First report on the occurrence of *Neseuretinus* and *Ovalocephalus* trilobites in the Middle Ordovician of Iran

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In the Derenjal Mountains of east Central Iran, the upper part of the Shirgesht Formation (uppermost Darriwilian) contains a distinct trilobite assemblage that includes *Neseuretinus birmanicus* and *Ovalocephalus* aff. *obsoletus* among others. Both genera were previously unknown in Iran. The occurrence of *Ovalocephalus* represents the earliest sign of westward taxon migration from China towards higher latitudes along the West Gondwanan margin, which may be related to global warming, after a short episode of cooler climate in the early to mid Darriwilian. Patterns of biogeographical distribution of *Ovalocephalus* and *Neseuretinus* suggest that Central Iran was part of an "overlap zone" where tropical and high latitude benthic taxa mingled.

Key words: Trilobita, palaeobiogeography, taxonomy, Ordovician, Darriwilian, Iran.

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Introduction

Ordovician trilobites of the Shirgesht Formation in the Derenjal Mountains of east Central Iran were revised recently by Bruton et al. (2004), but the Middle Ordovician fauna was mostly beyond the scope of that paper. There are some controversies about the upper age limits of the Shirgesht Formation. Early reports by Ruttner et al. (1968) gave evidence for the presence of Upper Ordovician rocks in the area. However, this was dismissed in later publications by Bassett et al. (1999) and Bruton et al. (2004), on the grounds that available data from studies of brachiopods and trilobites suggest that the age of the uppermost Shirgesht Formation cannot be younger than Arenig.

More recently, a Middle Ordovician age for the upper part of the Shirgesht Formation was supported by the discovery of a small ostracod fauna (Ghobadi Pour et al. 2006). The ostracod-bearing horizons also contain a moderately diverse trilobite assemblage, which includes *Birmanites* sp., *Deanaspis* sp., *Liomegalaspides* (= *Megalaspides*) *winsnesi* (Bruton, 2004), *Neseuretinus birmanicus* (Reed, 1906), *Ovalocephalus* aff. *obsoletus* (Zhou and Dean, 1986), *Radnoria simplex* (Kolobova, 1978) and *Thaleops* (*Amphoriops*) sp., among others. The occurrence of *Neseuretinus* and *Ovalocephalus* in this assemblage is of particular interest. Both taxa were relatively widespread within Gondwana and its associated terranes, but they have not been reported previously from Iran. Moreover, there are only a few reports of their co-occurrence in the same faunal assemblage, including the Upper Ordovician Şort Tepe Formation of the Turkish Taurides (Dean and Zhou 1988) and the Naungkangyi Group, northern Shan States, Myanmar (Burma) (Fortey and Cocks 1998). Areas occupied by these genera in the Mid and early Late Ordovician were otherwise separated. This peculiarity in the palaeogeographical distribution of *Neseuretinus* and *Ovalocephalus* may have important implications for the evaluation of the palaeogeographical position of Central Iran in the Middle Ordovician, which is discussed below.

Institutional abbreviations.—GSI, Geological Survey of India, Calcutta, India; NMW, National Museum of Wales, Cardiff, UK.

Other abbreviations.—Al, Aw, length and width of pygidial axis; Cl, Cw, length and width of cephalon; Gl, Gw, length and width of the glabella; N, number of measured specimens; PGl, PGw, length and width of preglabellar field; Pl, Pw, length and width of pygidium; ORl, ORw, length (sag.) and width of occipital ring; S, standard deviation; sag., sagittal; tr., transverse; X, average.

Geological setting

The studied trilobites were sampled from the upper part of the Shirgesht Formation in the Derenjal Mountains, about 65 km north of Tabas. The geology of the area was outlined by Ruttner et al. (1968) and by Bruton et al. (2004), but no detailed faunal logs were given in these publications and the lists of fossils characteristic of the Shirgesht Formation are composite. Recently, Ghobadi Pour et al. (2006: 552, fig. 2)

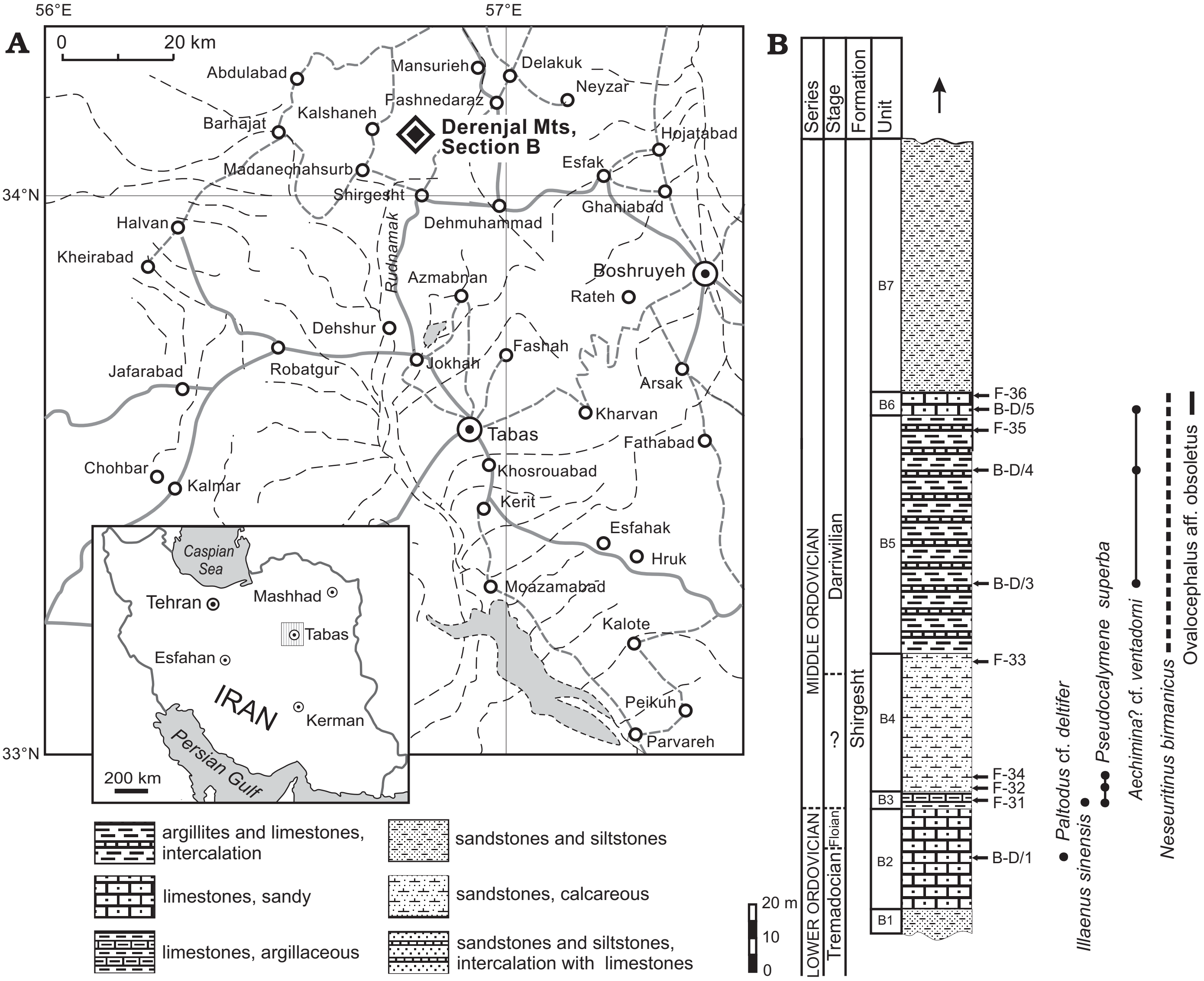


Fig. 1. Geographical map (**A**) showing the position of fossil locality in the Derenjal Mountains north of Tabas and stratigraphical column (**B**) through Section B in the upper part of the Shirgesht Formation, showing stratigraphical ranges of selected trilobite, ostracod, and conodont species (after Ghobadi Pour et al. 2006). The dashed line for *Neseuretinus birmanicus* indicates the position of specimens collected lose on the surface and therefore only in approximate stratigraphical position.

published a more detailed account of the faunal distribution through the upper part of the Shirgesht Formation exposed on the west side of Dahaneh Kolut (Section B). Units B5 and B6 of the section represent the main source of the trilobites studied and described in the present paper (Fig. 1). Geographical coordinates for the base and the top of Section B are 34°05'32" N and 56°47'7.3" E, and 34°05'21.7" N and 56°47'06.7" E respectively.

Unit B5, about 70 m thick, comprises intercalating green calcareous argillites and argillaceous limestones with abundant brachiopods, bryozoans, gastropod and cephalopod molluscs, trilobites, ostracods, and echinoderms. Most trilobites were collected as loose specimens through the unit (sample F-35). *Neseuretinus birmanicus* is relatively abundant and is represented mostly by complete, enrolled exoskeletons.

Unit B6, about 19 m thick, comprises characteristic brownish-red sandy limestones with abundant gastropod and cephalopod molluscs, ostracods, echinoderm columnals and rhombiferan *Heliocrinites* sp. (Lebfebvre et al. 2005; sample F-36), and trilobites including *Ovalocephalus* aff. *obsoletus* and a few *Neseuretinus birmanicus*.

There is a barren interval of intercalating siltstones and argillites up to 150 m thick in the uppermost part of the Shirgesht Formation (Unit B7).

Systematic palaeontology

The terminology and systematic classification follow that of the revised edition of the *Treatise on Invertebrate Palaeontology* (Whittington and Kelly 1997).

Class Trilobita Walch, 1771

Order Phacopida Salter, 1864

Suborder Cheirurina Harrington and Leanza, 1957

Superfamily Cheiruroidea Hawle and Corda, 1847

Family Pliomeridae Raymond, 1913

Subfamily Hammatocnemiinae Kielan, 1960

Remarks.—Yuan et al. (2003) gave a detailed description of *Ovalocephalus primitivus* (Lu, 1974) and pointed out a remarkable similarity in ontogenetic development with that of *Pliomerina* Chugaeva, 1958 (Edgecombe et al. 1999). Their assignment of Hammatocnemiinae, as a separate subfamily, within the family Pliomeridae is accepted here.

Genus *Ovalocephalus* Koroleva, 1959

Type species: *Ovalocephalus kelleri* Koroleva, 1959, Upper Ordovician, lower Katian, northern Central Kazakhstan.

Ovalocephalus aff. *obsoletus* (Zhou and Dean, 1986)

Fig. 2F–H.

Material.—NMW 2004.22G.575, complete enrolled exoskeleton (Gl-9.0, Gw-7.9; ORl-1.3, ORw-3.85, Cw>10.7); NMW 2004.22G.576, incomplete cephalon (Gl-8.0; ORl-1.3); 2004.22G.577, pygidium (Pl-4.6, Pw-8.7, Al-2.8, Aw-3.0); NMW 2004.22G.578, pygidium of meraspid (Pl-1.0, Pw-2.4, Al-0.8, Aw-0.9); all from sample F-36, Unit B6, Section B.

Description.—Exoskeleton elongate suboval, with finely granulated surface. Cranidium about 85% as long as wide with a strongly convex subtriangular glabella, about 115% as long as wide with a broadly rounded anterior margin; axial furrows deep, almost straight, strongly tapering backwards to the occipital furrow. Preoccipital ring short (sag.) with a pair of small preoccipital lobes abaxially. S1 shallow, transverse; S2 and S3 very short (tr.), inclined slightly posteriorly abaxially; S4 poorly defined, situated opposite to the anterior end of palpebral lobes. Occipital ring convex, about one third as long (sag.) as wide (tr.) and about 14–15% as long as the glabella. Palpebral lobes narrow (tr.) with the posterior end about half distance between S1 and S2. Postocular area of fixigena slightly transverse, subtriangular, gently curved downward abaxially. Posterior border convex, uniform in width (sag.); border furrow wide and deep. Librigena with a wide, convex border and holochroal eyes. Hypostome unknown. Thorax with nine thoracic segments.

Pygidium subtrapezoidal in outline, about half as long as wide, with a transverse, almost straight posterior margin; anterior pygidial margin strongly and evenly curved backwards. Axis weakly convex, about one third of maximum pygidial width, gently tapering posteriorly, with four axial rings. Terminal piece not laterally differentiated. Axial furrows distinct in the anterior half of pygidial length, fading posteriorly. Pleural field evenly convex with four pairs of pleural ribs strongly bending backwards abaxially. Three anterior pairs of pleural furrows well defined, fourth pair short (tr.) and shallow.

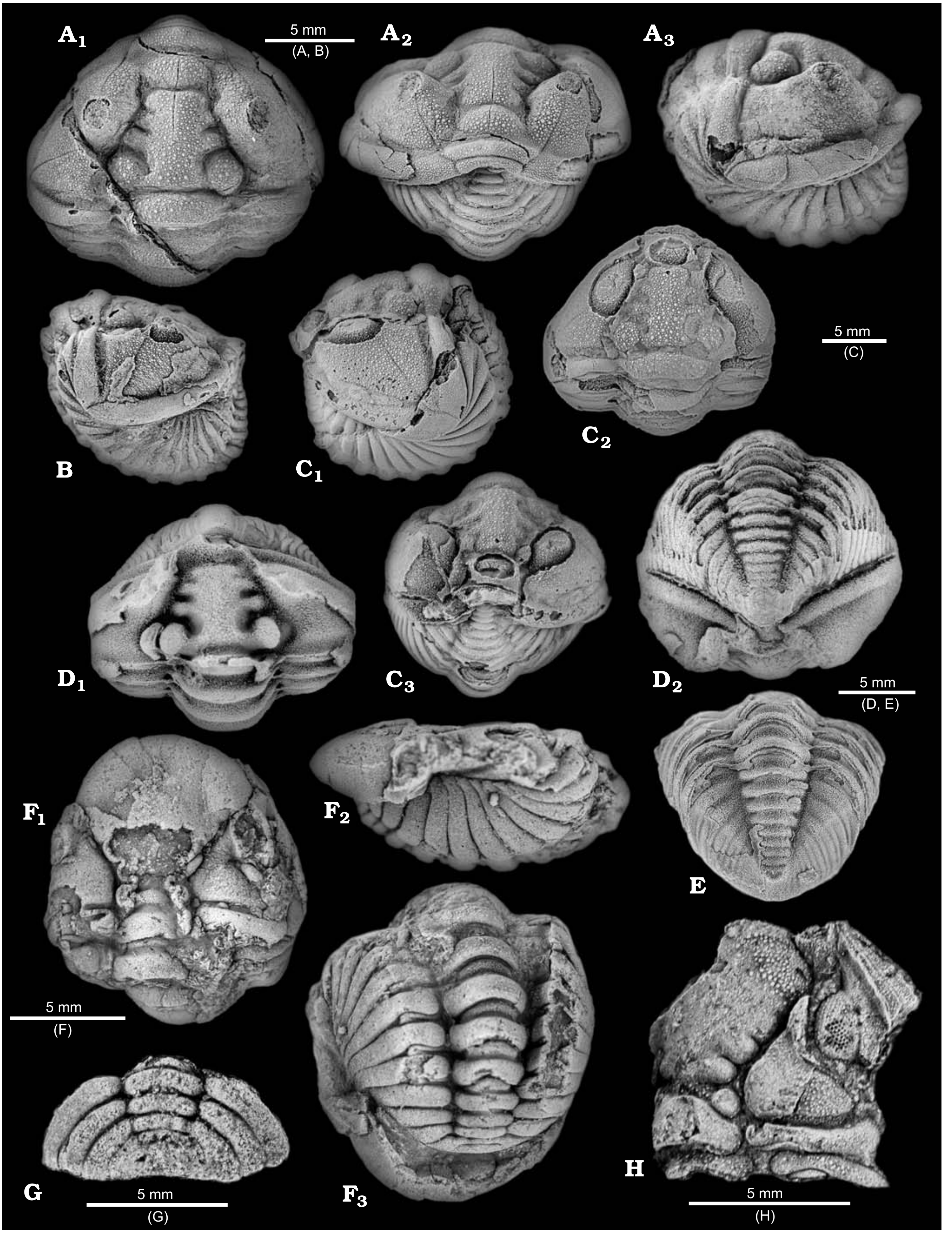
Discussion.—In the morphology of the pygidium, with pleural ribs strongly curved backwards abaxially and with three posterior ribs lacking free points, the specimens from the Shirgesht Formation resemble *Ovalocephalus obsoletus* (Zhou and Dean, 1986) from the Upper Ordovician Chedao Formation (lower Sandbian, *Nemagraptus gracilis* Biozone) of Gansu Province, north-west China, but they differ in having longer postocular fixigenae, a slightly more constrained posterior part of the glabella at L1 and L2, and a wider (sag.) posterior border.

Ovalocephalus aff. *obsoletus* also closely resembles *Ovalocephalus intermedius* (Lu and Zhou, 1979) from the lower Darriwilian of Inner Mongolia, north-west China in cranidial morphology, including an entire preoccipital furrow (S1), a relatively short (sag.) and narrow axial ring, and in the absence of S5. However, it differs in having shorter (tr.) S2–S4, in the position of the palpebral lobe posterior margin being slightly posterior to S2, and in finer granulose ornament. The taxonomic significance of these differences cannot be evaluated accurately, because the original description of *O. intermedius* is based on limited material and pygidial morphology remains unknown. In cranidial morphology, specimens of *Ovalocephalus* from Iran occupy an intermediate position between *O. intermedius* and *O. obsoletus*.

Ovalocephalus aff. *obsoletus* belongs to the "Species group 2 of *Ovalocephalus*" after Dean and Zhou (1988), in having the entire preoccipital ring (S1). Iranian specimens differ from *Ovalocephalus primitivus extraneus* (Lu and Zhou, 1979) from the Middle Ordovician of South China, in having a shorter (sag.) axial ring not exceeding 15% of glabellar length, more anterior position of the palpebral lobes with posterior ends situated about half distance between S1 and S2, and in the absence of S5. The pygidium of *Ovalocephalus* aff. *obsoletus* differs from most of the Upper Ordovician species of the genus, e.g., *Ovalocephalus yangtzeensis* (Lu, 1974) and *Ovalocephalus ovatus* (Sheng, 1964), in having pleural ribs bending strongly backwards. In width of the glabellar base (about 36% of cranidial width), *Ovalocephalus* aff. *obsoletus* occupies an intermediate position between *Ovalocephalus primitivus* (37–39%) and the Upper Ordovician species of the genus (34% and less), but it cannot be proved statistically significant from the available material (for details see also Yuan et al. 2003).

The pygidium of *Ovalocephalus* aff. *obsoletus* has some similarities to *Ovalocephalus plewesae* Fortey, 1997 from the Upper Ordovician Pa Kae Formation of southern Thailand, but it differs strongly in cranidial morphology, including a rounded, not pointed anterior margin of the glabella and obtuse genal angles of fixigenae lacking any trace of genal spines.

The only complete exoskeleton of *Ovalocephalus* aff. *obsoletus* has nine thoracic segments, whereas ten thoracic segments are typical for holaspides of *Ovalocephalus*. However, in length (about 2.5 mm), the specimen from Iran is


A1
5 mm
(A, B)
A2
A3
B
C1
C2
5 mm
(C)
D1
C3
D2
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(D, E)
E
F1
F2
5 mm
(F)
F3
G
5 mm
(G)
H
5 mm
(H)

comparable or slightly longer than complete exoskeletons of holaspides illustrated by Lu and Zhou (1979: pl. 2: 8, 11; pl. 4: 4). It is probable that the Iranian specimen represents a late meraspid, but in view of the significance of heterochrony in the evolution of *Ovalocephalus*, demonstrated convincingly by Yuan et al. (2003), a loss of thoracic segments in some species cannot be excluded.

Suborder Calymenina Swinnerton, 1915

Superfamily Calymenoidea Burmeister, 1843

Family Calymenidae Burmeister, 1843

Subfamily Reedocalymeninae Hupe, 1955

Genus *Neseuretinus* Dean, 1967

Type species: *Neseuretus* (*Neseuretinus*) *turcicus* Dean, 1967; Upper Ordovician, Sandbian, lower shale member of Bedian Formation, south-eastern Turkey.

Remarks.—In several publications an acute genal angle of fixigena in *Neseuretinus* was interpreted as bearing a short genal spine (Hammann and Leone 1997: text-fig. 28; Peng et al. 2000; Turvey 2005). However, this was based on imperfectly preserved cranidia without librigenae. The study of well preserved complete specimens of *Neseuretinus* from Iran shows convincingly that the species has evenly rounded lateral genal margins of the cephalon.

Neseuretinus birmanicus (Reed, 1906)

Fig. 2A–E.

1906 *Calymene birmanica* sp. nov.; Reed 1906: 71, pl. 5: 27.

1978 *Calymensun tingi* (Sun); Kolobova in Sokolov and Yolkin 1978: 133, pl. 26: 1–5.

2004 *Neseuretus ghavideli* sp. nov.; Bruton in Bruton et al. 2004: 140, pl. 10: 5–13.

2005 *Neseuretinus birmanicus* (Reed); Turvey 2005: 560, pl. 2: 1–9 (see Turvey 2005 for synonymy prior 2004).

Lectotype.—Cranidium (GSI 8341), selected by Turvey (2005: 560), Upper Ordovician, Sandbian (lower Caradoc), Naungkangyi Group, Kunkaw, northern Shan States, Myanmar (Burma).

Material.—Nine complete enrolled exoskeletons from sample F-35, including NMW 2004.22G.567, 568, 570, 571–573, 579–581; five variably preserved fragments of enrolled exoskeletons from sample F-35, including NMW 2004.22G.582–586; two thorax+pygidium, including NMW 2004.22G.574 from sample F-36 and 2004.22G.588 from sample F-35; one thorax from sample F-35, NMW 2004.22G.587; one pygidium from sample F-36, NMW 2004.22G.569; all from Units B5 and B6, Section B.

Description of Iranian specimens.—Cephalon with maximum length about 65–70% of maximum width at the level of L1. Glabella excluding the occipital ring truncated conical in outline, as long as wide with maximum width at mid point of L1, and about 70% as long as the cranidium. Anterior glabellar margin anteriorly slightly convex to almost transverse with curved margins, defined by a deep preglabellar furrow with a pair of distinct fossulae at abaxial terminations. Axial furrows deep, tapering anteriorly, becoming almost straight anterior of L1. L1 expanded laterally, almost hemispherical with evenly rounded outer margins. S1 deep, straight and slightly bent posteriorly anterior to L1, then strongly curved posteriorly adaxially. S2 and S3 deep, straight, slightly inclined posteriorly adaxially. Occipital ring about 25% of glabellar length and about 85% of maximum glabellar width, tapering near the outer margins. Occipital furrow deep, transverse medially, slightly curved posterior to L1. Preglabellar field strongly swollen medially, about 30–35% of cephalic length and about 65–75% as wide as the glabella. Anterior cranidial border pointed, subtriangular, arched in transverse profile. Anterior border furrow wide (sag.), well defined, shallow medially, slightly deepened abaxially. Rostral plate slightly narrower (tr.) than the anterior cranidial border. Postocular fixigenae subtriangluar, steeply sloping downward abaxially with acute genal angles. Palpebral lobes short, raised above the glabella, with a posterior margin situated opposite the mid point of L2 and the anterior margin situated slightly posterior to L3. Weakly defined, transverse eye ridge occasionally present. Posterior border furrow deep, transverse; posterior border convex, slightly widening (exsag.) abaxially. Librigenae sloping strongly abaxially with an evenly convex border widening posteriorly.

Thorax with strongly convex axis of about one third thoracic width and deep pleural furrows. It was described in detail by Bruton (Bruton et al. 2004).

Pygidium about 90% as long as wide. Axis strongly convex, subconical, about 90% as long as the pygidium and with width about half of maximum pygidial width. Axis with 8 axial rings and a small terminal piece with a rounded posterior margin. Axial furrows deep, converge posteriorly. Broadly arched postaxial ridge present between the terminal piece and posterior pygidial margin. Pleural field convex adaxially, steeply declined abaxially, with six pleural ribs; the most posterior rib weakly defined. First three pairs of pleural ribs slightly inclined posteriorly in proximity of the axial furrows, then strongly curved posteriorly with interpleural fur-

← Fig. 2. Phacopide trilobites from Middle Ordovician Shirgesht Formation of Iran. **A**–**E**. Reedocalymenid trilobite *Neseuretinus birmanicus* (Reed, 1906). **A**. NMW2004.22G.570, complete enrolled exoskeleton, sample F-35; A_1, dorsal view of the cephalon; A_2, anterior view of cephalon and pygidium; A_3, side view. **B**. NMW2004.22G.567, complete enrolled exoskeleton, sample F-35, side view. **C**. NMW2004.22G.568, complete enrolled exoskeleton, sample F-35; C_1, side view; C_2, dorsal view of cephalon; C_3, anterior view of cephalon and pygidium. **D**. NMW2004.22G.571, complete enrolled exoskeleton, sample F-35; D_1, dorsal view of cephalon; D_2, dorsal view of pygidium. **E**. NMW2004.22G.574, incomplete enrolled pygidium and part of thorax, sample F-35, dorsal view of pygidium. **F**–**H**. Pliomerid trilobite *Ovalocephalus* aff. *obsoletus* (Zhou and Dean, 1986) from sample F-36. **F**. NMW2004.22G.575, complete enrolled slightly crushed exoskeleton, sample F-36; F_1, dorsal view of cephalon and part of thorax; F_2, side view; F_3, dorsal view of pygidium and part of thorax. **G**. NMW2004.22G.577, dorsal view of pygidium. **H**. NMW2004.22G.576, dorsal view of incomplete cranidium.

rows originating at the bending point. Posterior pleural ribs strongly inclined posteriorly for entire length.

External surface of cephalon covered by coarse tubercles with fine granules in interspaces, surface of thorax and pygidium finely granulated.

Remarks.—Affinities of *Neseuretinus birmanicus* were discussed in detail by Turvey (2005). Study of the Iranian specimens reveals that they are identical in all characters to *Neseuretus ghavideli* Bruton (in Bruton et al. 2004), including the proportions of the cranidium, cephalon and pygidium; a long, swollen preglabellar field defined by the anterior border furrow; asymmetrically arranged tubercles and granules on the external surface; a subconical pygidial axis with up to 8 axial rings plus terminal piece and 6 pleural ribs reaching the posterior margin. This synonymous affinity was also pointed out by Turvey (2005) and Tuvrey and Siveter (2007).

Specimens of *Calymene* aff. *birmanica* from the Upper Ordovician of the Panj river basin, Pamirs, as described and illustrated by Weber (1948: pl. 10: 26–28) are probably conspecific with *Vietnamia pamirica* (Balashova, 1966) are not related to *N. birmanicus*.

Some minor differences in proportions as recorded in the description of the Iranian specimens by comparison with previously described specimens from Burma and Uzbekistan are mainly due to imperfect preservation of previously described disarticulated pygidia and cranidia, often distorted and strongly flattened.

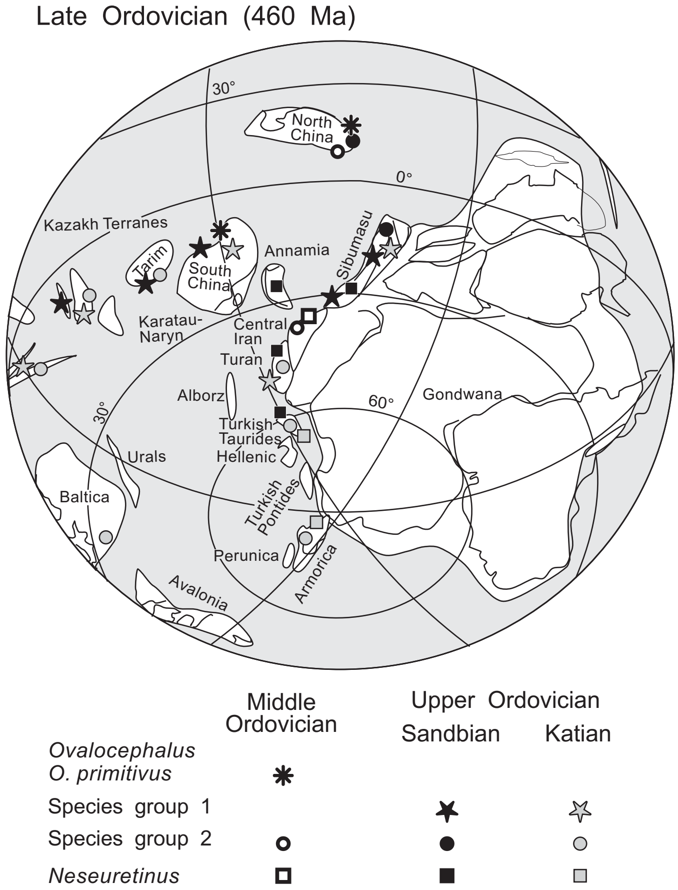

Fig. 3. Palaeogeographical reconstruction for the Middle Ordovician showing geographical distribution of biogeographically informative trilobite genera and species that occur in the upper Shirgesht Formation.

Age and biogeographical affinities of the fauna

According to Turvey (2005), *N. birmanicus* (Reed, 1906) is a senior synonym of *Neseuretus* (*Neseuretinus*) *turcicus* Dean, 1967 and this view is accepted here. Turvey also gave an account of the geographical distribution of the species, which is confined mostly to high and medium latitude peri-Gondwana, including Annamia, Sibumasu, Afghanistan, the Zerafshan Range in Uzbekistan (which was situated on the margin of the Turan microcontinent (Biske 1996)), Turkish Taurides and Armorica (Sardinia) (Fig. 3). With the exception of the Portixeddu and Tuviois formations of Sardinia, which are considered as lower Ashgill (Hammann and Leone 1997), all listed localities are usually dated as Caradoc (Upper Ordovician, probably, Sandbian). At the same time, the occurrence of *N. birmanicus* in South China was not confirmed in the revision of existing records (Turvey 2005: 564). There is also no record of the occurrence of *Neseuretinus* in Tarim, and Reedocalymeninae are remarkably absent in Kazakhstanian terranes, which were mostly located in low latitudes through the Middle and Late Ordovician (Fortey and Cocks 2003).

By contrast, during the Middle Ordovician *Ovalocephalus* was endemic to South China, North China and Tarim (Lu 1975; Lu and Zhou 1979; Zhou and Dean 1986), and only spread towards terranes of Kazakhstan and Central Asia (Koroleva 1959; Abdullaev 1972; Apollonov 1974) during the Late Ordovician, and then to Armorica (Hammann 1992) and Baltica (Kielan 1960). Remarkably, *Ovalocephalus* almost became a lazarus taxon in the late Darriwilian, prior to its geographical expansion. *Ovalocephalus* aff. *obsoletus* from the upper Shirgesht Formation probably fills this gap. The upper Darriwilian age of the locality was suggested earlier from the ostracod studies (Ghobadi Pour et al. 2006), whereas the occurrence of *N. birmanicus* supports a latest Middle Ordovician or younger age (for details see Turvey 2005). Iranian specimens show distinct similarity to *Ovalocephalus intermedius* (Lu and Zhou, 1979) from the lower Darriwilian of Inner Mongolia and to *Ovalocephalus primitivus extraneus* (Lu and Zhou, 1979), and can therefore be referred to the "Species group 2 of *Ovalocephalus*" after Dean and Zhou (1988), together with *Ovalocephalus globosus* (Abdullaev, 1972) from the Late Ordovician (probably early Katian) of the central Karakum desert (Turan Plate after Biske 1996); *Ovalocephalus kanlingensis* Zhang, 1981 from the Upper Ordovician of Tarim, North China (Zhou and Dean 1986, see also discussion on probable synonymy), Alai Range (Petrunina in Repina et al. 1975) and north-eastern Central Kazakhstan (Apollonov 1974); *Ovalocephalus plewesae* Fortey, 1997 from the Upper Ordovician, Sandbian of southern Tailand

Table 1. Measurements and basic statistics for cephala and pygidia of *Neseuretinus birmanicus* (Reed, 1906) from the sample F-35. Abbreviations: Cl, Cw, length and width of cephalon; Gl, Gw, length and width of the glabella; PGl, PGw, length and width of preglabellar field; ORl, ORw, length (sag.) and width of occipital ring; Pl, Pw, length and width of pygidium; Al, Aw, length and width of pygidial axis; X, average; S, standard deviation; N, number of measured specimens.

Cephala	Cel	Cew	Cel/w	Gl	Gw	Gl/w	Gl/Cl	Gw/Cw
2004.22G.568	12.2	17.3	70.5%	8.5	8.2	104%	70%	47%
2004.22G.569	13.7	19.4	71%	8.8	8.8	100%	64%	45%
2004.22G.567	12.5	16.5	76%	8.7	7.6	114.5%	70%	46%
2004.22G.570	11.2	16.7	67%	7.8	7.9	99%	70%	47%
2004.22G.571	9.8	17.2	57%	7.2	8.0	90%	73.5%	48%
2004.22G.572	11.4	17.0	67%	8	7.7	104%	70%	45%
N	6	6	6	6	6	6	6	6
X	11.8	17.35	68%	8.2	8.0	1.02	69%	46%
S	1.33	1.05	6.3	0.615	0.43	0.08	3	9.2

Pygidia	PGl	PGw	ORl	ORw	Orl/Gl	Pl	Pw	Al	Aw
2004.22G.568	3.4	3.8	2.2	6.5	26%				
2004.22G.569	4.6	5.8	2.0	6.9	23%	7.8	10.0	7.3	7.2
2004.22G.567	4.0	5.6	2.0	6.8	23%				
2004.22G.570	3.8	5.7	1.8	6.7	23%				
2004.22G.571			1.6	6.6		8.5	8.3	7.5	4.8
2004.22G.572			2.0	6.8					
2004.22G.573						8.5	9.4	7.5	4.8
N	4	4	6	6	6				
X	3.95	5.23	1.9	6.7	24%				
S	0.50	0.95	0.21	0.15	1.4				

(Sibumasu), and *Ovalocephalus tetrasulcatus* (Kielan, 1960), which was widespread in Baltica, Armorica (Spain) and Turkish Taurides (Hammann 1992; Dean and Zhou 1988). The occurrence of *Ovalocephalus* aff. *obsoletus* in Central Iran also represents the earliest sign of migration of *Ovalocephalus* outside South China and Tarim, and precedes subsequent westward migration of the lineage towards the Turkish Taurides and Armorica.

In the Late Ordovician there was considerable biogeographical differentiation in the distribution of *Ovalocephalus* as already recognised by Lu and Zhou (1979), and Zhou and Dean (1986). The biogeographical area of "Species group 2 of *Ovalocephalus*" closely followed the West Gondwanan margin, whereas "Species group 1", typified by such species as *Ovalocephalus kelleri* Koroleva, 1959, *O. ovatus* (Sheng, 1964) and *O. yangtzeensis* (Lu, 1974), was confined to north-eastern Central Kazakhstan, Tarim, South China, and Sibumasu, mainly in low southern latitudes (Fig. 3). In Kazakhstanian terranes, North China, Sibumasu and Central Asia (Alai and Turan microplates) species belonging to two groups co-occur. It is probable that differentiation of *Ovalocephalus* was climatically controlled.

The co-occurrence of *Ovalocephalus* and *Neseuretinus* in the Naungkangyi Group of northern Shan States requires special attention. As pointed out by Fortey (in Fortey and Cocks 1998), some specimens illustrated by Reed (1915: pl. 8: 8–10) as *Calymene lilluensis* Reed, 1915 and *Pliomera* (*Encrinurella*) *lingshangensis* Reed, 1906, must be reassigned to *Ovalocephalus*. The morphology of the illustrated cranidium shows distinct similarity to *Ovalocephalus yangtzeensis* in general outline of the glabella, characters of glabellar furrows (excluding S4 which was not shown on the figure) and small preoccipital lobes. Two pygidial internal moulds illustrated by Reed (1915) are strongly transverse, have a subtrapezoidal outline with slightly concave posterior margin and transverse pleural ribs only slightly inclined backwards, which also suggests affinity to *O. yangtzeensis*. Precise taxonomic attribution of the specimens from the Naungkangyi Group is impossible without direct observation, because of insufficient description and illustrations, but there is little doubt that they lack a complete preoccipital ring and must therefore be assigned to the "Species group 1" after Dean and Zhou (1988).

It is probable that the appearance of *Ovalocephalus* in the late Darriwilian of Central Iran and somewhat later appearance of the genus in the early Sandbian of Sibumasu may represent a sign of a warm water faunal invasion towards temperate latitudes, which related to global warming following an episode of cooler climate in the early to mid Darriwilian. The lower Darriwilian deposits in the Shirgesht section are barren. However, the upper Darriwilian part of the Shirgesht Formation can be correlated with the uppermost part (*Lenodus pseudoplanus* Conodont Subzone and higher) of the Lashkarak Formation in Simeh-Kuh, Eastern Alborz Mountains (Ghobadi Pour et al. 2007). The lower Darriwilian of Simeh-Kuh coincides with invasion of the *Neseuretus* biofacies, which was a sign of a cooler climate, and a period of a sea-level low-stand followed by a sea-level rise and invasion of a new, diverse benthic fauna (Ghobadi Pour et al. 2007; Ghobadi Pour 2008). Both in Central Iran and the Eastern Alborz the late Darriwilian faunal assemblages contain abundant plectambonitoidean and strophomenoidean brachiopods not characteristic of earlier faunas. In the Simeh-Kuh section the brachiopods include *Ishimia* (Ghobadi Pour 2008: fig. 3A, B), which is otherwise characteristic of the low latitude faunas of "East" Gondwana (Australia, Sibumasu, Tibet) (for detailed review see Cocks and Zhan 1998; Percival et al. 2001). Another new element typical elsewhere for the Middle Ordovician low latitude "East" Gondwanan faunas is the trilobite *Birmanites*, which occurs both in the upper Darriwilian part of the Lashkarak and Shirgesht formations (Ghobadi Pour 2008: fig. 3E, F). Diachronous biogeographical expansion of *Birmanites* towards "West" peri-Gondwana and Baltica during the Late Ordovician (Zhou and Dean 1986; Romano and Owen 1993; Fortey and Cocks 2003) mirrors that of *Ovalocephalus*.

Characters of sea level fluctuations during the Darriwilian documented for the Iranian sequence (Ghobadi Pour et al. 2007; Ghobadi Pour 2008) correspond closely with those of Baltica, where a regressive episode is documented for the lower to middle Darriwilian (Kundian Regional Stage), whilst the uppermost Darriwilian (Uhaku Regional Stage) represents a sea level high-stand (Nielsen 2004). According to Meidla et al. (2004) and Kaljo et al. (2007) a period of low-stand in the Kundian–Aserian coincides with low magnitude (1–3‰) positive stable carbon and oxygen isotope excursions suggesting a cooling event in Baltica.

The observed biogeographical patterns of distribution of *Ovalocephalus* and *Neseuretinus* suggest that Central Iran, together with Sibumasu and the Turkish Taurides, was part of an "overlap zone" (see also Fortey and Cocks 2003), where tropical and high latitude benthic taxa mingled, and which can be considered in the Ordovician as major gateways for latitudinal faunal migrations and exchange along the Gondwanan margin.

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