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Late Devonian and Carboniferous vertebrates from the Shishtu and Sardar formations of the Shotori Range, Iran

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Abstract – Frasnian to early Famennian microvertebrates from the Shishtu Formation of the Shotori Range, eastern Iran, include thelodont scales of *Australolepis seddoni*, phoebodont, protacrodont, and possible stethacanth, symmoriid, cladoselachian and ctenacanth shark teeth and scales. Also present are palaeoniscoid actinopterygian and sarcopterygian microremains including scales, as well as lepidotrichia and teeth of possible onychodontids and osteolepiforms. Orodontid shark teeth are reported for the first time from the *anchoralis–latus* Conodont Zone (Early Carboniferous) of Iran.

INTRODUCTION

Late Devonian fish have been reported from Iran since the 1930s (e.g., Golshani *et al.* 1972; Janvier 1977; Schultze 1973; Goujet and Janvier 1984). The first microremains, thelodont scales, were reported from the Early to Middle or early Late Devonian of Iran (Blieck and Goujet 1977; Turner and Janvier 1979; Blieck *et al.* 1980; Hamdi and Janvier 1981). Other workers, including Hairepetian and Gholamalian (1998), Long and Hairepetian (2000) and Dashtban (pers. comm.) have been collecting and preparing Devonian and Carboniferous micro- and macrovertebrate remains from central Iran and the Alborz region. Late Devonian (Famennian) microremains are now known (Long and Hairepetian this volume) from central Iran. Well-exposed Frasnian to Carboniferous sequences in the Shotori Range (Figure 1) have been producing microvertebrate remains as a by-product of acid-leaching for conodonts (Yazdi 1999). These materials are documented in this report, and their significance is discussed.

Yazdi (1995, 1998, 1999) and Yazdi and Ghazifard (1998) described the Shishtu Formation, and Yazdi (1998, 1999) described conodont assemblages from the Shishtu Formation, a sequence of about 580 m of limestones (various lithologies), cross-bedded arenites, gypsiferous shales and limestone, and minor dolomites. Two main sections have been sampled for conodont and microvertebrate data: at Kale Sardar where, *inter alia*, the late Frasnian, *rhenana* and *linguiformis* zones are present, and at Howz-e-Dorah where biostromal beds lacking chronologically constraining conodonts at the base of section are succeeded by a sequence spanning the interval from mid-Frasnian Early *hassi* Zone to latest Tournaisian *anchoralis–latus* Zone. Sample 101 came from an oolitic sandy horizon in this basal part of the succession almost 30 metres before the incoming of *Polygnathus aspelundi* and *P. capollocki*, indicative of the lower half of the Frasnian, late Early *hassi* Zone or older. Sample 103 at Howz-e-Dorah yielded numerous microvertebrate remains—early sharks and bony fishes—as well as abundant conodonts. It is a marker bed within the Shishtu Formation in the Shotori Range. Conodonts from this sample—*Icriodus alternatus* morph II, *I. alternatus mawsonae*, *I. iowaensis iowaensis*, *Polygnathus planarius*, *P. rabeti*, *Palmatolepis minuta minuta*, *Pal. quadrantinodosalobata*, *Pal. subperlobata* and *Pal. tenuipunctata*—are indicative of the *rhomboidea* to *postera* Conodont Zones (Yazdi 1999). Rounded microtektites(?) about 250µm diameter are also present.

Yazdi (1990, 1995, 1999) has reported conodonts and invertebrates from two Carboniferous horizons in the Shotori Range: a sample from a black limestone in the Sardar Formation with conodonts indicative of the *anchoralis–latus* Zone, and shark teeth from an imprecisely located crinoidal limestone at Howz-e-Dorah.

Specimens illustrated herein are housed in the Geology Department of Esfahan University (EUIM).

IMPLICATIONS

Devonian fish faunas of Western Gondwana (South America, Africa including the Middle East) were reviewed by Lelièvre et al. (1993). Janvier (1996) has emphasised the need to search non-

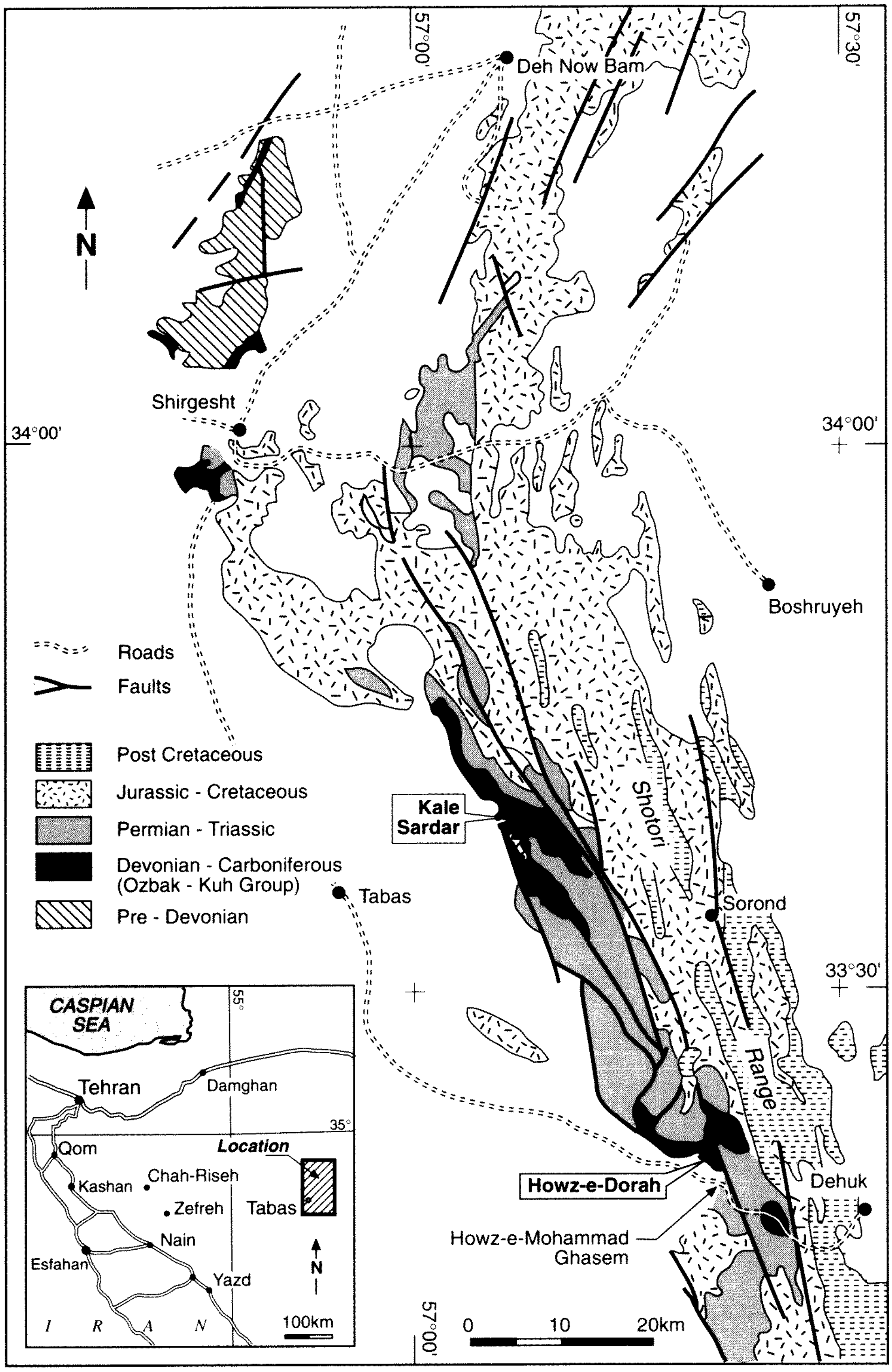

Figure 1 Regional geology and position of the two main sections (from Yazdi 1999).

traditional regions of the world for Palaeozoic fishes to increase our understanding of their evolution and biogeography; he highlighted important finds from former Gondwanan terranes. The new Late Devonian–Early Carboniferous records from eastern Iran presented herein help improve understanding of linkages between West and East Gondwana along the North Gondwana shoreline.

Thelodont scales are being recognised as important elements for helping resolve biostratigraphic problems in former Gondwanan terranes (Young 1996; Turner 1997; Trinajstic in press) and are proving useful in Silurian to late Frasnian shallow water environments where conodonts may be absent. Silurian (possibly Pridoli) thelodont scales have been reported from the Niur Formation of the Derenjal Mountains near Tabas in eastern Iran (Hamedi et al. 1997; Turner 1997). The presence of the thelodont

Australolepis seddoni low in the Shishtu Formation accords with an early–middle Frasnian age for the basal part of that unit. All thelodonts thus far known from Iran have greater affinity with those from eastern Gondwana than those from elsewhere (Turner 1997). The Shotori Range thelodont is consistent with a close link between Iran and Western Australia during the Frasnian.

Another group of vertebrate fossils, phoebodont shark teeth, has been found useful for biostratigraphic alignments in Middle to Late Devonian rocks (Ginter and Ivanov 1995; Young 1996). The phoebodont teeth found in the Shotori Range from the Famennian (Late Devonian) *rhomboidea* to *postera* Conodont Zones compare well with those presently being described from the Famennian elsewhere (e.g. Ginter and Turner 1999; Jones *et al.* in press). These sharks from shallow to medium depth waters (Ginter 1999) seem to have had a Prototethyan distribution, across the North Gondwana continental shelf.

Few orodontid shark teeth have been recorded for the Southern Hemisphere or from former North Gondwana terranes. Carboniferous fish have not previously been described from Iran. Orodontid sharks are typical for Lower Carboniferous shallow to mid-depth marine deposits particularly in Euramerica (mid-west USA and the Russian platform).

TAXONOMIC NOTES

A. DEVONIAN

Thelodonti

Australolepis seddoni Turner and Dring, 1981
Figure 2.1

cf. *Australolepis seddoni* Turner and Dring. Turner 1997, fig. 8.

Material

EUIM 601—a thelodont scale from sample 101, 55 m above the base of the Howz-e-Dorah section through the Shishtu Formation at Niaz-Kale, near Sardar, Tabas, eastern Iran.

Age

Frasnian (Late Devonian) older than *jamiae* Zone.

Description

A small head or cephalopectoral scale with few (less than six) crown ridges meeting in a prominent posterior point on the high crown (Figure 2.1). Anterior ridges bifurcate near the crown–neck interface. Base is wider than the crown with a large pulp cavity.

Remarks

The presence in the Shotori Range of Late Devonian thelodonts including a scale of *Australolepis seddoni* (Figure 2.1) accords with the conodont data. Sample 101 is a biostromal limestone with solitary corals dated by conodonts as older than *jamiae* Zone, i.e early to mid-Frasnian (Yazdi 1999, Fig. 5). The source horizon for *A. seddoni*, in the Gneudna Formation of the Carnarvon Basin of Western Australia, is now thought to be earliest Frasnian (Young 1996; Turner 1997; Trinajstic in press).

Turiniid thelodont scales have been recorded from elsewhere in northern and central Iran in the Cimerian Terrane (Lelièvre et al, 1993, fig. 7.2F,11, 14). They came from the late Early Devonian or early Middle Devonian Khush-Yeilagh [Khoshyeilagh, Khoshyelaq] Formation near Khush-Yeilagh in the eastern Alborz Mountains, north-east Iran (Turner, 1997, fig. 9.16). *Australolepis seddoni* illustrated here for the first time from the basal Shishtu Formation accords with broad correlation with the early Frasnian Gneudna Formation of Western Australia.

Placodermi

Placodermi undet.
Figure 5.1

Description

Rare trunk scales of placoderms from sample 103 have a few (six or less) raised tubercles (odontodes) with five to six radii placed centrally on a wide grooved platform base in the middle of polygonal six-sided scales.

Remarks

The wide ridge and groove "skirt" of the upper base is reminiscent of arthrodire scales found elsewhere in the Early Devonian (Burrow and Turner 1998).

Chondrichthyes

cf. Phoebodus rayi Ginter and Turner 1999
Figure 2.9, 12, Figure 4.2

Material

EUIM 609, 612—A considerable number of phoebodont teeth from sample 103, Howz-e-Dorah section through the Shishtu Formation at Niaz-Kale, near Sardar, Tabas, eastern Iran.

Age

Early Famennian (Late Devonian) *rhomboidea* to *postera* Conodont Zones.

Remarks

The tooth described here is close to *Phoebodus rayi* Ginter and Turner 1999 from the *crepida* zone of Melville Island (Arctic Canada) and elsewhere. Prospects appear good for refining the phoebodont biozonation suggested by Ginter and Ivanov (1995) on the basis of Iranian materials. Hampe (1998) recorded the first phoebodont tooth from Iran, a possible *P. gothicus* from the early to middle Famennian of Zunuz, NW of Tabriz. Janvier (1981) attributed a tooth from the Frasnian of Chanaruh to *Phoebodus* sp.; it looks like the tooth of a stethacanthid shark with a split lingual button.

Protacrodus sp. cf. *"P. aequalis" sensu* Ginter and Turner 1999

Figure 3.4, 6–7, 8?, 9–10; Figure 4.4

Material

EUIM 616–619, 621–622—A few protacrodont teeth and scales from sample 103, Howz-e-Dorah section, Shishtu Formation, at Niaz-Kale, near Sardar, Tabas, eastern Iran.

Age

Early Famennian (Late Devonian) *rhomboidea* to *postera* Conodont Zones.

Remarks

The teeth from the Shishtu Formation are closest to *Protacrodus aequalis* of Ginter and Turner (1999) from the Cape Fortune Member, Parry Islands Formation, Melville Island, Canada. The material from the Shishtu Formation and from Melville Island differ from the type species, *P. aequalis* Ivanov 1996 from the early Tournaisian of Russia, in having more and less separated cusps. The cusps in the conjoined teeth from Iran (Figure 2.9–10) are not so well defined and resemble eugeneodont teeth (Zangerl 1980), but isolated teeth (Figure 2.4, 6–7) have at least five well-separated cusps. Protacrodontid sharks were widely distributed in Late Devonian epicratonic seas (Ginter 1999).

Unidentified shark teeth

Figures 2.3, 10, 11; 3.1, 3; 4.5; 5.3

Remarks

The collections include several "cladodont" teeth not falling readily into currently recognised taxa. Some (Figure 2.3, 11, 3.3, 5.3) might be from an early stethacanth. Others (Figures 2.10, 3.1) include a symmoriid type with a pronounced labial median shelf. One tooth (Figure 4.5) has a large median cusp with coalescing cristae on the labial side and two widely splayed smaller lateral cusps; it might be from *Cladoselache* or a ctenacanth.

Janvier (1981) made the first study of Late Devonian shark teeth from the Kerman region of Iran, recognising *"Cladodus"* (already known to be a form genus), *Ctenacanthus*, *"Phoebodus"* (not *Phoebodus s.s.*) and *Protacrodus* species. He pointed out the difficulty of identifying detached teeth, scales and spines, but in the last decade much progress has been made in defining Palaeozoic shark teeth (e.g., Ginter 1998; Ivanov 1999). Most of the teeth which Janvier (1981, pl. II) referred to *"Cladodus"* appear to be stethacanth, ctenacanth or protacrodont teeth.

Shark scales

Figure 2.4–8, 5.6–8, 10

Remarks

Several specimens of ctenacanth type scales occur in sample 103. Most (Figures 2.4–7, 5.7, 10) are like forms illustrated as *Ctenacanthus* sp. from the Frasnian of Hootk by Janvier (1981, pl. IV). Some resemble those of *Maplemillia costata* Gross (1973) from the late Devonian (Famennian) Maple Mill Shale, USA. Other scales might belong to a stethacanthid shark (Figure 2.8) or are protacrodont scales (Figure 5.6). Other shark scales include branchial scales (Figure 5.5), and a hybodont type with neck foramina (Figure 5.8). Others, of uncertain origin, might be placoderm tubercles (Figure 5.9). "Cladodontid", ctenacanth and protacrodontid teeth and scales were reported from the Late Devonian (Frasnian) of Bidou, central Iran, by Janvier (1974), some from an articulated ctenacanth specimen.

Coprolites?

Figure 5.11

Also present in sample 103 from the Shishtu Formation in the Howz-e-Dorah section at Niaz-Kale are microcoprolites with distinct annular grooves. These may be shark coprolites though they do not have a spiral configuration.

Acanthodii

Acanthodes sp. indet.

Figure 4.6

Material

EUIM 628—a scale from sample 103, Howz-e-Dorah section through the Shishtu Formation at Niaz-Kale, near Sardar, Tabas, eastern Iran.

Age

Famennian (Late Devonian) *rhomboidea* to *postera* Conodont Zones.

Remarks

Typical of the *Acanthodes* type of scales, these have large relatively flat, smooth and shiny crowns on a relatively high rounded base. Such scales are relatively common from the Devonian to the Permian, but discrimination of taxa is difficult. Janvier (1974) has summarised acanthodian records from the Late Devonian of central Iran.

Osteichthyes

Osteichthyes undet.
Figures 4.8–11; 6.1–10

Remarks

Actinopterygians are possibly represented by ornamented bones (Figure 4.8–10) and palaeoniscoid scales and teeth (Figure 6.1–10); the latter resemble those of *Moythomasia* which have been reported previously from Iran (Bartram 1981); they appear to be close to *M. durgaringa* of the Frasnian of Western Australia (Trinajstic 1999). The denticulated bones (Figure 4.9–10) resemble those referred to palaeoniscoids by Bartram (1981, pl. 6E–F). One tooth type (Figure 4.11) has micro-ornament of small widespread tubercles on the enameloid surface.

Sarcopterygii indet.
Figures 2.2, 4.7

Sarcopterygian remains are represented by onychodontid teeth (Figure 2.2), possibly from from *Onychodus* s.s., a genus reported by Janvier (1974) from the Late Devonian (Frasnian) of Bidou, central Iran. Short pieces of jawbone with tooth sockets resemble those of the osteolepidid described from Kerman by Janvier and Martin (1979). Lepidotrichia with a cosmine-coated crown (Figure 4.7) also occur, together with cosmine bone fragments; they too may belong to such an osteolepidid.

B. CARBONIFEROUS

Chondrichthyes

Orodontidae gen. et sp. indet.
Figure 7

Material

Four teeth plus fragments of teeth, EUIM 657, from crinoidal limestone in the Sardar Formation at Howzen, Howze-Do-Rahi, Tabas, Iran.

Age

anchoralis–latus Conodont Zone (Early Carboniferous)

Description

A small block with crinoid ossicles, a coral, four complete orodontid teeth and fragments of four or five others. All teeth are laterally elongated; only the largest is apparently complete. It has a crown bearing a large central rounded dome and a series of lateral segments separated by deeply indented furrows. Another tooth is approximately 35 mm long along the crown by 5 mm high. Incomplete teeth are around 15 mm long.

Remarks

The Iranian orodontid teeth are similar to those described by St John and Worthen (1875) from the Kinderhook Formation of Iowa. Taxonomy of the group has been based largely on these elongated pavement teeth with complex ridged crown ornament. The teeth of *Orodus* Agassiz and those of eugeneodontid shark genera such as *Campodus* de Koninck and *Caseodus* Zangerl share similarities in their laterally elongated teeth with ridged buttresses. Zangerl (1981) preferred to place *Orodus* in a separate order, the Orodontida. A major revision of orodont teeth is needed to clarify taxonomy (Lebedev and V'yushkova 1993; Ivanov 1996).

This is the first record of Carboniferous orodontid sharks in the North Gondwana region. They are otherwise known from the Early Carboniferous from the USA, Britain and Ireland, Belgium, Russia, and eastern Australia.

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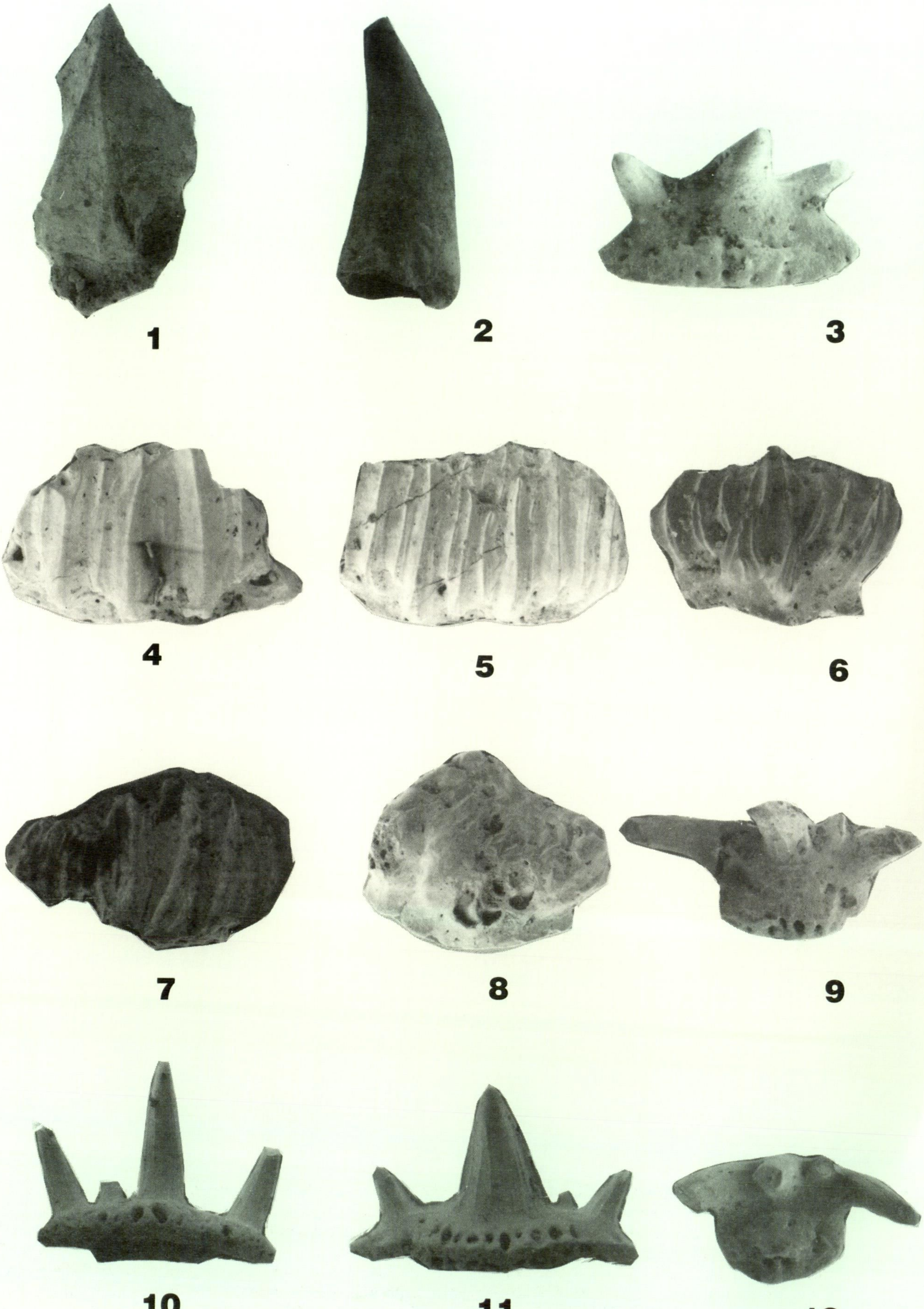
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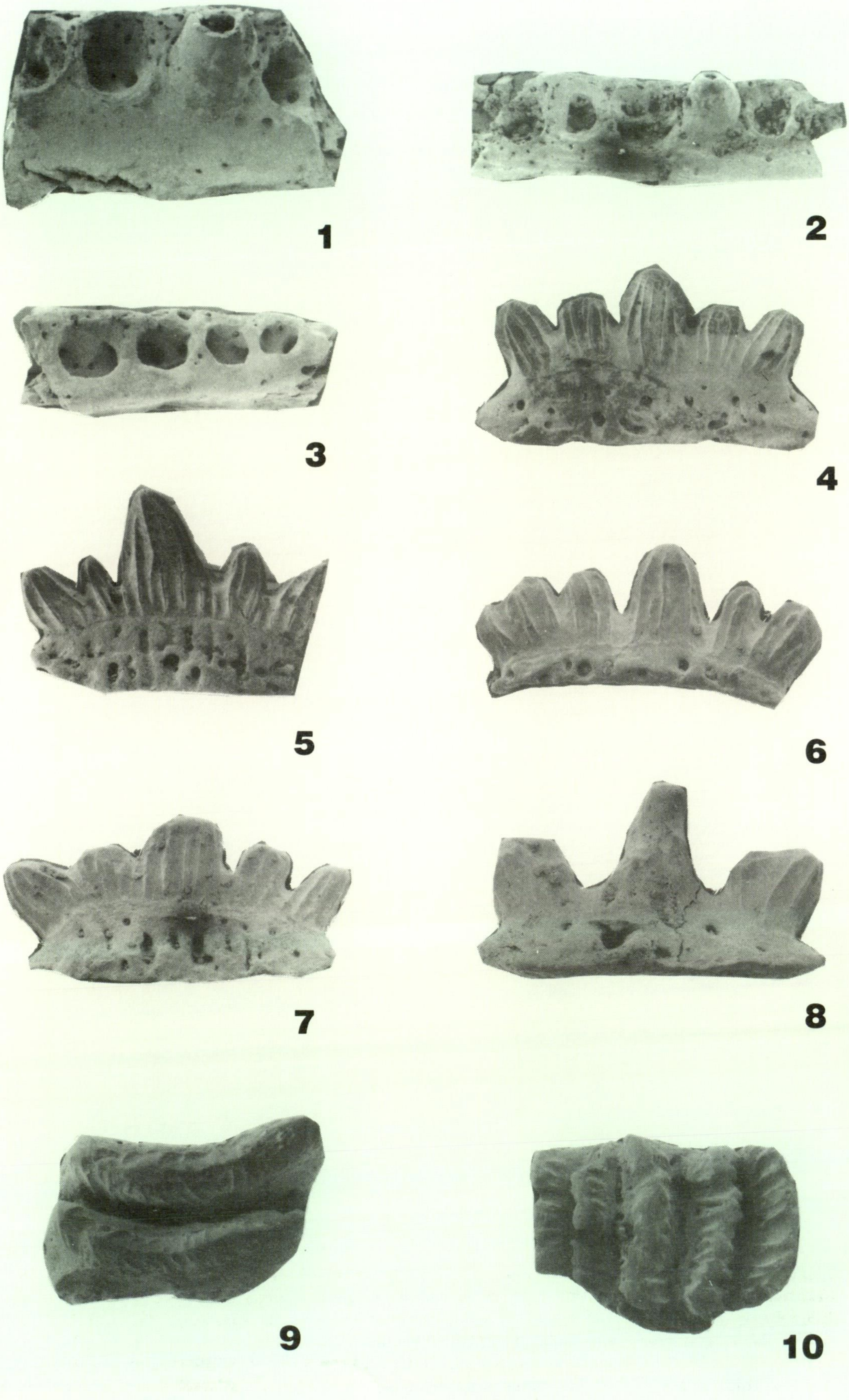
◀ Figure 2 1, *Australolepis seddoni*, scale EUIM 601, crown view, from sample 101, x 130. **2**, onychodontid tooth EUIM 602, lateral view, from sample 103, x 65. **3**, tooth of stethacanthid? shark EUIM 603, lingual view, from sample 103, x 90. **4**, ctenacanth scale EUIM 604, crown view, from sample 103, x 85. **5**, ctenacanth scale EUIM 605, crown view, from sample 103, x 85. **6**, ctenacanth scale EUIM 606, crown view, from sample 103, x 85. **7**, ctenacanth scale EUIM 607, crown view, from sample 103, x 85. **8**, stethacanth? head scale EUIM 608, crown view, from sample 103, x 85. **9**, cf. *Phoebodus rayi*, tooth EUIM 609, lingual view, from sample 103, x 75. **10**, tooth of symmoriid shark EUIM 610, lingual view, from sample 103, x 75. **11**, tooth of stethacanthid? shark EUIM 611, lingual view, from sample 103, x 65. **12**, cf. *Phoebodus rayi*, tooth EUIM 612, dorso-lingual view, from sample 103 x 75.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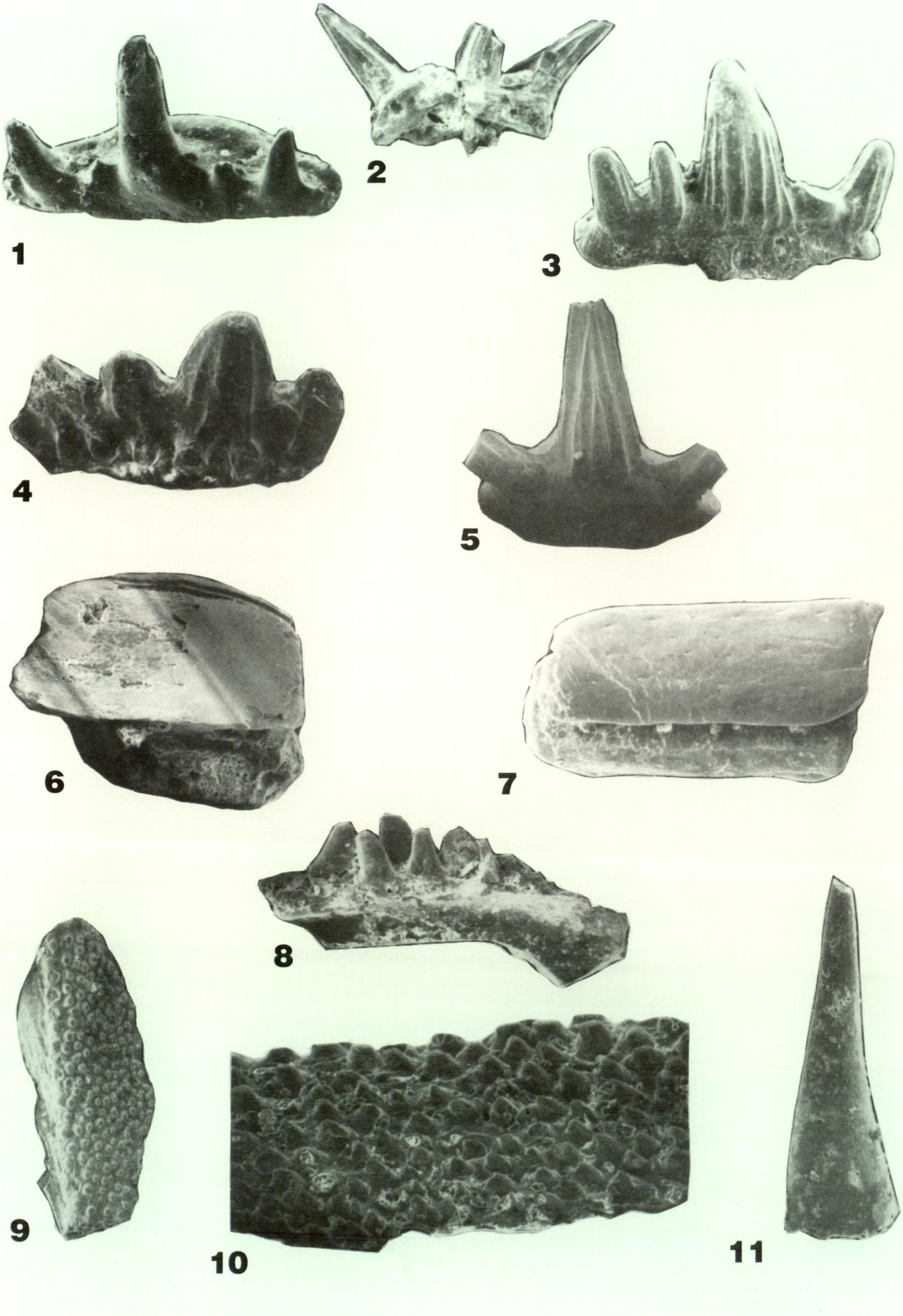
◀ **Figure 3** **1**, sarcopterygian jawbone EUIM 613, lingual view, from sample 103, x 65. **2**, sarcopterygian jawbone EUIM 614, lingual view, from sample 103, x 65. **3**, sarcopterygian jawbone EUIM 615, dorsal view, from sample 103, x 65. **4**, tooth of *Protacrodus* sp. EUIM 616, lingual view, from sample 103, x 70. **5**, tooth of *Protacrodus* sp. EUIM 617, lingual view, from sample 103, x 70. **6**, tooth of *Protacrodus* sp. EUIM 618, lingual view, from sample 103, x 70. **7**, tooth of *Protacrodus* sp. EUIM 619, lingual view, from sample 103, x 70. **8**, tooth of stethacanthid? shark EUIM 620, labial view, from sample 103, x 70. **9**, teeth of *Protacrodus* sp. EUIM 621, crown view, from sample 103, x 55. **10**, teeth of *Protacrodus* sp. EUIM 622, crown view, from sample 103, x 100.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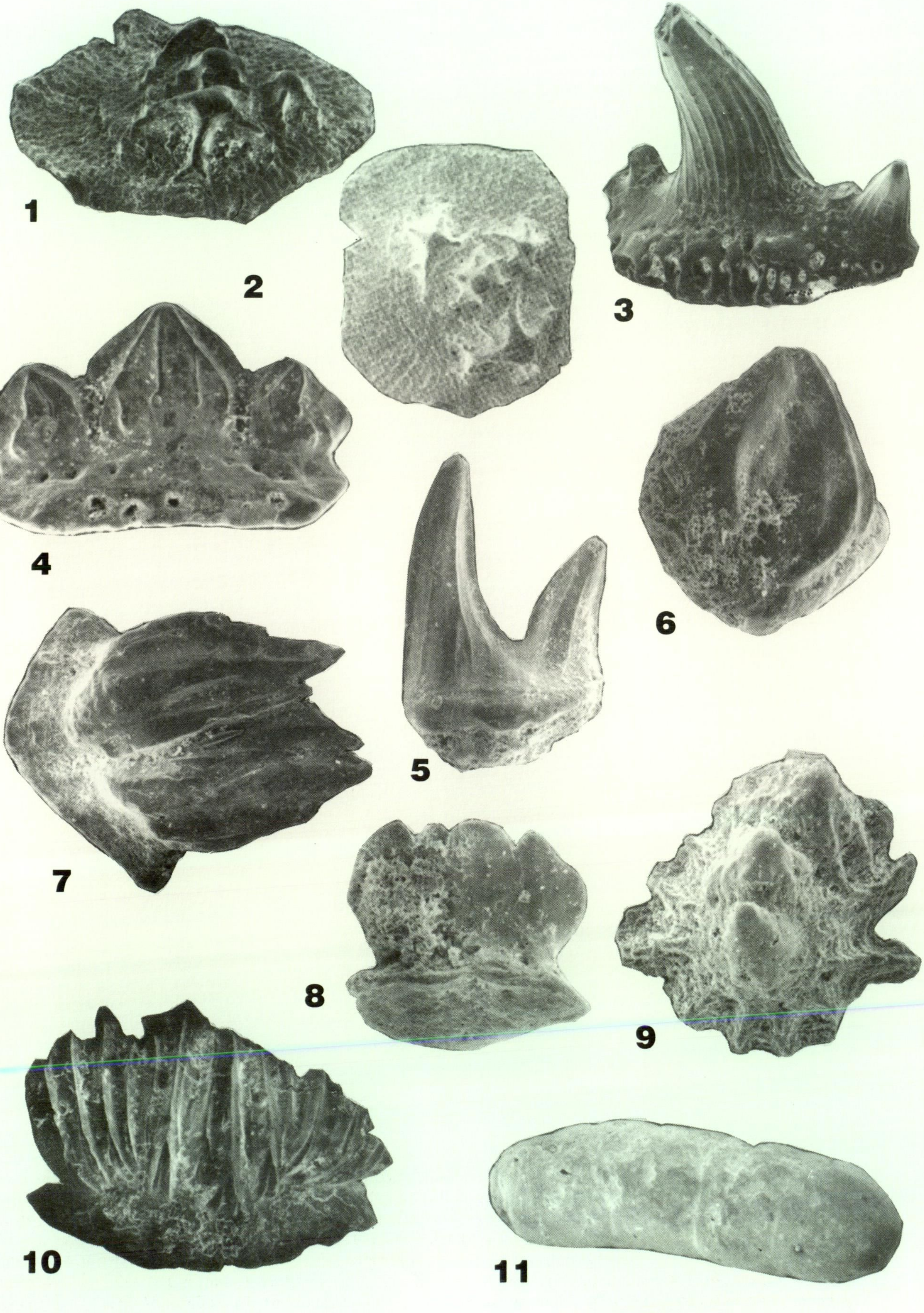
◀ Figure 4 **1**, tooth of symmoriid? shark EUIM 623, labial view, from sample 103, x 56. **2**, tooth of phoebodont shark EUIM 624, labial view, from sample 103, x 44. 3, tooth of stethacanthid? shark EUIM 625, labial view, from sample 103, x 44. **4**, tooth of *Protacrodus* sp. EUIM 626, labial view, from sample 103, x 48. **5**, tooth of ctenacanth? shark EUIM 627, labial view, from sample 103, x 30. **6**, *Acanthodes* sp. indet., scale EUIM 628, dorso-lateral view, from sample 103, x 110. **7**, sarcopterygian indet. lepidotrichium EUIM 629, dorso-lateral view, from sample 103, x 58. **8**, sarcopterygian? toothplated bone EUIM 630, lingual view, from sample 103, x 70. **9**, palaeoniscoid denticulated bone EUIM 631, dorso-lateral view, from sample 103, x 22. **10**, close up of denticulated surface EUIM 631 (same as 9), x 72. **11**, palaeoniscoid tooth EUIM 632, lateral view, from sample 103, x 58.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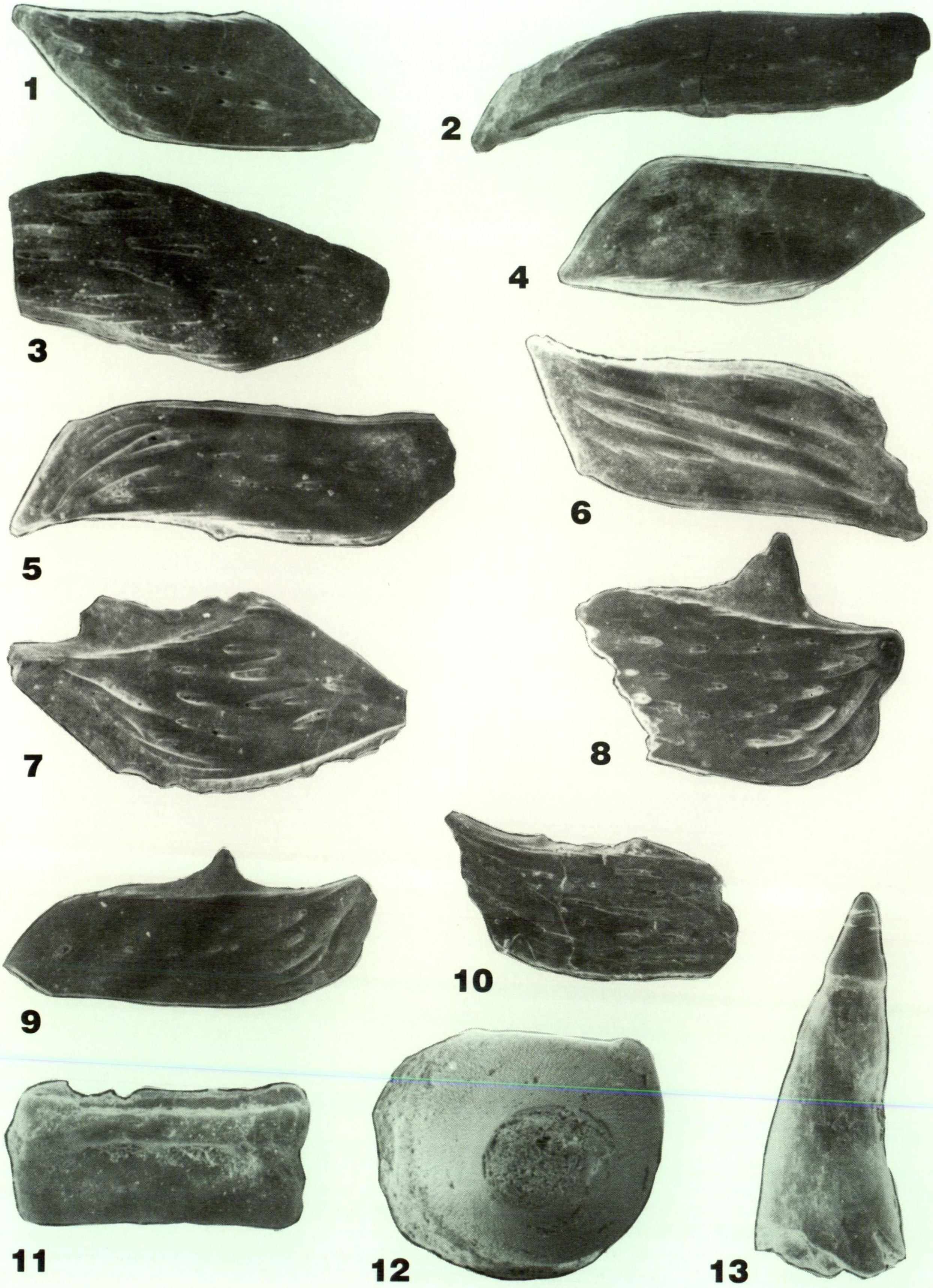
◀ **Figure 5** **1**, Scale of arthrodire fam., gen. et sp. indet. EUIM 633 from sample 103, lateral view, x 36. **2**, EUIM 634, crown view, x 30. **3**, tooth of stethacanthid? shark, EUIM 635 from sample 103, lingual view, x 30. **4**, tooth of protacrodont shark, EUIM 636 from sample 103, lingual view, x 74. **5**, possible branchial scale of unknown shark EUIM 637 from sample 103, 'labial' view, x 70. **6**, scale of *Protacrodus* type EUIM 638 from sample 103, crown view, x 100. **7**, ctenacanth scale EUIM 639 from sample 103, crown view, x 74. **8**, scale of hybodont? type EUIM 640 from sample 103, ventral view, x 74. **9**, scale of unknown shark (or placoderm?) EUIM 641 from sample 103, crown view, x 72. **10**, ctenacanth scale EUIM 642 from sample 103, crown view, x44. **11**, fish? coprolite, EUIM 643 from sample 103, crown view, x44.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◀ **Figure 6** **1–10**, actinopterygian palaeoniscoid scales *Moythomasia* sp. cf. *M. durgaringa* Gardiner and Bartram, 1977 EUIM 644–653 from sample 103, all in crown view. **1**, EUIM 644 x 46. **2**, EUIM 645 x 30. **3**, EUIM 646 x 44. **4**, EUIM 647 x 38. **5**, EUIM 648 x 38. **6**, EUIM 649 x 28. **7**, EUIM 650 x 36. **8**, EUIM 651 x 30. **9**, EUIM 652 x 38. **10**, EUIM 653 x 27 **11**, Palaeoniscoid lepidotrichia, EUIM 654 from sample 103, x 50, lateral view. **12**, Palaeoniscoid tooth type 1 EUIM 655 from sample 103, x 145, apical view. **13**, Palaeoniscoid tooth type 2 EUIM 656 from sample 103 x 44, lateral view.

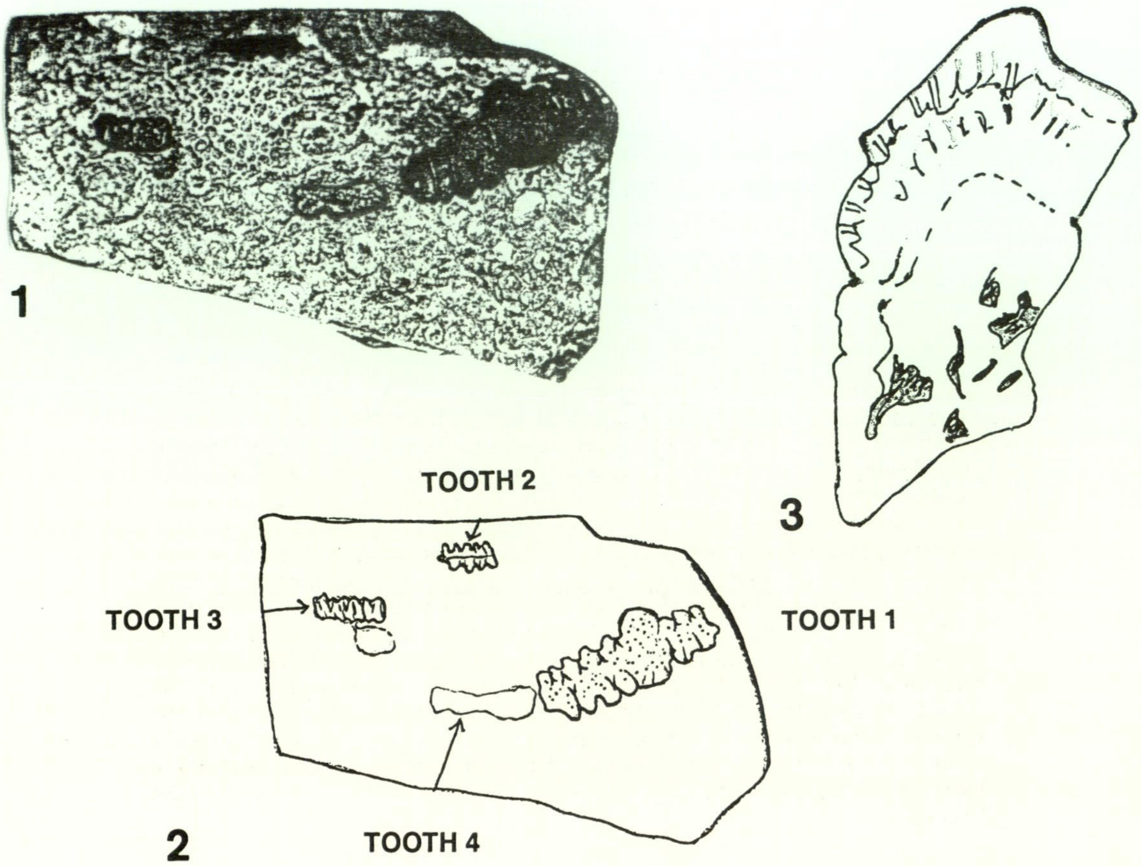

Figure 7 Orodontid teeth EUIM 657 from Early Carboniferous Sardar Formation, Howzen, Howze-Do-Rahi, Tabas, Iran. **1**, slab of crinoidal limestone with teeth in situ, x 1. **2**, diagram of slab showing position of teeth. **3**, sketch of cross-section of one tooth showing internal structure with an outer zone of tubular dentine (top) and inner zone of vascular osteodentine.