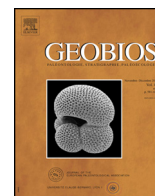




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Original article

First reported Late Ordovician trilobites from the High Zagros Ranges, Iran: A biogeographic link between Gondwanan Chinese and Mediterranean faunas[☆]

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ABSTRACT

The study of the Upper Ordovician in the Faraghan Mountains, southeastern Iran, reveals for the first time the presence of a low-diversity trilobite fauna in the middle member of the Seyahou Formation. Five genera and nine species have been identified, including *Dalmanitina* (*Dalmanitina*) *dargazensis* nov. sp. Four species are described under open nomenclature and the affiliation of four taxa was possible only to the generic level. Overall, this trilobite assemblage shows strong affinities with high-to-mid latitude, peri-Gondwanan faunas, and displays close similarities with taxa from the Mediterranean margin of Gondwana (mainly Sardinia and Bohemia/Perunica) and, to a lesser extent, with the Turkish Taurides. The age of the Iranian trilobite fauna is well constrained, due to its co-occurrence with chitinozoans, which reveal a biostratigraphic interval ranging from the upper part of the *Acanthochitina barbata* to the *Armoricochitina nigerica* zones, mid-to-late Katian in age.

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1. Introduction

Ordovician trilobites were hitherto unknown from the High Zagros Ranges. Though this region is presently located along the northeastern margin of the Arabian plate, it was an integral part of the “core” of Gondwana for most of the Phanerozoic (Torsvik and Cocks, 2011, 2013). Whereas the Late Ordovician trilobite faunas of the West Mediterranean Gondwana (including Armorica, Bohemia, Morocco, Spain, and Sardinia) are relatively well documented (for a synthesis, see Fortey and Cocks, 2003), knowledge of the Late Ordovician trilobites from the Arabian segment of Gondwana remains poorly constrained and based on a few publications (Dean, 1967; Fortey et al., 2011). A newly discovered Iranian trilobite fauna fills the stratigraphic gap between the Katian faunas previously described in the region, including those from the upper part of the Ra'an Formation in the Oman Mountains (Fortey et al., 2011), and the Şort Tepe Formation of the Hakkâri region in southeastern Turkey (Dean and Zhou, 1988).

2. Geological and stratigraphic setting

The Upper Ordovician stratigraphy of the Faraghan Mountains was recently outlined by Ghavidel-Syooki et al. (2011, 2014). The Ordovician exposures are subdivided into the Lower Ordovician (Tremadocian to Floian) Zard-Kuh Formation, the Lower-to-Upper Ordovician (upper Floian to Katian) Seyahou Formation, and the glaciogenic Dargaz Formation (Hirnantian). The Seyahou Formation is subdivided into three members:

- the lower heterolithic member, about 10 m thick, comprises black shales and sandstones with a phosphoarenite bed at the top;
- the middle heterolithic member consists of black and green shales and sandstones with thin interbeds of bioclastic carbonate siltstone and impure limestone, up to 450 m thick;
- the upper member, up to 390 m thick, includes rhythmic, thin-bedded claystone/sandstone couplets rich in ichnofossils.

The Lower-to-Middle Ordovician part of the succession is extremely condensed, with a paraconformity that marks the top of the above-reported phosphoarenite bed. This discontinuity

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Table 1
Distribution of the studied brachiopod species in the Seyahou Formation, Faraghan section.

Trilobite species	Fossil localities									
	1	2	3	4	5	6	7	8	9	10
<i>Deanaspis</i> sp. aff. <i>D. vysocanensis</i>						+	+	●	●	+
<i>Deanaspis</i> sp. 1	●									
<i>Deanaspis</i> sp. 2					●					
<i>Dalmanitina</i> (<i>Dalmanitina</i>) sp. cf. <i>D. (D.) acuta</i>	+		+							
<i>Dalmanitina</i> (<i>Dalmanitina</i>) sp.				●	+					
<i>Dalmanitina</i> (<i>Dalmanitina</i>) <i>dargazensis</i> nov. sp.							+	+	●	
<i>Sardoites</i> sp. cf. <i>S. pillolai</i>						+	+	+	+	+
<i>Nesuretinus</i> sp. aff. <i>N. malestanus</i>	●	+			+	+	+		●	●
<i>Iberocoryphe</i> sp.	+				+					

●: common species (50–10%); +: rare species (< 10% or less than 5 specimens). Fossil localities: 1, KF-6a; 2, MG10026; 3, MG10029; 4, MG10033; 5, MG10037; 6, MG10066; 7, Sy-A/4; 8, Sy-A/5; 9, MG10078 (=Sy-A/6); 10, Sy-A/7.

represents a pronounced stratigraphic gap, covering the entire Dapingian and the lower part of the Darriwilian Stage below the *Siphonochitina formosa* Zone (Ghavidel-Syooki et al., 2014). Ordovician deposits are overlain by the black graptolitic shales of the Sarchahan Formation, mainly Silurian (Llandovery to Wenlock) in age, but including graptolites from the latest Ordovician *Normalograptus persculptus* Zone in its basal part.

The trilobites described in this paper (Table 1) have been collected from the middle member of the Seyahou Formation (Ghavidel-Syooki et al., 2011), exposed only on the eastern flank of the Tang-e Pashagh Gorge, in the southern foothills of the Bone Mountain (Fig. 1). Trilobites were sampled from seven fossiliferous levels within a stratigraphic interval ranging from 84 m (sample KF-6a) to 262 m (sample MG10078 + 10.5 m) of the measured section, above a paraconformable discontinuity that marks the top of the phosphoarenite bed (Fig. 2). Chitinozoans characteristic of the *Acanthochitina barbata* Zone, including its index species, were recovered from sample MG10011, 33 m above the base of the Middle Ordovician, while the first occurrence of *Armoricochitina nigerica* (Bouché, 1965), the index species of the eponymous chitinozoan zone, is confirmed from an horizon ca. 193 m above the base of the Middle Ordovician.

Trilobites from the lower five fossiliferous levels (Fig. 2; samples KF-6a and MG10026–MG10037) occur in tempestite beds rich in coquinas composed of broken and disarticulated large bivalves and subsidiary brachiopods, gastropods and cephalopod

shells, bryozoans, crinoid and cystoid plates, and trilobite carapaces. The four uppermost trilobite-bearing levels (samples MG10066, Sy-A/4 (= Sy-A/5), MG10078 (= Sy-A/6), and Sy-A/7; Fig. 2) are recognized in monotonous claystones punctuated by a few fossiliferous levels, the latter characterized by impure limestone-to-calcareous sandstone beds, ca. 0.1–0.3 m thick. The trilobites are commonly disarticulated, variably compressed, and suffered little or no breakage. The associated faunal assemblage includes abundant brachiopods, ostracods and subsidiary bryozoans, cephalopods, gastropods, tentaculitids, and echinoderms.

3. Systematic palaeontology

The studied and illustrated specimens are housed in the Department of Geology of the National Museum of Wales, Cardiff, UK (acronym NMW). The terminology and systematic classification follow that of the revised edition of the Treatise on Invertebrate Palaeontology (Whittington and Kelly in Kaesler, 1997). All measurements are in millimetres.

Morphological abbreviations: Cl, Cw: maximum cranial length and width; Gl, Gw: maximum glabellar length (including glabella) and width; PGL, PGW: length and width of preglabellar field; PLl: length of palpebral lobes; PLA: distance between anterior termination of palpebral lobes and anterior margin; ORl, ORw: length (sag.) and width of occipital ring; Hl, Hw: hypostomal length and width; HML, HMw: hypostomal middle body length and

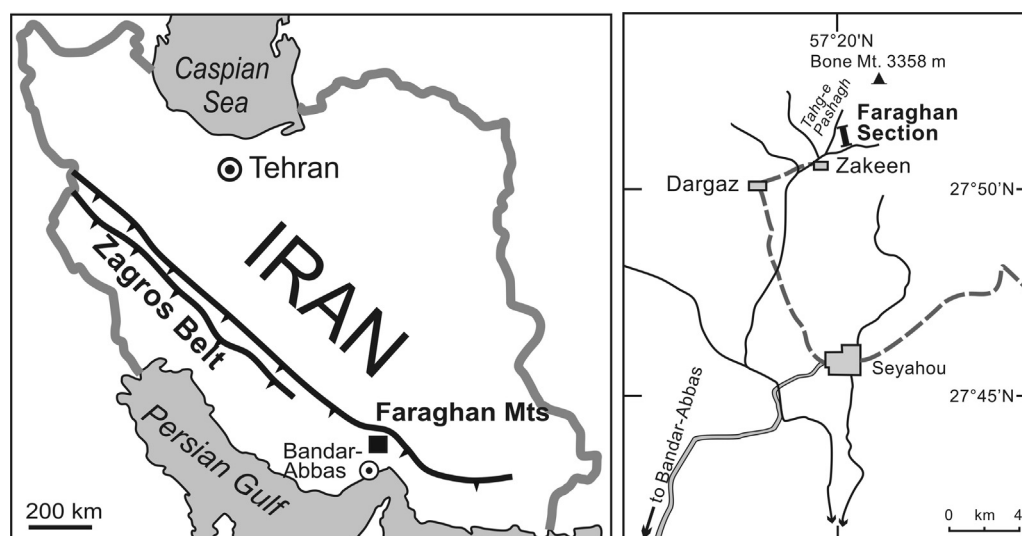


Fig. 1. Map of the Seyahou district in southeastern Iran with location of the Faraghan section.

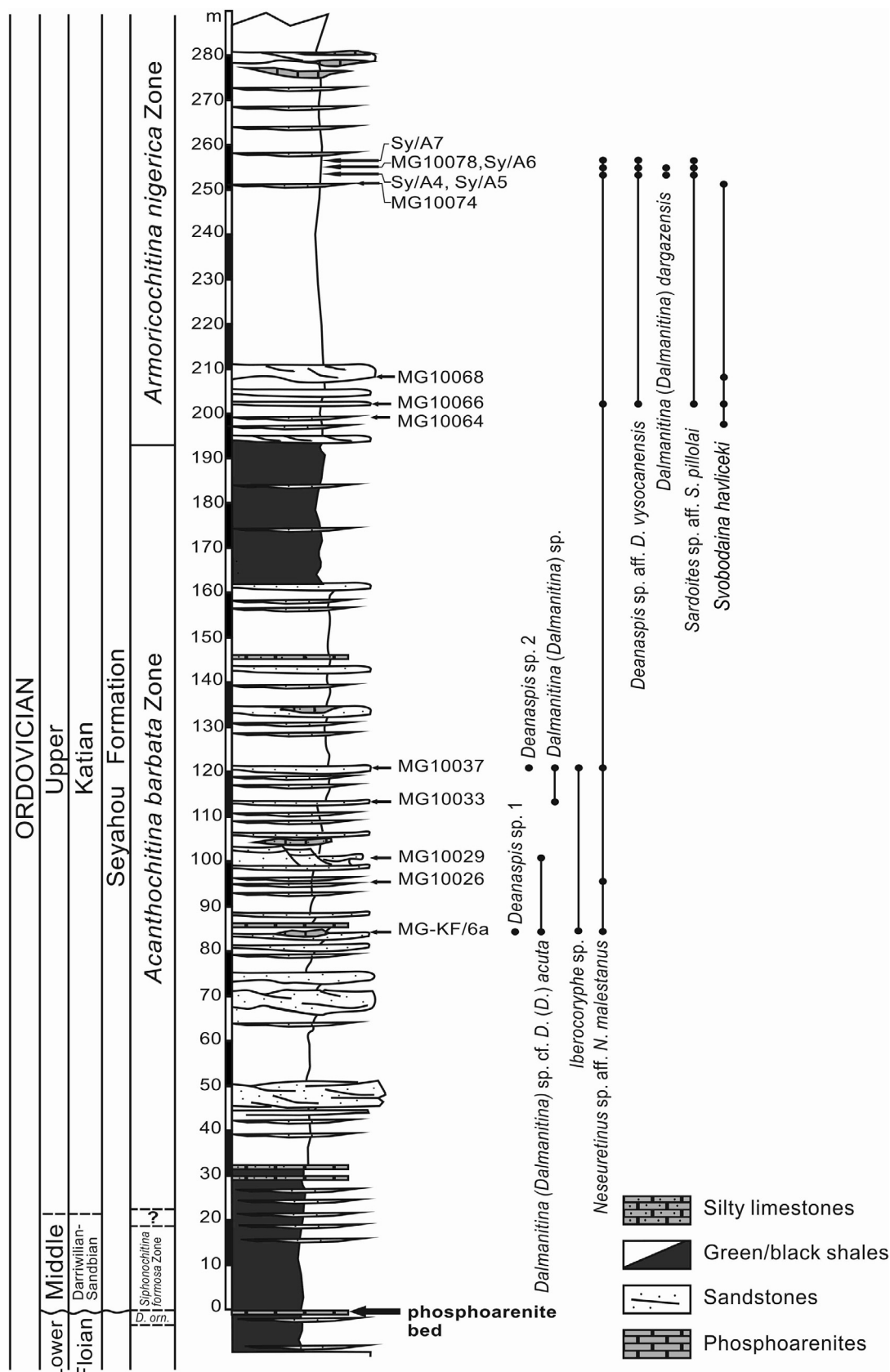


Fig. 2. Middle–upper Katian stratigraphic log from the eastern bank of the Tange–Pashag Gorge, showing stratigraphic position of fossil samples and ranges of trilobites. *D. orn.*, *Desmochitina ornensis* Chitinozoan Zone.

width; Pl, Pw: maximum pygidial length and width; Al, Aw: length and width of pygidial axis; sag.: sagittal; exsag.: exsagittal; tr.: transverse.

Order ASAPHIDA Salter, 1864

Family TRINUCLEIDAE Hawle and Corda, 1847

Subfamily MARROLITHINAE Hughes, 1971

Genus *Deanaspis* Hughes et al., 1975

Type species: *Deanaspis bedinanensis* (Dean, 1967), Caradoc (uppermost Sandbian–lower Katian) Bedinan Formation, south-eastern Turkey (by original designation).

Deanaspis sp. aff. *D. vysocanensis* (Příbyl and Vaněk, 1980)

Figs. 3(9–23), 4

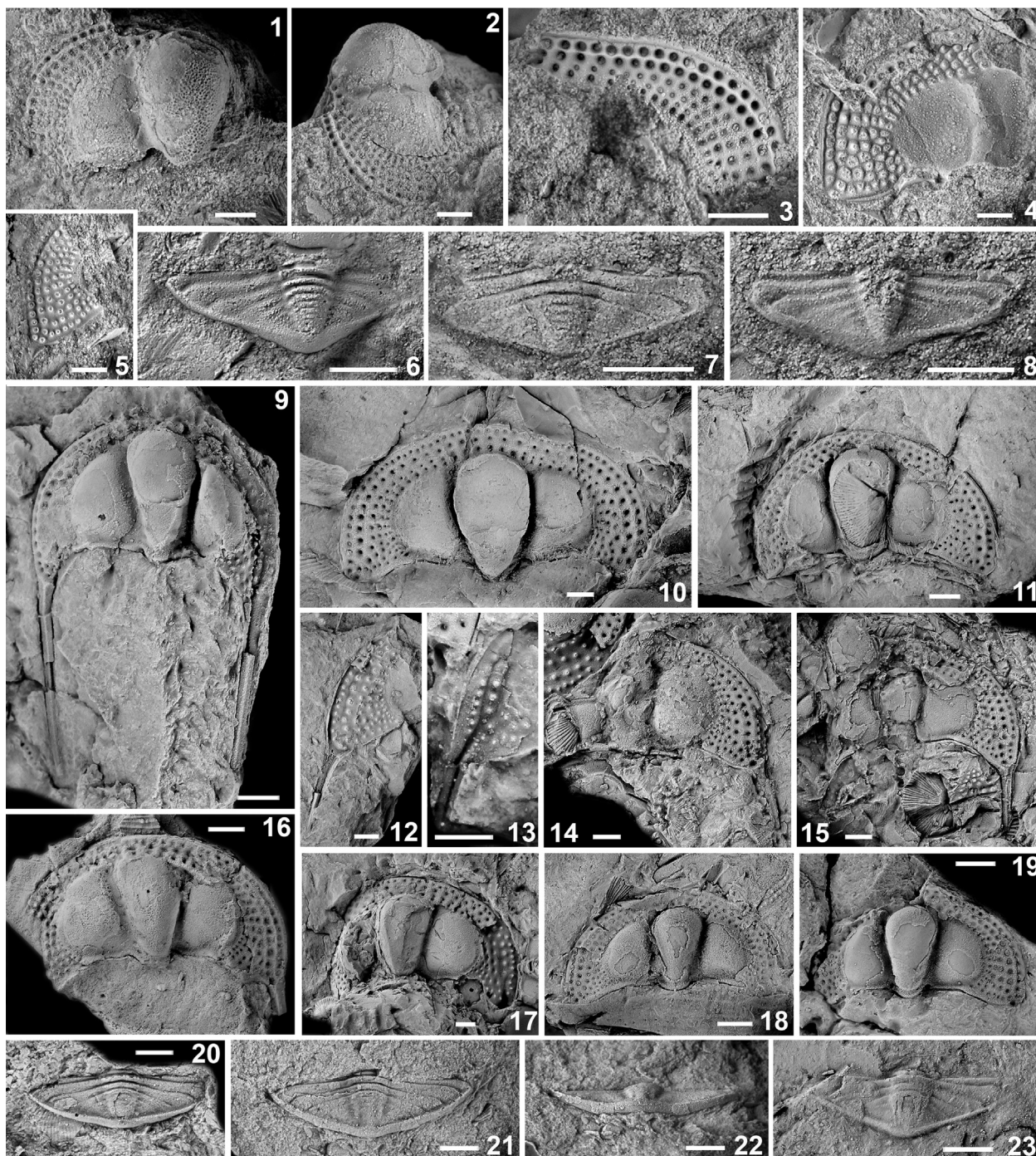


Fig. 3. 1–3, 5–7. *Deanaspis* sp. 2, sample MG10037; 1–2, incomplete cranidium, dorsal and side views, National Museum of Wales (NMW) 2008.35G.338; 3, part of left fringe, dorsal view, NMW 2008.35G.341; 5, part of left lower lamella and broken spine, external mould, NMW 2008.35G.589; 6–7, two pygidia, NMW 2008.35G.336, 337. 4, 8. *Deanaspis* sp. 1, level KF–6a; 4, NMW 2008.35G.522, incomplete cranidium showing external mould of the lower fringe; 8, NMW 2008.35G.335, pygidium. 9, 11, 15, 16, 19–23. *Deanaspis* sp. aff. *D. vysocanensis* (Příbyl and Vaněk, 1980), sample MG10078; 9, NMW 2008.35G.326, complete cephalon with long genal spines; 11, NMW 2008.35G.316, complete cephalon excluding genal spines; 15, NMW 2008.35G.306, incomplete cephalon; 16, NMW 2008.35G.324, incomplete cephalon; 19, NMW 2008.35G.327, incomplete cephalon; 20, NMW 2008.35G.447, pygidium, latex cast; 21, 22, NMW 2008.35G.446, pygidium, latex cast, dorsal and posterior views; 23, NMW 2008.35G.412a, incomplete pygidium. 10, 12–14, 17, 18. *Deanaspis* sp. aff. *D. vysocanensis* (Příbyl and Vaněk, 1980), sample Sy–A/6; 10, NMW 2008.35G.451, complete cephalon excluding genal spines; 12, NMW 2008.35G.323, interior of right part of upper lamella and partly broken spine; 13, NMW 2008.35G.303b, interior of left part of lower lamella and partly broken spine; 14, NMW 2008.35G.302, incomplete cephalon; 17, NMW 2008.35G.301, incomplete cephalon showing left lower lamella; 18, NMW 2008.35G.314, incomplete cephalon. All specimens from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. Scale bars: 2 mm.

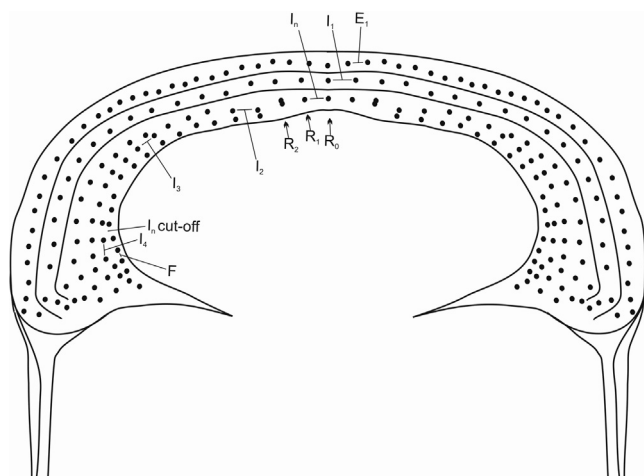


Fig. 4. Schematic drawing of *Deanaspis* sp. aff. *D. vysocanensis* (Příbyl and Vaněk, 1980) showing arrangement of pits on the fringe.

Material: Two incomplete cephalon, NMW 2008.35G.581, 582 from sample MG10066; four incomplete cephalon, NMW 2008.35G.485, 488b, 489, 490, from sample Sy-A/4; six incomplete cephalon, NMW 2008.35G.496–501, from sample Sy-A/5; two complete cephalon, NMW 2008.35G.326, 451, two lower lamellae of incomplete cephalon, NMW 2008.35G. 301, 311, 52 incomplete cephalon, NMW 2008.35G.302, 303a, 306, 314, 316, 324, 349, 350, 355b, 356b, 358, 360, 365–384, 406, 412b, 415–428, 456, 502–504, two incomplete external moulds of cephalon, NMW 2008.35G.429, 430, 16 broken half cephalon, NMW 2008.35G.312–327, one external mould of incomplete cephalon, NMW 2008.35G.319, one half upper lamella, NMW 2008.35G.323, one broken lower lamella, NMW 2008.35G.303b, one complete pygidium, NMW 2008.35G.318, one internal mould of complete pygidium, NMW 2008.35G.313, one nearly complete pygidium, NMW 2008.35G.412a, one internal mould of nearly complete pygidium, NMW 2008.35G.437, seven incomplete pygidia, NMW 2008.35G.438, 439, 441–445, one internal mould of complete pygidium, NMW 2008.35G.440, five external moulds of pygidia, including NMW 2008.35G.446–450, from samples MG10078 and Sy-A/6; three incomplete cephalon, NMW 2008.35G.502–504, from sample Sy-A/7.

Description: Cephalon almost semicircular in outline, about twice as wide as long (excluding genal spines). Glabella clavate, expanding forward, convex, about 1.5 times longer than wide, with maximum width at level of fossulae. Maximum glabellar width (tr.) almost the same as genal field width. Anterior one-fifth of the glabella overhanging fringe. Occipital ring narrow, less than 10% of glabellar length; occipital furrow well-developed; occipital spine not seen in available specimens. S1 at about one-fifth, S2 at about one third and S3 very faint, at about half glabellar length (sag.). Genal lobes evenly curved, almost as wide as glabellar width. Posterior border furrow moderately deep and wide. Fringe short (sag.) in front of glabella, including three arcs: E_1 , I_1 and I_n (Fig. 4). Genal spines long. Ridge of genal spine subdivided into two branches, confluent with girder and pseudogirder equally in lower lamella; E_1 extending to main ventral ridge of genal spine in lower lamella. Arc pits in E_1 slightly smaller, more numerous and out of phase in relation to pits of I_1 . Half-counts for 7 specimens are 23–29 pits for E_1 , 18–20 pits for I_1 , about 17 pits for I_2 starting at R_2 , 12 pits for I_3 starting at R_8 . Four I arcs and two flange pit arcs present; I_4 cut-off I_n at I_{n13-15} . True girder and internal pseudogirder equally developed, better expressed on interior of lower lamella. Glabella and genal fields covered with poorly preserved

reticulate sculpture observed in a few specimens. Hypostome and thorax unknown.

Pygidium subtriangular in outline, transverse; pygidial length (sag.) about 30% of maximum pygidial width. Posterolateral margin curved slightly sigmoidally. Axis subtriangular, gently convex, with up to 7 axial rings and very small triangular terminal piece tapering gently to posterior margin, terminating at posterior border; anterior axial width about one-fifth of maximum pygidial width. Posterior border vertical, relatively wide, convex, covered with fine terrace lines, and without occipital spine. Axial furrows wide, shallow, straight, tapering backward. Pleural field flat, limited laterally and posteriorly by slightly elevated rim running on margin of posterior border, with 5 pleural ribs, posterior one very faint.

Remarks: The measured ratios of the cephalon in the studied specimens are probably distorted by dorsal compression. Therefore, the lack of dorsal declination of the fringe could be related to secondary post-mortem deformation of the exoskeleton.

Shaw (1995) discussed in detail the affinities of *Deanaspis* and *Onnia*. Following his diagnoses, the Iranian specimens are assigned to *Deanaspis* because they have equal development of a true girder and an internal pseudogirder, and the ventral genal spine groove on the interior of the lower lamella runs directly into the true girder. Despite the absence of an occipital spine and the overall morphological characters, *Deanaspis* sp. aff. *D. vysocanensis* differs from *D. vysocanensis* (Příbyl and Vaněk, 1980), from the lower-middle Katian Vinice and Zahořany formations of the Prague Basin, Bohemia, in having a greater number of E_1 pits. According to Shaw (1995: p. 17) the Bohemian specimens have half-counts 23 and 21 for E_1 and I_1 pits, respectively, which is close to the lower limit of the range observed in the Iranian specimens.

The Iranian specimens are most similar to *D. sp. aff. D. vysocanensis* from the middle Katian Portixeddu Formation of southern Sardinia, Italy (Hammann and Leone, 1997: p. 65), although they differ from the latter in having more impressed lateral sulci on glabella, more numerous pits in arc E_1 [half-count 23–29 pits ($n=7$) by comparison with 23–26 in Sardinian specimens], a fewer pits in other arcs (e.g., I_1 , I_2 and I_3 ; half-count 18–20 pits in comparison to 20–23 for I_1 , about 17 pits in comparison to 18–21 for I_2 , 12 pits in comparison to 14–17 for I_3), smaller pits on the external side of the upper lamella, and pygidium with five (not four) distinctive pleural ribs.

The Iranian material differs from *Deanaspis bedinanensis* (Dean, 1967), from the Katian Lower Bedinan Shale Formation of the Turkish Taurides, in having fewer pits in E_1 and I_1 , (up to 29 instead of 36 for E_1 and up to 20 instead of 27 for I_1 ; nomenclature after Shaw, 1995), and a fewer pygidial axial rings and pleural ribs. The Iranian specimens are also different from *Deanaspis goldfussi* (Barrande, 1846), from the upper Sandbian–lower Katian Letná and Vinice formations of the Prague Basin, Bohemia (Shaw, 1995), in having a distinct S2 and a faint S3 and only two girders developed instead of three, and in the absence of the occipital spine.

Onnia superba (Bancroft, 1929), from the Onny Formation Shropshire (Owen and Ingham, 1988), shows similarity in the range of E_1 and I_1 pit numbers, while *D. aff. vysocanensis* differs from that species in having a more prominent true girder, the presence of S2 and S3, and the absence of occipital spine.

As pointed by Shaw (1995), an inferred evolutionary scenario for the Bohemian *Deanaspis* and *Onnia* species involves a considerable change in pit counts and development of the first internal pseudogirder. However, major evolutionary trends involving the girder and pseudogirder will only be revealed after the study of more specimens sampled at different stratigraphic levels.

Deanaspis sp. 1

Fig. 3(4, 8)

Material: One incomplete cranidium (external mould), NMW 2008.35G.522, eight fragmentary incomplete cranidia and fringes, NMW 2008.35G.523–528, 529a, 562, three fragmentary fringes, NMW 2008.35G.591–593, 595, one incomplete glabella, NMW 2008.35G.594, one complete pygidium (external and internal moulds), NMW 2008.35G.335, and one incomplete pygidium (external mould), NMW 2008.35G.590 from sample KF–6a.

Remarks: Incompletely preserved specimens from level KF–6a include a few fragmented cranidia and pygidia that do not exhibit diagnostic characters for a precise taxonomic determination. The presence of a well-developed girder with a direct connection to the spine ridge, which can be seen also as a deep groove between the true girder and the first pseudogirder, confirms the generic affiliation of the specimens to *Deanaspis*. Approximate half-count pits for E_1 is up to 21, and for I_1 is up to 20. This suggests almost equal numbers and size of E_1 and I_1 pits. There is also a trace of an occipital spine preserved in one specimen. The pygidial morphology and proportions of *Deanaspis* sp. 1 are similar to *Deanaspis* sp. aff. *D. vysocanensis* except in a narrower axis in *Deanaspis* sp. 1.

Minor differences in the cephalic morphology of *Deanaspis* are traceable from the lower to the upper part of the studied sequence. In particular, they include an increasing number of pits in E_1 in comparison with I_1 and a respectively slight decrease in the size of E_1 pits, an equal development of the true girder and the first internal pseudogirder in younger specimens, whereas the specimens from the lowermost part exhibit a distinct girder. Other evolutionary trends involve a loss of the occipital spine and a widening of the pygidial axis upsection.

Deanaspis sp. 2

Fig. 3(1–3, 5–7)

Material: One incomplete fringe, NMW 2008.35G.341, eight incomplete cranidia, NMW 2008.35G.338, 535–540, 589, two complete pygidia, NMW 2008.35G.336–337, and one external mould of pygidium, NMW 2008.35G.534, from sample MG10037.

Remarks: The presence of a well-developed true girder in some specimens, together with a deep groove between the true girder and the first pseudogirder, suggest a generic affiliation of the specimens to *Deanaspis*. The cephalic and pygidial morphology of *Deanaspis* sp. 2, including a convex glabella, an arrangement and size of pits on the fringe (including larger I_1 pits than E_1), a subtriangular pygidial outline, the presence of up to seven axial rings and five pleural ribs on the pygidium, as well as the proportions of the pygidium, are similar to *Deanaspis* sp. aff. *D. vysocanensis* sampled in the upper part of the section. However, other important features for precise identification, especially pit counts, are insufficiently preserved in the studied specimens, which precludes their species affiliation.

Order PHACOPIDA Salter, 1864

Family DALMANITIDAE Vogdes, 1890

Subfamily DALMANITININAE Destombes, 1972

Genus *Dalmanitina* Reed, 1905

Type species: *Phacops socialis* Barrande, 1846, from the Letná Formation, Beroun Series, Bohemia (by original designation).

Subgenus *Dalmanitina* (*Dalmanitina*) Reed, 1905

Dalmanitina (*Dalmanitina*) *dargazensis* nov. sp.

Figs. 5, 6

Derivation of the name: After Dargaz village, southeast of the type locality.

Holotype: NMW 2008.35G.317, cranidium (Cl = 21, including genal spine; Cw = 33; CMw = 18; Gl = 13.5; Gw = 12; PlI = 5.5; ORI = 2; ORw = 7.5), from sample Sy–A/6.

Paratypes: Two incomplete pygidia, including NMW 2008.35G.487, 488a, from sample Sy–A/4; two incomplete pygidia, including NMW 2008.35G.494, 495, from sample Sy–A/5; 10 complete pygidia, including NMW 2008.35G.308, 310, 300, 346–348, 344, 351, 359, 391, 393, 18 incomplete pygidia, including NMW 2008.35G.353–354, 355a, 404, 407, 470, 471–482, two cephalia, including NMW 2008.35G.458, 389, 28 incomplete cranidia, including NMW 2008.35G.348, 320–321, 317, 356a, 357, 315, 388, 395, 401, 403, 410, 457, 459, 460, 461, 462–469, 571, 585–587, one glabella, NMW 2008.35G.570, three broken thoraxes, including NMW 2008.35G.394, 413, NMW 414, and one broken librigena, NMW 2008.35G.409 from samples Sy–A/6 and MG10078.

Type locality and horizon: 254 m above the base of the middle member of the Seyahou Formation at Kuh-e Faraghan, north of Bandar-Abbas, South of Iran; Middle Katian part of the Seyahou Formation

Diagnosis: Glabella pear-shaped, axial furrows S1 oblique, bifurcated, S2 almost transverse extending to lateral furrow, S3 slightly sigmoidal running to widest part of frontal lobe. L1 rounded, longer than L2 at lateral furrow (exsag.), L3 subtriangular, as long as L1 + L2 (exsag.), frontal lobe transversely rhomboidal with acute anterolateral corners. Eyes crescentic, opposite to L2 and L3, with more than 30 vertical rows of lenses with up to six lenses per row on visual surface. Genal spines relatively long, developed as elongation of cephalic border, continuing curve of lateral cephalic margin. Cephalic surface covered with dense and relatively fine tubercles. Pygidium subtriangular, about 65% as long as wide with axis less than one third pygidial width, axial furrows well-defined; 10 to 11 axial rings plus terminal piece continuing to spine. Pleural fields with seven broad, well-defined pleural ribs. Interpleural furrows very narrow and shallow; pleural furrows deep and wide. Pygidial spine about one third pygidial length. Pygidial surface covered with coarse granules, fining posteriorly.

Description: Cephalon semicircular, about twice as wide as long. Glabella pear-shaped, convex, axial furrows shallow and wide, almost straight, converging posteriorly. Occipital ring about 10% of cephalic length (sag.), narrowing abaxially, occipital furrow shallow and wide, deepening abaxially. S1 oblique, pointed backward adaxially, bifurcated with posterior branch directed backward but terminating before reaching occipital furrow, and anterior branch running forward and inward, forming curved sulcus. S2 almost transverse extending to lateral furrow; S3 pointed backward adaxially, running forward, slightly sigmoidal, reaching widest part of frontal lobe. L1 narrowing adaxially whereas L2 narrowing abaxially, thus L1 longer than L2 at lateral furrow (exsag.); L3 subtriangular, as long as L1 + L2 (exsag.) (Fig. 5(1, 3, 4, 9)). Frontal lobe convex (tr., sag.), transversely rhomboidal in outline, expanding (tr.) outward, with acute anterolateral corners. Frontal lobe about 60% as long as wide and about 50% as long as glabella (including occipital ring). Eyes crescentic, opposite to L2 and L3, with more than 30 vertical rows of lenses, with up to six lenses per row on visual surface (Fig. 5(5, 10)). Eyes situated at about 50–60% of eye length from posterior border furrow. Posterior border furrow wide and moderately shallow. Posterior border slightly convex, strongly widening abaxially, merged with lateral border, forming wide subtriangular genal angle. Genal spines rectangular in cross-section, relatively long, formed as elongation of cephalic border, continues curve of lateral cephalic margin (Fig. 5(1, 2, 7)). Lateral border moderately narrow, gently convex in cross-section, as wide as doublure. Posterior branch of facial suture curved forward abaxially, then running backward close to margin before cutting it. Anterior branch of facial suture running to corner of frontal lobe and then around front of glabella. Cephalic surface covered with dense and

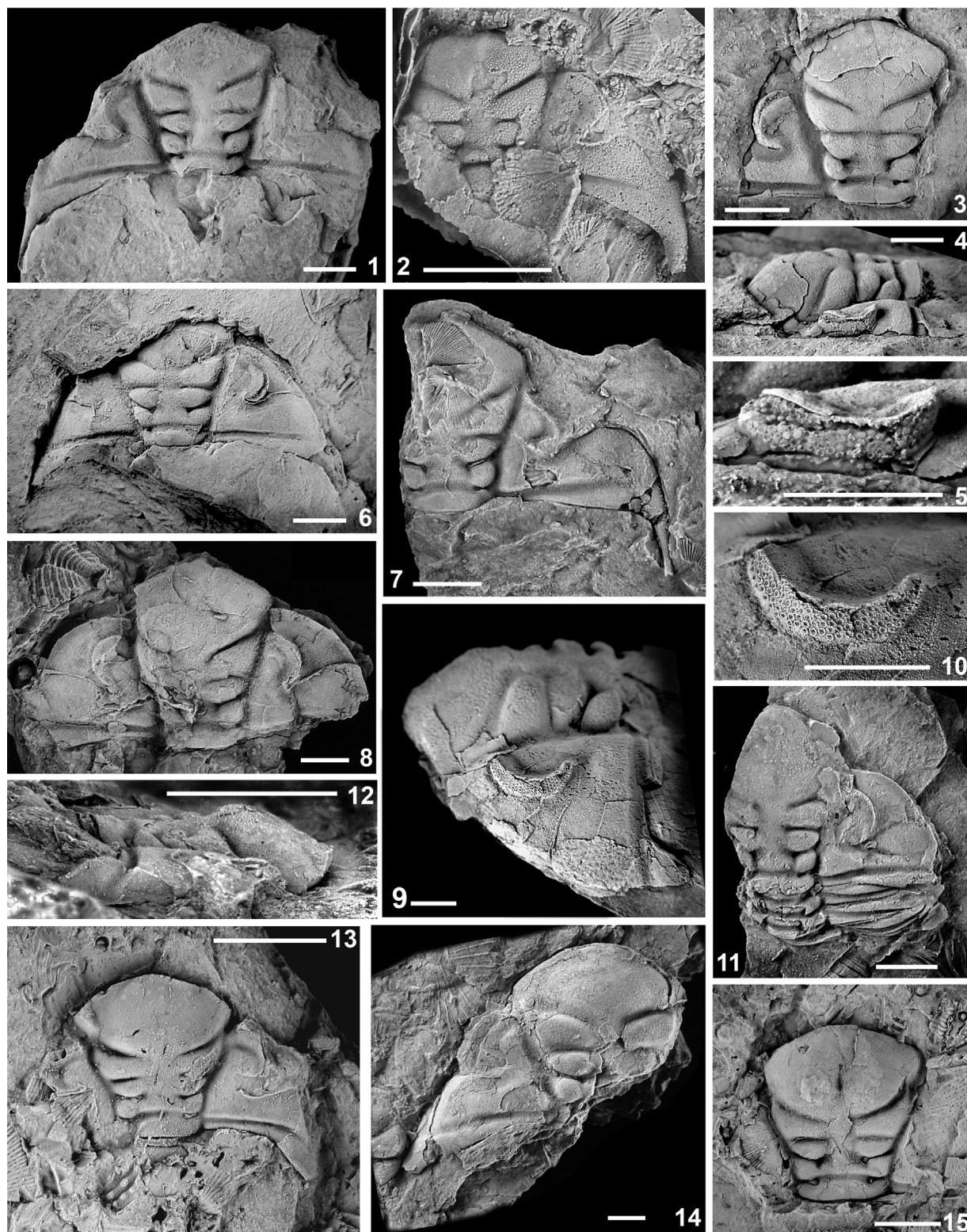


Fig. 5. *Dalmanitina (Dalmanitina) dargazensis* nov. sp. from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. **1**, National Museum of Wales (NMW) 2008.35G.317, holotype, incomplete cranidium, internal mould; **2**, NMW 2008.35G.572, incomplete cranidium, latex cast; **3–5**, NMW 2008.35G.403, incomplete cranidium, internal mould, dorsal and side views and a close view of left eye showing schizochroal lenses; **6**, NMW 2008.35G.389, incomplete cephalon, internal mould; **7**, NMW 2008.35G.315, incomplete cranidium, internal mould with a relatively long genal spine; **8**, NMW 2008.35G.587, incomplete cranidium and two thoracic segments, internal mould; **9**, NMW 2008.35G.458, incomplete cephalon, internal mould; **10, 11**, NMW 2008.35G.585, incomplete cranidium, side view and close view of eye showing schizochroal lenses; **12, 13**, NMW 2008.35G.458, incomplete cranidium, internal mould, side and dorsal views; **14**, NMW 2008.35G.586, incomplete cranidium; **15**, NMW 2008.35G.321, glabella and a part of fixigena, internal mould. **1, 3–8, 10, 11, 14**, level Sy–A/6; **2**, level Sy–A/4; **9, 12, 13, 15**, sample MG10078. Scale bars: 5 mm.

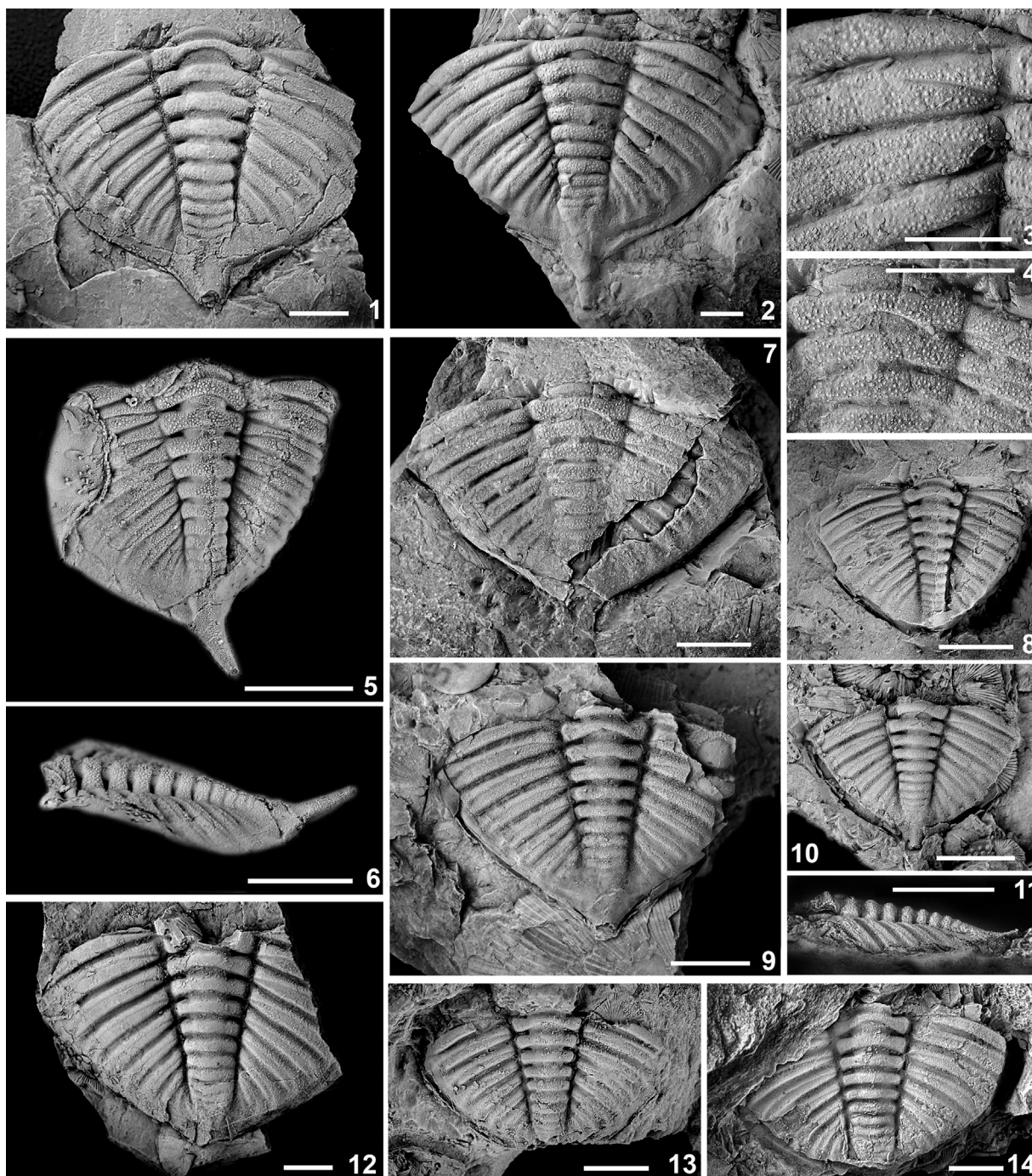


Fig. 6. *Dalmanitina (Dalmanitina) dargazensis* nov. sp. from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. **1**, National Museum of Wales (NMW) 2008.35G.391, pygidium with a part of spine; **2, 3**, NMW 2008.35G.393, pygidium, dorsal view and a close view of a part of pleural ribs showing coarse granulation; **4, 5**, latex cast, NMW 2008.35G.344, pygidium with an upward pointed spine, dorsal and lateral views; **6, 7**, NMW 2008.35G.359, pygidium with a broken spine, dorsal view and a close view of a few axial rings and part of pleural ribs showing coarse granulation; **8**, NMW 2008.35G.346, pygidium with broken spine, internal mould; **9**, NMW 2008.35G.310, incomplete pygidium with broken spine, internal mould; **10, 11**, NMW 2008.35G.300, pygidium with a part of spine, internal mould, dorsal and lateral views; **12**, NMW 2008.35G.308, incomplete pygidium with a broken spine, internal mould; **13**, NMW 2008.35G.404, pygidium with a broken spine, internal mould; **14**, NMW 2008.35G.347, incomplete pygidium with a broken spine, internal mould. **1, 4, 5, 9**, sample MG10078; **2, 3, 6–8, 10–14**, level Sy–A/6. Scale bars: 5 mm.

relatively fine granules (Fig. 5(2, 3)). Hypostome unknown. Thoracic segments typically dalmanitid with well-defined axis comprising about 25% of thoracic width.

Pygidium subtriangular, about 65% as long as wide in compressed specimens preserved in claystones. Axis slightly less than 30% as wide as pygidium, tapering backward at angle of about 10 degrees along first 7 axial rings and then parallel sided (Fig. 6(1, 2, 5)). Axial furrows well-defined, narrow on dorsal side of

exoskeleton. Ten to 11 axial rings plus terminal piece present with first 6–7 rings distinctly separated by wide and deep interrering furrows, whereas next 3–4 posterior rings poorly defined with narrow and shallow interrering furrows. Axis not clearly separated from posterior pygidial spine. Interrering furrows wide, deepening abaxially, and becoming narrower backward. Pleural field gently convex. Pygidial border slightly convex all the way, narrow, occupying less than one tenth of pygidial length (excluding spine).

Doublure confined to border. Pleural field with seven broad, well-defined, posterolaterally directed pleural ribs becoming strongly backwardly directed posteriorly, plus half rib. Interpleural furrows very narrow and shallow, pleural furrows deep and wide. Pygidial spine subrectangular in cross-section, relatively long and narrow, about one third as long as pygidium. Pygidial surface covered with coarse granules, becoming finer posteriorly (Fig. 6(3, 4)).

Remarks: *Dalmanitina (Dalmanitina) dargazensis* nov. sp. differs from *Dalmanitina (Dalmanitina) acuta* Hammann, 1971, from the lower–middle Katian Monte Orri Formation of Gonnese, SW Sardinia, in having a less convex glabella, longer and wider genal spines, a pygidium with seven pleural ribs (instead of six in *D. (D.) acuta*) and a smaller and narrower posterior pygidial spine. *Dalmanitina asta* Šnajdr, 1982 from the Bohdalec Formation (lower Katian) of Bohemia differs from the Iranian species in having wider and longer genal spines and very fine granules on the surface. Unlike the Iranian specimens, *Dalmanitina (Dalmanitina) proaeva* (Emmrich, 1839) from the lower Katian Zahořany Formation of Bohemia (Šnajdr, 1956) has 28 vertical rows of lenses, with up to eight lenses per row on visual surface, smaller genal spines, subrectangular in cross-section, slightly directed posteriorly adaxially, a rounded genal angle and eyes situated at the distance of 80% eye length from the posterior border (in comparison to 50–60% in the Iranian species).

Dalmanitina elfrida Šnajdr, 1982 from the uppermost Sandbian to lower Katian Vinice Formation of Bohemia is similar to *D. (D.) dargazensis* nov. sp. in having genal spines in line with the lateral cephalic margin, but differs in their smaller eyes situated more anteriorly and nearly straight pygidial axial furrows.

In comparison to the Iranian specimens, *Dalmanitina (Dalmanitina) socialis* (Barrande, 1852) from the Sandbian Letná Formation of Bohemia (Šnajdr, 1956) has smaller and more anteriorly-situated eyes opposite to mid L3, a shorter frontal lobe, much deeper and wider interpleural furrows, and narrower pleural furrows.

Specimens from the Lower Bedinan Shale Formation of the Turkish Taurides, assigned by Dean (1967) to *Dalmanitina proaeva proaeva* (Emmrich, 1839), share with the Iranian species the position of the genal spines, the cephalic morphology, and the number of pleural ribs and axial rings. However, the Turkish specimens differ in having a wider and longer pygidial spine, which exceeds the pygidial length, and a more triangular outline of the pygidium. There is little information about the cephalic and eye characters of the Turkish specimens, which makes further comparison impossible.

D. (D.) dargazensis nov. sp. differs from *Dalmanitina (Thuringaspis) lamarmorai* (Meneghini, 1880) from the Portixeddu Formation (middle Katian), as revised by Hammann and Leone (2007: p. 14), in cephalic morphology including a wider cephalon about 50% as wide as long [instead of 70% in *D. (T.) lamarmorai*], almost transverse (not inclined posteriorly adaxially) S2, more posterior position of eyes with posterior eye corners situated at about 50–60% of eye length from the posterior border furrow [instead of 60–90% in *D. (T.) lamarmorai*], a fewer number of eye lenses in vertical rows [six instead of 10 in *D. (T.) lamarmorai*]. In addition *D. (D.) dargazensis* nov. sp. has a transverse pygidium with 10–11 axial rings, while in *D. (T.) lamarmorai* the pygidium is almost as long as wide (without spine) with 13 axial rings of which three posterior rings are usually poorly defined.

Dalmanitina (Dalmanitina) sp. cf *D. (D.) acuta* Hammann, 1971 Fig. 7(1–6)

Material: One incomplete pygidium, NMW 2008.35G.552, one incomplete cranidium, NMW 2008.35G.553, from sample MG10029; three incomplete pygidia, NMW 2008.35G.530, 343, 547, two librigenae, NMW 2008.35G.569, 588, from sample KF–6a.

Remarks: The Iranian specimens share some similarities with *Dalmanitina (Dalmanitina) acuta* Hammann, 1971, from the lower–to–middle Katian Monte Orri Formation of Gonnese, SW Sardinia, described and illustrated by Hammann and Leone (2007): these include a short frontal lobe, longer glabellar lobes (sag. and exsag.), transverse S1, slightly curved forward S2 and S3 (Fig. 7(2)), short fixigenae (exsag.), a stout pygidium with six and a half pairs of pleural ribs, 10 axial rings plus a terminal piece, deep and wide pleural furrows narrower than pleural ribs (sag. and exsag.) and faint interpleural furrows, and a pygidial length/width ratio close to 2/3 (Fig. 7(1, 3)). Due to the insufficient number of specimens and poor preservation, their precise taxonomic affiliation is difficult.

Dalmanitina (Dalmanitina) sp. cf *D. (D.) acuta* differs from *Dalmanitina asta* Šnajdr, 1982, from the Bohdalec Formation (lower Katian) of Bohemia, in having a pygidium with narrower interpleural furrows, six pairs of pleural ribs and a half rib in comparison to the latter which has seven pairs plus one half rib. The Iranian pygidia also differ from *Dalmanitina elfrida* Šnajdr, 1982, from the Vinice Formation (upper Sandbian–lower Katian) of Bohemia, in having fewer pleural ribs (six instead of seven in *D. elfrida*) and more faint interpleural furrows and shallower pleural furrows. The Iranian cranidia are not well preserved and precise comparisons are not possible. *Dalmanitina (Dalmanitina) philippoti* Henry, 1980, from the upper Caradoc (lower Katian) Kermur Formation of the Armorican Massif, has the same number of pleural ribs but the interpleural furrows are deeper marked.

Dalmanitina (Dalmanitina) sp. cf *D. (D.) acuta* differs from *D. (D.) dargazensis* nov. sp., from the same section, in having a more convex and shorter frontal lobe of the glabella, fewer pleural ribs and a wider pygidial axis (Fig. 7(1, 3, 8)). It clearly differs from *Dalmanitina (Thuringaspis) lamarmorai* by a transverse pygidium almost two-thirds as long as wide with fewer axial ribs (10 instead of 13) and pleural ribs (six instead of seven).

Dalmanitina (Dalmanitina) sp.

Fig. 7(7–12)

Material: Six incomplete pygidia, NMW 2008.35G.544, 545, 558–561, two incomplete cranidia, NMW 2008.35G.575, 556, one incomplete glabella, NMW 2008.35G.546, one incomplete fixigena + spine, NMW 2008.35G.557, from sample MG10033; three incomplete glabellas, NMW 2008.35G.339, 541, 542, two incomplete pygidia, NMW 2008.35G.533, 340, from sample MG10037.

Description: Glabella strongly convex, glabellar furrows straight, narrow and shallow, frontal lobe long (sag., exsag.) and rhomboidal; S1 pointed slightly backward adaxially, bifurcated; S2 almost transverse, slightly curved forward, not cutting glabellar furrows (exsag.) (Fig. 7(11, 12)); S3 directed backward adaxially, sigmoidal; occipital ring very long, lateral border and posterior border wide and convex, merging at genal angle and forming thick base of genal spine (Fig. 7(10)); genal spine moderately long, pointed posterolaterally.

Pygidium with 6 pleural ribs and one half rib, about 9 axial rings plus terminal piece; interpleural furrows straight, wide and shallow; pleural ribs very broad; pleural furrows narrow; interpleural furrows very faint fading abaxially; border moderately narrow, widening posteriorly; doublure as wide as border; pygidial spine thickened at base, about one third as long as pygidium.

Remarks: *Dalmanitina (Dalmanitina) sp.* differs from *D. (D.) sp.* cf *D. (D.) acuta* Hammann, 1971, from samples KF–6a and MG10029 of the same section, and *D. (D.) acuta* Hammann, 1971, from the lower–middle Katian Monte Orri Formation of Gonnese, SW Sardinia (Hammann and Leone, 2007), in having wider pygidial pleural ribs, narrower pleural furrows, weaker interpleural furrows and a glabella with a longer frontal lobe with rhomboidal outline and sigmoidal S3. It also has a pointed genal

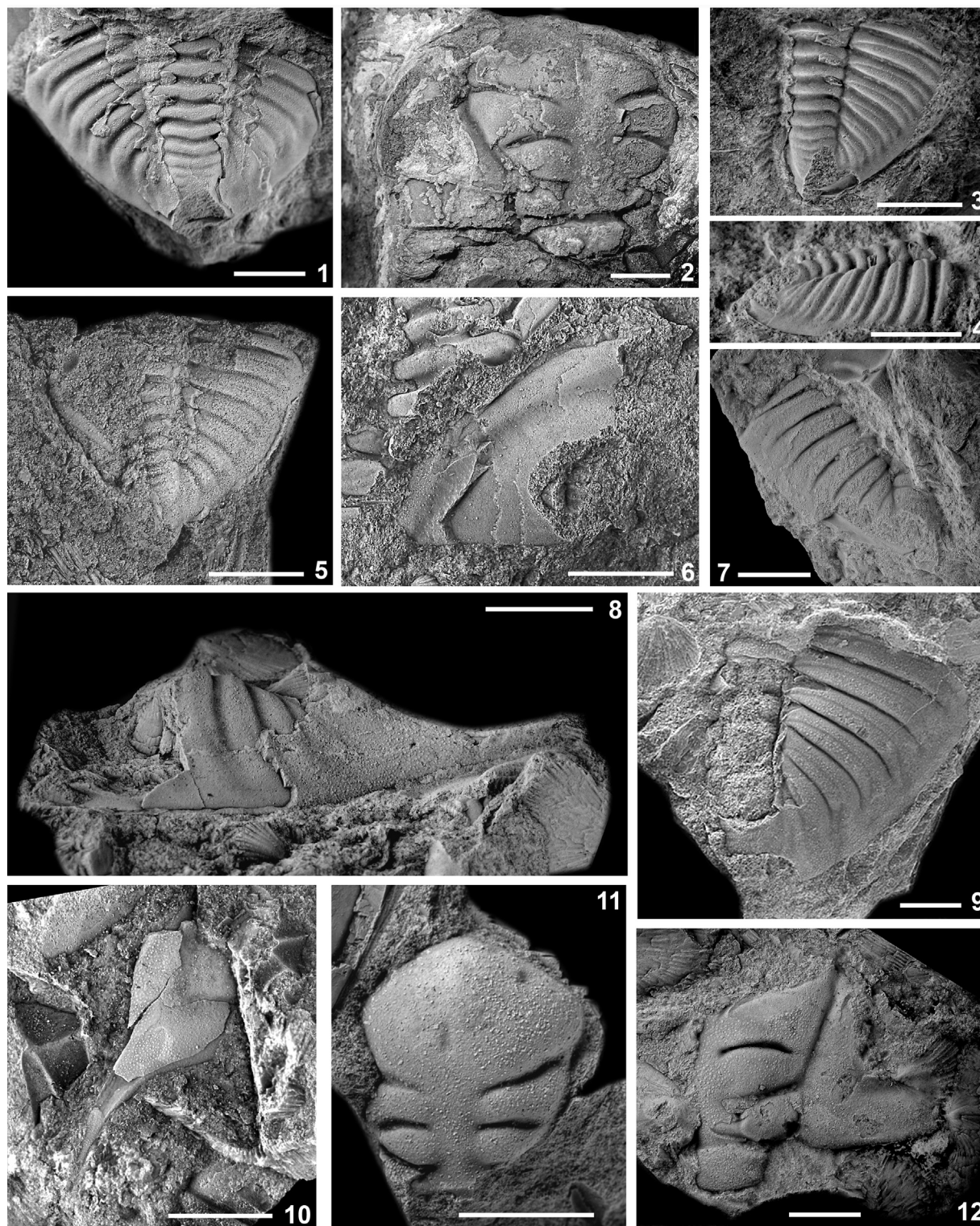


Fig. 7. 1–6. *Dalmanitina* (*Dalmanitina*) sp. cf. *D. (D.) acuta* Hammann, 1971; 1, National Museum of Wales (NMW) 2008.35G.552, incomplete pygidium; 2, NMW 2008.35G.553, incomplete cranidium. 3, 4, NMW 2008.35G.343, incomplete pygidium, dorsal and side views; 5, NMW 2008.35G.569, incomplete librigena, internal mould; 6, NMW 2008.35G.547, incomplete pygidium, internal mould; 1, 2, 5, sample MG10029; 4–5, sample KF-6a. 7–12, *Dalmanitina* (*Dalmanitina*) sp.; 7, NMW 2008.35G.544, incomplete pygidium; 8, incomplete pygidium with long spine, NMW 2008.35G.558; 9, NMW 2008.35G.340, incomplete pygidium; 10, NMW 2008.35G.557, incomplete fixigena+spine; 11, NMW 2008.35G.339, incomplete glabella; 12, NMW 2008.35G.556, incomplete cranidium; 7, 8, 10, 12, sample MG10033; 9, 11, sample MG10037. All specimens from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. Scale bars: 5 mm.

angle and a broad genal spine base unlike *D. (D.) acuta* Hammann, 1971, which has a rounded genal angle and a narrow-based genal spine. *D. (D.)* sp. differs from *D. (D.) dargazensis* nov. sp. from samples Sy-A/4, Sy-A/5, Sy-A/6, and MG10078 of the same

section, *D. (D.) proaeva* (Emmrich, 1839) from the lower Katian Zahořany Formation of Bohemia (Šnajdr, 1956; Havlíček in Chlupáč et al., 1998), and *D. (Thuringaspis) lamarmorai* (Meneghini, 1880) from the middle Katian Portixeddu Formation of Gonnese, SW

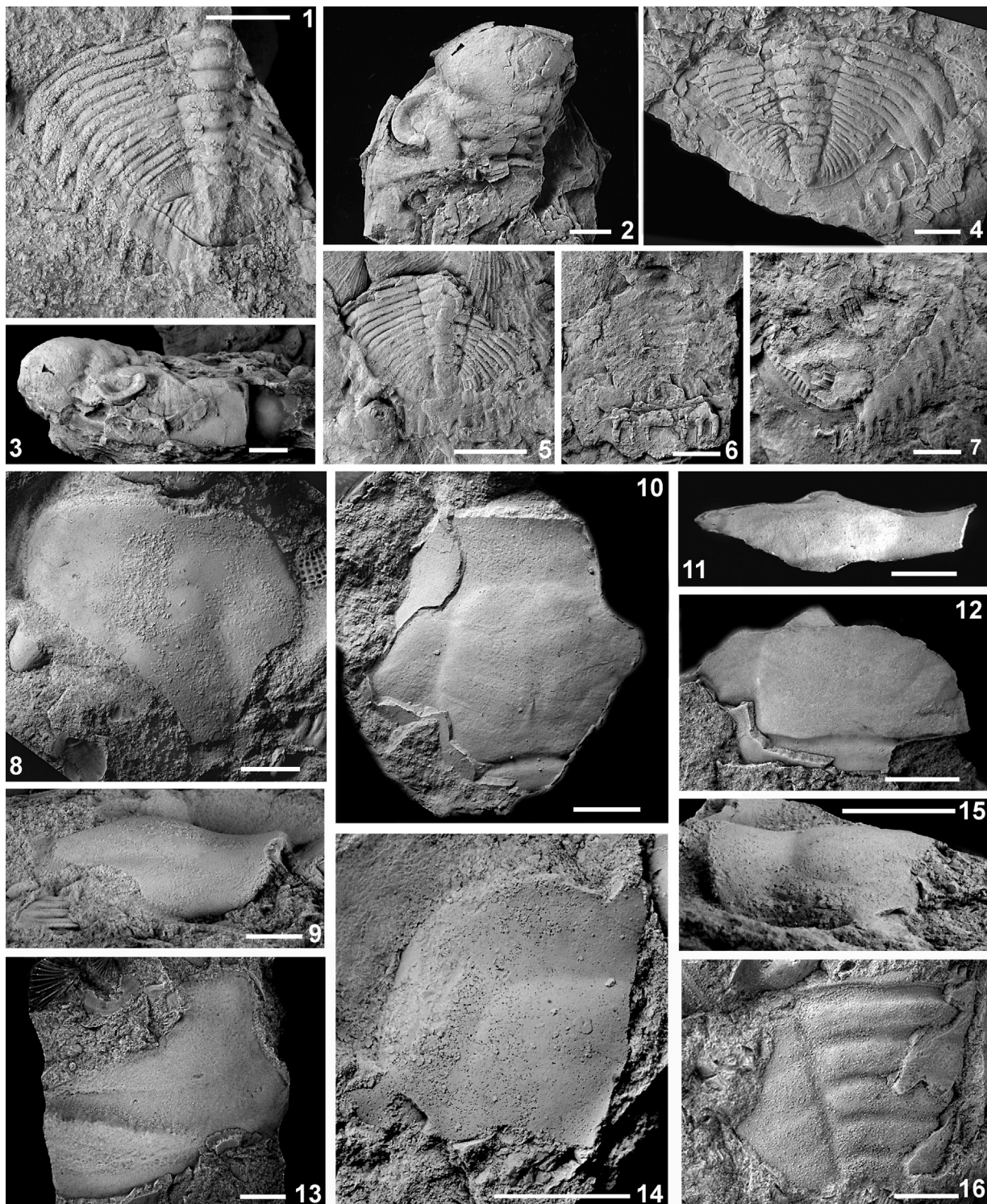


Fig. 8. 1–7. *Sardioites* sp. aff. *S. pillolai* Hammann and Leone, 2007; 1, National Museum of Wales (NMW) 2008.35G.452, holotype, incomplete pygidium, internal mould; 2, 3, NMW 2008.35G.486, incomplete cephalon, dorsal and side views; 4, NMW 2008.35G.549, incomplete pygidium; 5, NMW 2008.35G.454, incomplete pygidium; 6, NMW 2008.35G.550, incomplete pygidium, external mould with partial doublure and a few posterior spines; 7, NMW 2008.35G.554, incomplete pygidium with partial doublure and a few spines; 1, 5, level Sy–A/6; 2, 3, level Sy–A/4; 4, 7, level Sy–A/5; 6, level Sy–A/7. 8–16. *Iberocoryphe* sp.; 8, 9, NMW 2008.35G.555, incomplete cranidium, dorsal and side views; 10–12, NMW 2008.35G.331, incomplete cranidium, latex cast of external mould, side view of latex cast and internal mould; 13, NMW 2008.35G.532, incomplete fixigena; 14–15, NMW 2008.35G.568, incomplete cranidium; 16, NMW 2008.35G.342, incomplete pygidium, internal mould; 8, 9, sample MG10037; 10–15, level KF–6a; 16, sample MG10037. All specimens from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. Scale bars: 5 mm.

Sardinia (Hammann and Leone, 2007), in having an almost transverse S2, which is slightly curved forward and does not reach the glabellar furrows, a pygidium with six (not seven) pleural ribs and nine (not 13) axial rings (Fig. 7(7, 9)), and narrower and shallower pleural and interpleural furrows. The Iranian specimens

also differ from *D. (D.) socialis* (Barrande, 1852), from the Sandbian–lower Katian Letná Formation of Bohemia (revised by Šnajdr, 1956) and *D. (D.) ciliensis* Šnajdr, 1956, from the Sandbian Drabov Quartzites of Bohemia, in having a longer genal spine, S2 that does not reach the glabellar furrows, narrower pleural

furrows, and very faint interpleural furrows. *D. (D.)* sp. shows some similarities with *D. (D.)* n. sp. aff. *acuta* Hammann, 1971, described and figured by Henry (1980) from the upper Sandbian Postolonnec Formation of the Armorican Massif, including a long rhomboidal frontal lobe (sag.) with a medial longitudinal depression, almost transverse S2, which is slightly curved forward and does not reach the glabellar furrows, a cephalic posterior border widening abaxially and merging with the lateral border to form a wide base for medium-sized genal spines, a pygidium having broad pleural ribs, very narrow pleural furrows and very faint interpleural furrows. Further comparisons are not possible on the basis of the preservation and small number of Iranian specimens.

Subfamily EUDOLATITINAE Tomczykowa, 1991

Genus *Sardoites* Hammann and Leone, 2007

Type species: *Sardoites pillolai* Hammann and Leone, 2007 from the Portixeddu Formation TH 2b, late Beroun Series (mid Katian), Gonnese, SW Sardinia.

Sardoites sp. aff. *S. pillolai* Hammann and Leone, 2007

Fig. 8(1–7)

Material: One incomplete glabella, NMW 2008.35G.583, one incomplete pygidium, NMW 2008.35G.584, from sample MG10066; one incomplete cephalon, NMW 2008.35G.486, from sample Sy-A/4; two incomplete pygidia, NMW 2008.35G.549, 554, from sample Sy-A/5; four incomplete pygidia, NMW 2008.35G.452 (Pl = 15, Pw = 22, Al = 13, Aw = 6.2), 453, 454, 455, two juvenile incomplete pygidia, NMW 2008.35G.352, 551, from sample Sy-A/6; two incomplete pygidia, NMW 2008.35G.505b, 550, from sample Sy-A/7.

Description: Cephalon semicircular. Glabella pear-shaped, strongly convex, axial furrows shallow and wide, almost straight and diverging anteriorly. Preglabellar furrow narrow, curved forward. Occipital ring not well preserved, occipital furrow deep and wide. S1 transverse or slightly inclined backward adaxially, not bifurcated; S2 directed slightly forward abaxially; S3 curved backward, running forward to reach axial furrow near widest part of frontal lobe. L1 and L2 transverse, about same length (exsag.); L3 subtriangular, as long as L1 + L2. Frontal lobe convex (tr. and sag.), expanding (tr.) outward, transversely rhomboid in outline, with acute anterolateral corners; about 50% as long as wide and 50% as long as glabella (including occipital ring). Eyes semicircular, large, posterior end opposite anterior part of L1, extending forward to S3. Posterior border furrow narrow, moderately deep. Posterior border slightly convex, strongly widening abaxially to merge with lateral border, forming broad genal angle. Genal spine base very broad (Fig. 8(2)). Lateral border convex and narrow, confined to double. Posterior branch of facial suture transverse, slightly forward curved toward lateral margin. Anterior branch of facial suture running to corner of frontal lobe and runs around front of glabella along anterior border furrow. Thorax and hypostome unknown.

Pygidium subtriangular in outline, about two third as long as wide. Axis about 25% as wide and 80% as long as pygidium, with twelve axial rings plus terminal piece consistently tapering backward and terminating at border. Axial rings becoming shorter and narrower (sag.) backward, with posterior rings not well-defined. Posterior end of axis very weakly defined. Inter-ring furrows narrow, deepening abaxially. Axial furrows well-defined, narrow, straight, evenly curved backward. Pleural field gently convex. Border furrow wide and shallow. Border gently convex, narrow about one tenth as long as pygidium (excluding spines). Double confined to border. Twelve pleural ribs, well-defined, posterolaterally directed, becoming more posteriorly directed backwards, with most posterior ones running almost parallel to axial furrows. Interpleural furrows narrow and deep, fading

toward border. Pleural furrows as deep as interpleural furrows, running towards pygidial margin, weakening on border and continuing into posterior margins of pygidial spines. Pygidial margin with 12 pairs of spines plus short triangular median spine (Fig. 8(1, 5)). Eleventh pair of spines more pronounced (Fig. 8(1)).

Remarks: Iranian specimens differ from the types of *Sardoites pillolai* Hammann and Leone, 2007, in having a more convex glabella with longer L1 and L2 (exsag.), a wider frontal lobe, eyes placed more distantly from the glabellar furrows, a much wider base of the genal spine, a slightly wider pygidial axis, a narrower pygidial border, and longer pleural spines. They may represent a separate taxon, but because of inadequate preservation of the specimens available for study, they are left in open nomenclature.

Suborder CALYMENINA Swinnerton, 1915

Superfamily CALYMENOIDEA Burmeister, 1843

Family CALYMENIDAE Burmeister, 1843

Subfamily REEDOCALYMENINAE Hupé, 1955

Genus *Neseuretinus* Dean, 1967

Type species: *Neseuretinus (Neseuretinus) turcicus* Dean, 1967; Sandbian Lower Bedinan Shale Formation, Turkish Taurides.

Neseuretinus sp. aff. *N. malestanus* (Wolfart, 1970)

Figs. 9, 10

Material: Two external moulds of incomplete crania, NMW 2008.35G.574, 565, from sample MG10026; one incomplete pygidium, NMW 2008.35G.543, from sample MG10037; one hypostome, NMW 2008.35G.332 (Hl = 10.5; Hw = 11; Hml = 7.2; HMw = 4.5), six incomplete crania, NMW 2008.35G.512–513, 334, 516, 563, 564, three incomplete librigenae, NMW 2008.35G.333, 514–515, eight incomplete pygidia, NMW 2008.35G.517–521, 531, 548, 567, one external mould of pygidium, NMW 2008.35G.566, from sample KF-6a; two incomplete librigenae, NMW 2008.35G.576–577, one incomplete cranidium, NMW 2008.35G.578, two incomplete pygidia, NMW 2008.35G.579–580, from sample MG10066; two incomplete crania, NMW 2008.35G.484b, 493, one pygidium, NMW 2008.35G.484a, two incomplete pygidia, NMW 2008.35G.491, 492 from sample Sy-A/4; one cranidium, NMW 2008.35G.325 (Cl = 16; Cw = 32; Gl = 8; Gw = 9.5; PGI = 5.2; ORI = 2.5; ORw = 9), two external moulds of crania, NMW 2008.35G.396, 572, eight internal moulds of incomplete crania, NMW 2008.35G.307, 313 (Cl = 17; Gl = 9; Gw = 12.7; PGI = 6; ORI = 2.6), 345, 390 (Cl = 13.5; Gl = 7.5; Gw = 10; PGI = 4.5), 405, 411, 431, 432, four internal moulds of pygidia, NMW 2008.35G.304, 328, 386, 387, 11 internal moulds of incomplete pygidia, NMW 2008.35G.309, 397–400, 402, 433–436, 483, three internal moulds of incomplete librigenae, NMW 2008.35G.355c, 312, 408, from samples MG10078 and Sy-A/6; one internal mould of incomplete cranidium, NMW 2008.35G.505a, three internal moulds of incomplete librigenae, NMW 2008.35G.506–508, three internal moulds of incomplete pygidia, NMW 2008.35G.509–511, from sample Sy-A/7.

Description: Cranidium subtriangular, as wide as long. Glabella moderately convex (tr. and sag.), trapezoidal in outline, about 80% as long as wide, with maximum width at midpoint of L1. Glabellar length about 65% of cranial length (sag.). Glabellar length equal to 90% of maximum glabellar width at midpoint of L1. Anterior glabellar margin slightly convex forward to almost transverse, slightly concave in middle part. Preglabellar furrow deep with pair of distinct fossulae at abaxial terminations (Figs. 9(1), 10(1)). Axial furrows deep, narrowing anteriorly, gently convex abaxially. L1 expanded laterally, almost hemispherical with evenly rounded outer margins on internal mould, subquadrate on dorsal side; L2 subrectangular, obliquely directed; L3 short, subrectangular. S1 deep, straight, slightly bent posteriorly adaxially, then strongly curved backward shallows into occipital furrow. S2 deep, straight,

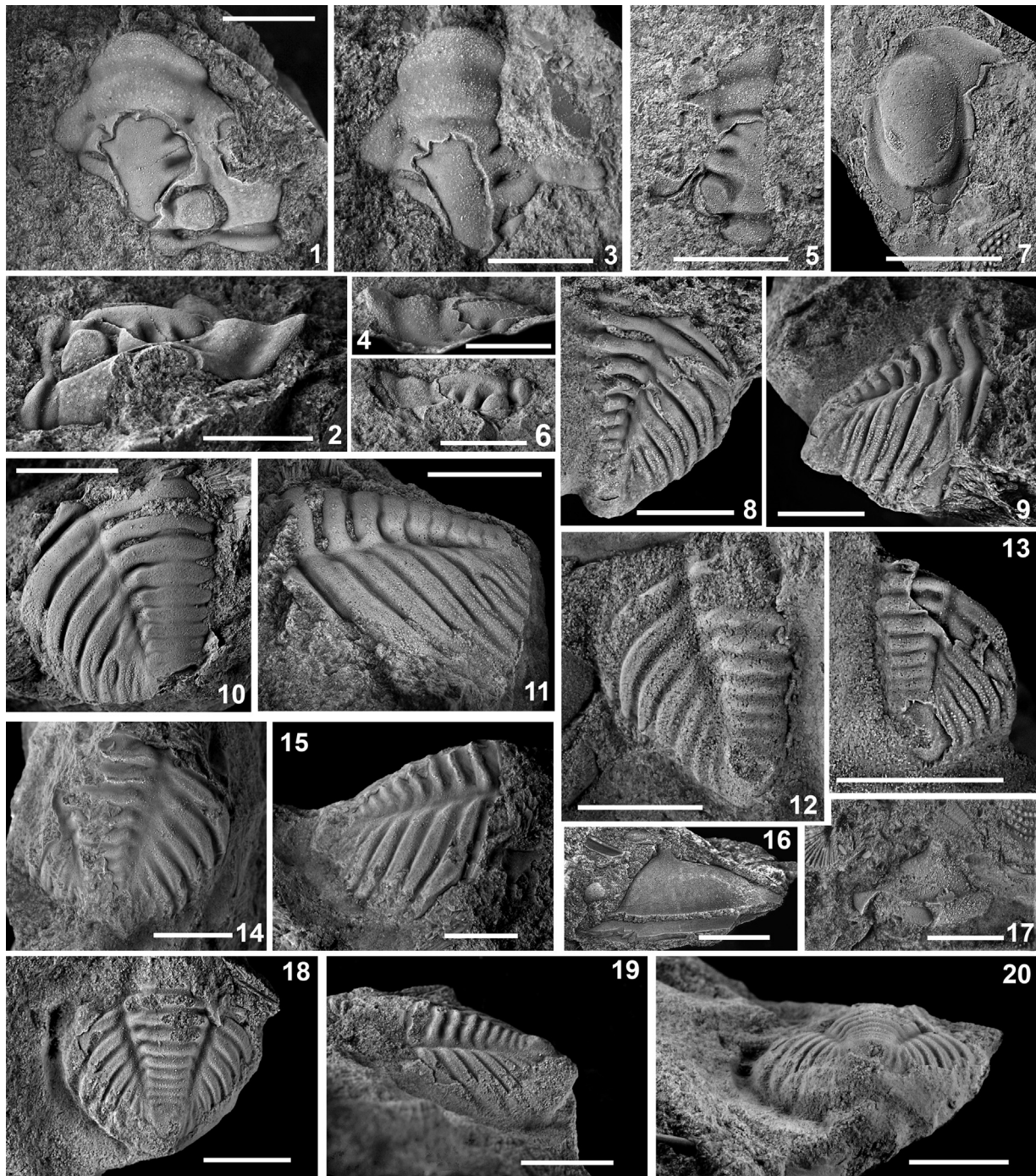


Fig. 9. *Neseuretinus* sp. aff. *N. malestanus* (Wolfart, 1970) from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. **1, 2**, National Museum of Wales (NMW) 2008.35G.512, incomplete cranidium, dorsal and side views; **3, 4**, NMW 2008.35G.516, incomplete cranidium, latex cast, dorsal and side views; **5, 6**, NMW 2008.35G.334, incomplete cranidium, dorsal and side views; **7**, NMW 2008.35G.332, hypostome, internal mould; **8, 9**, NMW 2008.35G.548, incomplete pygidium, dorsal and side views; **10, 11**, NMW 2008.35G.517, incomplete pygidium showing abnormal growth of pleural ribs on posterior part, dorsal and side views; **12**, NMW 2008.35G.543, incomplete pygidium, internal mould; **13**, NMW 2008.35G.519, incomplete pygidium; **14, 15**, NMW 2008.35G.520, incomplete pygidium, internal mould, dorsal and side views; **16**, incomplete librigena, internal mould, NMW 2008.35G.514; **17**, NMW 2008.35G.333, incomplete librigena; **18–20**, NMW 2008.35G.567, pygidium, dorsal, side and posterior views; 1–11, 13–20, level KF-6a; 12, sample MG10037. Scale bars: 5 mm.

parallel to S1, inclined less than 20° posteriorly adaxially. S3 deep, straight, inclined less than 40° posteriorly adaxially. Occipital ring about 15% of glabellar length (sag.) including occipital ring. Occipital furrow transverse, deepening abaxially. Preglabellar field strongly swollen (sag. and tr.). Anterior border subtriangular, convex in transverse profile (Fig. 9(4, 6)). Anterior border furrow wide (sag. and exsag.), very shallow medially, deepening slightly abaxially. Preglabellar boss swollen (tr. and sag.) occupying more

than half of preglabellar field length. Posterior border furrow transverse, deep and wide; posterior border slightly convex, widening (exsag.) abaxially. Librigena sloping strongly abaxially with evenly convex border. External surface of cranidium and librigena covered by coarse tubercles with interspersed fine granules.

Hypostome elongate, suboval in outline, about 80% as wide as long. Median body gently convex (Fig. 10(2)), suboval in outline,

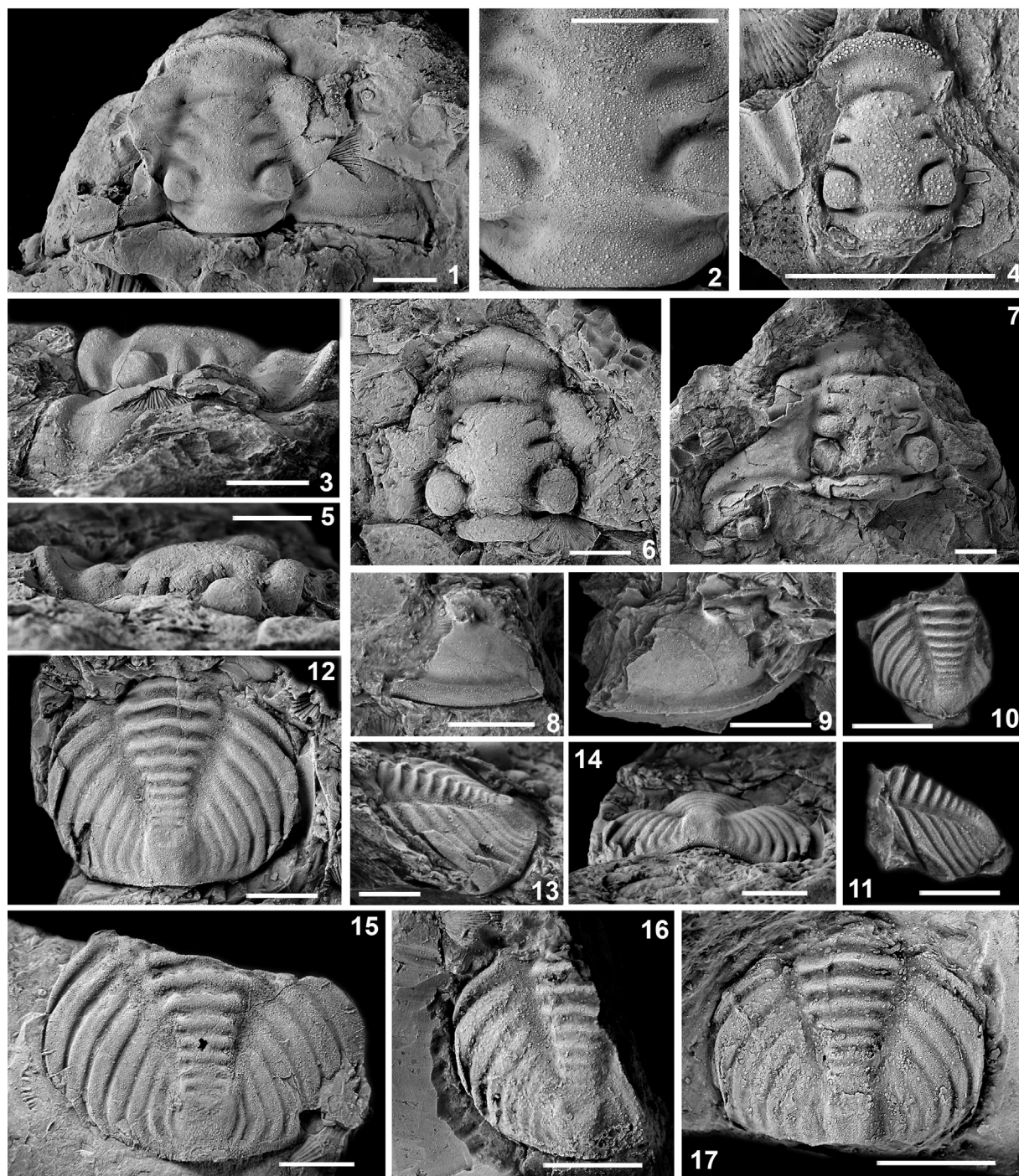


Fig. 10. *Neseuretinus* sp. aff. *N. malestanus* (Wolfart, 1970) from the Faraghan section, southeastern Iran; Seyahou Formation, lower–middle Katian, Upper Ordovician. 1–3, National Museum of Wales (NMW) 2008.35G.325, incomplete cranidium, dorsal view, close view of the glabella showing granulation, and side view; 4, NMW 2008.35G.405, incomplete cranidium; 5, 6, NMW 2008.35G.313, incomplete cranidium, internal mould, dorsal and side views; 7, NMW 2008.35G.345, incomplete cranidium; 8, incomplete librigena, internal mould, NMW 2008.35G.312; 9, NMW 2008.35G.408, incomplete librigena, internal mould; 10, 11, NMW 2008.35G.397, incomplete pygidium, internal mould, dorsal and side views; 12–14, NMW 2008.35G.304, pygidium, internal mould, dorsal, side and posterior views; 15, NMW 2008.35G.386, incomplete pygidium, internal mould; 16, NMW 2008.35G.309, incomplete pygidium, internal mould; 17, NMW 2008.35G.328, pygidium, internal mould; 1–3, 5–7, 9–17, level Sy–A/6; 4, 8, sample MG10078. Scale bars: 5 mm.

with long anterior lobe and smaller (sag.) posterior lobe separated by very narrow and shallow, middle furrow. Middle furrow curved backward (adaxially), and then turning to be fading posteriorly adaxially. Macula well-defined, obliquely suboval, situated on anterior surface of middle furrow. Lateral border slightly convex, narrowing anteriorly into shoulder. Posterior border divided medially by funnel-shaped notch occupying about 20–25% of hypostomal length. Anterior wings wide, inclined dorsally

abaxially. Anterior border wide, anterior border furrow shallow and moderately wide. Hypostomal suture curved forward. Thorax unknown.

Pygidium about 85% as long as wide, subtriangular, strongly convex. Axis funnel-shaped, about 85% as long and about 40–45% as wide as maximum pygidial width. Nine axial rings and small terminal piece with faint rounded posterior end of axis. Axial furrows shallow, deepening backward, widening forward, tapering

abaxially at about 20° along first seven rings then turned subparallel. Posterior pygidial margin poorly defined, connected with bilobate postaxial ridge. Pleural furrows deep; interpleural furrows shallow and narrow, more prominent posterior to fulcrum, less strongly impressed on dorsal side of pygidium, separating wider anterior pleural band from narrower posterior pleural band. Pleural field convex, steeply declined abaxially with short anterior half rib and seven pleural ribs; posteriormost rib weakly defined. Pygidial surface finely granulated.

Remarks: There are small variations in the cranidial morphology between the specimens of *N. aff. malestanus* from stratigraphically lower samples, including KF-6a and MG10037, and the upper ones, including MG10066, MG10078, Sy-A/4, Sy-A/6 and Sy-A/7; the latter exhibit a wider, slightly shortened and less swollen preglabellar field, a more rounded anterior margin, a shorter preglabellar boss, a deeper anterior border furrow, and a more strongly curved upward anterior border.

The Iranian specimens here identified as *Neseuretinus* sp. aff. *N. malestanus* are closely related to the topotypes of *N. malestanus* (= *Pharostoma malestana* Wolfart, 1970), from the Upper Ordovician of the Malestan District in eastern Afghanistan. In particular, they exhibit close similarities in the shape of the anterior cranidial border, a preglabellar field and pygidial morphology including a number of pleural ribs. By contrast, the Iranian specimens differ in having a longer preglabellar field, and a narrower and distinctly funnel-shaped pygidial axis. Due to poor preservation of the Afghan specimens, a more precise comparison is not possible.

Wolfart (1970) considered *N. malestanus* as a different species from *N. birmanicus* (Reed, 1906) because the former has a more rounded anterior margin of the cranidium and different pygidial morphology and number of pleural ribs. Dean (1975) also recognized that the Afghan specimens are different from the type species *N. turcicus*. Hammann and Leone (1997) reassigned the Afghan specimens to *Neseuretinus* and discussed their affinities in more detail. They considered them as very similar to *N. turcicus* Dean, 1967, based on a common shape of the anterior border; however, because of the poor preservation of Afghan specimens, their comparisons were not completely convincing.

The cranidial morphology of *Neseuretinus* is highly conservative except in some minor variations in the proportions and shape of the preglabellar field and the border. The main differences useful for taxonomic purposes at the species level can be found in the pygidial morphology, which is unfortunately unknown for the types of *N. turcicus*. The specimens described by Hammann and Leone (1997, 2007) may be indeed conspecific with the Turkish ones, but, as the pygidial morphology of the topotypes is still unknown, it cannot be established with confidence.

Dean (1967) discussed some differences in the cranidial morphology of *N. turcicus* and *N. birmanicus* (Reed, 1906), and noted a more pointed and much longer anterior cranidial border, a more convex preglabellar field, and a somewhat narrower glabella in the former species. His comparison was based on the study of a single incomplete cranidium (holotype) and he did not provide any information about other parts of the exoskeleton, most importantly on the pygidium. Nevertheless, a comparison between *N. birmanicus*, including the specimens from Central Iran (Ghobadi Pour and Popov, 2009) and Myanmar (Reed, 1915), and *N. turcicus*, including data from Turkey (Dean, 1967) and Sardinia (Hammann and Leone, 1997), reveals that the differences between these two species outlined by Dean are small, but consistent, and in our opinion are not due to differences in preservation or distortion, but reflect genuine morphological differences.

N. birmanicus (Reed, 1906) from the Shan States of Myanmar co-occurs with the *Saucrorthis* brachiopod association (Reed, 1915; Cocks and Zhan, 1998), which is confined to the Darriwilian in South

China and the Alborz Mountains of Iran (Ghobadi Pour et al., 2011a). Therefore, the Myanmar specimens are contemporaneous with the specimens from the Shirgesht Formation of Central Iran, which are also dated as late Darriwilian (Ghobadi Pour and Popov, 2009).

N. aff. malestanus differs from *N. birmanicus* (Reed, 1906) from the Darriwilian of the Shirgesht Formation in Central Iran in having a wider glabella, axial furrows becoming convex abaxially, a shorter frontal lobe, S2 and S3 with different angles inclined posteriorly adaxially, a wider occipital ring, a longer preglabellar field, a more rounded anterior border, a wider, less convex and funnel-shaped pygidial axis, a pygidium with nine rings and a small terminal piece, and seven pygidial pleural ribs instead of six pleural ribs and eight axial rings in *N. birmanicus* (Ghobadi Pour and Popov, 2009).

The specimens from Zagros differ from *N. turcicus* Dean, 1967, from the Lower Bedinan Shale Formation (lower Katian) of the Turkish Taurides and also from the specimens assigned to that species by Hammann and Leone (1997), from the middle Katian Portixeddu Formation of southern Sardinia, in having a slightly narrower glabella, a slightly longer preglabellar field and a boss, a wider pygidium with a funnel-shaped axis, with seven rather than six pleural ribs which are less inclined posteriorly.

Kolobova in Sokolov and Yolkina (1978) described and illustrated a few specimens from the presumably Sandbian Obikalon Beds of the Shahriyon Formation in Zerafshan Range, South Tien Shan, Uzbekistan as *Calymenesun tingi* (Sun, 1931). Hammann and Leone (1997) and later Turvey (2005) reassigned them to *N. birmanicus*. However, the insufficient description and illustration of these poorly preserved specimens do not provide enough information for the precise specific determination of these specimens.

Calymenesun longinasuta Dean and Zhou, 1988, from the Şort Tepe Formation of the Zap Valley in southeastern Turkey, was reassigned by Turvey (2005) to *Neseuretinus*, who considered *N. turcicus* and *N. birmanicus* as conspecific. It is not conspecific with *N. aff. malestanus*, because unlike the Iranian specimens, the Turkish specimens have a strongly pointed anterior cranidial border with a short frontal spike, a more strongly convex anterior border furrow, a longer (sag.) preglabellar field with a more strongly swollen preglabellar boss, and a pygidium with only seven axial rings and six pleural ribs.

Family HOMALONOTIDAE Chapman, 1890

Subfamily EOHOMALOTINAE Hupé, 1953

Genus IBEROCORYPHE Hammann, 1977

Type species: *Iberocoryphe verneuili* Hammann, 1977, Darriwilian 'Tristani' Sandstone, Central Iberia (by original designation).

Iberocoryphe sp.

Fig. 8(8–16)

Material: One incomplete cranidium and external mould, NMW 2008.35G.331, one incomplete fixigena, NMW 2008.35G.532, one incomplete cranidium, NMW 2008.35G.568, from sample KF-6a; one incomplete pygidium, NMW 2008.35G.342, and one incomplete cranidium, NMW 2008.35G.555, from sample MG10037.

Description: Cranidium convex, strongly effaced with transverse anterior margin. Glabella subrectangular, delineated by faint glabellar furrows, which slightly converge anteriorly adaxially. Preglabellar furrow transverse, weakly defined; preglabellar field moderately long and broad. S1 faint curved backward not merged with occipital furrow. Anterior border very narrow and transverse. Palpebral lobes small, semicircular, as high as glabella. Pygidium with very broad axis bearing more than five prominent (on internal mould) axial rings (posterior margin broken). Interringing furrows almost transverse, wide and shallow; axial furrows shallow, straight, converging posteriorly, pleural furrows very weak, fading posterolaterally.

Remarks: Incomplete specimens from the Faraghan Mountain should probably belong to *Iberocoryphe* Hammann, 1977. However, due to the fragmentary preservation of the studied specimens, a specific assignment is not possible. In particular they show some similarities with *Brongniartella levis* Dean, 1967 from the Lower Bedinan Shale Formation (Katian) of the Turkish Taurides. As Hammann (1983: p. 113) mentioned, the Turkish species must likely be reassigned to *Iberocoryphe*. Other species of *Iberocoryphe* are reported from the Upper Darriwilian–Sandbian of Spain and the Upper Ordovician ‘Grès de May’ Formation in France (Hammann, 1983: p. 113).

The Iranian specimens differ from *Eohomalonotus* Reed, 1918 in having faint, subparallel glabellar furrows, a weakly defined, transverse preglabellar furrow, a transverse anterior cranial margin, and very weakly defined, less posteriorly directed, pygidial pleural furrows. The specimens from the Zagros differ from *Platycoryphe* Foerste, 1919 in having a wide preglabellar field, subparallel glabellar furrows, a transverse preglabellar furrow and a less effaced pygidium.

4. Biostratigraphical and biogeographical significance of the fauna

According to the chitinozoan biostratigraphic chart published by Paris (1990) for the Mediterranean segment of Gondwana, all studied trilobites from the middle part of the Seyahou Formation are bracketed from the upper part of the *A. barbata* Zone to the lowermost part of the *Armoricochitina nigerica* Zone. Three slightly different trilobite associations can be identified in this interval, which are, in ascending order:

- the lowermost association, recovered from samples MGKF-6a, MG10026 and MG10029, includes *Deanaspis* sp. 1, *D. (D.)* sp. cf. *D. (D.) acuta*, *N. sp.* aff. *N. malestanus*, and *Iberocoryphe* sp. The specimens of *Deanaspis* sp. 1 are preserved as incomplete and disarticulated cephalons and pygidia, which make their affiliation at species level impossible; however, the presence of a true girder with a direct connection to the genal spine ridge leaves no doubts about their belonging to *Deanaspis*. *D. (D.)* sp. aff. *D. (D.) acuta* is a biostratigraphically significant species. In Sardinia, it occurs in the upper part of the Monte Orri Formation (horizon TH1b after Hammann and Leone, 2007). In Spain, according to Hammann and Leone (2007: p. 112), *D. acuta* appears slightly later in the “Bancos Mixtos” than in Sardinia. They suggest a correlation of the upper part of the Monte Orri Formation with the Bohdalec Formation of Bohemia and probably the Lower Bedinan Shale Formation of the Turkish Taurides. *N. sp.* aff. *N. malestanus* is assigned provisionally to the species originally described from the Upper Ordovician of eastern Afghanistan. Due to the imperfect preservation and illustration of the specimens in Wolfart (1970), a detailed comparison is difficult with the Iranian specimens, although they are probably conspecific on the basis of their pygidial morphology. The age of the types from Afghanistan is not known precisely, and the associated fauna includes only two species of poorly preserved brachiopods assigned to *Paracranios* and *Sowerbyella*. The occurrence of *Paracranios*, which is unknown from deposits older than the late Sandbian, suggests that *N. malestanus* is younger than *N. birmanicus* and probably confined to the Katian. *Iberocoryphe* is a long-ranging taxon that appears as early as the upper Darriwilian. In the Lower Bedinan Shale Formation of the Turkish Taurides, the genus co-occurs with *Deanaspis*, *Dalmanitina* (*Dalmanitina*) and *Neseuretinus* (Dean, 1967), although represented by different species;
- the second association has been recovered from samples MG10033 and MG10037. It includes *Deanaspis* sp. 2 and *Dalmanitina* (*Dalmanitina*) sp., which are somewhat different

from the representatives of the same genera in underlying beds, whereas *N. sp.* aff. *N. malestanus* and *Iberocoryphe* sp. are transitional. *Dalmanitina* (*Dalmanitina*) sp. is poorly preserved, but it is not conspecific to *D. (D.)* sp. aff. *D. (D.) acuta*. It shares distinct similarities with the specimens described by Henry (1980) as *D. (D.) n. sp.* aff. *D. (D.) acuta* Hammann from the upper Sandbian Postolonnec Formation in the Armorican Massif, but their taxonomic identity cannot be confirmed due to the poor preservation of the Iranian specimens;

- the third and youngest assemblage from the Faraghan section was recovered from samples MG10066, MG10078 (= Sy-A/6), Sy-A/4, Sy-A/5, and Sy-A/7. It includes *D. aff. D. (D.) vysocanensis*, *D. (D.) dargazensis* nov. sp., *Sardoites* sp. aff. *S. pillolai*, and *N. sp.* aff. *N. malestanus*. The species of *Sardoites* belongs to a genus previously known only from the lower part of the Portixeddu Formation in Sardinia (horizon TH2b of Hammann and Leone, 2007). The upper part of the Portixeddu Formation (horizon TH3a of Hammann and Leone, 2007) also contains *D. sp.* aff. *(D.) vysocanensis* and *Neseuretinus*, *Dalmanitina* (*Dalmanitina*), *Deanaspis*, but their species are different. Except *Sardoites*, all these genera also occur in the Lower Bedinan Shale Formation of the Turkish Taurides (Dean, 1967). According to Hammann and Leone (2007), the Portixeddu Formation of Sardinia can be correlated chronostratigraphically with the Bohdalec Formation and the lower part of the Králův Dvůr Formation from Bohemia.

Almost all the trilobite genera documented from the middle part of the Seyahou Formation, including *Dalmanitina* (*Dalmanitina*), *Deanaspis*, *Iberocoryphe* and *Sardoites*, display a strong Gondwanan signature and are confined in their biogeographical distribution to high-to-mid latitude peri-Gondwanan margins and terranes included in the Mediterranean region. As for *Neseuretinus*, a pattern of the geographic distribution of that taxon closely follows the Gondwana margin and probably was controlled by a cold water current running along the western coast of Gondwanaland (Ghobadi Pour and Popov, 2009).

A small Katian trilobite assemblage described and illustrated by Fortey et al. (2011) from the upper part of the Ra'an Formation in the Oman Mountains includes only three taxa: *Deanaspis goldfussii* sevenbergi (Hawle and Corda, 1847), *Dreyfussina* cf. *taouzensis* (Destombes, 1972), and *Vietnamia teichmulleri* (Hammann and Leone, 1997). Among them, only *Deanaspis* is shared with the Iranian trilobite assemblages, although they are represented by different species. A possible co-occurrence of trilobites from the Ra'an Formation with chitinozoans of the *Tanuchitina fistulosa* Zone (Fortey et al., 2011: p. 143) may suggest that the Iranian trilobite fauna from the Seyahou Formation is slightly younger.

A diverse trilobite fauna from the Şort Tepe Formation of the Hakkâri Region in southeastern Anatolia (Fig. 11) includes 23 trilobite genera (Dean and Zhou, 1988). With the exception of *Neseuretinus* (= *Calymenes*), none of them occurs in the Seyahou Formation, while *Dalmanitina* and trinucleids are absent. Among the genera documented from the Şort Tepe Formation of Hakkâri, *Birmanites*, *Ovalocephalus* and *Paraphillipsinella* make their earliest appearance in Eastern Gondwana (Kazakhstanian terranes, South and North China) and only in the late Katian migrated toward the Mediterranean Gondwana and Baltica (Turvey, 2005; Ghobadi Pour and Popov, 2009; Zhou and Zhen, 2009). *Sinocybele* is otherwise confined to the Australasian segment of Gondwana, its satellite plates and island arcs (Edgecombe and Webby, 2006; Zhou and Zhou, 2006; Ghobadi Pour et al., 2011b). Other components of the assemblage are cosmopolitan, but some of them, such as *Diacanthaspis*, *Dicranopeltis*, *Lichas*, *Miraspis* and *Phorocephala*, were confined mainly to low latitudes in the older faunas. Their appearance, as well as the immigration of Australasian taxa in the Mediterranean segment of Gondwana, can be considered as an

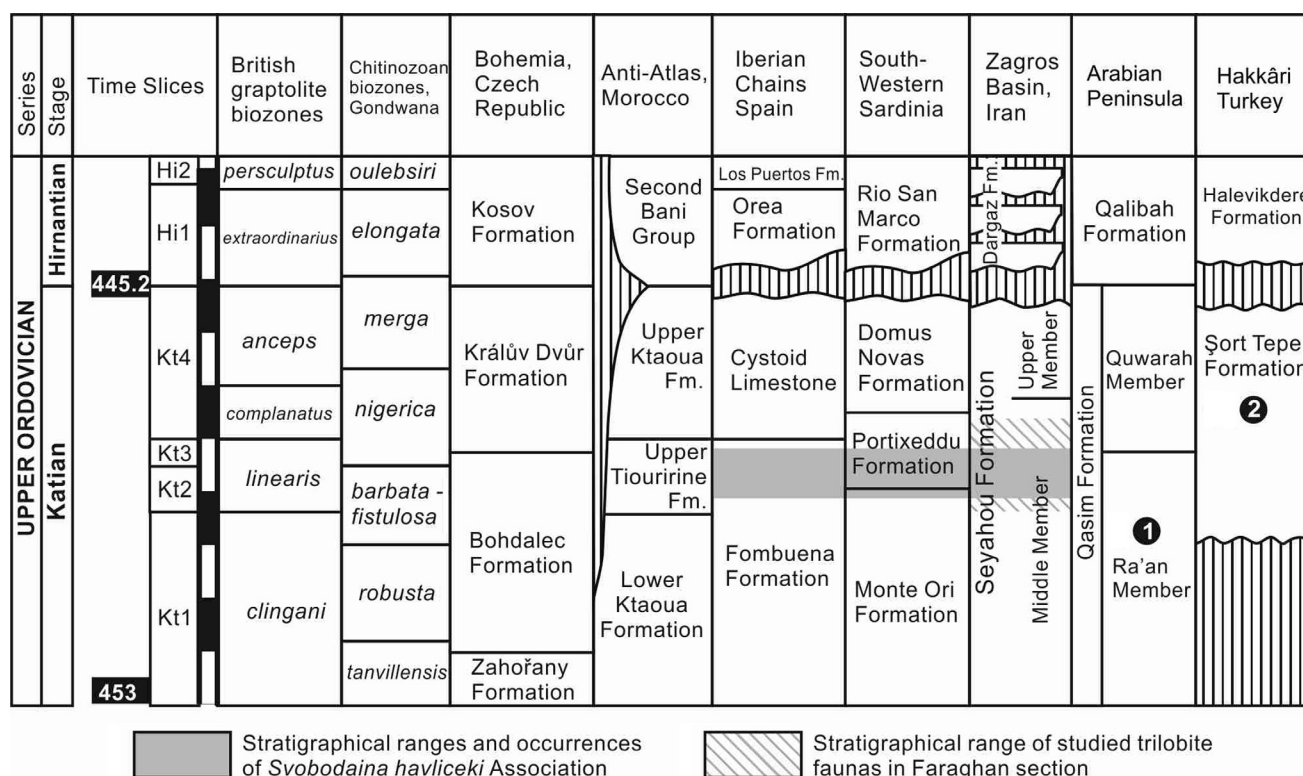


Fig. 11. Summarized Late Ordovician chrono- and lithostratigraphic chart of the Arabian and Mediterranean segments of Gondwana, based on Dean and Zhou (1988), Paris et al. (2007), Villas et al. (2002, 2006), Loi et al. (2010), Ghavidel-Syooki et al. (2011, 2015), and this work. ❶: approximate stratigraphical position of trilobite fauna from the upper part of the Rann Formation in the Oman Mountains; ❷: the Şort Tepe Formation of the Hakkâri Region in southeastern Anatolia (Dean and Zhou, 1988).

evidence for warming. Despite the lack of graptolites, the trilobite fauna of the Şort Tepe Formation is provisionally assigned to the *Dicellograptus complanatus* graptolite Zone (Dean and Zhou, 1988). Chitinozoans have only been reported from the lower part of the Şort Tepe Formation, below the trilobite-bearing strata, and they are indicative of the lower Katian (Paris et al., 2007). Although an age assessment of the fauna made by Dean and Zhou (1988) looks tentative, about that time the Mediterranean segment of Gondwana witnessed massive immigration of distinct benthic faunas previously restricted to low latitudes, e.g. Baltica and Laurentia (Villas et al., 2002). Boucot et al. (2003) also discussed a warming episode in the Mediterranean segment of Gondwana since the beginning of the *D. complanatus* Zone.

Fortey and Cocks (2003) pointed on a westward displacement of faunas that originated in China, resulting in the general homogenisation of trilobite assemblages across the Mediterranean margin of Gondwana in the Ashgill (= late Katian). The trilobite fauna of the Şort Tepe Formation can be considered as a sign of similar development in the Arabian segment of Gondwana. At that time, the Arabian segment of Gondwana, including present-day southeastern Turkey and Zagros, located along the western margin of Gondwanaland and was probably under the influence of the cool-water South Subpolar Current, running along the western Gondwanan coast (Wilde, 1991; Ghobadi Pour et al., 2011c: fig. 1). As a consequence of warming in the Mediterranean segment of Gondwana, the South Subpolar Current declined, leading to a distinct poleward faunal migration along the western Gondwanan coast.

There is growing evidence that from the beginning of the Katian, the Earth evolved into Icehouse conditions (Saltzman and Young, 2005; Page et al., 2007). Loi et al. (2010) and Videt et al. (2010) published a composite sea-level curve, based on a sequence-stratigraphic analysis of the Upper Ordovician sedimentary succession in the North African segment of Gondwana. They documented high-frequency sea-level fluctuations probably

controlled by orbital forcing, and three episodes of abrupt sea-level falls, exceeding 40 m during the Katian, which they considered as glacio-eustatic in origin and probably controlled by ice-cap to ice-sheet growths. One of these lowstands is recorded in the upper part of the *A. barbata* Zone (Upper Tiouririne Formation of the Anti-Atlas, Morocco). In the Zagros, it coincided with the proliferation of the low-diversity *Svobodaina havliceki* Brachiopod Association (Ghavidel-Syooki et al., 2015). Remarkably, the fourth-order sequences recognized in the Upper Tiouririne Formation also can be seen in the coeval interval of the Seyahou Formation in the Kuh-e Faraghan section (Ghavidel-Syooki et al., 2014; Figs. 2, 11), where they were accentuated by the migration of recurrent sandstone shoal complexes bearing a brachiopod assemblage characteristic of the *Svobodaina havliceki* Association (Villas et al., 2006; Álvaro et al., 2007; Colmenar and Álvaro, 2015). Its habitat is characterized as “shifting, medium-grained, sand substrates in high-energy environments of the shoreface” (Colmenar et al., 2013: p. 212). Steady sea-level rise in Zagros occurred just below the base of the *Armoricochitina nigerica* Zone (Fig. 2, samples MG10077, MG10078). Although there is little change in composition of the trilobite fauna at this level, it coincides with the invasion of a moderately diverse fauna of rhynchonelliform brachiopods assigned to the *Aegiromena-Hedstroemia* Association, characteristic of distant offshore substrates (Ghavidel-Syooki et al., 2015). The generic composition of that assemblage, including *Dalmanella*, *Iberomena*, *Jezercia*, *Kozlowskites*, *Onnizetina*, *Protomendacella*, and *Triplesia*, suggests strong links to contemporaneous brachiopod faunas of the Mediterranean Gondwana. It is likely that the newly discovered Katian trilobite fauna is slightly older than the trilobite fauna from the Şort Tepe Formation of the Hakkâri Region. Thus, it fills a stratigraphic gap between two previously reported Katian trilobite faunas of the Arabian segment preceding the time of increased southward migration of warm water faunas into temperate-to-subpolar latitudes of Gondwana.

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