

The latest Devonian (Famennian) phacopid trilobite *Omegops* from eastern Alborz, Iran

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Abstract. The Late Devonian (late Famennian) phacopid trilobites represented by *Omegops tilabadensis* sp. nov. are described and illustrated from the Khoshyeilaq Formation, eastern Alborz Mountains, North Iran. The species formed a monotaxic trilobite association inhabiting a shallow shelf together with diverse brachiopod communities dominated by the athyridides and spiriferides. Constant differences in pygidial morphology between the geographically separated *Omegops* species from the Middle East, Northwest China (Junggar) and West Europe plus the North African sector of Gondwana may suggest the existence of two geographically isolated *Omegops* lineages which diverged in pre-Strunian time. The occurrence of conodonts not older than the *Bispathodus costatus* Zone and the brachiopod *Rhipidomella michelini* gives a sufficient proof of the Strunian to early Tournaisian age of the uppermost part of the Khoshyeilaq Formation.

Key words: Devonian, Trilobita, Phacopida, Iran, Khoshyeilaq Formation.

INTRODUCTION

Iranian Late Devonian trilobites are presently best documented from Central Iran. They were described by Morzadec (2002) and Ghobadi Pour et al. (2013), who studied the taxa of the subfamily Asteropyginae, and Feist et al. (2003), who described several phacopide and proetide species from the Famennian of the Shotori Range. There is also a brief report on the occurrence of *Omegops cornelius* (Richter & Richter, 1933) in the uppermost Famennian of the Chahriseh section, south of Esfahan by Mistiaen et al. (2000). The only taxon properly documented from the Devonian of northern Iran is *Heliopyge sharudensis* (Pillet in Brice et al., 1974) from the Khoshyeilaq Formation (Givetian) of the eastern Alborz Mountains.

In their comprehensive revision of the Devonian stratigraphy of Iran Wendt et al. (2005, table 5) listed nine trilobite taxa including information on their occurrences. Remarkably, the Givetian fauna is dominated by the subfamily Asteropyginae, while the late Famennian trilobites are represented exclusively by the species of *Omegops*, which occur in the uppermost part of the Khoshyeilaq Formation. The list of the late Famennian trilobites given by Wendt et al. (2005, table 5) includes

Omegops cornelius (Richter & Richter, 1933), *Omegops accipitrinus accipitrinus* (Phillips, 1841) and *Omegops accipitrinus maretolensis* (Richter & Richter, 1933) from the uppermost Famennian (Strunian) of the Mighan section in the eastern Alborz Mountains; and *Omegops accipitrinus accipitrinus* and *Omegops paiensis* Farsan, 1998 from the Mazraeh-e-Kheradmand section of the northern slope of Kuh-e-Dosar, ca 60 km south of Yazd in Central Iran. None of these trilobites was properly described or illustrated except a single pygidium which was illustrated from the Mazraeh-e-Kheradmand section and assigned to *Omegops accipitrinus accipitrinus*; however, this identification looks problematic.

The phacopide trilobites are relatively common in the Sarcheshmeh Member (the uppermost Devonian unit of the Khoshyeilaq Formation) exposed in the eastern Alborz Mountains along the road connecting Shahrud and Azadshahr. They are represented, as noted above, by a single species. This fauna is the major objective of the present study.

The illustrated trilobite and brachiopod specimens were photographed using a digital camera Nikon D300S mounted on a Leitz Aristophot photomicrography stand. Prior to the photography, specimens were lightly coated with ammonium chloride. The conodonts (after coating

with gold palladium) were studied and photographed under a JEOL JCM-5000 Neoscope scanning electron microscope installed in the Department of Natural Sciences, National Museum of Wales, Cardiff.

GEOLOGICAL AND GEOGRAPHICAL SETTING

The sampled Upper Devonian to lower Carboniferous succession, here referred to as the Ghoznavi section (Figs 1, 2), is a natural outcrop located in the eastern Alborz Mountains northeast of Shahrud, on the west side of the road connecting Shahrud and Azadshahr, between the Ghoznavi Bridge and the Tilabad village. The Devonian to lowermost Carboniferous deposits in the area are assigned to the Khoshyeilaq Formation. The type section of this lithostratigraphical unit, formally

introduced by Bozorgnia (1973), is situated just 12 km southwest of the Ghoznavi section, north of the Khoshyeilaq village (Fig. 1). The most recent detailed account of the Devonian litho- and biostratigraphy of the area was given by Wendt et al. (2005) who provided also an extensive list of the late Famennian (Strunian) brachiopods from the Khoshyeilaq (informal units 41–43) and Mighan sections, while the Late Devonian bryozoans from Khoshyeilaq were described and illustrated by Tolokonnikova et al. (2011). The individual lithostratigraphical units introduced by Wendt et al. (2005) for the upper part of the Khoshyeilaq Formation in the type section are easily recognizable in the Ghoznavi section. The most detailed information on the conodont occurrences in the Khoshyeilaq section was presented by Ashouri (2006), who also proved the Carboniferous (Tournaisian) age of the uppermost part of the formation.

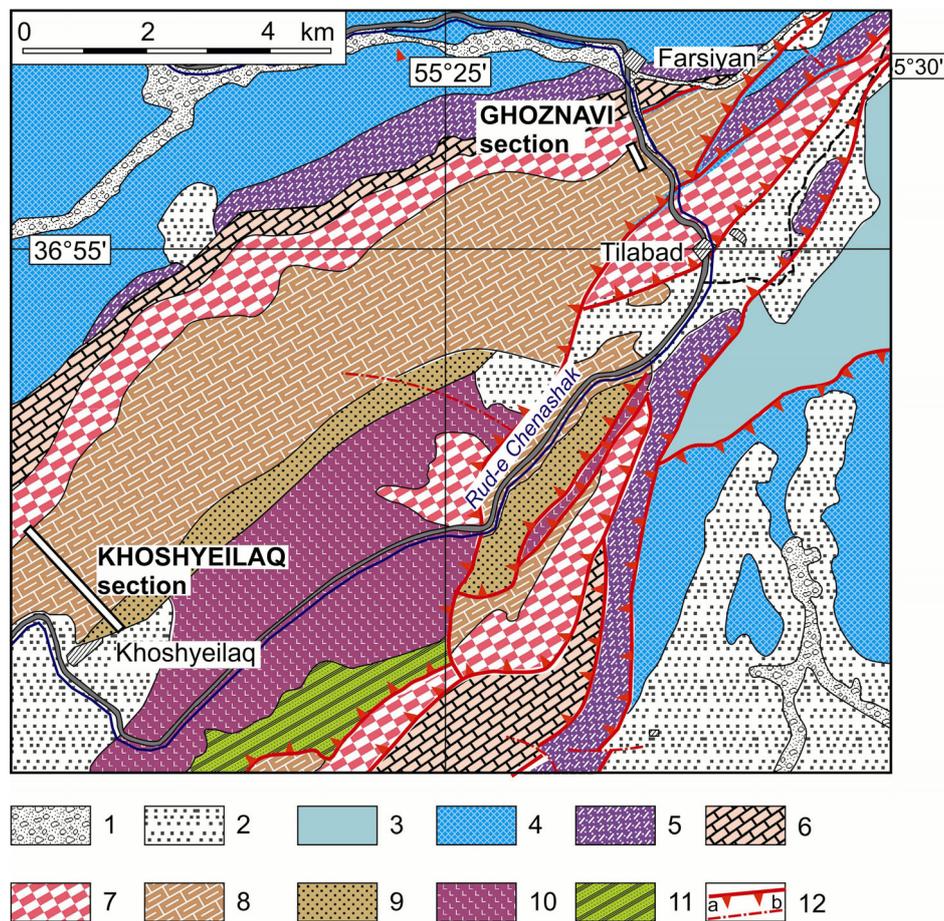


Fig. 1. Simplified geological map of the Khoshyeilaq area showing locations of the Ghoznavi and Khoshyeilaq sections (modified after Shahrabi 1990). 1, Late Quaternary alluvial deposits; 2, Quaternary, undifferentiated; 3, Cretaceous, undifferentiated; 4, Jurassic (Lar and Shemshak formations); 5, Triassic (Elika Formation); 6, Permian (Emarat and Ghoznavi formations); 7, Carboniferous (Toyeh Formation, Mobarak Group); 8, Middle Devonian, Givetian–Carboniferous, Tournaisian (Khoshyeilaq Formation, including the Sarcheshmeh, Shahvar and Tilabad members); 9, Middle Devonian, Emsian?–Eifelian (Mighan Member); 10, Silurian (Soltan Meidan Formation); 11, Upper Ordovician (Abarsaj Formation); 12, thrust faults (a) and faults (b).

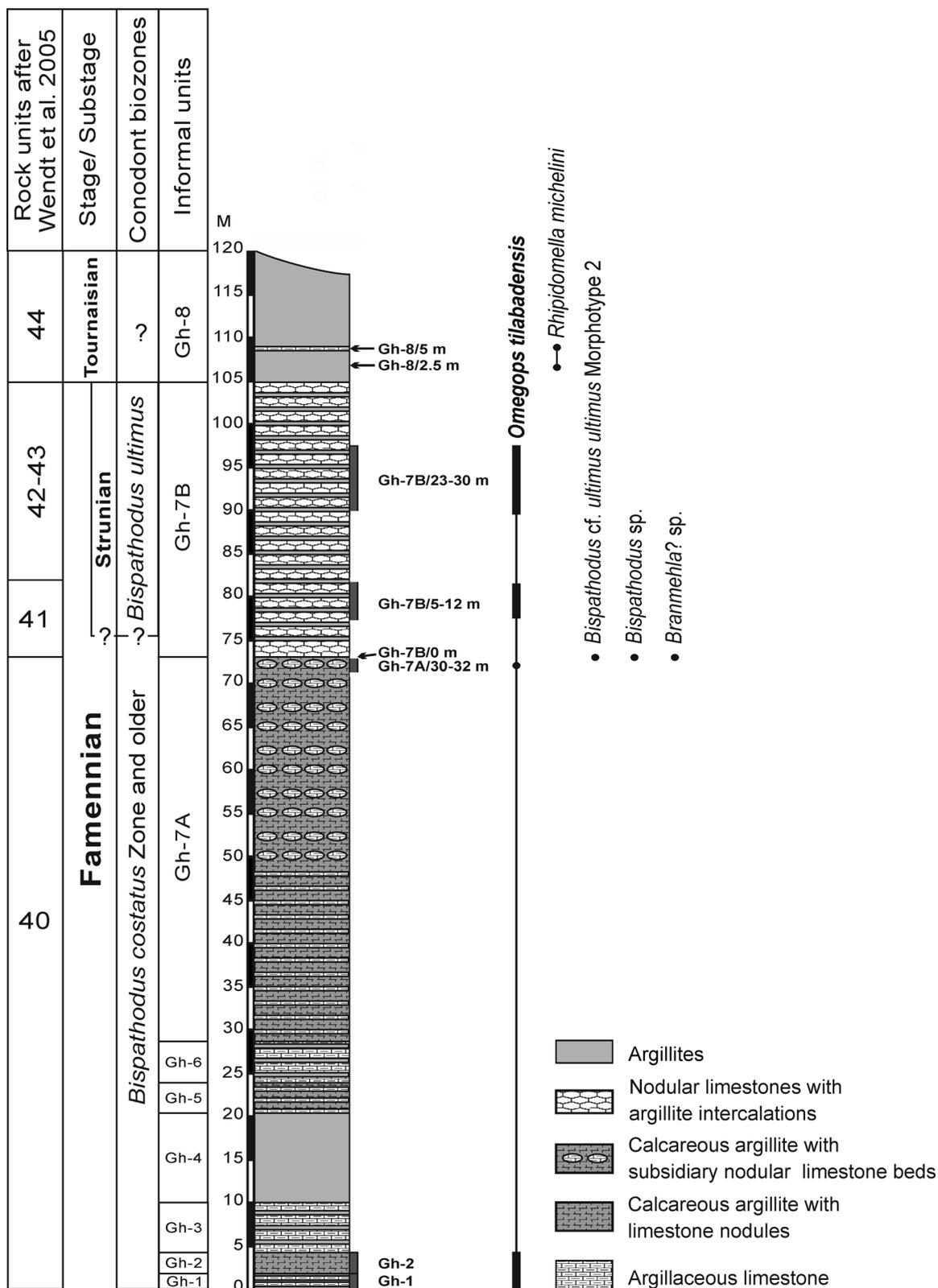


Fig. 2. Stratigraphical column of the Ghoznavi section, Upper Devonian–Lower Carboniferous Khoshyeiaq Formation, Sarcheshmeh Member, showing the horizons of fossil localities and stratigraphical ranges of trilobite, brachiopod and conodont species.

Alavi-Naini (2000) subdivided the Devonian succession in Khoshyeilaq into four formal members: (1) the Mighan Member, starting with polymict conglomerates succeeded by the heterolithic succession of red and white sandstones, siltstones and argillites, sometimes erroneously assigned to the Padeha Formation; (2) the Tilabad Member, comprising mainly limestones; (3) the Shahvar Member, containing siliciclastic rocks; (4) the Sarcheshmeh Member, including bioclastic and nodular limestones, and shales (units 31–44 of Wendt et al. 2005). Wendt et al. (2005) suggested that the base of the Khoshyeilaq Formation should be placed at the base of their Unit 16, which coincides with the onset of a fully marine sedimentation and probably with the base of the Tilabad Member of Alavi-Naini (2000). The estimated thickness of the Khoshyeilaq Formation in the type section is 925 m (Wendt et al. 2005). The Frasnian–Famennian boundary was provisionally placed by Wendt et al. (2005) in the lower part of the Sarcheshmeh Member (at the top of the informal unit 33), above the last occurrence of tentaculitids.

The base of the measured profile of the Ghoznavi section has geographical coordinates 36°55'24.6" N and 55°27'22.8" E. The observed succession in ascending order looks as follows (Fig. 2):

Unit Gh-1 – 2.0 m of dark grey, bedded argillaceous limestone with uneven bedding surfaces and numerous argillite intercalations 0.15–0.35 m thick. The unit contains abundant brachiopods, which often occur as articulated shells, and subsidiary trilobites (sample Gh-1).

Unit Gh-2 – 2.7 m of dark grey calcareous argillite with limestone nodules. The unit is rich in complete brachiopod shells and a few trilobites (sample Gh-2).

Unit Gh-3 – 6.2 m of dark grey limestone intercalating with calcareous argillites which occur in

proportion 50–50%. The thickness of individual layers varies from 0.1 to 0.3 m.

Unit Gh-4 – 1.4 m of dark grey argillites.

Unit Gh-5 – 3.5 m of dark grey argillites (individual beds up to 0.6 m thick) with subsidiary beds of limestone up to 0.35 m thick. The number of limestone beds increases significantly in the upper part of the unit.

Unit Gh-6 – 2.5 m of bedded limestone intercalating with argillites. Individual beds of limestone 0.25–0.35 m thick are separated by beds of argillite 0.10–0.25 m thick.

Unit Gh-7A – 42.4 m of calcareous argillite with subsidiary limestone beds. The lower 10.4 m with limestone beds up to 0.35 m thick is separated by beds of argillite up to 0.60 m thick. The upper 32 m comprises mainly calcareous argillite with subsidiary nodular limestone beds. The upper 16 m of the unit is rich in brachiopods and also contains a few trilobites (Fig 2; sample Gh-7A/30–32 m).

Unit Gh-7B – 33.5 m of dark grey nodular limestones with argillite intercalations. The unit contains abundant brachiopods, conodonts (Fig. 2, sample Gh-7B/0 m) and occasional trilobites (Fig. 2; samples Gh-7B/5–12 m and Gh-7B/23–30 m).

Unit Gh-8 – Dark grey argillites with a shell bed at 5 m above the base of the unit (sample Gh-8/5 m) containing the brachiopod *Rhipidomella michelini* (Léveillé, 1835) suggesting a Carboniferous (Tournaisian) age.

Units Gh-1 to Gh-7A of the measured succession correspond to Unit 40 of Wendt et al. (2005, fig. 10) in the Khoshyeilaq section, while Unit Gh-7B is probably stratigraphically equivalent to units 41–43 of Wendt et al. (2005). The only productive conodont sample Gh-7B/0 m, taken from the base of Unit Gh-7B, contains *Bispathodus* cf. *ultimus ultimus* (Bischoff, 1957) (Figs 2, 3D), *Bispathodus* sp. (Figs 2, 3E) and *Branmehla?* sp.

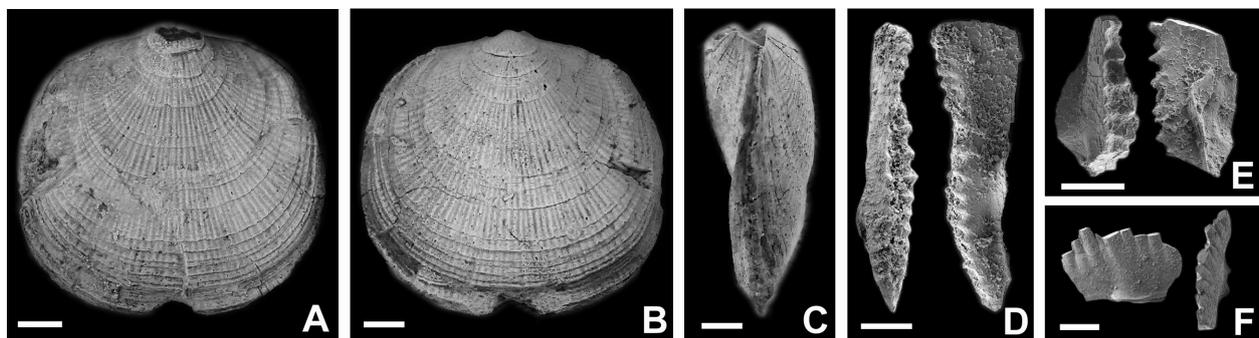


Fig. 3. Upper Devonian, Famennian, Khoshyeilaq Formation, Ghoznavi section, Eastern Alborz, NE Iran; **A–C**, *Rhipidomella michelini* (Léveillé, 1835), GUGM 1351, articulated shell, ventral, dorsal and side views, sample Gh-8/2.5 m; **D**, *Bispathodus* cf. *ultimus ultimus* (Bischoff, 1957), GUGM 1370, upper and side views, sample Gh-7B/0 m; **E**, *Bispathodus* sp., GUGM 1371, upper and side views, sample Gh-7B/0 m; **F**, *Branmehla?* sp., GUGM 1372, side and upper views, sample Gh-7B/0 m. Scale bars for A–C are 2 mm and for D–F 0.2 mm.

(Figs 2, 3F). *Bispathodus* cf. *ultimus ultimus* is represented by its early variant (Morphotype 2 of Ziegler & Sandberg 1984), which is probably an intermediate form between *Bispathodus costatus* (Branson, 1934) and *Bispathodus ultimus ultimus*, while *Bispathodus* sp. is represented by a fragment of an advanced bispathodid species, suggesting that the sampled horizon is not older than the *Bispathodus aculeatus* Zone. *Branmehla?* sp. has a relatively narrow stratigraphical range corresponding to the uppermost part of the Famennian to the lower Tournaisian. Thus, the conodont assemblage is indicative of an upper Famennian age, not older than the uppermost *Bispathodus costatus* Zone. These data are also in a good agreement with the provisional correlation of the uppermost part of the Sarcheshmeh Member (units 41–43) with the Strunian age suggested by Wendt et al. (2005).

The Devonian–Carboniferous boundary can be placed provisionally at the base of Unit Gh-8, at the top of the uppermost limestone beds. The only fossil in the lower part of the unit, which is a stratigraphical equivalent of Wendt et al. (2005) Unit 44 in the Khoshyeilq section, is the brachiopod *Rhipidomella michelini* (Léveillé, 1835) (Figs 2, 3A–C). It appears at 2.5 m above the base of Unit Gh-8 and forms a distinctive shell bed at 5 m above the base of the same unit (Fig. 2). This distinctive shell bed is apparently traceable also in the Khoshyeilq section (Wendt et al. 2005, fig. 10).

SYSTEMATIC PALAEOLOGY

The studied specimens are deposited in the Department of Geology, Golestan University (GUGM abbreviation for the Golestan University, Geology Museum) and in the British Geological Survey (BGS GSM). The terminology and systematic classification follow that of the new edition of the *Treatise on Invertebrate Paleontology* (Whittington & Kelly in Kaesler 1997).

Order PHACOPIDA Salter, 1864

Superfamily PHACOPOIDEA Hawle & Corda, 1847

Family PHACOPIDAE Hawle & Corda, 1847

Subfamily PHACOPINAE Hawle & Corda, 1847

Genus *Omegops* Struve, 1976

Type species. *Calymene accipitrina* Phillips, 1841, Upper Devonian Pilton Beds, England.

Species assigned. In addition to the taxa assigned to the genus in the original publication by Struve (1976, p. 435), it includes: (1) *Omegops tilabadensis* sp. nov., Khoshyeilq Formation (Upper Devonian, Famennian) of the eastern Alborz Mountains, Iran; (2) *Phacops* (*Omegops*) *paiensis* Farsan, 1998, late Famennian (Strunian) of Herat Province, Afghanistan; (3) *Phacops* (*Omegops*) cf. *cornelius* (Richter & Richter, 1933), Shishtu Formation (upper Famennian) of the Shotori Range, Iran; (4) *Phacops* (*Omegops*) sp., Yonghsien Formation (Upper Devonian, lower *Siphonodella praesulcata* Zone), Guilin, Guangxi, South China.

Omegops tilabadensis sp. nov.

Figures 4–6

?1998 *Phacops* (*Omegops*) *accipitrinus accipitrinus* (Phillips, 1841); Farsan, p. 25, figs 4, 8b; pl. 2, figs 1, 2.

?1998 *Phacops* (*Omegops*) *accipitrinus maretiolensis* Richter & Richter, 1933; Farsan, p. 26, figs 5, 8c; pl. 2, figs 3–5; pl. 3, fig. 4.

Derivation of name. After Tilabad village near the type locality.

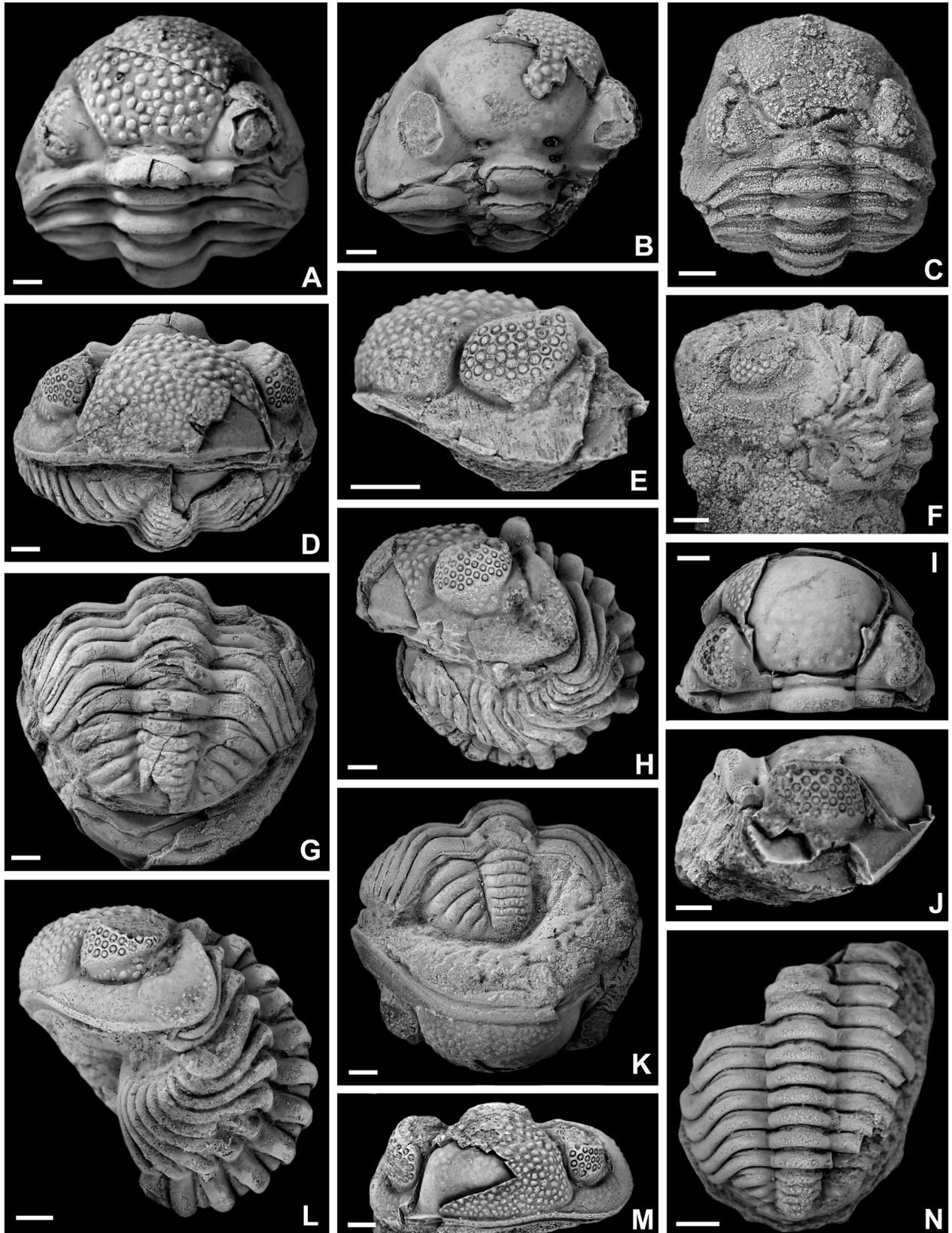
Holotype. GUGM 1359 (Fig. 4A, D, G, H), enrolled exoskeleton from sample Gh-1–Gh-2 (loose sample); Upper Devonian, Famennian, Khoshyeilq Formation, Ghoznavi Section, Eastern Alborz, Iran.

Paratypes. Two enrolled exoskeletons (GUGM 1359, 1362), two cephalothoraxes (GUGM 1360, 1367), two cephalata (including GUGM 1364), three incomplete cephalata, three pygidia, and one thoracopygon (GUGM 1366); one cephalon (GUGM 1362), and one thoracopygon (GUGM 1365) from sample Gh-2.

Other material. One incomplete cephalon from sample Gh-7A/30–32 m; one enrolled exoskeleton (GUGM 1361) from sample Gh-7B/5–12 m and one pygidium (GUGM 1369) from sample Gh-7B/23–30 m.

Diagnosis. Species of *Omegops* with a broadly and evenly rounded anterior margin of the glabella. Glabellar axial furrows almost straight, posteriorly and medially divergent at 40–45°. Eyes moderately high with up to 48

Fig. 4. *Omegops tilabadensis* sp. nov., Upper Devonian, Famennian, Khoshyeilq Formation, Ghoznavi section, Eastern Alborz, NE Iran; **A, D, G, H**, GUGM 1359, holotype, enrolled exoskeleton, sample Gh-1–Gh-2 (loose sample); **A, D**, dorsal and anterior views of cephalon; **G**, dorsal view of pygidium and attached thorax; **H**, side view; **B**, GUGM 1360, cephalothorax, dorsal view, sample Gh-1–Gh-2 (loose sample); **C, F**, GUGM 1361, cephalothorax, dorsal and side views, sample Gh-7B/5–12 m; **E**, GUGM 1364, cephalon, side view, sample Gh-1–Gh-2 (loose sample); **I, J**, GUGM 1363, cephalon, dorsal and side views, sample Gh-2; **K–M**, GUGM 1362, enrolled exoskeletons; **K**, dorsal view of pygidium; **L**, side view; **M**, anterior view of cephalon, sample Gh-1–Gh-2 (loose sample); **N**, GUGM 1365, thoracopygon, dorsal view, sample Gh-2. All scale bars are 2 mm.



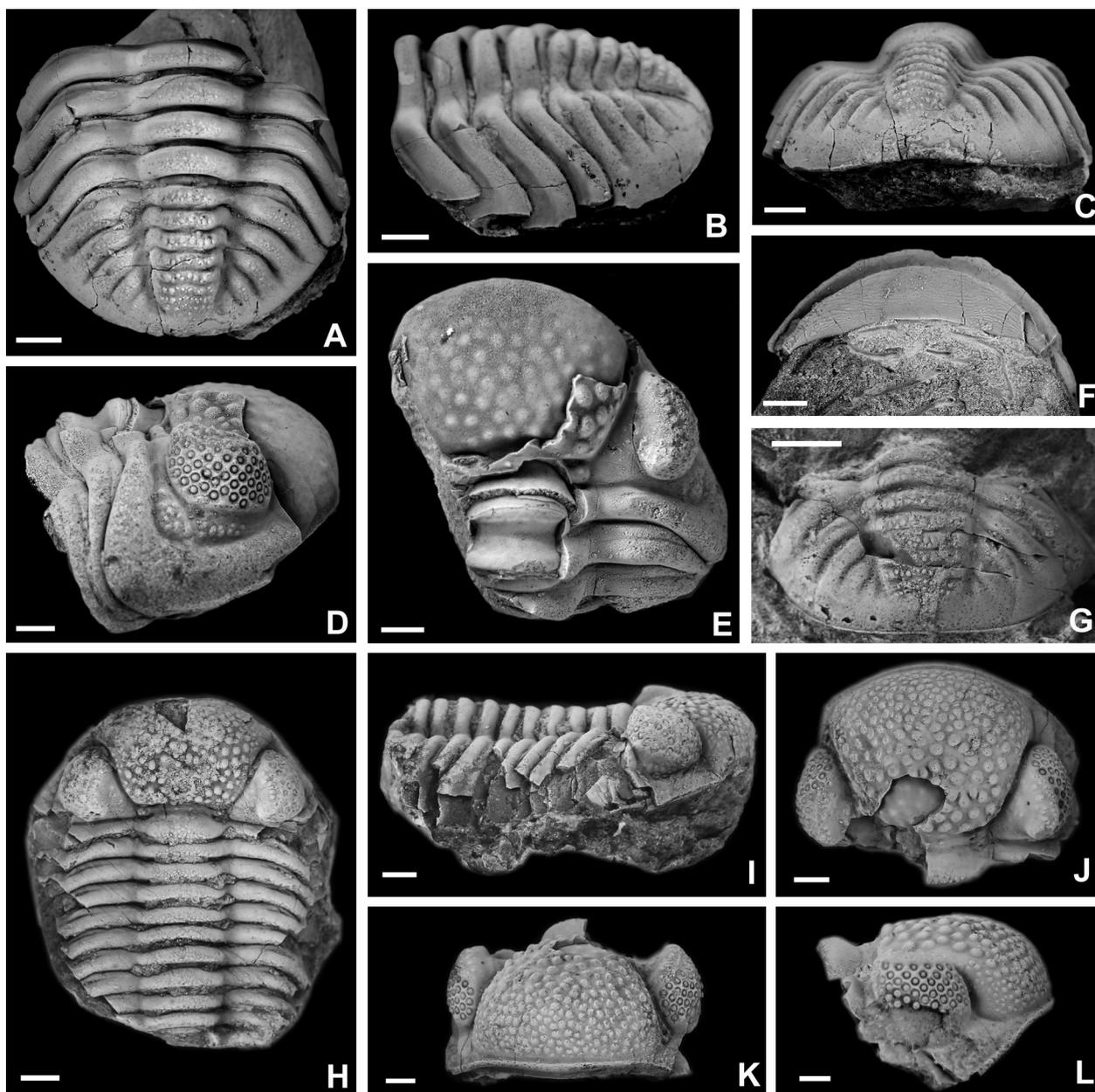


Fig. 5. *Omegops tilabadensis* sp. nov., Upper Devonian, Famennian, Khoshyeilaq Formation, Ghoznavi Section, Eastern Alborz, NE Iran; **A–C**, GUGM 1366, thoracopygon, dorsal and side views, sample Gh-1–Gh-2 (loose sample); **D, E**, GUGM 1367, incomplete cephalothorax, side and dorsal views, sample Gh-1–Gh-2 (loose sample); **F**, GUGM 1368, vincular furrow and post-vincular doublure, ventral view, sample Gh-1–Gh-2 (loose sample); **G**, GUGM 1369, pygidium, dorsal view, sample Gh-7B/23–30 m; **H, I**, GUGM 1349, cephalothorax, dorsal and side views, sample Gh-1–Gh-2 (loose sample); **J–L**, GUGM 1350, cephalon, dorsal, anterior and side views, sample Gh-7B/0–20 m. All scale bars are 2 mm.

large lenses arranged in up to seven horizontal rows and with up to four lenses in the vertical files. Postocular area of fixigena with up to eight coarse tubercles confined to the postocular pad. Pygidium with five pleural ribs. Pygidial axis up to 90% of pygidial length, very gently constrained posteriorly, with eight axial rings plus a very short terminal piece.

Description. Cephalon transverse, semicircular, almost 60% as long as wide. Glabella about 80% as long as wide and 60% as wide as the cephalon, extending to the cephalic border, densely covered with irregularly arranged coarse tubercles gradually decreasing in size anterior to palpebral lobes; lateral sides of glabella accentuated by a single row of small tubercles following

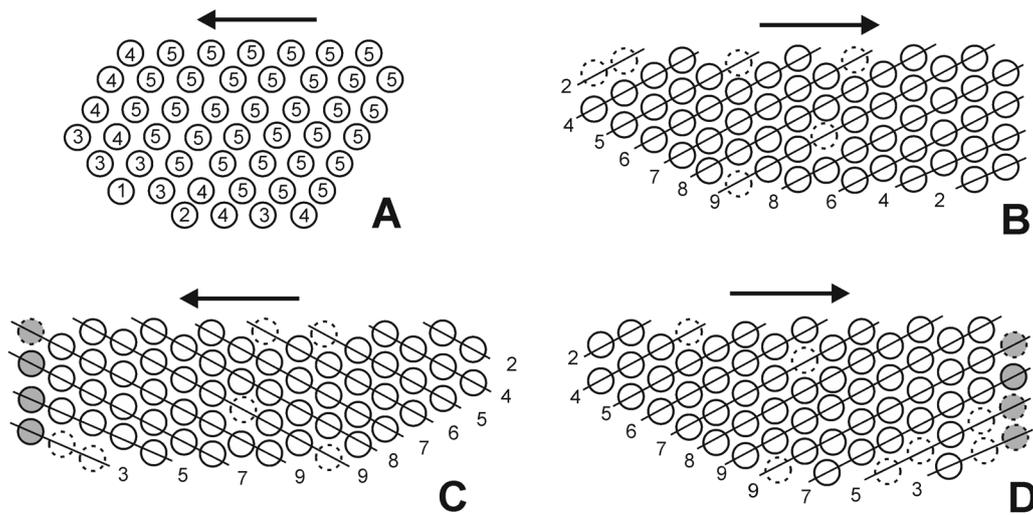


Fig. 6. A, lens formula diagram (after McKellar & Chatterton 2009) for *Omegops tilabadensis* sp. nov., Upper Devonian, Famennian, Khoshyeilaq Formation, Ghoznavi Section, Eastern Alborz, NE Iran, recording the number of individuals carrying a lens in each position shown on the diagram, lenses in equal height represent horizontal rows; **B–D**, schematic representation of eye lenses of *Omegops accipitrinus accipitrinus* (Phillips, 1841), Upper Devonian, Famennian, Devon, England, showing vertical rows and the number of lenses in spiral files; B, BGS GSM 7053, right eye, Pilton Beds at Croyde Bay; C, D, BGS GSM 7057, left and right eyes, Pilton Beds at ?Top Orchard Quarry, Pilton; lenses added to the eye visual surface in a larger individual shown by a grey circle. Anterior direction is shown by the arrow.

the axial furrows; maximum glabellar width at the anterior termination of axial furrows; transverse profile of the glabella strongly vaulted; sagittal profile evenly convex, more strongly curved between the anterior termination of palpebral lobes and the anterior border. Axial furrows deep, divergent at about 40–45°, almost straight posteriorly and medially, very gently curved inwards in front of palpebral lobes (Fig. 5H). Intercalating ring, transverse, weakly defined with a pair of small lateral nodes (Figs 4A, 5H); another pair of nodes situated on the small lateral lobes (L1), bounded laterally abaxially by shallow furrows (Fig. 5H). S1 transverse, incised laterally, shallowing adaxially. S2 and S3 absent on the dorsal glabellar surface and on the ventral side. Occipital furrow transverse, shallowing abaxially with deep apodemal pits at the lateral terminations. Occipital ring high, strongly vaulted in transverse and sagittal profiles, ornamented with fine tubercles, occupying 17% of cephalic length (sag.). Posterior border transverse in the middle and curved posteriorly adaxially in dorsal view, strongly convex in cross section. Posterior border furrow gradually fading adaxially, curving along the rounded genal angles. Anterior border narrow, ridge-like, delineated by the narrow and shallow border furrow. Palpebral furrows weakly defined, subparallel, very gently curved outwards. Palpebral lobes distinctly raised above the palpebral area, with the outer rim of faint densely spaced tubercles and the second inner row. Palpebral

area of fixigena very narrow (tr.), smooth or covered by a few small subconical tubercles. Eyes large, in dorsal view reaching lateral cephalic margin. Visual surface consisting of up to 48 lenses arranged in a distinct hexagonal pattern with up to seven horizontal rows in mature individuals (Figs 5D, 6A). Visual surface almost vertical, underlined by the concave band bearing a row of large tubercles bounded by distinct furrow separating the area from an outer surface of the librigena. Postocular area of the fixigena slightly inflated, smooth and narrow adaxially widening abaxially with a distinct postocular pad covered with eight large tubercles (Fig. 5D). Posterior branch of the facial suture placed in a deep postocular furrow. Vincular furrow evenly deep, evenly curved. Post-vincular doublure (Feist et al. 2016) almost flat, about three times as wide as the vincular furrow, ornamented with faint terrace lines (Fig. 5F). Hypostome not observed.

Thorax of 11 segments, slightly tapering posteriorly down to 90% of anterior width. Thoracic axial rings strongly arched, lacking lateral lobes, up to 38% as wide as whole segment in anterior segments and down to 31% in posterior segments; ornamented by small tubercles of varying sizes, gradually fading adaxially. Articulating half-ring smooth, bounded posteriorly by a deep ring furrow. Anterior bands of thoracic pleurae narrow (exsag.), smooth. Pleural furrow weakly defined abaxially, becoming prominent at the transition to a

fulcrum, then gradually fading adaxially. Posterior bands up to three times as wide as anterior bands, ornamented with patch of fine tubercles at the transition from the proximal part to the fulcrum. Articulating facet smooth with a gently concave surface.

Pygidium transverse, semioval, slightly more than half as long as wide. Pygidial axis conical, gently tapering posteriorly at 10–12°, almost 90% as long as pygidium and about 30% as wide as maximum pygidial width; eight axial rings plus a small terminal piece, separated by narrow, deep, almost transverse axial furrows. Two–three posterior rings short and weakly defined. Axial rings covered with small to medium-sized tubercles loosely arranged in one–two rows. Axial furrows wide and deep, moderately shallowing posteriorly. Pleural field gently vaulted, with five pleural ribs evenly bent posteriorly adaxially. Medial part of the pleural ribs covered with densely spaced large granules and small to medium-sized tubercles gradually fading outwards and inwards. Three anterior pairs of the pleural furrows narrow (exsag.) and deep, posterior fourth pair significantly shallower. Pygidial border smooth, weakly defined without border furrow.

Discussion. In its cephalic morphology *Omegops tilabadensis* shows similarity to the topotypes of *Omegops accipitrinus accipitrinus* as revised by Richter & Richter (1933), including the characteristic ornament of the postocular area of fixigena, which is smooth adaxially and covered with eight large tubercles abaxially. The most significant difference from the types of *Omegops accipitrinus accipitrinus*, including the lectotype (BGS GSM 7055) and the specimens described and illustrated by Salter (1864), is in the morphology of the eye visual surface, upon which are arranged up to 48 large lenses with no more than four lenses in the vertical row in the Iranian specimens, while in *Omegops accipitrinus accipitrinus*, it is covered by 56–70 smaller lenses with up to five lenses in the vertical row (Fig. 6B–D). Another difference is the axial glabellar furrows divergent in *Omegops tilabadensis* under an angle of about 40–45°, against 45–60° in *Omegops accipitrinus accipitrinus*. Also the palpebral area of fixigena is very narrow in Iranian specimens, while in dorsal view the eyes reach the lateral cephalic margin like in *Omegops accipitrinus insolatus* Struve, 1976, but unlike *Omegops accipitrinus accipitrinus*. The pygidial morphology of *Omegops accipitrinus accipitrinus* was described by Richter & Richter (1933) without illustration. No phacopid pygidia assignable to *Omegops accipitrinus accipitrinus* are reported from the type locality in the Pilton Quarry (North Devon, England); however, the phacopid cranidium (BGS GSM 7053) and associated

pygidium (BGS GSM 7056) illustrated by Salter (1864, pl. 1, figs 10, 14) were sampled from the Pilton Beds at Croyde Bay, Devon, England. Originally they were assigned by Salter to *Phacops latifrons* (Bronn, 1825), but subsequently included in the synonymy of *Omegops accipitrinus accipitrinus* by Richter & Richter (1933), which was also confirmed by Morris (1988) in his review of British trilobites. Our observation of the internal mould of the cranidium illustrated by Salter (1864) suggests that it exhibits characteristic features of *Omegops accipitrinus accipitrinus*, but the ornament of the postocular area of the fixigena is not preserved. The available data from earlier descriptions and illustrations suggest that the pygidium of *Omegops tilabadensis* differs from that of *Omegops accipitrinus accipitrinus* in having five (not six) pleural ribs and a relatively longer axis (90% against 75%) less strongly tapering posteriorly. The pygidium from the Famennian (Strunian) of the Mazraeh-e Kheradmand section in Central Iran illustrated by Wendt et al. (2005, pl. 9, fig. 7) does not belong to *Omegops accipitrinus accipitrinus* because it has only five (not six) pleural ribs and a long axis only slightly constrained posteriorly. This pygidium is similar to that of *Omegops tilabadensis*, but its specific discrimination cannot be made without data on cranidial morphology.

The pygidial morphology is known also for *Omegops accipitrinus maretolensis* and *Omegops accipitrinus bergicus* (Drevermann, 1902). Both have pygidia with 7–9 axial rings and six pleural ribs (Struve 1976), while in *Omegops tilabadensis* specimens with eight axial rings and five pleural ribs are invariably characteristic. *Omegops tilabadensis* also differs from *Omegops accipitrinus maretolensis* in having a relatively wider pygidial axis very gently tapering posteriorly. Though, unlike the Iranian specimens, the eye visual surface of *Omegops accipitrinus bergicus* illustrated by Farsan (1998, fig. 8a) has 61 lenses arranged in nine horizontal rows.

Omegops tilabadensis is comparable to *Omegops accipitrinus insolatus* Struve, 1976 in the position of the eyes and a very narrow palpebral area of fixigena. Iranian specimens mainly differ from the latter in having a divergence angle of the glabellar axial furrows not exceeding 45°, and in the ornament of a postocular pad covered with eight coarse tubercles. Due to the poorly preserved visual surface of eyes and the absence of data on the pygidial morphology of *Omegops accipitrinus insolatus*, more detailed comparison between these two taxa is impossible.

Farsan (1998) described and illustrated trilobite specimens from the late Famennian (Strunian) of several sections in Afghanistan, which he assigned to

Omegops accipitrinus accipitrinus, *Omegops accipitrinus maretioleensis*, *Omegops paiensis* and *Omegops cornelius* and gave a description of the eye visual surface for all of them. In his collection, both subspecies *Omegops accipitrinus accipitrinus* and *Omegops accipitrinus maretioleensis* co-occur in the same samples and have almost identical eye formulas, while they can be discriminated only in minor differences of cephalic ornament. Both subspecies differ from the types of *Omegops accipitrinus accipitrinus* in the morphology of the visual surface with up to 46 lenses arranged in seven horizontal rows (Farsan 1998, figs 4, 5), and unlike *Omegops accipitrinus (s.l.)*, they have a pygidium with only five (not six) pleural ribs (Farsan 1998, pl. 2, figs 1c, 2a, 5). On the other hand, in the cephalic and pygidial morphology they resemble closely *Omegops tilabadensis*. The major difference is in details of the individual lens arrangement on the eye visual surface. Therefore, the Afghan specimens described by Farsan (1998) can be questionably assigned to the newly introduced species. However, the precise taxonomic affiliation requires further study, which probably needs additional new material due to insufficient preservation of the cephalia illustrated by Farsan (1998).

Omegops tilabadensis shows distinct similarity to the Afghan *Omegops paiensis* Farsan, 1998 in cephalic and pygidial morphology. Except occasional occurrence of pygidia with four pleural ribs in the latter species, the major recognizable difference is in the eye morphology. *Omegops paiensis* has much higher eyes with 86 lenses on the visual surface arranged in up to 14 horizontal rows and with up to 7 lenses in vertical files, while the Iranian specimens have no more than 48 lenses arranged in 6–7 horizontal rows on the visual surface. While bimodal variability in eye lenses is documented for some phacopide taxa (e.g. Campbell 1967; Crônier et al. 2015), it has not been reported for any species of *Omegops* and it is not observed in *Omegops tilabadensis*. With growth, the new lenses in the latter taxon were added mainly anterodorsally (Fig. 6A). Therefore, strong differences in eye morphology can be taken as adequate to distinguish these two species.

Omegops tilabadensis differs from *Omegops cornelius* (Richter & Richter, 1933) in having a shorter and wider cephalon, a coarser tuberculation of the glabella, a shorter frontal glabellar lobe, a more vaulted glabella (tr., sag.), different ornaments of the postocular area of fixigena, a pygidium which has five (not six) pleural ribs, a slightly more transverse posterior pygidial margin and a less conical shape of the pygidial axis (see Struve 1976, p. 437, text-fig. 9). There is no sufficient data on the eye morphology of *Omegops cornelius*.

The taxonomic affiliation of the specimens from the Devonian (upper Famennian) of Afghanistan assigned

by Farsan (1998) to *Omegops cornelius* is questionable. They have up to 51 lenses on the eye visual surface and their eye formula is not very different from that of individuals assigned by Farsan in the cited publication to *Omegops accipitrinus accipitrinus* and *Omegops accipitrinus maretioleensis*. A less vaulted in the middle, but slightly hanging in front glabella was listed by Farsan (1998) as another difference between the Afghan specimens assigned to *Omegops cornelius* and those affiliated to the *Omegops accipitrinus* group. However, it may represent a preservational artefact because of sediment compression during lithification.

The specimens from the late Famennian of western Junggar, Xinjiang, northwest China, assigned to *Omegops cornelius* by Yuan & Xiang (1998), are not conspecific with that taxon, because they have a different pygidium with five pleural ribs and a longer axis, very slightly constrained posteriorly. The pygidium illustrated in the cited publication strongly resembles pygidia of *Omegops paiensis* and *Omegops tilabadensis* but differs in a greater number of the axial rings (9 instead of 7–8). In having moderately high eyes with 65–70 lenses on the visual surface, the Chinese specimen occupies an intermediate position between Afghan and Iranian materials. As no data have been provided on the detailed arrangement of lenses on the visual eye surface for the Chinese trilobite, further comparison is impossible. The species affiliation of the Chinese *Omegops* cannot be defined without restudy based on more representative and better preserved material.

DISCUSSION AND CONCLUSIONS

Crônier & François (2014) commented on a district bathymetrical gradient in the distribution of the Famennian phacopid taxa with *Omegops* restricted to a shallow marine environment. In eastern Alborz, *Omegops tilabadensis* is a minor component of a benthic fauna with abundant athyridide, rhynchonellide and spiriferide brachiopods that inhabited lime mud substrate rich in bioclasts within a shallow shelf setting offshore, which is consistent with the pattern established by Crônier & François (2014). Specimens of *Omegops* described and illustrated from the upper Famennian of the Middle East (Farsan 1998; Wendt et al. 2005 and authors' personal observations) and western Junggar, Xinjiang (Yuan & Xiang 1998) have minor but consistent differences in the pygidial morphology from the taxa originally described from West Europe (Richter & Richter 1933; Struve 1976), North Africa (Morocco) (Richter & Richter 1943; Struve 1970; Alberti 1972) and Kazakhstan (Weber 1937; Struve 1976). These include a different

number of pleural ribs and a relatively longer and less constrained pygidial axis in the *Omegops* specimens from the Middle East and western Junggar, which was within the margins of the Tarim microcontinent by the Late Devonian (Torsvik & Cocks 2017), versus a shorter, subconical axis in the European, North African and Kazakh individuals. These may indicate the existence of two separate lineages of *Omegops* evolved in the relative geographical isolation (Fig. 7).

In recent palaeogeographical reconstructions, Alborz, Central Iran and Afghanistan are usually positioned within the Gondwana margin where they occupied temperate latitude locations during the Late Devonian (Torsvik & Cocks 2017). Nevertheless, the existing record of rift-related Silurian and, probably, Devonian flood basalt volcanism (Wendt et al. 2005; Hairapetian et al. 2017) might have relation to a breakup of the Gondwana margin related to the opening of the Paleo-Tethys Ocean (Domeier 2018). While the tectonic history of the Iranian terranes through the Devonian Period remains obscure, extensive Late Devonian to Carboniferous carbonate sedimentation in Alborz and Central Iran is in favour of their location in low latitudes, probably as separate microplates, as it is inferred in Fig. 7. In that case almost all documented *Omegops* occurrences, except the North African sector of Gondwana, were confined to tropics and subtropics.

The stratigraphical range of *Omegops tilabadensis* in the Ghoznavi section may suggest that the divergence of these two lineages probably occurred in pre-Strunian time. It is likely that in addition to differences in the eye visual surface morphology and different cephalic ornaments including the ornament of the postocular area of fixigena, there are small but constant differences in the pygidial morphology important for the discrimination of *Omegops* species and subspecies.

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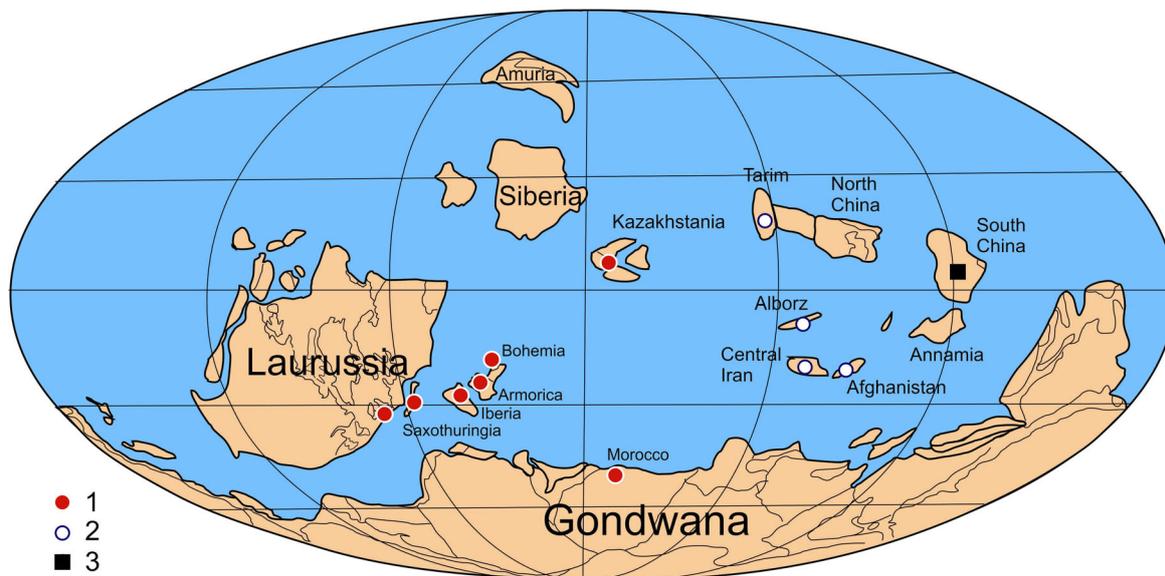


Fig. 7. Palaeogeographical reconstruction for the Late Devonian Epoch showing the geographical distribution of *Omegops* lineages: 1, taxa with six and more pygidial pleural ribs; 2, taxa with four to five pygidial pleural ribs; 3, pygidial morphology unknown. Position of major continents is mainly after Torsvik & Cocks (2017) with significant emendations for Australasian peri-Gondwana.

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**Hilis-Devoni (Famenne'i) phacopiidne trilobiit *Omegops*,
leitud Alborzi idaosast Iraanis**

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Hilis-Devoni (Famenne'i lõpuosa) phacopiidseid trilobiite esindab siinkirjeldatud *Omegops tilabadensis* sp. nov., mis on leitud Khoshyeilaqi kihistust Alborzi mäestiku idaosas Põhja-Iraanis. See liik moodustab trilobiitide koosluse, mis asustas madalat šelfimerd koos mitmekesise brahhiopoodide kooslusega, milles domineerisid athyriidide ja spiriferiidide liigid. Püsivad erinevused sabakilbi morfoloogias geograafiliselt eraldatud *Omegops*'i liikidel, mis on levinud Kesk-Ida aladel ja Loode-Hiinas (Junggaris) ning Lääne-Euroopas + Gondwana Põhja-Aafrika sektoris, võivad viidata kahe erineva *Omegops*'i arengurea olemasolule, mis lahkesid enne Struni aega. Konodontide leiud Khoshyeilaqi kihistust, mis ei ole vanemad kui *Bispathodus costatus*'e tsoon, ja brahhiopood *Rhipidomella michelini* esinemine samas on piisavad, dateerimaks selle kihistu ülaosa vanuseks Struni kuni varase Tournai aeg.