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Silurian thelodonts from the Niur Formation, central Iran

VACHIK HAIRAPETIAN, HENNING BLOM, and C. GILES MILLER

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Thelodont scales are described from the Silurian Niur Formation in the Derenjal Mountains, east central Iran. The material studied herein comes from four stratigraphic levels, composed of rocks formed in a shallow water, carbonate ramp environment. The fauna includes a new phlebolepidiform, *Niurolepis susanae* gen. et sp. nov. of late Wenlock/?early Ludlow age and a late Ludlow loganelliiform, *Loganellia* sp. cf. *L. grossi*, which constitute the first record of these thelodont groups from Gondwana. The phlebolepidiform *Niurolepis susanae* gen. et sp. nov. is diagnosed by having trident trunk scales with a raised medial crown area separated by two narrow spiny wings from the lateral crown areas; a katoporodid-type histological structure distinguished by a network of branched wide dentine canals. Other scales with a notch on a smooth rhomboidal crown and postero-laterally down-stepped lateral rims have many characters in common with *Loganellia grossi*. Associated with the thelodonts are indeterminable acanthodian scales and a possible dentigerous jaw bone fragment. This finding also provides evidence of a hitherto unknown southward dispersal of *Loganellia* to the shelves of peri-Gondwana.

Key words: Thelodonti, Phlebolepidiformes, Loganelliiformes, palaeobiogeography, Silurian, Niur Formation, Iran.

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Introduction

The Silurian record of vertebrates from Gondwana is restricted mainly to micro-remains, dissociated fin spines, and dental elements (Lelièvre et al. 1993; Burrow and Turner 2000), plus only one partial articulated specimen, the early teleostome *Yealepis douglasi* Burrow and Young, 1999. Most studies have focused on the eastern regions and include mainly ?Wenlock–Přidoli acanthodians, thelodonts, plus putative placoderm and stem osteichthyan remains from Australia (e.g., Turner and Pickett 1982; Turner 1986; Burrow and Simpson 1995; for a review see Burrow and Turner 2000) and middle Ludlow thelodonts and acanthodians from Irian Jaya (Turner et al. 1995).

Late Silurian faunas comprising mainly acanthodians from western and northern Gondwana, including Middle Eastern peri-Gondwanan terranes, have been little studied (Lelièvre et al. 1993). From western Gondwana, acanthodian and possible heterostracan micro-remains are known from the Late Silurian (Přidoli) of Algeria (Blieck 1982; Blieck et al. 1984) and latest Silurian acanthodian scales and jaw bone fragments from Bolivia (Janvier and Suarez-Riglos 1986). A diverse acanthodian fauna of Ludlow age is described from Portugal (Priem 1910), although Lelièvre et al. (1993) have suggested that this fauna could be younger than Late Silurian.

Silurian thelodont scales from Iran were first reported by Hamedi et al. (1997) from the Niur Formation in the Derenjal Mountains. The stratigraphic age of the scales is still problematic since the stratigraphic position of the sampled horizon was not given. Although never described or illustrated, these scales have subsequently been compared to *Turinia fuscina* (Young in Turner 1997).

The present paper describes an Iranian occurrence of phlebolepidiform and loganelliiform thelodonts; *Niurolepis susanae* gen. et sp. nov. and *Loganellia* sp. cf. *L. grossi* respectively, also from the Niur Formation. This is the first record of these groups in Gondwana and provides new evidence about the distribution of Silurian (Wenlock–Ludlow) faunas in peri-Gondwana. Acid preparation residues also include a few acanthodian micro-remains and were collected by detailed sampling of several horizons (S23, S28, S30, and S32) from a site in the Derenjal Mountains (Fig. 1).

Institutional abbreviations.—AEU, Museum of Azad University, Esfahan, Iran; NHM PM X, Department of Palaeontology, Natural History Museum, London, UK.

Geological setting

The reference section of the Silurian (late Llandovery to Přidoli) Niur Formation is situated on the eastern side of the Dahaneh Kolut Gorge in the south of the Derenjal Mountains, east central Iran (ca. 65 km N of Tabas; Fig. 1A, B), and was

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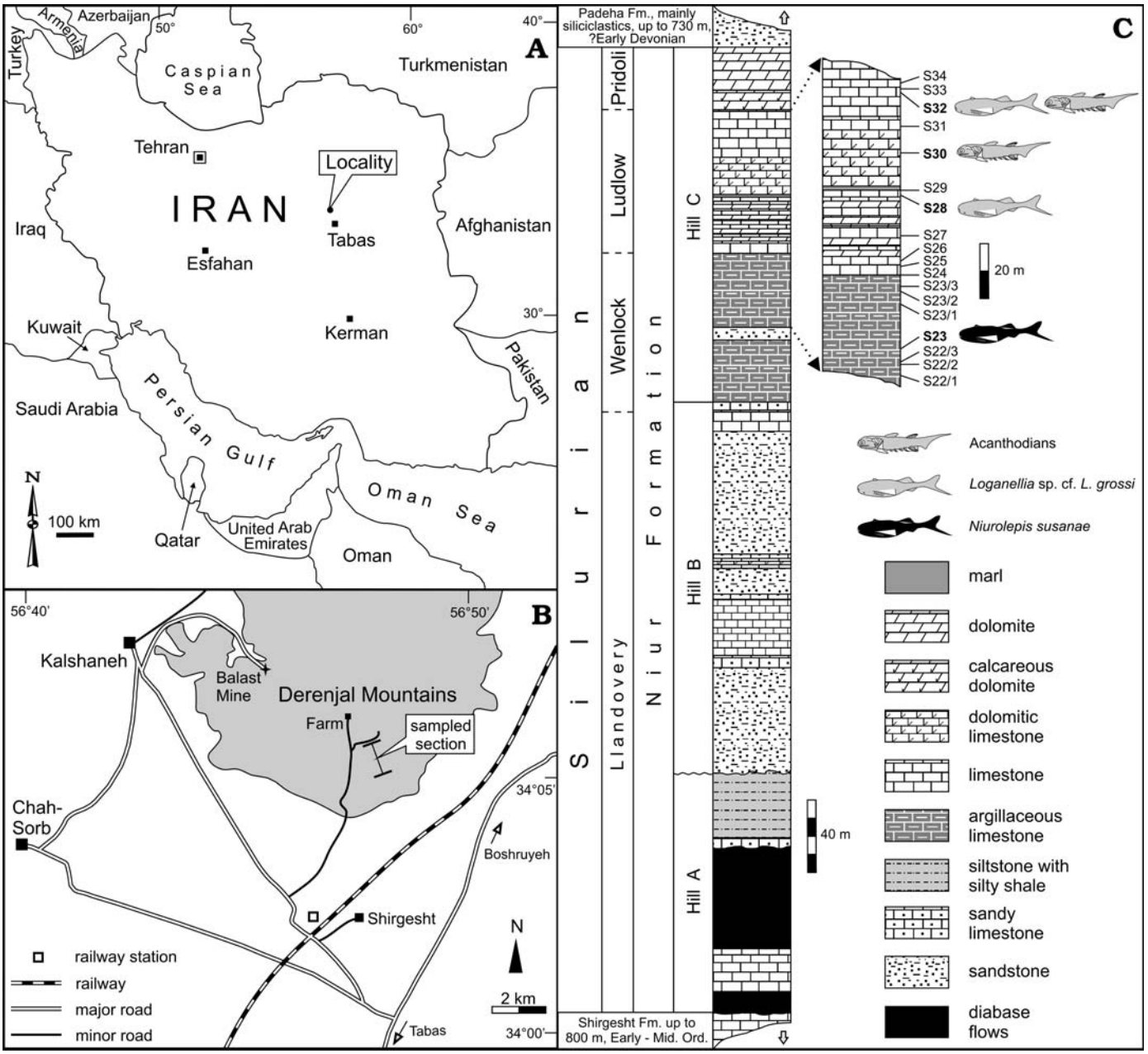


Fig. 1. **A**, **B**. The position of the Derenjal Mountains, north of Tabas, east central Iran, and the sampled section of the Niur Formation. **C**. Composite stratigraphic column of the sampled section showing fish-bearing beds.

first described by Ruttner et al. (1968). The Niur Formation type section in the Ozbak-kuh Mountains (ca. 90 km NE of the reference section) is considered to be faulted in the lower part and mainly composed of carbonates (Ruttner et al. 1968). The Silurian deposits in the reference section are exposed in three major Hills, A, B, and C (Fig. 1C), and combined, are about 550 m thick. The base of the section at Hill A is N 34°05'8.3"; E 56°48'14" at an altitude 1072 m above the sea level. The top of Hill C, close to the tentative boundary between the Niur and Padeha Formations is at N 34°04'44.66"; E 56°48'7.3" at an altitude of 1069 m. Hill A consists in ascending order of volcanic diabase flows of imprecise age (possibly Early Silurian), brown to grey limestones, and siltstones with silty shales which are rich in corals, brachiopods, crinoid ossicles, bryozoans and abundant ostracods. Hill B shows an alternation of sandstones and bioclastic sandy limestones; sometimes limestones yield abundant brachiopods, corals, gastropods, cephalopods, tentaculitids, conodonts, ostracods, and some trilobite fragments. The sequence on Hill C comprises dark grey argillaceous limestones that grade into dolomitic limestones and dolomites, with abundant brachiopods, gastropods, ostracods, and some coral and bryozoan colonies. All the fish-bearing beds are exposed on Hill C.

Although Ruttner et al. (1968) considered the contact between the base of the Niur Formation and the Early–Middle Ordovician Shirgesht Formation to be a transitional bound-

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ary, it is now considered to be faulted (Bruton et al. 2004; Ghobadi Pour et al. 2006). The Niur Formation is conformably overlain by a siliciclastic sequence (mostly sandstones) of the presumed Early Devonian Padeha Formation (Ruttner et al. 1968).

Despite abundant fossils, the Niur Formation of the Derenjal Mountains has remained little studied. Flügel (1969) described stromatoporoids, *Ecclimadictyon* and *Clathrodictyon* from Hills A and C respectively. Flügel and Saleh (1970) reported Llandovery rugose coral faunas of *Grewingkia*, *Schlotheimophyllum*, *Streptelasma, Tenuiphyllum*, *Tryplasma*, and *Paliphyllum*, from Hill A and the limestone beds in the middle part of Hill B; some rugose corals of Ludlow age including *Cystiphyllum* (*Holmophyllum*) and *Gyalophyllum* (*Coronoruga*) were also identified from Hill C. From the lower part of Hill A, Hubmann (1991a) described halysitid corals, including *Halysites*, *Eocatenipora*, and *Catenipora* of Llandovery age. Hamedi et al. (1997) suggested a Llandovery to Přidoli age for the Niur Formation based on preliminary lists of conodonts, ostracods and thelodonts.

Late Wenlock/?early Ludlow.—Sample S23 was collected from a grey sandy bioclastic limestone about 55 m above the base of Hill C. This sample lacked conodonts, but samples S24 and S25, which were collected at 27 m and 30 m above sample S23, contain elements of *Ozarkodina bohemica bohemica* (NHM PM X 3272–3273). This record suggests an age very close to the Wenlock–Ludlow boundary and sample S23 may therefore be of similar age, most probably late Wenlock. A microfacies analysis showed ostracod packstone with abundant quartz grains which is inferred to have been deposited on an inner carbonate ramp, probably in a shallow subtidal environment (Hasan Hejazi, personal communication January 2007).

Late Ludlow.—In sample S28 from a grey crinoid brachiopod packstone with bryozoan colonies, 111.3 m above the base of Hill C, some diagnostic conodonts *Ozarkodina crispa* and *Oz.* cf. *snajdri* (NHM PM X 3268–3270) occur, which suggests a late Ludlow age. Sample S30 was taken from a dolomitic limestone, 15.4 m above sample S28. Pelloid bioclastic packstone is dominated by rich shallow water assemblages of brachiopods and bryozoans. The association of conodonts retrieved from this level (on slide NHM PM X 3267), includes *Oz. crispa*, *Oz.* cf. *confluens*, and *Oz. remscheidensis* ssp. suggesting the late Ludlow. Sample S32 collected from a gastropod packstone/wackestone, at 22 m above sample S30 lacked conodont elements. However, some conodonts identified by Walliser in Ruttner et al. (1968), collected from the uppermost limestone level in Hill C, suggest a late Ludlow age.

Material and methods

Forty two calcareous samples were dissolved in a buffered solution of 10% acetic acid. Four samples (Fig. 1C) yielded fish micro-remains, some of which are particularly rich (S23 and S32). The scales in the residues vary from reddish brown to white and those from samples S28, S30, and S32 are extensively hypermineralised, preventing histological studies. Most specimens are covered with sand grains and calcite blades, which often makes photography and histological thin sectioning difficult. Specimens were picked from the residues using a Nikon SMZ-1 stereo microscope, and stored in cavity slides. All SEM micrographs were taken at the Institute of Palaeobiology, Polish Academy of Sciences (Warsaw, Poland) using a Philips XL 20. Histological studies and relevant photomicrographs were done from thin sections under a Nikon Eclipse E200 POL light-polarizing microscope equipped with a Nikon DS-L1 digital camera. For thin sectioning, the scales were fixed on glass with heated liquid Canada Balsam and one side of the scales polished. Reheating allowed the scales to be turned upside down and polished on the other side. Due to the fragility and the small size of scales, all were polished in water without any oxidised metallic powder.

Systematic palaeontology

Class Agnatha Cope, 1889

Subclass Thelodonti Kiaer, 1932

Order Phlebolepidiformes Berg, 1937

Family Katoporodidae Märss, Wilson, and Thorsteinsson, 2002

Genus *Niurolepis* nov.

Derivation of the name: From Niur Formation, and *lepis* (Greek), scale.

Type species: *Niurolepis susanae* gen. et sp. nov.

Diagnosis.— As for the species, by monotypy.

Stratigraphic and geographic distribution.— Late Wenlock/?early Ludlow; Niur Formation of east central Iran.

Niurolepis susanae gen. et sp. nov.

Figs. 2, 3.

Derivation of the name: After Dr. Susan Turner (Brisbane), in recognition of her contributions to Lower–Middle Palaeozoic agnathan fish studies.

Holotype: AEU 4105, trunk scale (Fig. 2F).

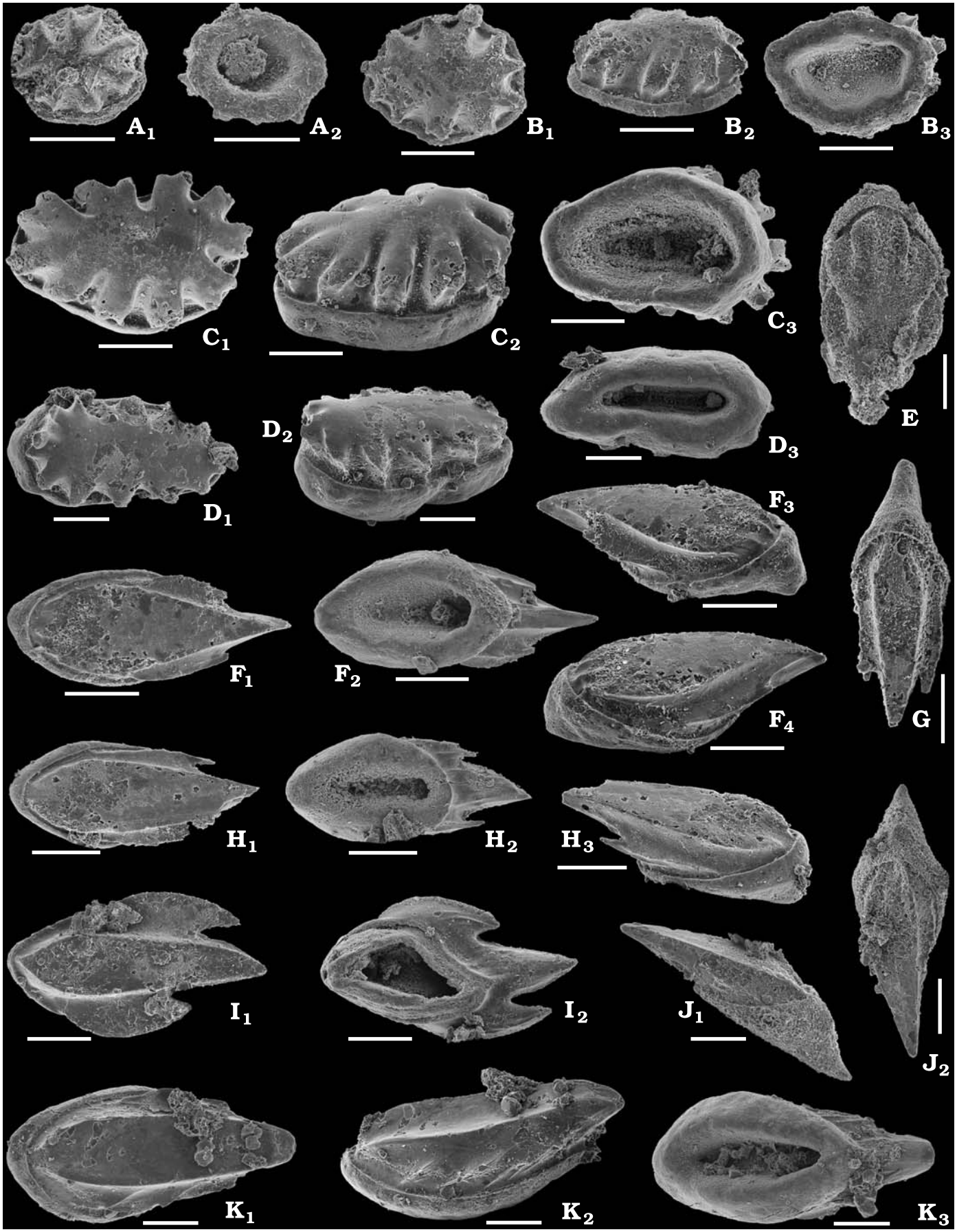
Type locality: Eastern side of the Dahaneh Kolut Gorge, Derenjal Mountains, east central Iran.

Type horizon: S23, grey sandy bioclastic limestone, ca. 55 m above the base of Hill C, reference section of the Niur Formation.

Material.—165 scales from sample S23.

Diagnosis.—Katoporodid with small to medium sized scales (up to 1 mm length); trident-like trunk scales with flat or slightly convex median crown area and one pair of lateral wings (areas); median crown area broad and elevated; lateral wings with posteriorly pointing apices; lower crown surface with fine longitudinal ridges beneath each narrow lateral wing and a median crest. The histological structure is characterised by branched wide dentine canals.

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Description

Morphology.—The morphological varieties recovered include head, transitional and trunk scales. Head scales (0.3–0.8 mm long, 0.25–0.4 mm wide) are rounded or oval, sometimes slightly elongated (Fig. 2A–D). The crown margins are deeply incised and have six to twelve, often bifurcating ribs. The crown surface is smooth and flat in small scales but more convex in elongated forms with a posteriorly elevated area. The neck is low and starts abruptly below the crown with a distinct step. The base varies from low (Fig. 2A, B) to relatively high (Fig. 2C, D). It has a large pulp depression, which is rounded or elliptical in outline.

Transitional scales (0.6–0.9 mm long, 0.4–0.5 mm wide) are fairly rare in residue samples, but one scale (Fig. 2E) shows rounded ribs, bifurcated at the crown anterior margin. The neck is low and the base is shallow with an elliptical pulp depression. An anterior spur is not developed in transitional scales but the base protrudes slightly anteriorly.

The trident-like trunk scales (0.5–1 mm long and 0.3–0.5 mm wide) are diagnostic and are characterised by three distinct crown areas; a raised broad median area and two lateral areas (wings) at a lower level. The flat or slightly convex median area covers three quarters of the crown surface and has a posteriorly pointing apex. The anteriormost part of the median area has two to four very short parallel ridges (e.g., Fig. 2F_3, F_4; AEU 4105); sometimes a shallow notch (e.g., Fig. 2H; AEU 4107) occurs. Each lateral wing has a posteriorly pointed spine and is separated from the median area and the neck by shallow grooves.

The lateral wing with smooth surface extends backwards from the middle of the crown and is rather narrow for most of its length. Behind the spiny end, the lateral wing is reduced to a narrow rim that extends to the crown posterior, just below the main surface of the median crown area (Fig. 2F_3, F_4).

The lower surface of crown has ridgelets that run from anterior of the spines to the posterior part. The lower crown surface also shows a very prominent and wide median crest (Fig. 2F_2, H_2). There is no microsculpture on the crown. The crown is inclined towards the anterior at an acute angle to the base. The neck is shallow and forms a distinct boundary with the base.

In trunk scales, the base is anteriorly protruded, making a single spur that varies in length from short to rather long (Fig. 2F–H, J); there is no additional basal projection. The pulp depression is also elongated, has an elliptical outline, and is situated close to the centre of the scale.

There are some rare additional scale forms in the collection. Only one rare scale seems to have two spines on each lateral wing. An asymmetrical scale shows a relatively narrow and smooth median area with flattened lateral wings and a distinct rim around the basal opening, perhaps from the pectoral or caudal fin regions (Fig. 2I). It has an irregular quadrangular base and an almost triangular pulp depression. The scale (Fig. 2K; AEU 4110) has an elliptical and concave median area lacking lateral wings. Instead, four distinct short ridges on the lateral sides of the crown and neck curve upwards posteriorly; each ridge raised centrally.

Histology.—Scales have branched wide dentine canals, which spring from the pulp depression and the pulp canal (Fig. 3A; AEU 4111). The dentine canals branch to numerous fine dentine tubules in the upper part of crown. The growth lines are distinct (Fig. 3B, C; AEU 4112–4113). The pulp canal is of medium length (1/3–1/4 of the scale length). The uppermost part of the crown is an enamel-like tissue and the boundary with the dentine portion seems to be transitional. A few wide dentine canals are present in the neck region. Tubules of Sharpey's fibres are placed on the base.

Discussion.—The histology of *Niurolepis* is most diagnostic and similar to that of the katoporodid-type structure. It differs from other groups of thelodonts, including typical taxa such as *Shielia* Märss in Märss and Ritchie, 1998, *Paralogania* Karatajātė-Talimaa, 1997, *Chattertonodus* Märss, Wilson, and Thorsteinsson, 2002, *Nikolivia* Karatajātė-Talimaa, 1978, *Canonia* Vieth, 1980, and *Glacialepis* Märss, Wilson, and Thorsteinsson, 2002, by having branched wide dentine canals with openings distributed evenly in the pulp depression. *Niurolepis susanae* gen. et sp. nov. differs from the other katoporodids, *Katoporodus* Turner and Peel, 1986, *Goniporus* Gross, 1967, *Overia* Soehn, Märss, Caldwell, and Wilson, 2001, and *Zuegelepis* Turner in Turner et al., 1999, by having a broader median area, and by lacking well developed and deeply ridged lateral areas. The phlebolepidid genera, *Erepsilepis* Märss, Wilson, and Thorsteinsson, 2002, *Helenolepis* Karatajātė-Talimaa, 1978, and *Phlebolepis* Pander, 1856, which all show histology similar to katoporodids, differ from *Niurolepis* by having numerous ridges on the crown and lacking trident-like trunk scales. *Niurolepis* differs from other morphologically similar shieliid genera such as, *Shielia* and *Paralogania*, by having a wider median area and by lacking spines at the margins of the lateral areas. Scales of nikoliviids, *Chattertonodus* and *Nikolivia* can be distinguished from those of *Niurolepis* as they have nikoliviid-type bases, smooth lower crown surfaces and wider lateral areas. The furcacaudiform *Canonia* has a flattened crown with longitudinally ridged median and lateral areas, a smooth lower crown surface, a relatively high smooth neck

← Fig. 2. The phlebolepidiform thelodont *Niurolepis susanae* gen. et sp. nov. from sample S23, late Wenlock / ?early Ludlow of the Niur Formation, east central Iran. SEM micrographs of scales comprising a morphological set. **A**. Head scale AEU 4100 in crown (A_1) and basal (A_2) views. **B**. Head scale AEU 4101 in crown (B_1), oblique lateral (B_2), and basal (B_3) views. **C**. Head scale AEU 4102 in crown (C_1), oblique lateral (C_2), and basal (C_3) views. **D**. Head scale AEU 4103 in crown (D_1), oblique lateral (D_2), and basal (D_3) views. **E**. Transitional scale AEU 4104 in crown view. **F**. Holotype, trunk scale AEU 4105 in crown (F_1), basal (F_2), and oblique lateral (F_3, F_4) views. **G**. Trunk scale AEU 4106 in crown view. **H**. Trunk scale AEU 4107 in crown (H_1), basal (H_2), and oblique lateral (H_3) views. **I**. Trunk scale AEU 4108 in crown (I_1) and basal (I_2) views. **J**. Trunk scale AEU 4109 in oblique lateral (J_1) and crown (J_2) views. **K**. Trunk scale AEU 4110 in crown (K_1), oblique lateral (K_2), and basal (K_3) views. Scale bars 0.2 mm.

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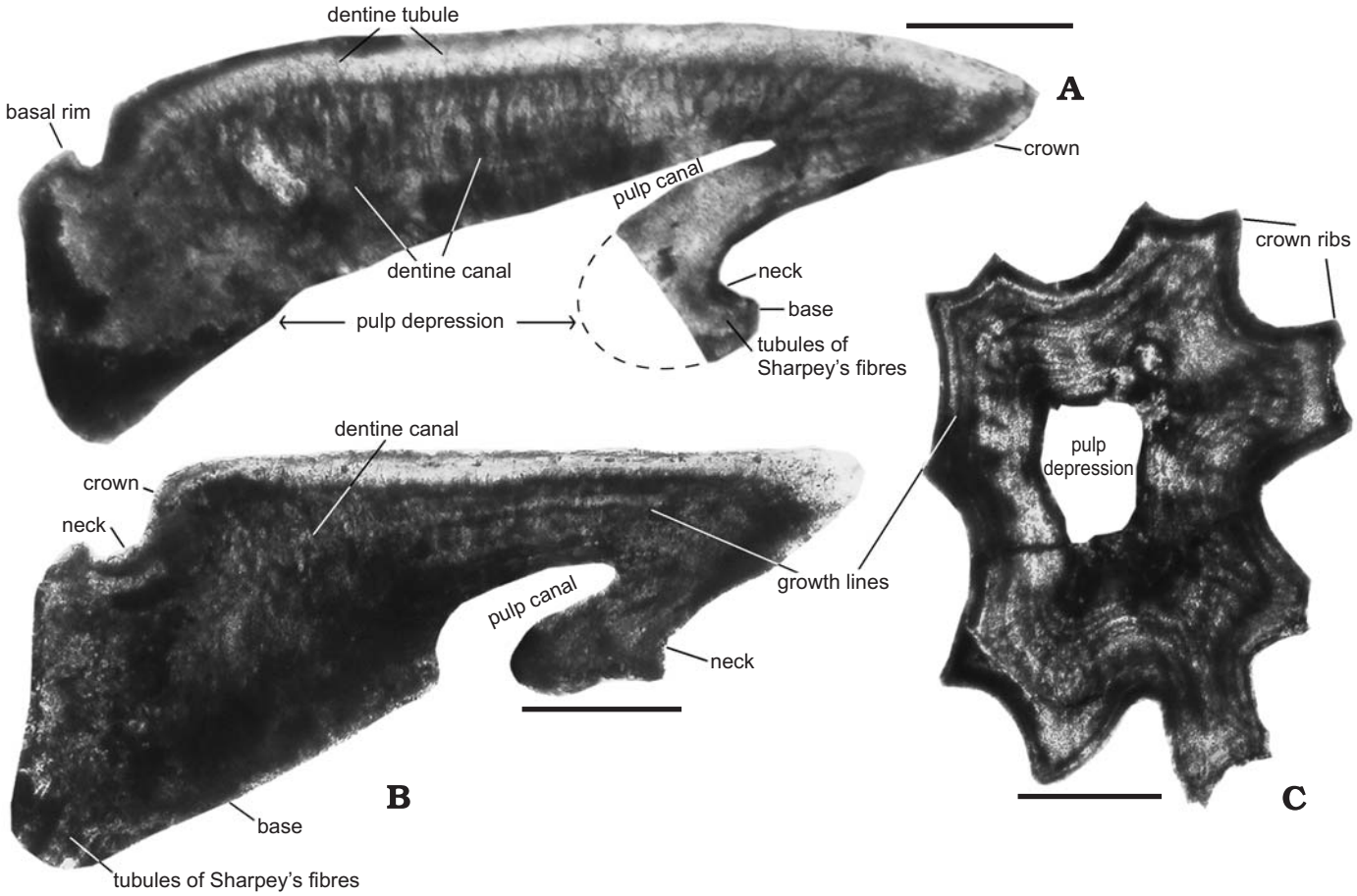


Fig. 3. The phlebolepidiform thelodont *Niurolepis susanae* gen. et sp. nov. from sample S23, late Wenlock / ?early Ludlow of the Niur Formation, east central Iran. Photomicrographs of thin sections. **A**. Vertical longitudinal section of a trunk scale AEU 4111. **B**. Vertical longitudinal section of a trunk scale AEU 4112. **C**. Horizontal section of a head scale AEU 4113. Scale bars 0.2 mm.

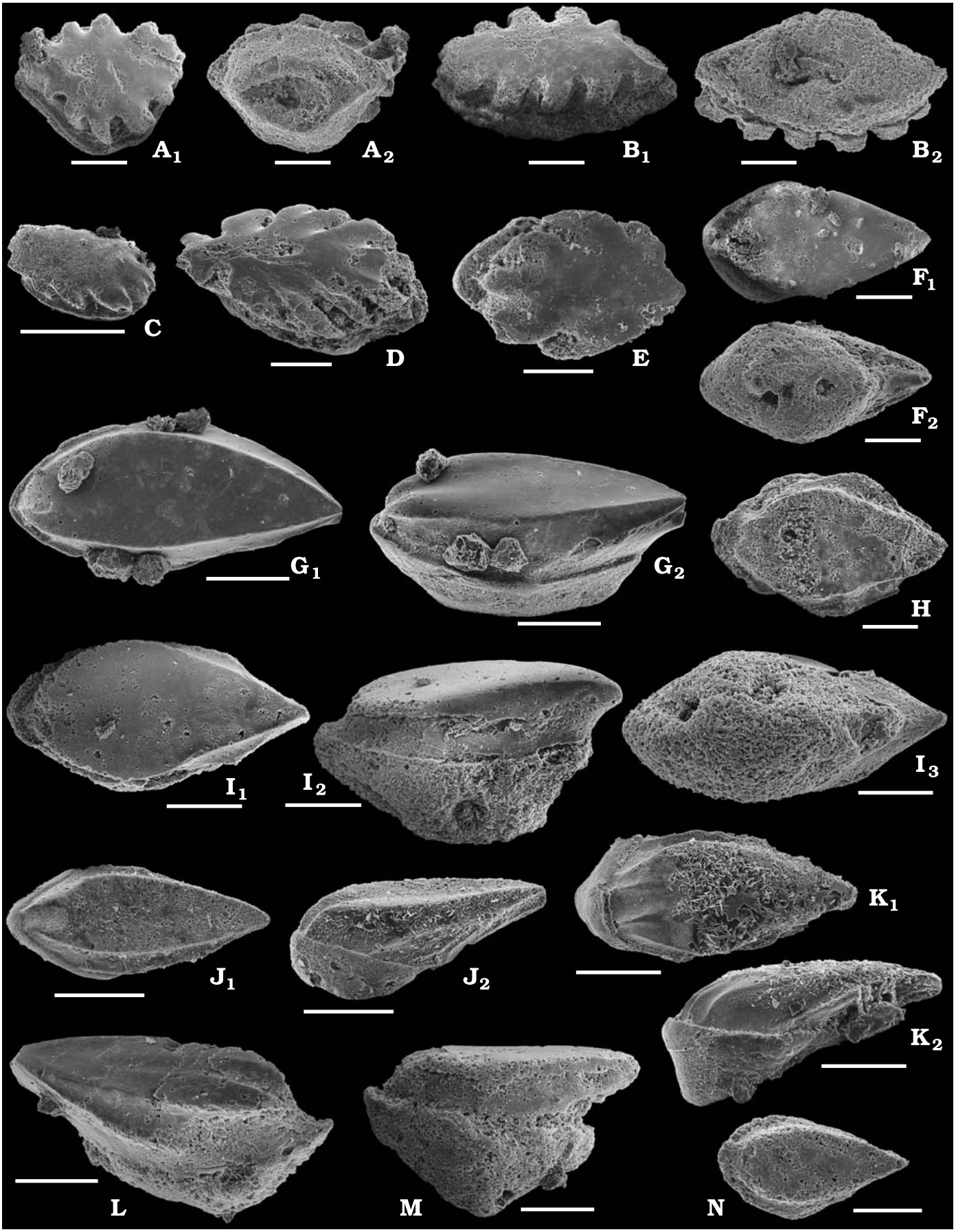
and a different base of low collar form around the pulp depression. *Niurolepis* differs from the talivaliid *Glacialepis* in having a narrower median area with spiny lateral wings, and ridged lower crown surface.

The southern hemisphere taxon, *Turinia fuscina* Turner, 1986 (figs. 2B–H, K–U; 3F) from the Late Silurian (most probably Ludlow–Přidoli; see also Burrow and Turner 2000 for age constraints) of the Silverband Formation, western Victoria, Australia is morphologically very similar to *N. susanae*. Like the Iranian scales, head and transitional scales show identical structure, and its trunk scales have a distinctly raised, wide median area on the crown with longitudinal lateral wings, but as Turner (1986: 58) stated, the lateral wings apparently do not reach the crown posterior. It seems that, the anteriormost part of the median area in eighteen paratypes of *T. fuscina* is smooth. Two scales illustrated by Turner (1986: figs. 2Q and 3F) seem to have more than two lateral wings. The histological structure of *T. fuscina* was not preserved, but Turner (1986) suggested based on broken scales that they may have turiniid-type histology. The morphological resemblances between *T. fuscina* and *N. susanae* may suggest that these two species are closely related and may be considered congeneric. However, such conclusion can only be drawn if both can be shown to have identical histological structures.

Among taxa recently described from the northern hemisphere, *Niurolepis susanae* shows similarities to those from the Early Devonian (Lochkovian) of the Ben Nevis Formation of Spitsbergen which Blom and Goujet (2002) attributed to a new species, *Turinia barentsia*. Like the Iranian specimens, its trunk scales have a distinctly raised, and anteriorly inclined

Fig. 4. The loganelliiform thelodont *Loganellia* sp. cf. *L. grossi* Fredholm, 1990 from late Ludlow of the Niur Formation, east central Iran. SEM micrographs of scales comprising a morphological set. Sample S32 (**A**, **B**, **D**–**F**, **H**, **I**, and **L**–**N**) and sample S28 (**C**, **G**, **J**, **K**). **A**. Head scale AEU 4114 in crown (A_1) and basal (A_2) views. **B**. Head scale AEU 4115 in oblique crown (B_1) and basal (B_2) views. **C**. Transitional scale AEU 4116 in oblique crown view. **D**. Transitional scale AEU 4117 in crown view. **E**. Transitional scale AEU 4118 in crown view. **F**. Trunk scale AEU 4119 in crown (F_1) and basal (F_2) views. **G**. Trunk scale AEU 4120 in crown (G_1) and oblique lateral (G_2) views. **H**. Trunk scale AEU 4121 in crown view. **I**. Trunk scale AEU 4122 in crown (I_1), lateral (I_2), and basal (I_3) views. **J**. Trunk scale AEU 4123 (most probably from the fin regions) in crown (J_1) and lateral (J_2) views. **K**. Trunk scale AEU 4124 in crown (K_1) and lateral (K_2) views. **L**. Trunk scale AEU 4125 in oblique lateral view. **M**. Trunk scale AEU 4126 in lateral view. **N**. Trunk scale AEU 4127 (most probably from the fin regions) in crown view. Scale bars 0.2 mm. →

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median area of the crown supported by two lateral wings, but the anterior median and lower crown areas are smooth. In some figured scales (Blom and Goujet 2002: pl. 2: 6, 7, 9), sometimes the lateral wing outwardly developed a flattened segment, midway to the crown posterior. Also, the base is oval and did not produce a spur, although to some extent, it protruded anteriorly. As with most turiniids, *Turinia barentsia* is also significantly larger than *Niurolepis susanae*.

There are other Early Devonian smooth forms of *Turinia* with a wide geographic distribution which can be compared to *N. susanae*. *T. pagei* (Powrie 1870) differs from the Iranian scales in having crenulated lateral wing margins, a ridged neck and a much longer basal process (e.g., Karatajūtė-Talimaa 1978). Scales of *T. polita* Karatajūtė-Talimaa 1978 have a smooth neck and an undivided crown surface with serrated margins, a smooth lower crown with median crest, and a deeper base (Karatajūtė-Talimaa 1978; Märss et al. 2006). Histologically, scale crowns of these early *Turinia* species (including *T. barentsia*) differ from those of the Iranian *Niurolepis* in having turiniid-type characters, with long straight and narrow dentine tubules that are often wider near the pulp cavity and pocket-like hollows.

Order Loganelliiformes Turner, 1991

Family Loganelliidae Märss, Wilson, and Thorsteinsson, 2002

Genus *Loganellia* Fredholm, 1990

Type species: *Thelodus scoticus* Traquair, 1898; Patrick Burn Formation, Priesthill Group, upper Llandovery, southern Scotland.

Loganellia sp. cf. *L. grossi* Fredholm, 1990

Fig. 4.

Material.—Seven scales from sample S28, 314 scales from sample S32, late Ludlow, Niur Formation, Derenjal Mountains, east central Iran.

Description

Morphology.—The collection from the Niur Formation contains all the main scale varieties. The head and transitional scales that dominate the collection, range from 0.15 to 0.9 mm in length, are rounded or elongate in outline, with a flat or convex crown surface and deeply crenulated margins (Fig. 4A–E; AEU 4115–4118). Diagnostic trunk scales (0.5–0.8 mm long and 0.3–0.4 mm wide) are characterised by a smooth rhomboidal outline and a flat or slightly convex crown (Fig. 4F–I, L–N; AEU 4119–4122, 4125–4127). A deep downward notch occurs at the anterior of the crown. Sometimes two short ribs appear on each side of the deep notch at the beginning of a wider crown anterior (Fig. $4K_1$). A postero-laterally downstepped lateral rim runs each side of the crown, extending at least two thirds the length of the crown. The posterior end of the crown is pointed. Possible fin scales (Fig. 4J, N) are smaller, and have a narrower crown. Scales have a deep base with one (Fig. $4A_2$), two (Fig. $4B_2$) or three pulp openings (Fig. $4F_2$). Some irregularly placed hollows (Fig. $4I_2$, I_3) are situated on the lateral side of the base which seem to be taphonomic artefacts.

Histology.—Due to poorly preserved material, histological studies have not been undertaken, but a pulp canal can be recognised in some examined thin sections.

Discussion.—The set of scales from the Niur Formation described here is similar to the type material of *Loganellia grossi*, from the Wenlock of the Slite Beds of Gotland, Sweden (Fredholm 1990; redescribed by Märss 1996) in most details of the crown structure of trunk scales, including the anterior notch. The specimens from the Baltic region, including those from Estonia (Märss 1996), differ from the Iranian specimens in having a shallower base.

Scales from the Samoilovich Formation of October Revolution Island, Severnaya Zemlya (Märss and Karatajūtė-Talimaa 2002), the Cape Philips Formation of Canadian Arctic Archipelago (Märss et al. 2006), and the Kap Moton Formation of Washington Land, north Greenland (Blom 1999), all of Wenlock age, have also been assigned to *L. grossi*. However, the Russian and the Canadian specimens differ from the Iranian scales in having a shallower anterior notch, a wider crown, and better developed lateral rims (Märss and Karatajūtė-Talimaa 2002: figs. 2N–S; Märss et al. 2006: pl. 3: 14, 15). A median posterior crest on the lower crown surface is also recognised in the north Greenland material (Blom 1999: fig. 3.3) and is not seen in the material described here.

Indeterminable acanthodians

Fig. 5.

Material.—Two scales and a jaw bone fragment from sample S30, nine scales from sample S32, late Ludlow, Niur Formation, Derenjal Mountains, east central Iran.

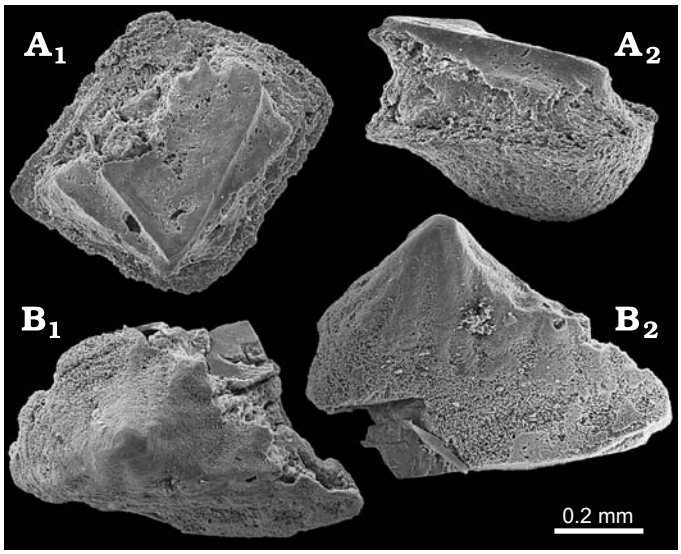


Fig. 5. Indeterminable acanthodians, SEM micrographs of micro-remains from sample S30, late Ludlow of the Niur Formation, east central Iran. **A**. Scale AEU 4128 in crown (A_1) and lateral (A_2) views. **B**. ?dentigerous jaw bone fragment AEU 4129 in occlusal (B_1) and lateral (B_2) views.

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Discussion.—These findings are the first illustrated acanthodians from the Silurian of Iran and the Middle East. The scales are of climatiid-type and have a diamond-shaped crown with a distinct neck (Fig. 5A; AEU 4128). The anterior part of the crown of the best preserved scale is badly damaged, so the positions of the anterior ridges are unknown. The crown slopes anteriorly toward the protruding base, which is deep anteriorly and shallow posteriorly, and separated from the neck by a pronounced rim.

One specimen (Fig. 5B; AEU 4129) is possibly a fragment of dentigerous jaw bone, in which a triangular tooth is ankylosed to the bone. The tooth is damaged or worn, but shows a semicircular horizontal section and irregular radial ridges.

Histological studies have not been attempted on these poorly preserved micro-remains.

Palaeobiogeographic significance

In the palaeogeographic reconstruction of Cocks and Torsvik (2002: fig. 8) for the late Early–Late Silurian, the Iranian terranes including central Iran (Lut), Alborz, Sanand and Zagros terranes were placed at 15–30° S palaeolatitude, composing Middle Eastern peri-Gondwanan/Gondwanan terranes (Fig. 6). East of central Iran, a vast shelf with a carbonate-siliciclastic sedimentation regime was formed whereas the Zagros and Sanand terranes were considered to be attached to the northern margin of Gondwana, showing lithological and faunal similarities to that of the Saudi Arabian domain (e.g., Lüning et al. 2000; Rickards et al. 2000; Ghavidel-Syooki and Winchester-Seeto 2004; Wendt et al. 2002, 2005; Ruban et al. 2007).

Loganelliiform and phlebolepidiform thelodonts have previously only been recorded from nearshore to outer shelf marine environments of Siberia, Tuva, northwestern Mongolia, Laurentia (Turner 1999); in Baltica thelodonts have been documented from lagoonal to "slope" (probably distal shelf) deposits (Märss and Einasto 1978). The stratigraphically important Wenlock species, *Loganellia grossi* Fredholm, 1990 was widely distributed, on the Kara terrane (Severnaya Zemlya), Laurentia (Canadian Arctic and north Greenland), and Baltica (Norway, Sweden, and Estonia), embracing ca. 15° N and S from equator (Fig. 6). Similar forms as *L.* cf. *grossi* were also recorded from the early–?middle Ludlow (Gorstian–?lower Ludfordian) strata of the Cape Phillips Formation in Canadian Arctic Archipelago by Märss et al. (2006). *Loganellia* sp. cf. *L. grossi* has been reported here in the late Ludlow strata of east central Iran, and provides new biogeographic information. It gives definitive evidence for the southward dispersal pattern of *Loganellia*, down to the shelves of the peri-Gondwana margin. It may be that Baltica (or south Laurentia) and northwestern Gondwana were closer than has been shown in most late Early–Late Silurian reconstructions, thereby allowing thelodonts to migrate possibly via carbonate platforms or mid-ocean islands, under palaeoclimatically controlled conditions.

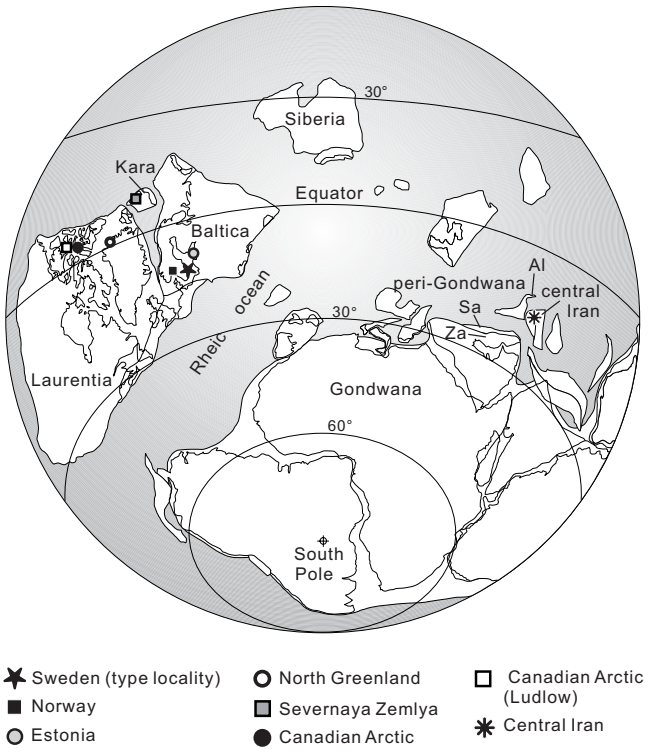


Fig. 6. The distribution of *Loganellia grossi* in Laurentia, Baltica, and Kara; *Loganellia* sp. cf. *L. grossi* in Canadian Arctic and the central Iranian terrane of peri-Gondwana in the Wenlock–Ludlow (base map from Cocks and Torsvik 2002, with modifications). Source of records: Wenlock—Severnaya Zemlya: Märss and Karatajūtė-Talimaa (2002); Canadian Arctic: Märss et al. (2006); North Greenland: Blom (1999), Norway and Sweden (type locality): Turner and Turner (1974), Fredholm (1990); Estonia: Märss (1986, 1996). Early–?middle Ludlow—Canadian Arctic: Märss et al. (2006). Late Ludlow—central Iran: this paper. Abbreviations: Al, Alborz; Sa, Sanand; Za, Zagros.

Probably the migration involved crossing the narrowed Rheic Ocean from Baltica (or southern Laurentia) to and along the North African shorelines and south European peri-Gondwanan/Gondwanan terranes. Further migration towards the east then allowed the migrating thelodonts to inhabit the shallow carbonate bank environments of the central Iranian terrane.

Another possibility is that the detached central Iranian terrane may have been further northwest from peri-Gondwana. This seems unlikely as there is currently no other reliable faunal or palaeomagnetic evidence. Future studies may shed more light on Silurian thelodont communities, particularly those from the northwestern and northern Gondwana margins, and will facilitate a better understanding of their biogeographic patterns.

Evidence from other fossil groups is also consistent with that of the thelodonts. During the Late Silurian–Early Devonian, the Rheic Ocean was not a major barrier against faunal and floral exchanges between southern Laurentia and north Gondwana. Marine and non-marine biogeographic patterns based on spores, macroplants, chitinozoans, acritarchs, brachiopods, and trilobites indicate broad similarities and sup-

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port that the Rheic Ocean separating southern Laurentia and northwestern Gondwana narrowed in the Late Silurian and Early Devonian (e.g., Wellman and Gray 2000; Boucot and Blodgett 2001; Richardson et al. 2001; Le Herisse 2002; Jaglin and Paris 2002; Rubinstein and Steemans 2002; Fortey and Cocks 2003; Raymond et al. 2006).

Studies on the halysitid coral, *Catenipora* with its species from the Niur Formation also suggested palaeobiogeographic relationships between north Gondwana and Laurussian terranes (Hubmann 1991a, b; Flügel and Hubmann 1993). Recent work on a Late Silurian actinocerid and orthocerid cephalopod fauna from south central Iran also revealed a close palaeobiogeographic affinity with northeastern Laurentia (Niko et al. 1999; see also Dastanpour et al. 2006 for the revised stratigraphic position and its probable age), although nautiloids had a trans-oceanic migration capability.

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