusp are missing. The remaining part of the tooth is composed of a broad central cusp, a basal part of a much smaller lateral cusp and a piece of a lingually extended base. The cusps are labio-lingually compressed and covered with strong cristae. Most cristae probably joined at the tips of the cusps, but there are also three or four on each side which run vertically and reach the mesio-distal ridge which connects the cusps. The tooth resembles *Protacrodus* sp. B, found from the upper Famennian of Utah (GINTER 2001, fig. 5A-C). It differs from *P. vetustus* in the strong compression of the cusps and from all known *Protacrodus* species in the unusual sculpture of the area between the cusps.

Genus *Dalmehodus* LONG & HAIRAPETIAN, 2000

TYPE SPECIES: *Dalmehodus turnerae* LONG & HAIRAPETIAN, 2000

Dalmehodus turnerae LONG & HAIRAPETIAN, 2000

MATERIAL: One specimen from Iran (EUIV 99.7.221, LONG & HAIRAPETIAN 2000, fig. 6g), Dalmeh, Early *expansa* Zone.

REMARKS: LONG & HAIRAPETIAN (2000) erected a new protacrodontid genus and species, *Dalmehodus turnerae,* based on three teeth from Dalmeh. These authors do not provide a formal diagnosis, but from the description the following sentence is the most important for the characterisation of the new taxon: "Unlike typical *Protacrodus* teeth the crown lacks a central main cusp but has a series of cusps varying in number from four (EUIV 99.9.232, Figure 6f) to eight (EUIV 99.7.221, Figure 6g) of nearly equal height." (LONG & HAIRAPETIAN 2000, p. 217). However, the holotype of the species (fig. 6f in LONG & HAIRAPETIAN 2000) is actually only half of a tooth, absolutely typical of *Protacrodus*, with a prominent (although broken) central cusp and three lower lateral cusps visible on the preserved side. It clearly corresponds to *P. vetustus*-like protacrodonts from Iran (see above). On the other hand, all eight cusps of a specimen figured in fig. 6g by LONG & HAIRAPETIAN (2000) are indeed virtually equal. The third tooth is strongly abraded, so nothing can be said about its cusps. Therefore we propose to retain the name *Dalmehodus turnerae* LONG & HAIRAPETIAN, 2000 temporarily only to the tooth which reflects the characteristic given in the original description, i.e. to the specimen EUIV 99.7.221 of the type material.

The "coarse reticulate pattern of ornamentation" of the basal part of the crown, presented by LONG & HAIRAPETIAN (2000, p. 216) as a diagnostic feature of the genus *Dalmehodus*, is common in several different Famennian protacrodontids and orodontids. It occurs in *Protacrodus* sp. A and "*Orodus*" sp. from Utah (GINTER 2001, fig. 6D-E, H), in *Deihim mansureae* gen. et sp. nov. from Iran (Text-fig. 10G), and in "Protacrodontidae cf. *Deihim mansureae*" from Morocco (Pl. 6, Fig. J). This pattern appears to be a result of an intersection between vertical cristae, typical of teeth of all protacrodontids, and the growth lines of the crown.

Superfamily Hybodontoidea ZANGERL, 1981
Family Polyacrodontidae GLIKMAN, 1964
Genus *Lissodus* BROUGH, 1935

TYPE SPECIES: *Hybodus africanus* BROOM, 1909

Lissodus sp.
(Text-fig. 12; Pl. 4, Figs A-C)

MATERIAL: 11 specimens from Iran: nine from Dalmeh, Early *expansa* Zone, and two from Mighan, *expansa* Zone.

DESCRIPTION: Teeth of *Lissodus* sp. have the narrow labial peg moderately developed. It can bear two small cusplets (Text-fig. 12F, H). The occlusal crest is well developed, usually crenulated, although crenulation can be partly lost due to abrasion or antemortem wear. The crest bears up to three lateral cusplets both mesially and distally (Text-fig. 12F, I). The crown is generally smooth, but in one specimen vertical striations occur on the lingual side (Text-fig. 12C-D). The central principal cusp is prominent and directed labially. The lingual margin is virtually straight in lingual view and straight to convex in coronal view. A horizontal, longitudinal crest occurs on both sides of the crown shoulder. The base is generally vertical, but can be slightly angled lingually, and it is perforated by many canal foramina and grooves.

The teeth vary from about 1 to 2.2 mm in mesio-distal width, but the labio-lingual dimension is rather stable (about 0.6-0.8 mm), so the proportions in narrower and wider specimens are different. In the narrowest specimens, the crown is reduced almost only to the principal cusp, the labial peg, and a single lateral cusplet on each side (Text-

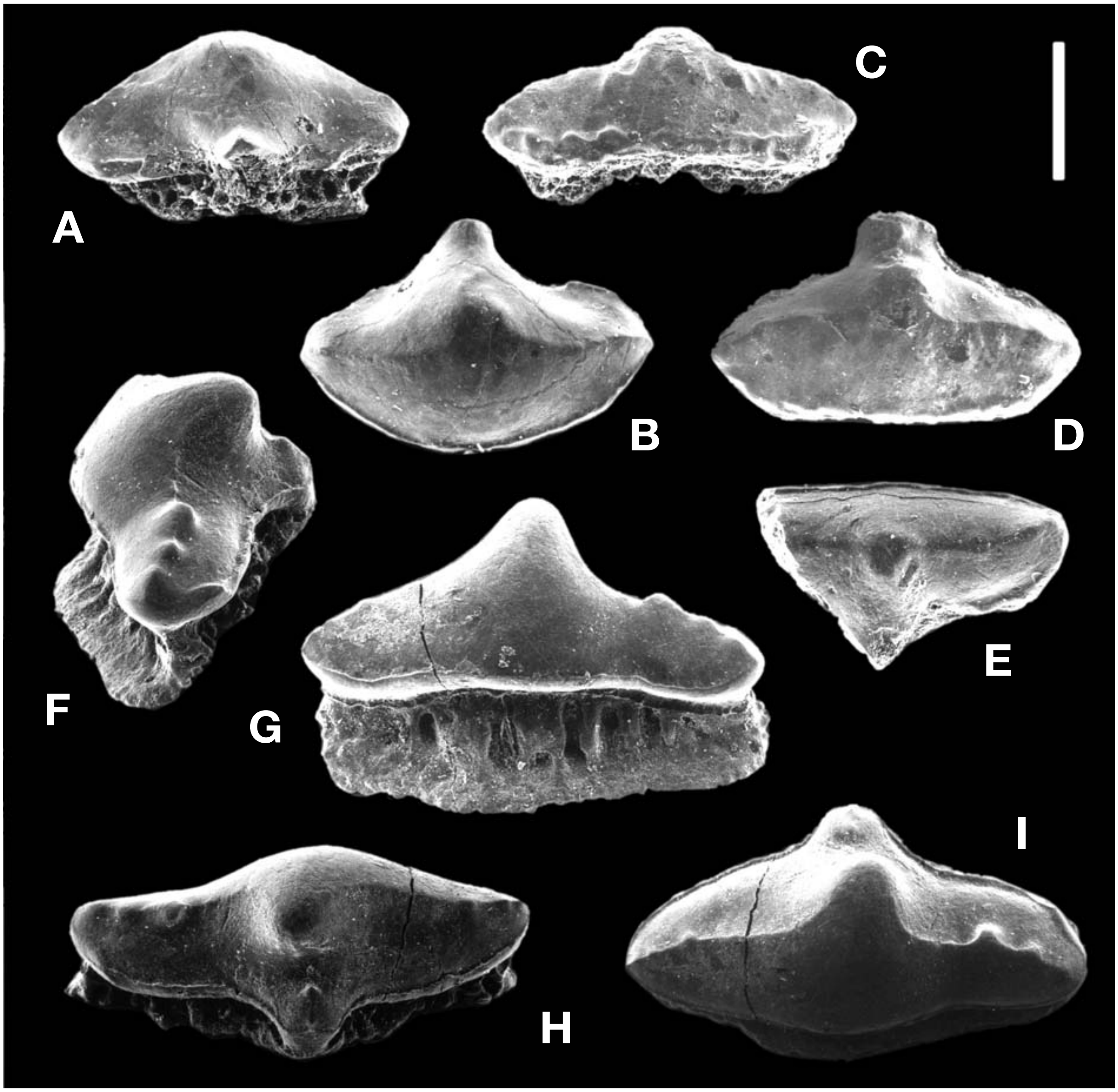


Fig. 12. *Lissodus* sp. from Iran, Dalmeh, sample 64. A-B – AEU 205, labial and occlusal views. C-D – AEU 206, lingual and occlusal views. E – AEU 207, occlusal view. F-I – AEU 208, lateral, lingual, occlusal/labial and occlusal views. Scale bar = 0.5 mm

fig. 12A-B). The lingual margin in such specimens is strongly convex. In wide specimens, the principal cusp is much less prominent in relation to the size of the tooth and a long, crenulated occlusal crest runs towards the mesial and distal ends of the crown (Pl. 4, Figs A-B). The lingual margins of such teeth are always straight or may even display a shallow concavity. Some specimens of *Lissodus* sp. are slightly asymmetrical, but this also would be a result of unequal abrasion or tectonic distortion (Pl. 4, Fig. B).

REMARKS: The teeth from Iran cannot be assigned to any of the species of *Lissodus* described by DUFFIN (1985) in his detailed revision of that genus. The only taxon to which *Lissodus* sp. is slightly similar is *L. selachos* (ESTES, 1964) from the Late Cretaceous. However, although the form of the labial peg and the lateral parts of the crown are similar in both species, the prominent, labially curved principal cusp of *L.* sp. is completely different from the indistinct, tubercle-like central cusp of *L. selachos* (DUFFIN 1985, pl. 1, fig. 1; 2001, fig. 38). The labial direction of that cusp was noted from an isolated crown of a Carboniferous tooth from the Iowa Point Shale (Lower Pennsylvanian) of Madison County, Iowa, illustrated by TWAY & ZIDEK (1983, fig. 77a) as the Subtype 107 and redrawn by DUFFIN (1985, text-fig. 10; 2001, fig. 6) as *Lissodus* sp. If this is indeed a fragment of a tooth of *Lissodus*, its labial peg is unusually broad and the lingual concavity of the crown margin is apparently present even in narrow specimens.

The discovery of *Lissodus* from Dalmeh and Mighan is the first published and illustrated record of this genus from the Devonian. The only earlier information about the occurrence of *Lissodus* in the late Famennian comes from DERYCKE & *al.* (1995). They note the presence of *Lissodus* sp. cf. *L. zideki* and *L.* spp. from the upper Famennian and Namurian A of Belgium. However, no descriptions or illustrations are provided.

Order Orodontiformes ZANGERL, 1981
Family Orodontidae DE KONINCK, 1878
Genus *Orodus* AGASSIZ, 1838

TYPE SPECIES: *Orodus cinctus* AGASSIZ, 1838

Orodus sp.
(Pl. 2, Figs I-J)

MATERIAL: 26 specimens from Iran, Dalmeh, Early *expansa* Zone.

DESCRIPTION: Teeth which are tentatively referred here to orodontids are mesio-distally elongated elements composed of a vertically directed base with many canal openings and grooves, similar to that of elongated specimens of *Lissodus*, and a compact crown with fused cusps. The crown can be smooth (Pl. 2, Figs I-J), can possess some remnants of cusps and their cristation, or can be coarsely cristate (LONG & HAIRAPETIAN 2000, fig. 5). Usually the central part of the crown is somewhat wider. There is a large size range of orodont teeth in Dalmeh; the mesio-distal dimension may vary from 1 to 23 mm. The largest tooth (EUIV 99.5.207, LONG & HAIRAPETIAN 2000, fig. 5a) was found on the rock surface.

REMARKS: Orodontids from Dalmeh are characterised by a morphology intermediate between protacrodontids, such as *Protacrodus* or *Deihim*, and crushing lateral teeth of hybodontoids (e.g. *Lissodus*). From protacrodontids they differ by further fusion of the cusps and possibly by partial replacement of orthodentine with osteodentine and tubular dentine (LEBEDEV & V'YUSHKOVA 1993). Judging only from tooth morphology, it is difficult to distinguish true orodonts from representatives of other chondrichthyans with similar feeding habits (e.g. eugeneodontids). We are also not sure if all teeth of *Orodus* sp. belong to the same or to several different species.

Elasmobranchii *incertae sedis*
Genus *Clairina* GINTER, 1999

TYPE SPECIES: *Phoebodus marocensis* DERYCKE, 1992

Clairina marocensis (DERYCKE, 1992)
(Pl. 11, Fig. E)

1992. *Phoebodus marocensis* sp. n.; DERYCKE, p. 31-32, fig. 10, pl. 1, fig. 4, 7, 8.
1995. "*Phoebodus*" *marocensis* DERYCKE; GINTER, fig. 4A.
1999. *Clairina marocensis* (DERYCKE); GINTER, p. 41, pl. 5, figs 1-5.

MATERIAL: One specimen from Morocco, Tizi Nersas, Late *expansa* Zone.

DESCRIPTION: The single tooth of *C. marocensis* unfortunately lacks the chevron ornamentation of the lingual side, typical of this species. However, the general outline of the crown, with five non-sigmoidal cusps lowering laterally, and the very short base almost lacking any articulation device, leave little doubt as to the affinity of this specimen.

STRATIGRAPHICAL RANGE: Famennian, *crepida* through Late *expansa* Zones.

New data on Famennian phoebodontids (M.G.)

Teeth belonging to virtually all known Famennian phoebodontid species (Text-fig. 13) were recovered from Iranian, Moroccan and Algerian sections. It seems likely that only *Ph. politus* and *Th. ferox* s.s. are missing (but see the next, palaeogeographic chapter and the description of *Ph. gothicus* from Iran). Moreover, two new taxa, *Ph. depressus* sp. nov. and *Ph. gothicus transitans* subsp. nov., were found. New records confirm certain earlier assumptions concerning the development of phoebodontid dentition in the Famennian and reveal new, hitherto unknown evolutionary stages of this group.

The origin and diversity of Ph. gothicus

In Iran, *Ph. gothicus* occurs in much older strata than in the other regions of the world. Thus far, the oldest record of this species came from a cephalopod limestone layer of the Early *marginifera* age from the Łagów-Dule section in the Holy Cross Mountains, Poland. All other records were either imprecisely dated or younger. In the Dalmeh section in Central Iran, *Ph. gothicus* was recovered, if the datings are correct, from the Middle or Late *crepida* Zone. It co-occurs here with rare *Ph. turnerae* and *Ph. typicus*. This suggests that *Ph. gothicus* might have evolved on the shelf of North Gondwana and subsequently, close to the early/middle Famennian boundary, migrated to the other regions. It is noteworthy that *Ph. gothicus* is still unknown from the Early *marginifera* Zone of Queensland and the South Urals, where only *Ph. typicus* and/or *Ph. turnerae* were found. It seems therefore that *Ph. gothicus* spread out first on the margins of Northwest Gondwana and southern Laurussia. By the end of the *marginifera* Zone it flourished in the shallow sea of Iowa (Gross 1973).

Intraspecific morphological variation and/or heterodonty in teeth of *Ph. gothicus* is high. In Iran, several new tooth morphotypes probably representing this species were found. Among the new forms, those with widening lingually bases, forming the shape of a pear or a spoon, or in some cases of a high trapezium are the most common. They are almost exclusive to Iran; a few similar teeth were observed in the upper Famennian of the Holy Cross Mountains (Ginter 1994). Although they might belong to some other, yet undescribed phoebodont species, such features as a length to width ratio of over 1.0 and the subcircular, centrally placed button are typical of *Ph. gothicus*. Moreover, transitional forms between such teeth and typical forms with "gothic" bases are observed. It appears likely that the dentition of an Iranian-style *Ph. gothicus* was composed of the following forms:

- very small, pentagonal teeth, with only three short, non-recurved, almost straight cusps (Pl. 1, Figs H-I);

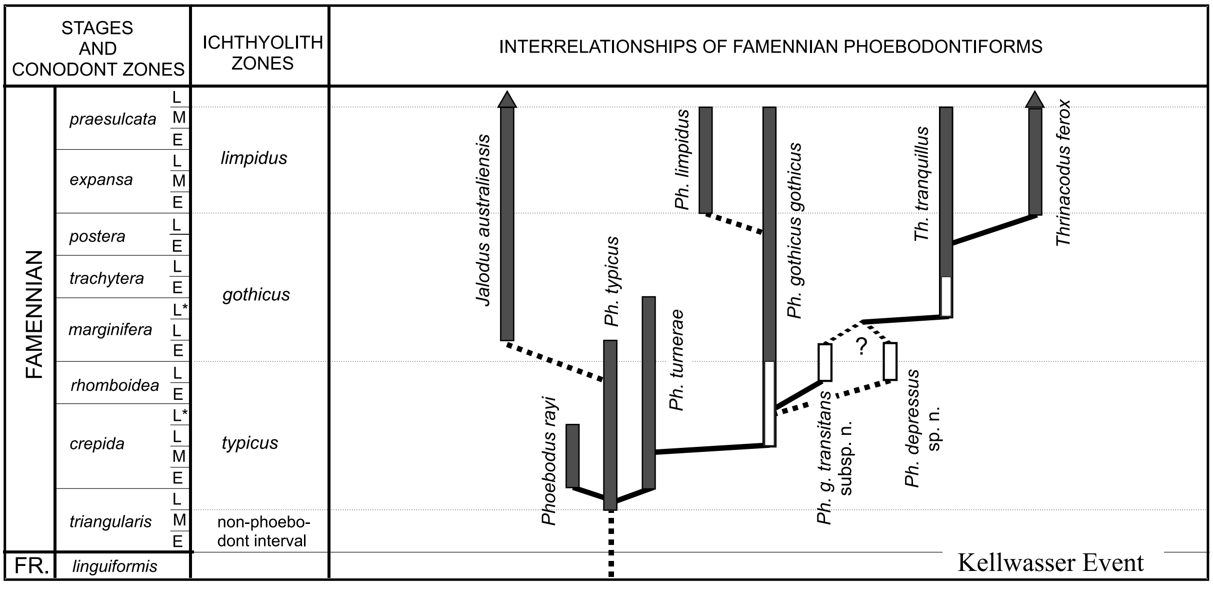


Fig. 13. Stratigraphical ranges and possible interrelationships of Famennian phoebodontiforms, against Standard Conodont Zonation (Ziegler & Sandberg 1984) and phoebodont-based ichthyolith zonation (Ginter & Ivanov 1995). Empty boxes – uncertain stratigraphic ranges. E – Early, M – Middle, L – Late, L* – Latest

such teeth represent the most distal part of a jaw or the embryonic stage;

- small, spoon-shaped with an obtuse lingual angle and a tricuspid crown composed of recurved, sigmoidal cusps (Text-fig. 6D-E; Pl. 1, Figs J-K; Pl. 3, Fig. A);
- trapezoid, with tricuspid crowns (Pl. 1, Fig. E);
- with parallel lateral rims of the base, a rounded lingual end, and three- to five-cusped crowns (Pl. 1, Fig. N; Pl. 2, Fig. G; Pl. 3, Fig. B);
- ogival (i.e. with the base shaped like a pointed gothic arch), usually with five-cusped crowns (Pl. 1, Figs F, L; Pl. 3, Fig. C).

Because of the high diversity of morphotypes among the teeth of *Ph. gothicus* it is difficult or sometimes impossible to clearly differentiate between this species and its presumed closest relative, *Ph. turnerae* (GINTER & TURNER 1999). There are intermediate forms resembling *Ph. turnerae* by their short and wide bases, but with the button situated centrally and the upper main foramen between the button and the lingual tip, which is typical of *Ph. gothicus*. Such specimens are generally referred to here as *Ph.* aff. *turnerae* (Pl. 3, Figs D-G; Pl. 7, Figs H-K). However, sometimes it seems more likely that such teeth actually belong to the dentition of *Ph. gothicus* in which they might have co-occured with typical, labio-lingually elongated specimens (compare Pl. 1, Figs G and L).

The origin of Thrinacodus

On the other hand, *Ph. gothicus transitans*, a new subspecies from the middle Famennian of Algeria, displays certain features thus far treated as unique to *Thrinacodus*. These are the asymmetry of the base and the rotation of the crown towards the base. The thrinacodont characters are only slightly marked in *Ph. g. transitans* and all other features (such as the size and position of the button and the main upper foramen) are typically phoebodont. Even the heterodonty is similar to that known from other localities rich in *Ph. gothicus* (compare Text-fig. 7J and Pl. 1, Fig. J).

Ph. depressus sp. nov. is another form which may pretend to be a link between *Phoebodus* and *Thrinacodus*. Its teeth are absolutely symmetrical, but the button and the labio-basal projection are very small (in *Thrinacodus* they are obsolete), the base is very long and there is a depression in the axial-lingual part, between two long lateral-lingual tips. Some teeth possess intermediate cusplets, unknown in thrinacodonts. Thanks to the occurrence of an unusual specimen of *Th. tranquillus* in an upper Famennian sample Ost-5 from the Ostrówka Quarry (Holy Cross Mountains, Poland; GINTER 1995, Fig. 4G; GINTER & IVANOV 1996, Fig 2B), it is possible to reconstruct further modifications of *Ph. depressus*. The tooth from Ost-5 has an axial depression between the lingual tips and a main upper foramen at the labial end of that depression, as in *Ph. depressus*. However, as usual in *Thrinacodus*, the crown was slightly vertically rotated in relation to the base (counterclockwise in this case) and there is neither a button nor a labio-basal projection present. The lingual tips of the base are of different length. It seems therefore that during the later evolution the teeth of forms more derived than *Ph. depressus* were subject to the complete reduction of intermediate cusplets, slight vertical rotation of the crown, partial reduction of one lingual tip and loss of articulation devices.

In typical, well preserved specimens of *Th. tranquillus*, traces of a shallow depression are visible, with a foramen at its labial end (Text-fig. 9G-H; GINTER 2000, Fig. 3B-F), but only one (probably mesial, see below) lateral-lingual tip occurs. In addition to the vertical rotation of the crown, a horizontal rotation, usually exceeding 10 degrees, is characteristic of such teeth. It is possible then that a part of the dental apparatus (for instance, teeth of the lateral rows) underwent further transformation: total reduction of the distal-lingual tip and a horizontal twist of the crown.

According to the scenario presented above, there is no place for *Ph. gothicus transitans* in the phylogeny of *Thrinacodus*. This would mean that the rotation of the crown in the former is a result of a parallel evolution. However, there is another possibility. The basal asymmetry in *Ph. g. transitans* is manifested in the occurrence of a mesial lobe and a shallow depression between the lobe and the axial-lingual part of the base (Text-fig. 7C, M, H, J). Transformation of such teeth into teeth typical of *Th. tranquillus* could have happened by a considerable lingually directed growth of the mesial lobe, loss of locking devices, further reduction of intermediate cusplets, and further vertical and horizontal rotation of the crown.

This discussion leads to several possible conclusions:

- *Th. tranquillus* derived from *Ph. depressus*;
- *Th. tranquillus* derived from *Ph. g. transitans*;
- sharks possessing typical teeth of *Th. tranquillus* derived from *Ph. g. transitans* and *Ph. depressus* is ancestral to the species which comprises teeth like that from Ost-5; consequently, *Thrinacodus* is polyphyletic;
- sharks possessing typical teeth of *Th. tranquillus* derived from *Ph. g. transitans*, but *Ph. depressus* is ancestral to the species which comprises teeth like that from Ost-5; consequently, *Ph. g. transitans* and *Ph. depressus* are conspecific.

Although the latter option seems improbable due to the large morphological distance between the teeth of

Ph. g. transitans and *Ph. depressus*, an argument exists in support of the idea. It is possible that the symmetrical teeth, currently assigned to *Ph. depressus*, and the subsymmetrical teeth of *Th. tranquillus* from Ost-5 are homologous and represent parasymphyseal tooth families. Weak crown/base asymmetry of the latter toothtype could be an indication for that. Consequently, *Ph. g. transitans*, as well as typical teeth of *Th. tranquillus*, might represent lateral components of the dentition. Such a relationship between the degree of asymmetry and the mesio-distal position of a tooth, appears to be common among the elasmobranchs (see Remarks to *D. mansureae* from Iran) and has previously been proposed for the dentition of *Th. ferox* (TURNER 1982, DUNCAN 1999, GINTER 2001). Usually the number of symmetrical or subsymmetrical frontal teeth is several times smaller than the number of lateral teeth displaying more or less distinct asymmetry. Such a difference is observed between the frequency of *Ph. depressus* (4 teeth) and *Ph. g. transitans* (14 teeth) in the sample from Gour Bedda.

The dentition of Th. tranquillus

The decision as to which phylogenetic scenario of those presented above is the most probable has some influence on the picture of *Th. tranquillus* dentition. Since three of the variants assume that all specimens currently referred to *Th. tranquillus* (GINTER 2000 and this paper) really belong to that species, that point of view is provisionally accepted here. In addition, the rule “the more distinct asymmetry, the more distal position of a tooth” will be applied. Based on such assumptions, and tentatively adding teeth of *Th.* cf. *ferox* (sensu GINTER 2000 and this paper) as possibly also belonging to *Th. tranquillus*, a hypothetical dentition model composed of 10 tooth families on each jaw ramus is proposed (a simplified reconstruction of its anterior part is presented in Text-fig. 14B). Four distinct tooth morphotypes could have occured in the dentition of *Th. tranquillus*.

1. Very small, entirely symmetrical teeth, composed of three very gentle, strongly recurved, sigmoidal cusps and a narrow, tube-like base (M1 in Text-fig. 14B; GINTER 2000, figs 3A, 4A-C). Such teeth might represent the symphyseal tooth family which, by analogy to the Recent *Chlamydoselachus*, can occur only on the lower jaw (Pfeil 1983, fig. 12.1). This morphotype is extremely rare. It conforms to the possible quantitative relation between such teeth and the other morphotypes in the dentition which probably would be no higher than 1:40 in our 10-row model. However, such teeth might also be rare because they actually come from an equivalent of pathological, additional rows, sometimes found in *Chlamydoselachus* (GUDGER 1937).

2. Teeth with slightly vertically rotated crowns, an axial-lingual depression on the upper side of the base and two uneven lingual tips (Text-fig. 14A.b; GINTER 1995, Fig. 4G; GINTER & IVANOV 1996, Fig 2B). Such teeth, described above as possible modifications of *Ph. depressus*, might have been situated in the parasymphyseal region and represent rows one and two (M2 in Text-fig. 14B).

3. The most common teeth of *Th. tranquillus* with the crown rotated vertically and horizontally, a very shallow lingual depression and only one lateral-lingual tip of the base developed (Text-fig. 14A.c). They would have occupied the middle lateral rows, from three to eight (M3 in Text-fig. 14B).

4. Relatively small teeth, referred here to as *Th.* cf. *ferox*, with short bases and asymmetrical, twisted crowns in which one lateral cusp is larger than the others (Text-fig. 14A.e). Such teeth might represent two angular tooth families.

Because all morphotypes but the first one are more or less asymmetrical, it is important to determine mesial and distal sides of a given tooth. Two obvious assumptions may help in solving this problem. A shark, in order to catch, hold and swallow prey, needs the tooth crowns be recurved inwards and backwards. The cusps cannot be directed outwards or forward. Furthermore, the most probable and useful direction of a tooth family, and consequently of overlapping toothbases, is roughly perpendicular to a jaw. Thus, it becomes clear that on the right ramus of a lower jaw the horizontal rotation of tooth-crowns must be counterclockwise. Therefore, the lingual tip of the most common morphotype 3 is always situated mesially. Knowing that, it follows that due to the vertical rotation the crowns turn mesially (i.e. clockwise on the right ramus of a lower jaw) and that the longer lingual tip in morphotype 2 is also mesial. The same reasoning can be applied to the position of the lateral lobe in *Ph. g. transitans* (Text-fig. 14A.d).

In spite of the vertical twist of the crown in morphotypes 2 and 3, such teeth still could have functioned with a normal, phoebodont-like position of the base, i.e. with the main upper foramen facing upwards or only slightly displaced distally. This means that the tooth-bases would have overlapped in a simple way. However, in morphotype 4 (= *Th.* cf. *ferox*; Text-fig. 14A.e), the whole tooth must have been turned distally and the main upper foramen was situated on the distal side of the base, because otherwise, the enormous mesial cusp would be directed downwards. Consequently, imbrication of tooth-bases could not have occurred. In fact, the lingual depression is virtually obsolete in morphotype 4 and the base is short and club-shaped. Probably, to connect the teeth in a tooth-family, the labio-basal depression of a younger tooth (Text-fig. 9D; Ginter 2000, fig. 2D) embraced the distal side of an older (more labial) one. It seems that no other interlocking took place.

In the most common, strongly asymmetrical morphotype of *Th. ferox* s.s. one of the lateral cusps is very large and the other two cusps are reduced, as in *Th.* cf. *ferox*. That was the reason for using this name in the description of the latter form by Ginter (2000). However, identification of tooth sides leads to the conclusion that in *Th.* cf. *ferox* the larger cusp is mesial (as noted above), but in *Th. ferox* it is always distal (compare Text-figs 15A.e and f). It appears likely that the latter teeth could have evolved from typical teeth of *Th. tranquillus* by further mesial, vertical rotation of the crown. During such a process, the mesial and central cusps became more and more useless. They were subject to continuous reduction and recurvature, until finally they were directed almost parallel to the base (Turner 1982, figs 2A-C, 3B-H; Ginter 2001, fig. 3D-E). In some cases, the mesial cusp is lost (Edwards & *al.* in prep., J. Talent's Canning Basin collection, Macquarie University). Probably, if the other cusps are

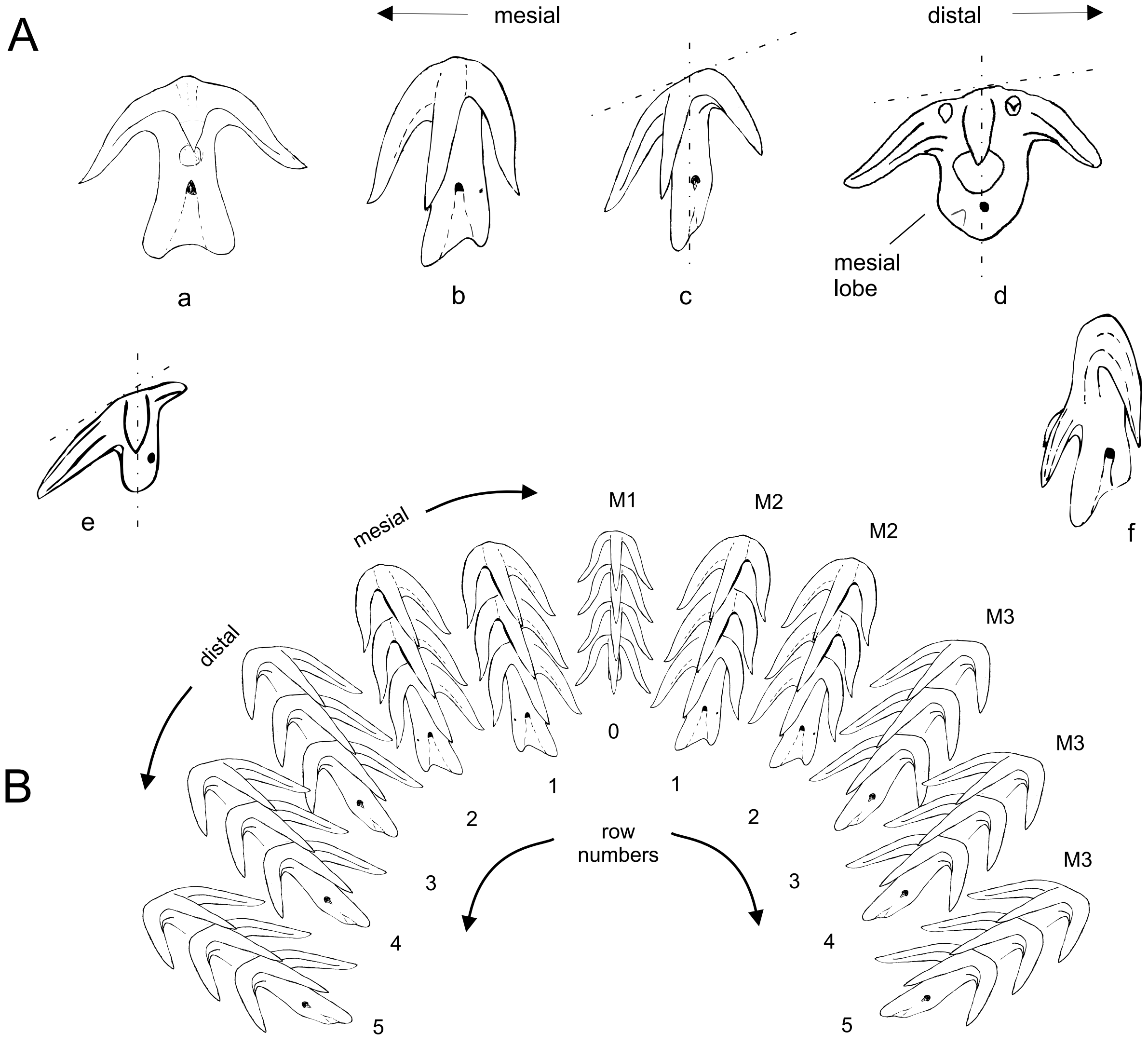


Fig. 14. A. Schematic drawings of phoebodont and thrinacodont teeth considered in the discussion on the origin and composition of *Thrinacodus* dentition; a – *Phoebodus depressus* sp. nov.; b – *Thrinacodus tranquillus* morphotype 2; c – the most common form of *Th. tranquillus* (morphotype 3); d – *Ph. gothicus transitans* sp. nov.; e – *Th.* cf. *ferox* (= *Th. tranquillus* morphotype 4); f – *Th. ferox* sensu stricto, asymmetrical tooth. B. Simplified, hypothetical reconstruction of the anterior part of the dentition of *Th. tranquillus*. M1-M3 – tooth morphotypes

strongly reduced, the distal cusp takes the almost upright position and the large part of *Th. ferox* dentition (except for the frontal region) looked like rows of single, strong hooks. It seems unlikely that *Th.* cf. *ferox* belongs to the dentition of *Th. ferox* s.s., because the process of becoming asymmetrical apparently was different in these two cases. Moreover, the former is unknown from the Lower Carboniferous in which the latter usually is abundant.

DISCUSSION (M.G., V.H. & C.K.)

Taxonomic composition of chondrichthyan assemblages

Central Iran and the Tafilalt Platform in Morocco are the regions of North Gondwana which have yielded the richest collections of Famennian chondrichthyan microremains thus far. They are also the only regions in which time-related changes of shallow water chondrichthyan faunas have been observed to date. Due to hiatuses and periodical occurrence of extremely shallow, terrigenous facies no undoubted middle Famennian sharks were recorded. However, quite a clear picture of the early Famennian and the early late Famennian assemblages can be drawn (Text-figs 15, 16). It is notable that generally, with a few important exceptions, the late Famennian faunas are more diverse, at the generic level, than the early Famennian ones. In the Tafilalt, this difference is almost negligible, and does not exceed two genera (five in the lower Famennian sample OEJ-1 to seven in the upper Famennian sample TN-2), and might be the result of the larger number of specimens in the upper Famennian samples. However, in Central Iran the late Famennian fauna consists of at least nine genera (sample 64 from Dalmeh section), whereas only three to a maximum of four genera were reported from all the lower Famennian localities.

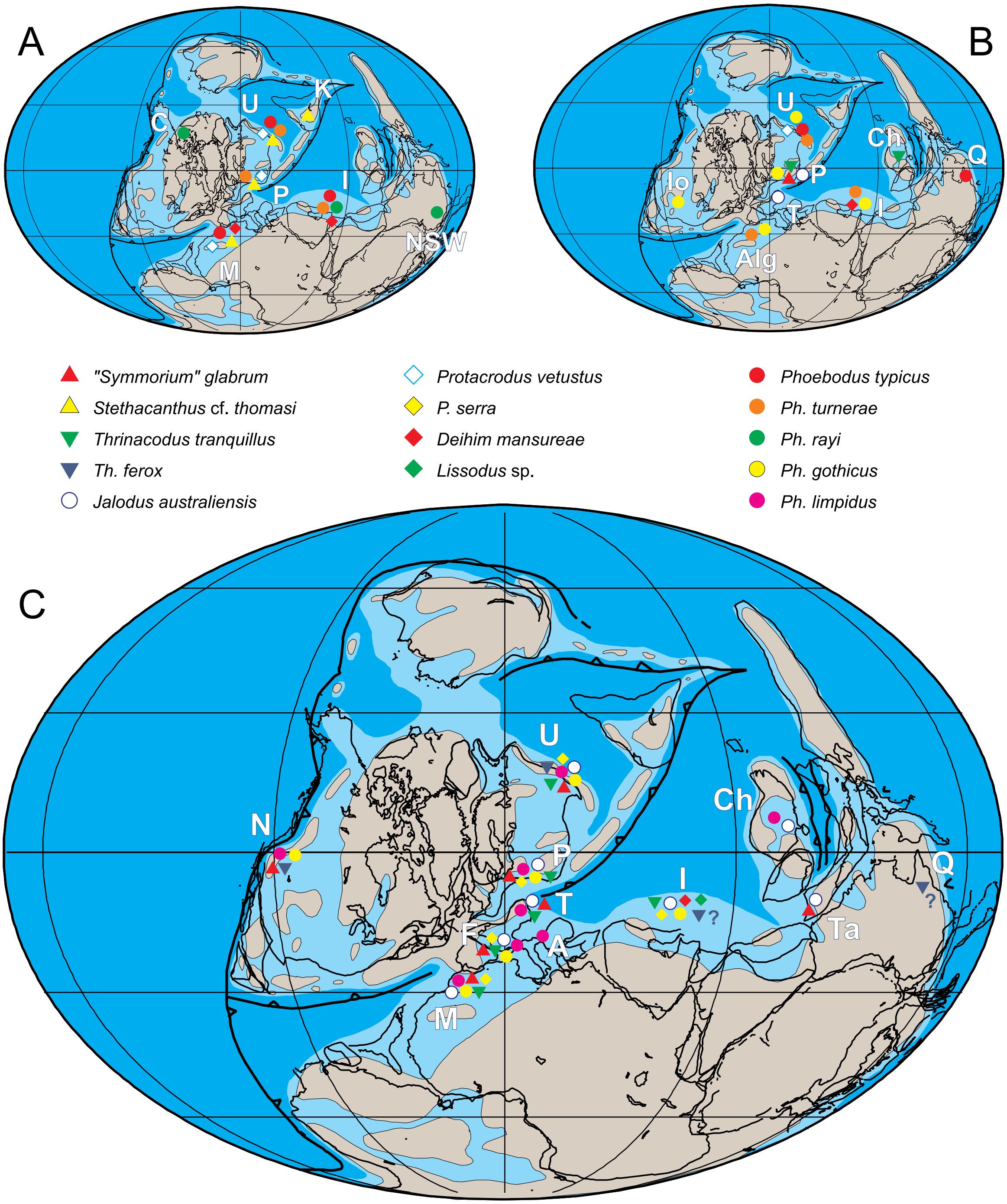
This diversity pattern reflects the continuous radiation of sharks in different environments during the Famennian, after the partial extinction related to the Kellwasser Event (GINTER & TURNER 1999). Two pelagic sharks, *Jalodus* and *Thrinacodus*, emerged in the middle Famennian and probably migrated to the North Gondwanan shallow shelves together with the transgression of the Early *expansa* Zone. Other new forms, characteristic of the late Famennian of Iran, could have evolved in this region or in areas with similar conditions. These are *Lissodus* and sharks with grinding teeth, called here orodonts. They are typical of the Carboniferous and as yet are unknown from rocks older than the *expansa* Zone.

Although almost all genera known from the lower Famennian of Central Iran and Tafilalt apparently can be found in the upper Famennian of these regions as well, in the Tafilalt there are important changes on the species level. The only Moroccan lower Famennian sample, OEJ-1 from the "placoderm bonebed" at Oum El Jerane, yielded 28 shark teeth. They are roughly equally distributed among *Phoebodus typicus*, protacrodontids (*Protacrodus vetustus* and a form resembling *Deihim mansureae*), "*Symmorium*" sp. B, and *Stethacanthus* cf. *thomasi*. None of these taxa was recovered from the upper Famennian of the Tafilalt. *Ph. typicus* is replaced here by *Ph. gothicus*, protacrodontids by *P. serra*, "*S.*" sp. B by "*S.*" *glabrum* and *S.* cf. *thomasi* by delicate stethacanthids with triangular bases (*Stethacanthus* sp.). Faunas from Central Iran show a different situation. In the five most probably lower Famennian samples (39 and TP of Dalmeh, R3 from Hodjedk, 38/23 from Hutk and 61/8 from Ali-Morad), the dominant species are *Ph. gothicus* (almost 60%) and *D. mansureae* (25%). The remaining 15% belong to typical early to middle Famennian phoebodonts, *Ph. typicus*, *Ph. turnerae* and *Ph.* cf. *rayi*, as well as to *Protacrodus* sp., and *Stethacanthus* sp. (different from *S.* cf. *thomasi*). "*Symmorium*" sp. B is absent. Unlike in the Tafilalt faunas, *D. mansureae* persists into the late Famennian in Central Iran, where it is known from the rich sample 64 from Dalmeh. *Ph. gothicus* continues to play an important role here (10%), although it is less abundant than *Thrinacodus*, protacrodonts or orodonts (about 20% each).

The data presented above show that already in the early parts of the Famennian, chondrichthyan communities of Central Iran and Tafilalt were slightly different and that the late Famennian change was more spectacular in Morocco than in Iran. Of course, all this discussion is based on the assumption that the samples TP and 39 from Dalmeh represent approximately the same, early Famennian age as the sample from Oum El Jerane, and not, for instance, the *marginifera* Zone. Difficulties with dating by conodonts in shallow water facies were mentioned in former chapters.

The transgression of the Early *expansa* Zone brought anoxic conditions to the Tafilalt Platform, with a high amount of clay minerals and organic matter, which resulted in formation of dark nodular ammonoid packstones. This facies is limited to the Early and Middle *expansa* Zones, and at Oum El Jerane, it is represented by two samples (OEJ-2 and 3) taken from two successive nodule layers. Chondrichthyan assemblages from these samples are very unusual and thus far unknown from any other upper Famennian locality. The very rich assemblage from sample OEJ-2 is characterised by a strong predominance of "*S.*" *glabrum*

(65%), a moderate number of stethacanthids (22%), and a complete absence of protacrodonts (or other sharks with crushing teeth). The number of phoebodonts is strongly reduced (only 1 specimen, less than 1%, of *Ph. gothicus*), but *Thrinacodus tranquillus* (counted here together with *Th.* cf. *ferox*) and *Jalodus* are present (7% and 5 %, respectively). The upper sample (OEJ-3) yielded a much smaller number of shark teeth (19 specimens), so the assemblage is not representative. However, it is remarkable that all the species found in OEJ-2 are present in OEJ-3, and vice versa. Protacrodonts are still absent, but a relatively large number (53%) of *Ph. gothicus*, compared to only 26% of "*S.*" *glabrum* may indicate some change in the environment.



Above a set of dark claystones and marls, from which chondrichthyan remains were not obtained, a pure limestone layer (*Gonioclymenia* limestone), most probably of Late *expansa* age occurs at Oum El Jerane. This unit is widespread in Tafilalt and it also crops out at Tizi Nersas. Three samples were processed for conodonts and ichthyoliths: OEJ-4 from Oum El Jerane and TN-1 and TN-2 from Tizi Nersas. The relative abundances of shark species in samples OEJ-4 and TN-1 are very similar, but slightly differ from those in TN-2. The first two samples are rich in *Ph. gothicus* (26 and 23%, respectively) and have no more than 25% of *Protacrodus serra*. In TN-2 there is only 9% of *Ph. gothicus* and 36% of *P. serra*. In the other respects all three samples from the *Gonioclymenia* limestone are almost identical. They contain *Th. tranquillus* (7-9%), "*S.*" *glabrum* (2-8%), and *Stethacanthus* sp. (32-39%). In addition, *Jalodus* was recorded from TN-1 and TN-2 (2 and 5%), a single specimen of *Clairina* from TN-2, and two teeth of *Ph. limpidus* (3%) from TN-1. The assemblage from sample OEJ-4 is the least diverse because of the small sample size.

Sample 64 from Dalmeh, representative for the late Famennian of Central Iran, yielded a chondrichthyan assemblage very different from all that we already know from North Gondwana. Among the 150 specimens, protacrodontids (*Protacrodus*, *Deihim* and *Dalmehodus*, altogether 29%), *Th. tranquillus* (23%), orodonts and *Lissodus* (23%), *Stethacanthus* sp. (11%), and *Ph. gothicus* (10%) are the most common. Only three specimens of *Jalodus* and three of *Bransonella*? sp. were found. The most important difference between this assemblage and all Tafilalt samples is the absence of "*S.*" *glabrum* and a high number and diversity of crushing or grinding teeth. Particularly the presence of *D. mansureae* and *Lissodus* in the upper Famennian was not previously recorded from elsewhere.

There are not enough shark teeth from the Mighan section (northern Iran) to present any reasonable analysis of assemblages. It can only be concluded that the chondrichthyan fauna of the *expansa* Zone must have been similar to that from Central Iran, with *Ph. gothicus*, *Th. tranquillus*, *Protacrodus*, *Lissodus* and stethacanthids. "*S.*" *glabrum*, *Jalodus* and *Ph. limpidus* were not found.

The early or middle Famennian assemblage from Gour Bedda, Algeria, is composed almost completely of phoebodonts (89%), probably belonging to three different species: *Ph. gothicus transitans*, *Ph. depressus* and *Ph.* aff. *turnerae*. The remaining 11% are represented by two cladodont species, "*Symmorium*" sp. A (two teeth) and *Stethacanthus* sp. (one tooth). Such a strong predominance of phoebodont sharks is rather strange, especially if we consider that the only conodonts found belong to the *Icriodus* group, known as shallow water indicators (e.g. SANDBERG & DREESEN 1984).

Palaeoecological implications

Chondrichthyan biofacies

Definitions of three biofacies, based on relative abundances of chondrichthyan teeth, were recently proposed by GINTER (2000, with modifications in 2001) for the open marine late Famennian environments. To make the definitions clearer, chondrichthyan taxa known from late Famennian pelagic and neritic facies were grouped in four basic morphoecological categories.

Fig. 15. Distribution of selected chondrichthyan species in A. early, B. middle, and C. late Famennian. Palaeogeographic background based on GOLONKA & *al.* (1994). A – Carnic Alps, Alg – Algeria, C – Canadian Arctic, Ch – South China, F – Montagne Noire (France), I – Iran, Io – Iowa, K – Kuznetsk Basin, M – Tafilalt (Morocco), N – Nevada and Utah, NSW – New South Wales, P – Holy Cross Mountains (Poland), Q – Queensland, T – Thuringia, Ta – Thailand, U – South Urals. Sources of information: **Early Famennian** – Arctic Canada: GINTER & TURNER (1999); South Urals: GINTER (1994), GINTER & IVANOV (1992, 2000); Kuznetsk Basin: IVANOV & *al.* (1992); Holy Cross Mountains, Poland: GINTER (1994, 1995), GINTER & IVANOV (2000); Tafilalt, Morocco: this paper; Iran: LONG & HAIRAPETIAN (2000), this paper; New South Wales: JONES & TURNER (2000). **Middle Famennian** – South Urals: GINTER (1994), GINTER & IVANOV (1992, 2000); South China: LELIÈVRE & DERYCKE (1998); Queensland: TURNER (1982), GINTER & TURNER (1999); Iowa: GROSS (1973); Holy Cross Mountains, Poland: GINTER (1990, 1994, 1995), GINTER & IVANOV (2000); Thuringia, Germany: GINTER (1999); Algeria: this paper; Iran: HAMPE (2000), LONG & HAIRAPETIAN (2000), this paper. **Late Famennian** – South Urals: GINTER (1994), GINTER & IVANOV (1992, 2000), IVANOV (1996); South China: WANG & TURNER (1985, 1995), WANG (1989); Queensland: TURNER (1982); Thailand: LONG (1990); Iran: LONG & HAIRAPETIAN (2000), this paper; Holy Cross Mountains, Poland: GINTER (1990, 1994, 1995), GINTER & IVANOV (2000); Thuringia, Germany: GINTER (1999); Montagne Noire, France: GINTER (2000); Tafilalt, Morocco: DERYCKE (1992), this paper; Nevada and Utah: GINTER (2001); Carnic Alps, Italy: BLIECK & *al.* (1998); The occurrences of *Thrinacodus ferox* were added here to show its possible wide distribution in late Famennian shallow water environments. Two specimens of that species were found from the alleged Famennian strata of Kerman province (Hodjedk area, southeastern Central Iran; K. RASHIDI's collection, Payam-e-Noor University, Ardekan), but the age of that material is still unconfirmed. Also, the age of samples from Australia which yielded the type series of *Th. ferox* (TURNER 1982) is actually unknown. It may belong to the late Famennian or the Early Carboniferous (TURNER, pers. comm.). Therefore, the only certain Famennian records of that species come from the South Urals (GINTER 1995, unillustrated) and Utah (GINTER 2001, fig. 3C-E).

1. Sharks with cladodont tooth-crowns (with the central cusp much higher than the lateral ones) which were fast-swimming surface hunters, generally eurytopic and resistant to environmental changes. Of the many described taxa which belong to this category, *Cladoselache*, *Stethacanthus*, and "*Symmorium*" *glabrum* need to be mentioned here.

2. Sharks with crushing or grinding teeth, supposed to have lived mainly in a photic zone and preying on benthic fauna, and therefore requiring well oxygenated waters down to the sea-floor. In this category protacrodontids and orodontids were originally included. Since a new shark with similar teeth, *Lissodus*, was found from the upper Famennian of Iran, it also will be placed in this category.

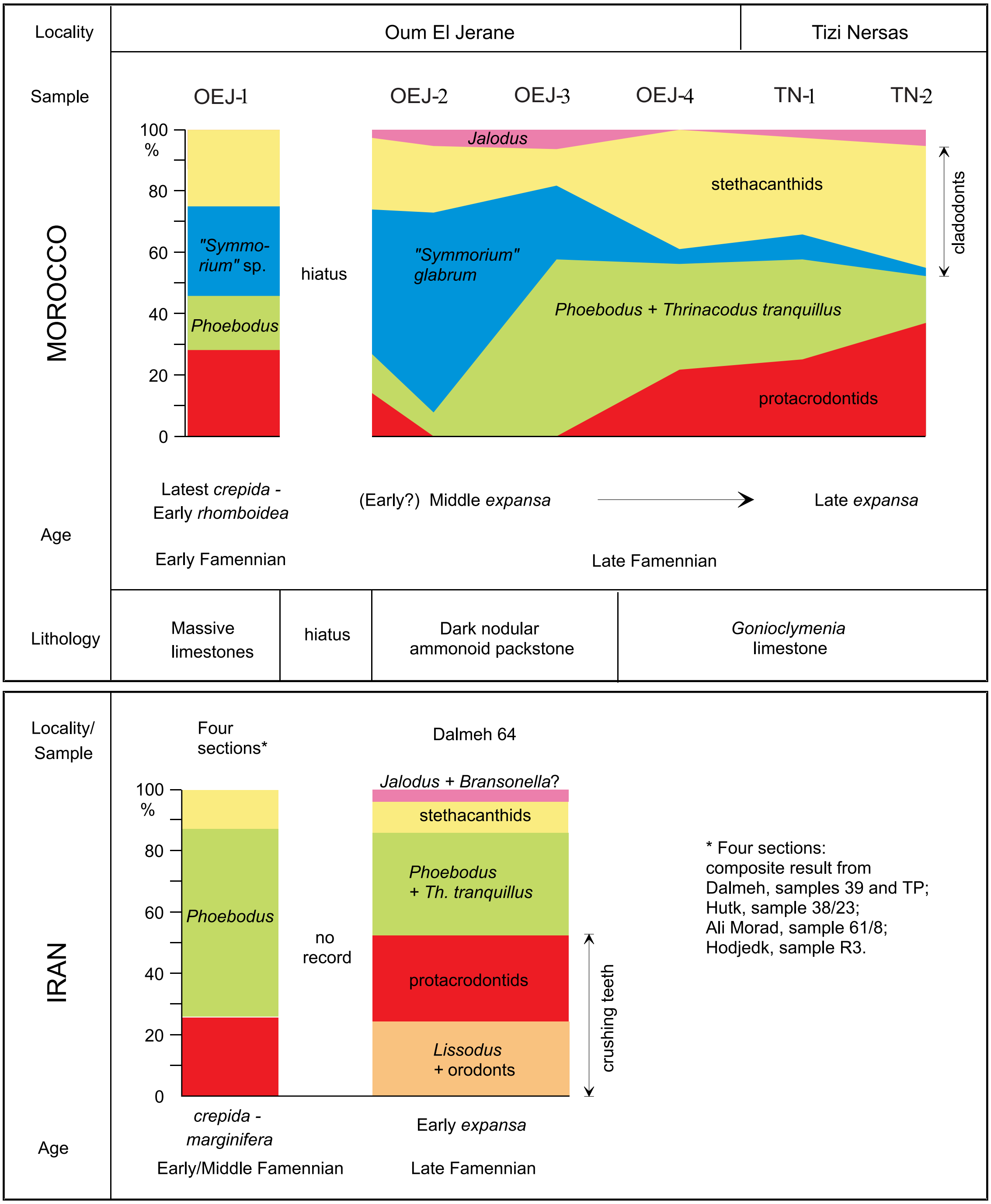


Fig. 16. Changes in taxonomic composition of chondrichthyan assemblages in the Famennian of Tafilalt Platform (Morocco) and Central Iran

3. Sharks with clutching or grasping teeth with delicate cusps and symmetrical to subsymmetrical crowns (phoebodont crowns), which probably lived mainly in the middle of the water column and hunted for relatively soft prey, such as unarmoured cephalopods or small actinopterygians, similarly to the Recent shark *Chlamydoselachus*. *Phoebodus* and *Thrinacodus tranquillus* belong to this category. They are typical of moderately deep to moderately shallow waters and could be vulnerable of anoxic conditions at the bottom, but apparently less than the protacrodontids.

4. *Jalodus,* an enigmatic genus (the feeding preferences of which are unknown), is predominant in the deep water facies of Thuringia and Thailand, common in moderately deep areas of the Holy Cross Mountains and Montagne Noire, and absent or very rare in shallow epicontinental seas. It is treated here as an indicator of proximity of a deep (oceanic?) realm.

The chondrichthyan biofacies were named after the most common representative of a predominating category. They are listed below, ordered according to the presumed water depth, from the deepest to the most shallow.

1. *Jalodus* biofacies: more than 25% of *Jalodus*, less than 25% of *Phoebodus* and *Thrinacodus tranquillus*, and less than 10% of protacrodontids, orodontids etc.
2. *Phoebodus* biofacies: more than 25% of *Phoebodus* and *Th. tranquillus*.
3. *Protacrodus* biofacies: more than 25% of protacrodontids and orodontids, less than 25% of *Phoebodus* and *Th. tranquillus*.

It is noteworthy that cladodonts were thus far not used in the definitions of biofacies, because of their eurytopic character.

The Late Famennian palaeoenvironments of chondrichthyans on the margins of North Gondwana

Hereafter, an ecological interpretation of late Famennian chondrichthyan assemblages from Morocco and Iran according to the biofacies model will be presented. Five samples are analysed: sample 64 from Dalmeh, samples OEJ-2, 3 and 4 from Oum El Jerane, and samples TN-1 and 2 from Tizi Nersas.

As previously mentioned, crushing and grinding teeth are very abundant and diverse in the sample from Dalmeh (Table 5). Their frequency altogether is very high and reaches 52%, which appears to clearly indicate the shallow water *Protacrodus* biofacies. However, phoebodontids are also very numerous (33%) and are represented by cosmopolitan species such as *Th. tranquillus*. Additionally to the facies of the deposits of the Early *expansa* Zone in the study area, this might reflect that Central Iran was a part of a vast shelf with very well developed, partly endemic, shallow water chondrichthyan fauna, but that the water column was high enough to allow phoebodontids to enter. Probably, the sea-floor morphology was highly differentiated and provided shallower areas which were inhabited by protacrodontids and slightly deeper channels which were probably visited by migrating phoebodontids. However, the deeper shelf and oceanic areas must have been very remote because of the small representation of *Jalodus* (2%) and complete absence of *Ph. limpidus*. The latter is known as the only phoebodont from the deep water assemblage of Thuringia (GINTER 1999) and the deep subtidal zone of Utah and Nevada (GINTER 2001), and can be considered therefore as a representative of *Phoebodus* with deeper water preferences than those of *Ph. gothicus*. The absence of "*S.*" *glabrum* from this area and its abundance in Thuringia and Thailand might indicate that it also preferred deeper basins. The frequency of stethacanthids is relatively low, but it is probably only a statistical effect of the extreme abundance of protacrodontids and orodontids.

Nothing can be said about the changes in Famennian chondrichthyan assemblages in Iran after the Early *expansa* Zone because of the lack of data. The situation is different in Morocco. There, the three successive samples from Oum El Jerane, supported by the samples from the nearby Tizi Nersas section, yielded much more information. A complete scenario of the evolution of palaeoenvironment on the Tafilalt Platform in the *expansa* Zone, and its influence on chondrichthyan communities, can be presented. After a period of regional erosion and possible emersion which took place in the middle Famennian, marine conditions returned to the area of Oum El Jerane. It appears likely that the extent of the transgression was increasing during the Early *expansa* and possibly also into the base of the Middle *expansa* Zone. This was the same global transgression that was noted for instance from Dalmeh and Mighan sections in Iran and from Nevada and Utah (SANDBERG & *al.* 1988, GINTER 2001), and which brought well oxygenated waters and a high diversity of benthic sharks to those regions. However, in the Tafilalt, the transgression had a completely different effect. The local basin was probably restricted, separated from the open sea by a kind of barrier, and a large amount of soft argillaceous sediment rich in organic matter accumulated on the bottom. The soft bottom and the decay of organic matter, resulting in the appearance of an anoxic water layer, were two factors that prevented the diverse benthic invertebrate fauna from settling in this area. This had an extensive influence on the taxonomic composition of the chondrichthyan fauna (Table 4). Sharks with crushing teeth disappeared. On the other hand, an incomparable number of cladodonts (87%) is observed, with "*Symmorium*" *glabrum* as a main constituent. Since *Jalodus* plays only an accessory role here and *Ph. limpidus* is absent, it seems that depth was not a factor determining such an unusual assemblage. Probably the only niche accessible for sharks were surface waters which, as noted above, were normally the realm of cladodonts accounting for their dominance here. It is worthwhile mentioning that a bispathodid conodont fauna with very few palmatolepids was recovered from sample OEJ-2, and that the dark nodular ammonoid packstones (represented by that sample) yielded an ammonoid assemblage, with numerous *Endosiphonites muensteri* (KORN 1999, KORN & *al.* 2000). When the picture is completed with a very poor record of benthic invertebrates (only a few crinoid sclerites), it becomes clear that the life was limited to the higher parts of the water column in which cladodont sharks, as top predators, hunted for clymeniids and other nektonic animals.

The chondrichthyan assemblage from sample OEJ-2 does not fit in any biofacies presented in the previous chapter. It is a regional anomaly and not much can be said about the depth of the basin. However, presence of ammonoids and diverse bispathodids suggests that it could not be very shallow. The next sample (OEJ-3), although taken from a higher level of the same lithological unit, reflects slightly different conditions. Unfortunately, the chondrichthyan fauna is much poorer, but if its composition is not a mere coincidence, it shows some trends. All species found in OEJ-2 are present in OEJ-3, protacrodonts are still absent, and among the cladodonts, "*S.*" *glabrum* still predominates over the stethacanthids, but the frequency of *Ph. gothicus* is much higher here than in the sample below (53%). This is rather strange, because thus far phoebodonts proved to be vulnerable to dysoxic conditions. Could this be a sign of shallowing? This can be supported by changes in conodont fauna. Of several different species of *Bispathodus* known from OEJ-2 only a eurytopic, long-living *B. stabilis* remained. It is possible that the environmental conditions were becoming unbearable for more and more taxa, while the basin was filled with sediment and the anoxic water zone expanded. The process ended with the deposition of much less fossiliferous dark claystones.

Probably in the second half of the *expansa* Zone, the hypothetical barrier between the Tafilalt area and the open sea disappeared. Oxic marine conditions returned to Oum El Jerane, accompanied by all morphoecological categories of chondrichthyans. As already noted, shark assemblages from the *Gonioclymenia* Limestone differ slightly from each other (Table 3). Samples OEJ-4 and TN-1 represent the intermediate *Phoebodus* biofacies, but with a rather high frequency of protacrodonts (22-25%), and sample TN-2 fits well in the shallow *Protacrodus* biofacies. It is unknown if this inconsistency truly reflects differences in space or time, such as shallowing of the basin, or if it is just a result of irregular distribution of ichthyoliths in rocks. The composite view of the three samples possibly gives the most correct answer as to the environment on the southern part of Tafilalt Platform by the end of the *expansa* Zone. The number of protacrodontids and phoebodontids is equal (28%), which formally places this assemblage in between the shallow and intermediate biofacies. The high frequency of stethacanthids (which were the only cladodonts on the shallow shelf of Central Iran) in relation to "*S.*" *glabrum* also indicates moderately shallow water conditions. This is supported by the rare occurrence of *Jalodus* and *Ph. limpidus*. However, the record of the three latter taxa indicates proximity of deeper water areas. The latter conclusion, together with the absence of orodonts and *Lissodus*, are the most important differences between this chondrichthyan community and that from Central Iran.

Comparisons with the other regions

Samples from the *Gonioclymenia* limestone. Diverse late Famennian assemblages, containing sharks of different feeding habits, and similar to that of the *Gonoclymenia* limestone, are common especially for the shelf areas between Laurussia and Gondwana (Table 5). Two localities have been the most thoroughly studied (GINTER 1990, 2000): Soureillé d'Izarne in the Montagne Noire (France) and the Ostrówka Quarry in the Holy Cross Mountains (Poland). The whole set of genera and species extracted from the *Gonioclymenia* limestone at Oum El Jerane and Tizi Nersas, except *Clairina*, is also present at these two localities. However, in contrast to the Tafilalt Platform, where the protacrodontids and phoebodontids are equally abundant or, sometimes (sample TN-2), the former predominate, the two European sections are evidently richer in phoebodontids. Moreover, the frequency of *Jalodus* is much higher at Soureillé d'Izarne and Ostrówka (15% and 24%, respectively) than at Oum El Jerane or Tizi Nersas. It is also interesting that, unlike in the Tafilalt, "*S.*" *glabrum* is more abundant than the stethacanthids in certain rich upper Famennian samples from Ostrówka. Otherwise, the frequency of *Ph. limpidus* alone may exceed 10%. The latter relationship was noted from Soureillé d'Izarne as well.

Chondrichthyan assemblages from Ostrówka and Soureillé d'Izarne are classic representatives of the *Phoebodus* biofacies. They come from similar environ-

Localities / Samples	Oum El Jerane OEJ-4		Tizi Nersas TN-1		TN-2		*Gonioclymenia* limestone comp.	
Species	%	ci [%]	%	ci [%]	%	ci [%]	%	ci [%]
Jalodus australiensis	0	—	2	± 3	5	± 6	2	± 2
Thrinacodus tranquillus	9	± 11	7	± 6	7	± 7	7	± 4
Phoebodus gothicus	26	± 17	23	± 10	9	± 8	19	± 6
Phoebodus limpidus	0	—	3	± 4	0	—	2	± 2
Protacrodus serra	22	± 16	25	± 10	36	± 14	28	± 7
"Symmorium" glabrum	4	± 8	8	± 6	2	± 4	5	± 3
Stethacanthus sp.	39	± 19	32	± 11	39	± 14	36	± 8
Clairina marocensis	0	—	0	—	2	± 4	1	± 1
Total specimens number	23		61		44		128	

Table 3. Relative abundances of late Famennian chondrichthyans in the samples from the *Gonioclymenia* limestone of Tafilalt Platform, Morocco. "*Gonioclymenia* limestone comp." means a composite result of samples OEJ-4, TN-1 and TN-2; ci – confidence interval

ments, but certainly deeper than that of the *Gonioclymenia* limestone. Nevertheless, all noted above taxonomic resemblances indicate that in the Late *expansa* Zone chondrichthyan communities of the Tafilalt Platform must have had significantly closer relations to those from the southern Laurussian shelves than was previously anticipated (see GINTER 2000).

Samples from the dark ammonoid packstones. The assemblage from sample OEJ-2, with the predominance of cladodonts as a result of probably euxinic conditions, is comparable to only one well known late Famennian environment, the Cleveland Shale Basin. The Cleveland Shale of Ohio has yielded many complete skeletons of fishes, mainly chondrichthyans and placoderms. The excellent preservation of cartilage and even traces of soft body parts of sharks is a result of reducing conditions at the bottom, protecting the carcasses from being disintegrated by benthic scavengers and aerobic bacteria (WILLIAMS 1990). It is also clear from the position of skeletons that the shark bodies were quickly buried in a muddy bottom. The chondrichthyan assemblage thus far described is composed mainly of cladodont sharks, attributed to *Cladoselache, Stethacanthus*, *Ctenacanthus* and *Tamiobatis* (WILLIAMS 1985, 1998, 2001), many of which are probably endemic species, not noted from elsewhere. A few isolated teeth of *Phoebodus politus* (NEWBERRY 1889) and several specimens of four different crushing tooth types were also found there. WILLIAMS (1990, p. 275) suggested that the presence of the latter teeth in the Cleveland Shale "may be due to rare 'visits', but at least one seems to have been eaten by a larger predator".

This short description indicates that in the Cleveland Shale and in the dark nodular ammonoid packstones of the Tafilalt both the ecology and the composition of shark communities, on the level of morphoecological categories, display considerable resemblances. Moreover, conodonts found in the gastric residues of sharks from Cleveland Shales belong mainly to *Bispathodus stabilis* (WILLIAMS 1990), a form typical of sample OEJ-2 (and particularly the slightly younger sample OEJ-3). Unfortunately, further comparison of these environments is limited by the fact that there are no data available whether there are any changes in chondrichthyan assemblages from the base to the top of the Cleveland Shale or from which level the conodonts were recovered.

We can compare the assemblage from the dark nodular ammonoid packstones with another rich sample, Bu-20 from the Buschteich Quarry in the East Thuringian Slate Mountains (GINTER 1999, text-figure 2). The age of this sample is close to the boundary between the Early and Middle *expansa* Zone and therefore it seems to be an exact time equivalent of sample OEJ-2 from Tafilalt (Table 4). The area of Buschteich in the late Famennian was probably situated on a low submarine rise, far from the shore or shallow shelf, surrounded by very deep basins, particularly well documented from the nearby Saalfeld region. Buschteich is the type locality for the *Jalodus* biofacies (GINTER 2000). The chondrichthyan assemblage from sample Bu-20 (58 teeth) is composed of 75% of *J. australiensis*, 4% of a strange thrinacodont form, 14% of "*S.*" *glabrum*, two broken cladodonts, two teeth of *Siamodus janvieri* and one of *Clairina marocensis*. Such taxonomic composition clearly reveals the difference between an open marine, deep-water environment (Bu-20) and a restricted, euxinic basin on a shelf (OEJ-2). However, it is uncertain if the clear predominance of *Jalodus* in Thuringia is only the effect of water depth and/or distance from land, or whether it was caused by some other factors preventing other sharks from entering that area.

Sample 64 from Dalmeh. The environment of the extensive, moderately shallow shelf, presumably characteristic of the *expansa* Zone of Central Iran appears to be similar to that of the areas between the Sevier Thrust System and the Transcontinental Arch in Utah, western USA (SANDBERG & *al.* 1988). Chondrichthyan remains are rare in the conodont samples from Utah and altogether only 50 shark teeth from the shallow subtidal zone were collected (GINTER 2001). The composite picture of the chondrichthyan assemblage from that zone (based on more than 20 samples) displays several differences, but also some similarities to that from Dalmeh (Table 5). First of all, the relative abundance of crushing teeth is high (44%), like in Dalmeh, and they are not limited to *Protacrodus*, but also several orodonts were found. Then, among cladodonts there are almost only stethacanthids, and "*S.*" *glabrum* is absent. Also, *Jalodus* is absent (in Dalmeh there are only three specimens) and a *Bransonella*-like tooth was found. In contrast, such important species for Dalmeh like *Th. tranquillus*, *D. mansureae* and *Lissodus* sp. are unknown from Utah and only two dubious specimens of *Ph. gothicus* were found there. The most striking difference is the occurrence of *Th. ferox* s.s. in several samples. GINTER (2001) suggested that the presence of *Th. ferox* in the shallow subtidal zone of Utah could have been environmentally controlled and that *Th. tranquillus* is therefore its open marine equivalent. However, the results from Dalmeh show that some factors other than water depth apparently caused the palaeogeographic distribution of these thrinacodont species. The lack of neritic *Deihim* and *Lissodus* in Utah is probably a good indication for geographic differentiation of shallow-water faunas separated by vast pelagic areas.

Final remarks

The discussion presented above confirms the idea that shark teeth can be useful tools for palaeoecological analysis of the late Famennian, if a statistically valid number of precisely dated specimens is available. The question then arises whether that methodology can be applied to earlier in the Famennian. From the data currently at hand, it seems that it might be problematic for several reasons. First of all, the diversity of chondrichthyans is much smaller. *Jalodus australiensis*, a probable deep water indicator, did not emerge at least until the Late *marginifera* Zone and it is unknown which shark could have been its morphoecological equivalent in the earlier times.

Localities / Samples	Buschteich Bu-20		Oum El Jerane OEJ-2		OEJ-3		*Gonioclymenia* limestone comp.	
Species	%	ci [%]	%	ci [%]	%	ci [%]	%	ci [%]
Jalodus australiensis	75	± 11	5	± 3	5	± 9	2	± 2
Thrinacodus tranquillus	3?	± 4	7	± 4	5	± 9	7	± 4
Phoebodus gothicus	0	—	1	± 1	53	± 22	19	± 6
Phoebodus limpidus	0	—	0	—	0	—	2	± 2
Protacrodus serra	0	—	0	—	0	—	28	± 7
"Symmorium" glabrum	14	± 8	65	± 8	26	± 19	5	± 3
Stethacanthus sp.	3?	± 4	22	± 7	11	± 14	36	± 8
Clairina marocensis	2	± 3	0	—	0	—	1	± 1
Siamodus janvieri	3	± 4	0	—	0	—	0	—
Total specimens number	58		119		19		128	

Table 4. Relative abundances of late Famennian chondrichthyans in samples Bu-20 from the Buschteich Quarry, East Thuringian Slate Mountains, Germany; OEJ-2 and OEJ-3 from Oum El Jerane, Tafilalt Platform, Morocco; and the *Gonioclymenia* limestone (see Table 3); ci – confidence interval

Then, it is quite probable that the phoebodonts occupied niches in shallower water than in the late Famennian. There are at least two examples in which samples have an extremely high frequency of *Phoebodus* in certainly shallow water environments. The first is the Cape Fortune Member of the Parry Islands Formation, Arctic Canada, in which over 90% of several hundred teeth belong to *Ph. rayi* (GINTER & TURNER 1999). The second is the sample from Gour Bedda in Algeria (see above), which yielded 25 phoebodonts and only 3 cladodonts. Also, a high phoebodontid/protacrodontid ratio in the lower Famennian of Central Iran (2.4) is in contrast to the result from the *expansa* Zone (0.6), whereas sedimentological data do not show any dramatic environmental change. Last but not least, horizons abundant in chondrichthyan microremains and index conodonts are much less common in the lower than in the upper Famennian. Therefore, data for correlation and comparison of environments are more scattered and difficult to obtain.

There are also several general limitations to the method, especially when compared to identification of palaeoenvironments by conodonts. First of all, usually the number of shark teeth extracted from a typical, 1-2 kg conodont sample is below 30 specimens, which makes the usefulness of such assemblages in statistics problematic. Furthermore, distribution of shark teeth in rocks is very irregular. Samples collected from the same locality and horizon, but in a distance of ten metres may yield a much different number of teeth and, to some extent, assemblages of more or less different taxonomic compositions (e.g. the Moroccan samples TN1 and TN2). Shark teeth reach the sediment surface mainly in two ways: as isolated elements shed by a fish during its life, and these should be disseminated more or less regularly all over the area; or together with a dead body. In the latter situation, unless the whole dentition is quickly dismembered and dispersed by scavengers and currents, it can be buried in place. A single dentition of an adult cladodont shark (e.g. *Cladoselache*, WILLIAMS 2001, fig. 11) has no less than 200 teeth, and a similar number can be estimated for phoebodonts, based on xenacanthid dentitions (e.g. *Triodus sessilis*, specimen M5458 from the J. Gutenberg University in Mainz, M.G. pers. obs.). Therefore, even if a part of such a dentition occurs in a sample, it is useless for palaeoecological reconstruction (although priceless for palaeontological description). To avoid such problems, it is highly advisable to take not one, but several larger samples from different points of a single horizon.

Localities / Samples	Nevada and Utah shallower zone		Dalmeh 64		Soureillé d'Izarne		*Gonioclymenia* limestone comp.	
Species	%	ci [%]	%	ci [%]	%	ci [%]	%	ci [%]
Jalodus australiensis	0	—	2	± 2	15	± 7	2	± 2
Thrinacodus tranquillus	0	—	23	± 6	23	± 9	7	± 4
Phoebodus gothicus	4	± 5	10	± 4	13	± 7	19	± 6
Phoebodus limpidus	4	± 5	0	—	13	± 7	2	± 2
Protacrodus spp.*	24	± 11	24	± 6	15	± 7	28	± 7
Deihim mansureae	0	—	5	± 3	0	—	0	—
orodontids	20	± 11	17	± 6	0	—	0	—
Lissodus sp.	0	—	6	± 3	0	—	0	—
"Symmorium" glabrum	0	—	0	—	2	± 2	5	± 3
Stethacanthus spp.	26	± 12	11	± 5	19	± 8	36	± 8
Clairina marocensis	0	—	0	—	0	—	1	± 1
Bransonella? sp.	2	± 3	2	± 2	0	—	0	—
Thrinacodus ferox	20	± 11	0	—	0	—	0	—
Total specimens number	50		150		87		128	

Table 5. Relative abundances of late Famennian chondrichthyans in the samples from the shallower zone of Nevada and Utah (GINTER 2001); sample 64 from Dalmeh, Central Iran; samples from Soureillé d'Izarne, Montagne Noire, France; and the *Gonioclymenia* limestone (see Table 3); ci – confidence interval; * including *Protacrodus serra* and *Dalmehodus turnerae*

CONCLUSIONS

In the early Famennian, Central Iran and the southern part of the Tafilalt Platform (Morocco) were occupied by roughly similar, moderately shallow water chondrichthyan faunas. Phoebodonts, protacrodontids and cladodont sharks were well represented, but the diversity was rather low. Data from a large part, if not the whole middle Famennian are missing due to hiatuses or the lack of record. The global transgression at the base of the *expansa* Zone reached both areas. It brought dramatically different conditions to each region and, therefore, resulted in development of substantially different shark faunas.

As an effect of the formation of an anoxic bottom water layer, a very special chondrichthyan assemblage, similar to that from the Cleveland Shale Basin in Ohio, developed in the Early/Middle *expansa* Zone of the Tafilalt. It is characterised by the predominance of cladodonts (mainly "*Symmorium*" *glabrum*) and the complete absence of benthic sharks with crushing teeth. In the Late *expansa* Zone, this assemblage was replaced by a more diverse association, composed of *Phoebodus gothicus*, *Ph. limpidus*, *Thrinacodus tranquillus*, *Jalodus australiensis*, *Protacrodus serra*, *Clairina marocensis*, "*S.*" *glabrum* and *Stethacanthus* sp. It is almost the same set of species as that known from the pelagic shelves between Laurussia and Gondwana, for instance from the Montagne Noire and the Holy Cross Mountains. This indicates close connections between the Tafilalt Platform and the open intercontinental sea. On the other hand, a higher frequency of protacrodontids in Morocco is probably the evidence of somewhat shallower environment here than in the former two regions.

In Dalmeh (Central Iran), the environment of the Early *expansa* Zone was quite similar to that from the early Famennian. High diversity of bottom-dwelling sharks with crushing or grinding teeth (protacrodontids, orodonts and *Lissodus* sp.), associated with abundant phoebodontids, indicate the conditions of a moderately shallow, oxygenated, extensive epicontinental sea, probably with a differentiated bottom relief. Presence of supposedly endemic shallow water taxa, such as *Deihim mansureae* and *Lissodus* sp., and the absence of several species characteristic of pelagic environments ("*S.*" *glabrum*, *Ph. limpidus*) may indicate a large distance between Central Iran and deeper marine areas on the North Gondwana margins.

The abundance of phoebodontiforms in the material from Morocco, Algeria and Iran yielded several new data about the evolution and ecology of this group in the Famennian. Originally, the lower boundary of the *gothicus* Zone of the phoebodont-based ichthyolith zonation was placed at the base of the Early *marginifera* conodont Zone (GINTER & IVANOV 1995). In many regions, from Iowa to Morocco, and to the South Urals, *Phoebodus gothicus* appears no earlier than that zone. However, it is highly probable that in Iran *Ph. gothicus* occurs already in the early Famennian, possibly even as early as the *crepida* Zone. This shows, if the samples are dated correctly, that the boundary mentioned above does not have a worldwide validity. It is possible that *Ph. gothicus* emerged in Iran and later migrated outwards.

Two new forms, *Ph. gothicus transitans* and *Ph. depressus*, which share certain important characters with both *Phoebodus* and *Thrinacodus* were found from Gour Bedda in Algeria. That discovery confirms the earlier ideas of possible close relationships between *Ph. gothicus* and *Th. tranquillus*. However, it is still unknown which of those intermediate forms belongs to the *gothicus-tranquillus* lineage. It is possible that *Ph. g. transitans* and *Ph. depressus* are actually conspecific, and that these two types of teeth belonged to the same dentition.

During the Famennian, environmental preferences of the phoebodontiforms appear to have changed from predominantly shallow water to more pelagic. In the middle and late Famennian, *Ph. gothicus* occupied similar or slightly more open marine niches to early Famennian phoebodonts. However, probably as a result of successive sea-level rises, at least two typically pelagic species emerged, viz. *Ph. limpidus* and *J. australiensis*. *Th. tranquillus* occurs in all the environments except for the shallowest which, however, could have been accessible to its supposed descendant, *Th. ferox*.

Some environmental differentiation in late Famennian cladodont sharks can also be observed. "*S.*" *glabrum* is quite common in sediments from deeper basins and flourishes in the regions with anoxic bottom conditions. In normal marine and well oxygenated waters on shallower shelves and platforms it gives way to stethacanthids.

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PLATE 1

A-F – Shark teeth from Iran, Ali-Morad, sample 61/8. A-B – *Protacrodus* sp., IGPUW/Ps/5/29, occlusal and lateral views. C-D – *Stethacanthus* sp., IGPUW/Ps/5/30, labial and oblique lingual views. E-F – *Phoebodus gothicus*; E – IGPUW/Ps/5/31, basal view; F – IGPUW/Ps/5/32, lateral view.

G-T – Chondrichthyan microremains from Iran, Hutk, sample 38/23. G-M – *Ph. gothicus*; G – IGPUW/Ps/5/33, transitional from *Ph. turnerae*, occlusal view; H-I – IGPUW/Ps/5/34, oblique lingual and occlusal views; J-K – IGPUW/Ps/5/35, occlusal and oblique lingual views; L-M – IGPUW/Ps/5/36, occlusal and labial views; N – IGPUW/Ps/5/37, occlusal view. O-Q – *Stethacanthus* sp., IGPUW/Ps/5/38, occlusal, lingual and labial views. R – *Deihim mansureae* gen. et sp. nov., IGPUW/Ps/5/39, morphotype 2, lingual view. S-T – Chondrichthyan scales, IGPUW/Ps/5/40-41.

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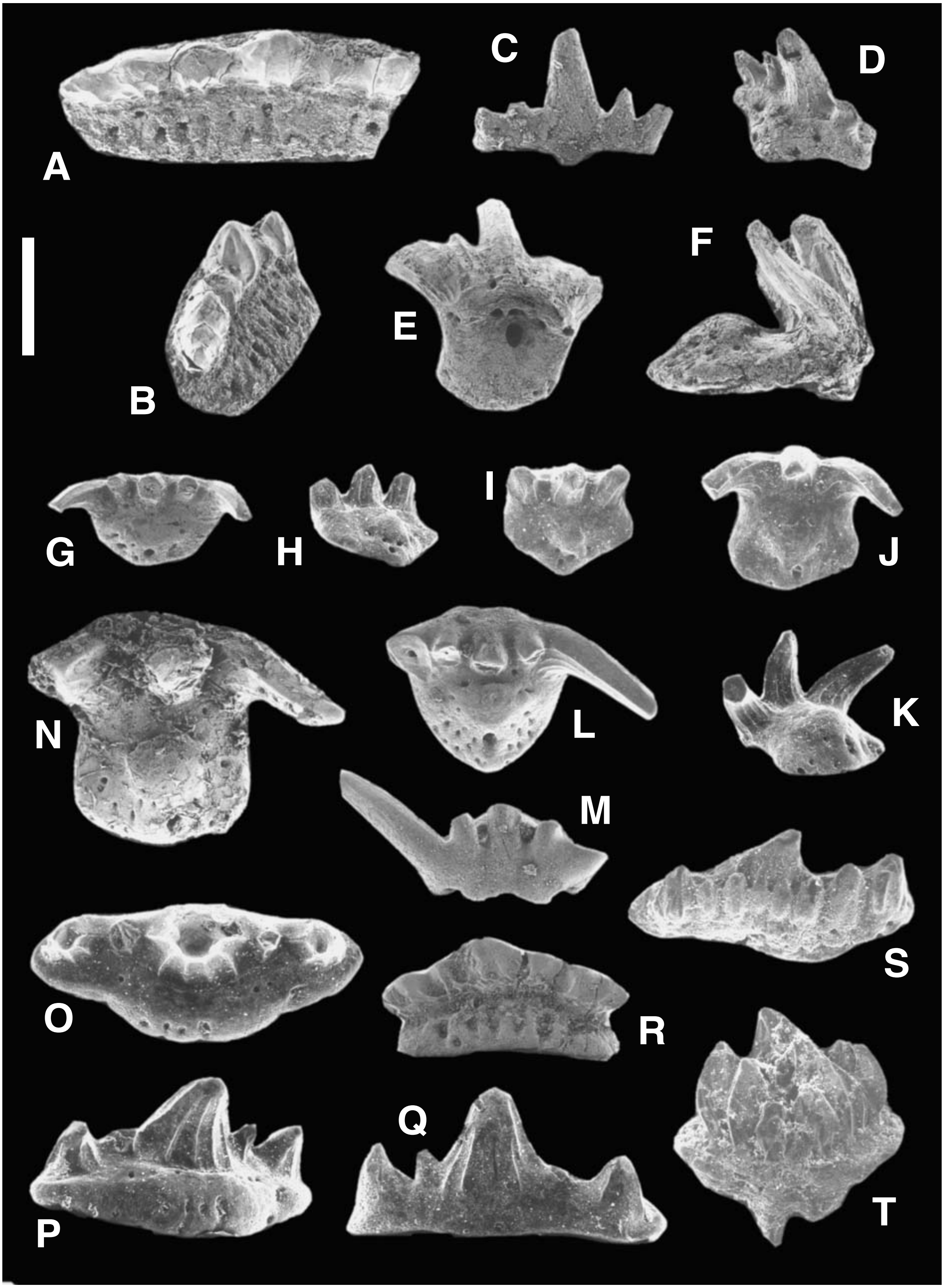
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PLATE 2

Shark teeth from Iran, Dalmeh, sample 64

A-D – *Jalodus australiensis*; A-B – AEU 209, labial and occlusal views; C-D – AEU 210, occlusal and labial views.
E-F – *Bransonella*? sp.; E – AEU 211, labial view; F – AEU 212, lingual view.
G – *Phoebodus gothicus*, AEU 213, occlusal view.
H – *Thrinacodus tranquillus*, AEU 214, occlusal view.
I-J – *Orodus* sp., AEU 215, occlusal and lingual? views.
K – ?*Deihim mansureae* gen. et sp. nov., AEU 216, isolated crown.
L-N – *Protacrodus serra* sp. nov., AEU 217, labial, mesial and lingual views.

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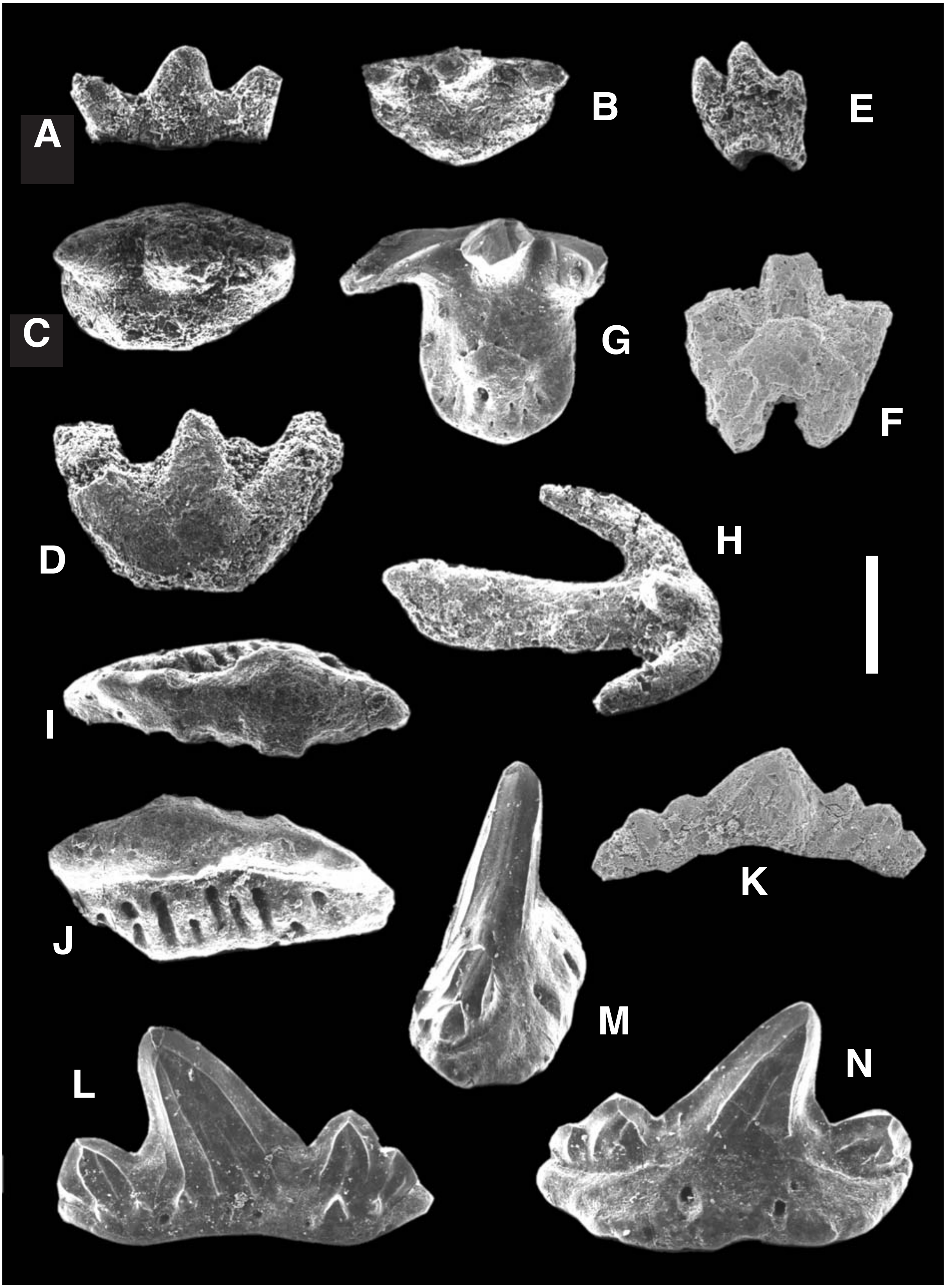
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PLATE 3

Shark teeth from Mighan, Iran

A-C – *Phoebodus gothicus*; A – AEU 218, sample 118, occlusal view, × 100; B – AEU 219, sample 131, occlusal view, × 60; C – AEU 220, sample 130, occlusal view, × 22.

D-G – *Ph.* aff. *turnerae*; D – AEU 221, sample 117, occlusal view, × 30; E – AEU 222, sample 117, occlusal view, × 23; F-G – AEU 223, sample 117, basal/labial and occlusal views, × 32.

H – *Thrinacodus tranquillus*, AEU 224, sample 134, occlusal view, × 70.

I-M – *Stethacanthus* spp.; I – AEU 225, sample 131, occlusal/lingual view, × 52; J – AEU 226, sample 113, lingual view, × 40; K – AEU 227, sample 131, basal/labial view, × 40; L-M – AEU 228, sample 113, labial and lingual views, × 52.

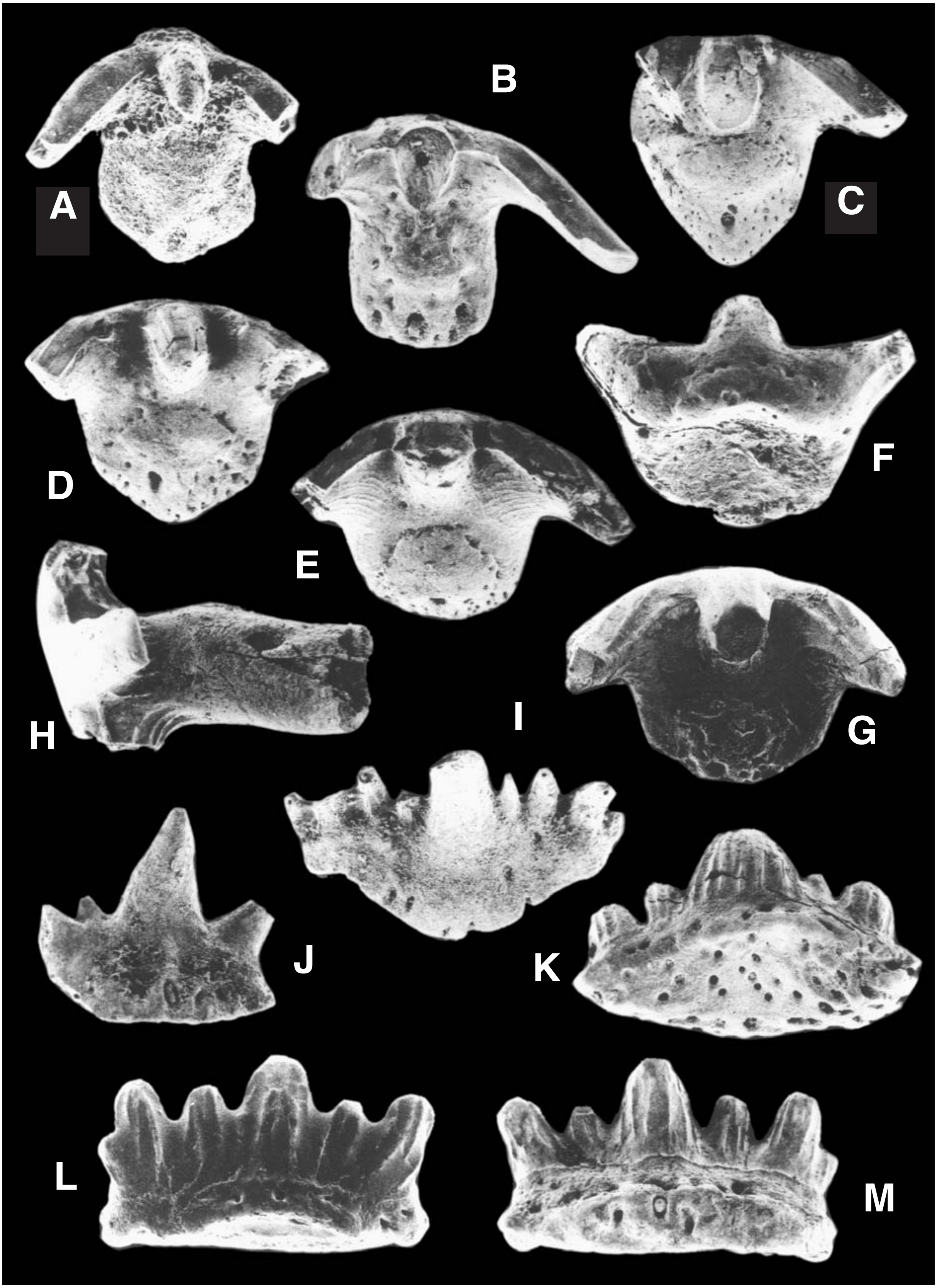
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PLATE 4

Crushing teeth from Iran. A-I from Mighan; J-K from Hodjedk, sample R3; L-N from Dalmeh, sample 39

A-C – *Lissodus* sp.; A-B – AEU 229, sample 129, occlusal and lingual views, × 25; C – AEU 230, sample 131, labial view, × 52.

D-E, H-I, N – *Protacrodus* spp. D-E – AEU 231, sample 117, occlusal and lingual views, × 41; H – AEU 232, sample 131, lingual view, × 43; I – AEU 233, sample 131, lingual view, × 30; N – AEU 234, isolated crown, × 40.

F-G, J-M – *Deihim mansureae* gen. et sp. nov. F-G – AEU 235, morphotype 3?, lingual and basal/labial views, × 52; J-K – Dubious specimen AEU 236, morphotype 4 without labial cusplets, oblique basal/labial view × 27 and lingual view × 32; L-M – AEU 237, morphotype 1, basal/labial and occlusal views, × 42.

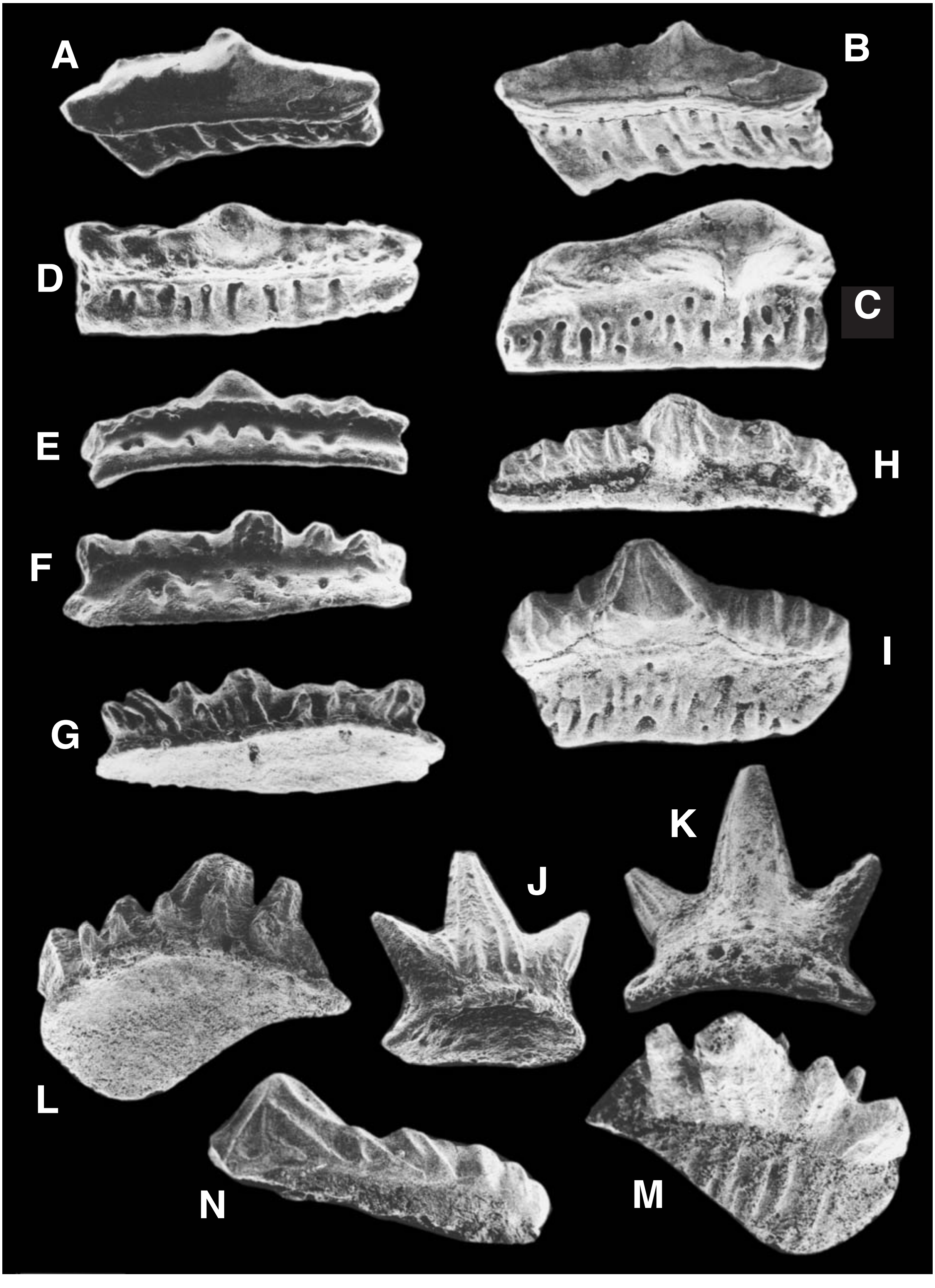
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PLATE 5

Protacrodontidae from Iran. A-F from Hodjedk, sample R3; G-I from Hutk, sample 38/23; J-Q from Dalmeh, sample 64

A-M – *Deihim mansureae* gen. et sp. nov.; A-C – AEU 238, morphotype 2?, labial, lingual, and occlusal views; D-F – AEU 239, morphotype 4, occlusal, lingual, and labial views; G-I – Morphotype 2; G – IGPUW/Ps/5/42, isolated crown; H – IGPUW/Ps/5/43, occlusal view; I – IGPUW/Ps/5/44, labial view; J – AEU 240, morphotype 1, occlusal view; K-M – Morphotype 3; K-L – AEU 241, labial and lingual views; M – AEU 242, occlusal view.

N-P – *Protacrodus serra*, AEU 243, labial, lingual, and occlusal views.

Q – *Protacrodus* sp., AEU 244, lingual view.

Scale bar = 0.5 mm

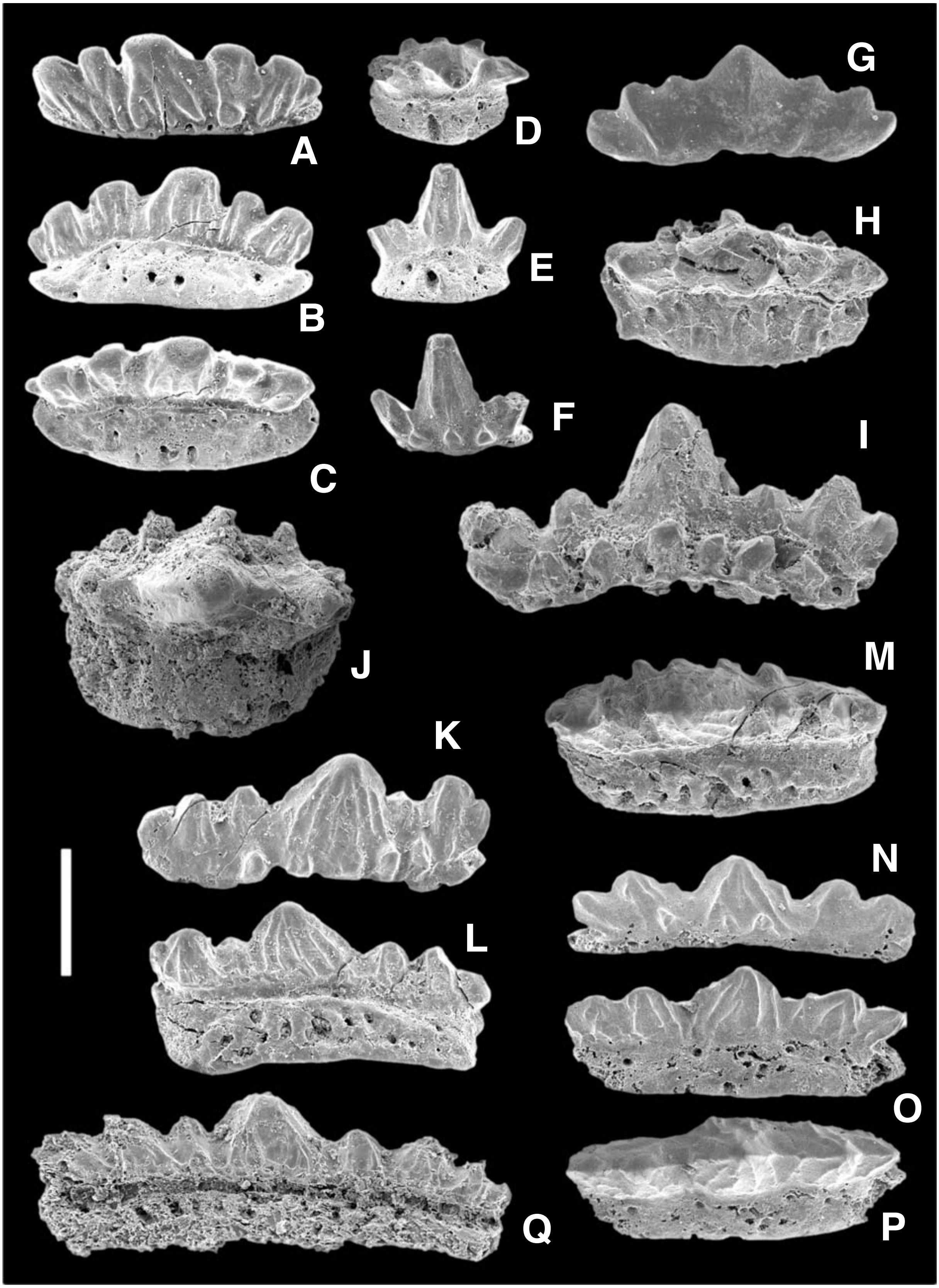
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PLATE 6

Ichthyoliths from Morocco, Oum El Jerane, sample OEJ-1

A-C – *Phoebodus typicus* (or *Ph. rayi*), IGPUW/Ps/5/44-46, occlusal views.
D-E – *Protacrodus* sp., IGPUW/Ps/5/47, occlusal and labial views.
F-K – Protacrodontidae cf. *Deihim mansureae*; F-H – IGPUW/Ps/5/48, labial, lingual, and occlusal views; I-K – IGPUW/Ps/5/49, labial, lingual, and occlusal views.
L – *Protacrodus vetustus*, IGPUW/Ps/5/50, labial? view.
M-N – Chondrichthyan or acanthodian branchial denticles, specimens IGPUW/Ps/5/51-52.
O-P – Chondrichthyan scales, specimens IGPUW/Ps/5/53-54.
Q-R – Acanthodian scales, specimens IGPUW/Ps/5/55.
S – Acanthodian symphysial tooth-whorl, IGPUW/Ps/5/56.

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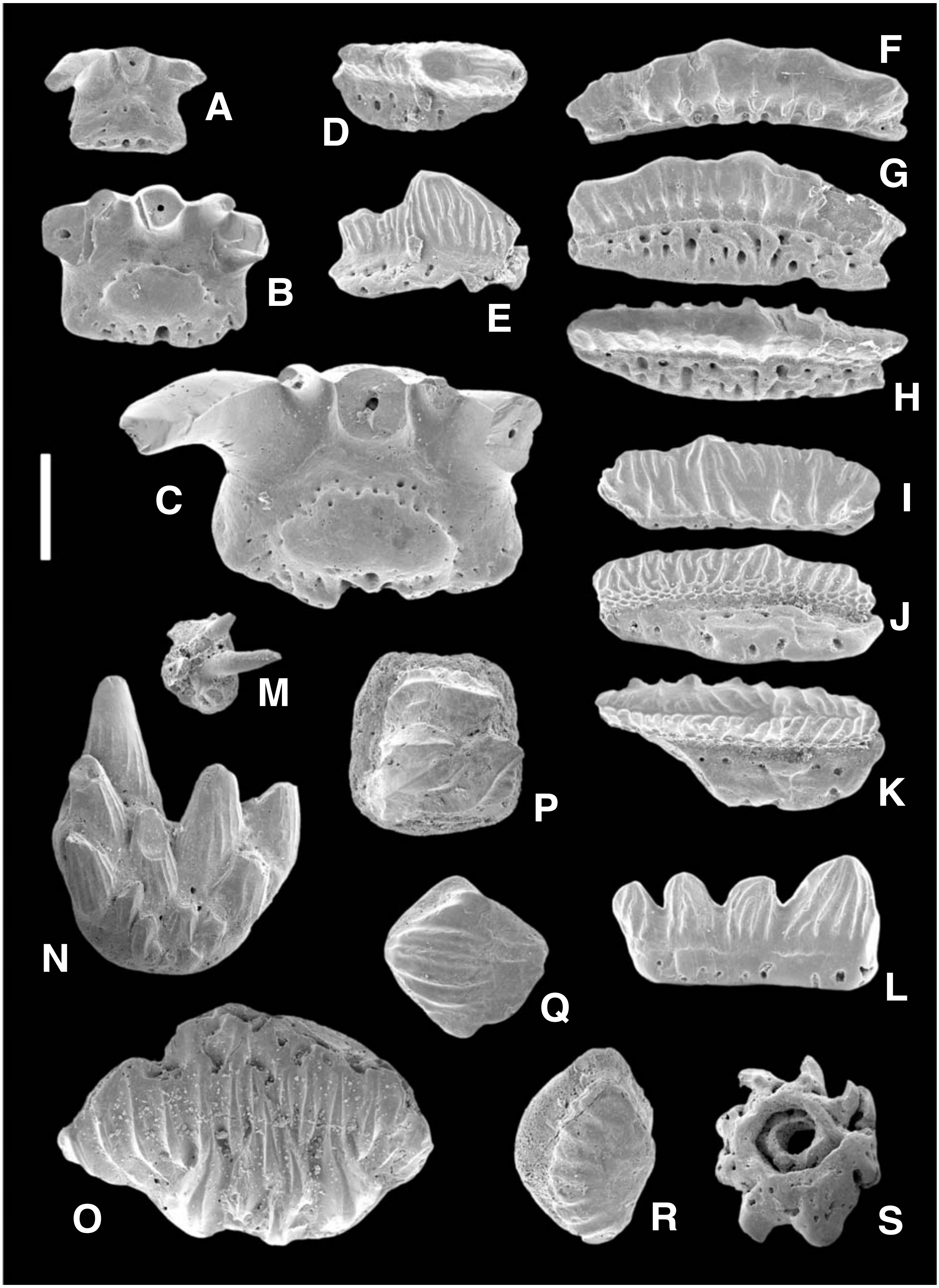
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PLATE 7

A-E – Cladodont teeth from Morocco, Oum El Jerane, sample OEJ-1. A-C – *Stethacanthus* cf. *thomasi*; A – IGPUW/Ps/5/57, lingual view; B – IGPUW/Ps/5/58, basal/labial view; C – IGPUW/Ps/5/59, unusual tricuspid tooth, labial view. D-E – "*Symmorium*" sp. B; D – IGPUW/Ps/5/60, occlusal view; E – Strongly abraded specimen IGPUW/Ps/5/61, occlusal view.

F-O – Ichthyoliths from Algeria, Gour Bedda, sample A-236. F-G – "*Symmorium*" sp. A, IGPUW/Ps/5/62, lingual and labial views. H-K – *Phoebodus* aff. *turnerae*; H-J – IGPUW/Ps/5/63-65, occlusal views; K – IGPUW/Ps/5/66, possibly *Ph. turnerae*, occlusal view. L-M – Acanthodian ("*Acanthodes*"-type) scales, IGPUW/Ps/5/100-101. N – Acanthodian gill-raker, IGPUW/Ps/5/67. O – Actinopterygian scale, IGPUW/Ps/5/68.

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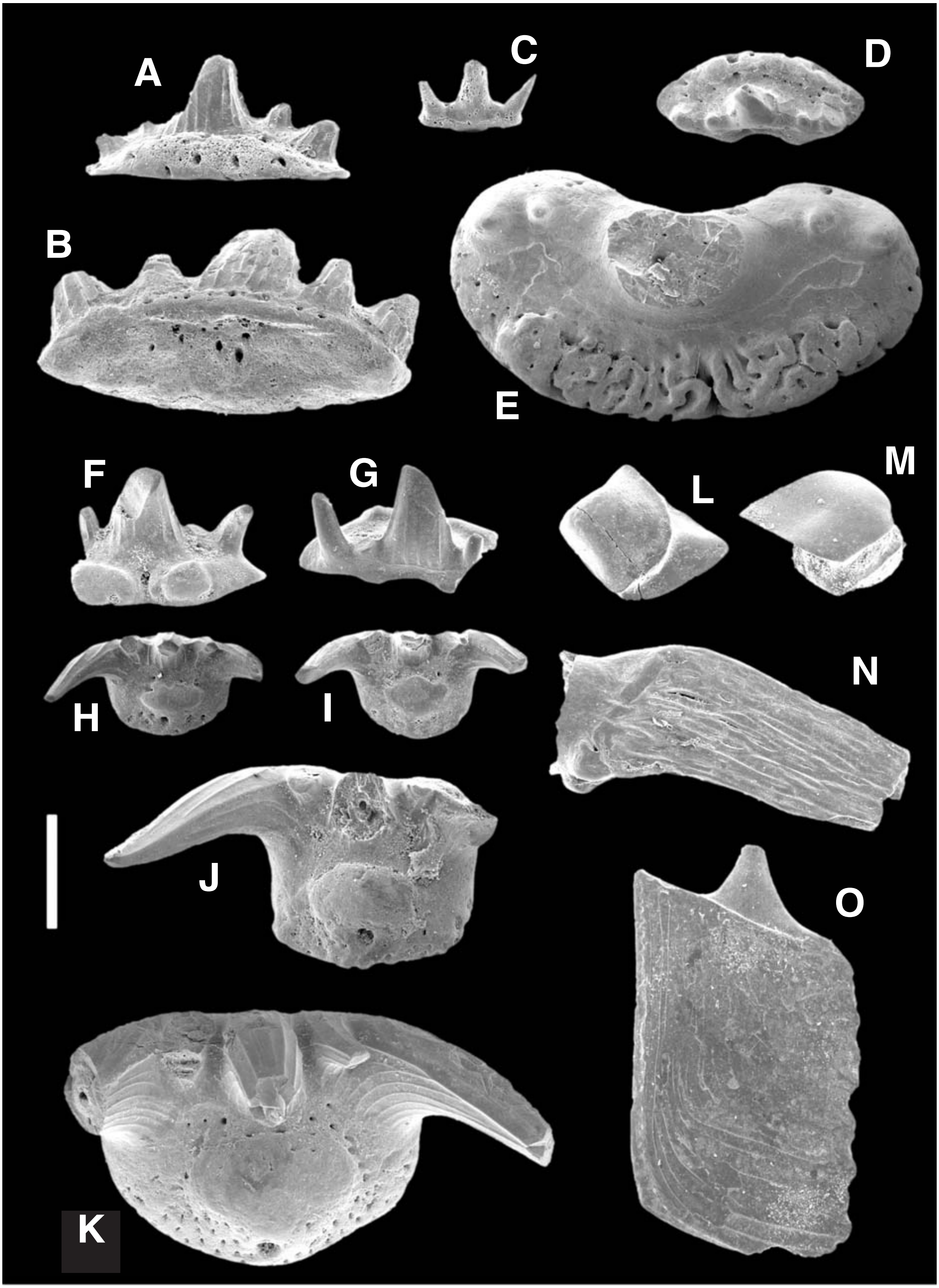
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PLATE 8

Phoebodontiformes from the late Famennian of Morocco

A-C – *Phoebodus limpidus* from sample TN-1; A – IGPUW/Ps/5/69, labial view; B-C – IGPUW/Ps/5/70, labial and lingual views.

D-J – *Jalodus australiensis*; D – IGPUW/Ps/5/71, sample TN-2, labial/basal view; E – IGPUW/Ps/5/72, sample OEJ-2, labial view; F-G – IGPUW/Ps/5/73, sample OEJ-3, occlusal and labial views; H-J – IGPUW/Ps/5/74, sample OEJ-2, oblique lingual, occlusal and labial views.

K-N – *Ph. gothicus* from sample OEJ-3, specimens IGPUW/Ps/5/75-78, occlusal views.

Scale bars = 0.5 mm

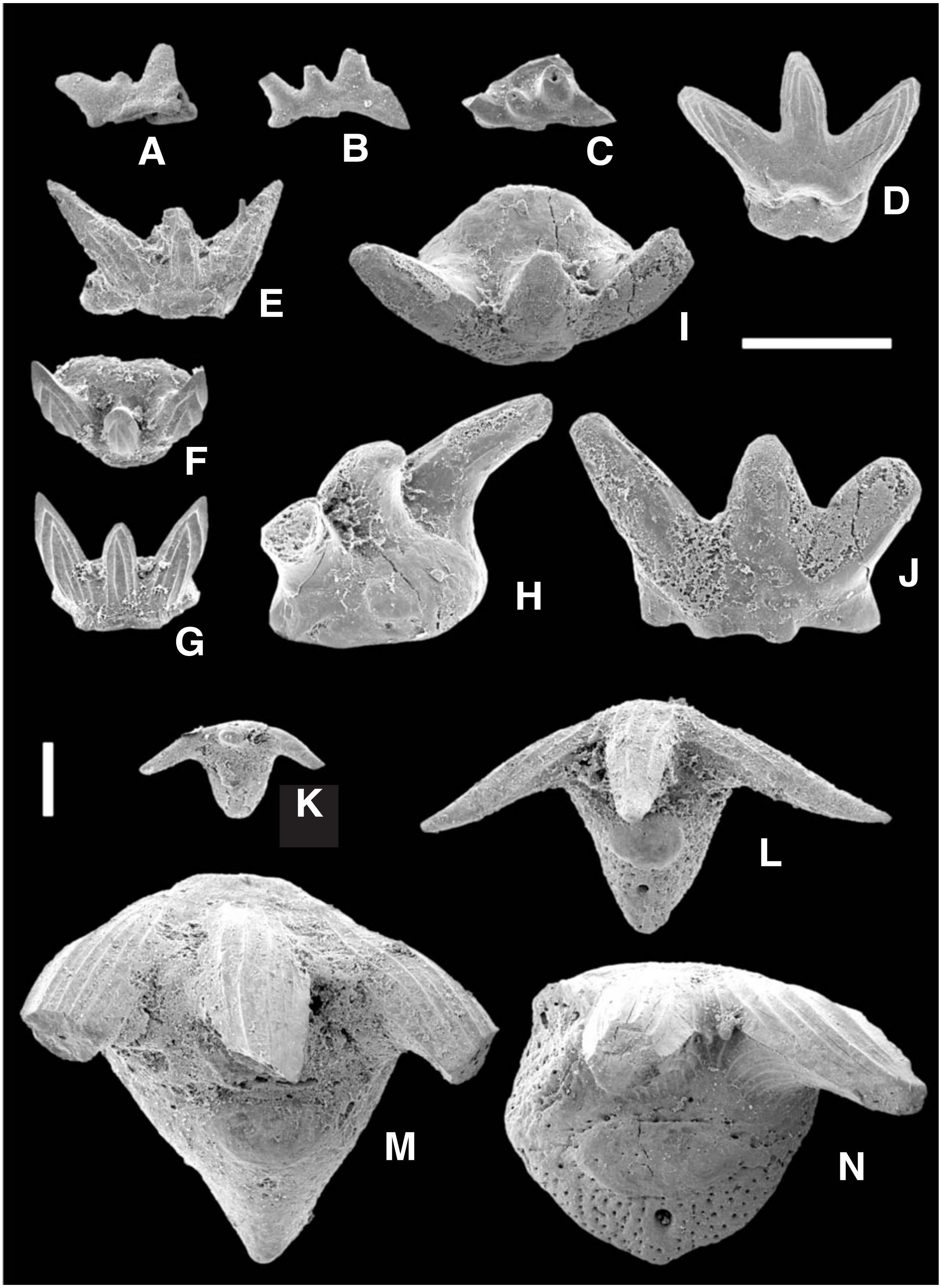
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PLATE 9

"*Symmorium*" *glabrum* from the late Famennian of Morocco, Oum El Jerane, sample OEJ-2

A-B – IGPUW/Ps/5/79, lingual and occlusal views;
C-D – IGPUW/Ps/5/80, lingual and occlusal views;
E-F – IGPUW/Ps/5/81-82, labial views;
G-H – IGPUW/Ps/5/83, occlusal and lingual views.
I – IGPUW/Ps/5/84, labial view.
J-K – IGPUW/Ps/5/85, lingual and labial views.

Scale bar = 0.5 mm

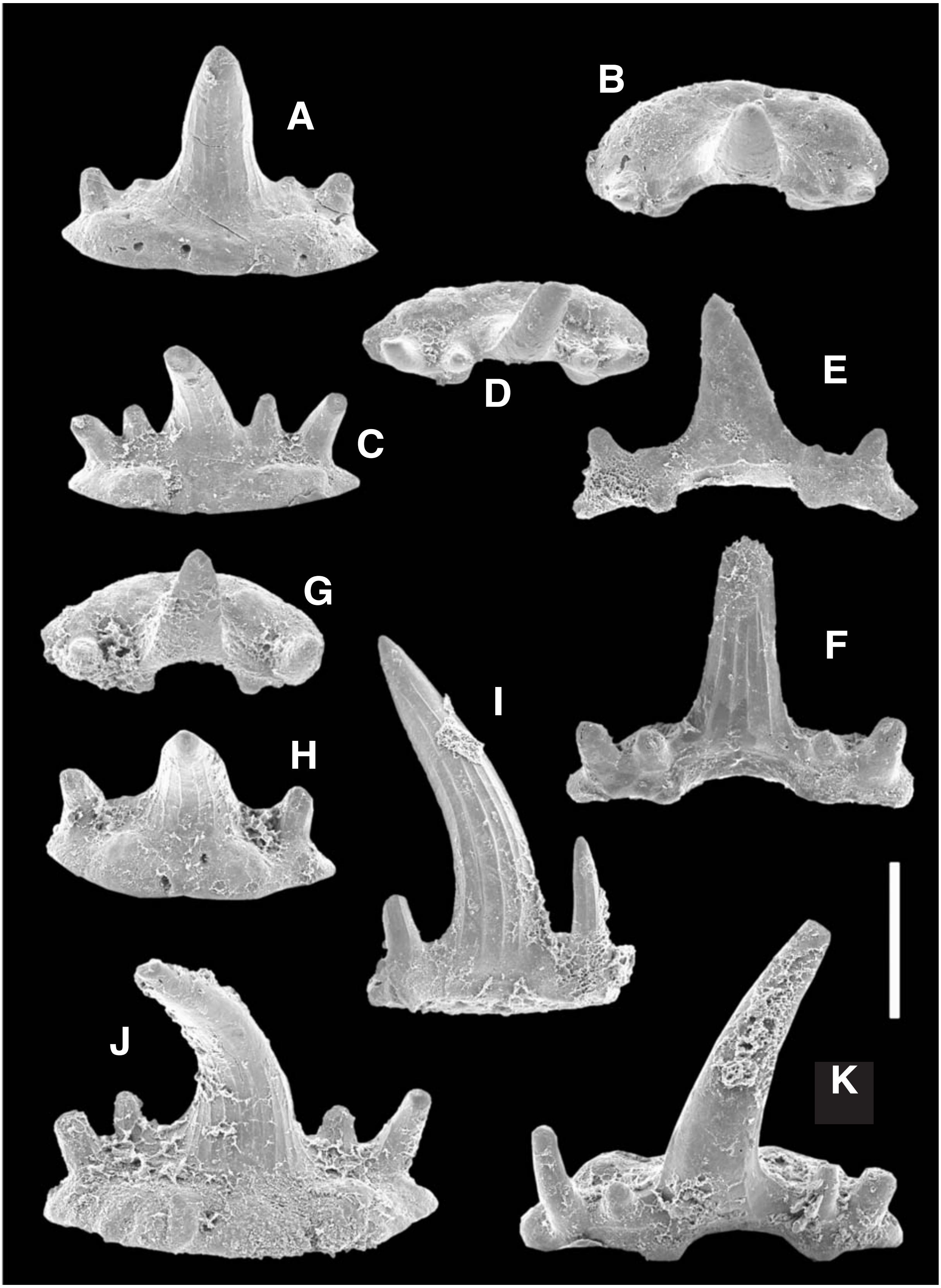
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PLATE 10

Stethacanthus sp. from the late Famennian of Morocco

A-B – IGPUW/Ps/5/86, sample TN-1, labial and lingual views;
C – IGPUW/Ps/5/87, sample TN-2, labial view;
D-J – From sample OEJ-2; D – IGPUW/Ps/5/88, labial view; E- F – IGPUW/Ps/5/89, basal and labial views; G – IGPUW/Ps/5/90, occlusal view; H-I – IGPUW/Ps/5/91, oblique lingual and labial views; J – IGPUW/Ps/5/92, occlusal view.

Scale bar = 0.5 mm

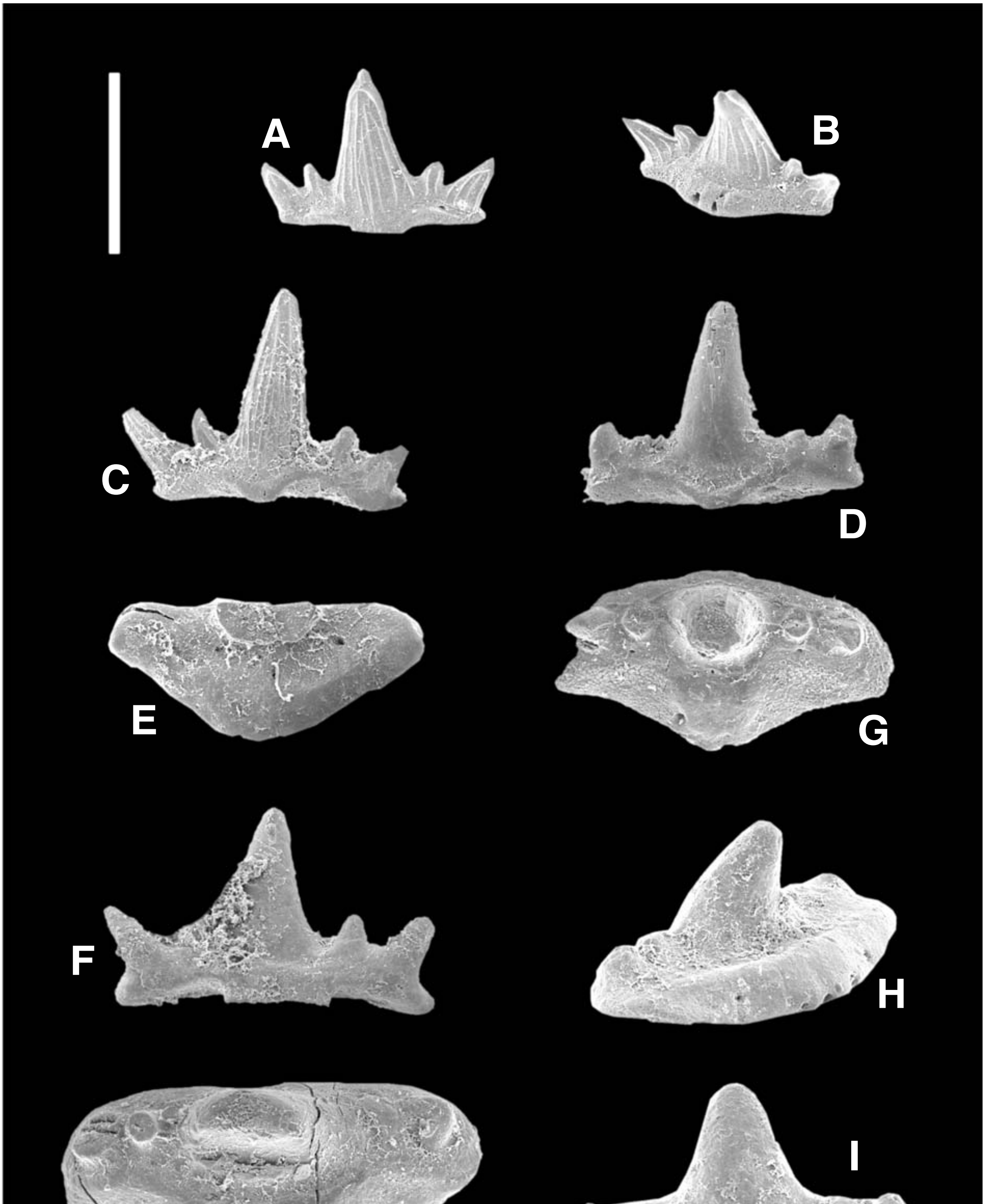
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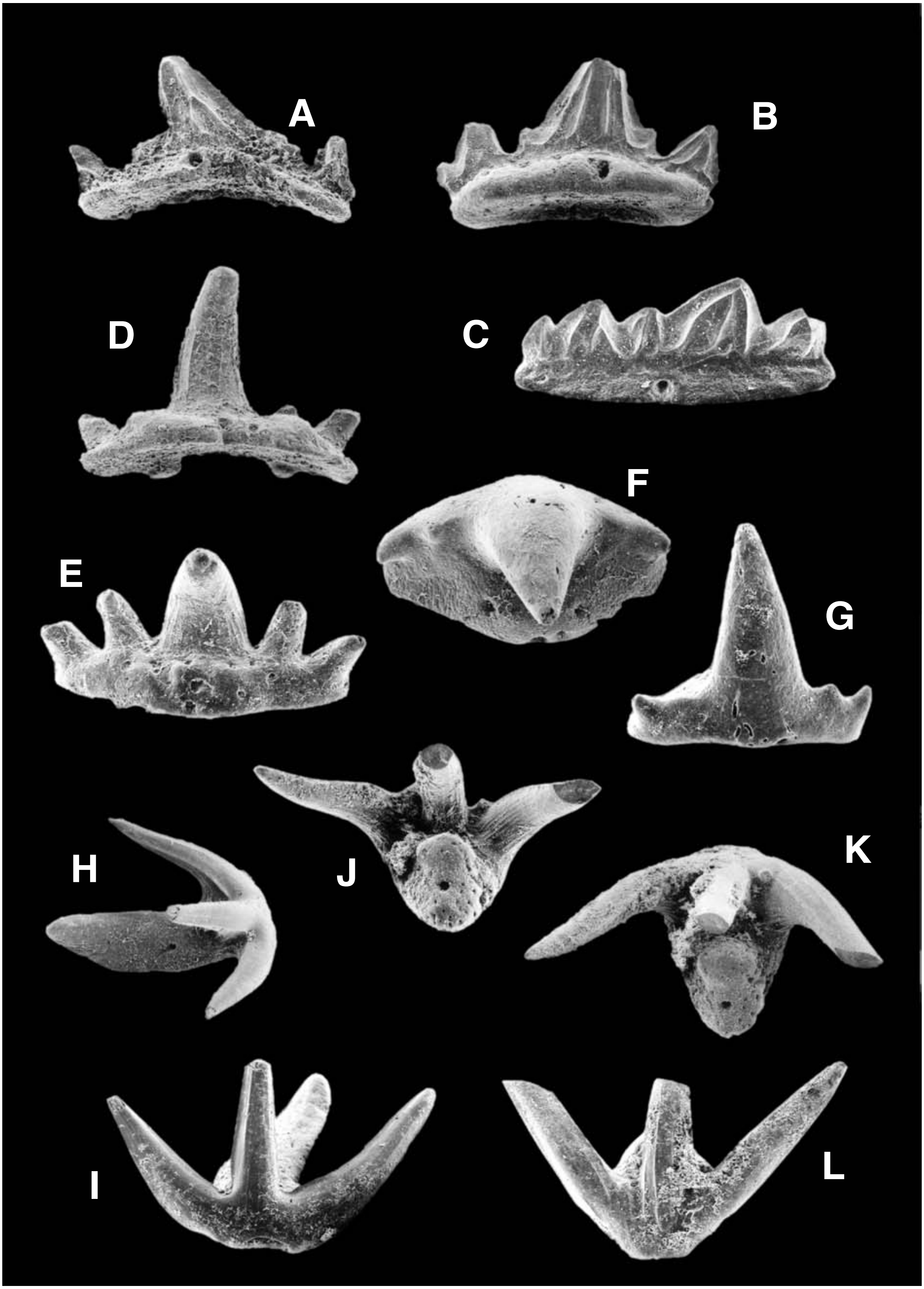
PLATE 11

Shark teeth from the *Gonioclymenia* limestone, late Famennian of Morocco, Tizi Nersas, sample TN-2

A-C – *Protacrodus serra* sp. nov., lingual views, IGPUW/Ps/5/92-94; A – Morphotype 1, × 71; B – Specimen intermediate between morphotypes 1 and 2, × 41; C – Morphotype 3, × 52.
D – "*Symmorium*" *glabrum*, IGPUW/Ps/5/95, lingual view, × 41.
E – *Clairina marocensis*, IGPUW/Ps/5/96, lingual view, × 49.
F-G – *Stethacanthus* sp., IGPUW/Ps/5/97, occlusal view × 71, labial view × 60.
H-I – *Thrinacodus tranquillus*, IGPUW/Ps/5/98, occlusal view × 21, labial view × 30.
J-L – *Phoebodus gothicus*, IGPUW/Ps/5/99, lingual, occlusal and labial views, × 19.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