

## Famennian microvertebrates from the Dalmeh area, central Iran

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**Abstract** – Late Devonian (Famennian) fish remains are here reported from limestones exposed in the Garigoon Mountains, near the village of Dalmeh, central Iran. The microvertebrate fauna includes the first records from Iran of some Devonian sharks, including *Phoebodus gothicus*, *Thrinacodus ferox*, *Stethacanthus* sp., *Protacrodus* sp. and *Orodus* sp. The new protacrodontoid *Dalmehodus turnerae* gen. et. sp. nov. is described herein. The presence of *Ph. gothicus* in the *crepida* zone makes this the earliest occurrences of the species. The actinopterygian *Moythomasia durgaringa*, previously known only from Australia, is here recorded from Iran in the early Famennian, extending the known age range for the species.

### INTRODUCTION

Although many sites yielding Devonian fish remains are now known from Iran (see Hairapetian *et al.*, this volume for a comprehensive review), few have yielded microvertebrates with biostratigraphically useful key taxa that add new information to the known age ranges or distributions of such taxa. In this paper we describe the microvertebrate faunas from the Garigoon Mountains, a site discovered by the junior author during mapping and sampling for conodonts in late 1998 (Figures 1, 2). The site is particularly significant because the vertebrate sites are well constrained by conodont faunas to within the Late *postera*-Early *expansa* zones of the Late Famennian. Figure 3 shows a detailed log of the stratigraphic section with all vertebrate-bearing samples indicated. Furthermore the first records of many taxa, previously known only outside of Iran are here recorded for the first time, allowing more precise palaeogeographic comparisons to be made with other regions within close proximity of the northern Gondwana margin.

The specimens were collected as bulk limestone samples by the junior author and dissolved in acetic acid and the insoluble residues sieved and picked. Some specimens, such as the larger orodont sharks teeth were collected as field specimens and left unprepared *in situ*.

Specimens are all numbered and housed within the collections of the Geology Department, University of Esfahan (prefix EUIV).

### SYSTEMATIC PALAEOLOGY

Subclass *Chondrichthyes* Huxley 1880

Infraclass *Elasmobranchii* Bonaparte 1838

### Order Indeterminate

Family Phoebodontidae Williams 1985

Genus *Phoebodus* St. John and Worthen 1875

#### Type Species

*Phoebodus sophiae* St. John and Worthen 1875

*Phoebodus gothicus* Ginter 1990

Figure 4 a, b, c, d, f, h, j

#### Material Examined

EUIV 99.8.222, is relatively complete but with the base broken off; EUIV 99.9.227 has the base well-preserved, central cusp present but missing the lateral cusps. EUIV 99.2.229 has the root well preserved but is missing the cusps, and both EUIV99.5.209 and 99.9.230 have the base of the cusps preserved and the root is complete.

#### Description

EUIV 99.8.222 superficially resembles teeth of *Jalodus australiensis* ('*Phoebodus*' *australiensis* Long 1990, Ginter 1999) because the base is not complete, giving the impression that the root is much shorter. However, the ornamentation on the cusps is of coarse widely separated striae as opposed to a chevron-type of layered ornamentation found in *Jalodus*. The presence of very minute accessory cusps seen as small circular basal sections (Figure 4 a) between the main cusps is a feature commonly seen on *Ph. gothicus* but never present in *Jalodus*, so on this basis we refer the specimen to *Ph. gothicus*. EUIV 99.9.227 (Figure 4c, e, f) is worn with lateral cusps missing, yet clearly shows the defining features of this species in having the base strongly produced lingually ending at a sharp point. It has three cusps, approximately equal in size (as shown



Figure 1 Map of Iran showing location of the Dalmeh section, north of Ardakan.

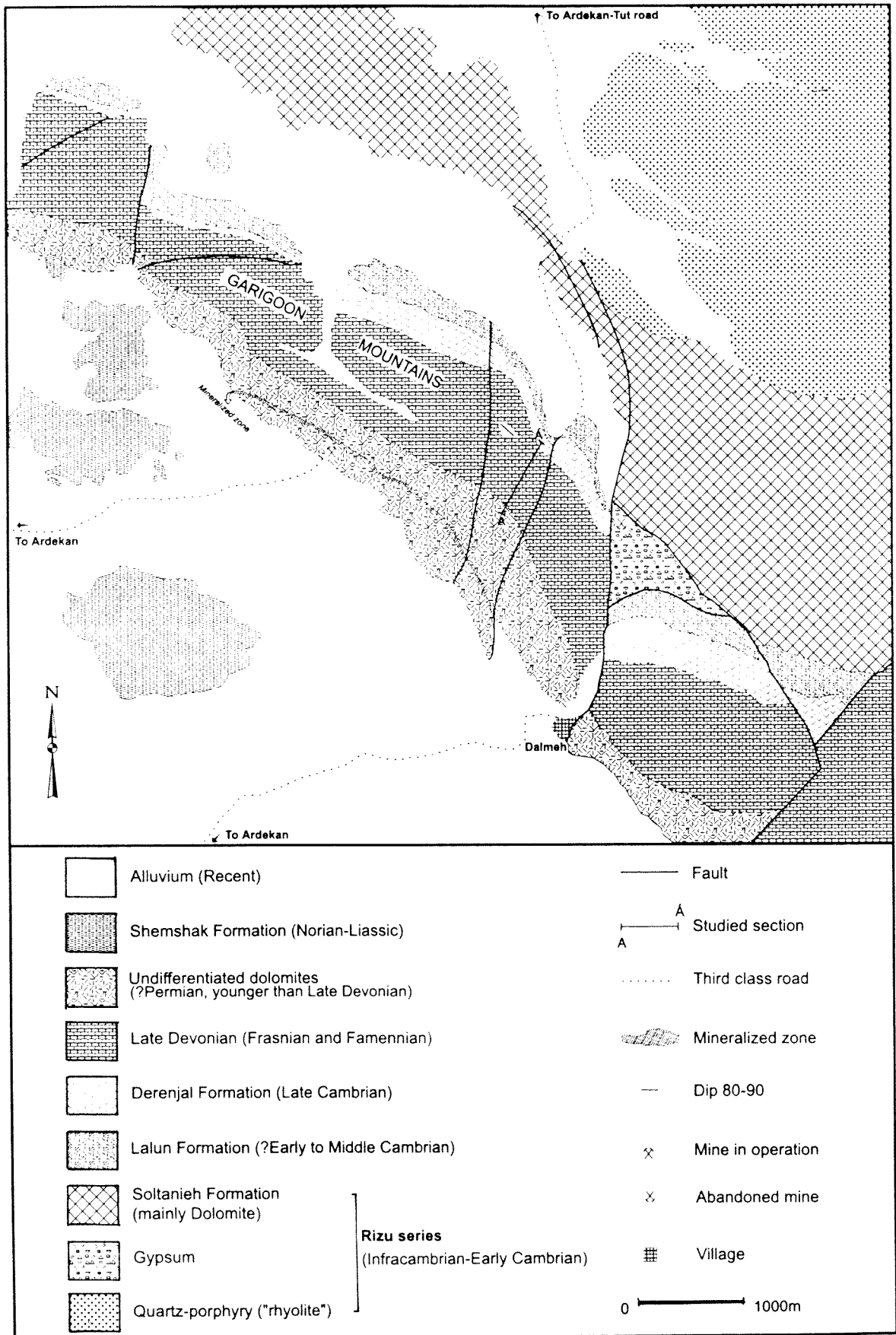
from the size of the cross-sections of the missing lateral cusps), the central cusp being only marginally smaller, and with two or three coarse ribs on the labial face of the preserved bases of the lateral cusps. The lingual face is not well preserved on the specimen. The base is closely comparable with type material from the Holy Cross Mountains of Poland illustrated by Ginter (1990, plate 2 figure 4), from the upper *expansa* or lowest *praesulcata* zones. Specimen EUIV99.9.229 (Figure 4d) has a typical elongated root of *Ph.gothicus* but is missing the cusps. Nonetheless it is clear that no accessory cusps are present between the three main bases of the cusps. Specimens EUIV 99.5.209 (Figure 4) and EUIV 99.9.230 (Figure 4j) both have a shorter base than the previous specimen with a well-developed

lingual boss. They show clear evidence of three main cusps without secondary cusps present. Both fall within the natural range of variation seen in *Ph.gothicus*, with close resemblances to other shorter-based specimens illustrated by Ginter (1990, plate 3, Figure 5c; Ginter 1999, plate 2, figures 4–5).

*Phoebodus ?gothicus* Ginter 1990  
Figure 4i, m, 6e

#### Material Examined

EUIV 99.7.219, a partial tooth with the main cusp preserved but lateral cusps broken off; (sample number 61) from the *postera* zone, Late Famennian; EUIV 99.7.216, a damaged tooth with cusps missing



**Figure 2** Detailed geological map of the Garigoon Mountains near Dalmeh, showing the distribution of Late Devonian sediments and position of where the stratigraphic section was measured (the line between the triangles, centre of map).

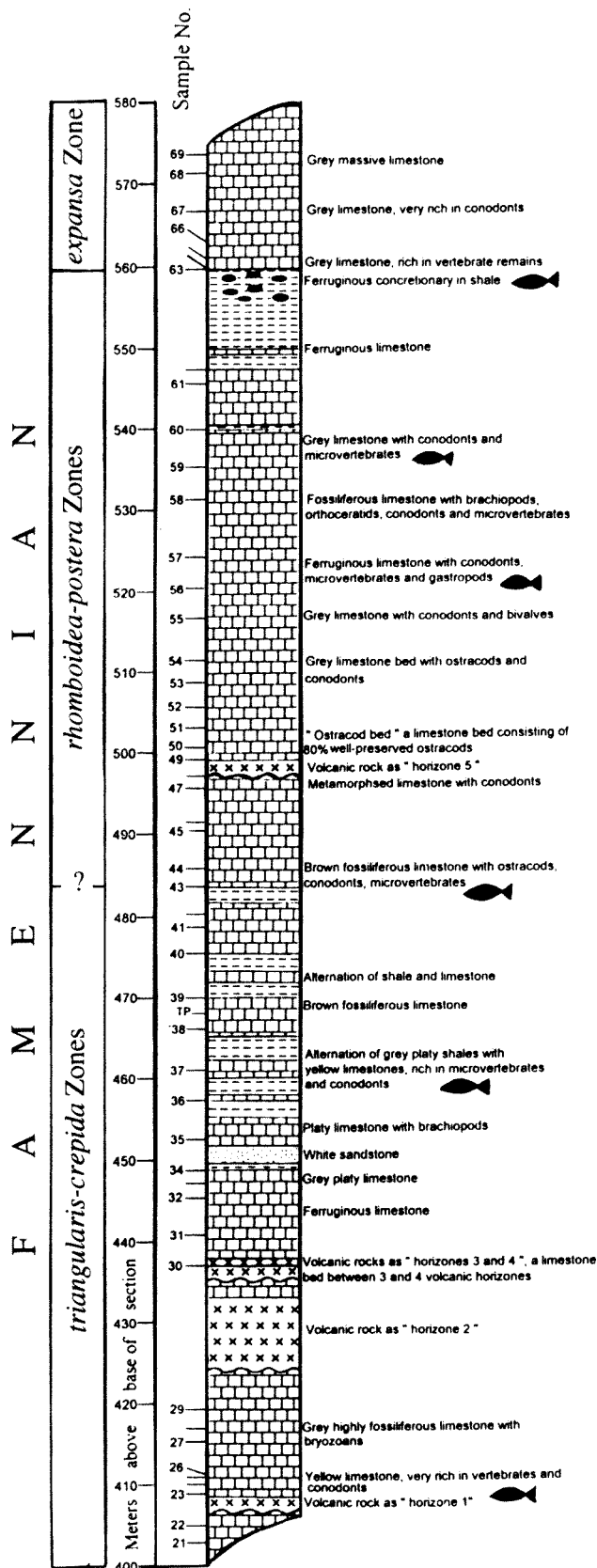


Figure 3 Stratigraphic column showing position of the fossil fish horizons in the Dalmeh section.

(sample 64); EUIV99.7.215, a poorly-preserved tooth with only the bases of the cusps preserved, root largely damaged (sample 39).

**Description**

EUIV 99.7.215 (Figure 4 i) is here considered to be a *Phoebodus* tooth as it has three almost equally sized cusps and a lingually well-developed root, so is most like a damaged example of *Ph. gothicus*. EUIV 99.7.216 (Figure 4m) also has three main cusps but they are worn and lacking any surface sculpture. The crown lacks intermediate cusps, and the specimen is here considered to be most likely a species of *Phoebodus*. EUIV 99.7.219 (figure 6e) has the main cusp on the crown well-preserved, showing distinct vertical ribbing. The lateral cusps are broken off but their basal sections shows they were relatively large cusps. The root is well-developed lingually. The wide lingual process of the root suggests that it is most closely aligned to *Ph. gothicus*, a common species within the *postera* zone.

**Stratigraphic range and distribution**

*Phoebodus gothicus* has been previously recorded ranging in age from the base of the *marginifera* zone right through to the end of the *expansa* zone of the Famennian (Ginter 1990, 1995, 1999, Ginter and Ivanov 1992, 1995a). It has been described from Germany (Thuringian Slate Mountains), Poland (Holy Cross Mountains), Russia (South Urals), possibly from Vietnam (*Phoebodus* cf. *Ph. gothicus*, Long 1993). The presence of *Ph. gothicus* in the *crepida* zone of Dalmeh, Iran, makes this the earliest occurrences of the species and a major extension of age range for the species.

**Genus *Thrinacodus* St John and Worthen , 1875**

**Type Species**

*Thrinacodus nanus* St John and Worthen 1875

***Thrinacodus* cf. *ferox* (Turner, 1982)**

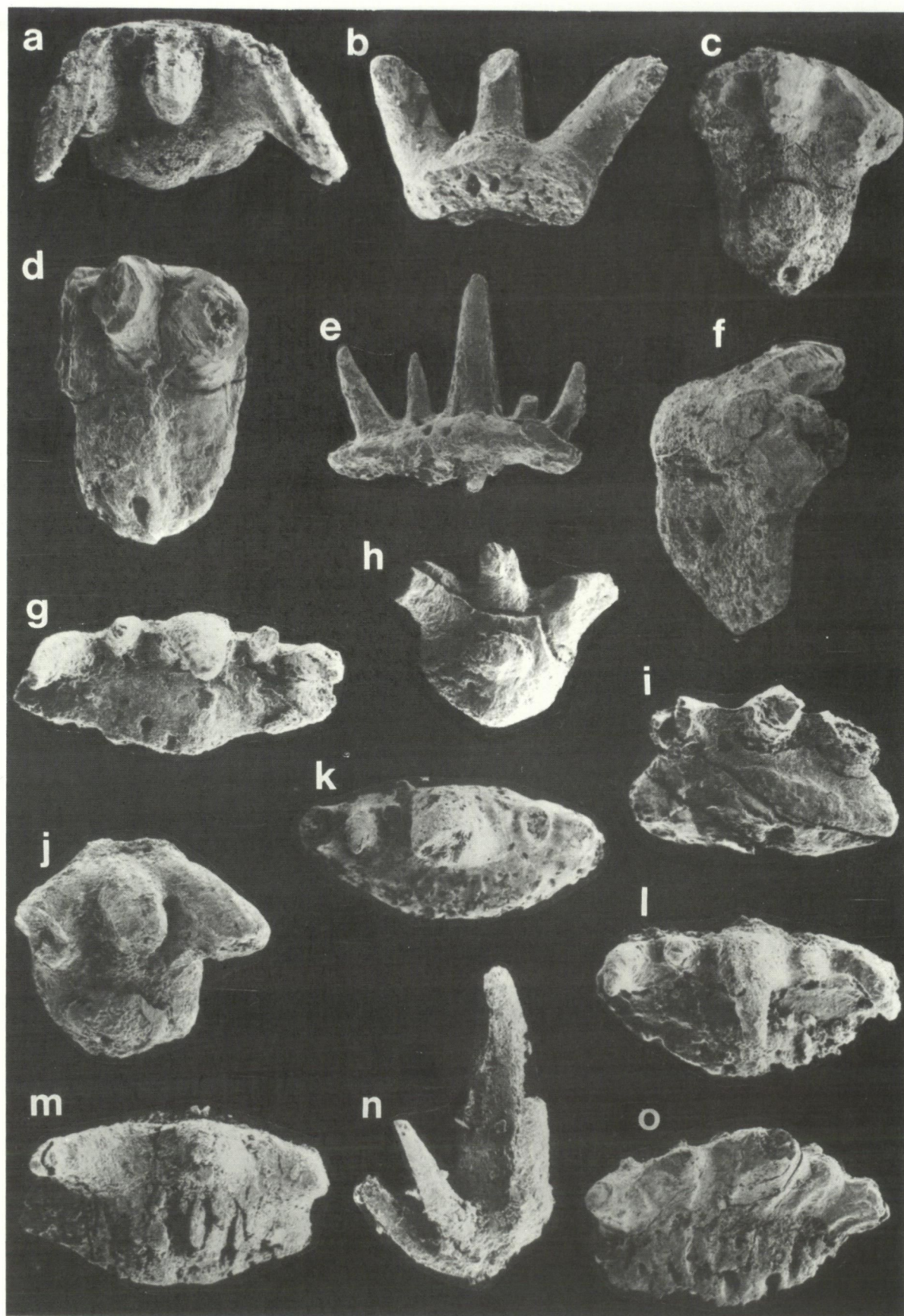
Figure 4 n

**Material Examined**

One specimen, EUIV 99.9.231, a fairly complete tooth showing the elongated base.

**Description**

The tooth shows the characteristic features of *Thrinacodus ferox* in having three strongly recurved, differently-sized grappling-hook like cusps on a very lingually elongated, evenly tapered base. The irregular, upturned shape of the lingual end of the base is reminiscent of the specimens illustrated by Ginter (1990, plate 3, figure 4) and Ginter and



**Figure 4** a, b, c, d, f, h, j. *Phoebodus gothicus*. a, b, EUIV99.8.222, a, occlusal view (x30); b, lingual view, showing broken root. c, f, EUIV99.9.227, c, occlusal view (x38), f, lateral view (x42). EUIV 99.9.229 occlusal view (x55). h, EUIV 99.5.209, occlusal view (x8). j, EUIV 99.9.230, occlusal view (x48). e, g, l, *Stethacanathus* sp. e, g, EUIV99.7.211, e, lingual view (x45), g, occlusal view (x60). l, EUIV 99.7.213, occlusal view (x60). m, *phoebodontid?* EUIV99.7.216, occlusal view (X33). o, *?Protacrodus* sp. EUIV 99.7.217, occlusal view (x33).

Ivanov (1996, figure 2A–D) from the Holy Cross Mountains, Poland. In this respect it also differs from specimens from Thailand and the Thuringian Slate Mountains which Ginter (1999) noted have similarities in having almost symmetrical crowns with a labio-basal depression.

#### Stratigraphic range and distribution

*Thrinacodus ferox* ranges from the end of the *marginifera* zone of the Famennian right through to the *sulcata* zone of the Tournasian (Ginter 1990, 1995, 1999, Ginter and Ivanov 1992, 1995b). It has been described from Germany (Thuringian Slate Mountains), Poland (Holy Cross Mountains), Russia (South Urals), Thailand (Long 1990), Australia (Turner 1982, 1983), China (Wang and Turner 1985) and possibly New Mexico (Kietzke and Lucas 1992). The specimen from Dalmeh, Iran, comes from the lower *expansa* zone, well within the known range for the species.

### Order Symmoriida

#### Family Stethacanthidae Lund 1974

#### Genus *Stethacanthus* Newberry 1889

#### Type Species

*Stethacanthus (Physonemus) altonensis* St. John and Worthen 1875

*Stethacanthus* sp.  
Figure 4 e, g, k, l

#### Material Examined

Three specimens, EUIV 99.7.211, EUIV 99.7.213 (both from sample number 37), EUIV 99.7.214 (sample number 43), all from the *crepida* zone of the early Famennian; all nearly complete teeth.

#### Description

These teeth all show characteristics more typically found in symmoriid and stethacanthid teeth but never in phoebodontids: the middle cusp is larger than the lateral cusps. The cusps are all quite straight-sided in lingual/labial views and gently recurved in occlusal view. The bases are approximately twice as broad as long (lingual-labial), apparently lack any development of a medial boss but may have one or two large nutritive foramina present (Figure 4 e, g, l). Small accessory cusps are present between the three main cusps on all of the specimens. The best preserved tooth (EUIV 99.7.211, Figure 4 e, g) closely resembles a similar tooth assigned to *Danaea* by Ginter (1990, plate 4, figure 7), but differs in that the central cusp of *Danaea* is curved slightly rostro-caudally, rather than symmetrical through its vertical plane. It

differs from similar teeth of *Stethacanthus thomasi* (Turner 1982) and forms attributed to *Stethacanthus* cf. *thomasi* (Ginter 1995) in the fewer numbers of lateral cusps, by its lesser degree of recurvature and absence of coarse ribbing on the cusps, yet has closer resemblance to teeth from the Thuringian Slate Mountains of Germany assigned to *Stethacanthus* sp. by Ginter (1999, plate 4 figures 1–5). The specimens illustrated by Ginter (1999) differ from the Dalmeh specimen in having a lingually pointed base and the main cusp is slightly curved rostrocaudally. The other specimens show similar morphology except that EUIV 99.7.213 (Figure 4 l) has a more convex outline to the root when seen in basal or occlusal views. The strong lingual curvature of the main cusps is also evident in this specimen.

#### Stratigraphic range and distribution

*Stethacanthus* is better known from articulated or partial skeletons of Carboniferous age (Zangerl 1981), although recently the famous articulated specimen previously referred to as the *Bearsden Stethacanthus* (as figured in Long, 1995 p.72–73) is now being described as a new genus by Coates and Sequiera (pers. comm. 2000). *Stethacanthus thomasi*, described by Turner (1982) from the presumed Famennian of Queensland and the Tournasian of Western Australia and New South Wales. *Stethacanthus thomasi* and *S.* cf. *thomasi* has been recorded ranging in age from the Early-Middle *expansa* zone.

### Order Euselachii

#### Superfamily Protacrodontoidea Zangerl 1981

#### *Dalmehodus* gen. nov.

#### Type Species

*Dalmehodus turnerae* sp. nov

#### Diagnosis

A protacrodontoid tooth having between four to eight relatively equally-sized broad-based cusps on a low, flat root. Lingually the crown has near vertical straition of widely-spaced ribs, labially the crown shows a coarse reticulate pattern of ornamentation. Each cusp has a corresponding large nutritive foramen adjacent to it in the root.

#### Remarks

Although only three specimens are known, the distinctive form of these teeth make them immediately separable from other known genera of Devonian sharks. Amongst the low crowned, multicuspid types of teeth only *Orodus* and *Protacrodus* are similar, yet in *Dalmehodus* there are numerous crowns, with distinctive ornamentation

arranged on a broad-based root. *Dalmehodus* therefore is distinguished from *Protacrodus* but its larger number of equal-sized cusps and broader tooth shape; from *Orodus* by the pointed cusps on the crown as opposed to the bulbous, durophagous dentition seen in *Orodus*. Although both *Siamodus* (Long 1990, Ginter 1999) and *Clairina* (Ginter (1999)) have multicuspoid teeth, these have linguad-labiad flattended cusps on a strongly arched base, so can readily be distinguished from the teeth of *Dalmehodus* gen nov.

#### Etymology

After the town of Dalmeh, central Iran, and the Greek 'odous' meaning 'tooth'.

#### *Dalmehodus turnerae* sp. nov.

Figure 6d, f, g

#### Type Material

Holotype is EUIV 99.9.232 (Figure 6f), from sample number 66, *expansa* zone of the early Famennian.

#### Material Examined

Two other specimens, EUIV 99.8.226 (from the lower Middle Famennian), EUIV 99.7.212 (sample number 64), from the *expansa* zone; both nearly complete teeth.

#### Etymology

In honour of Dr Susan Turner for her contributions to the study of vertebrate micropalaeontology.

#### Description

These teeth all show characteristic protacrodont form of the tooth being wide and low-crowned formed of several wide, low cusps, each with coarse, irregular ribbing. 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 6d) of nearly equal height. The cusps increase very slightly in height towards one end of the tooth. The root has large and numerous nutritive foramina that are closely packed together, each foramen corresponds to a cusp on the crown. The lingual side of the crown (Figure 6 d) shows near vertical, widely-spaced ribs, about four-five on each cusp. The labial face of the crown (Figure 6 f, g) has a more open, reticulate pattern of ridges on the cusps, which form strong ribs toward the apex of each cusp.

The morphology of *Dalmehodus* teeth suggest it is related to *Protacrodus*, with closest affinities to the *P. vetustus* morphotype in having many cusps on a broad, well-vascularised root.

#### Stratigraphic range and distribution

The three specimens of *Dalmehodus turnerae* gen et sp. nov. from Dalmeh, Iran, range from the lower Middle Famennian through to the *expansa* zone.

#### Family Protacrodontidae

##### ? *Protacrodus* sp.

Figure 4 o; 6 a, b, c, e

#### Type Species

*Protacrodus vetustus* Jaekel 1921 St. John and Worthen 1875

#### Material Examined

Four specimens, EUIV 99.7.217, (sample number 39); EUIV 99.7.218, EUIV 99.8.224, EUIV 99.7.220 (all from sample number 25), *triangularis-crepida* zones of the Early Famennian.

#### Description

Three specimens of chondrichthyan teeth are here provisionally referred to the Protacrodontidae, genus and species indeterminate. Specimen EUIV 99.9.217 (Figure 4o) has a well-preserved crown with 5 cusps, increasing in height towards the central cusp, and a wide root with large nutritive foramina. Specimen EUIV 99.7.218 (Figure 6a) shows a well-preserved crown of a tooth with a triangular main cusp, a few anastomosing ridges on the crown, as in some *Protacrodus* teeth. The base is missing. It is an asymmetrical tooth without well-defined lateral cusps although very small cuspules are present on one extremity of the cutting edge. The rounded surfaces of the ornamentation and absence of the root suggest the tooth has been abraded. It closely resembles the single known tooth of *Protacrodus orientalis* (Li 1988) in its overall high main cusp, weak development of lateral cuspules and widely-spaced anastomosing surface ornament on the crown. *P. orientalis* is distinguished by its many cuspules flanking the central main cusp, lacking on the Iranian specimen.

Another specimen, EUIV 99.7.220 (Figure 6 e) is a partial crown of a shark tooth possibly cogenetic with EUIV 99.7.218, except that it has more pronounced development of striae on the crown.

Specimen EUIV 99.8.224 (Figure 6 b, c) is a tooth with a blunt, rounded crown bearing a few ridges and grooves trailing one side of the crown. The base is broken, not showing the full extent of the root. We suggest it has protacrodontid affinities as the central main cusp is broad-based as in *Protacrodus*, and the few abraded ornamental ridges are widely-spaced on the crown. It shows no features that would link it to any other family of Devonian sharks, so we provisionally refer it also to ?*Protacrodus*.

**Stratigraphic range and distribution**

*Protacrodus vetustus* ranges from the late Frasnian *rhenana* zone through to the end of the Famennian (Ivanov 1995). The specimens from Dalmeš, Iran, range from from the lower Middle Famennian through to the *expansa* zone, well within the known range for the genus.

**Order Orodontida****Family Orodontidae DeKoninck 1878****Genus *Orodus* Agassiz 1838****Type Species**

*Orodus cinctus* Agassiz 1838

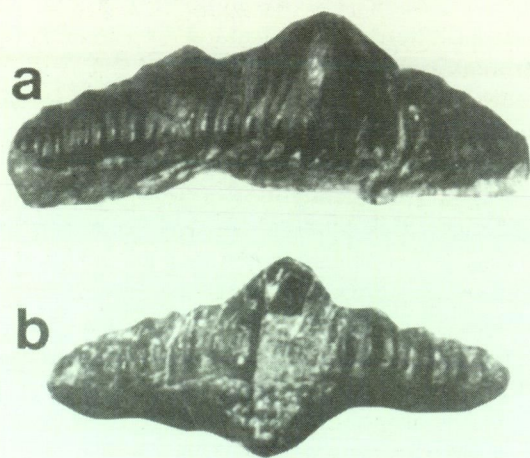
*Orodus* sp.  
Figure 5 a, b

**Material Examined**

Two specimens, EUIV 99.5.207 and EUIV 99.5.208 (sample number 64); from the Late *postera*- Early *expansa* zones.

**Description**

These teeth all show characteristic features of *Orodus* in having a central swollen bulbous crown with wide edges of finely crenulated ridges, which do not form a distinct cutting edge. The largest specimen from Dalmeš, EUIV 99.5.207 measures 23 mm in maximum length, and the main central cusp is 8 mm high, making it a very large tooth for a Devonian shark. This specimen is asymmetric in having the central large swollen cusp closer to one edge of the tooth, whereas EUIV 99.5.208, measuring 18 mm in maximum length, is a symmetrical tooth. The lateral ridged edges of the teeth are formed



**Figure 5** *Orodus* sp. teeth in crown view. a, EUIV 99.5.207 (x2.75), b, EUIV 99.5.208 (x3.3).

into lower swollen tuberosities, unlike the even crenulated occlusal edges of *Orodus greggi* from the Late Carboniferous of the USA (Zangerl 1981). The swollen array of tuberosities forming the crown of these two specimens is more reminiscent of the form of tooth seen in *Protacrodus* yet they clearly differ in being crushing teeth without a cutting edge.

**Stratigraphic range and distribution**

*Orodus* is typically known from the Carboniferous (Zangerl 1981), although Hussakof and Bryant (1918) record *Orodus devonicus* from the Late Famennian of the USA, although the exact stratigraphic placement for the species is uncertain, so it could well be from the Early Carboniferous. The specimens from Dalmeš, Iran, range from the lower Middle Famennian through to the *expansa* zone. As previous Devonian records of the genus are not well-dated, this could represent the first dated for the entry of the genus in the Late Devonian.

**Subclass Osteichthyes Huxley, 1880****Infraclass Actinopterygii Muller 1846****Order Palaeonisciformes Hay, 1929****Genus *Moythomasia* Gross 1950****Type species**

*Moythomasia perforata* (Gross 1942)

*Moythomasia durgaringa* Gardiner and Bartram  
1977

Figure 6 h, j, k, n

**Material Examined**

Four specimens, EUIV 99.9.233 -236, isolated scales (all from sample 37), *crepida* zone of the Lower Famennian.

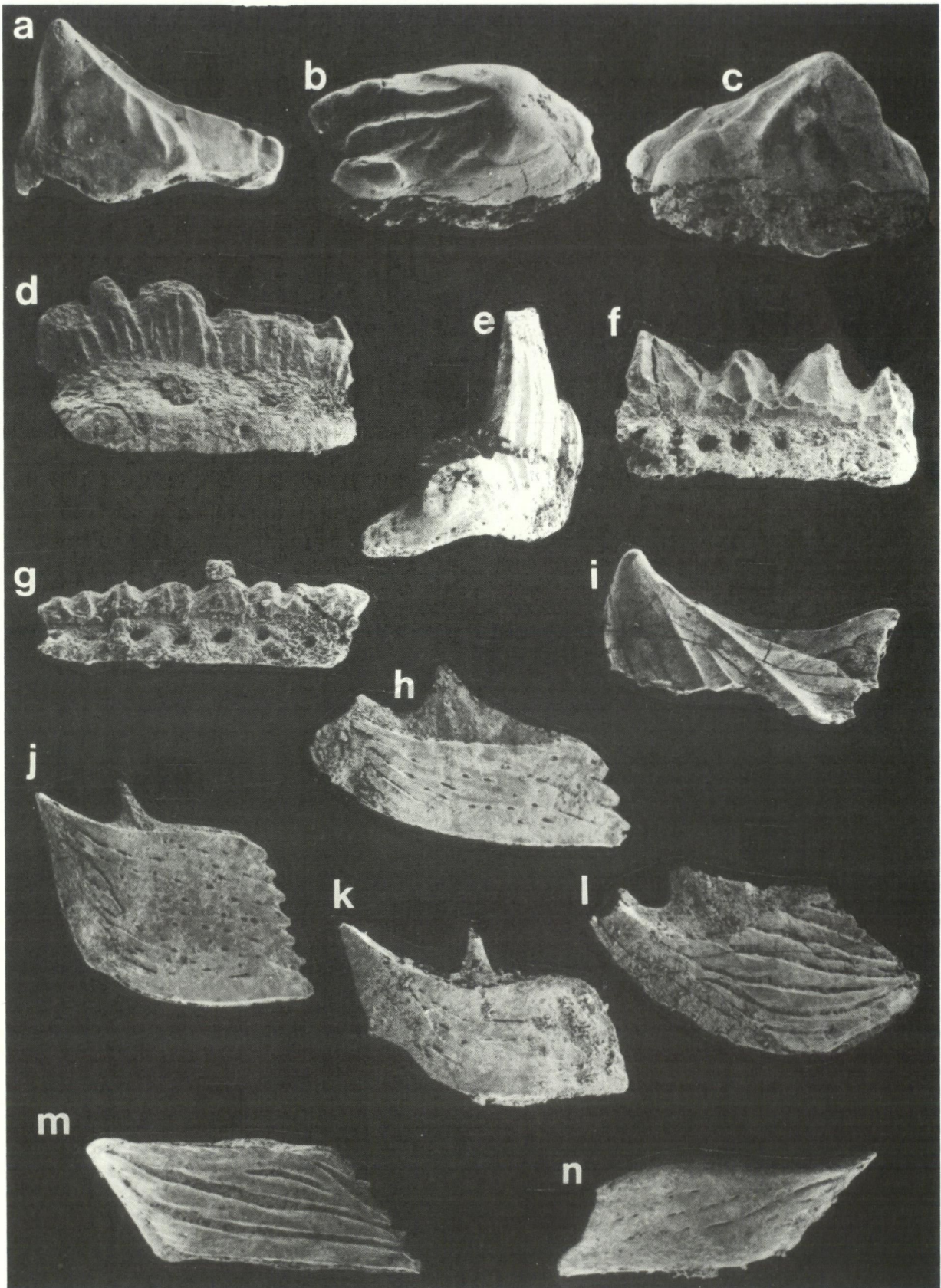
**Description**

Based on the work of Trinajstić (1999a, 1999b), who has identified various scale morphologies from the well-preserved Gogo Formation specimens of *Moythomasia durgaringa*, we can assign the Dalmeš scales to various parts of the squamation, based on the subdivision first proposed by Esin (1990). EUIV 99.9.234 is a type B scale of the anterior trunk region, just posterior to the operculum; EUIV 99.9.233 and EUIV 99.9.235 are type F scales, from the base of the fin. EUIV 99.9.236 is a type D scale from towards the tail region.

**Stratigraphic range and distribution**

The genus *Moythomasia* has so far been recorded from the Givetian-Frasnian stages only (Gross 1942,





**Figure 6** a–c *?Protacrodus* sp. a, EUIV99.7.218 (x43). b, c, EUIV99.8.224, b, occlusal view, c, lateral (lingual/labial?) view, (x54). d, f, g. *Dalmehodus turnerae* gen et sp. nov. d, EUIV99.8.226, lingual view (x40). f, Holotype, EUIV99.9.232 (x65) lingual view. g, EUIV99.7.221, lingual view (x65). e, *Phoebodus ?gothicus*, EUIV99.7.219 lateral view (x19). i, *? Protacrodus* sp. EUIV99.7.220 (x26). h, j, k, n, scales of *Moythomas*.

1950, Jessen 1968, Gardiner and Bartram 1977, Gardiner 1984, Lelievre *et al.* 1986, Trinajstic 1999a, 1999b). The Dalhmeh specimens are the first definitive record of the species *M. durgaringa* present in the Famennian, thereby extending the known age range for the genus.

### Genus and species indeterminate

Figure 6 l, m

#### Material Examined

Two specimens, EUIV99.9.237, and EUIV99.9.238, isolated scales (all from sample 37), *crepida* zone of the Early Famennian.

#### Description

EUIV 99.9.237 is a typical type B scale of the anterior trunk region, just posterior to the operculum. It differs from that of *Moythomasia* in having thick robust ornamentation of ganoine ridges and the dorsal peg is broader-based than in the equivalent scales of *Moythomasia* (eg Figure 6 j).

EUIV 99.9.238 (Figure 6m) is a type D scale from towards the tail region which also shows the same type of robust ganoine ridges as the previous specimen. Both of these scales differ from scales of *Mimia toombsi* (Trinajstic 1999b) in having the ganoine ridges more closely packed together.

#### Discussion

The Dalmech microvertebrate assemblage includes representative chondrichthyan and osteichthyan form taxa ranging in age from the upper *triangularis* zone of the Lower Famennian through to the *expansa* or basal *praesulcata* zone of the latest Famennian. The fauna includes a new genus and species of protacrodontoid *Dalmehodus turnerae*, shows an extension of the age range for *Phoebodus gothicus* downwards to the *expansa* zone, the first definite occurrence of *Orodus* sp. in the Late Devonian and the first record of *Moythomasia durgaringa* in the early Famennian and occurring outside of Australia. The presence of *Moythomasia durgaringa* in Iran further supports the close palaeogeographic affinities between Iran and Australia during the Late Devonian.

### ACKNOWLEDGEMENTS

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