Famennian survivor turiniid thelodonts of North and East Gondwana

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Abstract: Microvertebrate samples from the Upper Devonian Hojedk section, southeastern Iran, and the Napier Formation, northwestern Australia, have yielded scales of agnathan thelodonts, dated as early/mid-Famennian (*crepida–marginifera/trachytera* conodont zones). These scales are referred to *Arianalepis megacostata*, a new genus and species, and *Arianalepis* sp. indet., a second indeterminate species of this new turiniid genus. Further recorded scales of *Australolepis seddoni* from the Napier Formation confirm the age range for this taxon as extending into the late Frasnian. The new remains post-date the previously youngest thelodonts from Iran and Western Australia and provide the first evidence of thelodonts surviving the Frasnian–Famennian extinction events.

Thelodonts (jawless fishes) have a long history in the fossil record, appearing at least by the Late Ordovician (Turner *et al.* 2004) and becoming extinct at some point before the end of the Devonian along with most other agnathans, with the exception being the extant cyclostomes (Märss *et al.* 2007). Despite the relative lack of taxa based on articulated remains compared to scales (*c.* 25: *c.* 140), the latter have proved useful in biostratigraphic correlation for many decades, particularly for between shallow-marine and non-marine sequences (e.g. Turner 1993, 1997; papers in Blieck & Turner 2000). Although articulated taxa are fewer (Märss *et al.* 2007), most are known from Silurian deposits and none are known from the Southern Hemisphere or in post-Emsian or younger sediments. The youngest known occurrences of thelodont taxa were previously reported from Western Australia and Iran as isolated scales in Frasnian strata (Turner & Dring 1981; Trinajstic 2000, 2001; Turner *et al.* 2002; Trinajstic & George 2009) until the discovery in the early 2000s of the first Famennian thelodont scales from Iran (Hairapetian & Turner 2003; Turner & Hairapetian 2005; Hairapetian 2008).

Here we report in detail the first Famennian thelodonts that co-occur with conodont elements and jawed vertebrate assemblages in the Hojedk section in the north of Kerman, southeastern Iran (Fig. 1), and also the recent discovery of thelodont scales from a mid-Famennian sequence in the South Oscar Range, Canning Basin, northwestern Australia (Fig. 2). The Iranian scales are placed within a new turiinid genus *Arianalepis* gen. nov., which represents the youngest known thelodont remains; the Australian material is more sparse and so its assignment is less certain. These new discoveries furthermore support the closeness of faunal relationships in the mid-Palaeozoic of northern Gondwana, especially between Iran and Australia. In addition, the finds offer an opportunity to further establish and extend biostratigraphic schemes utilizing thelodont taxa in the Devonian (Turner 1997; Long & Trinajstic 2000; Young & Turner 2000).

Geographical and geological setting

Iran

The Hojedk section (*c.* 4 km west of Haruz village and *c.* 48 km north of Kerman; 30°43′N, 57°0′E; Fig. 1) is measured on the southeastern flank of Kuh-e-Kanseh Mountain, Kerman Province, central Iran. The stratigraphy of the Hojedk Devonian strata has recently been studied in detail by Wendt *et al.* (2005), Gholamalian & Kebriaei (2008)

From: Becker, R. T., Königshof, P. & Brett, C. E. (eds) *Devonian Climate, Sea Level and Evolutionary Events*. Geological Society, London, Special Publications, **423**, http://doi.org/10.1144/SP423.3

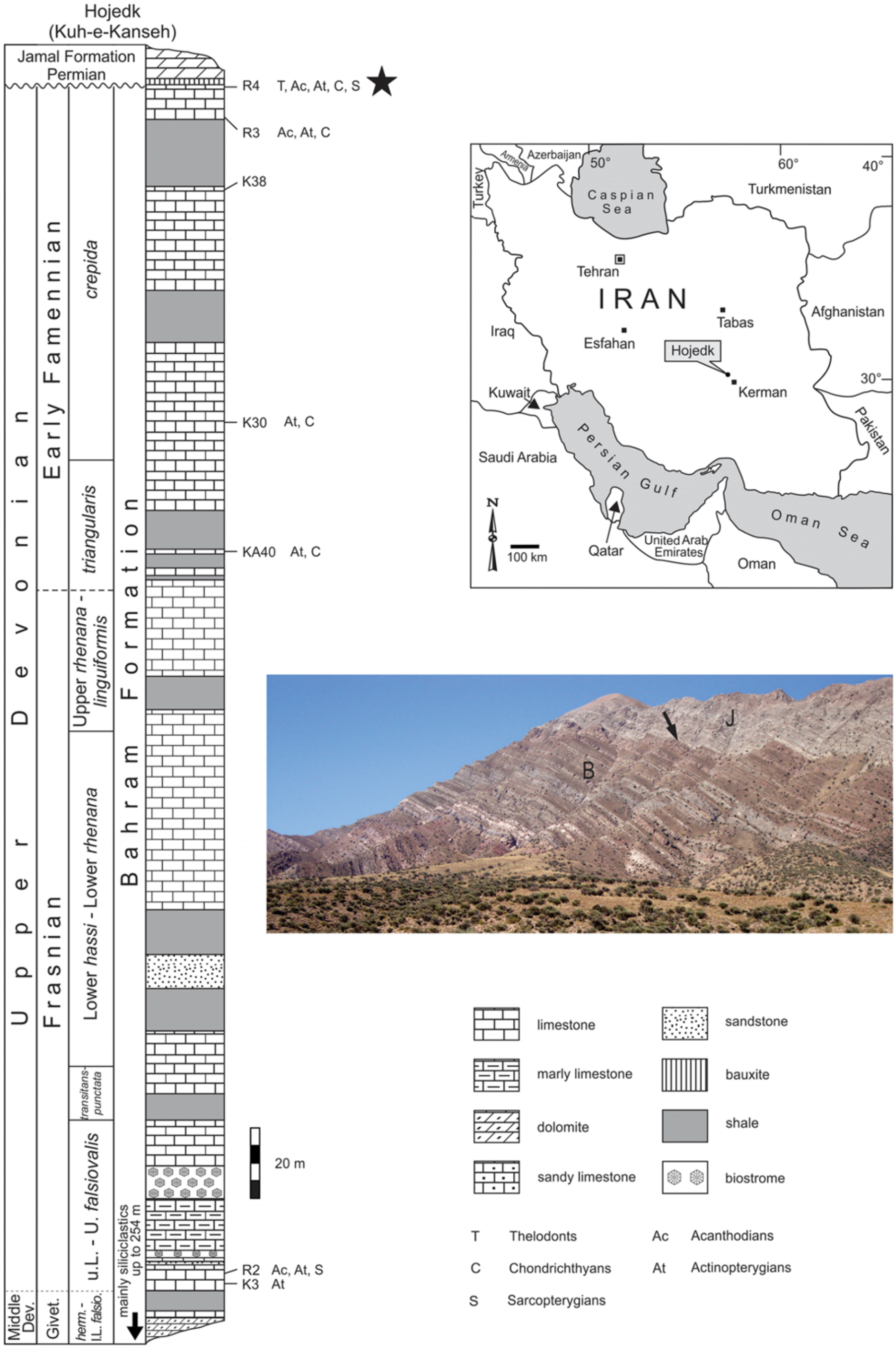

Fig. 1. Stratigraphy and location of the studied Iranian sequence. Simplified stratigraphic column of the Hojedk section in central Iran showing the main facies and fish-bearing horizons; the asterisk marks the bed with thelodont scales. Map of Iran showing the location of the section. Photograph of the Hojedk section showing the Bahram Formation (B) and the Permian Jamal dolomites (J). The distinct level of the unconformity is indicated by the arrow.

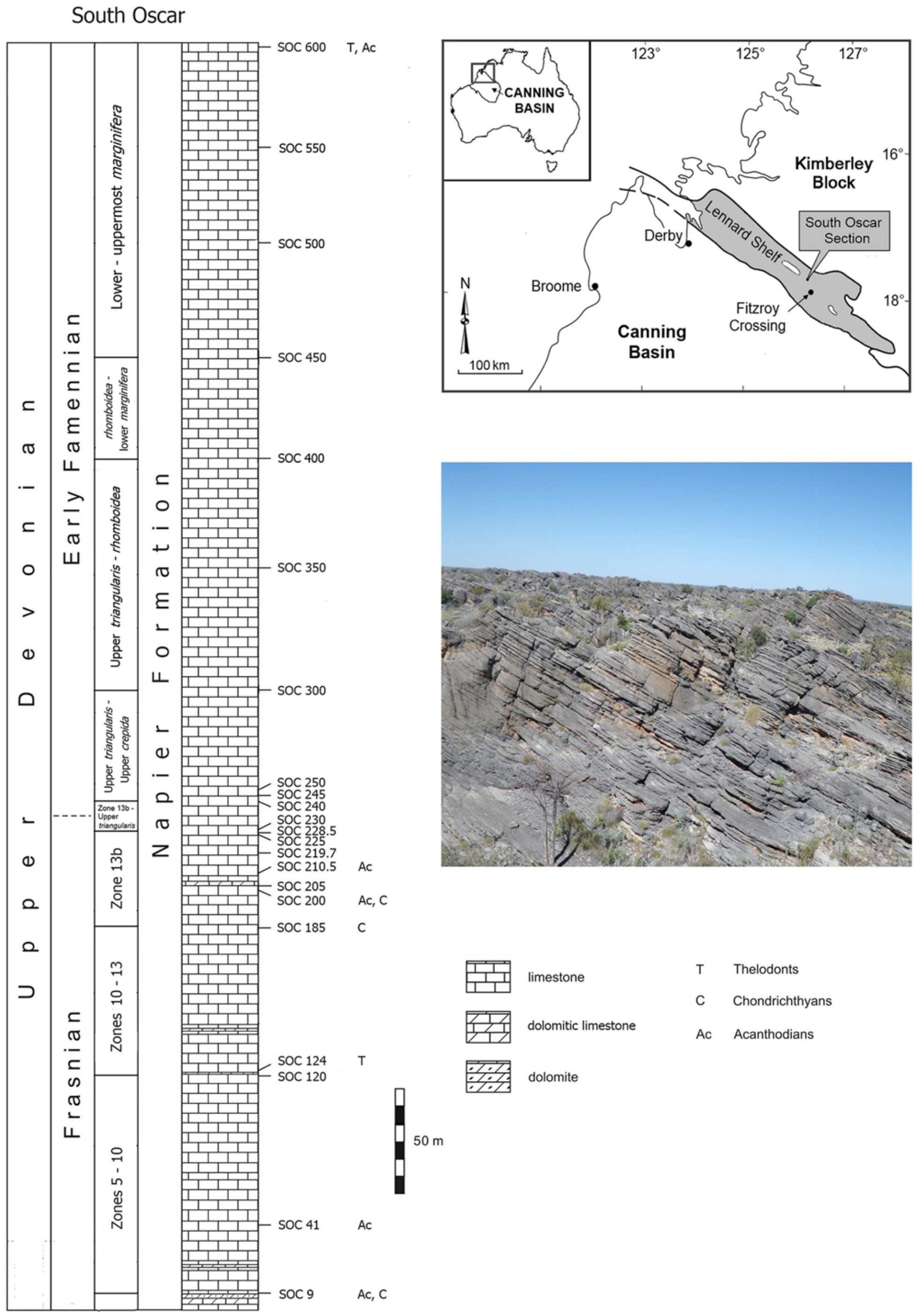

Fig. 2. Stratigraphy and location of the studied Australian sequence with simplified stratigraphic column of the South Oscar Range (SOC) section in the Canning Basin, Western Australia, showing the main facies and fish-bearing horizons (after Playton *et al.* 2013). Map of the Lennard shelf showing the location of the studied section, with inset map of Australia showing the location of the Canning Basin. Photograph of the South Oscar Range section in the Napier Formation.

and Gholamalian *et al.* (2013). The underlying Lower (?) Devonian/Eifelian Padeha Formation commences with a breccia unit followed by sandstones and dolomites. There is a disconformity at the top of the Padeha Formation, where a sandstone unit is overlain by a dolomitic horizon of the Bahram Formation containing small gastropods, large plates of the placoderm *Holonema* and plant remains; the unit has been dated as late Givetian based on conodonts (see Gholamalian & Kebriaei 2008). The limestones in the uppermost Bahram Formation are overlain with an apparent major temporal unconformity by dolomites of the Permian Jamal Formation. Conodont samples collected from the limestone beds in the upper part of the section, however, revealed an early Famennian age, from the Lower *Palmatolepis crepida* Zone (see Gholamalian & Kebriaei 2008, fig. 1, table 1, pp. 183–184).

The new thelodont material came from Sample R4, a red sandy limestone bed in the uppermost part of the section, just below the level of the Devonian/Permian unconformity (Fig. 1) (Hairapetian & Turner 2003; Turner & Hairapetian 2005; Hairapetian 2008). The bed is now dated as early Famennian based on conodonts and fish remains. Associated with the thelodont scales are conodont elements indicative of a shallow-water fauna, including *Icriodus alternatus* cf. *helmsi* Sandberg & Dreesen, 1984, *Icriodus cornutus* Sannemann, 1955, *Pelekysgnathus inclinatus* Thomas, 1949, *Polygnathus semicostatus* Branson & Mehl, 1934 and the *Polygnathus communis* group Branson & Mehl, 1934, dating of which spans the Middle–Upper *Palmatolepis crepida* Zone (Hairapetian 2008). The new thelodont taxon is associated with stratigraphical index chondrichthyan species from the Hojedk section (Fig. 1); the assemblage comprises several chondrichthyan and actinopterygian taxa, with shark teeth of phoebodonts *Phoebodus gothicus gothicus* Ginter, 1990, *Phoebodus turnerae* Ginter & Ivanov, 1992 and *Phoebodus* aff. *turnerae* Ginter & Ivanov, 1992, the protacrodonts *Protacrodus* sp. and *Deihim mansureae* Ginter, Hairapetian & Klug, 2002, the cladodontomorphs *Ctenacanthus* sp. and Elasmobranchii gen. et sp. indet., as well as sarcopterygian and actinopterygian scales, all supporting an early Famennian age (Ginter *et al.* 2002; Hairapetian 2008, fig. 4).

Australia

A section through the proximal slope facies of the Napier Formation was measured at South Oscar Range (17°55′S, 125°17′E; Fig. 2) (Playton *et al.* 2013), located along the southwestern edge of the Lennard Shelf in the Kimberley Region of NW Western Australia (Playford *et al.* 2009). The Napier Formation unconformably overlies Proterozoic basement and in outcrop ranges from early Frasnian to late Famennian. The lithology of the measured section is predominantly limestone with the basal part of the section comprising marginal and slope-derived mega breccias with minor dolomitic microbial boundstones, rudstones and breccias. The upper interval of the South Oscar Range section from approximately 185 m consists mainly of platform-derived skeletal packstone–grainstone facies as well as *in situ* stromatactoid boundstones and skeletal–peloid-coated packstones to grainstones. Overlying the mixed slope facies of the Napier Formation are the siliciclastic shelf deposits of the uppermost Devonian to Lower Carboniferous Fairfield Group (Playford & Lowry 1966). The Frasnian–Famennian boundary is placed within the upper part of the section, between 223.8 and 233.2 m, with its location based on conodont data (Hansma *et al.* 2015) in addition to the last occurrence of Frasnian stromatoporoids (Hurley 1986; Playford *et al.* 1989).

The new thelodont material comes from Sample South Oscar Range (SOC) 600 in the uppermost bed of the section and co-occurs with acanthodian and palaeoniscoid scales. This horizon has been dated as ranging from the Upper *Palmatolepis marginifera* to *Palmatolepis rugosa trachytera* conodont zones, which is supported by the overlap of *Palmatolepis gracilis gracilis* Branson & Mehl, 1934, and *Palmatolepis minuta minuta* Branson & Mehl, 1934 in Sample SOC 600. A lower *Palmatolepis rhomboidea* age is not supported because *Scaphignathus velifer* Helms, 1959 is not known below the Upper *Palmatolepis marginifera* conodont Zone within the Canning Basin and this taxon has been recovered below from Sample SOC 500 (Fig. 2). The Frasnian conodont succession at South Oscar Range is conformable with the Montagne Noire (MN) conodont zonation (Klapper 1989).

Additional thelodont scales identified here as *Australolepis seddoni* Turner & Dring, 1981 (Figs 3 & 4) have been found in the lower part of the section (SOC 124), dated as Frasnian MN Zone 10. Immediately above this horizon (MN 13b), there are shark teeth of *Stethacanthus* sp. as well as palaeoniscoid and acanthodian scales. The Frasnian part of the section has a diverse palmatolepid conodont fauna indicative of open-marine conditions (Sandberg & Ziegler 1979).

Material and methods

A buffered solution of 10% acetic acid was employed to extract the Iranian Sample R4 residue and specimens were then picked using a sieve of 0.177 mm mesh. Sixteen thelodont scales (Figs

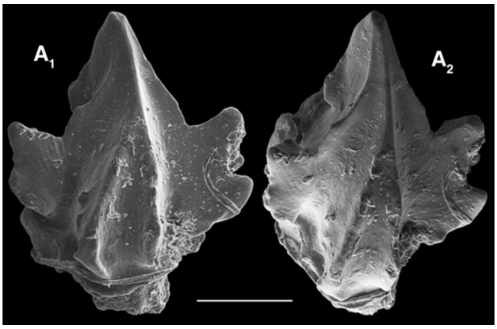

Fig 3. Scale of *Australolepis seddoni* WAM 13.10.2 from Sample SOC 124, South Oscar Range section, Canning Basin, Western Australia. A_1, dorsal view; A_2, dorsolateral view. Scale bar 0.2 mm.

5–7) have been found, most of which are broken and reddish brown in colour (Fig. 7). The scales are densely covered with adhering sedimentary quartz grains, which are not easy to remove with a needle (Fig. 7). Scanning electron micrographs were prepared in Esfahan with a Leica 360 scanning electron microscope and in the Institute of Palaeobiology, Polish Academy of Sciences (Warsaw, Poland) using a Philips XL 20. The Iranian specimens are deposited in the Department of Geology, Azad University, Esfahan (AEU).

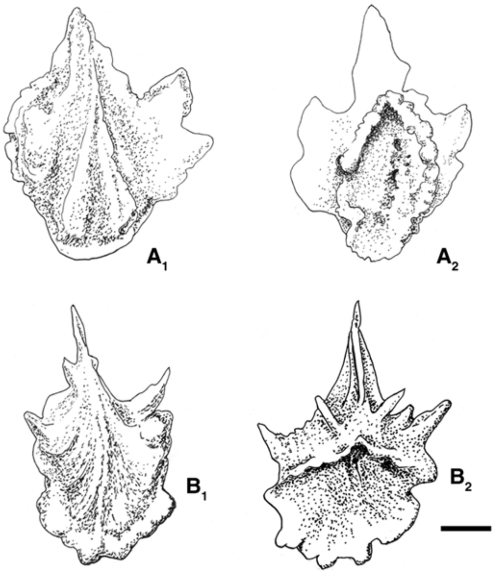

Fig. 4. Drawings of scales of *Australolepis seddoni* WAM 13.10.2 from Sample SOC 124, South Oscar Range section, Canning Basin, Western Australia. A_1, crown view; A_2, ventral view; B_1, crown view; B_2, ventral view. Scale bar 0.2 mm.

Bulk rock samples (20 kg) were taken within the measured South Oscar Range section. Acid digestion of the carbonates in 10% acetic acid and heavy-liquid separation of the residue was undertaken at Macquarie University and the fractionated residues returned for picking. One of two scales recovered from SOC 124 was photographed using a Zeiss EVO 40XVP and both scales were drawn while magnified using a binocular microscope. One scale from SOC 600 was photographed using a Leica XX2 V 7S stereomicroscope camera version 3.4.1 at the Western Australian Museum and drawn under a binocular microscope. Owing to the paucity and poor preservation of the SOC 600 scale, scanning electron microscope or histological work was not possible. Specimens are deposited in the Western Australian Museum (WAM).

The 13-fold Frasnian conodont zonation, first proposed for the MN succession (Klapper 1989) and subsequently modified to a 15-fold zonation (Girard *et al.* 2005), was used to describe the stratigraphic ranges of the conodont and vertebrate taxa recovered from the Canning Basin sections. The standard conodont zonation of Ziegler & Sandberg (1990) were used for both sections to describe Famennian age ranges and for the Frasnian in the Iranian sections, because the ranges of MN zonal markers have not yet been replicated for Iran.

SYSTEMATIC PALAEONTOLOGY

Thelodonti Jaekel, 1911

Order **Thelodontiformes** Kiaer in Kiaer & Heintz, 1932

Family **Turiniidae** Obruchev, 1964

Australolepis seddoni Turner & Dring, 1981
(Figs 3 & 4)

Material: WAM 13.10.2; one scale.

Locality and geology. South Oscar Range, Canning Basin, Western Australia (17°55′S, 125°17′E). Bed SOC 124, CZ 10, reef, margin and slope-derived skeletal limestone: Upper Devonian Napier Formation.

Stratigraphic range. Australia: Napier Formation, South Oscar Range, Canning Basin: MN Zone 10, MN Zones 6–10, Virgin Hills Formation, Horse Spring, Canning Basin; earliest Frasnian to MN Zone 10 in the Gneudna Formation type section, Carnarvon Basin, Western Australia (Turner & Dring 1981; Trinajstic 2000, 2001; Turner *et al.* 2002; Trinajstic & George 2009). In Iran the range extends from the early Frasnian *Mesotaxis falsiovalis* Zone, MN Zones 1–3, to, in the Chahriseh

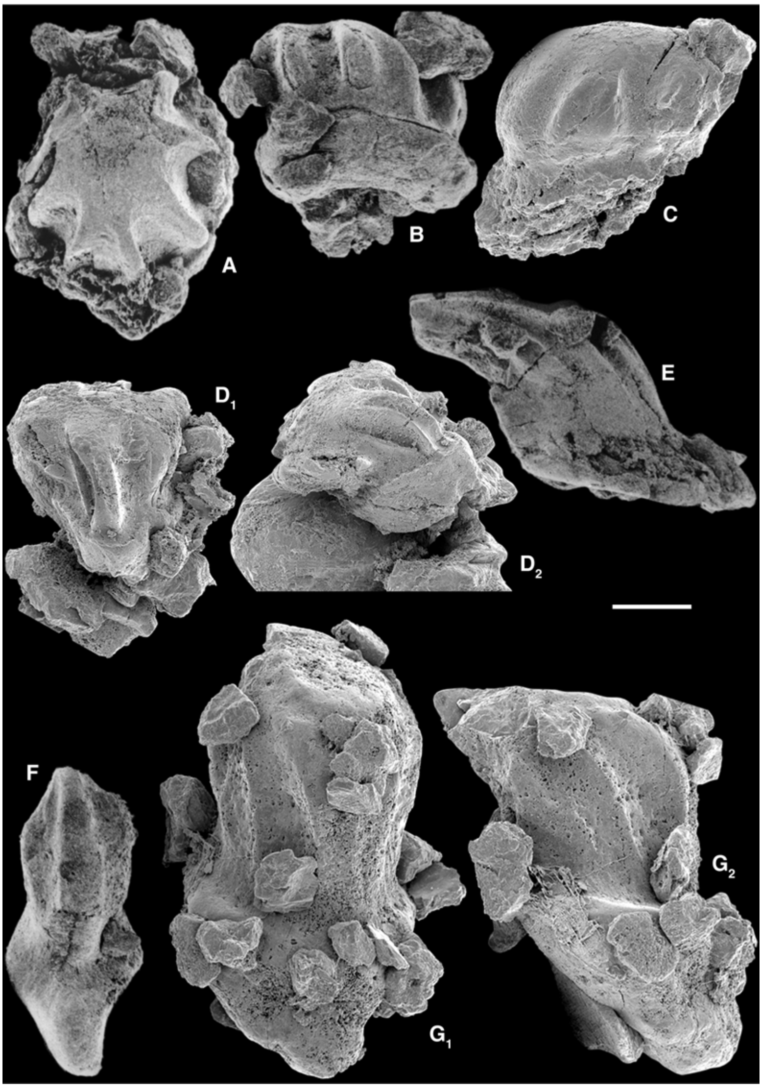

Fig. 5. Scanning electron micrographs of early Famennian thelodont scales of *Arianalepis megacostata* gen. et sp. nov. from sample R4, Hojedk, Kerman Province, Iran. A, B, head scales; C, cephalopectoral scale; and D–G, trunk scale. A, AEU 720 in crown view; B, AEU 721 in lateral crown view; C, AEU 722 in lateral view; D, AEU 723 in antero-crown (D_1) and lateral (D_2) view; B, AEU 724 in lateral view; F, AEU 725 in crown view; G, AEU 726, holotype in antero-crown (G_1) and lateral (G_2) view. Scale bar 0.2 mm.

section, *Palmatolepis hassi* Zone, MN Zone 10 (Hairapetian *et al.* 2000; Yazdi & Turner 2000).

Description. The scales measure less than 1 mm in length with an elliptical base and triangular crown, terminating in a sharp apex. The anterior face of the tripartite crown has two bifurcating ribs that fuse to form a single rib that extends to the crown apex (Figs 3 & 4, drawing A_1). The anterior ribs are ornamented with small tubercles (Fig. 4, drawing A_1). A well-developed, ridged lateral lappet is present at the medial region of the scale (Figs 3 & 4, drawings A_1, B_1). The lateral extent of the lappet curves posteriorally and bifurcates to form two anteriorward-pointing projections (Fig. 4, drawing B_1). The posterior lappets are reduced compared with the medial lappets and lack the terminal projections. The mesial face adjoins the central ridge. A shallow neck separates the crown from a narrow base, which does not possess an anterior spur. The base exhibits

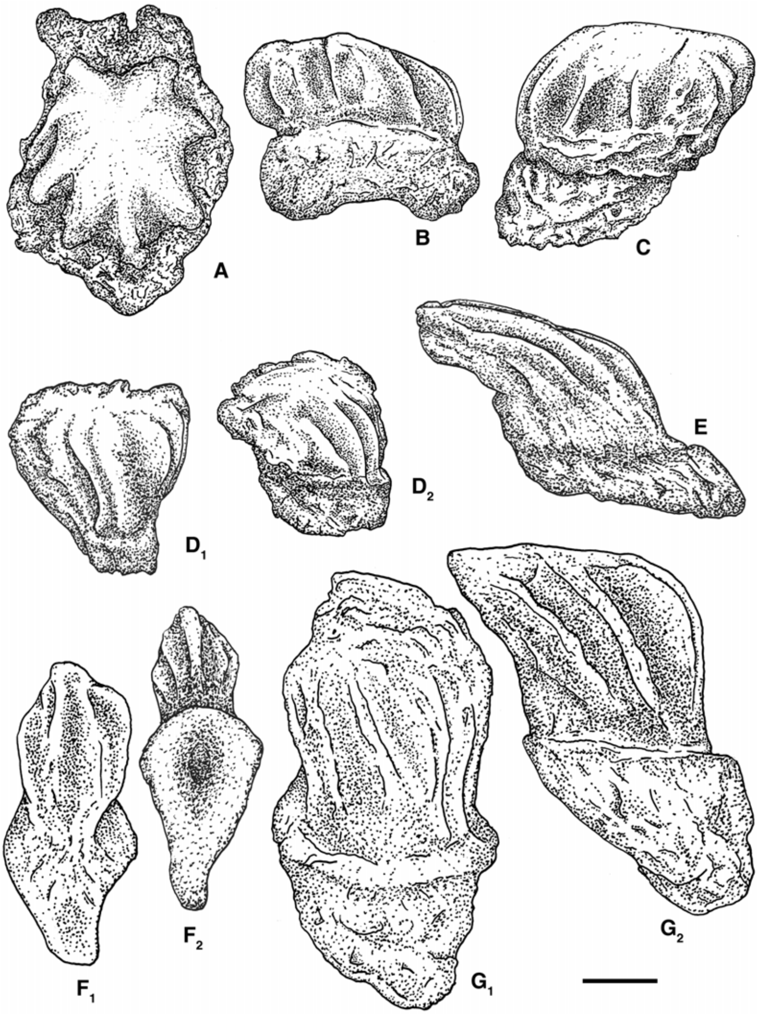

Fig. 6. Drawings of scales of *Arianalepis megacostata* gen. et sp. nov. from sample R4, Hojedk, Kerman Province, Iran. A, AEU 720 in crown view; B, AEU 721 in lateral crown view; C, AEU 722 in lateral view; D, AEU 723 in antero-crown (D_1) and lateral (D_2) view; E, AEU 724 in lateral view; F, AEU 725 in crown view (F_1) and ventral (F_2) view; G, AEU 726, holotype in antero-crown (G_1) and lateral (G_2) view. Scale bar 0.2 mm.

the lobate thickenings typical in scales of this species (Fig. 4, drawings A_2, B_2). An elongate pulp canal is visible on the underside of the scale.

Histology. As only two single scales were recovered no thin sections were made. However, the large pulp cavities are typical of turiniid histology (Märss *et al.* 2007).

Taphonomic analyses. The scale is pristine. The crowns are uniformly light brownish in colour with a white base, typical of thelodont scales, where the two hard tissues – dentine in the crown and neck, and aspidin in the base (see e.g. Märss *et al.* 2007) – are often present, with very different colours related to the varying mineralization effects based on the porosity of the tissue.

No diagenetic alteration is detectable and associated conodont remains have a conodont alteration index (CAI) of 0.5.

Remarks. These scales conform to the original diagnosis of *A. seddoni* (Turner & Dring, 1981) and are attributed to this taxon. Their small size, gracile construction, bifurcating crown ribs and smooth shallow neck, with a base wider than the crown, are all consistent with the type diagnosis. Small tubercles are present on the crown ribs, which are

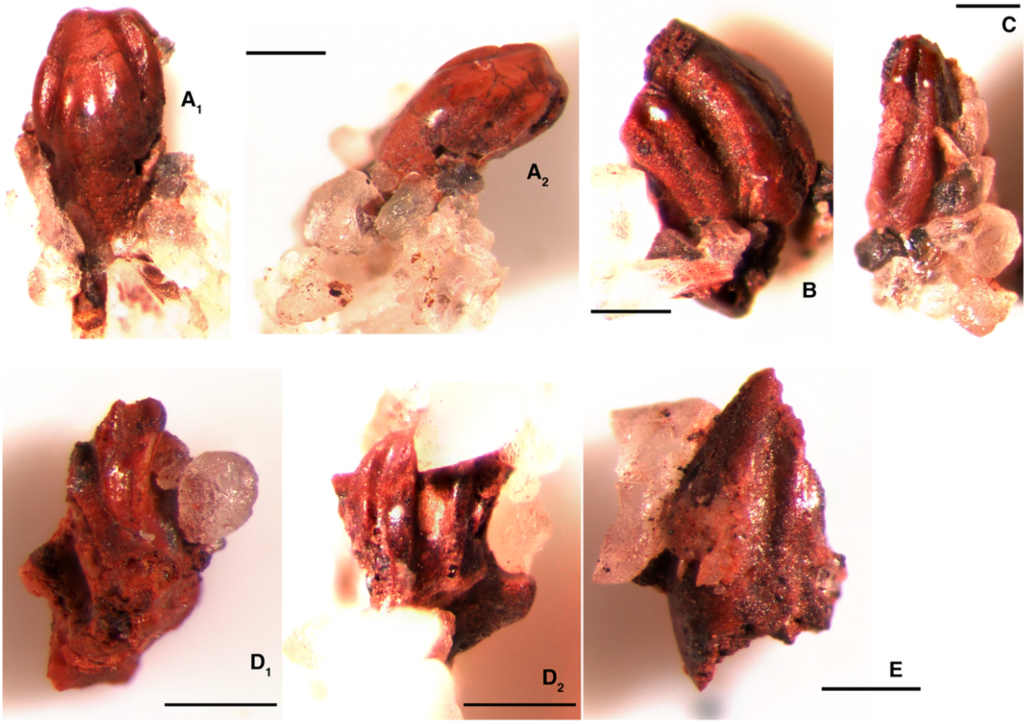

Fig. 7. Photographs of early Famennian thelodont scales from sample R4, Hojedk, Kerman Province, Iran, to show colour and taphonomic nature of the adhering quartz grains. (A) AEU 782 in crown ($\mathbf{A_1}$) and lateral-crown views ($\mathbf{A_2}$); (**B**) AEU 783 in lateral crown view; (**C**) AEU 783, in basal view; (D) AEU 784 in antero-crown ($\mathbf{D_1}$) and lateral-crown ($\mathbf{D_2}$) view; (**E**) AEU 785 in crown view. Scale bars, 0.2 mm.

also seen in scales from Horse Spring (Turner 1997; Trinajstic & George 2009). Following currently accepted concepts of squamation patterns (Märss *et al.* 2007), the scales originate from the cephalo-pectoral region of the body.

The scale conforms to those from the known uppermost range of *A. seddoni* (MN Zone 10) within Australia based on well-constrained conodont remains (Trinajstic & George 2009).

Genus *Arianalepis* gen. nov.

Etymology. From ‘Ariana’, an old name for the country of origin of the first Famennian thelodonts; and Greek: *lepis*, a scale.

Diagnosis. As for type and only species.

Stratigraphic range. Early Famennian, *crepida* Zone.

Type and only species. Arianalepis megacostata sp. nov.

Remarks. The Iranian and Western Australia thelodont scales are the youngest to be recorded to date; those from Iran were reported earlier and considered tentatively to be within the family Turiniidae, which is the only clade found thus far in post-Lochkovian Gondwana (Hairapetian & Turner 2003; Märss *et al.* 2007). Hairapetian & Turner (2003) and then Märss *et al.* (2007) retained them as an undetermined turiniid taxon. However, as there are significant morphological differences from earlier turiniid taxa and considering their much younger age, the new scales are referred here to a new genus (see further discussion below).

Arianalepis megacostata gen. et sp. nov.
(Figs 5–7)

Synonymy

2003 new turiniid Hairapetian & Turner: 26–27.
2005 new turiniid Turner & Hairapetian: 24.
2007 Turiniidae gen. et sp. indet. Märss *et al.*: 110.

Type specimens. Holotype: AEU 726, trunk scale (Figs 5, micrographs G_1, G_2 & 6, drawings G_1, G_2); paratypes: 15 scales (Fig. 7A–E), AEU 720–725, 782–790.

Type locality and stratigraphy. Section *c.* 4 km W of Haruz village; 30°43′N, 57°0′E, SE Kuh-e-Kanseh Mt, Hojedk, *c.* 48 km N of Kerman, central Iran. Sample R4, red sandy limestone bed, Bahram Formation, Late Devonian, early Famennian, *crepida* Zone.

Stratigraphic range. *Crepida* Zone, early Famennian.

Etymology. From Latin *mega* 'large' and *costata*, 'ribs' for the ribbed nature of the crowns.

Diagnosis. Turiniid with robust medium-sized scales with a few simple coarse ribs on crowns. Base is horizontally extended with anterior basal extensions.

Description. The scales all show a robust structure and measure less than 1 mm in length.

The head scales are rounded as in most thelodonts with robust crowns having a few, up to eight, strong ribs. There are eight ribs radiating from a high, rounded central apex to a shallow neck; wide troughs separate the ribs (Figs 5, micrographs A, B & 6, drawings A, B). Cephalopectoral scales are poorly preserved but can be seen to be more elliptical (Figs 5, micrograph C & 6, drawing C). The crowns exhibit simple coarse ribbing and well-developed bases.

Trunk scale crowns (Figs 5, micrographs D_2–G_2 & 6, drawings D_1, D_2, G_1, G_2) are characterized by simple coarse ribbing and a protruded, prominent median area, which can be flat and horizontally placed as in the holotype scale shown in Figure 5, micrograph G_1, G_2. One scale (Fig. 5, micrograph F) shows a smooth, wide median and two lateral areas at a lower level. Another scale shown in side view (Fig. 5, micrograph E) exhibits the high crown with ribs down to the shallow neck and the horizontally placed base with the scale axis at around 45°. Some indication of split ribs is seen in other scales (Fig. 7). The anterior base is developed into a single, thick basal root or spur, which extends in a lateral plane (Fig. 5, micrograph F). The holotype scale (Figs 5, micrographs G_1, G_2 & 6, drawings G_1, G_2) exhibits a relatively deeper base with an incomplete anterior anchoring root directed vertically downwards.

Unlike many turiniid taxa, especially in Gondwana (e.g. Turner 1997), there is no sign of micro-ornament on the crown surface of any scales but this is probably a factor of the removal of the external shiny layer of dentine (see taphonomic remarks below).

Histology. Owing to the relatively few scales and poorly preserved material, direct histological studies were not possible. However, all exhibit the typical single rounded pulp opening in the base found in thelodontidid scales as is usual in turiniids (cf. Märss *et al.* 2007); a quite large pulp cavity is seen in Figure 5, micrograph B, and remnants of the pulp canal in Figure 5, micrograph C. Based on comparison the crowns are formed of typical thelodont orthodentine and the base of aspidin. As noted above, the outer layer of dentine (vasodentine called 'enameloid' by some workers) is not as shiny as normal and the dentine tubules of the crown are exposed clearly in some scales (Fig. 5, micrographs G_1, G_2). The pulp cavity is relatively large and the scales are neither in their first dentine crown 'cap' stage nor senescent with large overgrown bases with closed pulp openings.

Taphonomic remarks. There are two possibilities that could explain why some of the Iranian thelodont scales are densely covered with adhering sedimentary quartz grains (e.g. Figs 5, micrographs G_1, G_2 & 7A–E). This could imply reworking and mean that the thelodont scales are older than the other remains, that is, not Famennian, and the presence in some scales of crown ribs divided into two might support this, as there is a similarity to the older Iranian turiniid *Turinia hutkensis* Blieck & Goujet, 1978. However, comparing the state of preservation of the thelodont scales with the other fish microfossils, they are identical in preservation and with the same deep red colour taken from the surrounding rock/grains. The conodont elements were also checked for evidence of reworking but all are light grey in colour, indicating an identical and low CAI, so that reworking does not seem to be a possibility.

Therefore, this leaves the alternative option that the fossils are diagenetically affected and therefore we need to look at post-depositional environmental conditions to account for these changes. The most likely explanation is that the phenomenon is a consequence of water chemistry after the scales were shed or lost from the dead animal; there is no sign of algal or fungal boring as seen in certain marginal environments (e.g. Märss *et al.* 2007). Other Gondwana samples of turiniid scales show similar adhering grains, such as those from central Australia and New Zealand, but these scales also show more extreme diagenetic effects such as silicification or loss of tissue structure (Turner 1997; Macadie 2002).

?*Arianalepis* sp. indet.
(Figs 8 & 9)

Material. WAM 13.10.1; one cephalopectoral scale.

Locality and stratigraphy. The South Oscar Range section (17°55′S, 125°17′E) lies 42 km NW of Fitzroy Crossing, South Oscar Range, Canning

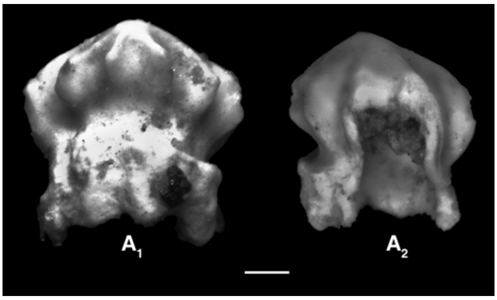

Fig. 8. Transmission microphotographs of scales of ?*Arianalepis* sp. indet. WAM 13.10.1 from sample SOC 600. A_1 and A_2 in lateral view. Scale bar 0.2 mm.

Basin, Western Australia. Sample SOC 600, white crinoidal packstone, Napier Formation, Late Devonian, Middle Famennian, *marginifera*/*trachytera* conodont zones.

Stratigraphic range. Middle Famennian, *marginifera*/*trachytera* conodont zones.

Description. The one almost complete specimen is a young, medium-sized (0.8 mm) robust scale with a small break anteriorly across the crown, neck and base (Figs $8A_2$ & 9, drawing A_{1-3}). The total range of the number of ribs cannot be determined; however, 12 broad crown ribs are reconstructed based on the spacing of the ten preserved ones. The ribs radiate from a dome-shaped apex with a centrally raised point directed posteriorly (Figs $8A_1$ & 9, drawing A_4). Two of the medial anterior ribs bifurcate halfway between the crown apex and neck–crown interface. Deep troughs separate the ribs, which diminish at a deep, narrow neck (Figs $8A_1$ & 9, drawing A_4). A series of small crenulations occurs on the terminal dorsal edge of each rib (Fig. 9, drawing A_2).

The base is approximately two-thirds the size of the crown and is separated by a high neck (Fig. 9, drawings A_2, A_3). The anterior portion of the base is broken (Figs $8A_{1-2}$ & 9, drawings A_2–A_4). The remaining preserved section indicates a roughly circular shape with a slight slope directed posteriorly. A large rounded pulp cavity and a pulp opening are present (Fig. 9, drawings A_2, A_3).

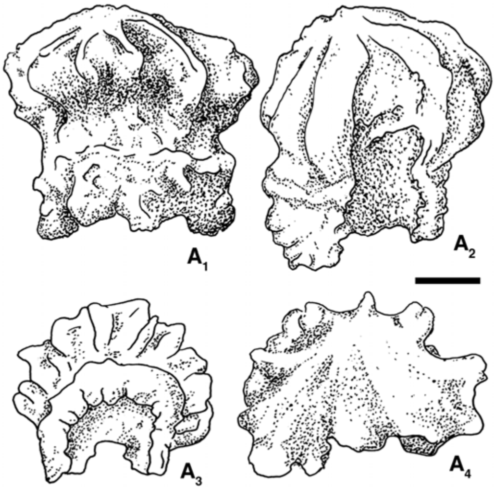

Fig. 9. Drawings of scale of ?*Arianalepis* sp. indet. WAM 13.10.1 from SOC 600. A_1 and A_2, lateral view; A_3, basal view; A_4, crown view. Scale bar, 0.2 mm.

Histology. Histology was not possible as only a single scale was recovered. However, the complete scale exhibits the typical large pulp cavity of a morphogenetically young turiniid scale where dentine has not yet grown centripetally to form a narrow pulp opening on the base.

Remarks. The scale from SOC 600 is referred tentatively to the new genus *Arianalepis* with indeterminate species, on the basis of similar morphology of a crown with few coarse ribs. Not being a body scale, however, specimen WAM 13.10.1 generally resembles all turiniid head scales and probably lacks diagnostic features. The head scale from SOC 600 has a higher number of radiating ribs: 12 compared with 8, and also seems to be more robust than the specimens from Hojedk. This might be because of normal variation, the different age of the scales, or dependent on the age of the individual animal (Märss *et al.* 2007).

Microcrenulation of scale crowns also seems to be phylogenetically significant in the Turiniidae; however, the relatively poor preservation of the Iranian scales means that micro-ornament is not preserved and, because most turiniid taxa do exhibit some ornament on the ribs, the crenulations in the Australian scale may just be due to variation within individual scales or within species.

For now we tentatively place the Australian scales within the genus *Arianalepis* gen. nov. based on the single scale.

Taphonomic analyses. The colour of the scale is uniformly white with no evidence of biogenic alteration.

Numerous, well-preserved acanthodian scales are also present within Sample SOC 600, suggesting a deeper-marine environment where thelodonts are relatively scarce (cf. Märss *et al.* 2007). The associated conodont elements are pristine with a CAI of 0.5. There is no evidence to suggest reworking in this sample as the conodont assemblage conforms to the other assemblages immediately below Sample SOC 600.

Comparison and discussion

The scales of *Arianalepis megacostata* gen. et sp. nov. from Hojedk are superficially more simple than other turiniid species from the Devonian of Gondwana and, interestingly, are most like those of the late Silurian *Turinia fuscina* Turner, 1986 of southern Australia, and mid-Late Devonian taxa, such as *T. hutkensis* Blieck & Goujet, 1978. The single complete scale from South Oscar Range shows some resemblance to the scales of *Jesslepis johnsoni* Turner, 1995 in being relatively robust, having bifurcating and deeply dissecting ribs, and a large pulp cavity. The complete scale from South Oscar Range can be distinguished based on the greater number of ribs, which do preserve microcrenulations.

The scales from Hojedk and South Oscar Range are distinguishable from any known species. Most interesting is that these youngest thelodont scales have large robust crowns and bases unlike the slightly older taxa known from Iran and Western Australia, especially *Australolepis seddoni*, which has delicate ribbing and sculpture on the crowns. Other older Devonian taxa from the same region are *Turinia antarctica* Turner & Young, 1992 and *J. johnsoni* from the Givetian of eastern Australia and Antarctica (Turner 1995, 1997).

T. hutkensis of Iran is most similar to scales from Thailand and Antarctica (see Turner & Young 1992; Turner 1997). Some of the *Turinia* cf. *hutkensis* scales from the Chahriseh locality resemble *Turinia pagoda* Wang, Dong & Turner, 1986 and *Turinia* spp. from the western Yunnan Province and *A. seddoni* in their out-turned ridges. Scales that share features with *T. hutkensis*, such as the tight crown double-ribbing, have also been found in the central Australian basins and were earlier

Table 1. *Turiniid taxa from the Middle (Givetian) and Upper (Frasnian and Famennian) Devonian of Gondwana*

Epoch/Age	Conodont zonation		Australia				Antarctica	Iran		China
			WA	NT	SA	QLD		SS	CEIM	
Famennian	*Si. praesulcata*									
	Pa. gracilis expansa									
	Pa. perlobata postera									
	Pa. rugosa trachytera									
	Pa. marginifera		? *Arianalepis* sp.							
	Pa. rhomboidea									
	Pa. crepida								*Arianalepis megacostata*	
372.2	*Pa. triangularis*									
Frasnian	*Pa. linguiformis*	MN 13 c								
		MN 13 b								
	Pa. rhenana	MN 13 a								
		MN 12								
		MN 11								
	Pa. jamieae									
	Pa. rhenana	MN 10	*Australolepis seddoni*					*Australolepis seddoni* *Turinia hutkensis*	*Australolepis seddoni* *Turinia hutkensis*	
		MN 9								
		MN 8								
		MN 7								
	Pa. punctata	MN 6								
		MN 5								
	Pa. transitans	MN 4								
	M. guanwushanensis (= *falsiovalis*)	MN 3					*Turinia antarctica*			
		MN 2								
382.7		MN 1								
Givetian	*norrisi*									
	K. disparilis			*Turinia* sp.						
	Sc. hermanni			?	*Turinia* sp.					
	Po. varcus			*Turinia* sp. cf. *T. pagoda*	?	*Jesslepis johnsoni*				*Turinia pagoda*
387.7	*Po. hemiansatus*									

CEIM, central–east Iran microcontinent; NT, Northern Territory; QLD, Queensland; SA, South Australia; SS, Sanadaj Sirjan; WA, Western Australia.

thought to be related to the older *Turinia australiensis* (Turner 1997: see Table 1). Could *Australolepis* be the result of paedomorphic evolution from *T. hutkensis* or *T. pagoda*? Heterochrony in the morphogenesis would leave all the scales with wide-open pulp cavities throughout life and shallow bases with only small anterior prongs, and with a base capable of only thickening sporadically, resulting in the lobate papillae that are typical of *A. seddoni* bases (cf. Fig. 4, drawing A_2). *Turinia hutkensis* and *T. antarctica* both share the fine ultrastructual lines on the crown, seen in earlier *T. australiensis* (see e.g. Turner 1997; Märss *et al.* 2007) but these are not apparent in *A. seddoni* (Fig. $4A_{1-2}$) or *A. megacostata* gen. et sp. nov. (Fig. 7, photographs A_1, D_2) although the latter does have the double ribbing seen in some scales of *T. hutkensis*.

Historically, studies on Laurasian/Laurentian thelodonts have been more numerous than those on Gondwana (Märss *et al.* 2007). This disparity began to be addressed especially during IGCP work from the 1980s onwards, when several new thelodont taxa and increased stratigraphic ranges were reported from Gondwanan faunas (e.g. Blieck *et al.* 1980; Turner *et al.* 1981, 2000; Turner 1986; Wang *et al.* 1986; Turner & Young 1992; Young & Turner 2000; Trinajstic 2001; Hairapetian 2008; Trinajstic & George 2009, table 1). Most notable was the discovery that thelodont taxa survived the Givetian–Frasnian boundary event (Turner & Dring 1981). Turiniid remains recovered from the Aztec siltstone in Antarctica (Turner & Young 1992) have shown a potential age range from the middle Givetian to the early Frasnian based on faunal association with *Antarctilamna* (Young 1993). However, the presence of the spore *Geminospora lemurata* Balme, 1960 has dated this unit as Givetian (Young 1988; Young & Turner 2000). Thelodont remains were first found in the Middle Devonian of Iran in the 1970s and other taxa in Australia, Thailand and China in conodont-dated strata (e.g. *J. johnsoni* in Queensland) (Turner & Janvier 1979; Blieck *et al.* 1980; Hamdi & Janvier 1981; Turner 1997).

The first early Frasnian thelodont scales, *A. seddoni*, were recorded from the Gneudna Formation, Carnarvon Basin, of Western Australia (Turner & Dring 1981). Spore assemblages (Balme 1988) gave a possible Givetian to Frasnian age for the lower part of the section; however, microvertebrate assemblages suggested a Frasnian age for the whole section (Trinajstic 2001). In the last decade thelodont scales identified as *T. hutkensis* and *A. seddoni* were reported from the early–middle Frasnian of Iran (e.g. Yazdi & Turner 2000; Turner *et al.* 2002) and poorly preserved scales possibly from *A. seddoni* were recovered from slightly younger Frasnian strata in the Canning Basin of Western Australia (Turner 1997, 1999). Until recently, this was the youngest record of any thelodont taxon (Turner 1997). Ranges for thelodonts have been further refined in Western Australia based on the co-occurrence of thelodonts and phoebodonts in conodont-dated sequences at Horse Springs, with the age range of *A. seddoni* extended into the upper Frasnian (Trinajstic & George 2009). Younger thelodont scales were recovered from younger early Famennian strata in the Canning Basin of Western Australia; however, as the preservation was poor these were not formally identified (Turner 1997, 1999). Subsequent studies by Hairapetian & Turner (2003) and Hairapetian (2008) reported the first Famennian scales in Iran.

Palaeobiogeography

The continuance of thelodont taxa into the Famennian may suggest a displacement post the Givetian–Frasnian extinction and the foundation of a refuge in Northern Gondwana (Kauffman & Harries 1996; Harries *et al.* 1996). As the Frasnian and Famennian turiniid fish are found in shallow to very shallow water, 'challenging' environments, for example, marginal, lagoonal and hyper-saline, were they then pre-adapted or opportunistic survivors and thus these new taxa are evidence of a survival lineage? There is no sign yet of any thelodont in the immediate earliest Famennian 'bloom' of recovery, but with evidence now in two disparate parts along the Palaeotethyan southern shore we consider *Arianalepis* gen. nov. as a Lazarus taxon.

Few agnathan fishes survived the massive Late Devonian extinctions and until recently only two thelodont taxa, *T. hutkensis* from the early–middle Frasnian of Iran (Turner *et al.* 2002) and *A. seddoni* from the early–late Frasnian (MN zones 6–10) of Western Australia and Iran (Yazdi & Turner 2000; Trinajstic 2001; Turner *et al.* 2002; Trinajstic & George 2009; Burrow *et al.* 2010) were known. However, now at least one thelodont genus with one or more species appears to have weathered the Frasnian–Famennian extinction and appears to represent a surviving Lazarus taxon (Kauffman & Harries 1996).

Australolepis seddoni is now known from the Gneudna and Virgin Hills formations of Western Australia and the Shotori Range and Chahriseh section of Iran (Turner 1997; Yazdi & Turner 2000; Turner *et al.* 2002; Trinajstic & George 2009). To date, scales have been recovered from different facies including distal and medial slope and back reef in the Canning Basin (Chow *et al.* 2013), as well as shallow carbonate ramp in Iran and the Carnarvon Basin (Hocking *et al.* 1987; Wendt *et al.* 2002; Trinajstic & George 2009). A few possible

Australolepis scales are recorded from the Late Devonian of Holy Cross Mountains (M. Ginter & S. Turner, pers. obs. 1990). The presence of thelodonts in sediments from Hull Range, Western Australia, has confirmed an early Frasnian age for these strata (Chow *et al.* 2013), where previously the date could only be constrained to the late Givetian–early Frasnian. This demonstrates again the utility of microvertebrates in general and thelodont scales in particular to help date strata where conodonts and other open-marine taxa are absent. The first appearance has been linked to conodonts by Long & Trinajstic (2000). The younger Frasnian *Australolepis* scales from the Horse Spring section (GK 364), Canning Basin, Western Australia, were also identified as *A. seddoni* (Trinajstic & George 2009). Scales from *A. seddoni* are therefore being reported from a number of sections throughout northern and East Gondwana and are proving useful for correlating early to late Frasnian sections.

Most thelodonts had died out in the Early to early Mid-Devonian and after this the only taxa are known outside of the Laurentian continental terranes (Turner 1997; Turner *et al.* 2004). Later Middle and Late Devonian thelodonts are known in East and northern Gondwana as far ‘south’ as Antarctica, that is, possibly up to 50–60°S in Gondwana (Turner 1997; Märss *et al.* 2007). From the records now available, it seems that the turiniids were most widespread in Gondwana in the Early to Mid-Devonian, with restriction in range by late Frasnian times to Iran and Western Australia.

The fact that at least a small population of thelodonts seems to have survived the Frasnian–Famennian Kellwasser extinction events and lived well into the Famennian is most surprising. We can only speculate on the factors that protected these turiniids from that dramatic time in vertebrate evolution (e.g. Hart 1996). However, it is clear that the area was home to several thelodont taxa from the late Silurian (Hamedi *et al.* 1997; Turner 1997; Hairapetian *et al.* 2008) onwards and their ability to adapt to high-latitude climatic zones must have been in their favour. Chen *et al.* (2002) have attributed a major transgression and eutrophic fluctuations that led to severe algal blooms especially in low-latitude continental shelves to related anoxic events. Now it is certain that least one thelodont taxon and possibly more did weather the Frasnian–Famennian extinction events with recovery and survival of the turiniids.

Blieck & Goujet (1978) and Turner (in Turner & Tarling 1982; Turner 1997) considered the relationship of Iranian thelodonts to others in Asian localities. We have seen above further evidence of the Gondwanan distribution of turiniid thelodonts and showed the links between Iran and Western Australia in the Mid- to early Late Devonian, supporting a Palaeotethyan dispersal route in shallow water between Gondwana and Euramerica

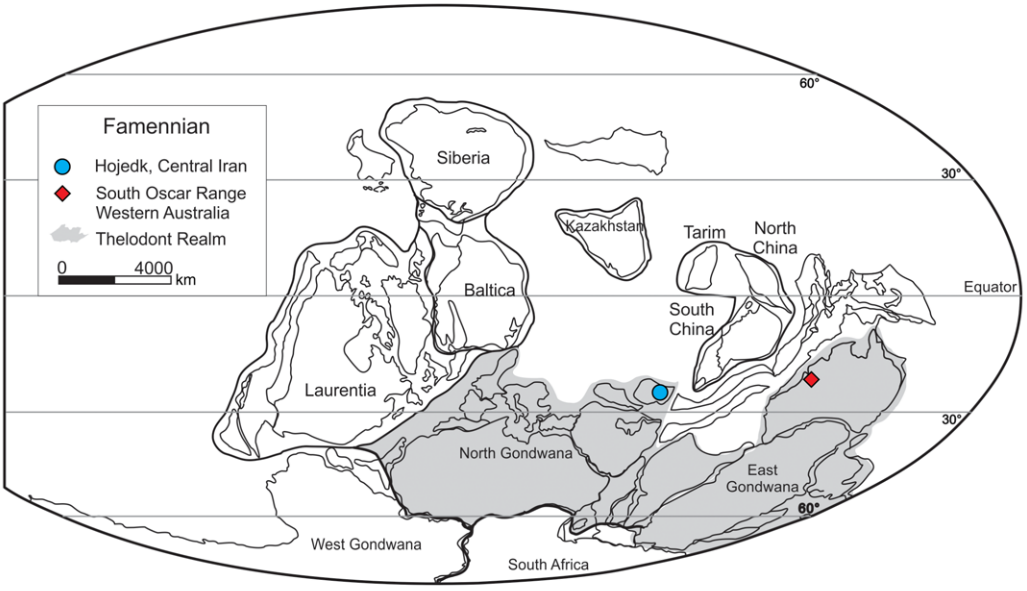

Fig. 10. Palaeogeographical map showing the position of the Famennian thelodont localities in southeastern Iran and Western Australia during the Late Devonian (Famennian). Base map after Golonka (2007) and Lebedev & Zakharenko (2010), with modifications.

(Laurentia) in the Mid–Late Devonian along the northern Gondwana shoreline. Other vertebrate taxa show a similar biogeographical pattern: Ginter *et al.* (2002) discussed the Famennian shark populations of the Palaeotethys; the youngest known ischnacanthiform *Grenfellacanthus zerinae* Long, Burrow & Ritchie, 2004 exhibits a similar pattern with a possible second species of *Grenfellacanthus* occurring in the early Famennian of Chahriseh, Iran (Long *et al.* 2004; C. Burrow, pers. comm. August 2013).

Lebedev & Zakharenko (2010) put forward a new hypothesis of vertebrate provinces for the Givetian, one of which is the Phyllolepid–Thelodont Province; several taxa of phyllolepid placoderms being endemic and earlier in East and northern Gondwana, whereas turiniid thelodonts occur there later. However, they seem to have been unaware that thelodonts did exist in western Gondwana in the Early Devonian (Turner *et al.* 2004) and also that thelodonts occur in the Broken River, North Queensland/China realm in the Mid-Devonian (Turner 1997). Nevertheless, their idea that this province might be extended into the Frasnian and beyond, because thelodonts are associated with key placoderms and chondrichthyans in northern Gondwana (Iran and Western Australia), offers a useful palaeogeographical model (Fig. 10), to which our new finds offer further support. Although they put northern Gondwana further south, the south of central Iran including Hojedk is positioned in the subtropics.

A different opinion on the palaeoposition of central Iran was presented on a recent map by Torsvik & Cocks (2013, fig. 10), which they considered at *c.* 40°S. This southern latitude still might be feasible as thelodonts are thought to have been able to live in relatively high latitudes (see Turner 1997).

Conclusions

The new genus and species of turiniid thelodont, *Arianalepis megacostata* gen. et sp. nov., found in the Upper Devonian (early Famennian) Bahram Formation of the Hojedk section of Iran, and a further uncertain species referred tentatively here to the same genus from the Upper Devonian (middle Famennian) Napier Formation of Western Australia, are younger than the previously youngest known thelodonts from Iran and Western Australia. These are the first thelodont scales known from the early–middle Famennian in both countries and worldwide, and their presence provides new data for biostratigraphic correlation between Iran and Australia. The conodont successions at South Oscar Range and in the Hojedk section constrain the dating.

Most agnathan fishes did not survive the Frasnian–Famennian event and so the presence of a survivor 'Lazarus' thelodont taxon is surprising. *Arianalepis megacostata* gen. et sp. nov. in northern Gondwana (central Iran) and the turiniid ?*Arianalepis* sp. indet. in East Gondwana (Western Australia) provide evidence of the only thelodont lineage surviving the Frasnian–Famennian extinction. These records extend the evolutionary history of the Thelodonti by some 2–6 Ma beyond the Kellwasser events into the *crepida* (Kerman) to Upper *marginifera*/*trachytera* (South Oscar Range) zones.

We emphasize here that it is now necessary to seek more diligently for further examples in the Famennian of the broad northern and eastern Gondwana area, especially in the carbonates of Western Australia.

VH thanks Prof Michal Ginter (Univ. Warsaw) for support and use of facilities in Warsaw. We thank Curtin University WA-OIGC/Applied Chemistry for use of facilities and acknowledge the use of equipment and scientific and technical assistance of the Curtin University Electron Microscope Facility, which has been partially funded by Curtin University, WA State, and Commonwealth Governments. Dr Mikael Siversson from the Western Australian Museum is thanked for photographic assistance and the use of facilities. KT and BR would like to further acknowledge funding from an Australian Research Council Grant (LP0883812), MERIWA, WA ERA, CSIRO, Buru, Chevron Australia Business Unit, Chevron Energy Technology Company, University of Greenwich, National Science Foundation and Chemostrat Inc. Field support and safety were provided by Wundargoodie Aboriginal Safaris and the Geological Survey of Western Australia. Thank you to the Mimbi Aboriginal Community, Mt Pierre Station and Fossil Downs, for field area access. BR acknowledges an Australian Postgraduate Award. This is a contribution to IGCP 596: 'Climate and biodiversity patterns in the Mid-Paleozoic (Early Devonian to Late Carboniferous)'.

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