

Early Frasnian acanthodians from central Iran

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Two vertebrate-bearing horizons in the basal Frasnian carbonate of the Chahriseh section, northeast of Esfahan, yielded microremains of thelodonts, placoderms, acanthodians, actinopterygians, chondrichthyans, and sarcopterygians, considerably expanding the vertebrate faunal list for the strata. Acanthodians comprise a diverse association of climatiids, diplacanthids, and ischnacanthiforms, including the previously recorded climatiid *Nostolepis* sp. cf. *N. gaujensis*, as well as one new climatiid genus and several taxa left in open nomenclature. Climatiid *Iranolepis ginteri* gen. et sp. nov. is diagnosed by having scales with a highly raised medial crown area separated by steep slopes from lateral crown areas; an odontocytic mesodentine of maximum extent in the crown, distinguished by extensive network of fine canaliculi with abundant tiny osteocytes; and a poorly developed strangewebe system. Other scales with fan-like symmetrically grooved crowns conform to the *Diplacanthus*-type histologically, and have many characters in common with *Milesacanthus antarctica* from the Aztec Siltstone of Antarctica. Osseous gnathal elements include mesodentulous tooth whorls from an ischnacanthiform or climatiid, and ischnacanthiform jaw bones with large chambers for vascular canals, distinctly separated cylindrical tooth cusps along the lingual ridge, and wide-based, triangular, weakly striated cusps on the main lateral ridge. The acanthodian association, accompanied by the Frasnian conodonts of the middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* zones and zonal thelodonts *Turinia hutkensis* and *Australolepis seddoni*, is proving useful for biostratigraphy, showing similarities with assemblages from both Gondwana and the Old Red Sandstone Continent.

Key words: Acanthodii, Ischnacanthiformes, Climatiidae, Diplacanthidae, scales, dental elements, histology, Devonian, Frasnian, Iran.

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Introduction

The Chahriseh section of the Upper Devonian sedimentary sequence (c. 55 km northeast of Esfahan; N 32°59', E 52°3'; Fig. 1), was first examined in the 1970s (e.g., Djafarian and Brice 1973; Zahedi 1976). The area constitutes the western sector of the central Iran structural zone and is confined to the east of Zagros Range. Most of the faults are predominantly oriented NW-SE, parallel to the main Zagros thrust fault (Zahedi 1976). In recent years, this fossiliferous section was the most interesting locality featured in several palaeontological and sedimentological works (e.g., Brice and Kebria-ee 2000; Mistiaen and Gholamalian 2000; Mistiaen et al. 2000; Safari and Kangazian 2003). The succession commences with a few meters of shallow water carbonates, gradating into thick siliciclastics and shallow water carbonates alternating with shale beds, ranging from basal Frasnian to almost the top of the Famennian (Gholamalian 2003; Yazdi et al. 2000). The Upper Devonian strata are overlain unconformably by a Permian mixed carbonates-siliciclastic sequence (e.g., Yazdi et al. 2000). The vertebrate remains were reported by Hairapetian and Gholamalian (1998), and Turner et al. (2002) described

thelodont (*Turinia hutkensis* Blicek and Goujet, 1978, *Australolepis seddoni* Turner and Dring, 1981) and acanthodian (*Nostolepis* sp. cf. *N. gaujensis*) scales from the basal part of an unnamed formation in the section.

Further investigations have provided additional, more diverse material from these bone beds (samples GI4 and H1 in Fig. 2), as documented in the present study. Besides numerous acanthodian microremains published here, the samples (particularly GI4) are also quite rich in thelodont scales (*Turinia hutkensis* and possibly *Australolepis seddoni*), placoderm scales and bone fragments (?*Holonema* sp. and probably a bothriolepid), actinopterygian scales (*Moythomasia* sp. and *Orvikuina*-like scales), as well as chondrichthyans (omalodontiform and phoebodontiform teeth) and sarcopterygian scales, teeth, tooth plates and bone fragments (porolepiform and dipnoan).

Based on some shallow water conodonts from sample H1, the age of this assemblage is determined as middle *Mesotaxis falsiovalis*–*Palmatolepis hassi* zones (Turner et al. 2002); the upper level (GI4) did not yield any conodont elements. Ghavidel-Syooki (2001) used some diagnostic miospores and acritarchs to confirm an early Frasnian age for

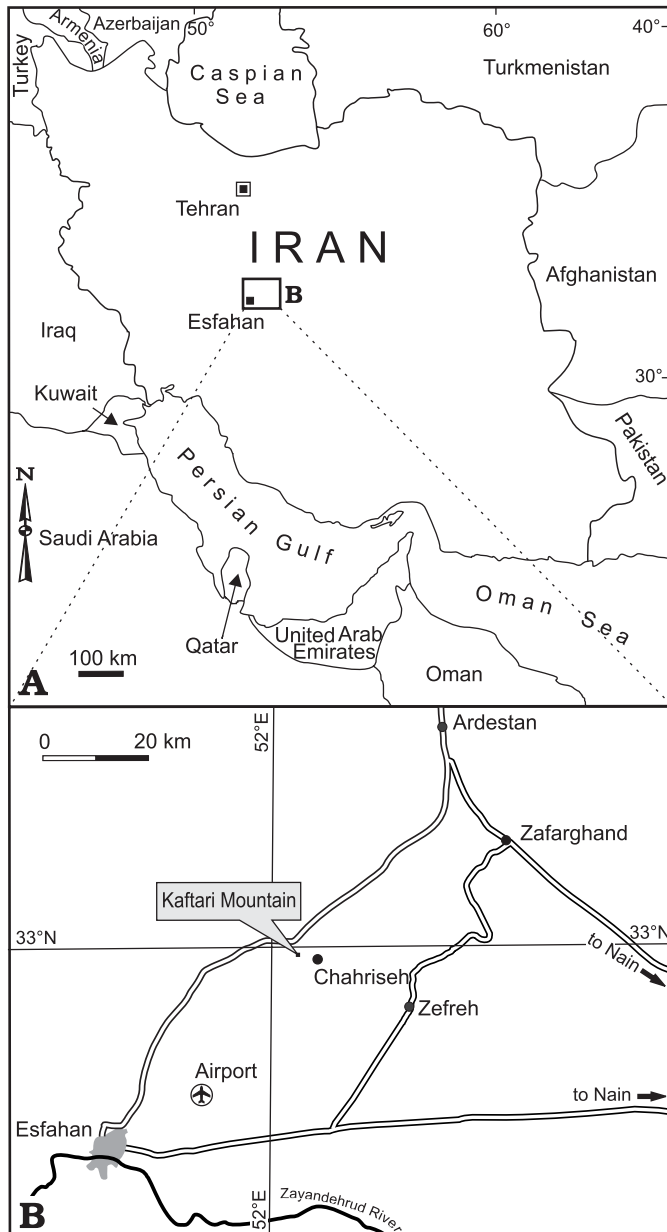


Fig. 1. Map of Iran (A) and close-up of the Chahriseh area showing location of the Kaftari Mountain section (B).

these fish bearing beds. From base to top, the lithology of this carbonate shows a shallowing trend. The microfacies of levels examined are characterised by bioclastic wackestone to mudstone (H1) and bioclastic packstone (GI4). Gyrogonites of *Sycidium*, the only known charophyte from the shallow-marine open shelf setting, are found in both horizons and one higher horizon (Monique Feist in Mistiaen et al. 2000). Associations of thelodonts and “nostolepid” acanthodians also suggest a shallow water environment (e.g., Turner 1999). Taking these lithological and palaeoecological data into consideration, the palaeoenvironmental interpretation is that both horizons were formed on a shallow shelf or even in a marginal marine environment in proximity to an emerged land mass during the early Frasnian.

Institutional abbreviations.—AEU, Museum of Azad University, Esfahan, Iran; EUIV, University of Esfahan, Esfahan, Iran; LIGG, Institute of Geology and Geography, Vilnius, Lithuania.

Material and methods

The calcareous samples were dissolved in a buffered solution of 10% acetic acid. Specimens were picked from the residues using a stereo microscope and stored in cavity slides. Most SEM photographs were taken in Esfahan with a Leica 360 Scanning Electron Microscope and a few were taken in the Institute of Palaeobiology PAN (Warsaw) using a Philips XL 20. Thin sections were made from selected specimens. The scales in particular are hypermineralised, multiply fractured (up to 14 diagonal cracks per 1 mm), and bored by fungal hyphae, hampering histological studies. These micro-cracks could have formed under the local tectonic activities along a fault where Upper Devonian deposits are in a sharp contact with Oligocene–Miocene fossiliferous marls and limestones.

Systematic palaeontology

Class Acanthodii Owen, 1846

Order Climatiformes Berg, 1940

Family Climatidae Berg, 1940

Genus *Iranolepis* nov.

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

Type species: *Iranolepis ginteri* gen. et sp. nov.

Diagnosis.—Climatiid acanthodian with medium to large (0.5–1.5 mm wide) scales. *Iranolepis* differs from all other climatids (for which scale structure is known) in having scale crowns with a highly raised, centrally depressed medial area bordered by steep slopes and separated from the lower lateral areas with all areas extending the entire crown length. It differs from *Nostolepoides*, *Tareyacanthus*, and *Cheiracanthoides* in having a low scale neck with large pores along the neck-base junction, and from *Nostolepis*, *Tareyacanthus*, *Endemolepis*, *Paranostolepis*, *Minioracanthus*, and *Euthacanthus* in having a rounded rhomboidal base which is shallow posteriorly and deep anteriorly, and protruding in front of the crown, and in having a different strangewebe system with short, narrow stranglakunae, weakly developed in the posterior crown part. It differs from *Nostovicina* and *Paranostolepis* in having odontocytic mesodentine forming a dense network of fine canaliculi incorporating abundant osteocytes in all growth lamellae of the central and anterior crown parts. *Iranolepis* differs from *Canadalepis*, *Minioracanthus*, *Watsonacanthus*, *Eifellepis*, *Hanilepis*, *Laliacanthus*, *Taimyrolepis*, and *Lijiangichthys* in having a vascular system comprising ascending, circular and radial canals in scale crown, and to those genera plus *Paranostolepis*, *Nosto-*

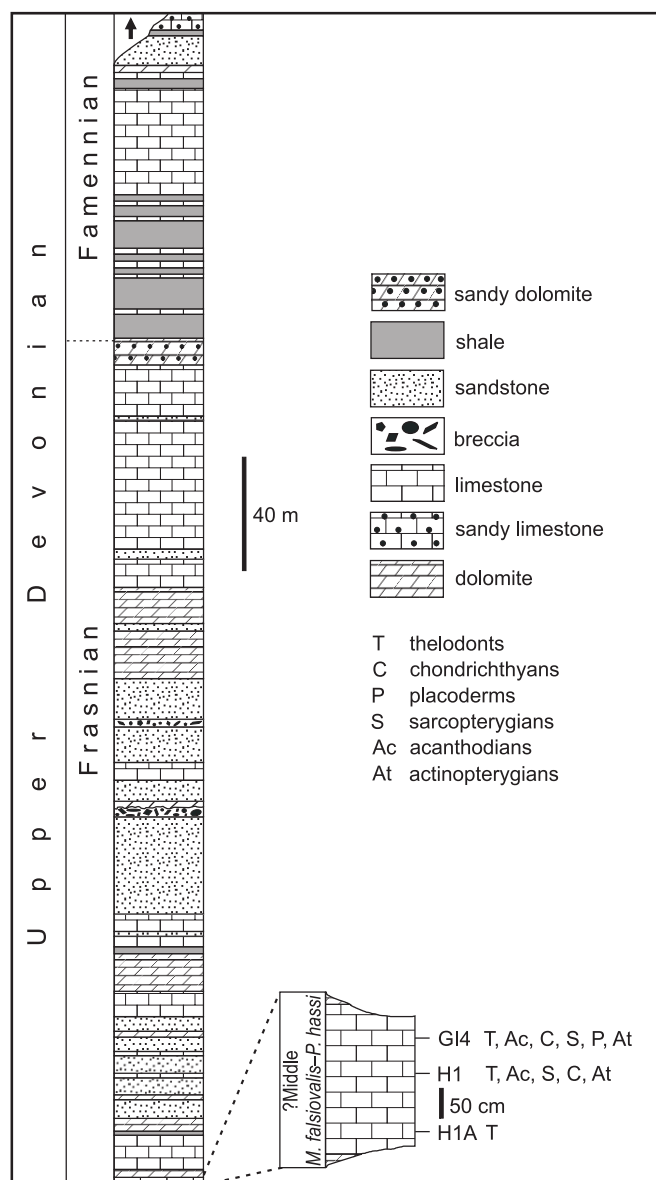


Fig. 2. Simplified stratigraphic column of the Chahriseh area with a magnification of the basal Frasnian deposits and position of acanthodian-bearing horizons H1 and GI4.

lepis, *Wetteldorfia*, and *Canadalepis* in having stranggewebe. It also differs from *Canadalepis* in having bundled rather than separate Sharpey's fibres.

Age and geographic distribution.—Late Devonian, early Frasnian, middle *Mesotaxis falsovalis* to *Palmatolepis hassi* conodont zones; unnamed formation of central Iran.

Iranolepis ginteri gen. et sp. nov.

Figs. 3, 4.

Holotype: AEU 301, flank scale (Fig. 3A).

Type locality: Chahriseh section, Kaftari Mt., central Iran.

Type horizon: GI4, the middle *Mesotaxis falsovalis* to *Palmatolepis hassi* conodont zones.

Derivation of the name: For Michal Ginter, in recognition of his work on teeth of Palaeozoic vertebrates.

Material.—Three scales from sample H1, 33 scales from sample GI4.

Diagnosis.—As for the genus *Iranolepis* gen. nov., by monotypy.

Description

Morphology.—All specimens examined are medium to large-sized, and identified as flank scales. The crowns are slightly elliptical, 0.6–1.7 mm long and 0.5–1.5 mm wide. A few scales have an elongated rhomboidal crown. Inclination of the crown plane varies from flat, to down sloped anteriorly toward the protruding base. An elliptical, highly raised medial area forms most of the crown plate; it is separated by steep slopes from the narrower lateral areas (Fig. 3A₁; AEU 301). Medial and lateral areas reach the posterior crown tip. The medial area is often shallowly depressed centrally and may carry one short anteriormost ridgelet. Rarely, the central depression is deep and furrow-like (Fig. 3C; AEU 303). Lateral crown areas are generally smooth, without ridges even along the anterior edge. A pair of additional weakly expressed oblique neck ridges may be present symmetrically on both sides of scales (Fig. 3A₃). Scale neck is slightly concave, decreasing from a medium height posteriorly to almost negligible where the anterior edge of the crown reaches the base. The lowermost neck has a row of large pores, with up to four opening on each lateral face at the base-neck junction (Fig. 3A₃, B₂). Scale bases are rounded rhomboidal, or rarely asymmetric rhomboidal, and separated from the anterior crown edge by a pronounced rim. Bases are shallow posteriorly (sometimes transversely concave), deepening to convex anteriorly and protruding beyond the crown antero-laterally, with the deepest point in front of or just below the anterior edge of the crown.

Histology.—The crown has up to six superpositional growth lamellae (Fig. 4D; EUIV 411), composed of odontocytic mesodentine (this mesodentine type with lacunae we distinguish to separate it from the syncitial mesodentine lacking lacunae: Karatajūtė-Talimaa and Smith 2003; Valiukevičius and Burrow 2005) and stranggewebe. Mesodentine is characterised by a dense network of fine, narrow and winding dentinal canaliculi (Fig. 4B₁, B₃; LIGG 3804) which extend from all sides of the abundant and small polygonal odontocytes. Odontocytes are large in the lower crown (neck) only, and are abundant in all growth zones (though fewer in the youngest lamellae). In the outer parts of the lamellae, canaliculi are mostly directed superficially (Fig. 4C₂; LIGG 3805), durodentine (*sensu* Gross 1971) is lacking. Stranggewebe is only present low in the posterior part of the crown/neck, and not in the primordial growth zone. The stranglakunae are short and narrow, and comparatively densely packed (Fig. 4C₁, D). Scales with reasonable preservation show wide, long radial vascular canals at the base-crown/neck junction and single branches of ascending and circular canals positioned in the inner/basal parts of growth zones (Fig. 4A). Scale bases are composed of highly cellular bone, and osteocyte cavities

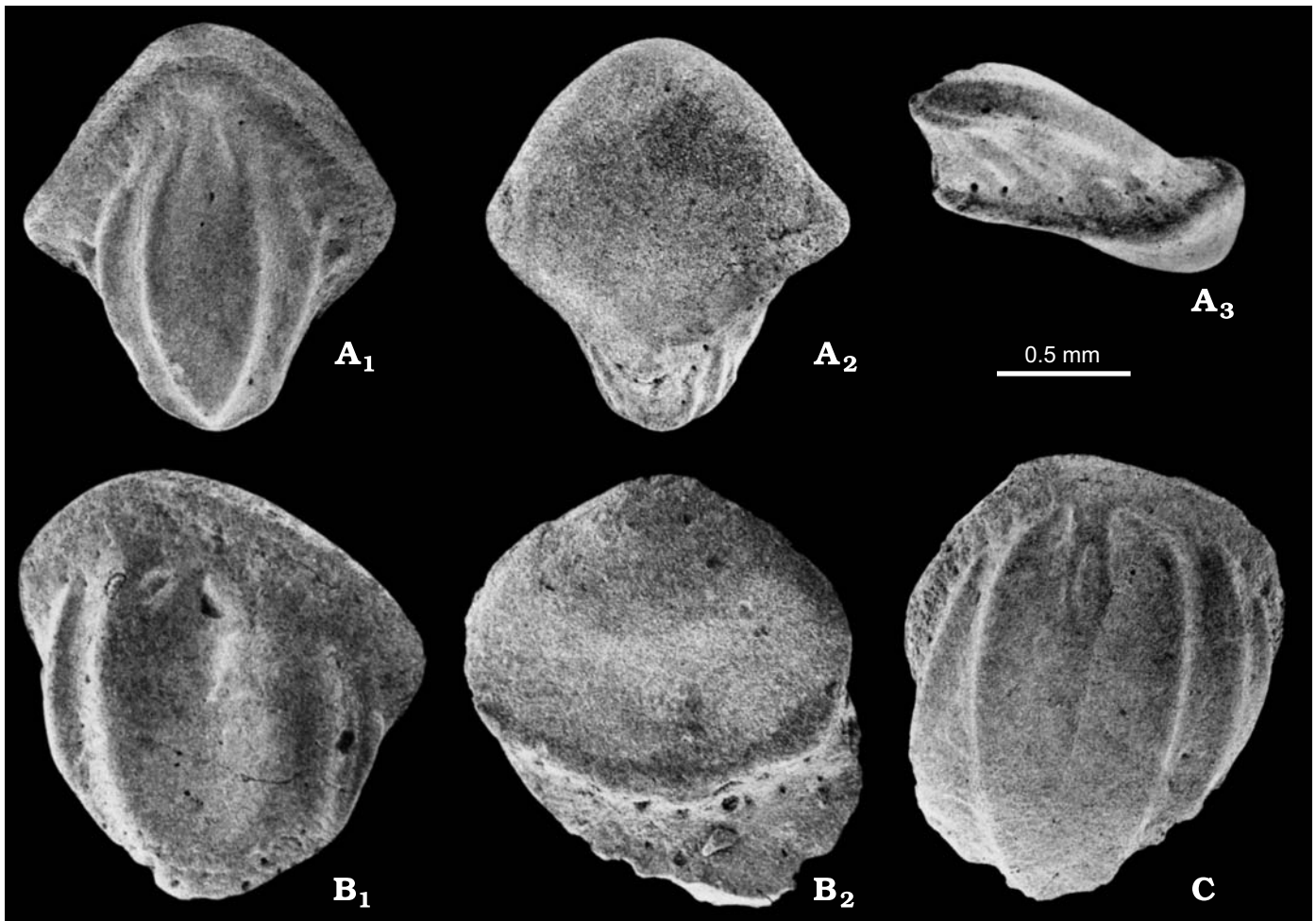


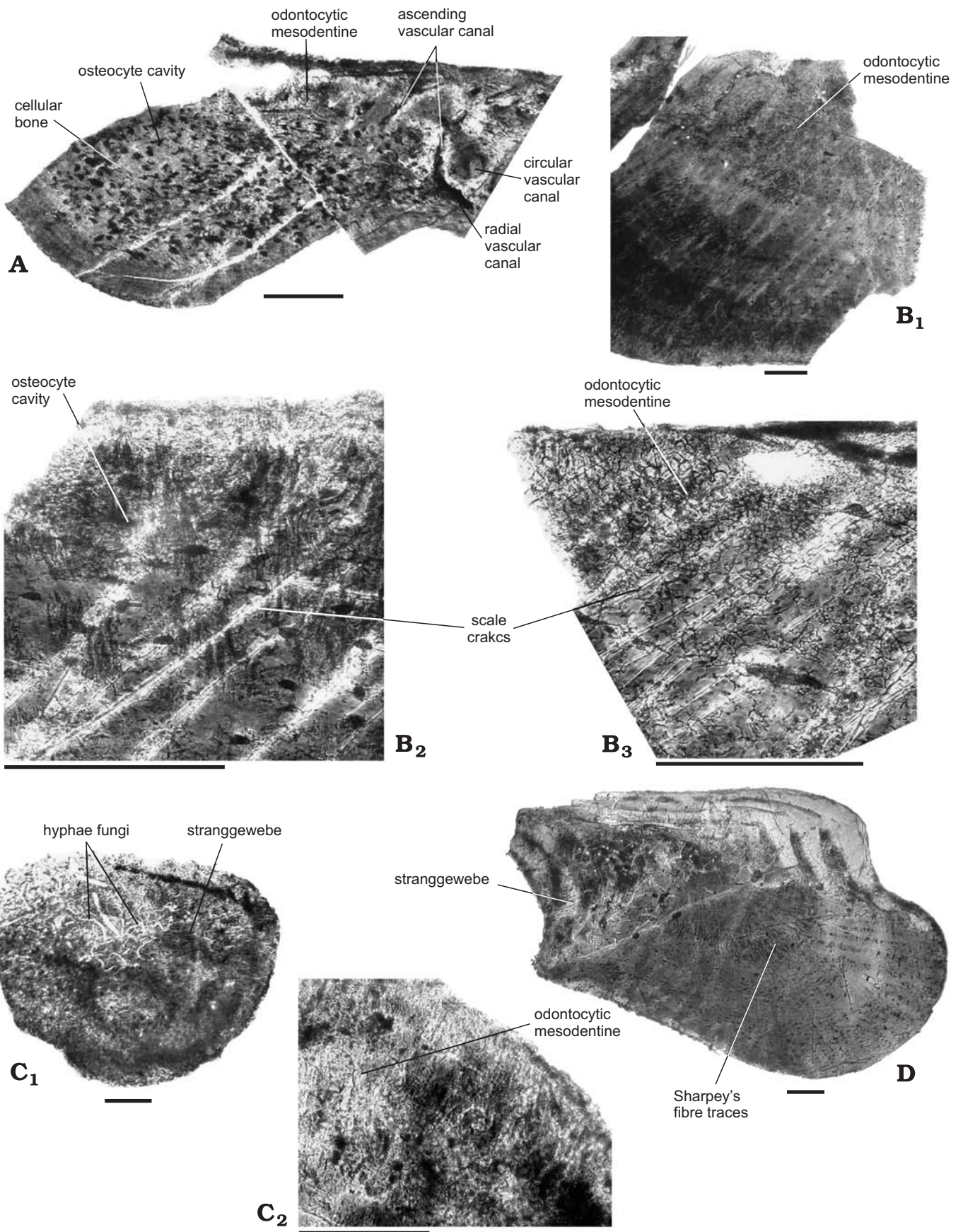
Fig. 3. Climaetid acanthodian *Iranolepis ginteri* gen. et sp. nov. from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. SEM micrographs of flank scales. **A.** Holotype, AEU 301 in crown (**A₁**, anterior upward), basal (**A₂**, anterior upward), and lateral (**A₃**, anterior to right) views. **B.** AEU 302 in crown (**B₁**) and basal (**B₂**) views. **C.** AEU 303 in crown view. In **B₁**, **B₂**, and **C** anterior is upward.

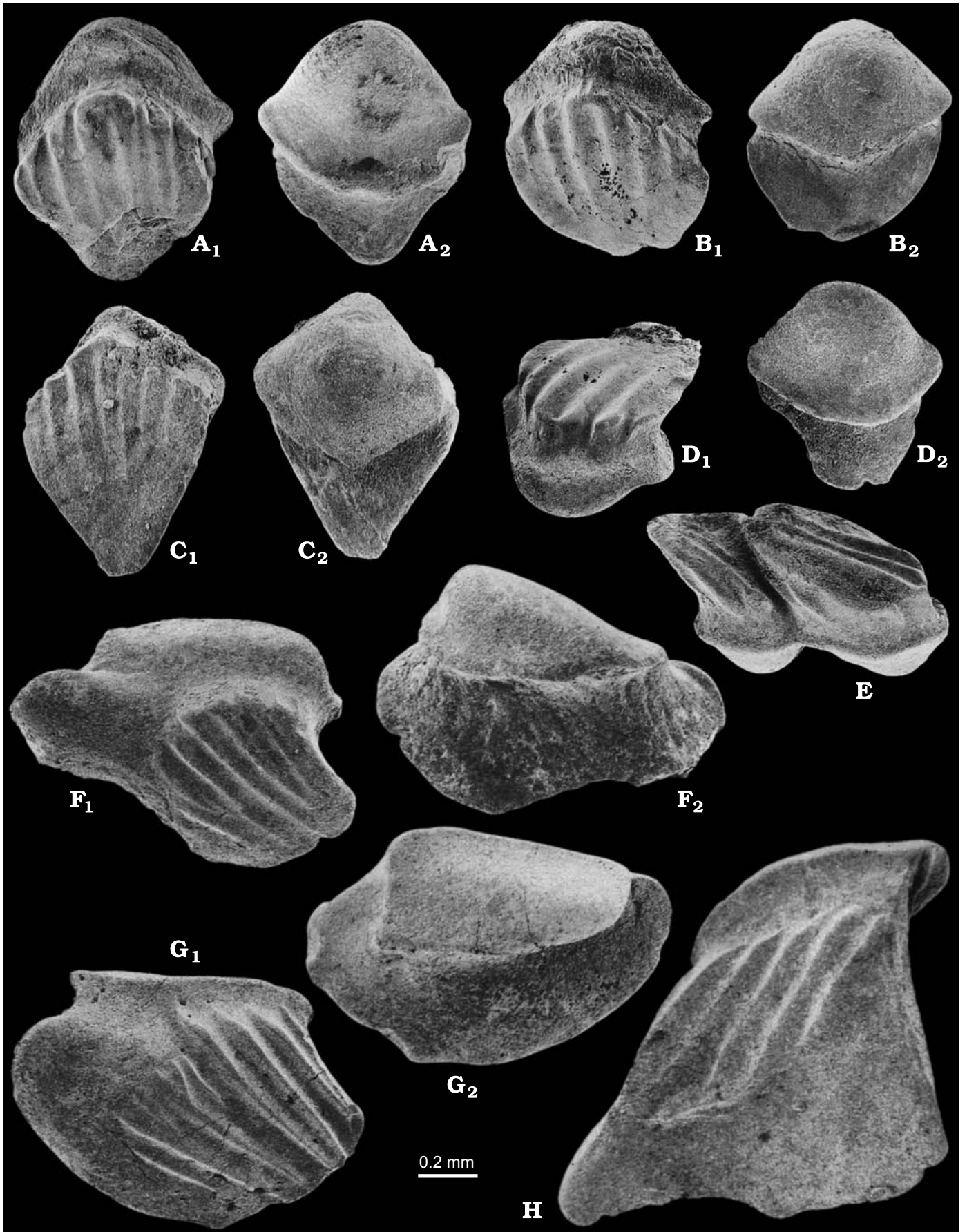
are distributed evenly throughout; the base forms a very low-angled pyramid (Fig. 4A; LIGG 3802). Osteocytes are of polygonal or spindle-like form (Fig. 4B₂) and oriented along the dense, thin growth lamellae. Osteocyte cells are interconnected by winding, narrow processes. Sharpey's fibre traces are bundled into long and narrow strips.

Discussion.—This taxon belongs to the climatiid acanthodians having robust but sparsely sculptured crowns, showing commonalities with representatives of some phylogenetic lineages of the *Nostolepis* sensu lato. Among taxa known from

the southern hemisphere, *Iranolepis ginteri* slightly resembles scales from the Broken River Group of North Queensland, Australia which De Pomeroy (1996) assigned to *Nostolepis* sp. 1 and *N.* sp. 2. Burrow (2002: 97–99, figs. 16, 17) erected a new species *Canadalepis basdenae* and included these two taxa in its synonymy. Burrow suggested that the younger stratigraphic occurrence (Givetian) for the first form could have been in a limestone clast reworked from the older horizon (Emsian). *Iranolepis ginteri* scales resemble those of *Canadalepis* in having tongue-shaped crowns, but differ in

Fig. 4. Climaetid acanthodian *Iranolepis ginteri* gen. et sp. nov. from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. Photomicrographs of thin sections of flank scales similar to the holotype. **A.** Thin section LIGG 3802. Vertical longitudinal section showing densely cellular bone in scale base and odontocytic mesodentine incorporating enlarged ascending, radial and circular vascular canals in crown. **B.** Thin section LIGG 3804. Vertical longitudinal section of a broken scale. **B₁**, fragment of a central scale part showing structure of base (lower left corner) and the lower part of crown (upward right); **B₂**, magnified area of the upper central base part with the spindle-like shaped osteocytes oriented along the growth lines and short perpendicular Sharpey's fibre traces, **B₃**, fine-celled mesodentinal network incorporating tiny polygonal osteocytes in scale crown (right corner) in a higher magnification. **C.** Thin section LIGG 3805. Vertical transverse section through the central part of scale. **C₁**, structure of cellular bone in scale base, and short-lacunal strangewebe and odontocytic mesodentine in crown; also fungal hyphae; **C₂**, the upper left corner of crown at higher magnification exposing canaliculi network and the cellularity of odontocytic mesodentine. **D.** Vertical longitudinal section of scale showing fully formed growth lamellae in crown and base, a networked odontocytic mesodentine in crown anteriorly (right part) and the strangewebe extent posteriorly, and cellular bone in scale base with long and narrow bundles of Sharpey's fibres. Thin section EUIV 411. Scale bars 0.1 mm. →





having low lateral crown areas, some stranggewebe, and bundled rather than separate Sharpey's fibres. Scales tentatively assigned to *Canadalepis*? sp. were identified in calcareous horizons of the upper Lower Devonian Jawf Formation of Saudi Arabia (Burrow et al. 2006: figs. 4.1–8, 4.14), and similar scales are found in calcareous facies of the late Middle Devonian (Givetian) Aztec Siltstone, Antarctica (CJB personal observation). The Saudi Arabian scales closely resemble those of *Iranolepis ginteri*, although the lower lateral crown areas are only variably present in the former; where these areas are lacking, multiple vertical ridgelets run from the lateral crown edges down to the base.

A northern hemisphere taxon with scales morphologically similar to those of *I. ginteri* is *Nostolepis valentinae* (Valiukevičius 2003a: figs. 20A–G, 21A–E) from the Lower Devonian (Lochkovian) of the Timan-Pechora region, Russia. A recent synopsis and revision of climatiiform acanthodians with the *Nostolepis*-type histological structure by Valiukevičius and Burrow (2005) renamed this taxon as *Pechoralepis valentinae*. Like the Iranian specimens, its scales have a distinctly raised, wide medial area on the crown with only one or two short anterior ridgelets, but the crowns are flat without a central depression. Also, the lateral slopes of the Timan-Pechora specimens are not as pronounced and rarely continue to the posterior crown tip; the scales lack large neck pores; and the odontocytic mesodentine in crowns is distinctly bone-like.

Genus *Nostolepis* Pander, 1856

Type species: Nostolepis striata Pander, 1856; Ohesaare Regional Stage, Pridoli, Upper Silurian. Ohesaare Cliff, Saaremaa, Estonia.

Nostolepis sp. cf. *N. gaujensis* Valiukevičius, 1998

Figs. 5, 6, 7.

2002 *Nostolepis* sp. cf. *N. gaujensis*; Turner et al. 2002: figs. 9A–H, 10A, B.

Material.—About 450 scales from sample H1, >800 scales from sample GI4, both middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* conodont zones of Chahrisheh section, Kaftari Mt., central Iran.

Description

Morphology.—Morphologically, specimens identified as flank scales (Fig. 5A–E; AEU 303–307) conform to the description in Turner et al. (2002), except that crowns carry 4–6 (not 4–5) ridges which decrease in height posteriorly and may fade out so that the posteriormost third of the crown is smooth.

Large asymmetric scales (Fig. 5F–H; AEU 308–310) are identified as lateral sensory line scales by comparison with the squamation of articulated climatiids (e.g., *Nostolepis decora* Valiukevičius 2003a) and *Acritolepis* (Valiukevičius 2003a) showing principal characters of the “*Pruemolepis*”

scale morphotype, which we regard as a growth form common to most climatiid and ischnacanthiform taxa (Burrow 2002). Scales vary greatly in shape and crown outline. Crowns are 0.6–1.8 mm long and 0.5–1.3 mm wide. Rounded, broadly elliptical or elongated trapezoidal crowns are common forms. The scales have no more than six longitudinal, often slightly oblique ridges, although some specimens have short additional ridgelets intercalated (Fig. 5G₁). Many specimens have a shallow antero-medial depression or sulcus at the neck-crown junction and one lateral (right or left) crown area unsculptured. Unlike the flank specimens (Fig. 5E), asymmetrical scales have no neck ridges converging into the postero-lateral crown edges. Scale bases are small and shallow, of irregular forms, most often narrowed and broadly elliptical to rounded-triangular (Fig. 5F₂, G₂).

Histology.—The three to five thick growth zones in crowns of flank scales (Fig. 6) are composed of an orthodentine-like tissue in the outer layer and odontocytic mesodentine in the deeper inner layer. The dentine is best preserved and most clearly seen in the anteriormost crown part forming almost all of the growth lamellae; it also extends into the thinner (outer) layers in the central crown part.

Unusually for climatiids, the dentine tubules are long, straight, rarely branching and the main canaliculi emanate from the rounded odontocyte lacunae (Fig. 6A₂; LIGG 3795). Odontocytes and branchings of the dentine tubules are concentrated in the basal parts of growth zones and are less numerous in the youngest (last) lamella. Thus, the tissue in the basal parts of growth zones resembles the odontocytic mesodentine characteristic of climatiids. The stranggewebe of the posterior crown part is only observed in the lower neck area and has fine, narrow and short stranglakunae connected by fine winding dentinal processes (Fig. 6B₂, C; LIGG 3796, EUIV 412).

The base pyramid is comparatively high and composed of cellular, fine-lamellar bone incorporating numerous osteocyte spaces lengthened and oriented along the growth lines (Fig. 6B₂, C).

The asymmetrical sensory line scales (Fig. 7; LIGG 3816–3818) are also characterised by superpositional growth of the crown, but growth zones are more numerous with up to 10 noted. Unlike flank scales, the orthodentine-like tissue is never observed in the anterior parts of crowns, which are composed of dense networks of odontocytic mesodentine, with stranggewebe in the posterior part of the crown (Fig. 7A₂, B₂). Odontocyte cells are comparatively larger and more densely concentrated, with more and wider processes emanating from all sides. Wide branches of ascending and radial dentine canals are also present in crowns, although only short lengths are preserved in the ground thin sections

← Fig. 5. SEM micrographs of scales of climatiid acanthodian *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, 1998 from early Frasnian, horizon GI4 of an unnamed formation in the Chahrisheh section, Kaftari Mt., central Iran. **A–E.** Flank scales, anterior upwards except for E, two scales in lateral view, anterior to right. **A.** AEU 303 in crown (A₁) and basal (A₂) views. **B.** AEU 304 in crown (B₁) and basal (B₂) views. **C.** AEU 305 in crown (C₁) and basal (C₂) views. **D.** AEU 306, in antero-lateral (D₁) and basal (D₂) views. **E.** AEU 307 in crown-lateral view. **F–H.** Specialised scales from the lateral sensory line, anterior upwards. **F.** AEU 308 in crown (F₁) and basal (F₂) views. **G.** AEU 309 in crown (G₁) and basal (G₂) views. **H.** AEU 310 in crown view.

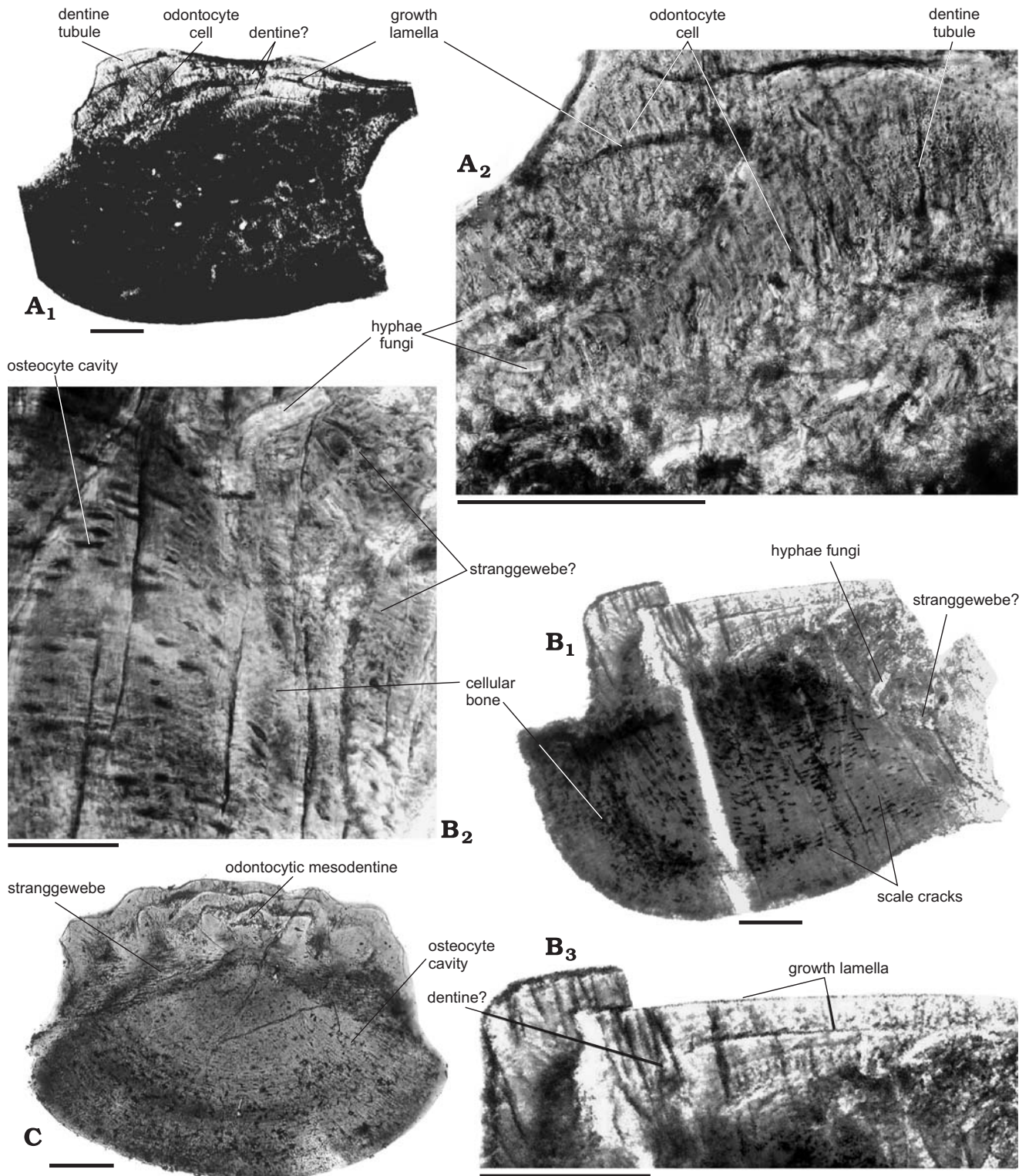


Fig. 6. Climatiid acanthodian *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, 1998 from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. Photomicrographs of thin sections of flank scales. Vertical longitudinal sections (A, B) and vertical transverse section (C) of the central part of scales. A. Thin section LIGG 3795. A₁, structure of ?orthodentine in the outer layers and odontocytic mesodentine in the inner parts of growth lamellae in crown anteriorly (left part); A₂, magnified area of the anterior crown part exposing unipolar, more outwardly-oriented dentine tubules emanating from large, rounded odontocytes. B. Thin section LIGG 3796. B₁, scale exposing cellular bone in base, portions of ?orthodentine and strangewebe tissues respectively in the anterior and posterior crown parts; B₂, orientation of elongated osteocyte cells along the growth lines in the apex of base, and probably strangewebe at the base/crown junction, at higher magnification; B₃, magnified part of the anterior crown with the orthodentine-like tissue. C. Thin section EUIV 412 showing a dense lamellarity of cellular bone in scale base with plenty of osteocytes, strangewebe in the lower crown, and partly bush-like odontocytic mesodentine in the outer parts of growth zones in crown. Scale bars 0.1 mm.

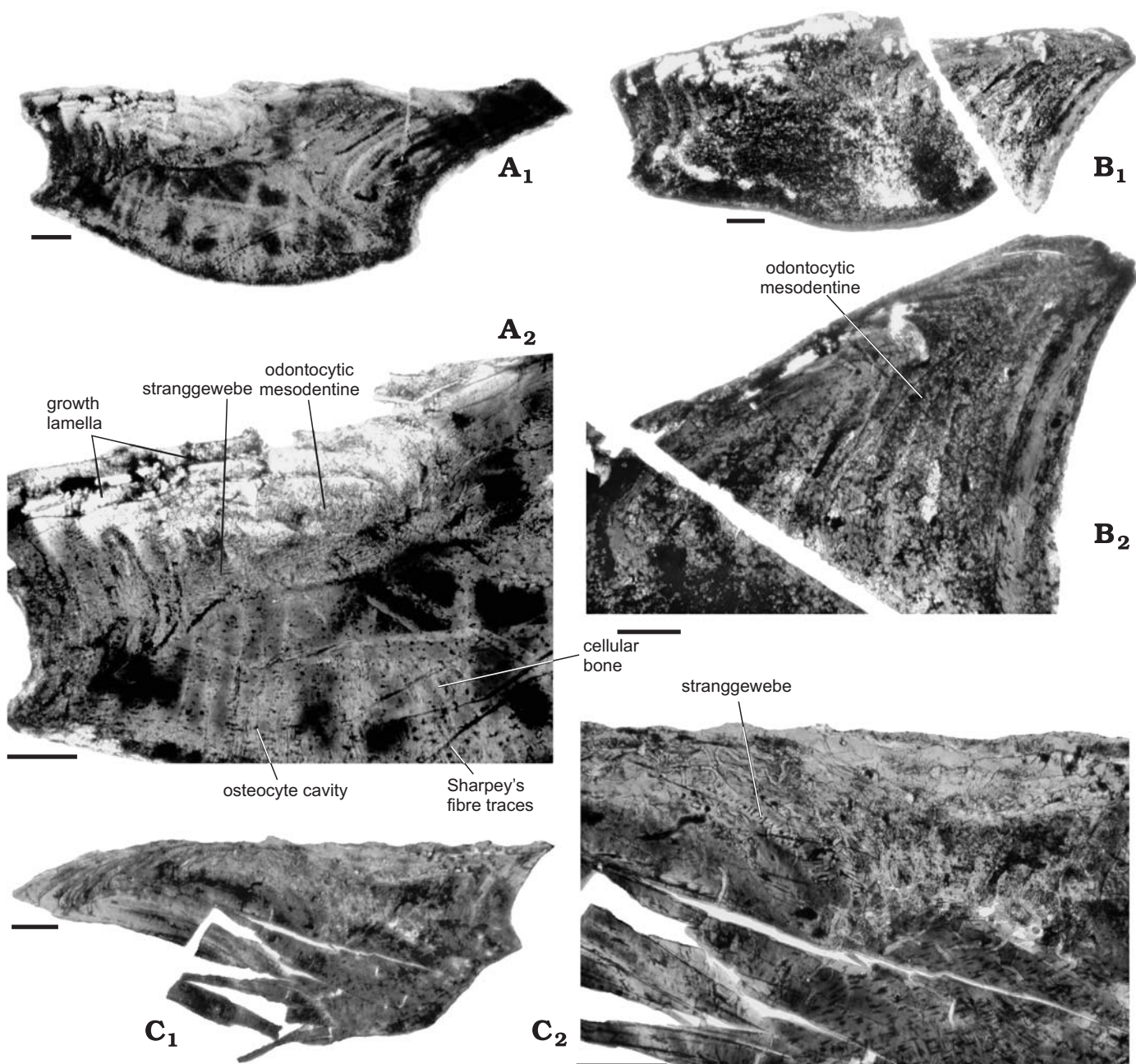


Fig. 7. Climaetid acanthodian *Nostolepis* sp. cf. *N. gaujensis* Valiukevičius, 1998 from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. Photomicrographs of vertical transverse sections of specialised scales from the lateral sensory line. **A.** Thin section LIGG 3816. A₁, general view of a scale sectioned through the central base part and showing growth characters; A₂, the anterior, left part of the same scale at higher magnification exposing distribution of densely cellular mesodentine and strangewebe in growth zones of crown, and structure of adjacent base part showing large numbers of osteocytes and long Sharpey's fibre bundles. **B.** Thin section LIGG 3817. B₁, structure of odontocytic mesodentine in the anterior crown part; B₂, finely networked mesodentine incorporating densely concentrated osteocytes in growth zones of crown, at high magnification. **C.** Thin section LIGG 3818 showing general view (C₁) and a small portion of the short-lacunal strangewebe developed in the crown amongst the odontocytic mesodentine (at higher magnification, C₂) characteristic of most of the crown. Scale bars 0.1 mm.

(Fig. 7A₂). Bases are comparable to those of flank scales, with thinly lamellar cellular bone.

Discussion.—Undoubtedly, the scales studied herein are from the same species as those identified by Turner et al. (2002: fig. 9A–H), from the same geological horizon of the Chahriseh section. The taxon belongs to the genus *Nostol-*

epis as it has scales with all the characteristic tissues composing crown and base which are diagnostic for the genus, in both articulated specimens and isolated microremains. The new material includes more morphological varieties of flank scales than previously recognised, and also specialised asymmetrical scales of a “*Pruemolepis*”-type having similar tissue microstructure.

Nostolepis spp. flourished in the uppermost Silurian and Lower Devonian in many regions worldwide, and showed wide variations in the sculpture on scale crowns: sharp ridges extending the whole crown length; sharp or rounded ridges, only on the anterior crown part; parallel, subparallel or radially-oriented ridges. Some species have a raised median area and lower lateral areas which may or may not be ridged.

Very few Middle or Late Devonian nostolepids are known, and most have scales with a relatively robust crown sculpture. The Iranian species is distinguished by broad parallel ridges extending at least two thirds of crown length, and configuration of the two median ridges. *Nostolepis gaujensis* (Valiukevičius 1998: pl. 8: 8) from the Baltic Upper Old Red Sandstone (Frasnian) facies has scales with four simple broad, rounded ridges extending almost the whole crown length with broad, shallow grooves between. It is comparable with the Iranian specimens in most details; in both, the broadest median ridges are joined by an arc-like rim along the anterior crown edge. Morphological differences between these taxa are the fewer ridges (four) and lower or almost negligible neck in scales of *N. gaujensis*. However, the latter was described based on only five scales, hardly encompassing the total scale diversity range in this taxon. The histological structure of *N. gaujensis* was not investigated. Scales from the ?Frasnian Cucho Formation of Colombia in South America have also been assigned to *Nostolepis* sp. cf. *N. gaujensis* (Burrow et al. 2003). Unfortunately, those scales were preserved only as hollow shells, and so their internal structure is unknown, but their morphology conforms to that of the Iranian and the type *N. gaujensis* scales.

Another representative from the Baltic, *Nostolepis kernavensis* (Valiukevičius 1985: pl. 1: 9–13) from the topmost Eifelian upper Narva Substage, differs in having two very robust median crown ridges which sometimes are converging posteriorly, or four median ridges meeting in two pairs posteriorly. Unlike the Iranian scales, ridges in *N. kernavensis* are high, with sharper crests, and grooves are deeper and narrower. Histological structure of the latter shares many characters in common with the Iranian *Nostolepis* sp. cf. *N. gaujensis*, even showing the relatively straight unipolar and perpendicularly-oriented dentine tubules in the anterior crown part (Valiukevičius 1985: fig. 2.4A, B), a feature rarely observed in climatiid acanthodians. The principal histological difference between the species is in the strangewebe, with more elongated and dense lacunae enveloped by an odontocytic mesodentine layer in each growth zone of *N. kernavensis*.

In the number and robustness of crown ridges, *Nostolepis* sp. cf. *N. gaujensis* slightly resembles scales from the Lochkovian and Pragian in Yunnan, China which Wang (2003: fig. 2A–D) assigned to *N. gracilis* Gross, 1947. Morphologically, the Chinese scales do not compare well with *N. gracilis* (shape of ridges differs, scales have a deep base protruding in front of the crown, no pores open out on the anterior crown part), and histological structure is not of the *Nostolepis*-type (very high apexed, thin-lamellar base composed of acellular bone, and no mesodentinal tissue in crown). The scales are

comparable with the Iranian ones in having 4–6 parallel ridges extending to the posterior crown part but never reaching its end. However, they differ significantly in having sharp crown ridges, a pair of short oblique neck ridges sloping down to the lateral corners of the base, and sometimes vertical ridges on the posterior neck.

Order Diplacanthiformes Berg, 1940

Remark.—Classification of the diplacanthids, including their higher taxonomical rank (order, suborder or family), has changed often since their assignment as a family of the Acanthodii by Woodward (1891). We will follow a proposal by Hanke et al. (2001) to revive the order Diplacanthiformes as a distinct assemblage of acanthodians which may or may not be closely related to armored “climatiiforms”. Characters by which the group is distinguished (when working on scales of articulated fish and in microremain assemblages) include the scale sculpture and histological structure of *Diplacanthus*-type (Valiukevičius 1985, 1995). *Diplacanthus*-type histology is characterised by a crown with superpositional lamellae formed of simple mesodentine and long branching vascular canals, and an acellular base pierced by multi-branched canals (Valiukevičius 1995).

Family Diplacanthidae Woodward, 1891

For a revised diagnosis of the family see Young and Burrow (2004), and the extended discussions on “diplacanthids” in Janvier (1996), Hanke et al. (2001), and Hanke and Wilson (2004).

Genus *Milesacanthus* Young and Burrow, 2004

Type species: *Milesacanthus antarctica* Young and Burrow, 2004; Portal Mountain and Mount Crean (Lashly Range), Victoria Land, Antarctica; the Aztec Siltstone, Givetian, Middle Devonian.

Milesacanthus sp. aff. *M. antarctica* Young and Burrow, 2004

Figs. 8, 9, and 10.

Material.—Ten scales from sample H1, 121 scales from sample GI4, both middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* conodont zones of Chahriseh section, Kaftari Mt., central Iran.

Description

Morphology.—All specimens examined are identified as flank scales. They are of a medium size; the largest reach 1.15 mm in length and width, but most are 0.6–0.8 mm. Crowns are flat, isometrically rhomboid, from slightly to distinctly rounded, or rarely with a subcircular outline. Crowns protrude beyond the base on all sides or at least posteriorly. Eight (only rarely), or most often twelve to fourteen subparallel ridges form a fan-like pattern over the crown. Ridge crests are flattened, decreasing gradually in height and narrowing towards the posterior, and extend the entire crown length (Fig. 8A₁; AEU 311), or else fade out leaving the

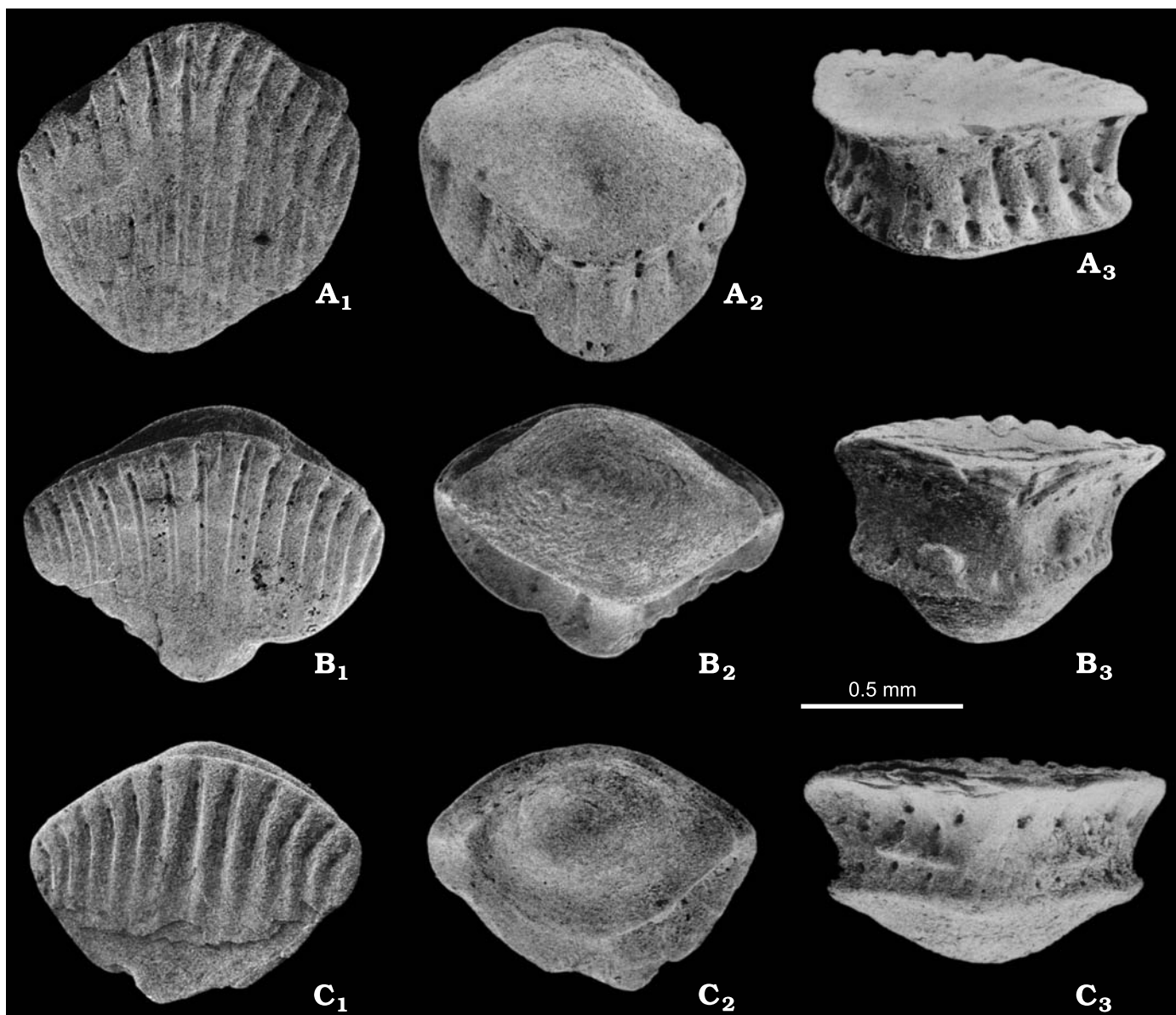


Fig. 8. Diplacanthid acanthodian *Milesacanthus* sp. aff. *M. antarctica* Young and Burrow, 2004 from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. **A.** AEU 311. **B.** AEU 312. **C.** AEU 313. SEM micrographs of flank scales in three positions respectively, in crown (**A**₁, **B**₁, **C**₁), basal (**A**₂, **B**₂, **C**₂), and postero-lateral (**A**₃, **B**₃, **C**₃) views. In **A**₁, **A**₂, **B**₁, **B**₂, **C**₁, and **C**₂, anterior is upward.

posteriormost crown part unornamented (Fig. 8B₁, C₁; AEU 312–313). One or two median ridges may show short bifurcations at the anterior crown edge. The flatness of ridges often gives the impression of deep, linear and narrow grooves on the crowns (especially in lateral view). Scales have well outlined, medium to high concave necks carrying large pores and two symmetrically positioned “warts” on the posterior faces. “Warts” may be circular (Fig. 8B₃) or transversely elongated (Fig. 8C₃) in outline. Very large pores (five-seven per side), arranged in three lines (Fig. 8A₃), open out from a complicated system (or systems) of canals. Some canals rise vertically and open out in the grooves of the anteriormost crown (Fig. 8B₁), while others extend diagonally through the posterior crown (Fig. 8A₂).

Scale bases are isometric or wide rhomboid, of medium convexity, with the deepest part centrally or, more frequently, slightly anteriorly.

Histology.—Scales have *Diplacanthus*-type histological structure. Up to ten thin growth lamellae in the crowns are composed of syncitial (non-lacunal) mesodentine and (particularly in the anterior crown) multiple-branching, long and winding ascending dentine canals (Figs. 9A, B₁, 10B₂) which have many narrow branchings of canaliculi. The posterior part of the crown is characterised by less branched, straighter ascending canals. The horizontal parts of growth zones in the crown plate have many narrow, short dentinal canaliculi directed perpendicularly outward and emanating from large

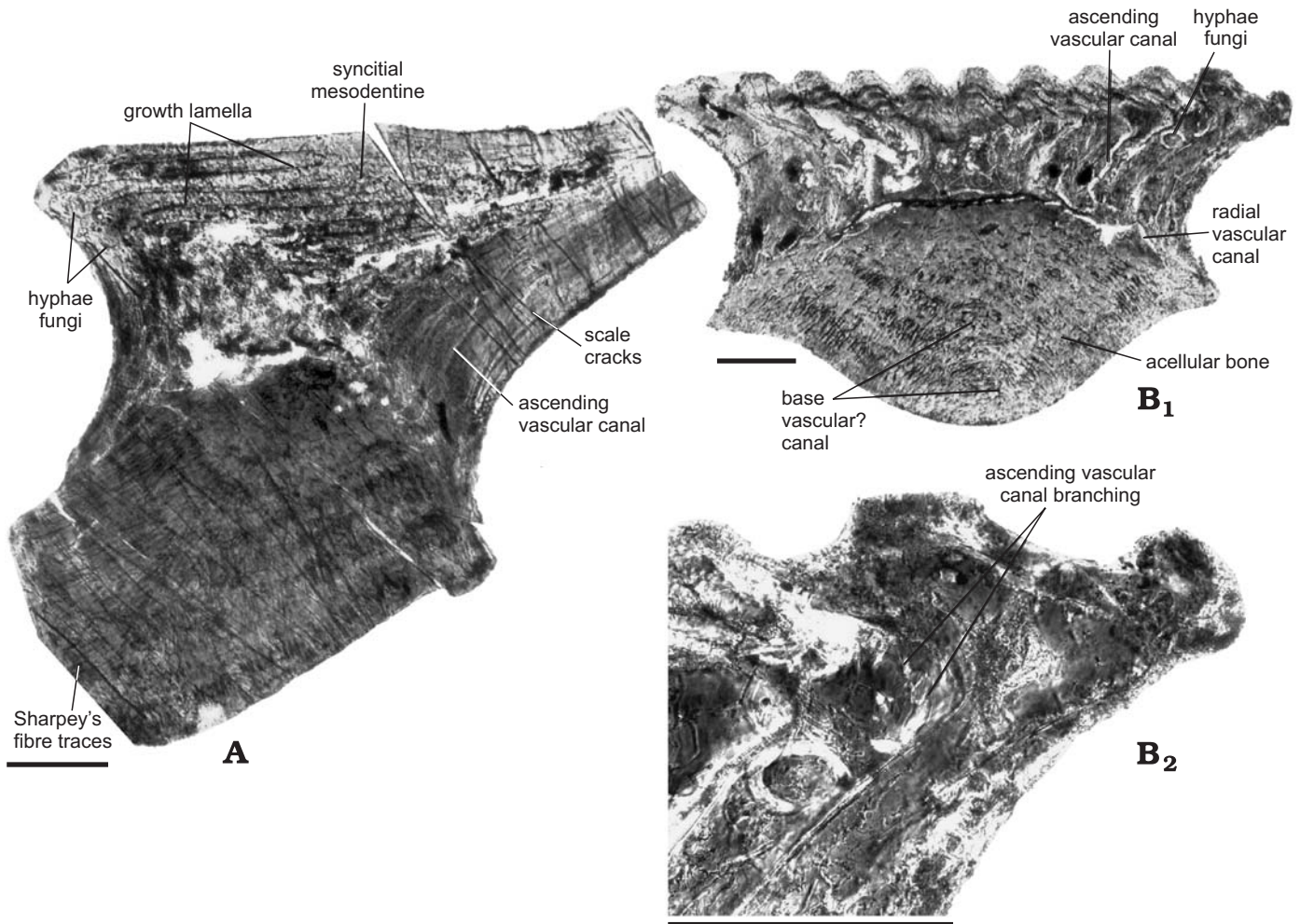
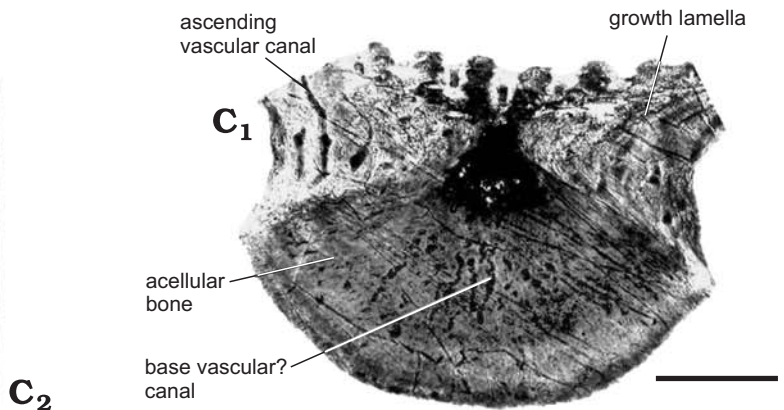
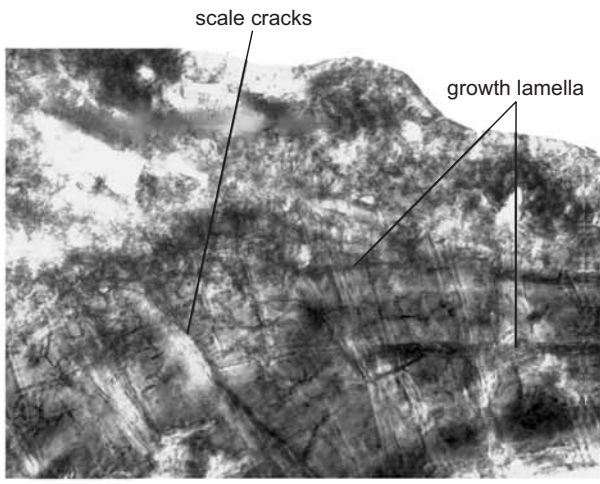
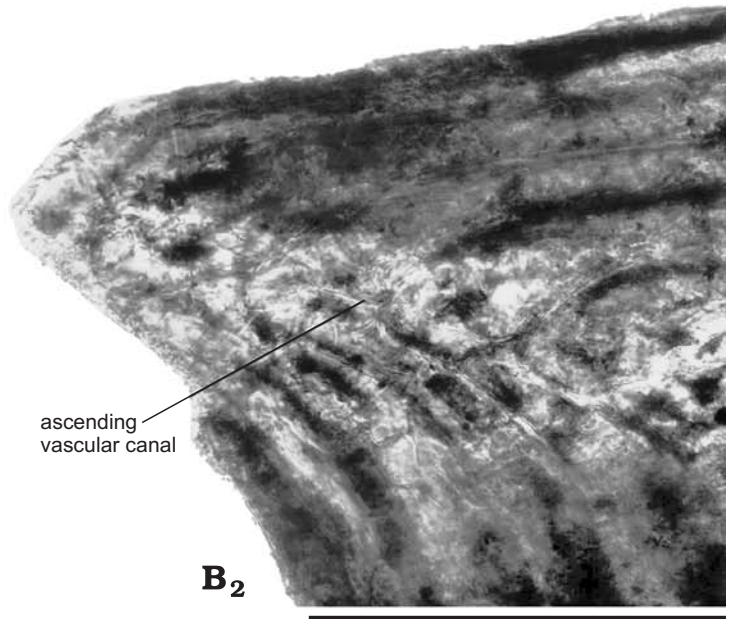
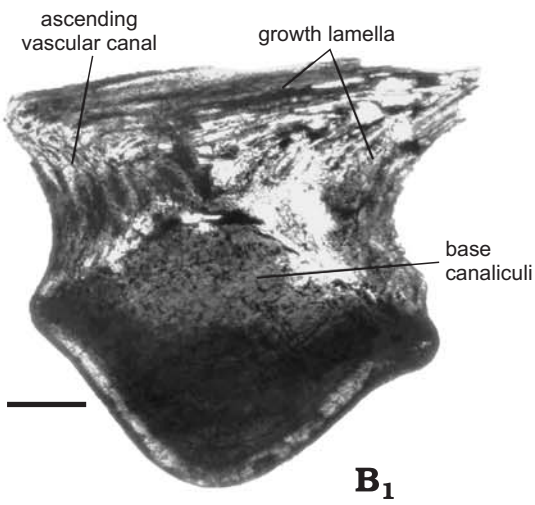
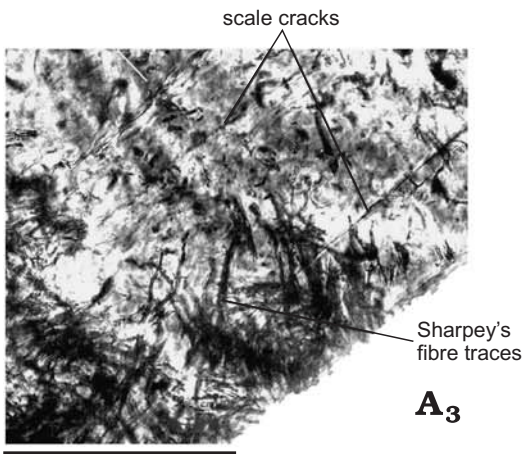
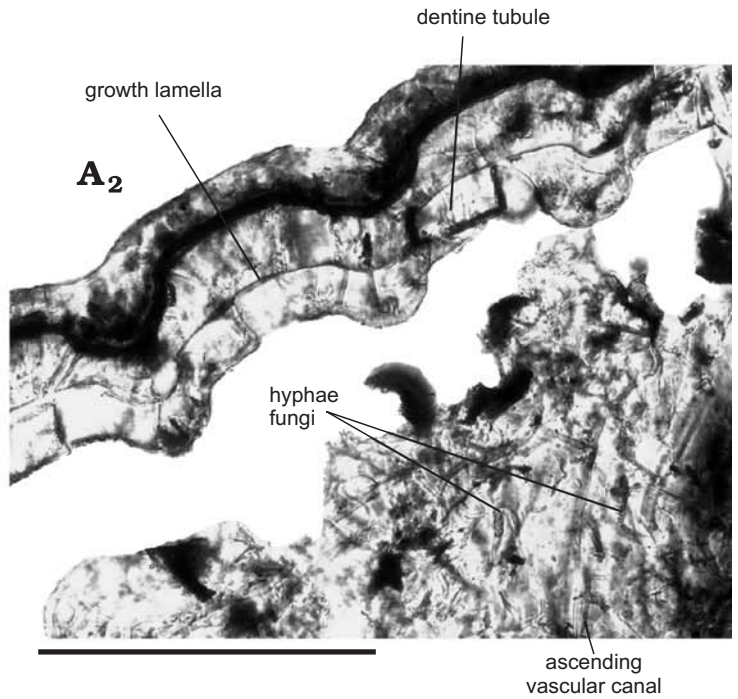
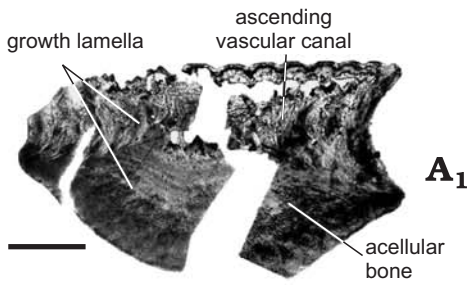


Fig. 9. Diplacanthid acanthodian *Milesacanthus* sp. aff. *M. antarctica* Young and Burrow, 2004 from early Frasnian, horizon GI4 of an unnamed formation in the Chahrisheh section, Kaftari Mt., central Iran. Photomicrographs of thin sections of flank scales in vertical longitudinal (A) and vertical transverse (B) sections. A. Thin section LIGG 3800. Structure of syncitial mesodentine with mainly upwardly directed dentine tubules in the upper crown part, unbranched ascending vascular canals in the lower crown part, and numerous elongated ?vascular canals and Sharpey's fibres piercing an acellular bone in scale base. B. Thin section LIGG 3801. B₁, ascending, radial and ?pore canals of the neck area, knot of canals in primordial zone, and small ?vascular canals in an acellular bone of base, all exposed in a section made through the anterior, most ridged crown part; B₂, positioning of fungal hyphae of a magnified area in the upper right corner of crown of the same scale. Scale bars 0.1 mm.

horizontal canals which run under the surface grooves (Figs. 9A, 10A₂, C₂). The primordial zone (first growth lamella) contains a knot of very densely interwoven canals (Fig. 9B₁). Pore canals are rarely observed in thin sections of crowns (possibly due to the preservation mode) and are distinguishable as rounded black spots (Figs. 9B₁, 10C₁) placed randomly at different heights in the neck area.

Scale bases are composed of acellular bone arranged in thin layers and pierced by long and straight Sharpey's fibres which would have given a strong anchorage in the corium. As well as short and winding canaliculi (canals of Williamson *sensu* Ørvig 1951), bases contain longer and wider canals (Fig. 10C₁) clearly distinguishable from the canaliculi.

Fig. 10. Diplacanthid acanthodian *Milesacanthus* sp. aff. *M. antarctica* Young and Burrow, 2004 from early Frasnian, horizon GI4 of an unnamed formation in the Chahrisheh section, Kaftari Mt., central Iran. Photomicrographs of histological structure of flank scales. A. Vertical transverse section of a scale with 13 grooves on crown, general view showing base composed of acellular bone and mesodentine crown filled by ascending vascular canals with plenty of smaller winding branches (A₁), upwardly directed narrow dentine canaliculi of the upper central crown part in a higher magnification (A₂), and bundles of Sharpey's fibres with incorporated ?vascular canals in the base of scale (A₃). Thin section LIGG 3797. B. Vertical longitudinal section LIGG 3798 of a similar scale, with short bifurcations of the flattened central ridges. B₁, thin and dense growth lamellae with long ascending dentinal canals in crown and short canaliculi in base; B₂, detail of the left upper crown part in a higher magnification. Structure of ascending dentine canals, composed of one long main branch and plenty of interconnecting branchings. C. Vertical transverse section LIGG 3799 of a similar scale but without ridge bifurcation. C₁, section exposing pore canals presumably distributed among the ascending vascular canals and a knot of dense canals attached to the primordial growth lamella, with clear enlarged canals in the acellular bone of base which shows fine lamellarity of growth zones; C₂, detail of the upper right crown part, magnified. Scale bars 0.1 mm.



Discussion.—*Milesacanthus antarctica* from the Givetian Aztec Siltstone of Antarctica was diagnosed on the skeletal structure of articulated fish and other isolated remains (scales and fin spines) discovered in the same horizons (Young and Burrow 2004). According to the diagnosis of the genus, scales "... are ornamented with 14–24 subparallel ridges or grooves extending from the anterior edge to at least mid-crown; scales have pore canal system in the anterior part of the crown with pore openings in the grooves and the lower neck ..." (Young and Burrow 2004: 26). Iranian specimens fit closely to *M. antarctica* according to scale size and crown/neck/base proportions and pore openings in the crown and neck. However, the crown ornamentation of the Iranian specimens (8–14 linear grooves rather than low flattened ridges) shows fewer grooves as compared to the Antarctic ones, and is more fan-like rather than the almost parallel ridges and grooves in *M. antarctica*. The bifurcation of ridges occasionally observed in the median crown of *M. sp. aff. M. antarctica* is not referred to in *M. antarctica*. Histological structure of the Antarctic scales is poorly preserved, but the illustrations of Young and Burrow (2004: fig. 3A–F) demonstrate a better developed system of branching pore canals and horizontal dentinal canals in the lower crowns, and a comparable appearance of ascending canals in the vertical growth zones. The possibly vascular canals in bases of the Iranian scales are considerably more pronounced in length and width than for the Antarctica scales, based on the small canaliculi fragments exemplified by Young and Burrow (2004: fig. 3D).

Morphologically, the Iranian scales resemble most closely an Emsian (Early Devonian) diplacanthid from the Jawf Formation of Saudi Arabia (Forey et al. 1992) which was recently studied in detail and described as *Milesacanthus ancestralis* Burrow, Lelievre, and Janjou (Burrow et al. 2006: figs. 7, 8). These scales were diagnosed by having six to eighteen subparallel longitudinal deep linear grooves rather than ridges on a flat crown, pores opening out in crown grooves and extending from a pore canal system in the anterior crown part, deep neck with lower and upper rows of large pores, and "warts" on the posterior neck. The Saudi scales differ from the Iranian ones in having a complicated syncitial mesodentinal network in the lower crown (neck area) filling the growth zones between the main branches of the ascending vascular canals (Burrow et al. 2006: fig. 8.1), and also lacunal widenings of dentine canals, particularly dense in the lower neck; and the horizontal canals running under the grooves of the crown plate are the longest and widest of the species compared, and supplied by numerous winding canaliculi (Burrow et al. 2006: figs. 7, 8).

Ectopacanthus? pusillus Valiukevičius, 1998 from the upper Lochkovian (Lower Devonian) of the Baltic region also shows some similarities with *Milesacanthus sp. aff. M. antarctica*. Its scales have nine to eighteen narrow ridges and linear fan-like grooves extending over the crown; some ridges bifurcate; scale neck is high and concave. However, the scales are tiny, ≤ 0.5 mm. Histologically, their crowns differ to those of the Iranian taxon in being composed of dentine

with a thick durodentine superficially, in up to twelve growth lamellae; their modified *Poracanthodes*-type structure was defined on the presence of radial, arcuate and ascending pore canals forming a system with openings only in the neck and not on the crown surface (Valiukevičius 1998: pl. 14: 2–4). The taxon was classified as an ischnacanthiform based on the pore canal system in the scales. Perhaps it might rather belong with *Milesacanthus* in a group of diplacanthids distinguished from the genus *Diplacanthus* by having scales with a crown sculpture mainly consisting of grooves, and an internal pore canal system.

Scales previously attributed to the genus *Diplacanthus* which resemble *Milesacanthus sp. aff. M. antarctica* in the crown sculpture are: (1) *Diplacanthus poltnigi* Valiukevičius, 2003b, which has 10 to 23 sub-parallel grooves extending the whole crown or fading out almost at the posterior corner; also attributed to this taxon are scales from the uppermost Emsian of Graz, Austria which Poltnig (1984: pl. 2: 1–7) assigned to *D. longispinus* Agassiz, 1845; and others from the upper? Lochkovian (Vieth 1980) or possibly Pragian (Langenstrassen and Schultze 1996) of Arctic Canada which Vieth (1980: pl. 5: 14a, b) assigned to *Nostolepis gracilis*; and (2) *Diplacanthus pechorensis* Valiukevičius (2003a: figs. 23G, H, 24D, E) from the Lochkovian to Pragian of the Timan-Pechora region (Russia) which have crowns ornamented with symmetric bipartite ridgelets and fan-like grooves, up to twenty on each side. The scales of both taxa have the *Diplacanthus*-type microstructure: crowns of mesodentine with upwardly directed bushy dentine tubules emanating from wide ascending and radial vascular canals (some of which arise high in the neck); no lacunae in dentinal canals nor pore canal systems present in crowns; acellular bone of scale bases pierced by long apically-directed vascular canals.

Diplacanthid spine fragments

Fig. 11.

Material.—Three spine fragments from sample GI4, middle *Mesotaxis falsovalis* to *Palmatolepis hassi* conodont zones of Chahriseh section, Kaftari Mt., central Iran.

Description

Morphology.—The longest fragment of fin spine is about 2.8 mm long and 0.5 mm wide (Fig. 11A; AEU 320), and (subcircular) crescent-like in cross-section. The hard tissue forming the spine is thickest along the leading edge, thinning slightly laterally, with a large circular central cavity which is wide open along the trailing edge of all fragments. Remnants of 5–6 smooth longitudinal parallel ribs extend almost the whole fragment length. The ribs are rounded-quadrangular with steep lateral faces; all are of equal width or with a slightly wider rib along the leading edge; ribs are separated by deep narrow uniform grooves. No pore openings are observed in the grooves; some large vascular canals are exposed in areas damaged during preparation or fossilisation; these canals become the grooves between the narrow ridges

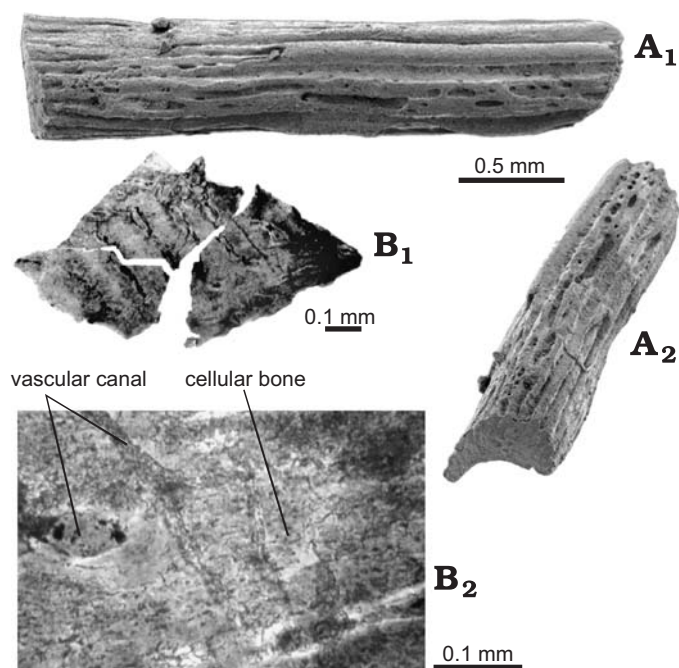


Fig. 11. Diplacanthid spine morphology and histology. Early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. **A.** AEU 320, fin spine in lateral (A_1) and leading edge (A_2) views. **B.** Histological microstructure of a diplacanthid fin spine. Vertical transverse section LIGG 3807 of spine fragment which had two rounded-quadrangular sculptural ribs (lost during sectioning, but were positioned at top). B_1 , general structure of an osseous vascularised tissue embracing all of the preserved spine; B_2 , abundant osteocyte cells densely displaced among the large vascular canals appeared in two perpendicular directions, longitudinal and transverse.

of the insertion area as exposed at the extreme left end of the fragment shown in Fig. 11A₁.

Histology.—The outer ribbed layer was lost during sectioning. The preserved part of the spine is composed of cellular bone (Fig. 11B; LIGG 3807) filled by long and wide longitudinal (linear in outline) and radial (subcircular in outline) vascular canals, with no surrounding osteons and without an inner lamellar layer around the central cavity. Polygonal osteocyte lacunae are disposed randomly throughout (Fig. 11B₂).

Discussion.—The few, small spine fragments collected through this study as isolated remains preclude a stricter taxonomical attribution because of absence of most diagnostic characters. However, straight spines with a rib pattern of 5–6 uniform ribs per side, separated by narrow grooves, suggest a diplacanthid rather than ischnacanthiform (or other) affinity. By these features, the Iranian diplacanthid spines resemble those of *Milesacanthus antarctica* (Young and Burrow 2004: figs. 4B–D, 5A–D) which have from three ribs (per side) plus a wider leading edge rib on the paired pectoral and pelvic spines, and up to five longitudinal ribs on the dorsal and anal spines. Tissues composing spines in *M. antarctica* articulated fish and isolated, better preserved spines (Young and Burrow 2004: fig. 5A, D) “...are quite vascular between the central cavity and the leading edge, with a radiating structure

more evident anteriorly” (Young and Burrow 2004: 34). The principal histological structures of spines were listed as: vascular canals surrounded by narrow denteons; the spines lack a subcostal canal; the thin inner spine layer presumed osseous. The Iranian spines also lack a subcostal canal, and similarly have regularly-spaced longitudinal and radial canals, but are mainly composed of a cellular bone with abundant osteocytes from below the ribs to the central cavity. However, in *Milesacanthus antarctica* spines, the thin inner lamellar layer is only developed in the exerted part, increasing in thickness distally. The proximal exerted part of the Saudi Arabian spines also lacks an inner lamellar layer (Burrow et al. 2006: fig. 9.11). Fine histological detail was not preserved in the spines from Antarctica and Saudi Arabia, so it is unclear if the lack of osteocytes in their thick osteodentine/cellular bone layer is an original absence or a result of preservation.

Order Ischnacanthiformes Berg, 1940

Family and genus indeterminate

?Ischnacanthiform tooth whorls

Figs. 12, 14A.

Material.—Two tooth whorls from sample H1, 17 tooth whorls from sample GI4, both middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* conodont zones of Chahriseh section, Kaftari Mt., central Iran.

Description

Morphology.—Tooth whorls consist of a slightly concave, arched (in lateral view) basal plate with tooth cusps increasing in height lingually (posteriorly). Basal plate is usually oval (Fig. 12F; AEU 319) to almost triangular (Fig. 12A–D; AEU 314–318) reaching a maximum width at the largest, terminal tooth at the lingual end. The labial (anterior) end is most tightly curved (Fig. 12E). Plates are 1.0–2.1 mm long and 0.6–1.1 mm wide. As a rule, the anterior (labial) part of whorls has uniform small tooth cusps placed randomly (Fig. 12A), or sometimes arranged in two or three transverse (Fig. 12D) or longitudinal (Fig. 12F) rows. The extreme anterior cusps are the smallest but cusps increase only slightly in size posteriorly. This anterior part with small cusps extends one-fourth to one-third of the whorl length. Behind this cluster, three large lingually bent teeth are placed linearly with the biggest one last in the row (Fig. 12A). The smallest whorls show these three principal teeth and only one to three low flat cusplets in the anterior part (Fig. 12B, C). All teeth and cusps are circular both basally and at the blunt apex; smooth, without sculpture and striation; and basally contiguous with adjacent cusps.

Histology.—The thin basal plate consists of dense lamellar bone incorporating large vascular canals (Fig. 14A₁; LIGG 3810). The overlying part is composed of ?osteodentine and odontocytic mesodentine without a superficial dentinal layer on the apices of tooth cusps. The tissue is highly vascularised, with numerous vascular (pulp) canals distributed

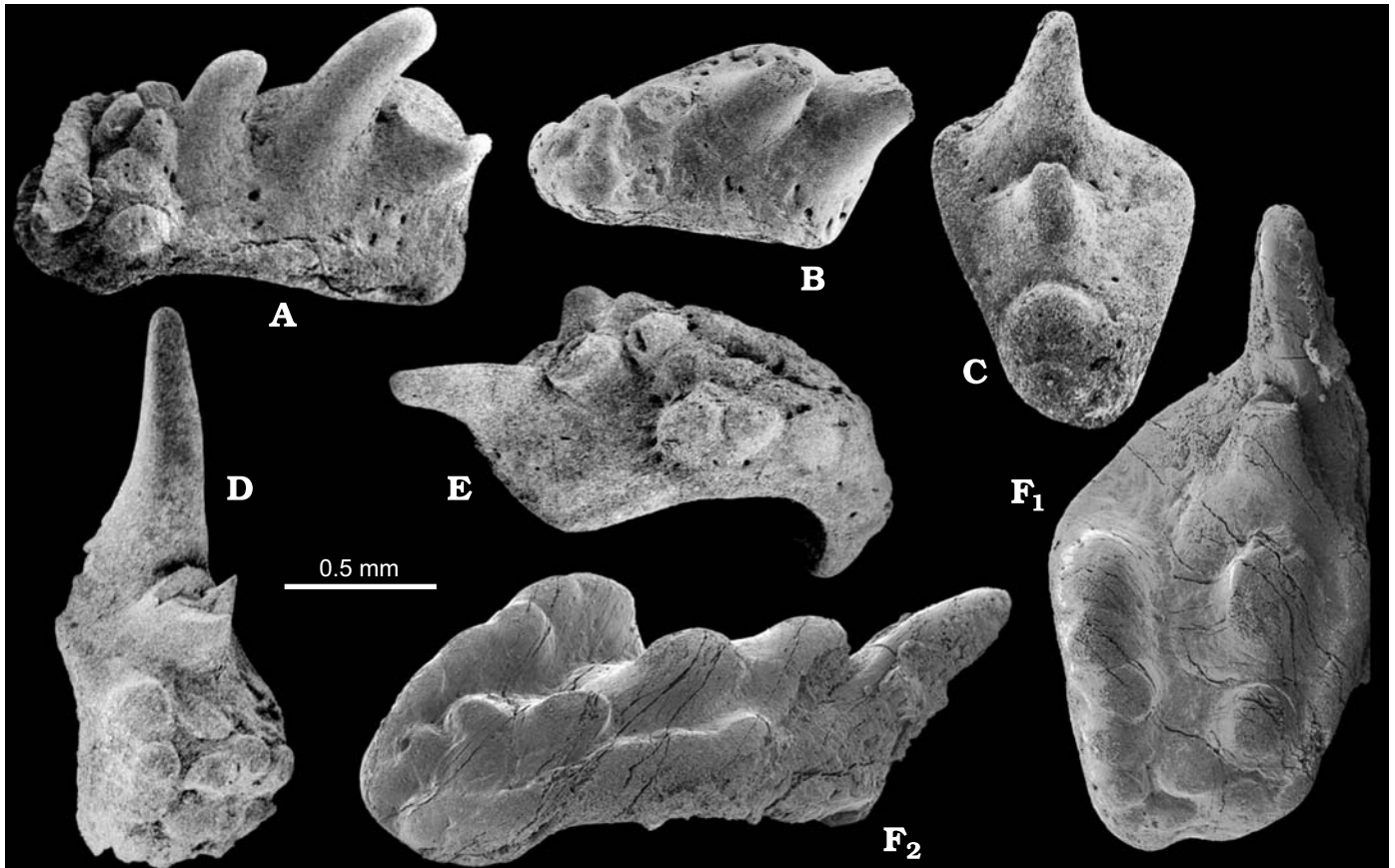


Fig. 12. SEM micrographs of ?ischnacanthiform tooth whorls from early Frasnian, horizon GI4 of an unnamed formation in the Chahrisseh section, Kaftari Mt., central Iran. A. AEU 314 in occluso-lateral view. B. AEU 315 in occluso-lateral view. C. AEU 316 in occlusal view. D. AEU 317 in occlusal view. E. AEU 318 in occluso-lateral view. F. AEU 319 in occlusal (F₁) and in occluso-lateral (F₂) views. A, B, and F₂ anterior to the left, C, D, and F₁ anterior to the page bottom, and E anterior to the right.

randomly in cusps and surrounded by a distinct denteonal layer (light strips in Fig. 14A₂; LIGG 3813). All space between these canals is occupied by bone-like tissue with densely distributed polygonal osteocyte lacunae from which emanate only short winding processes.

Discussion.—Tooth whorls are found in many ischnacanthiform acanthodians [genera *Ischnacanthus* Powrie, 1864, *Poracanthodes* Brotzen, 1934, *Gomphonchus* Gross, 1971, *Zemlyacanthus* Vergoossen, 1999 (new genus erected for *Poracanthodes menneri* Valiukevičius, 1992), *Radioporacanthodes* Vergoossen, 1999], but are also known in some climatiiform taxa, e.g., *Climatius reticulatus* Agassiz, 1845, *Nostolepis striata* Pander, 1856, *Ptomacanthus anglicus* Miles, 1973, *Brochoadmones milesi* Bernacsek and Dineley, 1977 (Gagnier and Wilson 1996), and *Acritolepis* Valiukevičius, 2003a. The Iranian whorls do not compare closely with those from any of these taxa. They only distantly resemble whorls of *Gomphonchus sandelensis* Gross, 1971 which were studied in detail from the *Beyrichia* Limestone (Silurian, Pridoli) erratics of northern Germany. The *G. sandelensis* whorls are usually tightly spiralled, with a main axial row of the largest teeth and two side rows of smaller teeth always present (Gross 1957: pls. 1, 2); tooth cusps are more lingually bent than in the

Iranian specimens, moreover, they may carry sharp lateral flanges or may be sculptured all around by low but distinguishable ridgelets (Gross 1957: pl. 1: 1, 6, 7). Apart from the three cusp lines mentioned, the most complicated whorls in *G. sandelensis* have numerous additional and smaller cusps between the main lines (Gross 1957: pl. 3: 4–6). Just one whorl figured by Gross (1957: pl. 2: 12) shows an anterior field of denticles or cusps, with a large central tooth behind. Histologically, whorls of *G. sandelensis* are distinguished by having a well separated lamellar bone base, a highly vascularised bony layer with osteocyte cells covering the base, and orthodontinous tooth cusps with regularly-spaced dentine tubules emanating from a single pulp canal (Gross 1957: fig. 3G, H).

The Early Devonian *Zemlyacanthus menneri* (Valiukevičius, 1992) has several forms of whorls. The largest, presumed to be a symphysial tooth whorl, consists of three monocuspid teeth arranged in a line, with only small additional denticles labially (Valiukevičius 1992: fig. 5A, B), on a weakly arched basal plate. The smaller whorls have three gently curved, lingually directed, tricuspid teeth each having a large cusp centrally and one smaller cusp symmetrically on each side (Valiukevičius 1992: fig. 7D); all cusps are contiguous basally. The three tissue layers seen in the tooth whorls

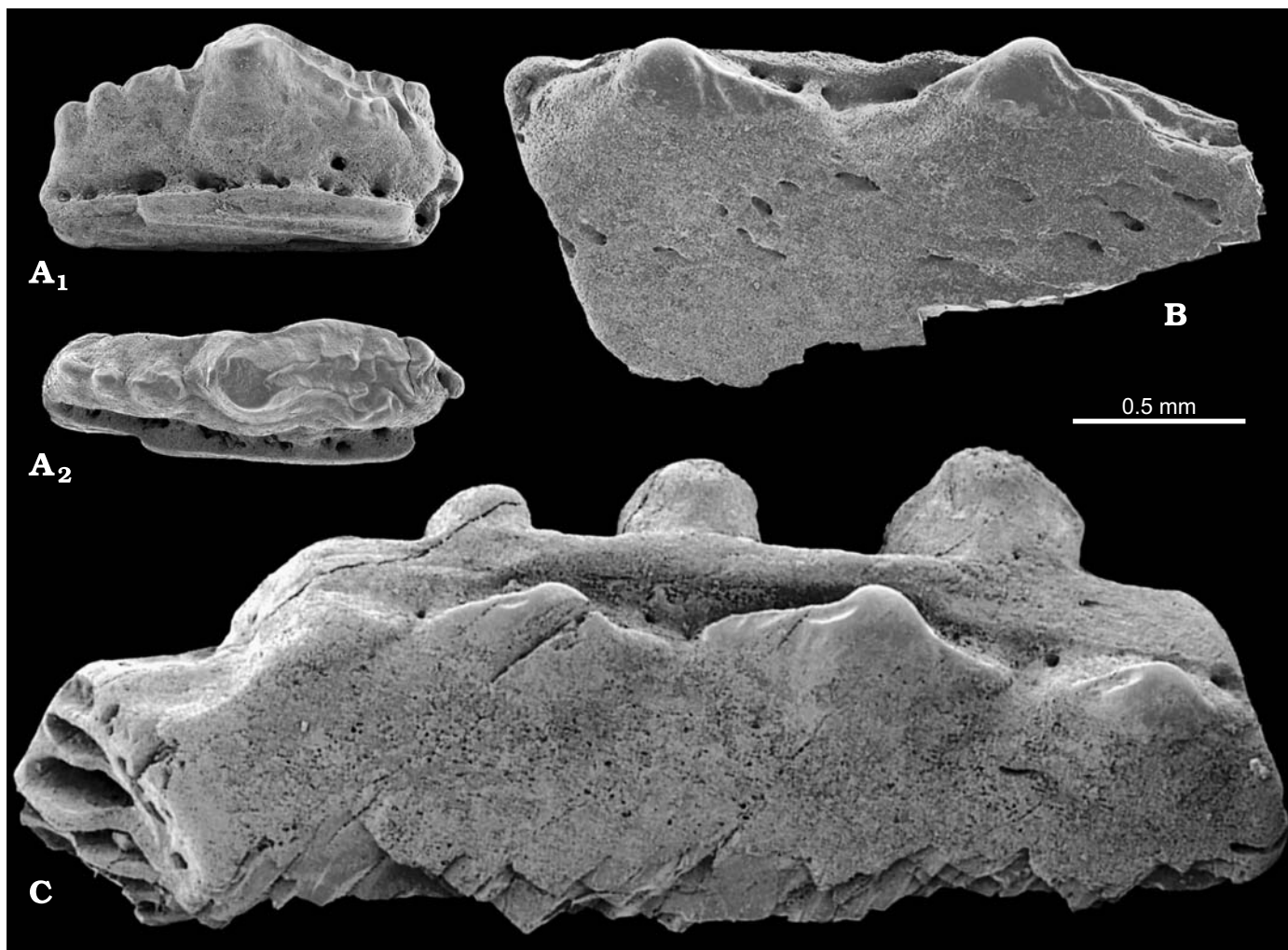


Fig. 13. SEM micrographs of ischnacanthiform jaw bone fragments from early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. **A**. First type of fragment. AEU 321 in mesial (A_1) and occlusal (A_2) views. **B**, **C**. The second type of fragment in occluso-lateral view. **B**. AEU 322. **C**. AEU 323.

of *Gomphonchus sandelensis* are present (Valiukevičius 1992: fig. 8H) with a distinction of having few pulp canals, with not even one at the teeth apices.

Tooth whorls of *Nostolepis striata* (the *Beyrichia* Limestone, Přidoli, Silurian, from the erratics of northern Germany) are composed of 3–4 teeth which have their long axes perpendicular to the length of the basal plate; cusps are almost without curvature, and they have (in lingual view) rounded-quadrangular sharp crests, with tooth rows separated from each other by distinct intervals. Whorls grew at the lingual end, by addition of a new portion of basal plate with a single tooth. They are composed of a bony basal layer which is distinctly thicker than in the ischnacanthiform whorls, vascularised bone forming a thin mid-layer, overlain by mesodentine (Gross 1971: figs. 11B, 13B; Denison 1979: fig. 7A) in which dentine tubules rise from a network of fine canals with lacunal swellings, becoming more orthodentine-like in a narrow superficial strip.

The Iranian tooth whorls resemble those from the Lower Devonian of Saudi Arabia (Forey et al. 1992: figs. 8, 9, Bur-

row et al. 2006: fig. 6.8–9). Forey et al. (1992) referred to them as ischnacanthid or cf. *Onychodus anglicus* Woodward (1888), whereas Burrow et al. (2006) referred them tentatively to the Ischnacanthiformes?, and compared them with isolated tooth whorls known elsewhere.

Ischnacanthiform dentigerous jaw bones

Figs. 13, 14B, C.

Material.—Eleven fragments from sample GI4, middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* conodont zones of Chahriseh section, Kaftari Mt., central Iran.

Description

Morphology.—The first type of jaw bone form is exemplified by a fragment (Fig. 13A; AEU 321) that is 1.25 mm long, with a tooth ankylosed to a thin lamellar bone plate. The tooth comprises an anterior flange (left part of 13A₁, A₂) having three cusps, each with an oval parabasal section, running along the jaw axis and joining into the anterior side of the large main tooth cusp, which shows a subcircular cross-

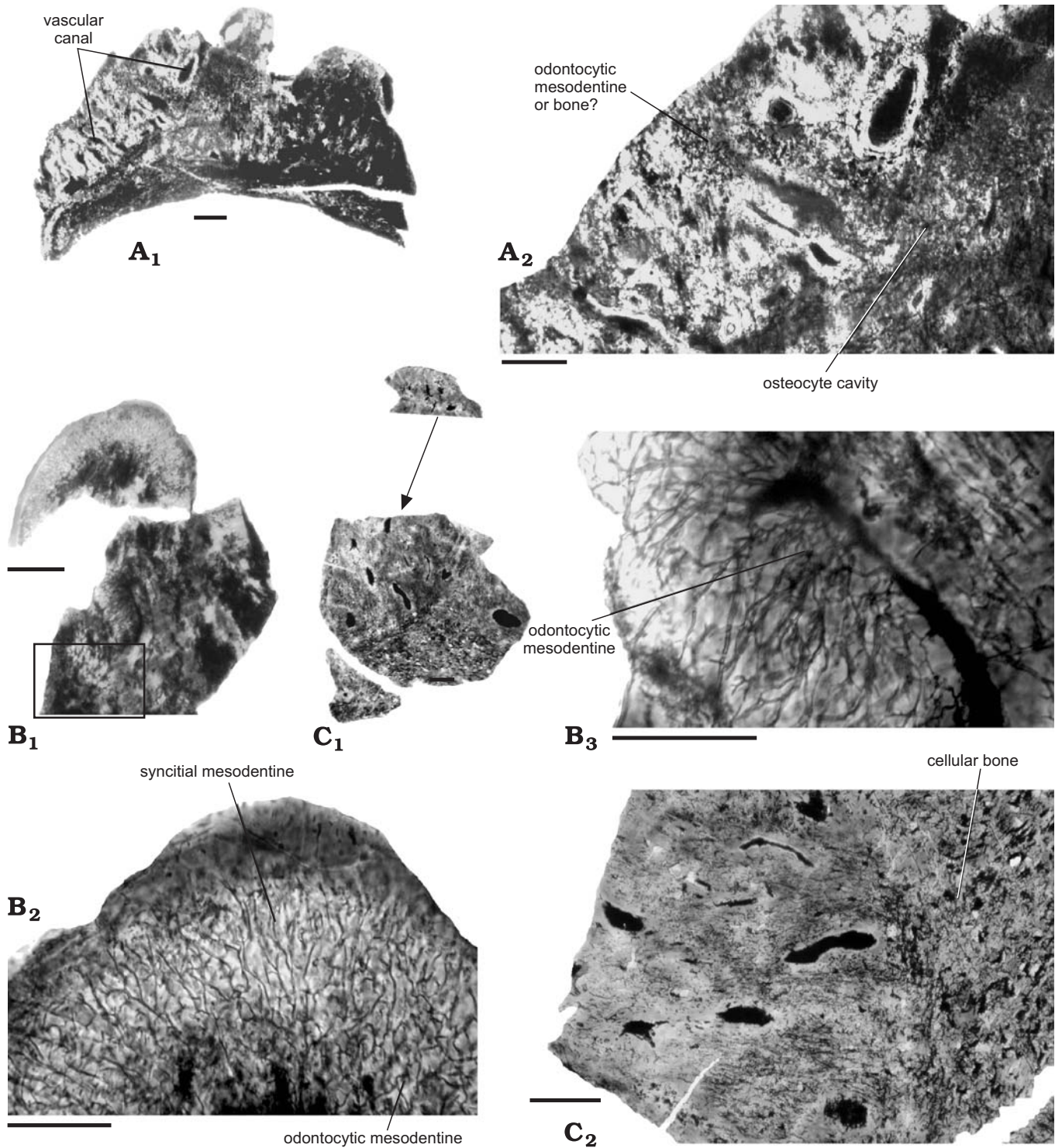


Fig. 14. Photomicrographs of histological structure of ?ischnacanthiform tooth whorl (A) and dentigerous jaw bones (B, C) in vertical longitudinal sections. Early Frasnian, horizon GI4 of an unnamed formation in the Chahriseh section, Kaftari Mt., central Iran. **A**. Thin section LIGG 3810 of a whorl with randomly displaced anterior tooth cusps of different size (left part in A₁) and an axial line of three larger cusps behind. A₁, high vascularisation of odontocytic mesodentine or bone tissue composing most of whorl; lamellar bone filling only thin basal plate; A₂, appearance of denteons (light strips surrounding dark vascular canals) and densely concentrated polygonal odontocyte cells characteristic of mesodentine/osteodentine in the intervascular space exposed in a central area of the same whorl, at higher magnification. **B**. Thin section LIGG 3813 of a single tooth cusp with the jaw bone portion from the presumed first type of jaw fragment showing general structure of tissues, with dentine canals in syncitial mesodentine of a cusp superficially grading to odontocytic mesodentine in a deeper layer (B₁), at higher magnification (B₂), and pulp canals with branching dentine tubules in odontocytic mesodentine which covers the basal osseous layer of the central cusp (B₃) (place indicated by rectangle in B₁). **C**. Thin section LIGG 3814 of a single tooth from the lingual row on a portion of jaw bone of the second type. The odontocytic mesodentine with large vascular canals extends to the cusp apex (C₁), grading into a cellular bone more deeply with increased density of osteocyte cells and wider vascular canals surrounded by thin osteons (magnified basal part of jaw bone, C₂). Scale bars 0.1 mm.

section where the tip is broken off or worn down. A pair of denticulated flanges (Fig. 13A₂) extends from the posterior side of the main cusp along the basal bone, decreasing in height and with a widening space between them away from the tooth apex. Numerous large circular vascular canals open out along the base of the tooth at the junction with the base of the jaw bone.

The second type of fragment (Fig. 13B, C; AEU 322) has low, long-based triangular teeth without secondary cusps, a lingual ridge with or without large cylindrical teeth, and basal bone with large longitudinal chambers separated from each other by comparatively thin-walled partitions. One example (Fig. 13C) is 3.75 mm long, and has a row along the occluso-lateral edge of three low triangular teeth with blunt apices and irregular radial ridges or striae. A robust ridge, transversely rounded-triangular, forms the lingual part of the jaw bone, and bears three teeth which are slightly closer together than the lateral teeth. The teeth in the lingual row are cylindrical, oval in parbasal section, with blunt, centrally rounded or laterally twisted apices. The largest, twisted tooth also has rounded lateral flanges. The two ridges are separated by a wide, moderately deep, pore-bearing longitudinal groove.

Histology.—Sectioned examples of jaw bone fragments show the structure of two teeth (Fig. 14B, C). LIGG 3813 (Fig. 14B), probably a secondary cusp from the first type of jaw fragment, is composed of a syncitial mesodentine superficially, with many dense, wavy dentinal canals with no or with rare and small lacunal widenings (right part in Fig. 14B₂), and without an outer orthodentine layer. Deeper in the tooth, the mesodentine gradually becomes odontocytic (Fig. 14B₂) with this tissue forming most of the tooth. Centrally in the tooth are wide, long (pulp) canals which have many canaliculi with lacunal widenings extending out from them, interspersed with odontocytes (Fig. 14B₃). The basal part of the tooth is composed of an osseous vascularised tissue.

LIGG 3814 (Fig. 14C), probably part of a cylindrical tooth cusp on the robust lingual ridge, is composed of a thin layer of odontocytic mesodentine superficially and vascularised cellular bone in the rest of the tooth and the basal jaw bone (Fig. 14C). Large vascular canals extend out to the mesodentine layer, and density of osteocyte cells increases in deeper layers of the jaw bone, where they became more oriented. Osteon structures, if present, are very thin.

Discussion.—Burrow (2004a, b) detailed the different forms and varieties of ischnacanthiform dentigerous jaw bones known worldwide from Silurian–Devonian deposits. The two different forms of jaw fragments from Chahriseh described here are possibly from the same taxon, with the first form being from the anterior part of the jaw bone (having a shelf-like basal bone, without a marked concavity for the jaw cartilage, and without a lingual ridge) and the second form being from the posterior part of the jaw bone (with a deep basal concavity which has been filled with horizontal bone trabeculae, a lingual tooth-bearing ridge, and short, worn lateral teeth). All late Middle to Late Devonian ischnacanthi-

forms (*Atopacanthus* Hussakof and Bryant, 1918, *Persacanthus* Janvier, 1977, *Grenfellacanthus* Long, Burrow, and Ritchie, 2004) have horizontal bone trabeculae within the jaw bone concavity. Long and Hairapetian (2000: fig. 6a–c) figured several teeth from an ischnacanthid jaw bone, misidentified as shark teeth ?*Protacrodus* sp., from the lower Famennian (*Palmatolepis triangularis*–*Palmatolepis crepida* zones) of the Dalmeh region, central Iran. These teeth, and those of *Persacanthus kermanensis* Janvier, 1977 (Frasnian, Iran), possibly *Persacanthus simpsonensis* Reed, 1986, *Atopacanthus? ambrockensis* Otto, 1999 (Eifelian Brandenburg Group, Germany), *Grenfellacanthus zerinae* Long, Burrow, and Ritchie, 2004 (Famennian Hunter Formation, New South Wales), and a taxon misidentified as ?placoderm from the ?lower Famennian Coffee Hill Member, New South Wales (Jones and Turner 2000: fig. 7.1–3) have lateral teeth (Janvier 1977: fig. 4C; Otto 1999: figs. 1I, 5C; Long et al. 2004: fig. 1A, C) similar to the teeth on AEU 321 (Fig. 13A), with a pair of denticulate flanges (presumed posterior); however, they lack the secondary cusps on the singular (presumed anterior) flange (a feature which is often present in Early Devonian ischnacanthiforms, including *Ischnacanthus*, *Poracanthodes*, *Xylancanthus* Ørvig, 1967, *Zemlyacanthus*). No other taxa are known to have the robust cylindrical cusps on the lingual ridge. Histological structure of the ?tooth cusp sectioned (Fig. 13B) compares with that of the secondary cusps of ischnacanthiform jaw bones from the Lower Devonian Connemarra Formation, New South Wales (Burrow 1995: fig. 6B). The jaw bone fragments could represent a new species, but the material in hand is too fragmentary and lacking in good diagnostic characters. Smooth-crowned acanthodian scales have been found with several Middle to Late Devonian ischnacanthiform jaw bones, but none were found in the Chahriseh residues. Such scales were found with the type specimens of *Persacanthus kermanensis* in the Frasnian of central Iran (Janvier 1977: fig. 4D).

Discussion

Taxonomic composition.—The basal Frasnian horizons of the Chahriseh section have yielded a diversified acanthodian association represented by climatiiforms, diplacanthiforms and ischnacanthiforms. The list includes:

Nostolepis sp. cf. *N. gaujensis*,
Iranolepis ginteri,
Milesacanthus sp. aff. *M. antarctica*,
 Diplacanthid fin spine fragments,
 Ischnacanthiform jaw bone fragments,
 ?Ischnacanthiform tooth whorls.

Nostolepis sp. cf. *N. gaujensis* resembles the type scales of the Baltic *N. gaujensis* in having broad rounded ridges extending almost the whole crown length and the broadest median ridges joined by an arc-like rim along the anterior crown edge. *N. gaujensis* from the Baltic, in distinction to the Iranian species, has fewer ridges (four) and a lower or almost

negligible neck. Histologically, *N. gaujensis* was not tested, thus it remains uncertain whether histological characters obtained from the Iranian specimens would correspond to the Baltic ones. Anyhow, the Iranian scales are ascribed to the genus *Nostolepis* in the family Climatiidae on the basis of histological characters, both strangewebe and odontocytic mesodentine structure, which are of primary taxonomical value.

Iranolepis ginteri belongs to a group of climatiid taxa having a sparse sculpture on scale crowns and distinguished by the highly raised medial area and well-developed lateral areas continuing the entire crown length. Its histological structure is of the classical *Nostolepis*-type characterised by particularly dense network of fine dentinal canaliculi with tiny osteocytes in most of the crown space, and by a strangewebe of short lacunae developed in a restricted posterior crown part.

Milesacanthus sp. aff. *M. antarctica* scales from Iran, with 8–14 linear grooves rather than low flattened ridges, have fewer grooves compared to the Antarctic ones, and a more fan-like ornament pattern when compared to the almost parallel grooves/ridges in *M. antarctica*. Histologically, the Antarctic scales have better developed pore canal and horizontal dentinal canal systems, allied with ascending canals in the vertical growth zones. The vascular canals in bases of the Iranian scales are pronounced in length and width, and the oriented dentinal canaliculi in the horizontal growth zones of the upper crown part correspond to the *Diplacanthus*-type structure. The diplacanthid fin spine fragments broadly resemble those of *Milesacanthus antarctica* in shape and ribs, but could belong to another species based on the wide extent of cellular bone/osteodentine composing most of the spine (except for the superficial ribbed part), and the lack of preservation of osteocyte cells in *M. antarctica*.

Tooth whorls with an axial line of large sharp teeth have traditionally been regarded as ischnacanthiform because they are widely found in ischnacanthiform genera, e.g., *Gomphonchus*, *Ischnacanthus*, *Poracanthodes*, and *Zemlyacanthus*. However, some climatiiforms are now known to have similar dental elements. The Iranian specimens show a climatiiform character in having a more osseous inner microstructure and an odontocytic mesodentine in the tooth bases, but are not comparable to any known taxa. It seems unlikely that they are from *Milesacanthus*, as diplacanthids lack teeth, and no such elements have been found in the Antarctic Aztec Siltstone samples. They could possibly be from one of the climatiid species from this locality; as noted earlier, scales similar to those of *Iranolepis ginteri* and the same form of tooth whorl have been identified in the Jawf Formation of Saudi Arabia.

Biostratigraphic significance.—The Chahrisah acanthodian assemblage shows marked similarities with the much richer fauna of the older Jawf Formation (Emsian) of Saudi Arabia, which includes *Milesacanthus ancestralis* scales and fin spines, *Iranolepis*-like scales, and the ischnacanthiform tooth whorls (Burrow et al. 2006). The rich Jawf Formation faunas include acanthodians with affinities to older Lochkovian fau-

nas from Spain and Brittany, and numerous placoderm taxa of which some appear related to Emsian taxa of south-eastern Australia. The acanthodian genera common to the Saudi Arabian and Iranian assemblages show a long stratigraphic range from late Pragian to early Frasnian. The faunal similarities are consistent with palaeogeographic reconstructions of Devonian (e.g., Scotese and McKerrow 1990; Golonka et al. 1994), which show Saudi Arabia and Iran as adjacent terranes, on the northern shelves of Gondwanaland.

The newly collected material from the Chahrisah area, despite its fragmentary character, adds knowledge to the relatively poorly known Upper Devonian acanthodian biostratigraphy. As mentioned, a single acanthodian *Nostolepis* sp. cf. *N. gaujensis*, comparable with the original Baltic taxon, was previously described from these horizons (Turner et al. 2002), allowing a tentative correlation with the Frasnian Šventoji Formation of the Baltic. This formation was attributed to the *Devononchus concinnus* acanthodian zone by the association of dominant *Devononchus* and rarer *Acanthoides?*, *Diplacanthus*, and *Nostolepis gaujensis* (Valiukevičius 1998), and also cf. *Rhadinacanthus* and cf. *Homalacanthus*. Comparable associations are widely distributed on the East European Platform (Timan-Pechora region, North Urals, Belarus, Main Devonian Field) but they do not contain *N. gaujensis*, the only fossil common for both regions, the Baltic and Iran. The age of the Šventoji Formation was disputed until recently; some researchers attribute its lower (main) part to the Gauja Formation in Latvia and Estonia, and to the upper Givetian based on correlation with the Timan-North Urals regions and miospore and vertebrate content (Mark-Kurik et al. 1999). Thus, if based on the presence of *N. sp. cf. N. gaujensis*, a Frasnian age for the Chahrisah horizon is not necessarily confirmed, but it could indicate the Givetian/Frasnian boundary sequences of rocks. *N. sp. cf. N. gaujensis* has also been recorded from micaceous siltstone lenses in the upper Frasnian Cucho Formation, Colombia, where it is associated with a fin spine and scales of diplacanthid *Florestacanthus morenoi* Burrow, Janvier, and Villarroel, 2003.

Another taxon worth mentioning for correlational discussions is *Milesacanthus* sp. aff. *M. antarctica*. *M. antarctica* occurs in the Aztec Siltstone fauna of Antarctica which is now considered Givetian in age rather than Upper Devonian as it was previously assessed. Young and Burrow (2004) defined its Givetian age without indication of conodont zone; Young and Turner (2000) attributed it to the *Polygnathus varcus* conodont zone, and Turner (1997) treated it as early Givetian based on the *Turinia antarctica* thelodont zone.

The Iranian acanthodian association containing at least one new climatiid and possibly two ischnacanthiform taxa, does not contradict the early Frasnian age of the Chahrisah horizon proposed on the presence of conodonts from the middle *Mesotaxis falsiovalis* to *Palmatolepis hassi* zones and of *Australolepis seddoni* (Turner et al. 2002). The early Frasnian *Australolepis seddoni* thelodont zone is recorded by occurrences in the Shotori Range of Iran and the Gneudna

Formation in Western Australia (Turner 1997; Turner et al. 2002).

Turinia hutkensis, the other thelodont found in the association, has a late Givetian age at the type locality, but Turner (1997) considered it to range from late Givetian to early Frasnian. This range is also supported by the two most valuable zonal acanthodians, *Milesacanthus* sp. aff. *M. antarctica* and *Nostolepis* sp. cf. *N. gaujensis*.

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