A new early Silurian prioniodontid conodont with three P elements from Iran and associated species

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A prioniodontid conodont *Arianagnathus jafariani* gen. et sp. nov. from the late Llandovery part of the Niur Formation of the Derenjal Mountains, East Central Iran had an apparatus bearing 3 pairs of P elements. Pa elements of its apparatus are closest to those of *Icriodella sandersi* (Llandovery–Wenlock boundary interval, Wales, Great Britain) in the weak development of an icrion. Due to the small sample size not all S-elements have been identified but those present are similar to those described in the *Icriodella* and *Icriognathus* apparatuses. Based on similarities with previously described apparatus *Notiodella* we suggest that *Arianagnathus jafariani* gen. et sp. nov. probably had an apparatus of 17 elements. *Arianagnathus* is therefore an important additional example that has potential for aiding the future revision of the palaeobiological arrangement of elements within and the phylogeny of conodont apparatuses with 3 P elements, one of which is icrion bearing. The completely known apparatus of associated *Ozarkodina derenjalensis* sp. nov. shows similarity to some unnamed *Ozarkodina* from Wales, Great Britain. Many of the conodonts found in the Llandovery part of the studied section are cosmopolitan; the new conodont species seem to have their possible closest relatives in Avalonia.

Key words: Conodonta, taxonomy, Silurian, Llandovery, Iran.

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Introduction

Illustrations and identifications of conodonts have recently been published from a section located in the Derenjal Mountains, East Central Iran (Fig. 1; Männik et al. 2013). The fauna includes a taxon with three pairs of P elements described below as *Arianagnathus jafariani* gen. et sp. nov. (named temporarily gen. et sp. nov. A aff. *Icriodella*? *sandersi* Mabillard and Aldridge, 1983; Männik et al. 2013). One of its P elements is icrion-bearing. A natural assemblage containing 17 elements including three pairs of P elements (one of which is also icrion-bearing) was described under a new genus *Notiodella* from the Upper Ordovician Soom Shale of South Africa (Aldridge et al. 2013). The discovery of bedding plane assemblages of *Notiodella* raises many questions regarding the composition of apparatuses assumed only from discrete element collections, particularly those with three pairs of P elements. One of the questions is related to the higher classification of icrion bearing taxa, another to the palaeobiological arrangement of elements in such apparatuses. Disarticulated collections of *Arianagnathus* gen. nov. from Iran provide another example of a genus with three P elements to add to several previously described genera and one that potentially conforms to the arrangement of the newly described apparatus *Notiodella*. A thorough revision of these taxa, their apparatus structures and phylogeny is required. Undoubtedly more material, both of *Arianagnathus* and also bedding plane assemblages of other taxa will be required to properly answer these questions. While this paper does not set out to do this, it provides a useful additional example to add to the data associated with these groups.

Both *Notiodella* and *Arianagnathus* gen. nov. are geographically limited (South Africa and Iran, respectively) and demonstrate great similarity to *Icriodella*. *Icriodella* is also sporadically distributed but known from Avalonia, Baltica, and Laurentia. Although the latest palaeogeographical reconstruction shows that present-day Iran was located far away from Baltica and Laurentia, on the other side of the Rheic Ocean, this seems not to have been a major migration barrier

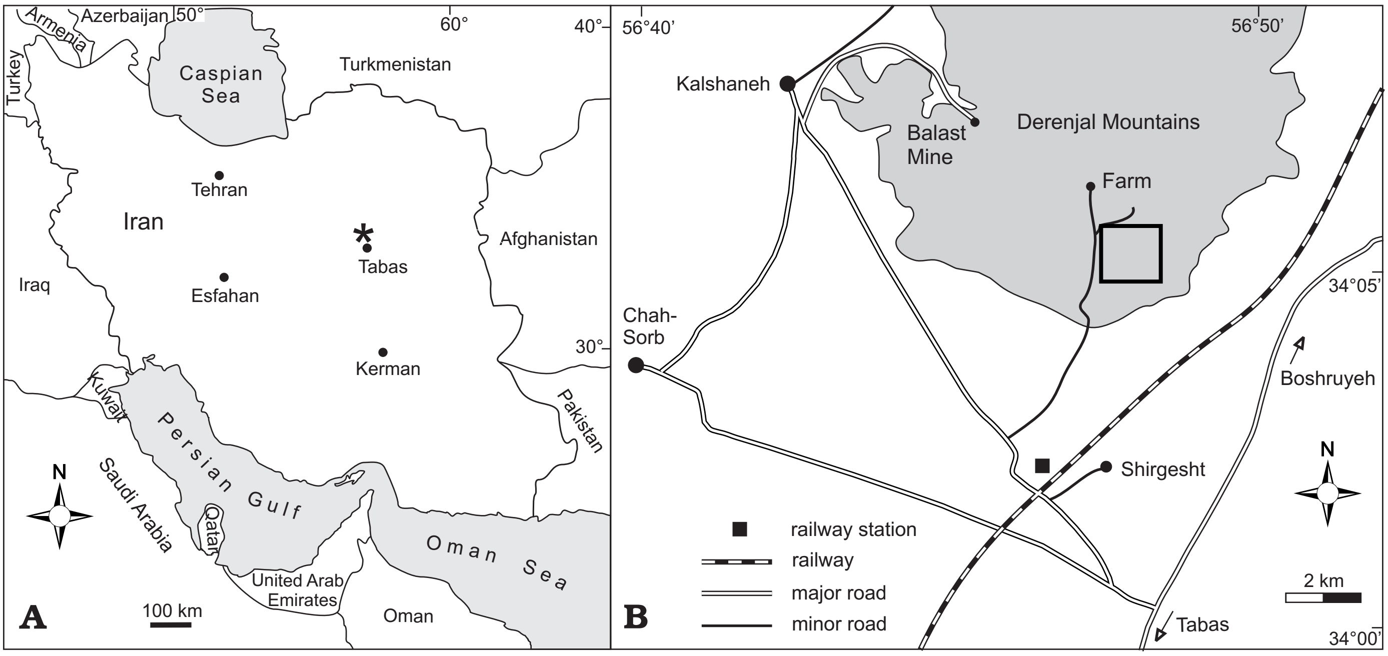


Fig. 1. A. Location of the study area in East Central Iran (asterisk). **B**. Studied area in the Derenjal Mountains (open frame indicates location of studied sections).

for many different organisms including the conodonts. Many of the conodonts found in the Llandovery part of the studied section of the Niur Formation are cosmopolitan. Several of the new conodont taxa (including *Arianagnathus* gen. nov.) to be described in this paper seem to have their possible closest relatives in Avalonia on the other side of the Rheic Ocean in the Marloes Bay section, SW Dyfed, Wales (Männik et al. 2013). Phlebolepidiform and loganelliiform thelodonts recovered from the part of the formation deposited in a shallow water carbonate ramp environment also provide evidence of a hitherto unknown southward dispersal of the thelodont genus *Loganellia* to the shelves of peri-Gondwana (Hairapetian et al. 2008). Nonpalaeocope ostracods recovered from the basal part of the formation, despite their mid-palaeolatitude peri-Gondwanan setting and isolation from low palaeolatitudes, show striking affinities with Late Ordovician and Early Silurian ostracod faunas of palaeo-equatorial/tropical Laurentia (Hairapetian et al. 2011). Conodonts from this section located in the Derenjal Mountains, East Central Iran, have high biostratigraphic potential and could be used for general regional Palaeozoic palaeogeographic reconstructions.

Institutional abbreviations.—NHMUK PM, Department of Earth Science, Natural History Museum, London, UK.

Other abbreviations.—CAI, Colour Alteration Index.

Geological setting

The Niur Formation of Iran has been dated as Llandovery to Pridoli by various authors on the basis of its conodont, ostracod, thelodont, coral, and brachiopod faunas (e.g., Ruttner et al. 1968; Aldridge in Hamedi et al. 1997; Hairapetian et al. 2008, 2011; Männik et al. 2013). Some authors suggest that the uppermost part of the formation is Devonian in age (Walliser in Ruttner et al. 1968; Weddige 1984). Lists of Silurian conodonts occurring in the formation have been published by Ruttner et al. (1968) and Hamedi et al. (1997). Key conodont taxa recovered from the Niur Formation have underpinned recent studies on thelodonts (Hairapetian et al. 2008), nonpalaeocope ostracods (Hairapetian et al. 2011) and brachiopods (Hairapetian et al. 2012) and have helped to date the new taxa described in these papers. A review of all conodont studies concerning the Niur Formation, including lists of identifications as well as a review of all previous faunal studies can be found in Männik et al. (2013). As the emphasis of that study was to present the fauna in a stratigraphical context some taxa requiring further study were illustrated in open nomenclature with the intention of later describing them in more detail. The samples requiring further study and with the richest faunas were mainly from Llandovery age carbonate rocks in the middle part of the section. These were deposited in a shallow water carbonate ramp environment. This paper concentrates on this part of the section and aims to describe the new taxa previously left in open nomenclature.

The reference section of the Silurian Niur Formation is located about 65 km north-west of Tabas on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran, and has a total thickness of 551.75 m. The Silurian outcrops are exposed on three major hills A–C. The conodonts described here come from samples from Hill B, from the topmost Unit 6 (S12), from Unit 7 (S15–S17) and from Unit 11 (S18 and S19) (Fig. 2). Full details of all samples studied for conodonts from the section have been pro-

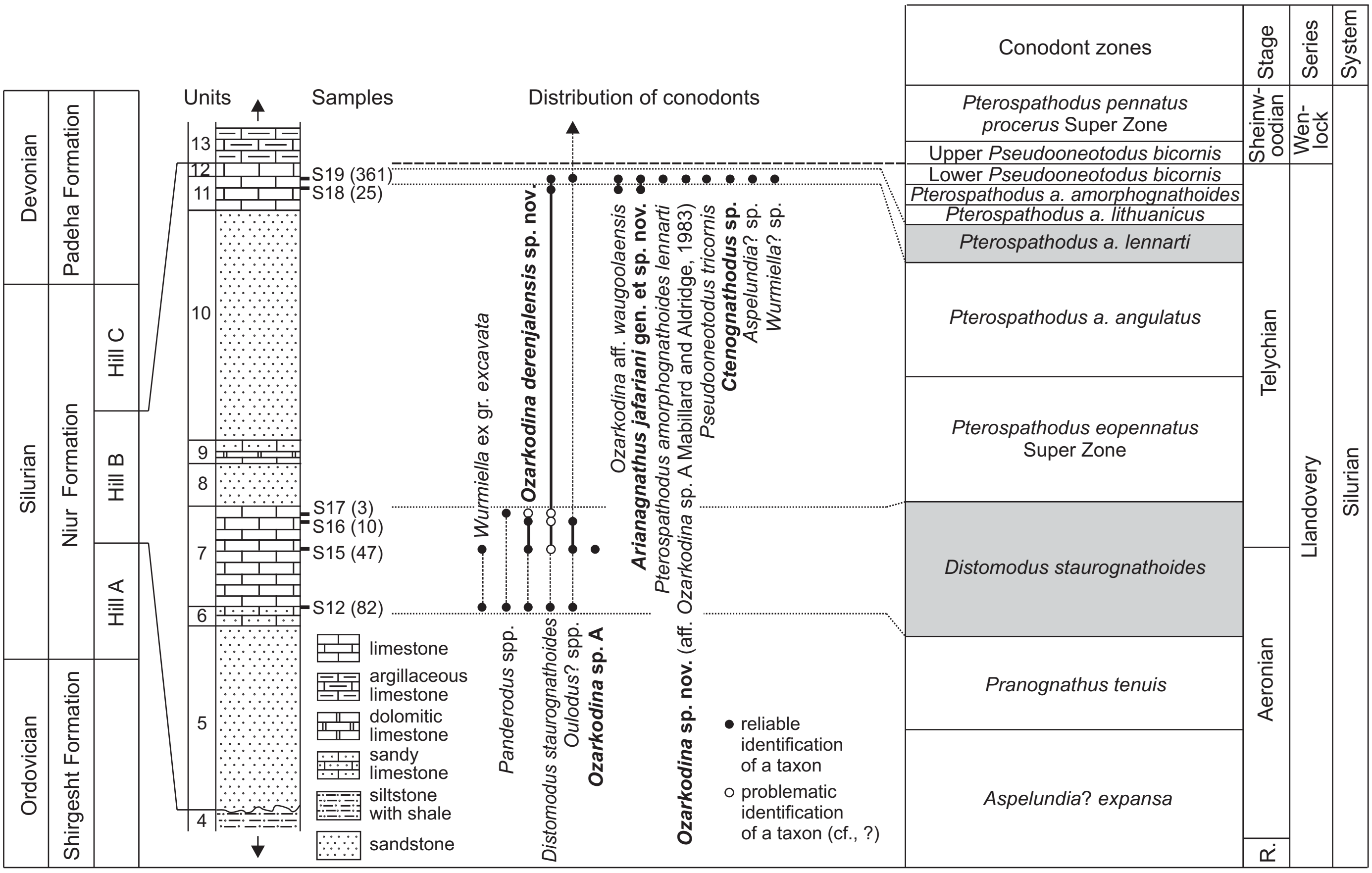


Fig. 2. Distribution of conodonts in strata exposed on Hill B, for details see Männik et al. (2013). Arrows below and above the log indicate that the section continues in both directions. Samples: location and number of sample (total number of specimens in a sample), only productive samples are indicated. Taxa in bold are described in this paper, arrow at the upper end of distribution line of *Oulodus* spp. indicates that this taxon also occurs in higher strata. Conodont zones modified from Cramer et al. (2011), grey boxes indicate zones which were recognised in the studied section. Abbreviations: a., amorphognathoides; R., Rhuddanian.

vided by Männik et al. (2013); a description of the samples studied here are included below.

Sample S12 was taken 6.48 m from the base of Unit 6 that consists of 6.72 m of thinly bedded brown sandy limestone with silicified brachiopods. Samples S15–S17 come from the upper half of Unit 7, S15 was taken 19.40 m, S16 28.50 m, and S17 31.00 m above the base of the unit. This unit consists of 33.80 m of medium to thin bedded grey to brown bioclastic packstone and grainstone rich in brachiopods, corals, bryozoans, orthoconic nautiloids, and tentaculites. Flügel and Saleh (1970) reported the Llandovery rugose corals *Grewingkia*, *Schlotheimophyllum*, *Streptelasma, Tenuiphyllum*, *Tryplasma*, and *Paliphyllum*, from Hill A and the limestone interval in the middle part of Hill B where our samples were taken. The conodont *Distomodus staurognathoides* (Walliser, 1964) in sample S12 indicates that this level, and the strata above, cannot be older than mid Aeronian. This agrees with the dating based on ostracods; *Pachydomella wolfei* Copeland, 1974, *Steusloffina cuneata* (Steusloff, 1895), *Arcuaria*? *triangulata* Neckaja, 1958 and *Punctobeecherella punctata* Copeland, 1974 in association with pentamerid brachiopods from Hill A (Unit 2) suggest a mid Aeronian age for these strata (Hairapetian et al. 2011). Hence, it is evident that samples S12–S17 were taken from strata no older than mid Aeronian but probably latest Aeronian or earliest Telychian in age (Männik et al. 2013). Sample S18 was taken 7.80 m and S19 10.77 m above the base of the Unit 11 that consists of 11.67 m of thinly bedded grey bioclastic mudstone, wackestone and grainstone with brachiopods and corals. Männik et al. (2013) report *Pterospathodus amorphognathoides lennarti* Männik, 1998 from sample S19 indicating a roughly mid-Telychian age for this level. Only the last two samples yield *Arianagnathus* gen. nov., 4 specimens in sample S18 and 174 in sample S19. In the last sample it forms about 48% of the assemblage.

Material and methods

Samples were collected in 2004 and 2007 and ranged in size from 0.5 to 3 kg. All samples were dissolved in a buffered solution of 10% acetic acid using standard methods and productive samples yielded between 2 and 361 conodonts. The lowest sieve size was 15.6 μm and each residue was picked in its entirety without using heavy liquid separation techniques. Illustrated specimens were gold-palladium coated and photographed using a Phillips XL-30 scanning electron microscope at the Natural History Museum. Preservation of the material is quite poor as most of the specimens are broken. The conodonts are brown to dark brown in colour (CAI = 3–4) and no white matter is visible. All figured specimens and assemblage slides are deposited at the NHMUK.

Where positional homology of elements in an apparatus has been determined, either from natural assemblages or through direct comparison with natural assemblages, we follow homology-based notation identifying P_1–P_4, M, and S_0–S_4 (P_n–S_n) elements outlined by Purnell et al. (2000). When there is no evidence for homology between different element types, the traditional Pa, Pb, Pc, M, Sa, Sb, Sc notation introduced by Sweet and Schönlaub (1975) and modified by Cooper (1975) and Sweet (1981, 1988) has been followed. In descriptions of elements the terms "anterior", "posterior", "lateral", "inner", "outer", "upper", and "lower" are used in the conventional sense for isolated conodont elements (see Sweet 1981, 1988), and do not refer to biological orientation in the animal.

Composition of the new apparatus

Reconstructions of conodont apparatuses are mainly based on scattered elements dispersed in the sediment after the death and decomposition of the animals. On rare occassions, parts of or complete apparatuses as fused clusters or bedding plane assemblages can be found. However, only such finds provide unequivocal evidence about the structure of conodont apparatuses and can be used as templates for the reconstruction of the apparatuses of taxa that are known only from scattered elements. Based on the available natural assemblages two main groups of apparatuses composed of ramiform and/or platform elements are known: apparatuses of 15 (most common) and of 19 elements. The second group is currently represented only by the genus *Promissum*. Recently, a natural assemblage of a new conodont taxon, *Notiodella keblon*, containing 17 elements was described from the Upper Ordovician Soom Shale of South Africa (Aldridge et al. 2013). This apparatus comprises three paired P elements (P_1, P_2, and P_3; P_1 is icrion-bearing), paired M, S_1, S_2, S_3, and S_4 elements, and an unpaired S_0 element. This was the first time that a 17-element apparatus plan has been unequivocally demonstrated in conodonts.

The new Iranian apparatus, *Arianagnathus* gen. nov., also has three pairs of P elements (Pa, Pb, Pc). Additionally, paired M, Sc, Sb_1, Sb_2 and an unpaired Sa element can be recognised in our collection. Some other Silurian prioniodontid apparatuses are also known to include three pairs of P elements, for example *Pranognathus* (Männik and Aldridge 1989), *Astropentagnathus* (Armstrong 1990), and *Coryssognathus* (Miller and Aldridge 1993). All these reconstructions are based on assemblages of discrete elements only. In general morphology, the new apparatus displays great similarity to that of *Icriodella*. However, only two pairs of P elements (Pa and Pb) are known in the *Icriodella* apparatus (Sweet 1988), although Aldridge et al. (2013), based on great general similarity between the *Icriodella* and *Notiodella* apparatuses, proposed that there might be a third P element in the *Icriodella* apparatus. This still remains to be shown. Following the cladistic classification of Donoghue et al. (2008) in which *Icriodella* is placed in the Family Balognathidae, Aldridge et al. (2013) assign *Notiodella*, like the similar *Icriodella*, to the same family. However, they do not exclude the possibility that the inclusion of additional (new) icrion-bearing taxa to the analysis, might result in the resolution of a distinct clade referable to the family Icriodontidae Müller and Müller, 1957. Dzik (1991) has previously suggested that *Icriodella* might be accommodated in this family. As the apparatus of *Arianagnathus* gen. nov. described below is closest to *Notiodella* and as *Notiodella* was assigned to the family Balognathidae sensu Donoghue et al. (2008) by Aldridge et al. (2013), we tentatively consider this new taxon also to be a representative of the same family. The Icriodontidae/Balognathidae family issue may only be resolved when/if further bedding plane material is uncovered. Until then we follow the classification of Donoghue et al. (2008) in the following systematic section.

Systematic palaeontology

Phylum Chordata Bateson, 1886

Class Conodonta Eichenberg, 1930

Division Prioniodontida Dzik, 1976

Family ?Balognathidae Hass, 1959

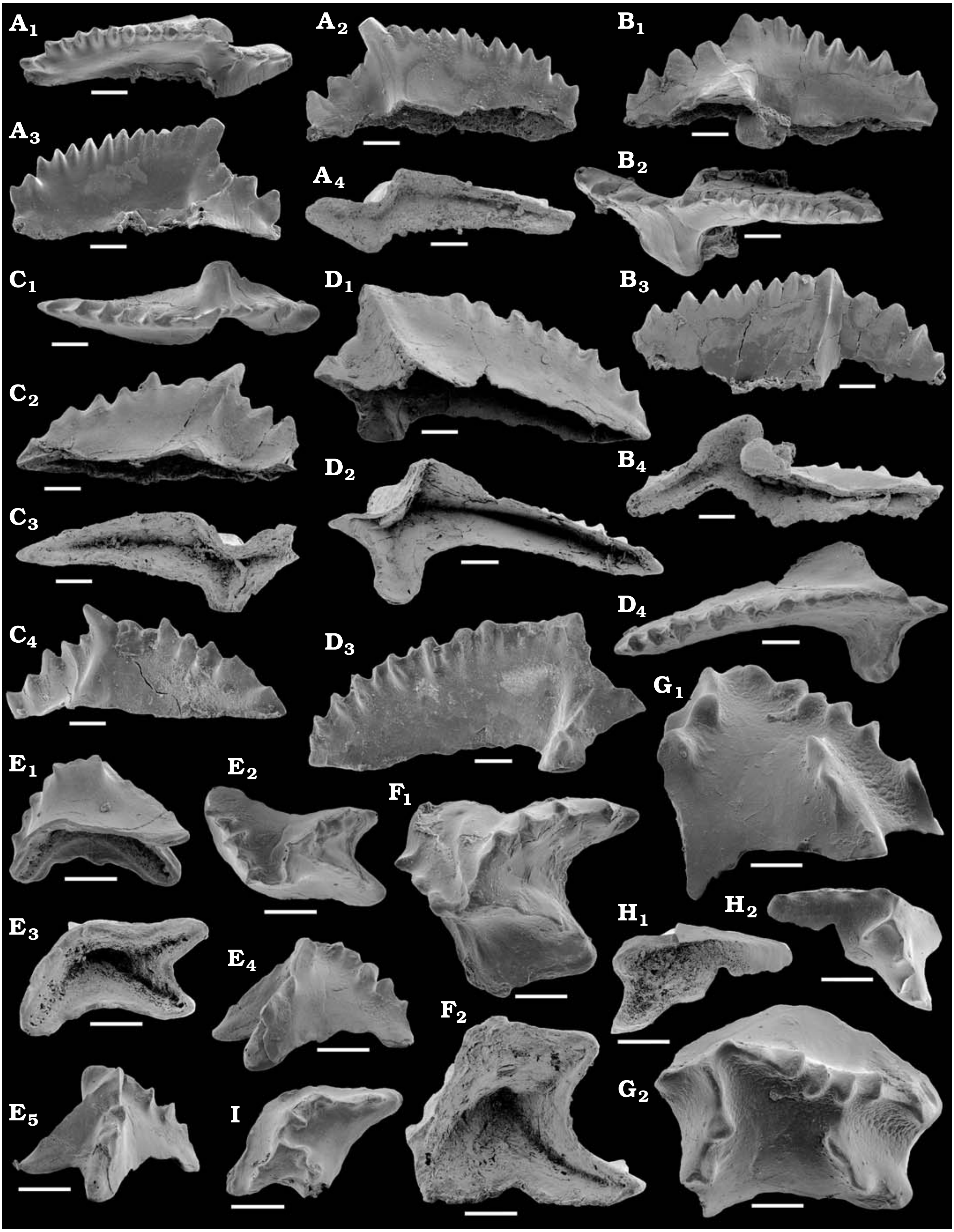
Genus *Arianagnathus* nov.

Etymology: After *Ariana*, older Latinized geographical name of the eastern part of the country from which the type material originated.

Type species: *Arianagnathus jafariani* sp. nov., by monotypy; see below.

Diagnosis.—An apparatus consisting of at least 14 paired elements: Pa, Pb, Pc, M, Sc, Sb_1, Sb_2, and a single symmetrical Sa element. Pa, Pb, and M elements are diagnostic: Pa element pastiniscaphate, thin-walled and broad-based with short posterior process bearing low, broad denticles, anterior

Fig. 3. Prioniodontid conodont *Arianagnathus jafariani* gen. et sp. nov from Llandovery (Silurian) of Derenjal Mountains, East Central Iran, Hill B → (sample S19). **A–D**. Pa elements. **A**. Sinistral element, NHMUK PM X 3623, in upper (A_1), inner lateral (A_2), outer lateral (A_3), and lower (A_4) views. **B**. Dextral element, NHMUK PM X 3603, in outer lateral (B_1), upper (B_2), inner lateral (B_3), and lower (B_4) views. **C**. Dextral element, NHMUK PM X 3624, in upper (C_1), inner lateral (C_2), lower (C_3), and outer lateral (C_4) views. **D**. Sinistral element, NHMUK PM X 3625, in inner lateral (D_1), lower (D_2), outer lateral (D_3), and upper (D_4) views. **E–I**. Pb elements. **E**. Dextral element, NHMUK PM X 3626, in inner lateral (E_1), upper (E_2), lower (E_3), outer lateral (E_4), and posterior (E_5) views. **F**. Dextral element, NHMUK PM X 3604, in upper (F_1) and lower (F_2) views. **G**. Dextral element, NHMUK PM X 3627, in outer lateral (G_1) and upper (G_2) views. **H**. ?Sinistral element, NHMUK PM X 3628, in lower (H_1) and upper (H_2) views (posterior process preserved). **I**. Dextral element, NHMUK PM X 3629, in upper view. Scale bars 0.1 mm.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process long with low denticles that thicken perpendicular to the blade to form short ridges of icriodelliform aspect that widen towards termination of process. Pb element pastiniscaphate, sub-triangular to quadrangular in upper view with widely opened deep basal cavity. Three main processes bearing rows of low denticles with the main denticle row arranged sigmoidally, also with short ridges of icriodelliform aspect perpendicular to the blade that are better developed distally. M element dolabrate with short anticusp and denticulate posterior process, on which denticle at the base of the cusp partly overlaps it.

Stratigraphic and geographic range.—Telychian (Llandovery, Silurian); Iran.

Arianagnathus jafariani sp. nov.

Figs. 3, 4.

?1980 *Ozarkodina* n. sp. A. Helfrich, 1980; Helfrich 1980: 568, pl. 1: 13–15. Pa element.

2013 Gen. et sp. nov. A (aff. *I.*? *sandersi* Mabillard and Aldridge, 1983); Männik et al. 2013: 10, fig. 4: r–s. Pa and Pb elements.

Etymology: After late Professor Mohammad Ali Jafarian (Esfahan), in recognition of his studies on Late Devonian brachiopods and regional stratigraphy.

Holotype: NHMUK PM X 3626, Pb element (Fig. 3E).

Type locality: A section located about 65 km north-west of Tabas, on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran; Hill B, uppermost Unit 11 (sample S19).

Type horizon: *Pterospathodus amorphognathoides lennarti* Conodont Zone, Telychian, Llandovery, Silurian.

Diagnosis.—Same as for genus.

Material.— 178 specimens: Pa element, 80; Pb, 16; Pc, 26; M, 26; Sc, 2; Sb_1, 10; Sb_2, 13; Sa, 5.

Description.—*Pa element* (Fig. 3A–D): Pastiniscaphate, very slightly S-shaped in upper view, with a stout low posteriorly inclined cusp situated close to posterior end of element. Anterior process long, slightly curved to outer side of element, and bearing up to 13 low denticles which thicken perpendicular to blade forming short ridges of icriodelliform aspect that get progressively wider from mid-blade towards termination of process. Height of anterior process decreases gradually away from cusp and more rapidly towards termination of process. Process can end abruptly or taper to a point. Posterior process short with 3–5 low, broad denticles that rapidly decrease in height distally. Basal cavity deep, thin-walled and open below entire element. Inner lateral flare of cavity lip located beneath cusp, usually bears distinct medial ridge that extends into lateral face of cusp (Fig. $3A_2$, B_3, C_2, D_1). Outer lateral flare of cavity lip better developed and slightly to posterior of inner flare. Some specimens also bear a distinct medial ridge on outer flare extending into lateral face of first or second denticle on posterior process and not up side of cusp (Fig. $3B_1$, B_2, C_4, D_3). Some larger specimens with outer flare developed into short process with indistinct distal denticles (Fig. $3D_3$, D_4).

Pb element (Fig. 3E–I): Pastiniscaphate, sub-triangular to quadrangular in upper view with three main processes bearing rows of low denticles with main denticle row arranged sigmoidally. On dextral elements main row of denticles curve smoothly into an S-shape (Fig. $3E_2$, F_1, G_2, I), on sinistral elements (Fig. 3H?) probably a reverse S-shape, although only specimen is incomplete. Denticles in main denticle row widen distally to short ridges of icriodelliform aspect. Cusp at junction point of processes, indistinct from denticles. Basal cavity deepest below the cusp and opens along the whole element. On larger specimens, more quadrangular in outline (Fig. $3F_1$), margins of basal cavity become strongly flared and additional ridges, sometimes denticulated, appear on the outer side between the main rows of denticles (Fig. $3G_2$).

Pc element (Fig. 4A, B): Pastinate with tall slightly curved cusp. Cusp triangular in transverse section, anterior and posterior edges sharp, inner face almost flat. All three processes short and pointed towards base with up to three low denticles. Distinct ridge continues up outer face of cusp from denticles on base of outer lateral process (Fig. 4A, B_1). Basal cavity deeply excavated and extends below entire element.

M element (Fig. 4C, E): Dolabrate with tall inwardly inclined and blade-like cusp. Anterior and posterior edges of cusp sharp, outer lateral face gently convex, inner lateral face gently convex near cusp tip but becoming increasingly convex downwards to produce an inwardly flared basal cavity margin. Margin is pinched at base of cusp; occasionally a weak ridge is developed at this point and extends to base of cusp. Anterior edge of cusp continues to short anticusp. Posterior process straight, inclined downwards and bearing up to four tall, discrete denticles. Denticle closest to cusp inclined inwards towards base of cusp and partly overlaps it on inner side (Fig. $4C_1$, C_2, E_2). Basal cavity triangular and deep, extending below whole element.

Sc element (Fig. 4D): Bipennate with short posterior and inner lateral processes both probably bearing a single denticle. Inner lateral process slender and inwardly pointed; posterior process denticle better developed with broad base. Basal cavity deep beneath cusp and filled with well preserved basal body.

Sb_1 element (Fig. 4F, J): Asymmetrical tertiopedate with

Fig. 4. Prioniodontid conodont *Arianagnathus jafariani* gen. et sp. nov. from Llandovery (Silurian) of Derenjal Mountains, East Central Iran, Hill B (sample S19). **A**, **B**. Pc elements. **A**. Dextral element, NHMUK PM X 3630, in outer lateral view. **B**. Sinistral element, NHMUK PM X 3631, in outer lateral (B_1), inner lateral (B_2), and lower (B_3) views. **C**, **E**. M elements. **C**. Dextral element, NHMUK PM X 3632, in lower (C_1), inner lateral (C_2), posterior (C_3), and outer lateral (C_4) views. **E**. Dextral element, NHMUK PM X 3634, in inner lateral (E_1) and lower (E_2) views. **D**. Sc element, NHMUK PM X 3633, in outer lateral (D_1), lower (D_2), and inner lateral (D_3) views. **F**, **J**. Sb_1 elements. **F**. Dextral element, NHMUK PM X 3635, in posterior (F_1), outer lateral (F_2), and inner lateral (F_3) views. **J**. Sinistral element, NHMUK PM X 3639, in posterior (J_1) and outer lateral (J_2) views. **G**. Sa element, NHMUK PM X 3636, in lateral (G_1) and posterior (G_2) views. **H**. Dextral Sb_2 element, NHMUK PM X 3637, in posterior (H_1) and inner lateral (H_2) views. **I**. Dextral Sb_2 element, NHMUK PM X 3638, in posterior (I_1), lower (I_2), and outer lateral (I_3) views. Scale bars 0.1 mm. →


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H2
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I2
I3
J1
J2

reclined cusp. Anterior face of cusp rounded, posterior face bears a medial ridge that extends to denticle row on long slightly downward and inwardly curved posterior process. The process bears up to six laterally compressed, irregular, erect denticles that are slightly fused at base. Cusp continues downwards to an adenticulate inner lateral process. A distinct high ridge is present on inner lateral side of cusp and continues along entire length of process. Steeply downwardly directed outer lateral process bears 1–4 denticles. Basal cavity full of basal body in all specimens available.

Sb_2 element (Fig. 4H, I): Asymmetrical tertiopedate with tall reclined cusp. Morphologically, Sb_2 element almost identical to Sb_1 element. Sb_2 element differs as both lateral processes are denticulated and bear up to three denticles. Inner lateral process of Sb_2 element curved slightly inwards rather than as continuation of cusp as on Sb_1 element.

Sa element (Fig. 4G): Alate and morphologically similar to the Sb_2 element. The main difference is that the Sa element is symmetrical. Both lateral processes bear up to three compressed denticles.

Remarks.—*Arianagnathus jafariani* gen. et sp. nov. displays features characteristic of several known apparatuses. As noted above, the apparatus of *Arianagnathus* is most similar to *Notiodella*. However, in *Notiodella* two P elements (P_1 and P_2) are pastinate and one (P_3) makellate (or modified pastinate) (Aldridge et al. 2013) whereas in *Arianagnathus* only one P element (Pc) is pastinate, other two (Pa and Pb) are pastiniscaphate. One of the morphologically closest is also *Icriognathus* from the earliest Llandovery (Rhuddanian) of Estonia (Männik 1992). However, the Pa element of *Icriognathus* has poorly developed parallel rows of three denticles on the anterior process (Männik 1992: pl. 1: 2, 3, 7, 10, 12, 14, pl. 2). Undescribed collections (PM unpublished material) suggest that these become better developed in specimens from younger strata. The second P (Pb) element of *Icriognathus* is also pastinate (ambalodiform) with a distinct cusp (Männik 1992: pl. 1: 1) and a third P element has not been found. The M and S elements of *A. jafariani* gen. et sp. nov. are also similar to elements in the *Icriodella*, *Pranognathus* and *Pterospathodus* apparatuses. The apparatus of *Icriodella* has a pastinate second P element with a tall stout cusp (Sweet 1988: fig. 5.18) and is lacking a third P element. The *Pranognathus* Pa element has five well developed processes each of which bears a single row of denticles, Pb and Pc elements are pastinate the first one with three primary and one secondary process (Männik and Aldridge 1989: text-fig. 5D–H, I, V–X) and the second with three primary processes (Männik and Aldridge 1989: text-fig. 5J, K; Y, Z). Both elements have a distinct cusp. *Pterospathodus* has four pairs of P elements two of which (Pb_1 and Pb_2) are angulate, the Pa is carminate or pastinate and Pc pastinate with a distinct cusp (Männik 1998). Helfrich (1980: pl. 1: 13–15) figured elements from Virginia and Maryland, United States that are morphologically quite similar to the Pa element of *A. jafariani* gen. et sp. nov. These elements identified by Helfrich (1980) as *Ozarkodina* n. sp. A occur together with *Pterospathodus amorphognathoides* Walliser, 1964, i.e., in strata of roughly the same age as the Iranian material. Unfortunately, the illustrations of the elements of *P. amorphognathoides* in Helfrich (1980: pl. 1: 1–6, identified as *Carniodus carnulus* Walliser, 1964; pl. 2: 17–19) are of too poor quality to allow identification of its subspecies and further refinement of the age. The illustrations of *Ozarkodina* n. sp. A in Helfrich (1980) do not allow detailed comparison of these specimens with the Pa element of *A. jafariani* gen. et sp. nov. as only lateral views of them are illustrated.

Several elements of *A. jafariani* gen. et sp. nov. are very similar to elements in the apparatus of *Icriodella*? *sandersi* Mabillard and Aldridge (1983: 33, pl. 2: 1–10). According to the original description by Mabillard and Aldridge (1983: 33), the apparatus of *I.*? *sandersi* contains a straight thin-walled broad-based P element with icriodelliform denticulation on its anterior process which is very similar to the Pa element of *A. jafariani* gen. et sp. nov. However, the Pa element in *I.*? *sandersi* is almost straight whereas that in *A. jafariani* gen. et sp. nov. is slightly S-shaped in upper view, its anterior process slightly curved to the outer side and posterior process curved to the inner side of the element. The anterior process of the Pa element of *A. jafariani* gen. et sp. nov. is also longer and usually bears more than 10 denticles instead of the 4 to 7 characteristic of the Pa element of *I.*? *sandersi*. Additionally, the M element of *I.*? *sandersi* lacks the characteristic denticle closest to the cusp of *A. jafariani* gen. et sp. nov. that is inclined inwards towards the base of the cusp and partly overlaps it on the inner side. In addition, our restudy of the 247 specimen collection of *I.*? *sandersi* made by Mabillard and Aldridge (1983) did not show any elements similar to the Pb element recognized in the *A. jafariani* gen. et sp. nov. apparatus.

The Pb element identified here is considered part of the *A. jafariani* gen. et sp. nov. apparatus mainly because of its great general morphological similarity to the Pa element: both have thin-walled wide and deep basal cavities and, most importantly, both elements bear rows of denticles that in distal parts of the processes are laterally thickened to short ridges of icriodelliform aspect. All three P elements occur in association with the other unusual elements figured here as part of the *Arianagnathus* apparatus and this, as well as the similar style of denticulation for two of them, is the main reason for suggesting the apparatus has three P elements.

Stratigraphic and geographic range.—Type locality and horizon only.

Division Ozarkodinida Dzik, 1976

Suborder Ozarkodinina Dzik, 1976

Family Spathognathodontidae Hass, 1959

Genus *Ozarkodina* Branson and Mehl, 1933

Type species: *Ozarkodina typica* Branson and Mehl, 1933; Ludlow, Silurian; Lithium, Missouri, USA.

Ozarkodina derenjalensis sp. nov.

Fig. 5A–I, K.

2013 *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. C Mabillard and Aldridge, 1983); Männik et al. 2013: 10, fig. 4o, P_1 element.

Etymology: After the Derenjal Mountains in the East Central Iran.

Holotype: NHMUK PM X 3640, P_1 element (Fig. 5A).

Type locality: A section located about 65 km north-west of Tabas, on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran; Hill B, uppermost Unit 6 (sample S12).

Type horizon: *Distomodus staurognathoides* Conodont Zone, Aeronian?, Llandovery, Silurian.

Material.— 48 specimens: P_1 element, 29; P_2, 11; M, 2; $S_{3–4}$, 4; $S_{1–2}$, 1; S_0, 1.

Diagnosis.—P_1 element carminate with distinct inclined cusp and gap or lower denticle located just to anterior. On all elements basal cavity relatively small and round, narrow inverted zone on blades of mature specimens.

Description.—*P_1 element* (Fig. 5A, E, F): Carminate, blade straight, elongate with lower edge straight or nearly straight. Cusp broad and low, posteriorly inclined, slightly to posterior of mid-length of blade; gap or lower denticle just to anterior. Anterior blade higher than posterior, bearing six to seven broad, erect denticles. Posterior blade with up to six posteriorly inclined denticles, generally less prominent than those of anterior, but on smaller specimens are almost same size. Denticles less fused on juvenile (Fig. 5E_1, E_2) and more completely fused on mature specimens (Fig. 5A_1, A_2, F_1). Basal cavity shallow, almost symmetrical and rounded on mature specimens (Fig. 5A_3, F_2); more tapered to anterior and posterior on smaller specimens (Fig. 5E_3). Cavity widest below lowest denticle just anterior of cusp and extends as a narrow groove below blades with narrow inverted zone better developed to posterior but can be on both blades of larger specimens.

P_2 element (Fig. 5B, C, G): Angulate, blade high, straight and strongly arched. Cusp prominent, posteriorly inclined, with sharp edges and lenticular section. Denticles laterally compressed, relatively short, fused at least until upper third of height, and generally decrease steadily in size distally on both processes. Upper parts of all denticles (including cusp) slightly inwardly curved. Lateral faces smooth, with weak thickening mid-blade on larger specimens creating a lenticular cross-section. Basal cavity small, slightly flared and deepest below cusp; almost symmetrical and rounded on mature specimens (Fig. 5C) but tapers to anterior and posterior on smaller specimens. Below processes cavity continues as narrow groove and becomes inverted on posterior blade of larger specimens (Fig. 5C).

M element (Fig. 5D): Bipennate. Cusp broken in both elements available. Preserved part of cusp asymmetrically lenticular in section; outer lateral face gently convex, inner lateral face strongly convex. Anterior process with one or two denticles. Posterior process very gently curved, bears at least six fused denticles. Cavity flared slightly inwards at base of cusp to produce small lip, continues as narrow groove below posterior process with well-developed inverted basal cavity.

$S_{3–4}$ element (Fig. 5I): Bipennate with laterally compressed, posteriorly inclined cusp. Preserved part of posterior process in specimens available straight, bearing fused?, compressed, posteriorly inclined denticles. Anterior process curving strongly downwards and slightly inwards, bearing up to eight compressed denticles. Basal cavity shallow and narrow, slightly flared beneath cusp, and continues as narrow groove below processes. Away from cusp, below posterior process, basal cavity becomes inverted.

$S_{1–2}$ element (Fig. 5H): Digyrate, cusp posteriorly inclined with ridge on inner surface producing elongated triangular section. Processes form an angle of about 90°. Anterior process with about four relatively wide, discrete, compressed and inwardly curved denticles. Posterior process bears up to eight slender denticles that are fused at least in their lower parts. Basal cavity flared more strongly on inner side below ridge on cusp; below processes cavity continues as narrow groove.

S_0 element (Fig. 5K): Alate, with a cusp lenticular in section with sharp lateral edges. Posterior face of cusp with wide prominent axial ridge at preserved part of base. Lateral processes slightly curved to posterior and directed quite steeply downwards making an angle of about 90º. Both processes bear at least six compressed, relatively discrete short denticles. Basal cavity flared below posterior ridge on cusp and continues below processes as narrow groove; cavity inverted below processes near base of cusp. Basal body fills cavity in single specimen available.

Remarks.—P_1 elements of the apparatus identified here as *Ozarkodina derenjalensis* sp. nov. bear some similarity to those described by Mabillard and Aldridge (1983: pl. 3: 9, 10) as *Ozarkodina* sp. C. However, our specimens differ by having shorter and higher blades and less prominent cusps. Based on the illustrated specimens of *Ozarkodina* sp. C the inverted basal cavity also appears to be absent on the Mabillard and Aldridge (1983) specimens.

Stratigraphic and geographic range.—Aeronia–Telychian (Llandovery, Silurian); Iran.

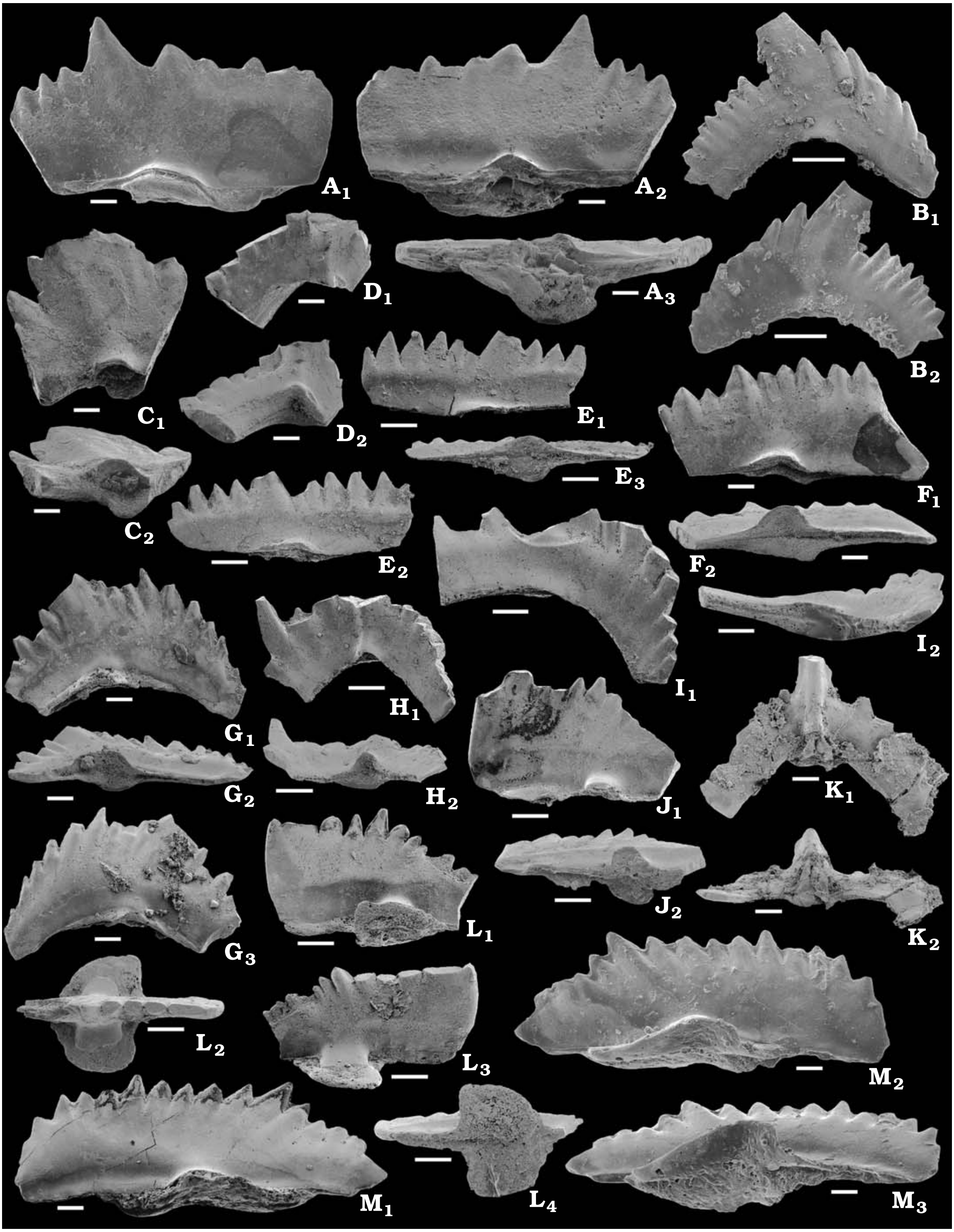
Ozarkodina sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983)

Fig. 5J, L.

2013 *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983); Männik et al. 2013: 10, fig. 4h, P_1 element.

Material.—P_1 element, 2 specimens from a section located about 65 km north-west of Tabas, on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran; Hill B, uppermost Unit 11 (sample S19). *Pterospathodus amorphognathoides lennarti* Conodont Zone, Telychian, Llandovery, Silurian.

Description.—*P_1 element* (Fig. 5J, L): Carminate, straight, laterally compressed with a straight to slightly arched lower edge in lateral view. Anterior blade short and high, bears 6–7 fused and compressed denticles which are inclined to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posterior proximally and more erect distally. Second denticle from anterior margin about twice as wide as all other denticles on blade. Cusp indistinct as all adjacent denticles are similar in size. From immediately above basal cavity, height of denticle row decreases rapidly towards posterior margin, although this margin is not preserved on specimens available. Preserved part of posterior process bears 5 low, posteriorly inclined denticles of irregular height and width. Both processes slightly thickened mid-blade, parallel to basal margin. Basal cavity shallow, strongly flared beneath cusp with prominent asymmetrical lobes, probably extending as shallow groove beneath entire blade as well preserved basal body present below entire element.

Remarks.—P_1 elements of *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983) resemble *Ozarkodina* sp. A of Mabillard and Aldridge (1983: pl. 3: 7, 8) in general configuration only. Both taxa have short P_1 elements with a high anterior blade and denticles on the posterior blade that rapidly decrease in height from the cusp. Morphological differences are evident between these two taxa. According to Mabillard and Aldridge (1983), the Pa (= P_1) element of *Ozarkodina* sp. A has 3–4 short, erect, broad denticles of subequal size on its anterior blade whereas our specimens have relatively small denticles with one considerably larger denticle in the anteriormost part of the blade. The cusp of *Ozarkodina* sp. A is broad and distinct whereas our specimens have cusps that do not differ in size from the other denticles. The P_1 element basal cavity of *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983) is shorter but more strongly flared than in *Ozarkodina* sp. A.

Ozarkodina sp. 1

Fig. 5M.

2013 *Ozarkodina* sp. nov. A; Männik et al. 2013: 10, fig. 4f, P_1 element.

Material.—P_1 element, 1 specimen from a section located about 65 km north-west of Tabas, on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran; Hill B, Unit 7 (sample S15). *Distomodus staurognathoides* Conodont Zone, Aeronian?, Llandovery, Silurian.

Description.—*P_1 element* (Fig. 5M): Carminate, straight, laterally thickened below denticle row, with basal margin very gently curved downwards in lateral view. Anterior blade twice as long as posterior blade, bears 9 fused denticles which are posteriorly inclined near to cusp, becoming more erect distally. Cusp inclined to posterior and slightly higher than adjacent denticles. Posterior blade bears 5 denticles that become smaller and increasingly inclined towards posterior distally. Basal cavity flared more strongly on the inner side of the specimen and almost at mid-point of specimen; cavity completely filled with well preserved basal body.

Remarks.—Männik et al. (2013) suggested that this could represent a new species. As only a single P_1 element of the apparatus has been found it is not possible to discuss its relation to other species of *Ozarkodina*.

Genus *Ctenognathodus* Fay, 1959

Type species: *Ctenognathus murchisoni* Pander, 1856; Wenlock, Silurian; Rootsiküla, Estonia.

Ctenognathodus sp.

Fig. 6A–D, F.

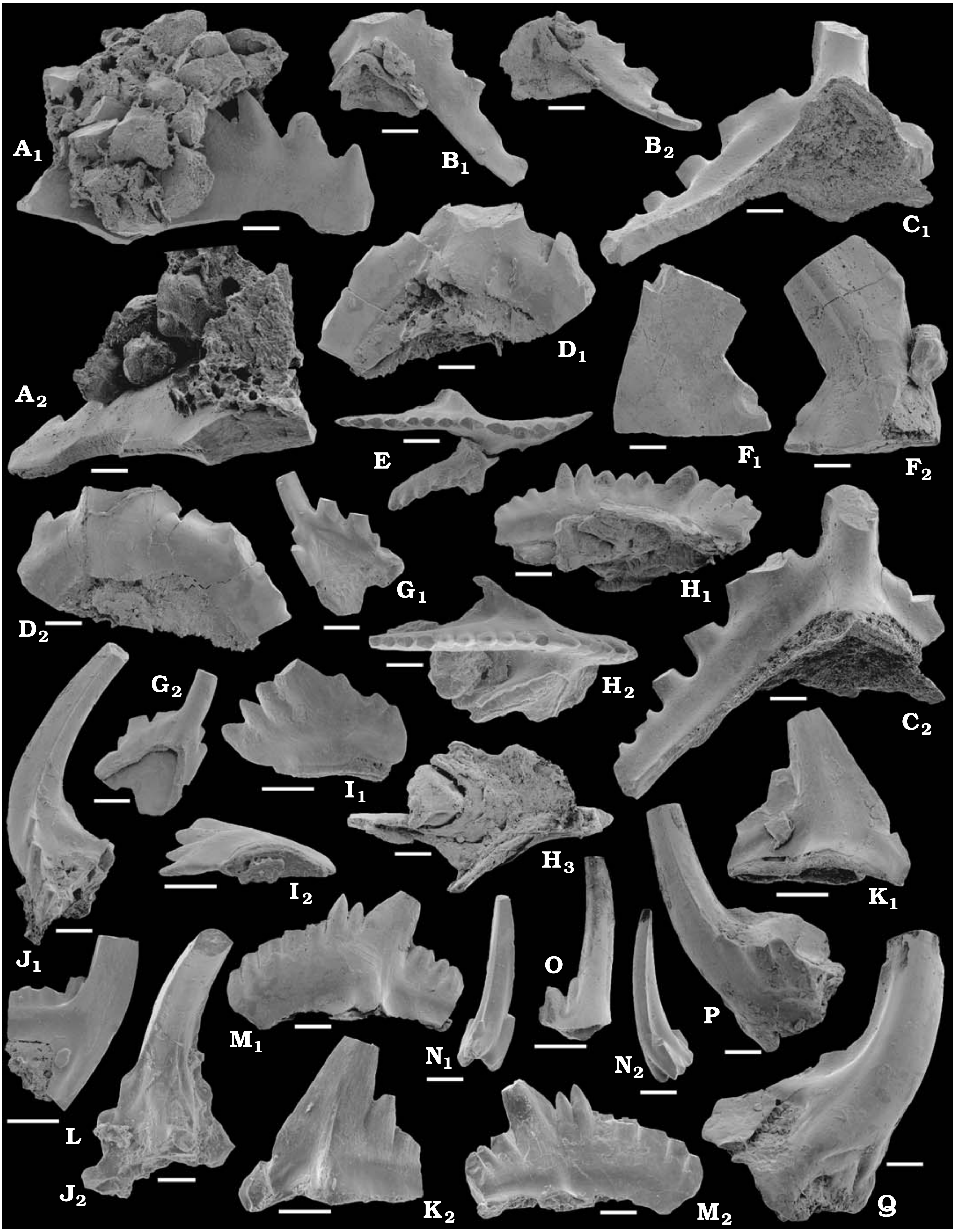
Material.— 5 specimens: P_1 element, 1; P_2, 1; $S_{1–2}$, 2; S_0?, 1; from a section located about 65 km north-west of Tabas, on the eastern side of the Dahaneh-e-Kolut Gorge in the Derenjal Mountains, East Central Iran; Hill B, uppermost Unit 11 (sample S19). *Pterospathodus amorphognathoides lennarti* Conodont Zone, Telychian, Llandovery, Silurian.

Description.—*P_1 element* (Fig. 6A): Carminate with straight, thick blade and basal margin gently curved downwards in lateral view. Denticles broad, discrete and triangular in lateral view with V-shaped gaps between them. Only anterior blade preserved. Narrow, groove-like basal cavity below entire preserved part of blade with narrow inverted zone.

P_2? element (Fig. 6F): A single fragment representing base of cusp and part of blade just below it. Posteriorly inclined cusp laterally compressed with sharp anterior and posterior edges and bears a distinct longitudinal ridge in mid-part of the inner lateral face. Other face of cusp smooth and slightly convex.

$S_{1–2}$ element (Fig. 6B, C): Digyrate. Cusp with sub-lenticular section that is almost sub-circular in larger specimens but with distinct anterior and weak posterior ridges. Anterior process mainly straight but slightly twisted and curved inwards distally. Anterior process bears up to 5 laterally slightly compressed, discrete widely spaced denticles with sharp

← Fig. 5. Ozarkodinid conodonts from the late Llandovery part of the Niur Formation of the Derenjal Mountains, East Central Iran, Hill B. **A–I**, **K**. *Ozarkodina derenjalensis* sp. nov. **A**, **E**, **F**. P_1 elements. **A**. Sinistral element, NHMUK PM X 3640, in outer lateral (A_1), inner lateral (A_2), and lower (A_3) views, sample S12. **E**. Dextral element, NHMUK PM X 3644, in outer lateral (E_1), inner lateral (E_2), and lower (E_3) views, sample S15. **F**. Sinistral element, NHMUK PM X 3645, in outer lateral (F_1) and lower (F_2) views, sample S12. **B**, **C**, **G**. P_2 elements. **B**. Sinistral element, NHMUK PM X 3641, in outer lateral (B_1) and inner lateral (B_2) views, sample S15. **C**. Dextral element, NHMUK PM X 3642, in inner lateral (C_1) and lower (C_2) views, sample S12. **G**. Dextral element, NHMUK PM X 3646, in inner lateral (G_1), lower (G_2), and outer lateral (G_3) views, sample S15. **D**. Dextral M element, NHMUK PM X 3643, in inner lateral (D_1) and lower (D_2) views, sample S15. **H**. Sinistral $S_{1–2}$ element, NHMUK PM X 3647, in inner lateral (H_1) and lower (H_2) views, sample S15. **I**. Dextral $S_{3–4}$ element, NHMUK PM X 3648, in inner lateral (I_1) and lower (I_2) views, sample S15. **K**. S_0 element, NHMUK PM X 3650, in posterior (K_1) and lower (K_2) views, sample S15. **J**, **L**. *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983). **J**. Dextral P_1 element, NHMUK PM X 3649, in outer lateral (J_1) and lower (J_2) views, sample S19. **L**. Dextral P_1 element, NHMUK PM X 3596, in outer lateral (L_1), upper (L_2), inner lateral (L_3), and lower (L_4) views, sample S19. **M**. *Ozarkodina* sp. 1, sinistral P_1 element, NHMUK PM X 3595, in inner lateral (M_1), outer lateral (M_2), and lower (M_3) views, sample S15. Scale bars 0.1 mm.



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edges, lenticular sections, and wide U-shaped gaps between them. Denticles decrease rapidly in width (?and height) from cusp towards distal end of process. Posterior process almost missing in both specimens available. Basal cavity filled with well preserved basal body below cusp and part of anterior process. At end of anterior process basal body is missing. Here cavity is narrow and a separate pit is visible below final denticle (Fig. 6C_1).

S_0? element (Fig. 6D): Alate. Only short parts of lateral processes preserved bearing discrete, slightly compressed denticles separated by U-shaped gaps. Cusp broken off but sub-circular in section at base. Basal cavity widest beneath cusp, with anteriorly and posteriorly flared lips better developed to posterior. Basal cavity completely filled with basal body.

Remarks.—The apparatus is poorly represented and the element available poorly preserved. However, the general morphology of specimens available (robustness, discrete laterally more or less compressed denticles, etc.) suggest that this apparatus, most probably, belongs to *Ctenognathodus*.

Conclusions

Presented here is a description of a new genus and species of conodont, *Arianagnathus jafariani* gen. et sp. nov., that appears to back up the idea that icrion bearing apparatuses can have three pairs of P elements as shown by Aldridge et al. (2013). *A. jafariani* gen. et sp. nov. but also *Ozarkodina derenjalenis* sp. nov. and *Ozarkodina* sp. nov. (aff. *Ozarkodina* sp. A Mabillard and Aldridge, 1983) seem to have possible closest relatives in Avalonia, in the Marloes Bay section, SW Dyfed, Wales (Mabillard and Aldridge 1983). Several other conodont taxa found in the Llandovery part of the Derenjal section are cosmopolitan and indicate that the described material comes from strata of late Aeronian–mid Telychian age (Männik et al. 2013; this paper). Some new material described here is based on small collections and as a result we have continued to leave it in open nomenclature. Collecting more material from the Niur Formation in Iran can possibly answer some of the questions that remain regarding these taxa as well as determining whether the *Arianagnathus* gen. nov. apparatus has 17 elements. The collections described here are significant as this area of the world has been little studied for conodonts. The new taxa described here have potential for future biostratigraphical work but also to answer questions regarding the Lower Palaeozoic palaeogeographical history of this important region.

← Fig. 6. Ozarkodonid and prioniodontid conodonts from the late Llandovery part of the Niur Formation of the Derenjal Mountains, East Central Iran, Hill B. All specimens from sample S19, except J, P, Q, sample S12. **A**–**D**, **F**. *Ctenognathodus* sp. **A**. P_1 element, NHMUK PM X 3651, in lateral (A_1) and lower (A_2) views. **B**, **C**. S_{1-2} elements. **B**. Dextral element, NHMUK PM X 3652, in inner lateral (B_1) and lower (B_2) views. **C**. Sinistral element, NHMUK PM X 3653, in lower (C_1) and inner lateral (C_2) views. **D**. S_0 element, NHMUK PM X 3654, in posterior (D_1) and anterior (D_2) views. **F**. Dextral P_2 element, NHMUK PM X 3656, in outer lateral (F_1) and inner lateral (F_2) views. **E**, **G**–**I**, **K**–**O**. *Pterospathodus amorphognathoides lennarti* Männik, 1998. **E**, **H**. Sinistral Pa elements. **E**. NHMUK PM X 3655, in upper view. **H**. NHMUK PM X 3598, in inner lateral (H_1), upper (H_2), and lower (H_3) views. **G**. Sinistral Sc_1 element, NHMUK PM X 3657, in inner (G_1) and outer (G_2) lateral views. **I**. Sinistral Pb_2 element, NHM PM X 3597, in outer lateral (I_1) and lower (I_2) views. **K**. Dextral Pc element, NHMUK PM X 3659, in inner (K_1) and outer (K_2) lateral views. **L**. Dextral Sc_2 element, NHMUK PM X 3660, in inner lateral view. **M**. Dextral Pb_1 element, NHMUK PM X 3599, in outer (M_1) and inner (M_2) lateral views. **N**. Sinistral Sb_2 element, NHMUK PM X 3661, in posterior (N_1) and inner lateral (N_2) views. **O**. Carnuliform element, NHMUK PM X 3662, in lateral view. **J**, **P**, **Q**. *Distomodus staurognathoides* (Walliser, 1964). **J**. Sa element, NHMUK PM X 3658, in lateral (J_1) and posterior (J_2) views. **P**. Dextral Sb element, NHMUK PM X 3663, in outer lateral view. **Q**. Sinistral Sc element, NHMUK PM X 3664, in outer lateral view. Scale bars 0.1 mm.

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