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Two new early balognathid conodont genera from the Ordovician of Oman and comments on the early evolution of prioniodontid conodonts

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Reports of Ordovician conodonts from the Arabian region of the Gondwanan margin are extremely rare. Here we provide a description of the apparatus of two new conodont genera and species *Aldridgeognathus manniki* and *Omanognathus daiqaensis*, based on discrete elements recovered from the Am5 Member of the Amdeh Formation, Darriwilian, Ordovician of the Sultanate of Oman. The apparatuses contain 17 and 15 elements respectively and both possess three pairs of P elements. The apparatus structure of *Omanognathus* is similar to the bedding plane assemblage defined genus *Notiodella* (=*Icriodella*) but differs in that as yet only 15 elements rather than 17 have been identified.

Aldridgeognathus has similar P elements to the early Silurian apparatus *Pranognathus* but differs in the possession of a geniculate M element and a *Baltoniodus*-like S element array. *Aldridgeognathus* does not easily fit with either the 17 element *Notiodella* (*Icriodella*) or the 19 element *Promissum* templates and suggests that there may be other 17 element Ordovician apparatus templates with very similar or duplicated elements in the P element positions. A cladistic analysis based on the dataset of Donoghue (2008) confirms that both new genera should be classified with the Balognathidae and suggests that they, along with another newly described three P element bearing genus *Arianagnathus* are more derived than *Baltioniodus* and *Prioniodus* but ancestral to *Icriodella*, *Sagittodontina*, *Promissum* and *Notiodella*. The exact position of *Aldridgeognathus* is not well resolved in respect to the newly described *Arianagnathus* or *Omanognathus*. These new taxa add little to attempts to correlate the Arabian Peninsula with other palaeogeographic regions but may prove useful for future correlation within the region and provide data to test the hypothesis of Dzik (2015) that the origins for prioniodontid conodonts lie in high latitudes during the Ordovician.

Keywords: Conodonts, prioniodontids, Balognathidae, *Aldridgeognathus* *Omanognathus*, Ordovician, high-latitude, Gondwana, Darriwilian, Oman.

Introduction

Bergström *et al.* (2009) noted a general scarcity of graptolites and almost total absence of conodonts in the Lower and Middle Ordovician of the Gondwanan region including the Arabian Peninsula where the material described here was collected. A summary of Ordovician South Gondwanan faunas and correlation by Gutiérrez-Marco *et al*. (2016) also notes a relative scarcity of conodont faunas in the region. This, allied to the presence of largely endemic shelly faunas, has led to difficulties in correlating the successions in this region with the Bergström *et al.* (2009) global chronostratigraphic scheme. Since 2009, additional conodont data has been published from the Ordovician of the Arabian Peninsula area including the Floian-Darriwilian of the Rann Formation of the United Arab Emirates (Fortey *et al.* 2011) and from the early Darriwilian of the Seyahou Formation, Faraghan Mountains, Iran (Ghavidel-Syooki *et al.* 2014). Conodonts had been recovered from the Hanadir Shale, Darriwilian of Saudi Arabia (see single specimen figured in Purnell 1995 and list of Vaslet, 1990) but as yet, the fauna has not been completely described. Heward *et al.* (2016) figured conodonts from the Am5 Member of the Amdeh Formation in a review article. However, they suggested that until more Ordovician conodont material is recovered from the Arabian margin, the fauna has greater phylogenetic than biostratigraphic significance and suggested a further multielemental study of the fauna was necessary to properly classify the material. Dzik (2015) has suggested that examples of conodont apparatuses with 17 elements were present in high latitude exotic refugia and gave rise to many of the lineages we see in an early Silurian conodont acme, citing an example of a new conodont genus *Moskalenkodus* from Siberia. The aims of this contribution are: to describe the full apparatus of two new 15 and 17 element balognathid conodont genera from the Ordovician of Oman; to provide data on conodont occurrences from the Arabian margin of Gondwana; to enhance the potential for conodont correlation within the region and with wider palaeogeographical areas; and to provide new evidence towards the debate on the origins of prioniodontid conodonts from high latitude areas.

Geological setting

Lithostratigraphy and environment

Conodont samples were collected as part of a study of the Am5 Member of the Amdeh Formation of the Sultanate of Oman carried out to investigate lateral equivalents and analogues of reservoir and seal intervals for hydrocarbons in the subsurface of northern Oman (Heward *et al.* 2016). That study concludes that the Amdeh Formation is probably the seaward continuation of the Darriwilian Saih Nihayda Formation of the Ghaba Salt Basin of northern Oman. The Am5 sections that provided this conodont fauna at Wadi Daiqa and Hayl al Quwasim (Fig. 1) are dominated by quartzitic sandstones, shales, and bivalve-rich shell beds, interpreted to have been deposited in storm-dominated shelf, shoreface and deltaic environments. Trace fossils referable to the *Cruziana* and *Skolithos* ichnofacies are common (Davies and Sansom, 2009). Two rare nodular carbonate beds a few tens of centimetres thick produced conodonts of colour alteration index 3–4 indicating a palaeo-temperature of 150– 200°C caused by regional, late Cretaceous, greenschist facies metamorphism (Heward *et al.* 2016). The lithology and general shallow water environment of the Amdeh Formation is not one that would normally be targeted for conodont faunas and the conodonts we describe here are, in common with those from elsewhere within the region, recovered from concretionary, bioclastic, ooidal or griotte-like nodular carbonates. Within the Amdeh Formation they probably represent the deepest water (tens of metres deep) part of the sequence but within a regional context they are correlated with high stands, as seems typical for Ordovician conodont faunas recovered elsewhere within the Arabian Plate (Fig. 2). The two nodular limestones that have yielded conodonts occur just below and a little above the probable location of the Maximum Flooding Surface MFS O30 in the outcrop section (Fig. 2, Heward *et al.* 2016). This MFS is currently interpreted to be mid Darriwilian, ca. 462-3 Ma.

Biostratigraphy

Earlier studies of the Amdeh Formation yielded trilobites, brachiopods, acritarchs, chitinozoans, trace fossils, fragments of conodonts and partly decalcified shell beds consisting mainly of bivalves (Lovelock *et al.* 1981; Le Métour *et al.* 1986; Villey *et al.* 1986). However, the Formation contains very few age diagnostic fossils and a rough age for the whole of the Amdeh was given as Lower to Middle Ordovician based on acritarchs, chitinozoans and trilobites. An assignment of a Darriwilian age for the Upper Siltstone Member (Am5) was based on the recovery of the acritarch *Arkonia* from Wadi Qahza (Lovelock *et al.* 1981). The identification of *Neseuretus tristani* from Member Am5 in Wadi Daiqa, Hayl al Quwasim and from (Am4 or 5?) shell beds near Dim, suggests correlation with sections in Iberia and elsewhere in southern Europe (Fortey & Morris 1982; El- Khayal & Romano 1985; Heward *et al.* 2016). More recent discoveries (Sansom *et al.* 2009) from Member Am5 have included fragments of scales and plates of the arandaspid fish *Sacabambaspis* typical of very shallow marine habitats prone to seasonal influxes of freshwater and terrigenous sediment that have been recorded from similar arandaspid bearing sites around the margins of Gondwana (Davies and Sansom 2009). The new arandaspid finds as well as articulated mouldic remains of the early crinoid *Iocrinus* (Donovan *et al.* 2011) were both dated ?Dapingian-Darriwilian using acritarchs and chitinozoa. Subsequent work on the acritarch floras of both the outcrops and the subsurface Saih Nihayda Formation has refined the age of the Am5 Member to early-late Darriwilian (Booth in Heward *et al.* 2016).

Materials and methods

Sampling

The five samples that yielded conodonts were taken from two nodular carbonate horizons in Wadi Daiqa (C2008, C2009, C2010, and C2012) and Hayl al Quwasim (C2011) with sample weights ranging between less than a kilogramme and 5kg (Table 1). Heward *et al.* (2016; figs 3-5) have provided detailed logs of the sections showing positions of samples and a full geological overview of the shallow-water storm-dominated shelf, shoreface and delta deposits that comprise the Amdeh 5 sequence together with its regional setting.

Sample processing and illustration

Samples were processed in buffered 10% acetic acid using the method described by Jeppsson *et al.* (2009) and separated in a solution of sodium polytungstate at a specific gravity of 2.80. All samples were sieved into a 75 microns to 2 mm fraction, which was then passed through a sediment splitter if necessary. Except for C2008 that was picked fully, only an 8th of each residue was picked in its entirety as the samples dissolved producing very large residues. Percentages of sample picked are shown in Table 1. All samples produced large acid residues dominated by heavy phosphatic or iron encrusted fragments rendering separating and picking of complete residues impractical. Specimens were illustrated using one of four different scanning electron microscopes that were available at the Natural History Museum during the timescale of the project: Hitachi S-2500, Phillips XL-30, FEI Quanta 650 FEG and Zeiss Ultra Plus Field Emission Scanning Electron Microscope.

Cladistic analysis

Two cladistic analyses were carried out based on the characters and dataset for complex platform conodonts of Donoghue *et al*. (2008). The first analysis used TNT version 1.5 (Golobov and Catalano 2016) to provide a parsimony consensus tree using the implicit numeration setting. The second used Mr Bayes MKV and gamma model of Lewis (2001) with 4 discrete gamma categories, running the analysis for 5,000,000 generations, discarding the first 25% of trees as burn in to produce a probabilistic Bayesian Maximum Likelihood tree.

Repository

Figured specimens and assemblage slides are deposited at the Natural History Museum, London and are prefixed by NHMUK. Details of these slides and additional SEM images are available via the NHMUK Data repository http://data.nhm.ac.uk/.

Systematic Palaeontology

Positional homology of some of the elements the apparatuses described have been determined through direct comparison with the natural assemblages of *Notiodella keblon* Aldridge *et al.*, 2013 and *Promissum pulchrum* Kovács-Entrödy, 1977 in Theron & Kovács Entrödy, 1986 so we follow homology-based notation identifying P_1–P_3, M, and S_0–S_4 (P_n–S_n) elements as outlined by Purnell *et al.* (2000). When no positional homology can be inferred we use the more traditional Pa-Pc, M, Sa, Sb1, Sb2, Sc notation. Following the suggestion of Purnell *et al.* (2000) we have used terms "anterior", "posterior", "lateral", "inner", "outer", "upper", and "lower" in inverted commas to show they are used in the conventional sense for isolated conodont elements and do not refer to biological orientation in the animal. Reasons for assignment of higher taxonomic levels are given in the discussion section.

Phylum **Chordata** Bateson, 1886
Class **Conodonta** Eichenberg, 1930
Order **Prioniodontida** Dzik, 1976
Family **Balognathidae** Hass, 1959
Genus *Aldridgeognathus* gen. nov.

Derivation of name

After the late Prof. Richard J. Aldridge, university lecturer and PhD supervisor who inspired CGM and many others to take up the study of conodonts. He worked extensively on Silurian and Ordovician conodonts

Type for genus and only species

Holotype *Aldridgeognathus manniki* gen. et sp. nov. (Figs 3 C, F, I), Pa element, NHMUK PM X 3692. All other figured material in Figs 3-5 is considered to be Paratype.

Diagnosis

17 element apparatus with 3 paired P elements. Pa and Pb almost identical; Pb has an almost straight blade while Pa has a kink mid-blade and its bifurcated lateral process is curved further backwards. Pastinate Pc element with one process with a flared basal cavity. Geniculate M element and S element array with distinctive irregular denticulation.

Remarks

P elements with a simple outer lateral process and a bifurcating inner lateral process are found in several genera including the Ordovician *Complexodus* (eg Dzik 2015, figs 7, 8), *Sagittodontina* (eg Dzik 2015, fig. 12), *Lenodus* (eg Löfgren 2003), *Amorphognathus* (eg Bergström and Leslie 2010, fig. 5) and the Silurian *Pterospathodus* (eg Männik 1998). However, the material described here is closest to the early Silurian *Pranognathus* Männik and Aldridge, 1989 when only the Pa and Pb elements are considered. The material belongs to a different genus if the whole apparatus is taken into consideration as *Aldridgeognathus* has two very similar P elements, a geniculate rather than a makellate M element and a different style of denticulation on the S elements (compare with *Pranognathus*, Männik and Aldridge 1989, text-fig. 5). The *Aldridgeognathus* M element is very similar to that of *Complexodus* as reconstructed by Dzik (2015, figs 7Q, R), which also shares a very similar pastinate element that we have suggested is the Pc element of *Aldridgeognathus*. This element is similar to *Baltoniodus* ambalodontiform elements (Löfgren 1978, plate 12). The S elements described here under *Aldridgeognathus* also have a very similar style of denticulation to *Baltoniodus* (eg. Agematsu et al 2007, fig. 10; Tetraprioniodontiform elements of Löfgren 1978, plate 12; McCracken and Nowlan 1989 pl. 1, figs 1-3, 5; Viira *et al.* 2006, pl. 1, fig 10), a genus that also bears a quadriramate S element (see Sd element of Agematsu et al 2007, fig. 10). *Amorphognathus* and *Rhodesognathus* also have a quadriramate Sd element but at present we suggest that this *Aldridgeognathus* element is most similar morphologically to the Sb1 element described here so consider this an Sb2 element. This point emphasizes our choice of using Sa, Sb, Sc and Sd notation that implies no positional homology. As the material described here in a multielemental context appears to share characters across a wide range of Ordovician and early Silurian conodont taxa,we choose to erect a new genus and species.

Species *Aldridgeognathus manniki* gen. et sp. nov.

(Figs 3-5)

2016 Pterospathodontidae gen et sp. nov. Heward *et al.* Figs 10d-h

Derivation of name

After Dr Peep Männik of Tallinn Technical University, Estonia, who defined *Pranognathus* with Prof. Richard J. Aldridge.

Type

As for genus.

Diagnosis

As for only species.

Material

476 individual elements consisting of 26 Pa, 113 Pb, 135 Pc, 29 indeterminate P, 70 M, 25 Sa, 16 Sb1, 27 Sb2 , 17 Sc and 9 Sd elements.

Occurrence

Early Darriwilian, Am5 Member, Amdeh Formation of Wadi Daiqa and Hayl al Quasim, samples C2008, C2009, C2010, C2011, C2012 (Fig. 1 and Table 1).

Description

Pa

Pastiniscaphate element, blade distinctly sigmoidal in upper view with slightly posteriorly inclined narrow and short cusp at mid element (Figs 3A-F, H, K, L). On outer side of element, cusp extends as a ridge and subsequently as a slightly posteriorly directed denticulate lateral process with style of denticulation similar to that of blade. This lateral process is broken on almost all examples of these elements from the collection but the best preserved specimens show that this lateral process can be almost 2/3rd the length of the anterior process and almost as long as the posterior process (Fig. 3K). Bifurcating inner lateral process located away from base of cusp at start of posterior process and curves to the anterior with the anteriormost bifurcation curved forward so it is almost pointing in the same direction as the anterior process. Bifurcations of inner lateral process appear adenticulate but the surface is irregular and the triangular outline that the bifurcations produce in lateral view is disrupted by some irregular nodular features. Anterior process slightly longer than posterior and with more crowded denticles, particularly at the base of the cusp. Posterior process with denticles that increase in width and become more discrete towards termination of process. Anterior and posterior processes appear to have a slightly angular relationship but basal margin is often poorly preserved and difficult to distinguish. Basal cavity extends under entire element but is usually filled with sediment.

Pb

(Figs 3G,J, M-X) Pastiniscaphate element with almost straight blade in upper view with slightly posteriorly inclined stout and short cusp at mid element. On outer side of element, cusp extends as a ridge and subsequently as a slightly posteriorly directed denticulate lateral process with style of denticulation similar to that of blade. As with Pa element, this lateral process is broken on almost all examples of these elements with only one specimen in the collection preserving this process in its entirety (Figs 3O,R). Bifurcating inner lateral process is more regular than for the Pa element with bifurcations extending at 45 degrees to the blade in upper view creating a lateral process that is much more triangular in outline both in lateral and upper view. Like the Pa element, the upper surface of the bifurcations appear adenticulate but the surface is disrupted by some irregular nodular features. Anterior and posterior processes are about the same length with denticles more crowded on anterior process and larger specimens. Basal margin of anterior and posterior processes appear to be straight but basal margin is often poorly preserved and can be difficult to distinguish. Basal cavity extends under entire element on rare occasions when it is not filled with sediment or basal body.

Pc

Pastinate pyramidal element with three processes and tall thin cusp, triangular in section and curved gently to posterior (Figs 4A-H,J). Margins of cusp sharp with outer lateral edge drawn out into a process that can be adenticulate or have one to three denticles at its termination just below basal margin. Denticles on anterior process much more crowded than those on posterior with denticle nearest cusp almost indistinguishable from base of cusp. Posterior process with much more discrete denticulation and in oral view the inner margin is flared with its widest point at mid blade. Basal cavity on most elements filled with sediment but in rare specimens shows that it extends below entire element and is deepest below cusp and point of maximum flaring of cavity lip on posterior process.

M

Geniculate element with tall erect cusp that increases in width slightly at base before tapering gradually to a sharp point (Figs 4I,K-S). Surface of cusp pinched at base forming a ridge that extends almost to tip and forming sharp flattened margins of the cusp. Large anticusp is swollen at basal cavity margin but thin and flattened on outer margin. This margin is often broken in the material and rarely preserved to the termination of the anticusp; some specimens show possible denticulation towards this termination but this could also be related to *post-mortem* breakage of the margin which is very thin at this point. Upper margin is very slightly convex and, like the outer margin of the anticusp, is thin and often broken, particularly towards termination. Basal cavity extends under entire element and is broadly flared beneath upper margin of element rather than beneath cusp. Basal margin is incompletely preserved in most of the material so figured specimens chosen to represent best-preserved material. Angle between basal margins in these specimens just over 90 degrees.

Sa

(Figs 5 A-G) Alate element with short inwardly curved cusp of circular section. Lateral processes curved downwards so at termination they are almost pointed in opposite direction to cusp. Denticles on lateral processes fused at base, tall and slender when preserved and point almost in same direction as cusp.

Posterior process incomplete in many of specimens but appears to extend as long as lateral processes and bears short stubby isolated denticles. Basal cavity extends under whole element with basal body often present producing a triangular cavity margin to reflect three processes.

Sb1

(Figs 5 H-J) Similar to Sa element but with asymmetrical arrangement of lateral processes either side of cusp. Juvenile specimens, as do smaller Sa elements, bear much less crowded denticles.

Sb2

(Figs 5K, L, O &P) Quadriramate element with four processes bearing descrete denticles of triangular outline; basal body preserved between these processes giving rhomboidal overall shape to element. Cusp curved slightly laterally, short and circular in section; ridges near base reflect the position of each process but do not continue to point of cusp.

Sc

(Figs 5L, M,Q-S) Asymmetrical tertiopedate element with flattened striated cusp that bears a ridge reflecting the short adenticulate inner lateral process. Outer lateral process that is continuation of cusp bears up to four slender and pointed denticles, with denticles at base of cusp closely fused to a smaller denticles. Posterior process longest and bearing irregular fused denticulation; at base of cusp a series of smaller fused denticles is proceeded by two large and broad denticles separated by a narrow gap. Specimens in the collection other than those figured here have a tendency to have broken at this point. For specimens where this process is better preserved, this style of low narrow and high wide alternating denticulation is seen to continue.

Sd

(Figs 5T-W) Similar to Sc element but with adenticulate outer lateral process and denticulate inner lateral process.

Remarks

The Am5 conodont fauna is low diversity and contains two different sets of S elements (Table 1) that we have assigned to the P elements based on size differences and similarity in denticulation. We discount the possibility of the two similar P elements belonging to closely related taxa as the distribution of elements across the samples analysed suggests a regular co-occurrence (Table 1). We suggest that they are two distinct P elements rather than ontogenetic variants as there is a clear difference in the curvature of the blades across a range of sizes in specimens of both morphologies and on the rare occasion that the bifurcating process is preserved, the Pa element has one process curved further backwards.

Genus *Omanognathus* gen. nov.

Derivation of name

After Oman where the first specimens were found.

Type for genus and only species

Holotype *Omanognathus daiqaensis* gen. et sp. nov. (Figs 6 N, Q), P_3 element, NHMUK PM X 3673, sample C2009. All other figured material in Figs 6 and 7 is considered to be Paratype.

Diagnosis

Apparatus of 15 robust large elements with 3 distinctly different icrion bearing P elements. M element makellate. S element array large and bearing regular style of short, well-spaced denticles of circular section and with Type II growth of Donoghue (1998).

Remarks

The possession of three icrion bearing P elements allows direct comparison with the bedding plane assemblage of *Notiodella keblon* as described by Aldridge *et al.* (2013) with the two pastinate and single pastinate pyramidal elements bearing a striking resemblance to those of *Notiodella*. Aldridge *et al.* (2013) suggested that *Notiodella* could be synonymous with *Icriodella* but differed only in the nature of its M element, which for *Icriodella* is geniculate. The M element described here as part of the *Omanognathus* apparatus is makellate. It should be noted that Dzik (2015) and Bergström and Ferretti (2015, fig. 12) have also suggested that *Notiodella* is a junior synonym of *Icriodella* and that one of the three P elements is an M element. We are in agreement with the arguments presented by Bergström and Ferretti (2015, p. 24-25) that these two genera are almost certainly synonymous but argue that the apparatus of *Omanognathus* is sufficiently different that we should create a new genus. A more detailed comparison of the *Icriodella keblon* and *Omanognathus* apparatus structures is given later, but currently only 15 rather than 17 elements have been recognised for *Omanognathus daiqaensis*. This material also has a very similar denticulation to the S elements of *Icriodella keblon* but the ramiform elements suggest Type II growth (see Donoghue 1998), where the processes comprise discrete complex units that became sequentially fused to the distal end of the process rather than Type 1 element morphogenesis typical of *Icriodella keblon* where each denticle possesses a discrete crown and basal body and apparently grew independently of its neighbours. Aldridge *et al.* (2013) also suggest that the 'outer lateral' process is probably denticulate, whereas the S_3 elements for this new apparatus are denticulate only on the posterior process. The P_1 element here is similar to that of *Icriodella* cf. *I. praecox* Lindström *et al.*, 1974 (see Dzik 2015, fig. 10). Aldridge *et al.* (2013) note that if discrete P_1 elements of *Notiodella* had been recovered, they would probably be classified under *Icriodella* and the same could be said of *Omanognathus*. Bergström (1983) figures similar elements as Pa (Figs 6A,B) and Pb (Figs 6C,D). An element figured as a tertiopedate S element of *Icriodella praecox* by Bergström (1983, fig. 6H) similar to our fig 9E but the denticulation is quite different and we have recovered only a single element (Table 1) so are reluctant to include it in this apparatus at present, particularly as the overall morphology of this S element is quite different and we only have one specimen. The P elements show a similar arrangement to *Gamachignathus ensifer* McCracken *et al.*, 1980 although it must be noted that Bergström and Ferretti (2015) consider *Gamachignathus* to be a junior synonym of *Birksfeldia*. Again the S elements are different in their denticulation which is more regular for *Omanognathus* rather than alternating. We suggest that this material is very similar to both *Notiodella* and *Icriodella* but different enough, particularly in the growth style of the S elements and the makellate M element, to be distinct from both these genera. More detailed discussions of the apparatus architecture, familial classification and phylogenetic significance follow later.

Species *Omanognathus daiqaensis* gen. et sp. nov.

(Figs 6-7)

2016 Balognathidae gen et sp. nov. Heward *et al.* Figs 10a-c

Derivation of name

After Wadi Daiqa, Oman where the first specimens were found.

Type

As for genus.

Diagnosis

As for only species.

Material

93 individual elements (Table 1) consisting of 14 P_1, 11 P_2, 25 P_3, 5 indeterminate P, 15 M, 6 S_0, 2 S_1, 7 S_2, 2 S_3 and 6 indeterminate S elements.

Occurrence

Early Darriwilian, Am5 Member, Amdeh Formation of Wadi Daiqa and Hayl al Quwasim, samples C2008, C2009, C2010, C2011, C2012 (Fig. 1 and Table 1).

Description

P_1

Pastinate element, blade curved gently inwards in upper view with low, broad cusp at mid element that becomes lower and less distinct in larger specimens (Figs 6A-H, J, K, M). On outer side of element, cusp extends as a narrow ridge that runs at an angle of about 70-80 degrees to the basal margin and forms a short adenticulate lateral process. In oral view, cavity lip on inner side of anterior process is gently flared in larger specimens and more distinctly flared in smaller ones. Anterior process just slightly longer than posterior with both processes having denticles near termination of process and often an adenticulate ridge close to base of cusp, particularly in larger specimens. Denticles in smaller specimens are equilateral triangular in outline in lateral view but denticles on all processes, particularly those near the termination of process, appear as icrions. Anterior and posterior processes appear to have a very slightly angular relationship in lateral view giving a generally elongate triangular shape to element. Basal cavity can be seen to extend under entire element on rare occasions when it is not filled with sediment or basal body; basal margin is often poorly preserved and difficult to distinguish clearly.

P$_2$

Pastinate pyramidal element with three similarly sized processes and short thin erect cusp, triangular in section (Figs 6T-Y). Margins of cusp sharp with outer lateral edge drawn downwards into adenticulate process. Denticles on anterior and posterior processes, like P$_1$ and P$_2$ elements are confined to terminations of processes, much better developed in smaller specimens and become more fused so that larger specimens are almost adenticulate. Icrions are clearly visible on all specimens and are best developed towards termination of processes. Basal cavity margin slightly flared on posterior process with cavity extending under entire element but always complete with sediment or basal body.

P$_3$

(Figs 6L, N-S) Pastinate element that in upper view has almost straight long anterior blade; posterior process bifurcates in a fish-tail pattern on other side of short erect cusp. Like P$_1$ element, on outer side of element, cusp extends as narrow ridge forming short adenticulate lateral process; unlike P$_1$ element, process makes an angle of 90 degrees to basal margin. In oral view, cavity lip on both sides of anterior process is gently flared; flaring near the cusp on the outer and near the termination on inner side. Denticulation similar to P$_1$ element with both processes more denticulate near termination of process and adenticulate close to base of cusp, particularly in larger specimens. Larger specimens also show development of icrions. Basal margin straight with basal cavity extending under entire element.

M

Makellate element with short stubby erect cusp; pinched slightly at base to produce cross section with sharp flattened margins and flaring of basal cavity lip immediately below cusp (Figs 7A-G, I). Large anticusp has similar pinched, sharp, often broken margin that may look denticulated near base of cusp but is certainly denticulated towards termination of process. Style of denticulation similar to upper margin that has short stubby fused denticles that are almost equilateral triangular in lateral view. Cavity extends under whole element and is deepest below cusp; angle between two processes and angle between basal margins less than 90 degrees, although basal margins variably preserved.

S_0

(Figs 7H, L, J-K) Alate element with stubby cusp of circular section. Lateral processes with regular style of closely spaced denticles that in better-preserved specimens appear to be of similar height and width, covering entire length of process. Basal body fills gap between processes and it is difficult to see extent of basal margin, particularly when this is not preserved completely. Posterior process with similar style of denticulation.

S_1

(Fig. 7M, O) Similar to S_0 element but with cusp curved towards one lateral process and asymmetrical arrangement of lateral processes either side of cusp.

S_2

(Fig. 7N) Asymmetrical tertiopedate element with flattened striated cusp that bears a ridge on base reflecting a long adenticulate inner lateral process that has almost same aspect as outer lateral process. Outer lateral process also adenticulate. Posterior process longest with gently convex upper margin bearing short fused denticles near base of cusp, followed by five taller more discrete denticles and finally a set of shorter fused denticles near termination of process.

S_3

(Fig. 7P-R) Similar to S_2 element but outer lateral process bisects inner later and posterior processes and upper margin of posterior process straight rather than gently convex.

Remarks

As with the only other platform bearing species in this restricted fauna *Aldridgeognathus*, these P, M and S elements have been grouped together based on their relative size and similarities in denticulation. All elements in the *Omanognathus* apparatus are larger and more robust than those described here under *Aldridgeognathus*.

Order Protopanderodontida Sweet, 1988

Family Drepanoistodontidae Fahraeus and Nowlan, 1978

Genus *Drepanoistodus* Lindström, 1971

Drepanoistodus sp.

(Fig. 8)

2016 *Drepanoistodus* sp. Heward *et al.* Figs 10h-k

Material

27 individual elements consisting of 1 oistodiform (r), 3 (possibly 4) suberectiform (p), 8 drepanodiform (q_1), 9 drepanodiform (q_2) and 5 indeterminate elements. Notation (r, p, q) after Barnes *et al*. (1979).

Occurrence

Early Darriwilian, Am5 Member, Amdeh Formation of Wadi Daiqa, samples C2008, C2009, C2010, C2011 and C2012 (Fig. 1 and Table 1).

Description

Oistodiform (r)

(Fig. 8A) Cusp reclined, straight, sharp; posterior margin straight, sharp anterior margin very slightly convex. Slightly convex upper edge of base short, sharp with angle of 45° with posterior margin. Symmetrical, almost flat inner and outer faces produce cusp of lenticular section. Basal margin broadly convex, almost forming a semicircle; antero-basal corner curved and cavity slightly open to anterior. Cavity lips slightly more flared to posterior with shallow basal cavity.

Suberectiform (p)

(Fig. 8B) Cusp proclined to erect, slightly curved with sharp posterior margin almost straight, and sharp anterior margin very slightly convex. Upper edge of base short and not completely preserved in available specimen, but appears straight with sub-rounded junction with cusp and angular relationship of 110–130° between cusp and posterior margin. Lateral faces symmetrical with mid-laterally inflated, lenticular cross section. Basal cavity margin incomplete but appears pinched to anterior and straight to slightly undulatory. Elements are thermally mature so extent of cavity within element not visible; most elements also have sediment in cavity.

Drepanodiform (q_1)

(Figs 8C, D, E) Cusp reclined, sharp posterior and anterior margins with posterior very gently curved and anterior regularly curved. Anterior margin may be drawn out into a keel towards basal margin, posterior margin also keel-like at junction with base. Upper edge of base straight, sharp with rounded junction with base of cusp. Outer and inner faces broadly convex giving symmetrical cusp section. Basal margin almost straight on one lateral face of element and more convex on the other, when completely preserved with basal outline lenticular.

Drepanodiform (q_2)

(Figs 8F- H) Cusp erect, curved just above base then straight. Anterior margin gently and regularly curved over entire length, posterior margin gently curved near base then straight. Antero-basal margin almost 90° with basal margin. Both margins less keel-like than q_1 element forming regular lenticular section and smooth broadly rounded faces to element. Upper edge of base straight, gently rounded junction with posterior margin of cusp. Basal margin straight to very gently convex with lenticular basal outline much less flared than q_1 element.

Remarks

The number of elements in the collection is too small and they are not well enough preserved to definitively place a specific name on this *Drepanoistodus* material. The oistodiform element is usually the most distinctive but the single example of this element in the collection does not correspond to any previously published reconstructions of the *Drepanoistodus* apparatus. Some authors have recognised three variations within drepanodiform (q) elements of this apparatus (eg Cooper 1981, Dzik 1983 and Fåhræus and Hunter, 1985) and we have tentatively identified two. It is interesting to note that our material differs from the single element of *Drepanoistodus* figured by Purnell (1995) from the co-eval Hanadir Shale of Saudi Arabia which has a much more reclined cusp and a more pinched antero-basal margin. The single indeterminate coniform (Fig. 8I) does not belong with the *Drepanoistodus* apparatus but almost certainly suggests that there is more than one coniform taxon present. Some very poorly preserved elements could be placed with *Cornuodus* (see Löfgren 1998) but more material is needed to show this definitively.

Order Prioniodontida Dzik, 1976

Family Periodontidae Lindström , 1970

Genus *Microzarkodina* Lindstrom, 1971

aff. *Microzarkodina* sp.

(Fig. 9)

Material

8 individual elements consisting of 5 Pa, 1 Sa, 1 Sb and 1 Sc.

Occurrence

Early Darriwilian, Am5 Member, Amdeh Formation of Wadi Daiqa, sample C2010 only (Fig. 1 and Table 1).

Description

P (Figs 9A-D, I) carminate to slightly angulate elements with well-developed cusp of triangular outline and keeled edges. Anterior and posterior processes roughly similar in length, taper gradually to termination and each bear 4-5 discrete regular denticles of similar outline to cusp. Aboral margin straight to very slightly concave and flared only very slightly below cusp giving element a flattened cross section. One element (Fig. 9C) is slightly less flat and may represent a Pb rather than a Pa element. Basal cavity very shallow in all elements.

Sa (Fig. 9D) alate symmetrical element with discrete elongate denticles with u-shaped gaps between that resemble separation of denticles towards termination of P elements. Neither lateral process preserved in only specimen available but suggests that angle between processes slightly less than 90°. Short adenticulate posterior process that follows from base of cusp of u-shaped cross section. Basal cavity shallow and extends under entire length of preserved element.

Sb (Fig. 9E) Digyrate element with long cusp of similar u-shaped section to Sa element. Denticles smaller and more slender than other elements figured here. Basal margins of processes form angle of 45-50° basal cavity extends under entire element but is full of sediment in only specimen available.

Sc (Fig. 9F) dolabrate cordylodiform flattened element with gently reclined cusp of lenticular section. Posteriorly inclined denticles on posterior process descrete with similar u-shaped gaps to other elements suggested to be in this apparatus.

Remarks

The P elements described here most closely resemble *Microzarkodina ozarkodella* the youngest species of a genus that is found throughout the Darriwilian of the Baltic (Löfgren and Tolmacheva 2008, figs 1, 11). The other rare S elements have tentatively been placed with these P elements as they are confined to sample C2010 of this study and other elements eg the Sc element (Fig. 9F) resemble other elements figured as part of the *Microzarkodina* apparatus (see Löfgren and Tolmacheva 2008, fig 8 AJ *Microzarkodina parva* Sc element from the *Trapezognathus quadrangulum* Subzone, of Gillberga, Sweden and Löfgren 2003, fig. 7T *Microzarkodina parva* Sa). The small number of elements present precludes naming a new taxon until more material is recovered. It is also possible that these elements belong to more than one taxon as the Pa element figured here is similar to McCracken and Nowlan (1989, pl. 3, fig. 14) figured as a "*Plectodina*" *tenuis* juvenile g element. Other elements appear similar to elements of *Spinodus* as they have discrete denticles with large u-shaped gaps (e.g. Armstrong 2000, pl. 7, fig. 13).

Comparison with Ordovician conodont apparatus templates

There have been many previous attempts to reconstruct taxa based on collections of discrete elements but this process is open to personal interpretation and biases introduced during sampling, processing or deposition (Purnell & Donoghue 2005, Jeppsson 2005). Männik and Aldridge (1989) were first to suggest that some apparatuses, i.e. *Pterospathodus* and *Pranognathus* possessed three pairs of P elements. Other authors have suggested that overrepresentation of particular elements in discrete element collections could be explained by duplications in some element positions within the apparatus. Löfgren and Zhang (2003) suggested Pb, Sb and Sc duplication for *Baltoniodus*, *Lenodus* and *Eoplacognathus* on this basis. M element duplication in the apparatus of *Microzarkodina* was postulated for similar reasons by Löfgren and Tolmacheva (2008) and for various early prioniodontid taxa by Dzik (2015). Our material can add little to the debate on elemental duplication but does provide details of two new Ordovician genera based on discrete elemental reconstructions that possess three distinct pairs of P elements, a state that Donoghue *et al.* (2008, fig. 13) suggested was fairly uncommon. *Arianagnathus* with 3 P elements, described from discrete elements by Männik *et al.* (2015) from the early Silurian of Iran, can also be added to the list. There is direct evidence that some Ordovician conodonts possessed three or four pairs of P elements in the South African Soom Shale bedding plane assemblages of

Icriodella keblon (Aldridge *et al.* 2013) and *Promissum* (Aldridge *et al.* 1995) respectively. We agree with Viira *et al.* (2006, p. 226) that discussions relating to the apparatus structure of new genera should be in the context of these well-described and well defined bedding plane assemblage templates rather than other reconstructions based on discrete element collections.

Aldridgeognathus

The 17 element apparatus described here for *Aldridgeognathus* fits with the *Icriodella keblon* apparatus plan in terms of the numbers of elements recognised. The Pa and Pb elements in *Aldridgeognathus* are almost identical to each other, differing only in the curvature of the main denticle row and the more backwardly directed bifurcating process in the Pa element (Fig. 3). *Promissum* has almost identical pastinate pyramidal P elements in the P_2 and P_3 positions so close duplication of similar types of elements in Ordovician apparatuses is not uncommon. We have herein called the pastinate pyramidal element Pc as we are uncertain how to place it in the context of either the *Icriodella keblon* or *Promissum* apparatus plans. Based on morphology, a similar element is in the P_2 position for *Icriodella keblon* but we suggest it is unlikely that it is positioned between two almost identical elements for *Aldridgeognathus* considering that in the *Promissum* apparatus plan the identical elements are situated together in the P_2 and P_3 positions. All three P elements in *Icriodella keblon* are different in morphology unlike the *Aldridgeognathus* P elements. The pyramidal elements in *Promissum* are to the posterior of the angulate P element hence our assignment of Pc to the pastinate pyramidal element in *Aldridgeognathus*. As *Aldridgeognathus* does not appear to fit with either the *Promissum* or the

Icriodella keblon template, we chose not to assign P_1, P_2 and P_3 element positions as this suggests positional homology (Purnell *et al.* 2000). Instead we use Pa, Pb and Pc but would suggest that until the unlikely event of a bedding plane assemblage of this, or a closely related taxon being found, this is the most likely order of arrangement of the P elements in the apparatus. There are similar issues with the S elements as *Aldridgeognathus* has a Sb_2 element with four processes, but there are no quadriramate S elements in either *Icriodella* or *Promissum*. Other Ordovician genera, for example *Baltoniodus*, *Rhodesognathus* and *Amorphognathus* do have quadriramate S elements as mentioned in the remarks for the species description above. The geniculate *Aldridgeognathus* M element is also a major variation from the makellate M elements bearing two and three processes of *Icriodella keblon* and *Promissum* respectively.

Omanognathus

Aldridge *et al.* (2013, p. 261) suggested that bedding plane assemblages of *Icriodella keblon* from the Soom Shale of South Africa represent a "new template for use in the reconstruction of apparatuses from the collections of dispersed elements, particularly for those with icrion-bearing P_1 elements and perhaps for other balognathids." In contrast to the *Aldridgeognathus* apparatus, there is a clear match with the *Icriodella keblon* template for the *Omanognathus* P elements and to a large extent the M and S element array. The pastinate pyramidal element we describe can clearly be placed between the two other P elements so positional homology can be inferred and the use of the $P_{1\text{-}3}$ element notation is facilitated. Presently we have only identified 15 elements in this apparatus, which would suggest that an ozarkodinid plan may be a possibility (Purnell and

Donoghue, 1997, 1998). However, ozarkodinid apparatuses are restricted to two P elements and the presence of icrions in all three P elements suggests a closer association with balognathids, particularly *Icriodella keblon*, with its icrion bearing P_1 element. It may be that with further sampling, another S element type could be found as the collection currently consists of low numbers of identifiable S elements (Table 1). Aldridge *et al.* (2013) also note that the *Icriodella keblon* S_3 and S_4 elements are very similar so it may be that this element is duplicated in the apparatus described here. We choose the element with the lateral process that bisects the two other processes as the S_3 element as it is most similar to the element figured as S_3 by Aldridge *et al.* (2013, fig. 10D).

Familial classification and phylogenetic implications

Various attempts have been made at a higher-level classification covering all known genera for the conodonts including Sweet (1988), Dzik (1991) and Aldridge and Smith (1993). More recently Donoghue *et al.* (2008) used a cladistic approach to group a set of genera with well-defined apparatus plans into families and provide a phylogeny for complex conodonts. Graphical representations of phylogenetic relationships for conodonts have been presented by Sweet (1988) and Dzik (1991) based on a stratophenetic approach. Using a similar approach, Stouge & Bagnoli (1999) presented a hypothesis of relationships and a suprageneric classification of some Ordovician prioniodontid conodonts. Dzik (2015) used the chronophyletic approach outlined by Dzik (2005) to suggest evolutionary relationships for early prioniodontid conodonts. Figure 10 summarises some of these phylogenies and indicates a clear lack of consensus for the early evolution of prioniodontid conodonts.

Omanognathus

One of the key questions relating to the familial classification of *Omanognathus* is identifying whether it should be placed within the Balognathidae Hass , 1959 the Icriodellidae Sweet, 1988 or the Icriodontidae Müller and Müller, 1957. All of these families contain taxa with icrion bearing P elements. Donoghue *et al.* (2008, fig. 13) suggested that the possession of three pairs of P elements in the balognathid clade may be fairly restricted. However, Aldridge *et al.* (2013) followed Donoghue *et al.* (2008, fig. 13, table 2) in assigning the three P element bearing *Icriodella* (as *Notiodella*) to the Family Balognathidae but suggested that including further icrion bearing taxa to the analysis might show a distinct clade referring to the Family Icriodontidae, including both *Notiodella* and *Icriodella*. Details and results of a re-run of Donoghue's analysis including these newly described taxa is included in the next section. Above we suggest that *Omanognathus* has similarities with *Notiodella, Icriodella* and *Gamachignathus* (*Birksfeldia* according to Bergström and Ferretti, 2015). Dzik (2015) places all these taxa within the Icriodontidae (Fig. 10) as well as suggesting that the third P element in *Notiodella* is an M element and that *Icriodella* and *Notiodella* are synonymous (see also discussion in Bergström and Ferretti 2015). Our *Omanognathus* material differs in that the three P elements are not makellate, or indeed geniculate. We don't therefore consider any of them to be M elements or that our material suggests duplication in any of the element positions. For that reason we suggest that, based on morphology of the whole apparatus, *Omanognathus* should at present be placed within the basal balognathids, particularly as *Icriodella* has yet to be shown to have three P elements in its apparatus.

Aldridgeognathus

Heward *et al.* (2016) while illustrating only the P and M elements, tentatively suggested that this taxon should be assigned to the Pterospathodontidae (Heward *et al.* 2016, fig. 10) based on its similarity to *Pranognathus* and *Pterospathodus* but suggested that a full reconstruction of the apparatus was necessary to properly place this material within a family. As mentioned above, the 17 element *Aldridgeognathus* apparatus does not clearly fit with any previously described genus. Its Pa elements are most similar to *Pranognathus* but share characteristics with *Complexodus, Sagittodontina, Lenodus, Amorphognathus* and *Pterospathodus.* Its M elements are most similar to *Complexodus,* while its Pc element and S element array most closely resemble *Baltoniodus*. Those taxa have been assigned to four different families by various authors including the Balognathidae, Pterospathodontidae, Icriodellidae and Prioniodontidae (see Fig. 10 for examples of three of them; additionally Aldridge and Smith (1993) included *Pranognathus* in the Pterospathodontidae). The 17 element arrangement as shown for *Aldridgeognathus* suggests a closer affinity to the balognathids such as *Icriodella keblon* rather than the established 15 element apparatus with two sets of P elements that is well established for the ozarkodinid conodonts (Purnell and Donoghue 1997, 1998). This would suggest that a balognathid, icriodontid or prioniodonitid affinity is more likely. Donoghue et al (2008, fig. 13) suggested that *Pterospathodus* resolves with the balognathids so our material which shows strong affinities to *Pranognathus* and *Pterospathodus* while showing similarities to balognathids such as *Sagittodontina*, *Lenodus* and *Amorphognathus*, would support this case. We suggest that a balognathid assignment is most likely. Stouge and Bagnoli (1999) suggested, based largely on the evolutionary diagram of Dzik (1976) and patterns in Ordovician conodont apparatus structures, that *Baltoniodus* be placed within superfamily Prioniodontoidea another superfamily alongside their Balognathoidea within their Order Prioniodontida. At the time, they were not able to suggest a relationship between these two groups. We would suggest that our material could represent a Darriwilian basal member that branched off into either of these groups. Based on his apparatus reconstruction of *Complexodus,* Dzik (2015) suggested that *Complexodus* was an underived member of the Prioniodontida close to the Balognathidae with a possible relationship to the Pterospathodontidae. He suggested that it may have had a duplication in the M element pair although the two elements would have been morphologically similar. We suggest that it is dangerous to infer duplication of element types when there is no evidence. However, our *Aldridgeognathus* collections support the idea that some early prioniodontid conodonts could have possessed very similar P elements (see Pa, Pb here) and that duplications, such as seen in the 19 element apparatus of *Promissum*, could be more common than is evident from discrete element collections.

Dzik (2015) and Aldridge and Wang (2010, p. 40) have mentioned that a diagnostic feature for *Pterospathodus* is a suppressed anterior (“outer lateral”) process and that this would have been fully developed in ancestral forms. Our material would suggest that this is the case. Dzik (2015, fig. 13) also suggests that the balognathids are rooted in the Early Ordovician high latitude continents of Baltica and Yangtse. In presenting a reconstruction for *Moskalenkodus*, he also suggests that 'conodonts with apparatuses of high complexity, with at least 17 elements, were diverse in exotic refugia much before their Early Silurian acme' (Dzik, 2015, p. 1). The two conodont apparatuses described in this paper shows that the little studied peri Gondwananan area around the Arabian Peninsula is one such exotic refugia but also has a great deal to offer in the study of origins and evolution of basal prioniodontid conodonts.

Cladistic analysis

Two cladistic analyses were carried out based on the characters and dataset for complex platform conodonts of Donoghue *et al*. (2008). Genera chosen from this dataset have been identified as members of the Order Prioniodontida by Donoghue *et al.* (2008). *Paracordylodus* was chosen as outgroup taxon. As well as *Aldridgeognathus* and *Omanognathus*, other potential balognathid taxa were added as their apparatuses have been reconstructed from discrete collections since the cladistic analysis of Donoghue *et al.* (2008) including *Arianagnathus* Männik et al., 2015 and *Complexodus* as reconstructed by Dzik (2015). *Pranognathus* was also added as it has been identified here as similar to *Aldridgeognathus* but no further reconstructions of the apparatus have been published since Männik and Aldridge defined the genus in 1989. Finally, *Notiodella* Aldridge *et al.*, 2013 was added as a new balognathid bedding plane assemblage and to test synonymy with *Icriodella*.

The first analysis used TNT to provide a parsimony consensus tree that was not well resolved (Fig. 11A) based on four shortest trees (see Supplementary Information). The second tree produced with the MrBayes MKV and Gamma model produced a single probabilistic Bayesian Maximum Likelihood tree (Fig. 11B). The Bayesian Maximum Likelihood tree and the all of the parsimony derived trees had several common features that help to resolve some of the issues raised earlier in this paper following observations of morphological characters and previously published ideas on phylogenetic relationships. The new taxa described here and *Arianagnathus* are placed firmly within the Family Balognathidae, are more derived than *Baltoniodu*s and *Prioniodus* but ancestral to *Icriodella*, *Sagittodontina*, *Promissum* and *Notiodella*. There is no evidence for *Aldridgeognathus*, *Omanognathus* or *Arianagnathus* belonging to an icriodontid clade or that such a clade exists. However, the analyses suggest that *Notiodella* is more closely allied to *Icriodella*, *Promissum*, and *Sagittodontina* than to the icrion bearing *Omanognathus*. The analysis does not confirm or reject that *Icriodella* and *Notiodella* are synonyms as they are rooted in an unresolved polytomy. None of the trees support the model of Dzik (2015) where *Complexodus* and *Pranognathus* belong to a different family than *Prioniodus* and *Baltoniodus*. Likewise, as previously suggested by Donoghue *et al.* (2008), it does not support the phylogenetic model of Stouge and Bagnoli (1999) where *Baltoniodus* and *Prioniodus* are in a separate family from *Sagittodontina*, *Amorphognathus* and *Promissum*. The exact position of *Aldridgeognathus* is not well resolved in respect to the newly described *Arianagnathus* or *Omanognathus*. In some of the parsimony trees (see Supplementary information) it is seen as being ancestral to both and in others as a sister group.

Correlation with other peri Gondwanan conodont faunas

Records of conodonts are rare in Ordovician peri Gondwanan sediments. An occurrence of Tremadocian conodonts was reported by Droste (1997) from core of the Barakat Formation in an undisclosed well in northern Oman. Coeval faunas to those described here, but probably from a more seaward location, in the Ayim Member of the Rann Formation in the UAE are dominated by *Eoplacognathus* with small numbers of *Complexodus* (Fortey *et al.* 2011). Vaslet (1990) lists conodonts identified by Weyant as *Oistodus abundans*, *Baltoniodus variabilis*, *Drepanodus suberectus, Drepanodus homocurvatus*, *Saggitodontus* sp. *Cordylodus* sp. *Keislognathus* sp. and *Hibbardella* from the Hanadir and Ra'an members of the Qasim Formation. A log of this section with distribution of these taxa was later reproduced by Simmons *et al*. (2007, fig. 11). Purnell (1995) illustrated a single element of *Drepanoistodus* from the Hanadir Shale of Saudi Arabia. The Hanadir Shale conodonts have yet to be described in detail but could yield similar faunas to those described here. Ghavidel-Syooki *et al.* (2014, p. 684) mention material that is slightly older (early Darriwilian) from the Zagros of Iran that is yet to be worked up. Shallow-water conodont faunas in the Ordovician are ephemeral, particularly from those seemingly tightly constrained depositional environments represented within Amdeh 5 that have yielded pteraspidomorph fish such as *Sacabambaspis* (Davies & Sansom 2009; Heward *et al.* 2016), so it is not unusual to find that the material described here does not correspond with any previously described faunas. Additionally, this region corresponds to the Shallow Sea Realm of Zhen & Percival (2003) and Bergström *et al.* (2009, p. 101) referred to "serious difficulties to correlate the successions in this area with the new global chronostratigraphy" due to a lack of conodont faunas described from the Middle East. This fauna does not help to solve this issue but is an important addition to the fossil record of early prioniodontid conodonts and may prove useful in the future to aid correlation within the Middle Eastern region.

Conclusions

Two new conodont genera are described from the Darriwilian, Ordovician of the Sultanate of Oman, the 17 element *Aldridgeognathus manniki* and the 15 element *Omanognathus daiqaensis*.

Other conodonts present include *Drepanoistodus* and aff. *Microzarkodina*, although these need further study as very few elements have been recovered so far.

Aldridgeognathus does not fit with any known apparatus template as it differs from both the 17 element *Icriodella keblon* and the 19 element *Promissum* apparatus plan. It suggests that other 17 element apparatus architectures could be represented amongst the Ordovician conodonts.

The apparatus structure presented for *Aldridgeoagnathus*, particularly the similar but not identical P1 and P2 elements suggests that duplication of P elements in Ordovician conodonts may be more common than can normally be shown from discrete element collections.

Omanognathus shows a very similar apparatus structure to *Icriodella keblon* but potentially differs in the growth mechanism of its S elements and that a final paired S element is missing.

We suggest that both these new taxa are members of the Family Balognathidae along with the recently discovered *Arianagnathus*, and *Icriodella keblon*. They are more derived than *Prioniodus* and *Baltoniodus* but considered to be ancestral to *Icriodella*, *Promissum*, and *Sagittodontina*.

The little studied conodont faunas of the peri Gondwanan region around the Arabian Peninsula are an exotic refugia for early prioniodonontid conodonts and have great potential for helping refine origins and evolution of basal prioniodontid conodonts particularly from samples approximating to Cambro-Ordovician maximum flooding surfaces in the Oman region which appear to yield exceptionally well preserved faunas such as those documented here.

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Text Figures and Tables

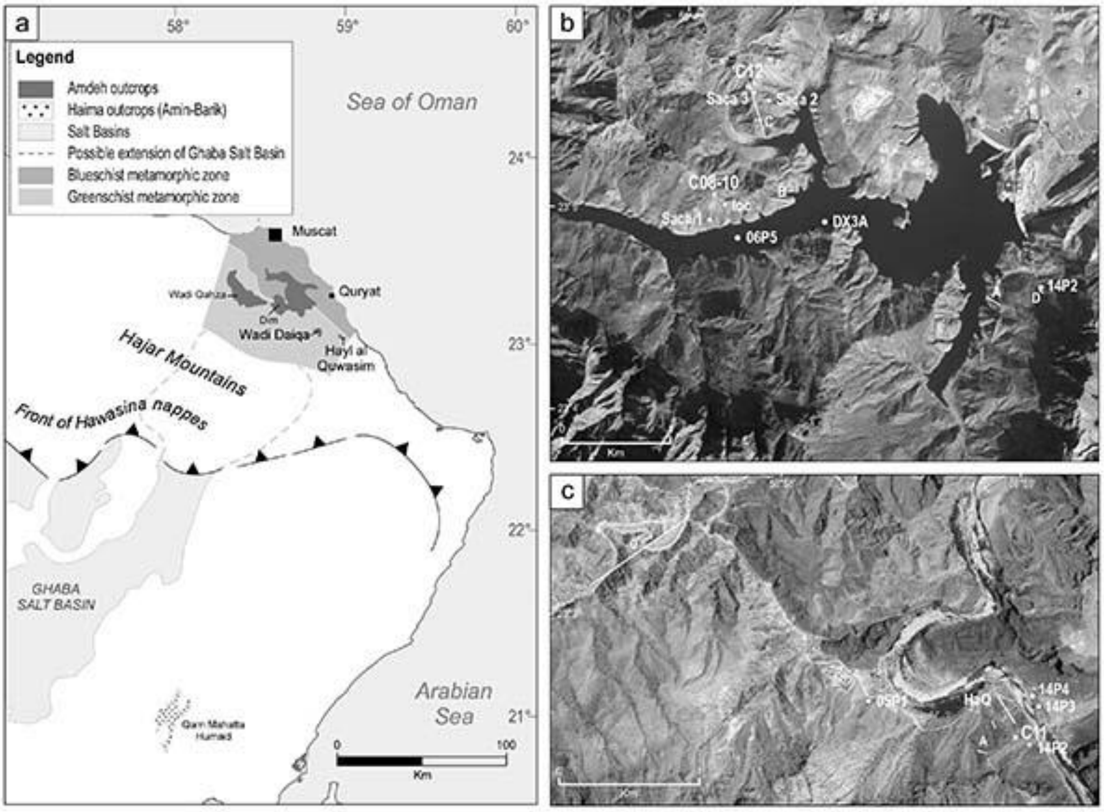

Figure 1. **A**, Outcrops of the Amdeh Formation on the southern rim of the Saih Hatat window of the Al Hajar Mountains of the Sultanate of Oman. **B**, locations of measured sections and samples in Wadi Daiqa. Palynology samples e.g. DX3A, conodont samples = C8-10, C12, Ioc = *Iocrinus* and Saca = *Sacabambaspis* locations. Quickbird image 1-5-2013 ©Digital Globe. **C**, Location of measured sections 0 and A at Hayl al Quwasim showing palynology samples e.g. 05P1, conodont sample location C11. HaQ = village. Quickbird image 1-5-2013 ©Digital Globe. (after Heward *et al.* 2016, figs 1-3).

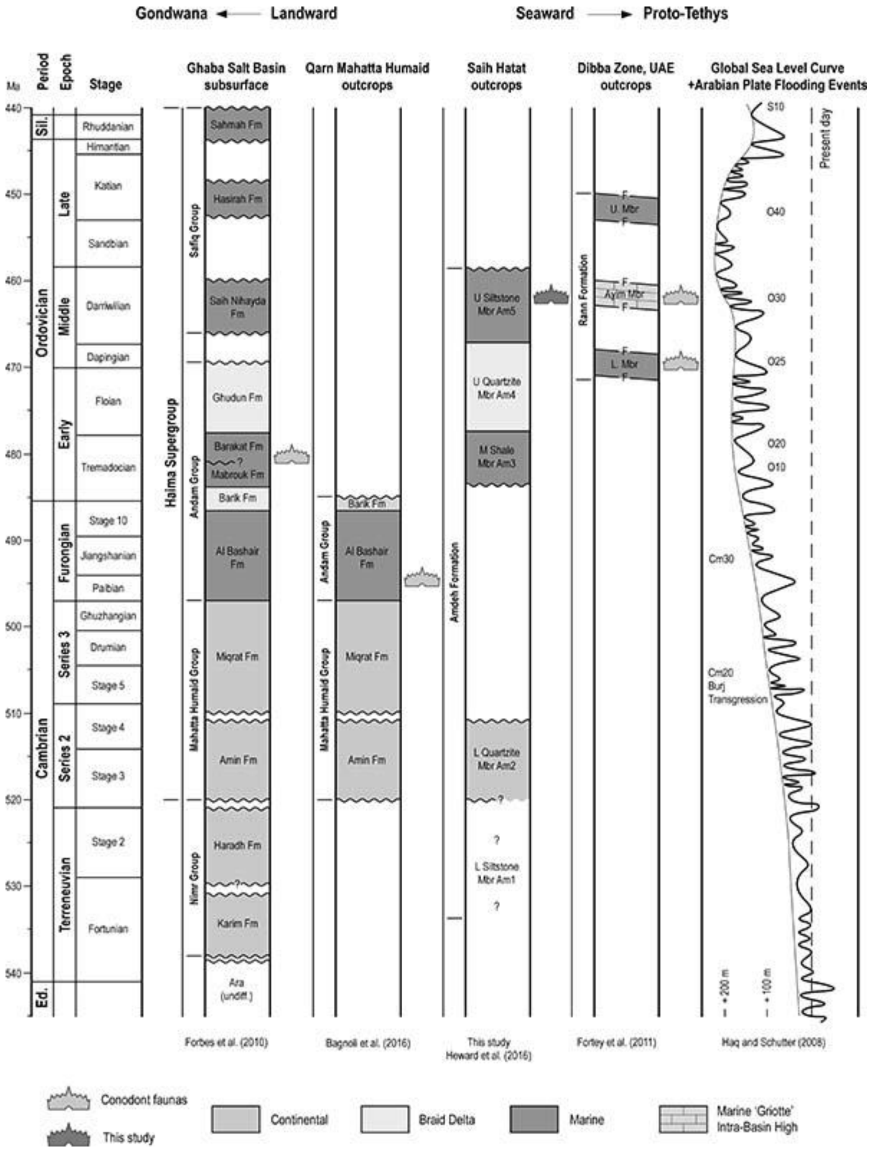

Figure 2. Cambro-Ordovician lithostratigraphy in the Oman area showing positions of Arabian Plate Flooding Events (prefixed by Cm for Cambrian, O for Ordovician, S for Silurian) and described conodont faunas against a global sea level curve.

					Aldridgeognathus manniki gen. et sp. nov											*Omanognathus daiqaensis* gen. et sp. nov												*Microzarkodina* sp				*Drepanoistodus* sp.						
Sample name	Section	sample dissolved (g)	percentage picked	conodonts/kg	P1	P2	P3	P indet	M	S0	S1	S2	S3	S4	S indet	P1	P2	P3	P indet	M	S0	S1	S2	S3	S indet	Indet S0	P	Sa	Sb	Sc	oistodiform r	suberectiform p	drepanodiform q1	drepanodiform q2	indet	indet coniforms	Total elements per sample
C2008 (S4)	Wadi Daiqa	531	100	207	5	16	42	20	5	4	5	3	4	1	1		1	2					1									1	1	2	3	4	110
C2009 (conodont bed)	Wadi Daiqa	6804	13	94	11	19	8	2	11	5	1	1	2	1		5	2	5		5			1			1						1	7	3	1	11	80
C2010	Wadi Daiqa	6124	13	393	3	68	60		53	12	9	18	11	7	2	9	5	18	3	10	5	1	3	2	1	1	5	1	1	1	1	1		4		2	301
C2011	Hayl al Quwasim	2780	13	58	1	1	4	6			1	1					2		2						2										1	3	20
C2012	Wadi Daiqa	2394	13	181	6	9	21	1	1	4		4					1				1	1	2		3							?1				2	54
Totals					26	113	135	29	70	25	16	27	17	9	3	14	11	25	5	15	6	2	7	2	6	2	5	1	1	1	1	4	8	9	5	22	565

Table 1. Counts of individual conodont elements from each sample showing total amount of sample dissolved (g) and percentage of residue picked to obtain counts.

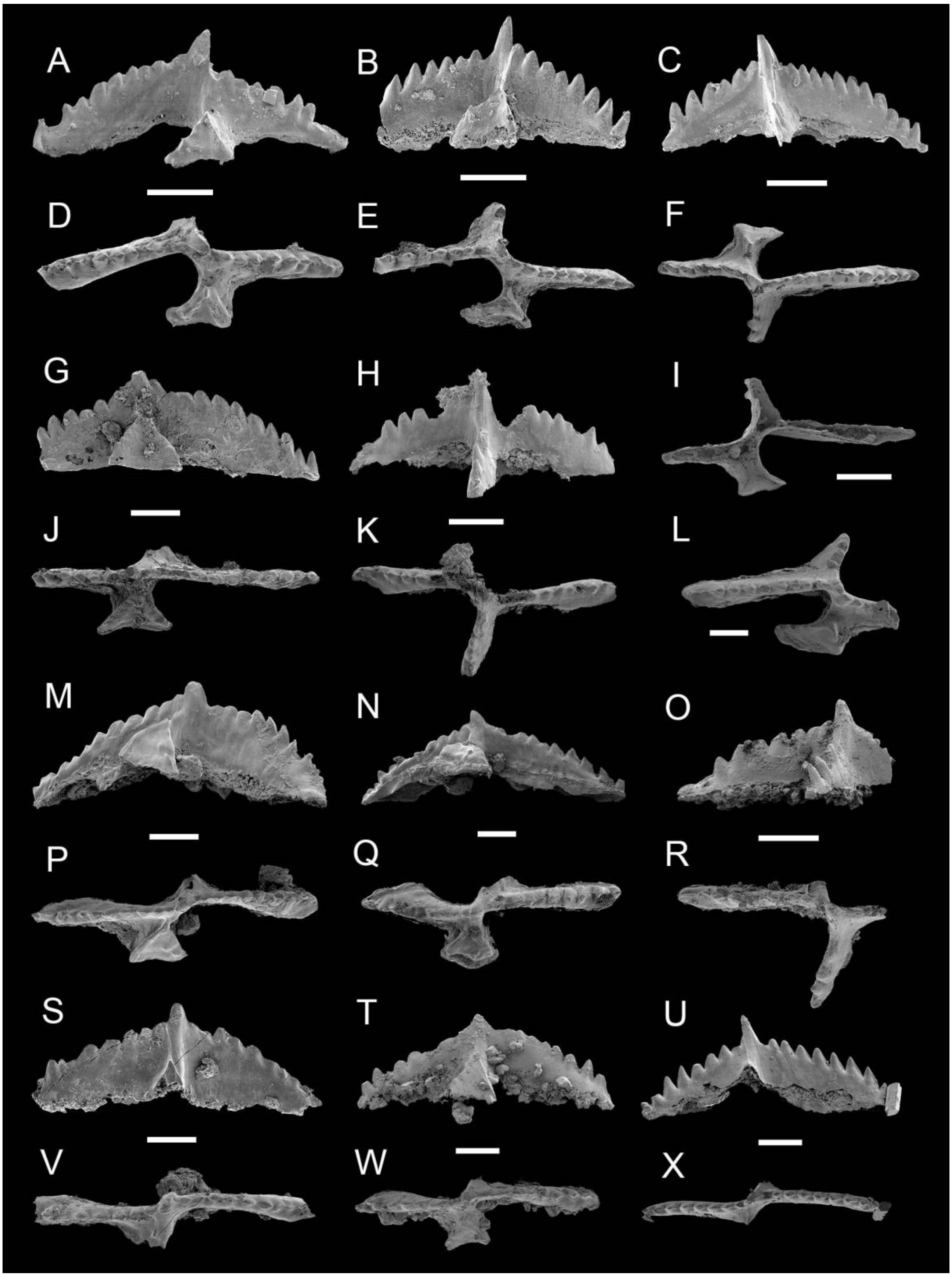

Figure 3. *Aldridgeognathus manniki* gen et sp. nov. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, sample C2010 unless stated. Scale bar for all specimens 200 microns. **A, D**, Pa element, (NHMUK PM X 3674), "inner lateral" and "oral" view. **B**, **E**, Pa element, (NHMUK PM X

3691), “inner lateral” and “oral” view. **C, F, I,** holotype Pa element, (NHMUK PM X 3692), “outer lateral”, “oral” and “aboral” view. **G, J**, Pb element, (NHMUK PM X 3693), C2009, “inner lateral” and “oral” view. **H, K**, Pa element, (NHMUK PM X 3694), “outer lateral” and “oral” view. **L**, Pa element, (NHMUK PM X 3695), “oral” view. **M, P**, Pb element, (NHMUK PM PX 3677), C2009, “inner lateral” and “oral” view. **N, Q**, Pb element, (NHMUK PM X 3696), C2012, “inner lateral” and “oral” view. **O, R**, Pb element, (NHMUK PM PX 3697), “outer lateral” and “oral” view. **S, V**, Pb element, (NHMUK PM X 3698), “inner lateral” and “oral” view. **T, W**, Pb element, (NHMUK PM X 3699), “inner lateral” and “oral” view. **U, X**, Pb element, (NHMUK PM X 3676), “inner lateral” and “oral” view.

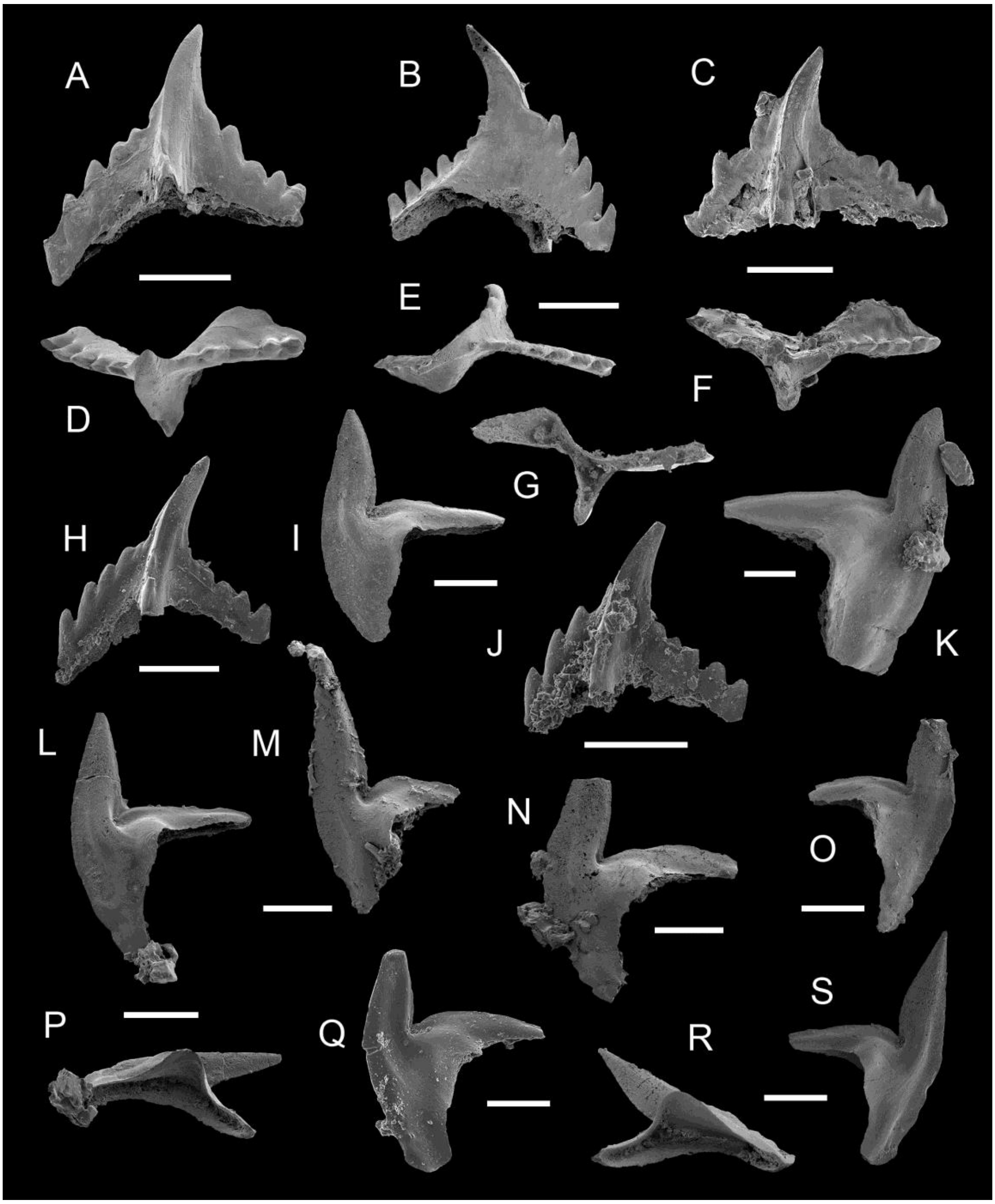

Figure 4. *Aldridgeognathus manniki* gen et sp. nov. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, sample C2010 unless stated. Scale bar for all specimens 200 microns. **A, D**, Pc element, (NHMUK PM X 3675), C2009, "outer lateral" and "oral" view. **B, E, G**, Pc element, (NHMUK PM X 3700), "inner lateral", "oral" and "aboral" view. **C, F**, Pc element, (NHMUK

PM X 3701), "outer lateral" and "oral" view. **H**, Pc element, (NHMUK PM X 3702), C2008, "outer lateral" view. **I**, M element, (NHMUK PM X 3678), C2009 "lateral" view. **J**, Pc element, (NHMUK PM X 3703), C2008, "outer lateral" view. **K**, M element, (NHMUK PM X 3704), "lateral" view. **L**, R, M element, (NHMUK PM X 3705), "lateral" and "oral" view. **M**, M element, (NHMUK PM X 3706), "lateral" view. **N**, M element, (NHMUK PM X 3707), "lateral" view. **O**, M element, (NHMUK PM X 3708), "lateral" view. **R, S**, M element, (NHMUK PM X 3710), C2008, "lateral" and "oral" view. **Q**, M element, (NHMUK PM X 3709), C2008, "lateral" view.

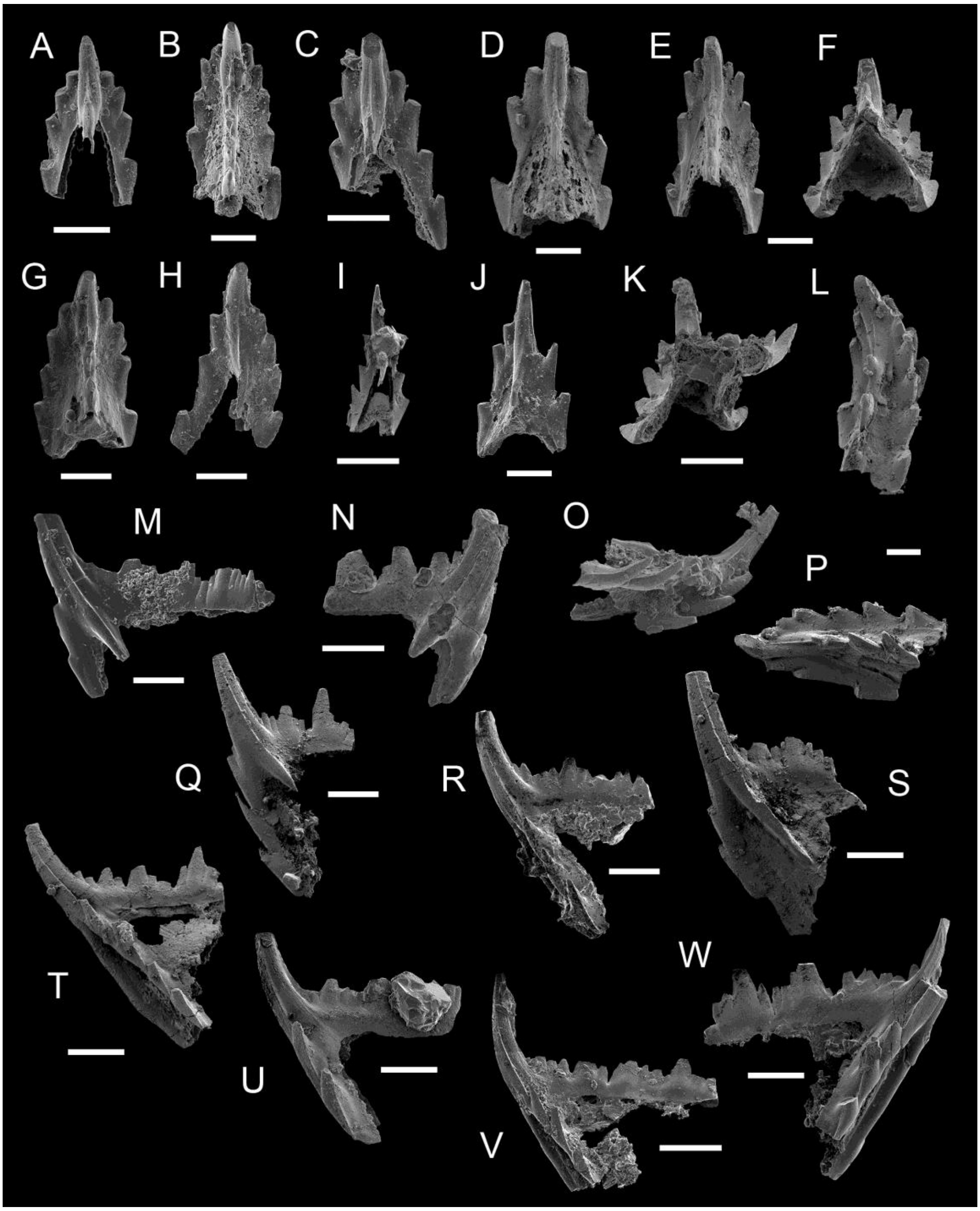

Figure 5. *Aldridgeognathus manniki* gen et sp. nov. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, sample C2010 unless stated. Scale bar for all specimens 200 microns. **A**, Sa element, (NHMUK PM X 3711), C2008, "posterior" view. **B**, Sa element, (NHMUK PM X 3712), C2008, "posterior" view. **C**, Sa element, (NHMUK PM X 3713), C2008, "posterior" view. **D**, Sa element, (NHMUK PM X 3714), "posterior" view. **E**, F, Sa element,

(NHMUK PM X 3715), "posterior" and close up "aboral" view.**G**, Sa element, (NHMUK PM X 3716), "posterior" view. **H**, Sb1 element, (NHMUK PM X 3717), C2008, "posterior" view. **I**, Sb1 element, (NHMUK PM X 3718), "posterior" view. **J**, Sb1 element, (NHMUK PM X 3719), C2008, "posterior" view. **K, O**, Sb2 element, (NHMUK PM X 3720), "aboral" and oblique "lateral" view. **L, P,** Sb2 element, (NHMUK PM X 3721), "posterior" and oblique "lateral" view. **M**, Sc element, (NHMUK PM X 3722), C2008, "lateral" view. **N**, Sc element, (NHMUK PM X 3723), "lateral" view. **Q**, Sc element, (NHMUK PM X 3724), "lateral" view. **R**, Sd element, (NHMUK PM X 3725), "lateral" view. **S**, Sc element, (NHMUK PM X 3726), "lateral" view. **T**, Sd element, (NHMUK PM X 3727), "lateral" view. **U**, Sd element, (NHMUK PM X 3728), "lateral" view. **V**, Sd element, (NHMUK PM X x3729), "lateral" view. **W**, Sd element, (NHMUK PM X 3730), "lateral" view.

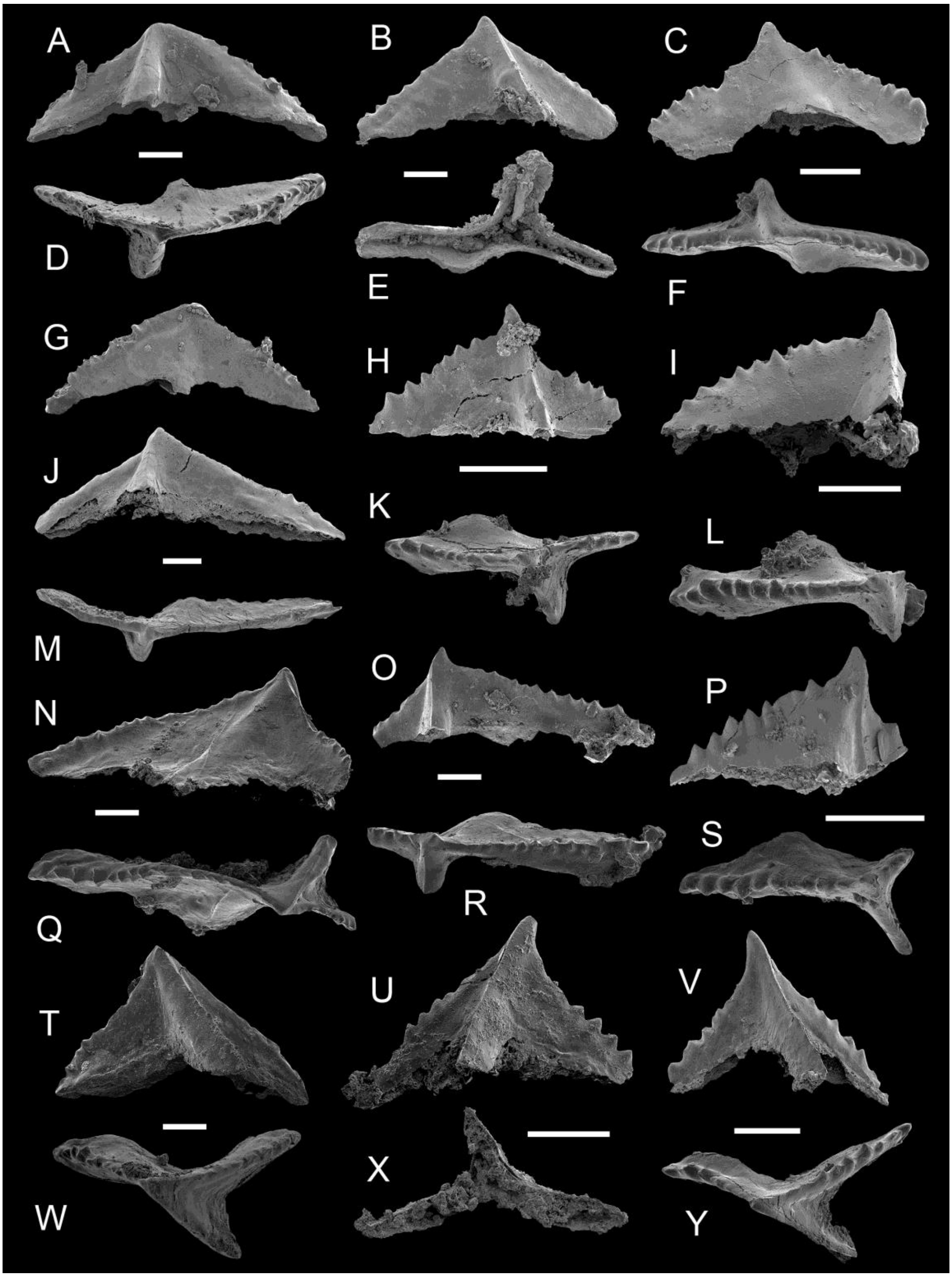

Figure 6. *Omanognathus daiqaensis* gen et sp. nov. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, sample C2010 unless stated. Scale bar for all specimens 200 microns. **A, D, G**, P_1 element, (NHMUK PM X 3731), "outer lateral", "oral" and "inner lateral" view. **B, E**, P_1

element, (NHMUK PM X 3732), “outer lateral” and “aboral” view. **C, F**, P_1 element, (NHMUK PM X 3733), “inner lateral” and “oral” view. **H, K**, P_1 element, (NHMUK PM X 3734), “outer lateral” and “oral” view. **I, L**, P_3 element, (NHMUK PM X 3735), “outer lateral” and “oral” view. **J, M**, P_1 element, (NHMUK PM X 3671), C2008, “outer lateral” and “oral” view. **N, Q**, holotype, P_3 element, (NHMUK PM X 3673), C2009, “inner lateral” and “oral” view. **O, R**, P_3 element, (NHMUK PM X 3736), “outer lateral” and “oral” view. **P, S**, P_3 element, (NHMUK PM X 3737), “outer lateral” and “oral” view. **T, W**, P_2 element, (NHMUK PM X 3738), C2008, “outer lateral” and “oral” view. **U, X**, P_2 element, (NHMUK PM X 3739), “outer lateral” and “aboral” view. **V, Y**, P_2 element, (NHMUK PM X 3740), “outer lateral” and “oral” view.

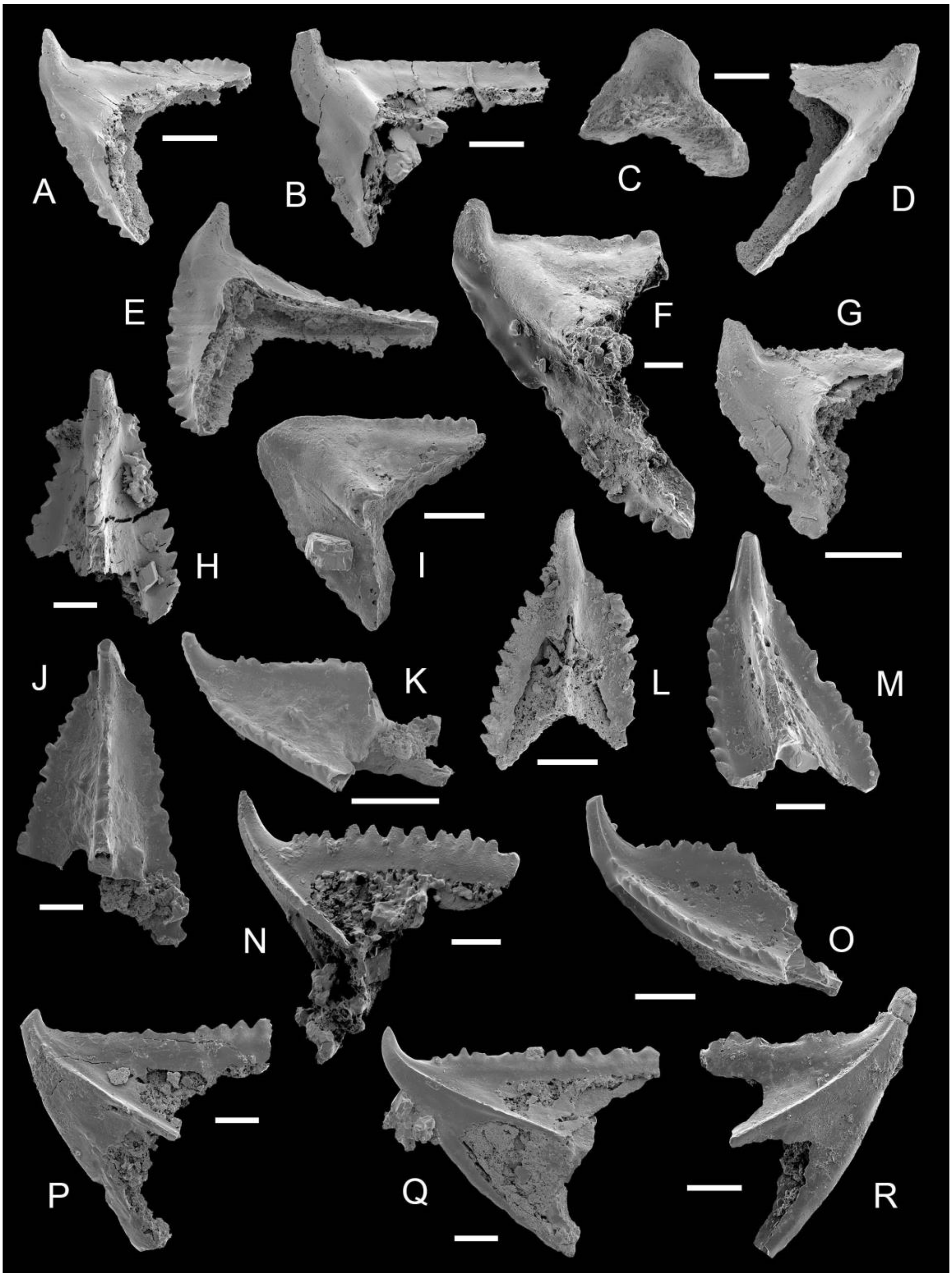

Figure 7. *Omanognathus daiqaensis* gen et sp. nov. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, sample C2010 unless stated. Scale bar for all specimens 200 microns. **A, E**, M element, (NHMUK PM X 3741), "lateral" and oblique "oral" view. **B**, M element, (NHMUK PM X 3742), "lateral" view. **C, D**, M element, (NHMUK PM X 3743), "oral" and "lateral"

view. **F**, M element, (NHMUK PM X 3745), C2009, "lateral" view. **G**, M element, (NHMUK PM X 3746), "lateral" view. **H**, S_0 element, (NHMUK PM X 3744), "posterior" view. **I**, M element, (NHMUK PM X 3747), "lateral" view. **J, K**, S_0 element, (NHMUK PM X 3749), "posterior" and oblique "lateral" view. **L**, S_0 element, (NHMUK PM X 3748), "posterior" view. **M, O**, S_1 element, (NHMUK PM X 3750), "posterior" and "lateral" view. **N**, S_2 element, (NHMUK PM X 3751), "lateral" view. **P**, **S_3** element, (NHMUK PM X 3752), "lateral" view. **Q**, S_3 element, (NHMUK PM X 3753), "lateral" view. **R**, S_3 element, (NHMUK PM X 3754), C2009, "lateral" view.

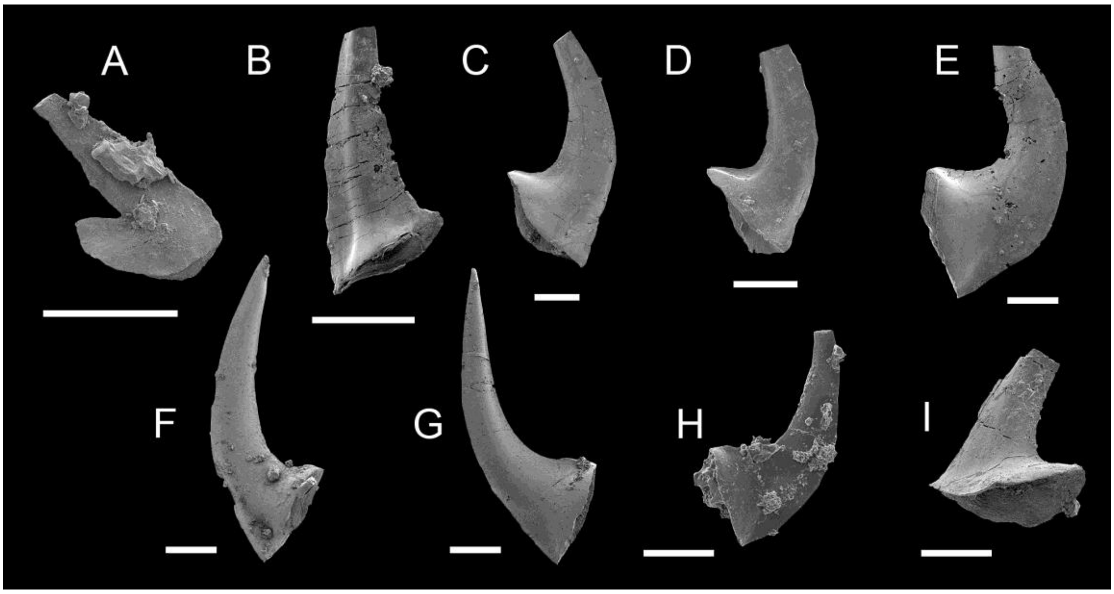

Figure 8. *Drepanoistodus* sp. Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman. Scale bar for all specimens 100 microns. **A**, oistodiform r element, (NHMUK PM X 3681). C2010. **B**, suberectiform p element, (NHMUK PM X 3755), C2009. **C**, drepanodiform q_1 element, (NHMUK PM X 3679), C2009. **D**, drepanodiform q_1 element, (NHMUK PM X 3756), C2008. **E**, drepanodiform q_1 element, (NHMUK PM X 3757), C2008. **F**, drepanodiform q_2 element, (NHMUK PM X 3758). C2010. **G**, drepanodiform q_2 element, (NHMUK

PM X 3759). C2010. **H**, drepanodiform q_2 element, (NHMUK PM X x3682), C2009. **I**, indet. coniform element, (NHMUK PM X 3680), C2009.

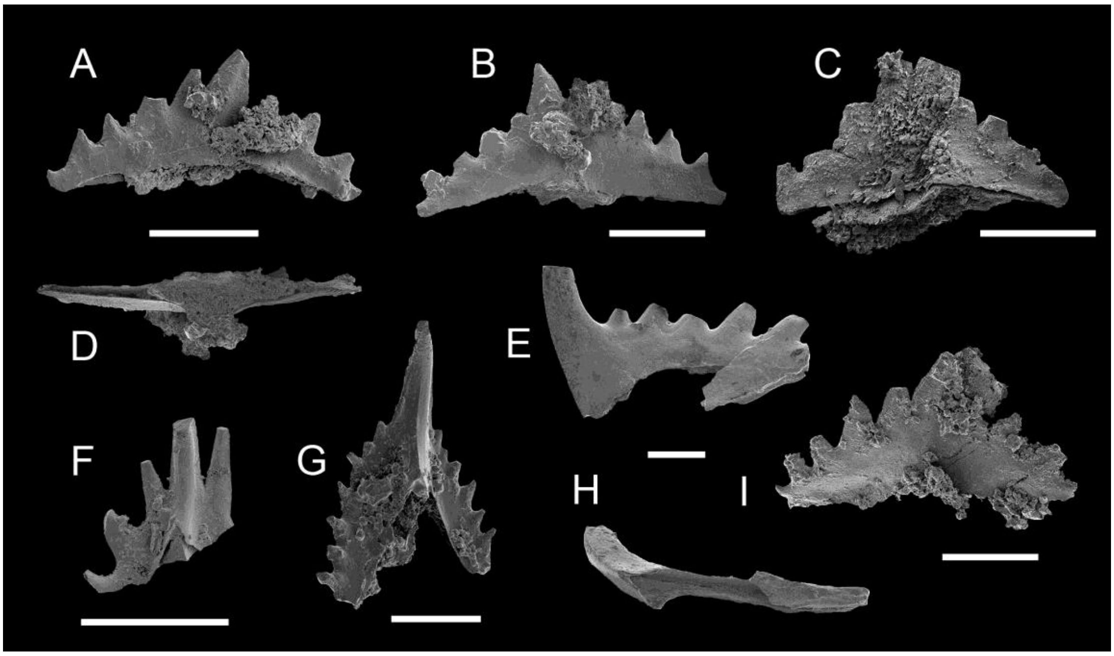

Figure 9. aff *Microzarkodina*, Middle Ordovician, Darriwilian, Am 5 Member, Amdeh Formation, Wadi Daiqa, Oman, all sample C2010. Scale bar for all specimens 100 microns. **A, D**, P element, (NHMUK PM X 3772). **B**, P element, (NHMUK PM X 3773). **C**, P element, (NHMUK PM X 3774), **E, H**, Sc element, (NHMUK PM X 3777). **F**, Sa element, (NHMUK PM X 3775). **G**, Sb element, (NHMUK PM X 3776). **I**, P element, (NHMUK PM X 3778).

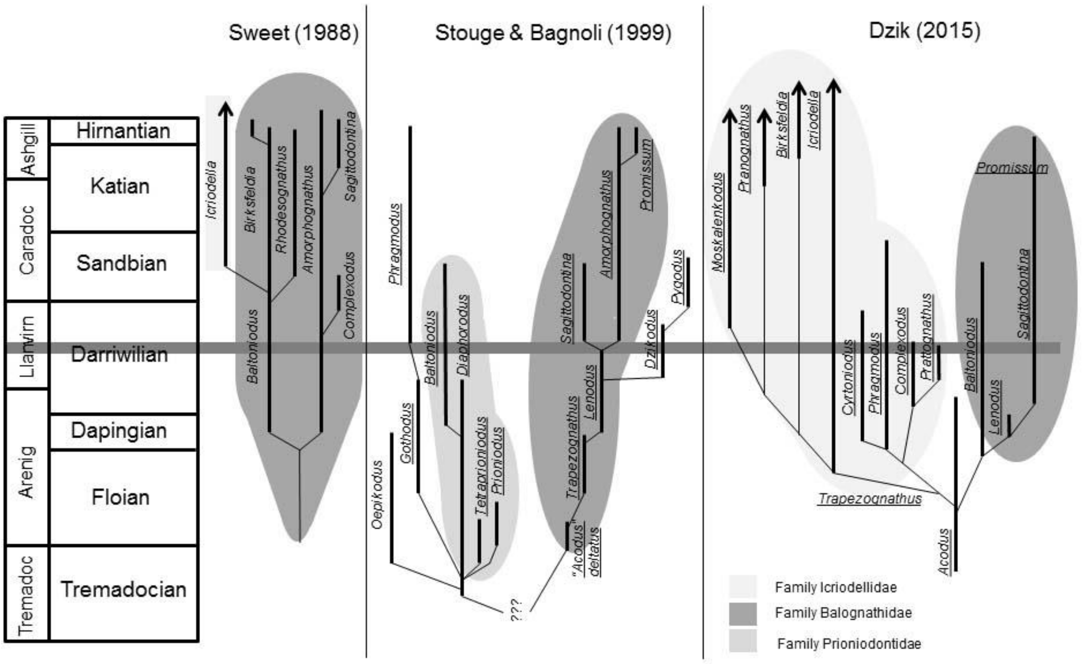

Figure 10. Stratophenetic representations of the early evolution of prioniodontid conodonts after Sweet (1988), Stouge and Bagnoli (1999) and Dzik (2015). The shaded horizontal bar represents the approximate age of the Amdeh Formation samples. *Gamachignathus* has been replaced by *Birksfeldia* as it is considered a junior synonym by Bergström and Ferretti (2015).

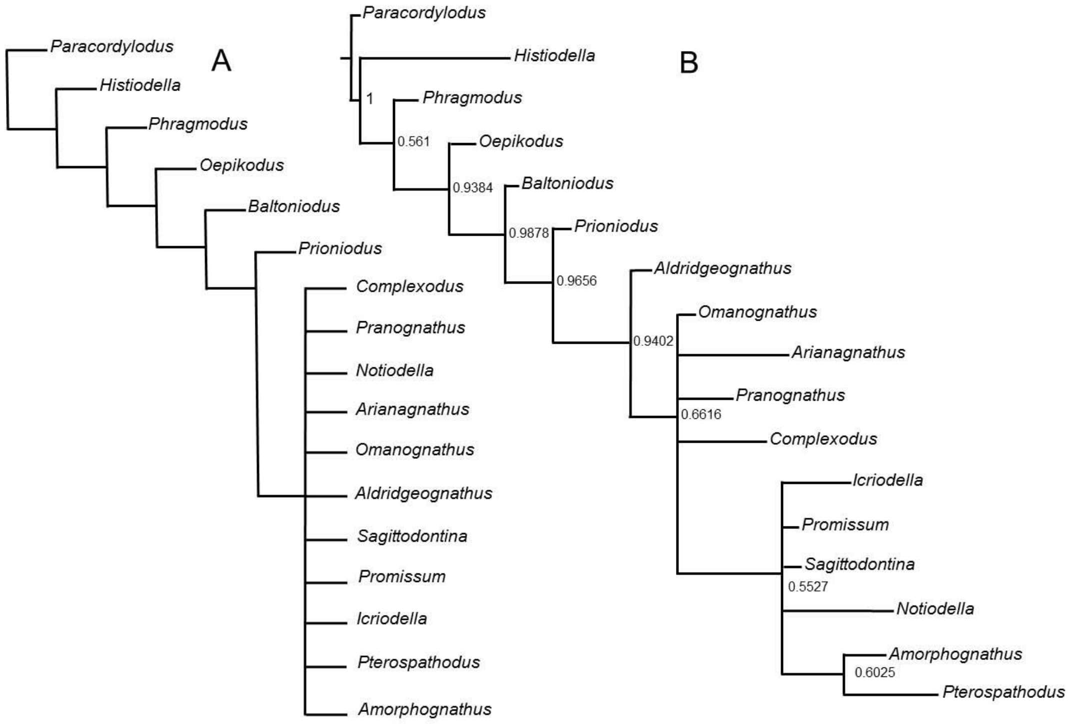

Figure 11. Trees for Balognathid conodonts following cladistic analysis using the Donoghue *et al.* (2008) dataset with additional taxa. **A**, poorly resolved parsimony consensus tree produced by TNT. **B**, probabilistic Bayesian Maximum Likelihood consensus tree produced using MrBayes MKV and Gamma model.