Early Ordovician (Tremadocian) brachiopods from the Eastern Alborz Mountains, Iran

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Abstract. Six linguliform and two rhynchonelliform brachiopods, including three new species *Eurytreta ahmadii*, *Wahwahlingula kharbashi* and *Nanorthis bastamensis* are described from Tremadocian strata (*Paltodus deltifer deltifer* conodont Biozone) in the Deh-Molla area southwest of Shahrud, Northern Iran. The fauna is dominated by micromorphic lingulides and acrotretides and shows distinct similarity to the contemporaneous micromorphic brachiopod association from Tremadocian chalcedonites of the Holy Cross Mountains, Poland. New data on the early ontogeny of the enigmatic lingulide *Diencobolus* show a very distinct pattern, including the presence of a metamorphic protegulum ornamented with flat-based pits and a single pair of larval setal bundles, which links this taxon to *Paterula* and suggests close phylogenetic relationships of both taxa to the Discinoidea.

Key words: Brachiopoda, taxonomy, ontogeny, Ordovician, Tremadocian, Iran.

INTRODUCTION

The Ordovician brachiopod faunas of Iran are still very poorly documented. In particular, Early Ordovician brachiopods are presently known only from a single section in the Eastern Alborz Mountains, where they were reported from the uppermost Tremadocian *Paroistodus proteus* Biozone and overlying Floian deposits (Popov et al. 2008, 2009a). The newly discovered brachiopod fauna from the Deh-Molla section, which co-occurs with conodonts of the *Paltodus deltifer deltifer* Biozone, bridges the gap between earlier described faunas and the Cambrian (Furongian) brachiopod associations of the Mila Formation (Popov et al. 2009b). The linguliform brachiopods are represented by six taxa, including *Acrotreta dissimilis* (Biernat, 1973), *Akmolina minor* (Biernat, 1973), *Diencobolus* sp., *Elliptoglossa* sp., *Eurytreta ahmadii* sp. nov. and *Wahwahlingula kharbashi* sp. nov. The assemblage shows distinct similarity to the association of micromorphic lingulates described earlier by Holmer & Biernat (2002) from Tremadocian chalcedonites of the Holy Cross Mountains, Poland, where they also occur in association with conodonts of the *Paltodus deltifer* Biozone. Only two rhynchonelliform brachiopods have been found through the Tremadocian interval of the sequence, including *Nanorthis bastamensis* sp. nov. and *Tritoechia* sp.

GEOLOGICAL SETTING

The brachiopod fauna described in the present work was sampled in the Deh-Molla area about 15 km southwest of the city of Shahrud in the Eastern Alborz Mountains (Fig. 1). The only published source on the Ordovician sequence in the vicinity of Shahrud is a paper by Ghavidel Syooki (2006), where he reported for the first time on the presence of Tremadocian deposits north of the Kalat-e Molla village and subdivided the Cambrian (Furongian)–Ordovician sequence into six acritarch assemblage zones. He referred the Lower Ordovician part of the sequence to the Lashkarak Formation, which is discontinuously overlain by the Upper Ordovician deposits referred to the Ghelli Formation. However, the lithostratigraphical subdivision of the Ordovician in the Alborz Mountains is currently under revision and therefore it is not used in our paper.

The studied section is exposed on the southern side of the unnamed valley about 1 km northeast of the Qalyankesh Mountain, close to the Shahrud University mine at about 8.5 km north of the Kalat-e Molla village. The Cambrian–Ordovician boundary in the section is placed provisionally at the base of the unit of green and grey argillite (up to 58 m thick) with several thin beds of bioclastic limestone (Fig. 2). The lowermost sample (DM-A/5, geographical coordinates 36°21′21.12″N,
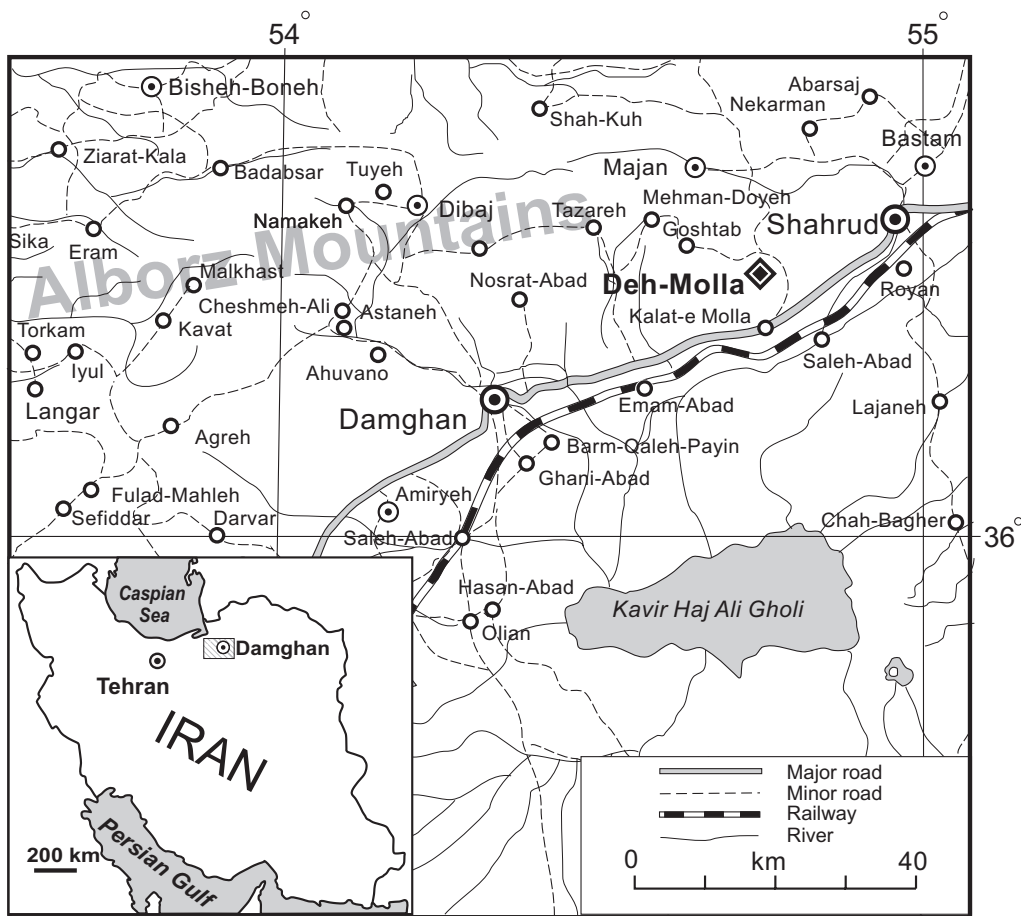
Fig. 1. Geographical map showing the position of the Deh-Molla section southwest of Shahrud.

54°44′44.1″E) was taken from the argillite at 15.5 m above the base of the unit, containing abundant trilobites, including *Asaphellus inflatus* Lu, 1962; *Chungkingaspis sinensis* (Sheng, 1958); *Conophrys simehensis* Ghobadi Pour, 2006; *Dactylocephalus mehriae* Ghobadi Pour, 2006; *Geragnostus* sp. and a few brachiopods, including *Eurytreta* sp. and *Nanorthis bastamensis* sp. nov.

The main part of the brachiopod collection was sampled from four beds of bioclastic limestone in the middle of the unit. Two uppermost limestone horizons yielded an abundant conodont fauna indicative of the *Paltodus deltifer deltifer* Biozone.

Sample DM-A/7 was taken at 21.4 m above the base of the unit. It contains brachiopods *Eurytreta ahmadii* sp. nov. and *Wahwahlingula kharbashi* sp. nov.

Sample DM-A/8 was taken at 29.8 m above the base of the unit. The brachiopod assemblage from that sample includes *Acrotreta dissimilis*, *Diencobolus* sp., *Elliptoglossa* sp., *Eurytreta ahmadii* and *Wahwahlingula kharbashi*, which occur in association with spicules of hexactinellide sponges and ostracods.

Sample DM-A/9 was taken from the base of a grey bioclastic limestone bed at 38.9 m above the base of the unit. It contains the brachiopods *Acrotreta dissimilis*, *Diencobolus* sp. and *Wahwahlingula kharbashi*.

Sample DM-A/10 was taken from the top of the same limestone bed at about 0.3 m above the sample. It contains brachiopods *Acrotreta dissimilis*, *Akmolina minor*, *Eoconulus* sp., *Eurytreta ahmadii* and *Wahwahlingula kharbashi*.

Sample DM-A/9B was taken from the base of the uppermost limestone bed at 41.75 m above the base of the unit and sample DM-A/9A was collected from the same bed just 5 cm above the previous sample (geographical coordinates 36°21′22.5″N; 54°44′44.88″E, altitude 1645 m). They contain rhynchonelliform brachiopods including abundant *Nanorthis bastamensis* and a few *Tritoechia* sp., linguliform brachiopods *Acrotreta dissimilis*, *Akmolina minor*, *Diencobolus* sp., *Eurytreta ahmadii* and *Wahwahlingula kharbashi*. Sample DM-A/10A was taken from the upper part of the bed at 0.35 m above sample DM-A/9A, containing
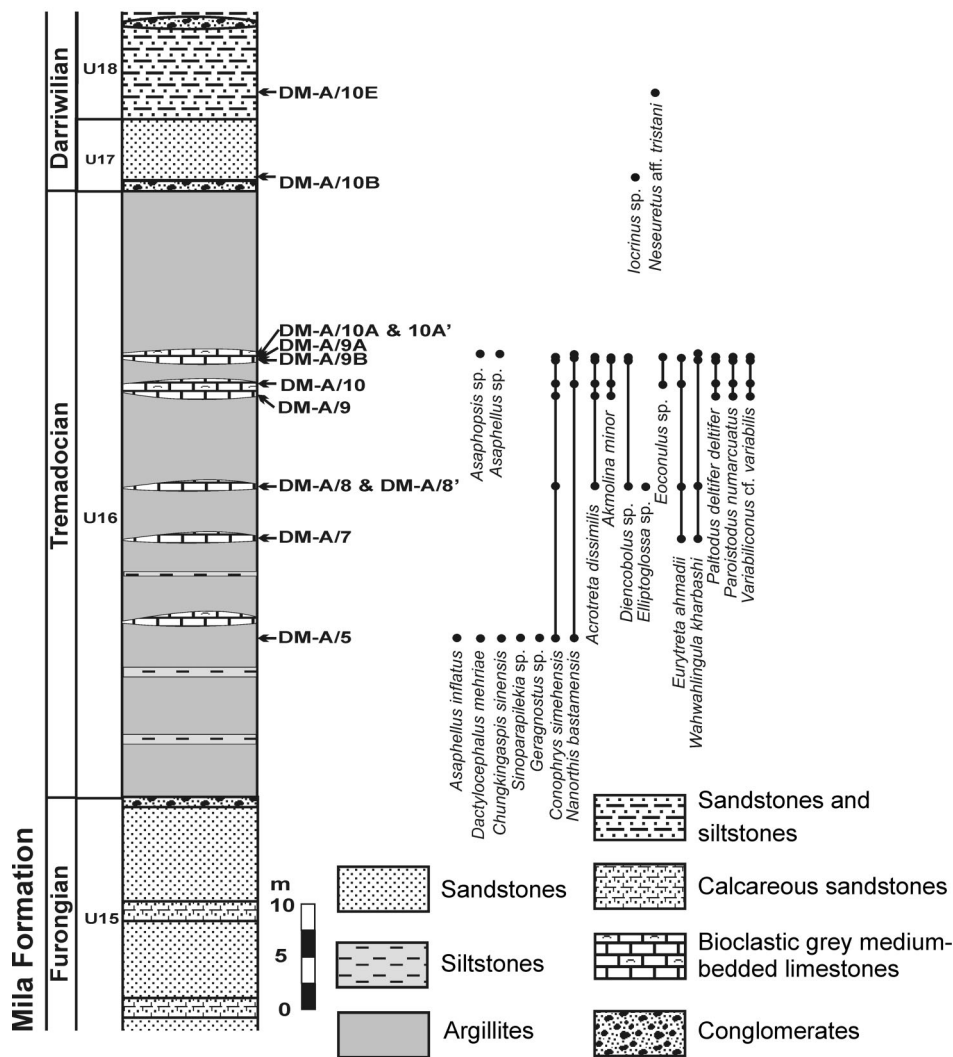
Fig. 2. Stratigraphical column of the Lower Ordovician sediments in the Deh-Molla section showing the position of samples and stratigraphical distribution of brachiopods, selected trilobites, echinoderms and conodonts.

numerous trilobites *Asaphellus* sp. and *Asaphopsis* sp. which occur in association with numerous ostracods.

The Tremadocian deposits are overlain unconformably by a sandstone unit with the up to 1 m thick bed of a pebbly conglomerate at the base. The Darriwilian age of the sandstones is confirmed by the occurrence of the trilobite *Neseuretus* aff. *tristani* (Brongniart in Desmarest, 1817) (for more comments see Ghobadi Pour et al. 2007).

In comparison to the Simeh-Kuh section, which is situated in the vicinity of Damghan about 50 km west of Deh-Molla (Ghobadi Pour 2006; Popov et al. 2008), the Tremadocian part of the Ordovician sequence in the studied section is condensed, while a significant interval from the uppermost Tremadocian *Paroistodus proteus*

Biozone to the Darriwilian Stage is missing. In the absence of diagnostic conodonts, the Lower Ordovician boundary in both sections is defined by the appearance of the characteristic *Asaphellus–Dactylocephalus* Association (for further discussion see Ghobadi Pour 2006), which includes *Asaphellus inflatus*, *Chungkingaspis sinensis* and *Dactylocephalus*. According to Peng (1990a, 1990b), in South China, the trilobite association with *Asaphellus inflatus* and *Dactylocephalus* spp. appears near the base of the Tremadocian. In particular, in the western Hubei Province, this assemblage appears in the Nantsinkwan Formation above the local *Monocostodus servierensis–Cordylodus intermedius* conodont Biozone of the uppermost Cambrian age. Therefore, the position of the Cambrian–Ordovician boundary in the Deh-Molla section

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is placed significantly higher than it was previously defined by Ghavidel Syooki (2006), approximately 35 m above his local Acritarch Assemblage Zone III.

SYSTEMATIC PALAEONTOLOGY

Abbreviations for parameters measured on specimens are (in millimetres): W, L, T = maximum width, length, thickness of the shell; Lv, Ld = maximum length of ventral and dorsal valve; Il, Iw = maximum length and width of pseudointerarea/interatarea; Pl = median length of pseudointerarea; Cw, Cl = width, length of cardinal muscle field; Sa = length of dorsal median septum; Sm = position of maximum height of dorsal median septum; Vl = length of visceral area; BBl = length of brachiophore basis; Ml = length of ventral muscle field; Mw = width of ventral muscle field. The morphological terminology used here for the linguliform brachiopods follows that of Holmer & Popov (in Kaesler 2000).

The illustrated and described material is housed in the National Museum of Wales, Cardiff (NMW). The cited specimens from Poland are deposited in the Institute of Palaeobiology Warsaw (ZPAL Bp).

Subphylum LINGULIFORMEA Williams et al., 1996
Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family OBOLIDAE King, 1846
Subfamily ELLIPTOGLOSSINAE Popov & Holmer, 1994
Genus *Elliptoglossa* Cooper, 1956

Type species. *Leptobolus*? *ovalis* Bassler, 1919; Upper Ordovician, Katian, Martinsburg Formation, Pennsylvania, USA.

Elliptoglossa sp.
Figure 3J

Material. NMW 2008.35G.160, incomplete dorsal valve from locality DM-A/8.

Remarks. A single dorsal valve is characterized by the marginal umbo, and well-defined limbus, which are characteristic of *Elliptoglossa*. There are only three other described Tremadocian species, all restricted in their geographical distribution to Gondwana and Baltica (Popov & Holmer 1994; Mergl 2002), including *Elliptoglossa polonica* Holmer & Biernat, 2002 and *Elliptoglossa linguae* (Westergård, 1909) and *Elliptoglossa celdai* Mergl, 2002. All these species differ from each other mainly in the shape of the vestigial ventral pseudointerarea. There is no doubt about generic attribution of the specimen, but in the absence of data on the dorsal valve morphology its precise taxonomic discrimination down to the species level cannot be made.

Family PATERULIDAE Cooper, 1956
Genus *Diencobolus* Holmer, Popov, Koneva & Bassett, 2001

Type species. *Diencobolus simplex* Holmer, Popov, Koneva & Bassett, 2001; Cambrian, Guzhangian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau Range, Kazakhstan.

Remarks on the ontogeny. The finely pitted micro-ornament of the larval and adult shell in *Diencobolus* was reported previously by Holmer et al. (2000, 2001) and by Holmer & Biernat (2002), but no further details were provided. The Iranian specimens of *Diencobolus* sp. exhibit a larval shell, about 180 μm wide, surrounded by a distinct halo. The second halo delineates a circular swollen area about 60 μm in diameter, which most probably represents a metamorphic protegulum. The surface of the protegulum is differentiated into a single pair of lateral lobs terminated anteriorly near the halo and divided medially by a shallow cleft (Fig. 3K). The protegulum and the larval shell are ornamented with shallow, densely placed flat-based pits varying from 4.5 to 5.1 μm in diameter (Fig. 3H). The mature shell surface is also bearing flat-based imprints, but the diameter of pits is only 2.8 to 3.2 μm and they are more deeply impressed than the juvenile pits (Fig. 3I).

The dorsal metamorphic protegulum of *Diencobolus* shows distinct similarity to the 'first-formed shell' of

Fig. 3. A–E, **G**, *Wahwahlingula kharbashi* sp. nov.; A, B, NMW 2008.35G.169, ventral valve exterior, pitted microornament of adult shell, sample DM-A/7; C, NMW 2008.35G.170, incomplete ventral valve, pseudointerarea, sample DM-A/7; D, NMW 2008.35G.173, incomplete dorsal valve exterior, sample DM-A/8; E, NMW 2008.35G.171, incomplete ventral valve interior, sample DM-A/8; G, NMW 2008.35G.172, incomplete dorsal valve interior, sample DM-A/7. **F, H–I, K–O**, *Diencobolus* sp.; F, H, K, NMW 2008.35G.161, incomplete dorsal valve exterior, pitted ornament of larval shell, enlarged larval shell (ls) and metamorphic protegulum (pt) showing paired lobes (L1) separated by median cleft, and halo (h) marking outer border of larval (brephic) shell, sample DM-A/8; I, L, NMW 2008.35G.162, dorsal valve, oblique posterior view and enlarged surface of mature shell with finely pitted microornament, sample DM-A/9A; M, N, NMW 2008.35G.222, incomplete dorsal valve exterior, enlarged surface of mature shell showing flat-based pits, sample DM-A/8; O, NMW 2008.35G.223, incomplete ventral valve interior, sample DM-A/9B. **J**, *Elliptoglossa* sp., NMW 2008.35G.160, incomplete dorsal valve interior, sample DM-A/8. All specimens from the Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone of the Deh-Molla section.
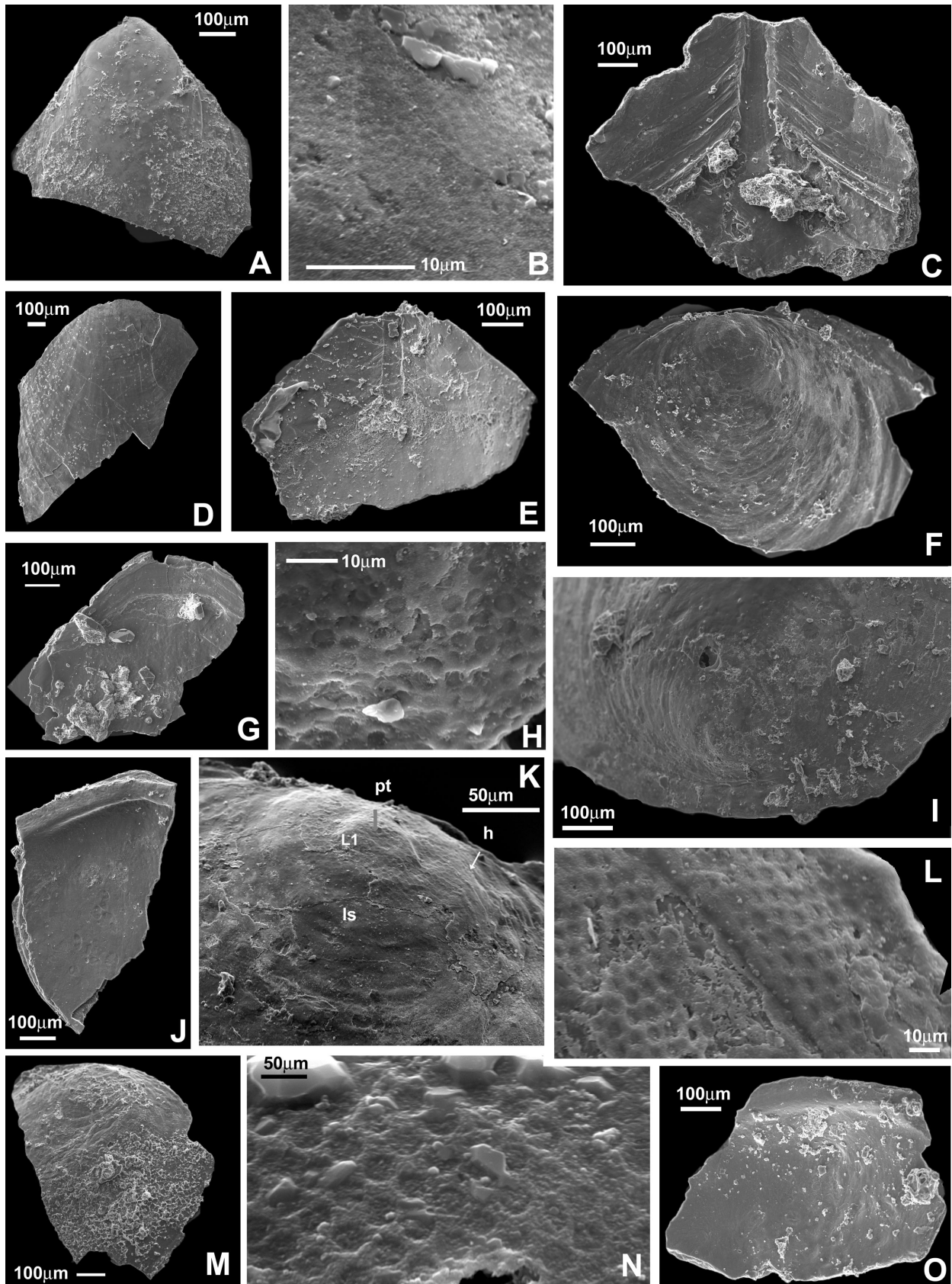
Paterula described in detail by Williams (2003, p. 70, text-fig. 2). In both genera the dorsal metamorphic shell is only about 60 μm; it bears a pair of lateral lobes and is ornamented with flat-based imprints. The only difference is that the diameter of pits in *Paterula* (on average 2.3 μm) is significantly smaller than in *Diencobolus* sp. The 'brephic zone' on the *Paterula* dorsal forms a narrow band just 7 μm wide, ornamented by elliptical pits. It is succeeded outwards by the mature shell ornamented with characteristic rhombic imprints. In *Diencobolus* the larval shell outside the protegulum, which in the ontogenetic sequence is comparable to the area of the 'brephic zone' after Williams (2003, text-fig. 2C), is significantly larger and shows no change in characters of flat-based imprints unlike *Paterula*. The most significant change in the shell ornamentation occurs outside the second halo, which forms the boundary with the mature shell.

It is unclear if the metamorphic shells of *Diencobolus* and *Paterula* represent the embryonic protegulum formed shortly before hatching, or if these shells were secreted by the whole surface of the mantle at the beginning of a free swimming stage, as in discinids (Chuang 1977). By analogy with the paterinides (Williams et al. 1998), the paired lobes in both genera can be interpreted as showing the position of two larval setal sacks. The slight wrinkling of the shell surface suggests that the metamorphic protegulum in both genera was flexible and most probably not mineralized.

The closest analogy to the ontogenetic pattern observed in *Diencobolus* and *Paterula* can be found in the extant discinids. According to Lüter (2001), *Discinisca* sp. cf. *tenuis* develops a pair of larval setal bundles at the end of the embryonic stage shortly before hatching. However, larval setae are becoming lost at the beginning of the free swimming stage and are absent at the stage when the protegulum is secreted (Chuang 1977). It is possible that larval setae in *Diencobolus* and *Paterula* were lost later in metamorphosis, shortly after the metamorphic protegulum was formed. The second halo in *Diencobolus* and the outer boundary of the 'brephic zone' in *Paterula* most probably mark a transition from the pelagic to the benthic stage of the life cycle. It may suggest that the pelagic stage in *Paterula* was significantly shorter than that of *Diencobolus*.

Data on the ontogeny suggest that *Diencobolus* and *Paterula* are closely related and they show more similarity to discinoids than to other lingulide families in the development pattern. It supports an earlier suggestion by Holmer & Popov (in Kaesler 2000) and Williams (2003, text-fig. 6) that the family Paterulidae represents a sister group of Discinoidea.

Diencobolus sp.
Figure 3F, H, I, K–O

Material. NMW 2008.35G.223, incomplete ventral valve interior, sample DM-A/9B. NMW 2008.35G.161, 222, incomplete dorsal valves, sample DM-A/8. NMW 2008.35G.162, incomplete dorsal valve, sample DM-A/9A. NMW 2008.35G.223, incomplete ventral valve, sample DM-A/9B.

Remarks. The Iranian shells show a finely pitted surface of the larval and adult shell, a moderately convex sagittal profile more strongly curved in the umbonal area in the dorsal valve, whereas a single ventral valve shows a submarginal umbo. All listed features are characteristic also of *Diencobolus subovalis* Holmer & Biernat 2002 from the Lower Ordovician, Tremadocian chalcedonites, Wysoczki, Holy Cross Mountains, Poland; however, the Iranian shells lack a ventral visceral platform that is characteristic of the Polish species. The only other known Ordovician species of the genus is *Diencobolus naukatensis* (Holmer, Popov & Bassett, 2000) from the Lower Ordovician (presumably Floian) olistolith in the Silurian Pulgon Formation of the Alai Range in southern Kyrgyzstan. Both species are closely similar in the dorsal valve morphology and can be distinguished mainly in the position of the ventral umbo, which is submarginal in *Diencobolus subovalis* and excentric in *Diencobolus naukatensis*. In addition, the latter species also lacks a ventral visceral platform.

Genus *Wahwahlingula* Popov, Holmer & Miller, 2002

Type species. *Lingula antiquissima* Jeremeyew, 1856; Cambrian (Furongian)–Lower Ordovician (Tremadocian), Tosna Formation, northwestern Russia.

Wahwahlingula kharbashi sp. nov.
Figures 3A–E, G; 4

Derivation of name. After Kuh-e Kharbash south of type locality.

Holotype. NMW 2008163, ventral valve (Lv = 3.2, W = 2.7, Il = 1.1, Iw = 2.0, Vl = 1.8), Lower Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone, sample DM-A/10A, Deh-Molla section, Eastern Alborz Mountains, Iran.

Paratypes. Figured specimens: NMW 2008.35G.169, ventral valve; NMW 2008.35G.172, incomplete dorsal valve; sample DM-A/7. NMW 2008.35G.170, 171, incomplete ventral valves; NMW 2008.35G.173, incomplete dorsal valve; sample DM-A/8. NMW 2008.35G.164,
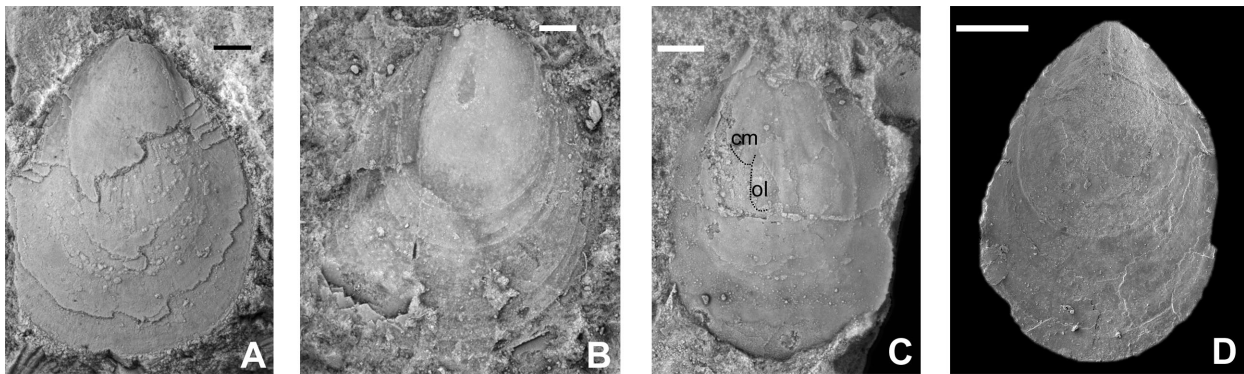
Fig. 4. *Wahwahlingula kharbashi* sp. nov.; **A**, NMW 2008.35G.164, exfoliated ventral valve exterior, sample DM-A/9B; **B**, NMW 2008.35G.165, dorsal valve exterior, DM-A/10A; **C**, NMW 2008167, dorsal external mould, DM-A/10A; **D**, NMW 2008163, holotype, ventral valve interior, DM-A/10A. All specimens from the Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone of the Deh-Molla section. Scale bars are 1 mm.

exfoliated ventral valve (Lv = 7.0, W = 5.9, T = 0.6), sample DM-A/9B. NMW 2008.35G.165 (Ld = 8.0, W = 6.1); NMW 2008167 (Ld = 6.7, W = 4.8, Vl = 3.9) dorsal valves; sample DM-A/10A.

Other specimens: NMW 2008.35G.224.1–3, incomplete ventral valves; NMW 2008.35G.224.4–5, incomplete dorsal valves; sample DM-A/7. NMW 2008.35G.225.1 incomplete ventral valve; NMW 2008.35G.168, 225.1, 224, dorsal valves; sample DM-A/9B. Total 9 ventral and 9 dorsal valves.

Diagnosis. Shell elongate, suboval, with a large ventral pseudointerarea occupying about three fourths of maximum shell width and an undivided dorsal pseudointerarea. Larval shell smooth; adult shell finely and densely pitted. Ventral interior with a large visceral area occupying posterior half of the valve. Dorsal interior with a weakly impressed visceral area extending anteriorly up to 60% of valve length and bisected by the long, faint median ridge.

Description. Shell slightly dorsibiconvex, elongate suboval in outline, about 120–140% as long as wide. Ventral valve with a pointed umbo and with maximum width slightly anterior to midlength. Ventral pseudointerarea wide, subtriangular, occupying up to 75% of maximum valve width. Pedicle groove shallow and narrow with steep slightly divergent margins. Propareas low, concave in transverse profile, with fine flexure lines expressed by a deflection of growth lines. Dorsal valve gently convex with a low, crescent-shaped, undivided pseudointerarea not raised above the valve floor. Larval shell completely smooth, almost subcircular in outline, about 270–360 μm across, delineated by a strong rim. Shell surface of the brephic and adult shell finely and densely pitted with subcircular pits slightly exceeding 1 μm across.

Ventral visceral area weakly impressed, with the anterior border situated slightly posterior to midlength. Dorsal interior with a weakly impressed visceral area about 60% as long as the valve. Anterior border of the visceral area with a short median tongue occupied mainly by a pair of weakly impressed outside lateral muscle scars. Central muscle scars large, elongate suboval, situated posterior to midvalve. Visceral area bisected by a long, faint median ridge more prominent anterior to midlength. Posterolateral dorsal muscle fields slightly thickened, but individual muscle scars indiscernible. Dorsal *vascula lateralia* arcuate, submarginal.

Remarks. Unlike *Wahwahlingula antiquissima* (Jeremeyew, 1856) revised by Popov et al. (1989, 2002), the Iranian shells have a suboval, rather than a subtriangular shell outline, a larger ventral pseudointerarea occupying about three fourths of maximum shell width, a much smaller size of the pits, which only slightly exceed 1 μm across, and they lack a median groove on the dorsal pseudointerarea. The characters of the microornament on the larval shell of *Wahwahlingula antiquissima* are as yet unknown.

Wahwahlingula kharbashi sp. nov. differs from *Wahwahlingula sevierensis* Holmer et al., 2005 from the Ibexian, House Limestone and Fillmore Formation of Utah, USA, in having a smooth larval shell, a large ventral pseudointerarea and a distinct median ridge crossing the dorsal visceral area.

Wahwahlingula? *emanuelensis* Brock & Holmer, 2004, from the Floian, Emanuel Formation in Western Australia, is also characterized by a smooth larval shell and finely pitted microornament of the brephic and adult shell, but it differs from the newly described species in having an elongate suboval, rather than a teardrop-

shaped outline, a wider ventral pseudointerarea and a long median ridge bisecting the dorsal visceral area.

Shells of *Wahwahlingula*? sp. from the Tremadocian *Drepanoistodus proteus* Biozone of Simeh-Kuh, Eastern Alborz Mountains, Northern Iran, briefly described and illustrated by Popov et al. (2008), are too poorly preserved to make a more detailed comparison. They are characterized by a microornament of hemispherical pits 5–8 mm across, which is significantly larger than that in *Wahwahlingula kharbashi*, and probably are not conspecific.

<div align="center">

Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893
Genus *Acrotreta* Kutorga, 1848

</div>

Type species. *Acrotreta subconica* Kutorga, 1848; Lower Ordovician, Floian (Billingenian), St Petersburg Region, northwestern Russia.

<div align="center">

Acrotreta dissimilis (Biernat, 1973)
Figure 5A–L, N–P

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1973 *Spondylotreta dissimilis* Biernat; p. 78; pl. 11; figs 2–9; pl. 12, figs 1, 2.
2002 *Acrotreta dissimilis* (Biernat); Holmer & Biernat, p. 149, fig. 7.

Holotype. ZPAL Bp XV/10d, ventral valve; Lower Ordovician, Tremadocian chalcedonites, Wysoczki, Holy Cross Mountains, Poland.

Material. Figured specimens: NMW 2008.35G.173, ventral valve, sample DM-A/8. NMW 2008.35G.176, 178, 179, 226, ventral valves; NMW 2008.35G.175, incomplete dorsal valve; sample DM-A/9. NMW 2008.35G.174, 177, incomplete dorsal valves, sample DM-A/9A. NMW 2008.35G.180, 181, incomplete dorsal valves, sample DM-A/10.

Other specimens: NMW 2008.35G.229.1–15, incomplete ventral valves; NMW 2008.35G.229.16–24, incomplete dorsal valves; sample DM-A/8. NMW 2008.35G. 227, 230.1–3, incomplete ventral valves; NMW 2008.35G.230.4, incomplete dorsal valve; sample DM-A/9. NMW 2008.35G.231.1–9, incomplete ventral valves, sample DM-A/9A. NMW 2008.35G.228, 232.1–6, incomplete ventral valves; NMW 2008.35G.232.1, incomplete dorsal valve; sample DM-A/9B. NMW 2008.35G.233.1–14, incomplete ventral valves; NMW 2008.35G.233.15–16, incomplete dorsal valves; sample DM-A/10. Total 54 ventral and 17 dorsal valves.

Discussion. In spite of incomplete preservation, the specimens of *Acrotreta* from the Deh-Molla section show close similarity to the topotypes of *Acrotreta dissimilis* (Biernat, 1973) in characteristic features of shell morphology and they are considered here as conspecific. In particular, they are characterized by (1) a procline to catacline ventral valve with height not exceeding commissural shell length and an evenly convex sagittal profile of the ventral pseudointerarea, (2) a narrow dorsal pseudointerarea occupying less than half of maximum shell width, (3) a poorly defined median buttress and (4) a low dorsal median septum. There are minor differences of the Iranian shells from topotypes, including a larger (up to 90 μm wide) pedicle foramen and a slightly smaller (less than 225 μm across) larval shell in comparison to the topotype specimens.

Acrotreta dissimilis is considered as the earliest known species of the genus (Holmer & Biernat 2002). It differs from *Acrotreta curvata* Klouček, 1919 from the Lower Ordovician, Třenice Formation of Bohemia revised by Mergl (2002) in having a ventral valve as a low cone with not exceeding commissural shell length in height, an almost flat sagittal profile of the dorsal valve, a significantly lower and shorter apical process, weakly impressed ventral mantle canals and dorsal cardinal and central muscle scars. A detailed discussion of the affinity of *Acrotreta dissimilis* to the derived species of the genus (e.g. *Acrotreta subconica* Kutorga, 1848 and *Acrotreta korinevskii* Holmer & Popov, 1994) was given by Holmer & Biernat (2002).

Fig. 5. A–**L**, **N**–**P**, *Acrotreta dissimilis* (Biernat, 1973); A, NMW 2008.35G.173, ventral valve posterior view, sample DM-A/8; B, C, NMW 2008.35G.174, incomplete dorsal valve exterior, pitted microornament of larval shell, sample DM-A/9A; D, F, NMW 2008.35G.175, incomplete dorsal valve, microornament of mature shell, exterior, sample DM-A/9; E, H, NMW 2008.35G.176, ventral valve, oblique lateral view, posterior view, sample DM-A/9; G, NMW 2008.35G.177, incomplete dorsal valve interior, sample DM-A/9A; I, NMW 2008.35G.178, incomplete ventral valve exterior showing pedicle foramen crossing the boundary of the larval shell, sample DM-A/9; J, NMW 2008.35G.179, incomplete ventral valve interior, sample DM-A/9; K, NMW 2008.35G.180, incomplete dorsal valve interior, sample DM-A/10; L, NMW 2008.35G.181, incomplete dorsal valve interior, sample DM-A/10; N–P, NMW 2008.35G.226, incomplete ventral valve, exterior, oblique posterior view and enlarged larval shell showing pedicle foramen, sample DM-A/9. **M**, *Eurytreta ahmadii* sp. nov.; NMW 2008.35G.182, dorsal valve interior, sample DM-A/10. All specimens from the Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone of the Deh-Molla section.
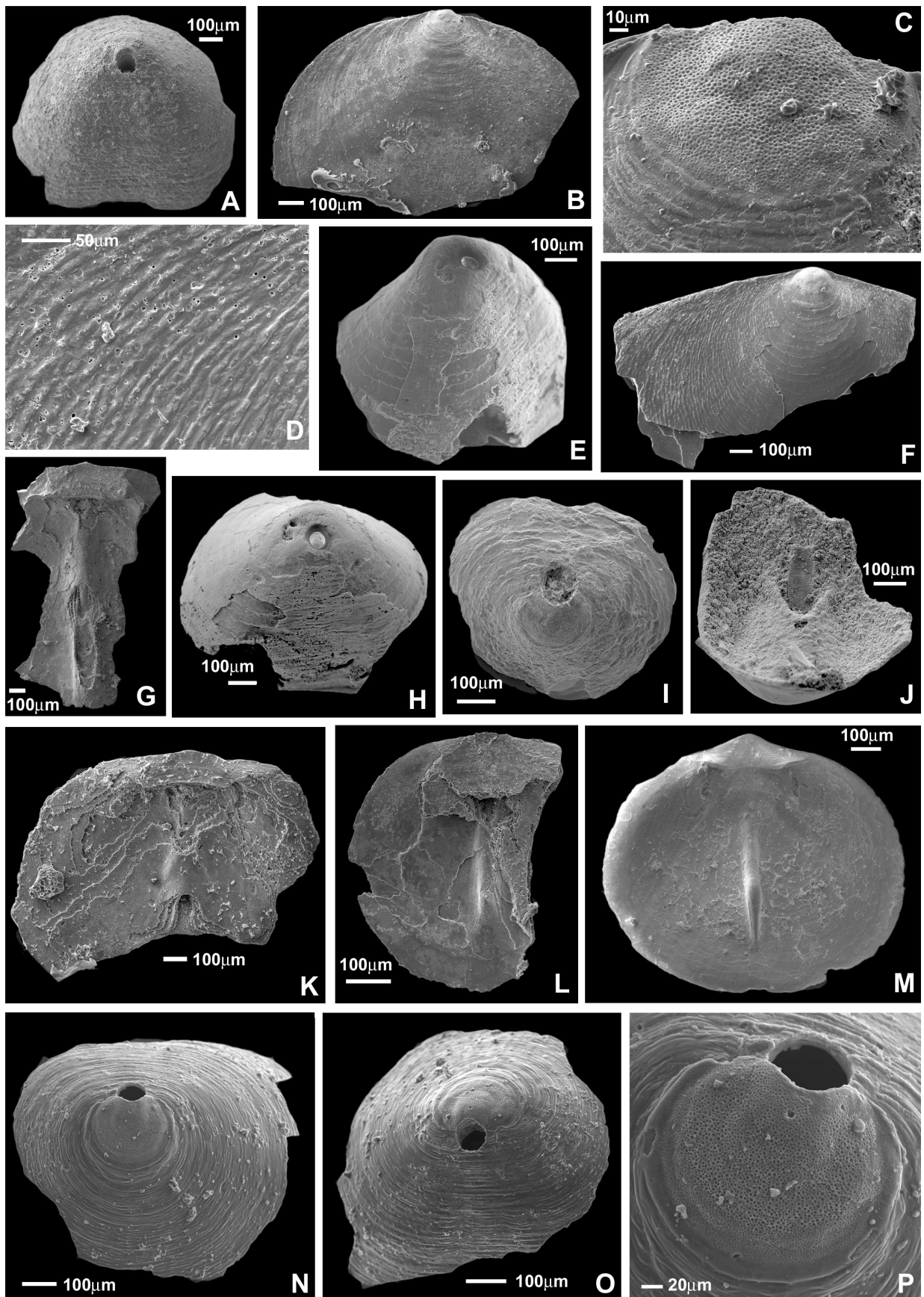
Genus *Eurytreta* Rowell, 1966

Type species. *Acrotreta curvata* Walcott, 1902, Lower Ordovician, Tremadocian, Pogonip Limestone, Eureka district, Nevada, USA.

Eurytreta ahmadii sp. nov.
Figures 5M; 6; 7Q

?2008 *Eurytreta* sp.; Popov, Ghobadi Pour, Hosseini & Holmer, p. 21, fig. 8J.

Derivation of name. After Hasan Ahmadi, geologist from Golestan University, Gorgan, in appreciation of his contribution to the study of the area.

Holotype. NMW 2008.35G.189 (Ld = 1.11, W = 1.30, Iw = 0.56, Cl = 0.45, Cw = 0.82, Sm = 0.65, Sa = 0.90), dorsal valve, Lower Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone, sample DM-A/9A, Deh-Molla section, Eastern Alborz Mountains, Iran.

Paratypes. Figured specimens: NMW 2008.35G.183 (Lv = 0.22, W = 0.44), ventral valve, sample DM-A/7. NMW 2008.35G.184, 185, ventral valves; NMW 2008.35G.187 (Ld = 0.60, W = 0.66, Iw = 0.27, Cl = 0.25, Cw = 0.36, Sm = 0.33, Sa = 0.49), dorsal valve; sample DM-A/8. NMW 2008.35G.186, 235, ventral valves; NMW 2008.35G.188, dorsal valve; sample DM-A/9A. NMW 2008.35G.190, ventral valve; NMW 2008.35G.182 (Ld = 0.87, W = 1.01, Iw = 0.46, Cl = 0.36, Cw = 0.69, Sm = 0.52, Sa = 0.74), dorsal valve; sample DM-A/10.

Other specimens: NMW 2008.35G.242.1–3, incomplete ventral valves, sample DM-A/7. NMW 2008.35G.236, 240.1–6, incomplete ventral valves; NMW 2008.35G.240.17–19, dorsal valves; sample DM-A/9A. NMW 2008.35G.237, 238, 241.1, 2, incomplete ventral valves; NMW 2008.35G.239, 241.13–15, dorsal valves; sample DM-A/10. Total 20 ventral and 10 dorsal valves.

Diagnosis. Ventral valve about 70% as high as long with maximum height at the umbo and almost straight anterior and posterior slopes in a sagittal profile. Ventral deltoid pseudointerarea slightly apsacline to almost catacline. Dorsal pseudointerarea up to 46% of maximum valve width. Ventral interior with a prominent narrow subtriangular intertrough. Dorsal interior with a low, triangular median septum. Dorsal cardinal muscle fields large, weakly impressed. Dorsal central muscle scars and vascular canals indiscernible.

Description. Ventral valve subconical, about 70% as high as long with the maximum height placed at the apex. Sagittal profile of the anterior valve slope almost straight; the lateral slopes are gently and evenly convex. Deltoid pseudointerarea slightly apsacline to almost cataline, straight in the sagittal section, with a weakly defined intertrough. Pedicle foramen small, rounded, about 30 μm in diameter, placed within the larval shell. Dorsal valve transversely oval in outline, 88–90% as long as wide with a weak sulcus slightly more prominent anterior to midlength. Dorsal valve sagittal profile gently convex with maximum height near the larval shell outer boundary. Dorsal interarea slightly anacline, 41–46% as wide as the valve, occupied mainly by a gently concave median groove. Larval shell up to 210 μm wide, ornamented by hemispherical pits of two sizes with larger pits 2.5–3.6 μm across and smaller pits varying from 1.3 to 1.9 μm across.

Ventral interior with a long, narrow, subtriangular apical process, placed anterior to the internal pedicle opening and widening anteriorly. Ventral mantle canals baculate with slightly divergent *vascula media*. Dorsal interior with slightly thickened elongate suboval cardinal muscle fields occupying 55–68% of maximum valve width and 41–42% of sagittal length. Central muscle scars and dorsal mantle canals indiscernible. Median buttress low, subrectangular, merged with a low subtriangular median septum extending anteriorly for 81–85% of valve length and with the highest point situated almost at midvalve.

Discussion. The only previous report on the occurrence of *Eurytreta* in the Tremadocian of Iran was given by Popov et al. (2008). The dorsal valve of *Eurytreta* sp. from the upper Tremadocian deposits of the Simeh-Kuh

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Fig. 6. *Eurytreta ahmadii* sp. nov.; **A**, **B**, NMW 2008.35G.183, ventral valve, oblique posterior and ventral views, sample DM-A/7; **C**, NMW 2008.35G.184, ventral valve interior showing apical process, sample DM-A/8; **D**, NMW 2008.35G.185, ventral valve lateral view, sample DM-A/8; **E**, **F**, **N**, NMW 2008.35G.186, ventral valve exterior, enlarged umbonal area showing pitted larval shell and pedicle foramen, sample DM-A/9A; **G**, NMW 2008.35G.187, dorsal valve interior, sample DM-A/8; **H**, **I**, **L**, NMW 2008.35G.188, dorsal valve umbonal area, dorsal and oblique lateral view, sample DM-A/9A; **J**, **K**, NMW 2008.35G.189, holotype, dorsal valve interior, oblique lateral view of interior, sample DM-A/9A; **M**, NMW 2008.35G.190, ventral valve oblique posterior view, pitted microornament of larval shell, sample DM-A/10. **O–Q**, *Akmolina minor* (Biernat, 1973); O, P, NMW 2008.35G.245, ventral valve, oblique posterior and oblique lateral views, sample DM-A/9; Q, NMW 2008.35G.246, dorsal valve exterior, sample DM-A/9. All specimens from the Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone of the Deh-Molla section.
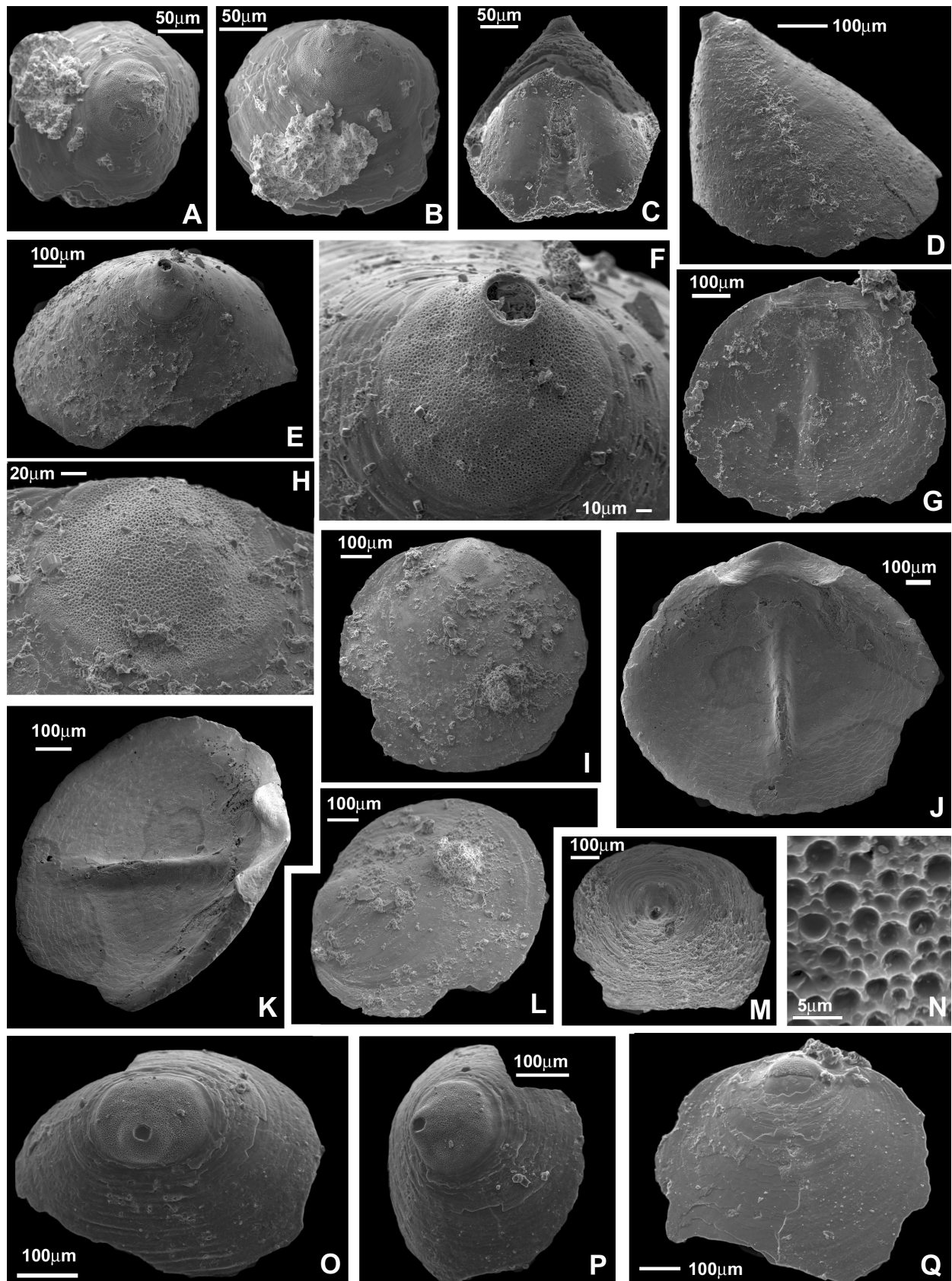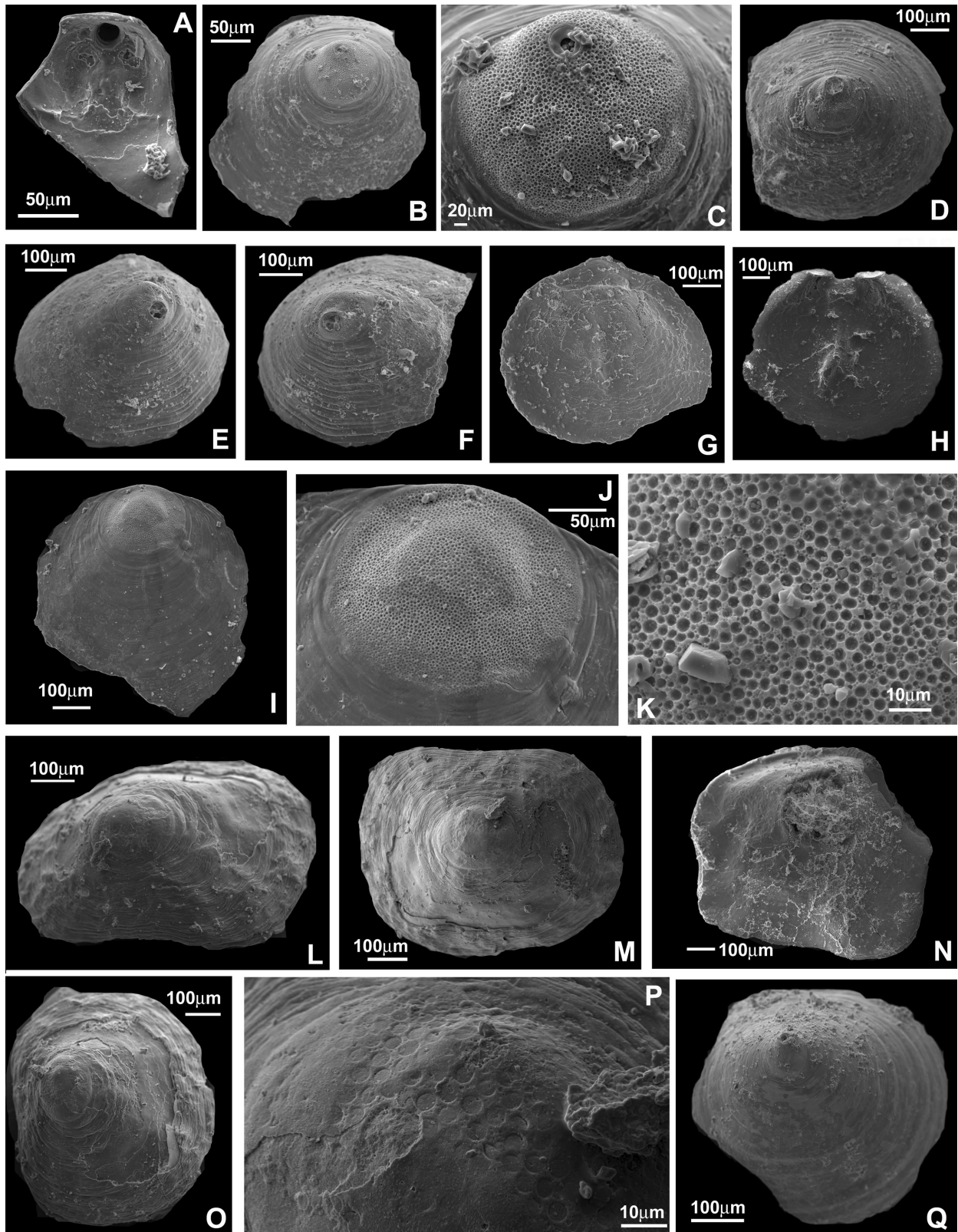
section in the Eastern Alborz Mountains illustrated in that publication is more likely conspecific with the shells of *Eurytreta ahmadii* from the Deh-Molla section.

Eurytreta ahmadii shows similarity to *Eurytreta fillmorensis* Holmer et al., 2005 from the upper Tremadocian Fillmore Formation of Utah, USA, in having a low subtriangular dorsal median septum with the highest point at midvalve and to *Eurytreta chabakovi* (Lermontova in Lermontova & Razumovskii, 1933) from the upper Tremadocian to lower Floian of the South Urals (Popov & Holmer 1994) in having a less strongly convex and only slightly apsacline ventral valve with the almost straight sagittal profile of the anterior slope, a wider dorsal pseudointerarea exceeding half the maximum valve width. In comparison with *Eurytreta fillmorensis*, Iranian shells have a larger dorsal larval shell, which is more than 210 μm wide, and a much coarser and strongly differentiated pitted microornament of the larval shell.

Eurytreta ahmadii differs from the type species *Eurytreta curvata* (Walcott, 1902) and *Eurytreta belli* (Davidson, 1868) as revised by Sutton (in Sutton et al. 2000) in having (1) less transverse commissural outline, (2) a more strongly convex ventral valve, (3) almost straight sagittal profile of the anterior and posterior slopes and maximum height at the umbo, (4) a more prominent, narrow subtriangular apical process, (5) large, but weakly impressed cardinal muscle fields and (6) indiscernible dorsal central muscle scars.

Another Tremadocian species *Eurytreta sabrinae* (Callaway, 1877) was revised and discussed in detail by Sutton (in Sutton et al. 2000). These shells are up to three times larger than those of *Eurytreta ahmadii*. They also differ in having (1) a less convex ventral valve on average only half as thick as long, (2) an evenly convex sagittal profile of the ventral valve anterior to the apex, (3) a low, broadly triangular apical process and (4) a long, strongly thickened median septum lacking a definite apex.

Family EPHIPPELASMATIDAE Rowell, 1965
Genus *Akmolina* Popov & Holmer, 1994

Type species. Akmolina olentensis Popov & Holmer, 1994, Cambrian, Furongian, Kujandy Formation, Aksak-Kujandy Mountain, northeastern Central Kazakhstan.

Akmolina minor (Biernat, 1973)
Figures 6O–Q; 7A–K

1973 *Eurytreta minor* Biernat; p. 74; pl. 9, figs 1–6; Fig. 26.
2001 *Eurytreta minor* Biernat; Holmer, Popov, Koneva & Bassett, 2001, p. 93; pl. 26, figs 1–10 (full synonymy).
2002 *Eurytreta minor* Biernat; Holmer & Biernat, p. 162; fig. 10A–K, N, O.

Holotype. Bp XV/16n, ventral valve; Tremadocian chalcedonites; Wysoczki, Holy Cross Mountains, Poland.

Material. Figured specimens: NMW 2008.35G.191, 192, 196 ventral valves; 2008.35G.193–195 dorsal valves; sample DM-A/10. NMW 2008.35G.245, ventral valve, sample DM-A/9. NMW 2008.35G.246, dorsal valve, sample DM-A/9A.

Other specimens: NMW 2008.35G.247, 248, ventral valves, sample DM-A/9B.

Discussion. The major morphological features of the Iranian shells match well with the description of the species given by Holmer & Biernat (2002) and Popov & Holmer (1994), however, the generic affiliation of *Akmolina minor* to *Eurytreta*, accepted in these publications, is questionable. In particular, unlike other species of *Eurytreta*, it is characterized by (1) a procline ventral pseudointerarea, (2) an apical process occluding the umbonal area with a short ridge in front of the internal foramen (Fig. 7A), (3) a poorly developed, transverse median buttress and (4) a low to vestigial dorsal median ridge. Most of these features can be found in early ephippelasmatids, in particular in *Akmolina* (Popov & Holmer 1994, p. 125; Holmer et al. 2001). Unlike most species of *Eurytreta* with an almost perfectly conical larval shell (Fig. 6E, F), the larval shell of *Akmolina minor* is strongly swollen anterior to the foramen and has a short external pedicle tube resembling genera of the family Ephippelasmatinae. Remarkably the specimens, originally described as *Eurytreta? exigua* Popov (in Koneva & Popov 1988) from the uppermost Tremadocian (lower *Paroistodus proteus* Biozone) of the Malyi Karatau Range, Kazakhstan, and later included into the synonymy of *Eurytreta minor*

Fig. 7. A–K, *Akmolina minor* (Biernat, 1973); A, NMW 2008.35G.191, ventral valve interior showing internal pedicle tube and apical process; B, C, K, NMW 2008.35G.196 ventral valve exterior, umbonal area, details of pitted microornament; D–F, NMW 2008.35G.192, ventral valve exterior, oblique lateral and oblique posterior view; G, NMW 2008.35G.193, dorsal valve interior; H, NMW 2008.35G.194, dorsal valve interior; I–K, NMW 2008.35G.195, dorsal valve exterior, umbonal region showing larval shell; all from sample DM-A/10. **L–P**, *Econulus* sp.; L, M, O, P, NMW 2008.35G.197, dorsal valve, oblique posterior, dorsal, oblique lateral view, enlarged umbonal area showing flat-based pits, sample DM-A/9A; N, NMW 2008.35G.198, dorsal valve, interior, sample DM-A/10. **Q**, *Eurytreta ahmadii* sp. nov.; NMW 2008.35G.235, ventral valve exterior, sample DM-A/9A. All specimens from the Ordovician, Tremadocian, *Paltodus deltifer deltifer* Biozone of the Deh-Molla section.

by Holmer et al. (2001), were referred by Popov & Holmer (1994) to *Akmolina*.

The main differences of *Akmolina minor* from *Akmolina olentensis* include a faint dorsal median ridge and a vestigial apical process occluding the umbonal area, whereas in the latter species it is reduced to the short median ridge supporting the internal pedicle tube.

Family EOCONULIDAE Cooper, 1956
Genus *Eoconulus* Cooper, 1956

Type species. *Eoconulus rectangulatus* Cooper, 1956; Middle Ordovician, Darriwilian, Pratt Ferry Formation, Alabama, USA.

Eoconulus sp.
Figure 7L–P

Material. Figured: NMW 2008.35G.197 (Ld = 0.46, W = 0.66), dorsal valve, sample DM-A/9A. NMW 2008.35G.198, dorsal valve, sample DM-A/10.

Other specimens: NMW 2008.35G.243, 244, dorsal valves, sample DM-A/10.

Remarks. The unnamed species is represented in the collection by four dorsal valves, which are characterized by a moderately high conical shape, transverse subrectangular outline about 70% and an excentric position of the umbo. The larval shell is up to 200 μm wide and 165 μm ornamented with circular flat-bottomed pits about 4.5–5.0 μm in diameter, surrounded by small hemispherical pits up to 0.7 μm across.

Due to the strongly variable shell morphology precise taxonomic discrimination of *Eoconulus* dorsal valves is difficult and often impossible on the limited material. Together with shells of *Eoconulus* sp. from Tremadocian chalcedonites of Wysoczki in the Holy Cross Mountains, Poland, illustrated by Holmer & Biernat (2002), Iranian specimens are the only known Tremadocian representatives of the genus.

Subphylum RHYNCHONELLIFORMEA
Williams et al., 1996
Class STROPHOMENATA Williams et al., 1996
Order BILLINGSELLIDA Schuchert, 1893
Superfamily POLYTOECHIOIDEA Öpik, 1934
Family TRITOECHIIDAE Ulrich & Cooper, 1936
Genus *Tritoechia* Ulrich & Cooper, 1936

Type species. *Deltatreta typica* Schuchert & Cooper, 1932 from the Lower Ordovician, Arbuckle Limestone of Oklahoma, USA.

Tritoechia sp.
Figure 8K, L

Material. Figured specimen: NMW 2008.35G.199, ventral valve; NMW 2008.35G.200, dorsal valve; sample DM-A/9B.

Other specimens: NMW 2008.35G.201–203, dorsal valves. All specimens from sample DM-A/9B.

Remarks. A few specimens of *Tritoechia* sp. are characterized by an apsacline ventral interarea with a convex pseudodeltidium, long, slightly divergent dental plates flanking a strongly elongate subtriangular muscle field and saccate ventral mantle canals. They resemble *Tritoechia florentinensis* Laurie, 1980 from the Lower Ordovician Florentine Valley Formation of Tasmania and *Tritoechia tokmakensis* Popov et al., 2001 from the Lower Ordovician, Floian, Kurday Formation of southern Kendyktas Range, Kazakhstan, in general shell shape and in characters of dental plates and the muscle field, but poor preservation of Iranian specimens makes further comparison difficult.

Class RHYNCHONELLATA Williams et al., 1996
Order ORTHIDA Schuchert & Cooper, 1932
Suborder ORTHIDINA Schuchert & Cooper, 1932
Superfamily PLECTORTHOIDEA Schuchert in
Schuchert & Le Vene, 1929
Family NANORTHIDAE Havlíček, 1977

Remarks. Williams & Harper (in Selden 2007) reassigned *Nanorthis* to the family Plectorthidae. As a result, the family Nanorthidae was suppressed and the new family Archaeorthidae within the superfamily Orthoidea was introduced to include other genera previously assigned to Nanorthidae. According to Benedetto (2007, p. 275), *Nanorthis* and *Kvania* (Havlíček, 1994) are closely related genera. He considered these two genera within the emended family Nanorthidae, which was reassigned to Plectorthoidea. Following the argument given by Williams & Harper (in Selden 2007) and Benedetto (2007), it seems most practical to retain the family Nanorthidae for the earliest known plectorthoids *Nanorthis* and *Kvania*.

Genus *Nanorthis* Ulrich & Cooper, 1936

Type species. *Orthis hamburgensis* Walcott, 1884, Lower Ordovician, Tremadocian, Manitou Limestone, Colorado, USA.

Remarks. Benedetto (2007) proposed an emended diagnosis of *Nanorthis* to include shells with multicostellate ornament, a low notothyrial platform and a distinct dorsal median septum (e.g. *Nanorthis calderensis*
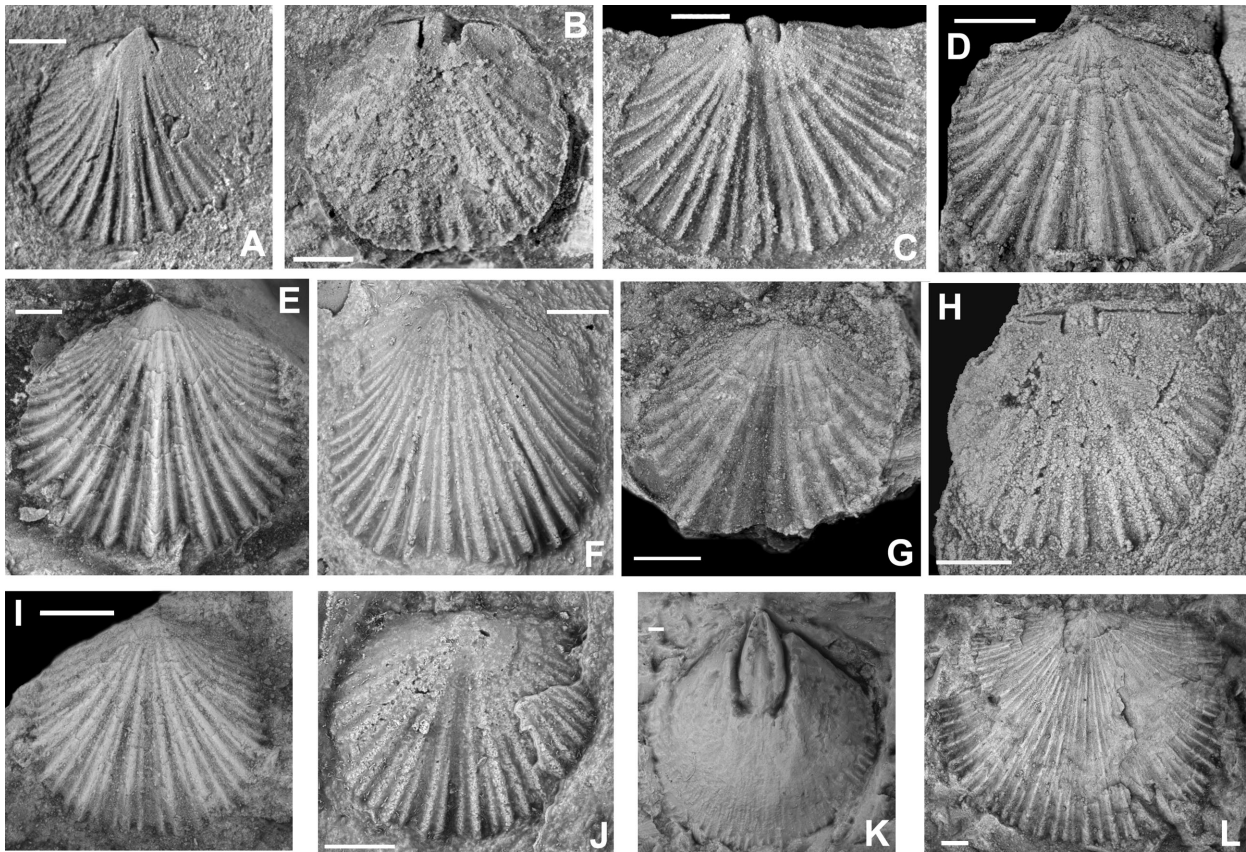
Fig. 8. A–J, *Nanorthis bastamensis* sp. nov.; A, NMW 2008.35G.205, ventral internal mould, sample DM-A/5; B, NMW 2008.35G.206, dorsal internal mould, sample DM-A/5; C, NMW 2008.35G.204, holotype, dorsal internal mould, sample DM-A/5; D, NMW 2008.35G.207, ventral valve exterior, sample DM-A/9B; E, NMW 2008.35G.208, ventral valve exterior, sample DM-A/9B; F, NMW 2008.35G.209, latex cast of ventral valve exterior, sample DM-A/5; G, NMW 2008.35G.210, dorsal valve exterior, sample DM-A/9B; H, NMW 2008.35G.211, dorsal internal mould, sample DM-A/5; I, NMW 2008.35G.212, dorsal valve exterior, sample DM-A/9B; J, NMW 2008.35G.213, dorsal internal mould, sample DM-A/5. **K**, **L**, *Tritoechia* sp.; K, NMW 2008.35G.199, ventral internal mould, sample DM-A/9B; L, NMW 2008.35G.200, dorsal valve exterior; sample DM-A/9B. All bars 1 mm.

Benedetto, 2007 and *Nanorthis purmamarcaensis* Benedetto in Benedetto & Carrasco, 2002), which are rather different from the type species and the Iranian shells described below as *Nanorthis bastamensis*. The two latter taxa are characterized by a significantly smaller shell size, have a distinctly fascicostellate ornament and lack a dorsal median ridge (Ulrich & Cooper 1938, pp. 88, 89).

Nanorthis bastamensis sp. nov.
Figure 8A–J

Derivation of name. After the ancient city of Bastam situated in the vicinity of Shahrud.

Holotype. NMW 2008.35G.204 (Ld = 4.2, W = 5.2, BBl = 0.5), dorsal internal mould, Lower Ordovician, Tremadocian, sample DM-A/5, Deh-Molla area, Eastern Alborz Mountains, Iran.

Paratypes. Figured specimens: NMW 2008.35G.205 (Lv = 3.9, W = 4.0, Mw = 0.9, Ml = 0.75), ventral internal mould; NMW 2008.35G.209 (L = 4.5, W = 4.9), ventral external mould; NMW 2008.35G.211, 213 (Ld = 3.3, W = 3.9, Iw = 2.85), dorsal internal moulds; sample DM-A/5. NMW 2008.35G.206 (Ld = 3.9, W = 4.3, BBl = 0.6), dorsal internal mould, sample DM-A/5. NMW 2008.35G.207 (Lv = 2.9; W = 3.4, Iw = 2.7), 208 (Lv = 4.6, W = 5.1), ventral valves; NMW 2008.35G.210 (Ld = 3.4, W = 3.7), 212 (Ld = 3.0, W = 3.3, Iw = 2.4), dorsal valves; sample DM-A/9B.

Other specimens: NMW 2008.35G.217, 218.1–6, 219, ventral internal and external moulds; NMW 2008.35G.220.1–7, 221, dorsal internal and external moulds; sample DM-A/5. NMW 2008.35G.216.1–3, ventral valves; NMW 2008.35G.213, 216.4–6, dorsal valves; sample DM-A/9B. NMW 2008.35G.215, ventral

valve, sample DM-A/10A. Total 6 ventral and 6 dorsal valves, 10 ventral and 12 ventral and dorsal internal and external moulds.

Diagnosis. *Nanorthis* with subcarinate ventral valve about as long as wide, fascicostellate radial ornament with up to 42 costellae, closely placed brachiophores with subparallel bases and a weakly defined dorsal median ridge.

Description. Shell ventribiconvex, subcircular in outline, about 90% as long as wide. Hinge line about three quarters maximum shell width at midlength; cardinal extremities broadly rounded. Anterior commissure gently unisulcate. Ventral valve moderately convex, subcarinate. Ventral interarea strongly apsacline with an open, narrow subtriangular delthyrium. Lateral profile of the dorsal valve gently convex with maximum height at about one fourth valve length from the umbo. Dorsal interarea linear, anacline. Dorsal median sulcus shallow and narrow, originating at the umbonal area. Radial ornament fascicostellate with 14–19 primary costae and up to 32–42 angular ribs. Ventral median rib slightly accentuated.

Ventral interior with small teeth, supported by thin, divergent dental plates. Ventral muscle field small, subtriangular, weakly defined anteriorly, occupying less than one fourth sagittal valve length. Adductor scars weakly impressed, broadly subtriangular, about equal length with flanking diductor scars. Dorsal interior with short, blade-like brachiophores flanking a narrow, almost subquadrate notothyrial cavity. No cardinal process and notothyrial platform. Dorsal adductor muscle scars indiscernible.

Remarks. *Nanorthis bastamensis* differs from *Nanorthis hamburgensis* (Walcott, 1884) in having subparallel brachiophore bases and complete absence of the notothyrial platform and the cardinal process. Ulrich & Cooper (1936, 1938) mentioned the presence of the rudimentary cardinal process and the notothyrial platform in the original diagnosis of the genus, but the presence or absence of these features in *Nanorthis hamburgensis* was not specified; however, a rudimentary notothyrial platform occurs in most of the illustrated specimens and a faint, ridge-like cardinal process can be seen on some illustrated shells (e.g. Ulrich & Cooper 1938, pl. 12, fig. 23).

In having a subcarinate ventral valve *Nanorthis bastamensis* resembles *N. carinata* Laurie, 1980 from the Lower Ordovician Florentine Valley Formation of Tasmania. However, it differs from the latter by a significantly smaller shell with a coarser, fascicostellate ornament and subparallel brachiophore bases.

Iranian specimens are characterized by a small shell with a fascicostellate radial ornament, a narrow hinge line and a subcarinate ventral valve externally similar to *Kvania*. However, *Nanorthis bastamensis* differs from the species assigned to *Kvania* (Benedetto 2007) in

having short, subparallel brachiophore plates not convergent towards the bottom and without tendency to form a septalium-like structure.

DISCUSSION AND CONCLUSION

As it was shown in the analysis of biodiversity patterns by Bassett et al. (1999), linguliform brachiopod biodiversity declined significantly by the end of the Cambrian. The early Tremadocian linguliform brachiopod associations are usually oligotaxic, often including species of acrotretides *Eurytreta* and *Ottenbyella*, lingulides of the family Elkaniidae and occasionally siphonotretides (Popov & Holmer 1994; Holmer et al. 2001, 2005; Popov et al. 2002). The lingulate brachiopod faunas documented from the *Paltodus deltifer* Biozone of the Eastern Alborz Mountains and Poland (Biernat 1973; Holmer & Biernat 2002) show clear signs of the beginning of recovery. They are still of relatively low taxonomic diversity, yet incorporate the ephippelasmatids, earliest *Elliptoglossa*, *Eoconulus* and *Acrotreta*. All these taxa diversified and became widespread later in the Ordovician.

The Iranian Tremadocian fauna contains two species, *Acrotreta dissimilis* and *Akmolina minor*, common with the contemporaneous linguliform microbrachiopod association from Tremadocian chalcedonites of the Holy Cross Mountains, Poland (Holmer & Biernat 2002). However, it does not contain siphonotretides, which are abundant in the Cambrian (Furongian) and Lower Ordovician of the Simeh-Kuh section, just 50 km west of the Deh-Molla section (Popov et al. 2008).

Another similar linguliform microbrachiopod assemblage was reported earlier from the Lower Ordovician (presumably Floian) olistolith in the Silurian Pulgon Formation of the Alai Range in southern Kyrgyzstan (Holmer et al. 2000). The Kyrgyzian fauna also contains *Acrotreta*, *Diencobolus* and *Eoconulus* represented by different species, which occur in association with *Ombergia mirabilis* Holmer et al., 2000, otherwise known only from the Hunnebergian Regional Stage of Baltoscandia.

The paterulid *Diencobolus* is transitional from the Cambrian and its relation to *Paterula*, which appears in the late Floian, is uncertain. However, new data on the early ontogeny of *Diencobolus* show a very distinct pattern, which links this taxon to *Paterula* and suggests close phylogenetic relationships of both taxa to early discinoids.

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Vara-Ordoviitsiumi (Tremadoci) brahhiopoodid Ida-Alborzi mägedest Iraanist

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Põhja-Iraani Tremadoci kihtidest (*Paltodus deltifer deltifer*'i konodonditsoon) on kirjeldatud kuus liiki lingulaate ja kaks liiki rünhonelliforme, sh kolm uut liiki: *Eurytreta ahmadii*, *Wahwahlingula kharbashi* ning *Nanorthis bastamensis*. Uuritud fauna on väga sarnane samaealise brahhiopoodikooslusega Püha Risti mägedest (Poola) ja selles domineerivad mikromorfsed linguliidid ning akrotretiidid. Uued andmed linguliidi *Diencobolus* varajasest ontogeneesist kinnitavad selle taksoni sugulust perekonnaga *Paterula* ja viitavad fülogeneetilistele seostele ülemsugukonnaga Discinoidea.