BioOne COMPLETE

A New, Morphologically Diverse Permian Trilobite Fauna from Oman

Authors: Fortey, Richard A., and Heward, Alan P.

Source: Acta Palaeontologica Polonica, 60(1) : 201-216

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00106.2014

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

A new, morphologically diverse Permian trilobite fauna from Oman

RICHARD A. FORTEY and ALAN P. HEWARD



Fortey, R.A. and Heward, A.P. 2015. A new, morphologically diverse Permian trilobite fauna from Oman. *Acta Palaeontologica Polonica* 60 (1): 201–216.

A newly discovered trilobite fauna from the early to middle Permian Qarari Unit of northeastern Sultanate of Oman is described. It comprises exceptionally complete and well-preserved examples of five proetoid species, belonging to genera typical of an eastern Tethyan region extending through southern Asia to Timor. The shallow shelf fauna compares closely with one of Artinskian age from Afghanistan. Permian species previously assigned to *Paladin* are here considered unrelated to this predominantly Carboniferous clade, and are placed in a new ditomopygine genus, *Simulopaladin*, type species *Simulopaladin tridentifer* sp. nov. Three other ditomopygine species are described: *Hentigia ornata* sp. nov., *Iranaspidion elephas* sp. nov., and *Acanthophillipsia felicitae* sp. nov. The proetid *Triproetus bonbon* sp. nov. is the most complete material known of a more widespread genus.

Key words: Trilobita, palaeogeography, Permian, Oman.

Richard Fortey [R.Fortey@nhm.ac.uk], Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK;
Alan Heward [alan@midfarm.demon.co.uk], 23 Croftdown Court, Abbey Road, Malvern WR14 3HZ, UK.

Received 2 July 2014, accepted 24 September 2014, available online 30 December 2014.

Copyright © 2015 R.A. Fortey and A.P. Heward. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Towards the end of their long history trilobites are often portrayed as being in decline. But new genera and species continued to evolve in the Permian (Owens 2003) and at a few localities trilobites continue to be a significant part of the fauna. The trilobites reported here were discovered and collected by APH over the last four years from a new and richly fossiliferous locality in northeastern Oman. They are well-preserved in full relief in a limestone matrix, and are among the most informative specimens of this age ever to have come to light. They occur alongside a diverse fauna of echinoderms, brachiopods, and fusulines that are typical of an eastern "Tethyan" Permian fauna that was recognised from Timor in the early part of the twentieth century (Gheyselinck 1937). Related proetoid trilobites occur sporadically through southern Asia and the Far East, although many previous papers figure fragmentary sclerites that provide an inadequate basis for comparison with the beautiful new material. Nonetheless, an extensive faunal province typified by endemic ditomopygine trilobites can be recognised. In this paper we describe the new trilobite locality and its fauna, with notes on its correlation.

Institutional abbreviations.—NHMUKPI, Natural History Museum, London, UK; prefix It applies to the trilobite collections there.

Other abbreviations.—Used in trilobite descriptions are standard: sag., sagittal; exsag., exsagittal; tr.,transverse; L, glabellar lobe; S, glabellar furrow.

Geographic and geological setting

Field occurrence.—The trilobite fauna described below are from outcrops of the Qarari Unit on the Batain Plain of Ash Sharqiyah province in the northeast of the Sultanate of Oman. Most of the specimens are from the weathered surface of a 450 m^2 outcrop of marly limestone in a tributary of Wadi Khawr al Jaramah (Fig. 1). The trilobites are preserved with their original cuticle and include many that are enrolled. Other enrolled samples are from a smaller mound around 170 m to the north-northeast. Disarticulated trilobite fragments were also observed in a rudstone bed of the Qarari Unit at a hill located northwest of Bu Fashiqah. Trilobite fragments were also collected from steeply dipping beds of limestone bounding a wadi draining the southwest flank of Jebel Qarari and a 1.5 cm enrolled trilobite photographed in

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

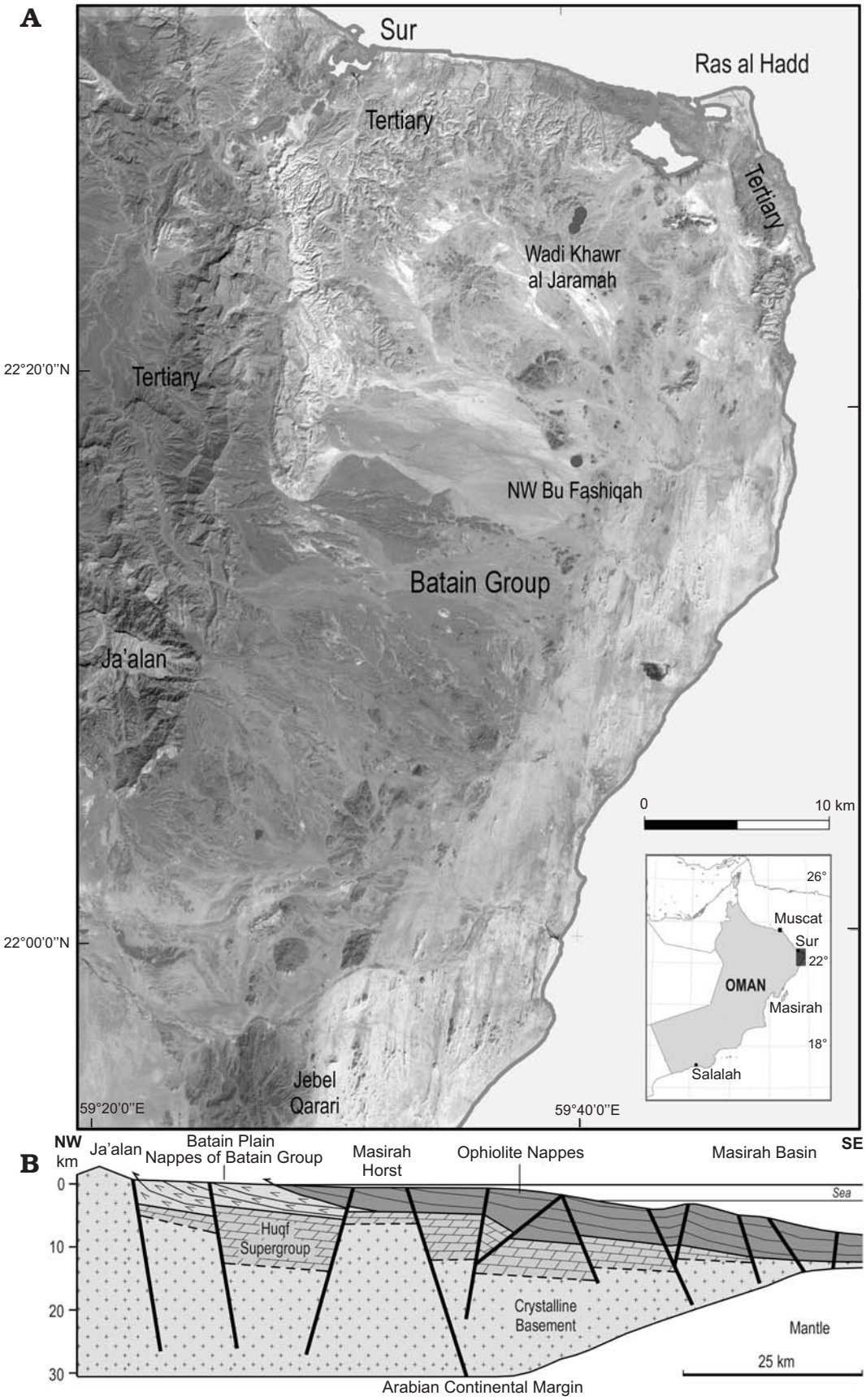


Fig. 1. Location map (**A**) and structural cross-section (**B**) showing the allochthonous Batain nappes and Masirah ophiolites of northeastern Oman (modified from Peters et al. 2001).

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

situ. This is probably location 604 of Shackleton et al. (1990) from which *Paladin* sp. was originally identified by Robert M. Owens, later re-assigned to *Triproetus* (see below).

Regional geology.—The Batain Plain is underlain by autochthonous Neoproterozoic rocks known from outcrops at Jebel Ja'alan, oil exploration wells and seismic lines (Fig. 1; Beauchamp et al. 1995; Mount et al. 1998). These autochthonous rocks are overlain by an allochthonous wedge of thrust and intensely deformed sediments of the Batain Group. They are capped along the coast and in Masirah Island by a stack of ophiolite nappes (Immenhauser et al. 2000; Peters et al. 2001). The nappes of the Batain Group and the ophiolites were obducted perhaps hundreds of kilometres from the Batain Basin north-westward over the eastern margin of the Arabian plate around 65 million years ago. The detachment of this sedimentary pile and its obduction with a stack of ophiolites has been related to the counter-clockwise rotation of India during its separation from the Seychelles (Immenhauser et al. 1998). Autochthonous Late Palaeocene to Miocene deposits cover parts of the Batain Plain.

The Batain Group was originally interpreted as a mélange by Shackleton et al. (1990) but Immenhauser and colleagues (1998) subsequently argued for much greater structural continuity. The Qarari Unit typically occurs as isolated hills and outcrops ranging in size from kilometres long and hundreds of metres thick, as at Jebel Qarari, to a few tens or hundreds of square metres, as at Wadi Khawr al Jaramah. The typical appearance of outcrops of the Qarari Unit is of grey, thinly bedded (5–25 cm), fine-grained limestone that sometimes contain partings of yellow marl. The Qarari limestone beds appear as diagenetic segregations and they are locally nodular and cherty. There are occasional grainstone and rudstone beds, but few sedimentary structures other than large horizontal arthropod burrows and the trace fossils *Zoophycos*, *Chondrites*, and *Ophiomorpha*. Notably no *Cruziana* have been observed. The impression is of quiet muddy shelf carbonates that accumulated in oxygenated conditions below normal storm-wave base. Previous interpretations of depositional environment of the Qarari Unit are of a low-energy, hemipelagic, shelf or toe of slope setting (Immenhauser et at. 1998; Hauser et al. 2002).

Macrofossils (brachiopods, crinoids, blastoids, corals, bryozoa, trilobites, ammonoids, bivalves, etc.) occur in the marlier intervals and vary from rare, most commonly, to abundant, as at Wadi Khawr al Jaramah. Preservation is sometimes excellent with little evidence of disaggregation, transportation or reworking, or indeed the spectacular deformation that is exhibited by other intervals of the Batain Group (e.g., the chevron-folded ribbon cherts of the Wahrah Formation). A conodont colour index of 1 for samples from the Qarari Unit implies a temperature of about 50°C for the Permian (Giles Miller personal communication 2014), equivalent to a maximum burial depth of around 1000 m.

The Batain Basin appears to have been an early, failed, southerly-orientated arm of Meso-Tethys. Palaeomagnetic data from the Masirah ophiolites indicate that the ophiolite of the lower thrust sheet formed close to Indian margin and the Kabul Block 150 million years ago (Immenhauser et al. 2000). It is not clear where the much older Qarari carbonates accumulated in relation to Arabia, India and Afghanistan, and perhaps the trilobites support deposition closer to the latter than the former, as described below. Age equivalent deposits in interior Oman are the continental clastics of the Gharif Formation and the transgressive carbonates of the Lower Khuff.

Age of the fauna.—The Qarari Unit is the oldest interval of the allochthonous Batain Group known to date. The limestone beds were considered Early to Late Permian based on brachiopods and corals from Jebel Qarari and the "Black Hills" (Shackleton et al. 1990), Wordian on unpublished ammonoids from Jebel Qarari (Immenhauser et al. 1998) and Murgabian on conodonts and ammonoids from northwest Bu Fashiqah (Peters et al. 2001). It appears some of these ammonoids may have been misinterpreted and there is thus some uncertainty over this assignment. Webster and Sevastopulo (2007) compared blastoids and a crinoid from the Jebel Qarari area with faunas from Western Australia and Timor and considered them probably Artinskian. An extensive fauna of echinoderms from the Wadi Khawr al Jaramah outcrops is currently being described by Webster and Waters and they regard this fauna as most likely Artinskian (Gary Webster, personal communication 2014). Fusulinids from the same Wadi Khawr al Jaramah outcrops that yielded the trilobites herein were interpreted as Kubergandian (Leven and Heward 2013; range: Kungurian–Roadian). However this assignment is based on only two species of *Parafusulina*, one of them new, and the uncertainty of correlating between the Tethyan and International time scales was noted. Conodonts extracted from samples collected at Wadi Khawr al Jaramah and Jebel Qarari are interpreted as Kungurian and Wordian, respectively (Lance Lambert, personal communication 2014) based on the occurrence of *Mesogondolella zsuzsannae*, *Sweetognathus guizhouensis*, and *Hindeodus excavatus* at the former, and *Mesogondolella siciliensis* at the latter. The closest comparison of the trilobites described below is with Artinskian faunas, but since the species are new this is not definitive, and the conodont evidence points to a slightly younger age.

Comparison with other Permian trilobite faunas.—The fauna from Wadi Khawr al Jaramah is well preserved, and is an important new addition to the Permian trilobite faunas of the Arabian Peninsula. Three previous spot faunas have been described from Oman. Goldring (1957) described *Pseudophillipsia* species from Wadi Lusaba and nearby outcrops of the Lower Khuff Formation in interior Oman that are unmatched in the present fauna and are of Wordian age (previously considered Artinskian). Becq-Giraudon and Pillevuit (1995) have figured two small faunas of "Murgabian–Midian" (approx. Capitanian) age from the Maqam Formation (Sumeini Group) and the Rustaq Formation (Hamrat Duru Group) of northern Oman, neither of which species are similar to the new finds. These authors comment that their faunas occupy two different hab-

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

itats, one shallow-water, even reef-like, and the other deeper water. Bruton (1996) figured a *Triproetus* species (fide Owens 2003) under the name *Paladin* (*Neokaskia*) sp. from the Qarari Limestone of Jebel Qarari, northeastern Oman. This species is similar to, but not identical with a new species of *Triproetus* from Wadi Khawr al Jaramah.

We can conclude that our fauna is not one hitherto recognised in Oman, although from the same stratigraphical unit as finds at Jebel Qarari where a free cheek has been collected indistinguishable from that of *Triproetus bonbon* sp. nov. While the limestone facies in which they occur is indicative of a shelf environment, it is clear that the bottom conditions were sufficiently quiet not to disarticulate the enrolled trilobites after death. It is possible that their death was caused by a sudden crisis, prompting them to enrol, with subsequent rapid burial protecting them from subsequent disturbance. The closest fauna described previously is that of Haas et al. (1980) from Artinskian limestone deposits in Afghanistan. These authors comment that they were deposited at between 10 and 30 m water depth. However, much of the Afghan material is disarticulated. With their thick cuticles, coarsely sculpted in some species, and very large eyes it is plausible that the Oman faunas lived under similar marine conditions, reflected in closely comparable species of *Hentigia* and *Simulopaladin* gen. nov., although some preservation details must have been different to account for the many articulated enrolled specimens in our collection.

The Oman fauna is part of a much more extensive Permian palaeotropical eastern "Tethyan realm", extending from Sicily through Asia Minor (Turkey, Iran), Afghanistan, Pakistan, the Malay Peninsula, Japan, and Guizhou Province, southern China. A species of *Iranaspidion* described below is compared with the type species from Iran, and similar species occur in Japan. The type species of *Simulopaladin* gen. nov. is very similar (possibly identical) to a species from Afghanistan, and also compared with material from Guizhou Province, South China, and Thailand. *Acanthophillipsia* has previously been reported only from southern China. The majority of these occurrences range in age from Artinskian to Wordian. Given that the taxa reported below are new species the trilobites alone cannot refine the age determination.

Systematic palaeontology

Class Trilobita Walch, 1771

Order Proetida Fortey and Owens, 1975

Family Phillipsiidae Oehlert, 1886

Subfamily Ditomopyginae Hupé, 1953

Remarks.—Higher level classification of the trilobites described below has been contentious, with some authors placing them in Phillipsiidae (e.g., Owens 2003) and others in Proetidae (e.g., Jell and Adrain 2003). However, a cluster of taxa around *Ditomopyge* does seem to comprise a compact group, and this subfamily is retained here. Ditomopygine trilobites are divided into at least 17 genera (Owens 2003) and the characters discriminating them are relatively few, and often a matter of degree rather than "presence or absence". The group as a whole would benefit from a critical cladistic analysis. Unfortunately, not all the type species are known from complete material. Here we add a few, very well-preserved species which should add clarity to future character coding, which we are mostly placing in previously established genera, basing our assignments particularly on criteria listed in Haas et al. (1980), Owens (1983), and Liebermann (1994). We suggest below a few additional characters that may prove of service as synapomorphies defining phylogenetically-based genera: in *Hentigia* the reduced genal spines, wedge shaped glabella with short lateral glabellar furrows, and flattened tubercular sculpture; in *Iranaspidion*, the longitudinally subdivided based of the composite anterior glabellar lobe and spinose genal ridge; in *Acanthophillipsia* coarse, encrinurid-like tuberculation and uniquely longitudinally divided cephalic border. Permian species hitherto accommodated within *Paladin* are not considered related to that predominantly Carboniferous Laurentian genus and are the basis of a new genus, *Simulopaladin*, typified by a pyriform glabella with an occipital ring with three turbercles, and wide, flat cephalic borders. The course of the facial sutures in the described species are all basically similar and the "greek letter" system often used in proetoids is not considered necessary here. However, we remove *Triproetus* from Ditomopyginae and place it in Proetidae, since it lacks the typical glabellar structure of ditomopygines and has a short pygidium with few segments.

All the species described below are known with certainty only from the type locality.

Genus *Hentigia* Haas, Hahn, and Hahn, 1980

Type species: *Hentigia bulbops* Haas, Hahn, and Hahn 1980; Artinskian (Permian), central Afghanistan, original designation.

Discussion.—The genus *Hentigia* was established to include two species from the early Permian of Afghanistan. Several specimens of the type species show tubercles on the posterior part of the composite anterior glabellar lobe (Haas et al. 1980: pl. 1: 4, pl. 2: 2). A species from Oman displays remarkably coarse glabellar tuberculation, which we regard as a further expression of the same feature. It is also variably developed from one specimen to another, and often does not extend on to the antero-median part of the glabella over an area probably corresponding with part of the middle body of the hypostome on the venter. The trilobite fauna from Oman is possibly younger than that from Afghanistan, and the coarse sculpture might be regarded as a derived character relative to *H. bulbops*.

Hentigia ornata sp. nov.

Fig. 2.

Etymology: Referring to elaborate cephalic sculpture.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Type material: Holotype: well preserved nearly entire exoskeleton, NHMUKPI It 29079. Paratypes: enrolled exoskeletons, NHMUKPI It 29077, 29081–29084, 29137, 29138 (unfigured); cephalic shield, NHMUKPI It 29078, 29080.

Type horizon: Kungurian–Roadian (Permian).

Type locality: Allochthonous limestone, Wadi Khawr al Jaramah, Oman.

Diagnosis.—*Hentigia* with coarse, but low tubercles on much of the glabella; basal glabellar lobes expand outwards forwards. Pygidium with about 20 axial rings and 9–10 pleural ribs, the first carrying strong adaxial knob.

Description.—Trilobite is 1–1.5 cm diameter when encapsulated, when pygidial margin extends beyond cephalic shield. Posterior part of glabella is not much higher than eyes, more convex anteriorly. Glabella in dorsal view length (sag.) 1.42–1.47 times maximum width across anterior lobe, which is 1.27–1.36 times transverse width of occipital ring. Swollen front part of glabella has an almost perfectly circular outline. Posterior part comprises occipital ring and transverse basal median lobe of similar length (sag.), the latter tapering forwards. Both are well defined by deep occipital furrow and S1. Basal lateral glabellar lobes are inflated, and extend well forwards from median lobe where they slope outwards towards the eyes. Their outline varies from comma-shaped to triangular. They are set off from the composite anterior glabellar lobe by a deep furrow, which however includes a small, subtransverse inflated ridge in some specimens. The anterior glabellar furrows are little more than furrows separating particularly inflated, flattened tubercles representing lobes L2–4. This arrangement is best illustrated on a small cephalon (Fig. 2B) displaying less developed tuberculation, showing three pairs short, forwardly inclined glabellar furrows, the outer ends of the most anterior being opposite the front of the eyes. The expression of the glabellar lobes varies from prominent and inflated, to relatively subdued. On the most tuberculate examples the lobes themselves carry further tubercles, as do the basal and lateral glabellar lobes. The tubercles extend towards the axial line, but do not quite reach it, or become very subdued antero-medially; again, this is variable. Usually prominent median tubercle on occipital ring, where the latter is widest. Axial and preglabellar furrows uniformly deep. Elevated semicircular palpebral lobes about one-third (exsag.) dorsal glabellar length, may be wrinkled or feebly tuberculate. Facial sutures of usual proetoid form outlining spine-like postocular cheeks that essentially comprise somewhat more than half the proximal part of posterior border. Anteriorly divergent sections track the outline of the frontal glabellar lobe until converging across vertical part of anterior border, bending ventrally, and then becoming transverse as rostral suture to meet at midline. The cranidial border narrows medially but is still visible in dorsal view, although the major part of it is bent down vertically. Here it abuts the large transverse rostral plate (Fig. 2F) that carries a pair of inflated bosses at its outer edge.

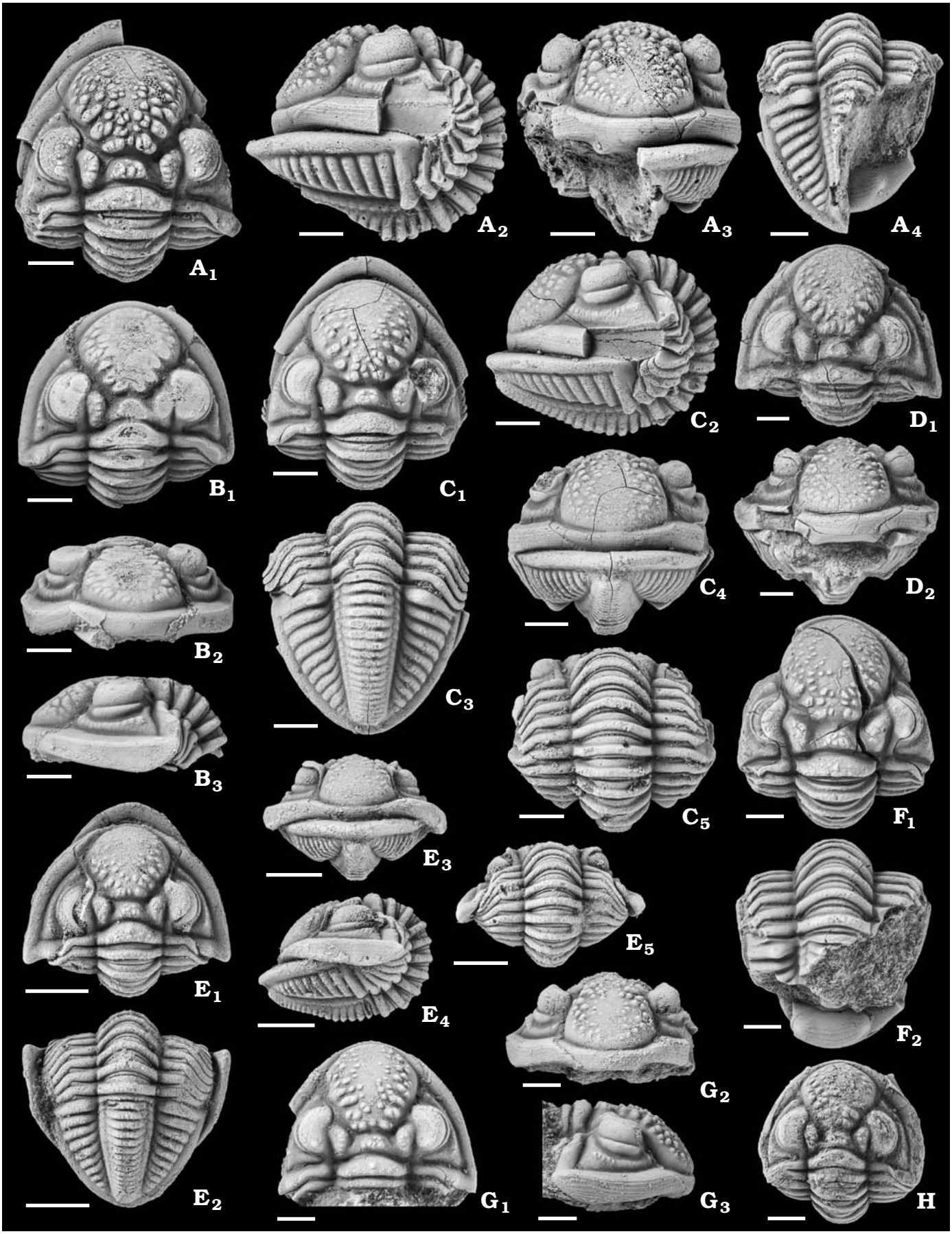
Free cheek lacks genal spine, genal corner rounded to almost rectangular in dorsal view. Posterior border widens laterally, and curves backwards, adaxially to nick point where cut by facial suture. Lateral border mostly comprises a steep, near vertical wall; it narrows towards the genal angle. Genal field is narrow (tr.) such that on many specimens it is anteriorly no wider than the very prominent eye socle at its widest, and equally inflated there, but posteriorly less so. It may carry weak tubercles adjacent to the deep furrow outlining the base of the eye socle, which is prominent, convex, widest medially. The base of the eye is also marked by a deep furrow, which is narrower than that at the base of the socle. Visual surface is twice as long as high in lateral view. Genal doublure reflexed up to border furrow making a marginal tube around cephalon. Vertical part of genal border carries sculpture of fine raised lines parallel to margin.

Thorax has nine segments of usual proetoid type with preannular half rings visible in enrolled specimens. Pleural tips flatten out distally. Long narrow axial rings may be slightly tuberculate. The tips of the first three segments are concealed beneath the edge of the free cheek during enrolment. In this case, the telescoped parts of the posterior six segments remain visible in lateral view, with just the tips tucked under the cheek edge. This area is backed by a wider plate of doublure.

Pygidium 0.75–0.80 times as long as wide, surrounded by well-defined and convex border with almost circular cross section. Ten pleural ribs are defined by deep furrows, and they are not further subdivided; the tenth rib could be regarded as no more than a triangular inflated area. The anterior rib runs into the border, from which the posterior ribs are separated by a deep border furrow. Proximally it carries an extraordinary boss or knob, which marks the point at which the wide facet ends, it can be large enough to overhang the rib behind. This knob appears to be a feature of later ontogeny as it is more subdued on the smallest enrolled specimen (Fig. 2E). Axis occupies no more than 0.4 maximum pygidial width at front of pygidium and tapers to border furrow, but more strongly after the fourth or fifth ring. On most specimens there are seventeen or eighteen rings, of which the first six are more convex (tr.) and clearly defined than those that follow. It has been remarked before (e.g., Lerosoy-Aubril and Angiolini 2009) that the proximal convexity of the axis in these Permian trilobites continues the curve of the thoracic axis as seen during enrolment, such that the maximum axial transverse convexity is at the third ring, not anteriorly as in most trilobites. Depressed lateral areas marking muscle insertion run along the lateral margins of the axis almost to the tip. Narrow ring furrows extend as far as this area.

Discussion.—*Hentigia bulbops* Haas, Hahn, and Hahn, 1980, from Afghanistan shares many features with *H. ornata*, differing obviously in its wedge shaped, rather than spherical anterior part of the glabella; although it has a tuberculate glabella, this is much less coarse than in the species from Oman. The basal glabellar lobes in *H. bulbops* taper forwards or at most expand very slightly, whereas in *H. ornata* they frequently push into the palpebral area. The pygidium of *H. bulbops* lacks the peculiar anterior pair of bosses seen in the new species, although its anterior rib pair is particularly prominent. Glabellar shape in *H. planops* Haas, Hahn and

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Hahn, 1980, is more like that of *H. ornata*, but its surface sculpture is even more subdued than that of *H. bulbops*, and it has also less curved palebral lobes and a longer eye than *H. ornata,* underlain by a much lower, less well defined eye socle.

Genus *Iranaspidion* Kobayashi and Hamada, 1978

Type species: *Iranaspidion sagittalis* Kobayashi and Hamada, 1978; Guadaloupian (Permian), central Iran.

Discussion.—*Iranaspidion* is close to *Ditomopyge* and *Pseudophillipsia* as Kobayashi and Hamada (1978: 157) recognised, and it may not survive a critical analysis of ditomopygine phylogeny. In reviews of Permian genera Owens (1983, 2003) cautiously retained it, noting its similarity to *Pseudophillipsia* (*Carniphillipsia*) particularly. A new species from Oman serves to further reduce the distinction between these various taxa. Like the type species of *Iranaspidion* it possesses a shallow, but distinctive median furrow or sulcus at the posterior end of the composite anterior glabellar lobe in front of a deep S1, but it lacks the transversely divided basal lateral glabellar lobes included by Owens (1983) as a character of *Iranaspidion*; it is more like *Ditomopyge* in this character. The development of the two nodes on L1 in the type species is, however, variable, being less on the holotype than on another specimen figured by Kobayashi and Hamada (1978: fig. 1a). However, since it is possible that the posteromedian sulcus is a synapomorphy of *I. sagittalis* and *I. elephas* sp. nov. it does potentially have generic significance. It is not present on the type species of *Pseudophillipsia* (*Carniphillipsia*), *P. ogivalis* Gauri, 1965. For the moment we employ *Iranaspidion* as the genus to receive the new species, while noting the reservations expressed by Owens (1983).

Iranaspidion elephas sp. nov.

Fig. 3.

Etymology: From Latin *elephas*, elephant; referring to prominent cheek tubercles, and the form of the hypostome.

Type material: Holotype: complete enrolled exoskeleton, NHMUKPI It 29087. Paratypes: enrolled exoskeletons, NHMUKPI It 29076, 29086, 29092, 29091 (prepared to show hypostome); unfigured, NHMUKPI It 29021, 29110–29120 (almost complete with hypostome); cephalon, NHMUKPI It 29090; pygidia, NHMUKPI It 29085, 29094, unfigured, NHMUKPI It 29122–29136, 29145; cephalic doublure, NHMUKPI It 29088; pygidial doublure, NHMUKPI It 29089.

Type horizon: Kungurian–Roadian (Permian).

Type locality: Allochthonous Qarari limestone Wadi Khawr al Jaramah, Oman.

Diagnosis.—*Iranaspidion* with undivided basal glabellar lobes; genal ridges end posteriorly in prominent bosses; sculpture of sparse subdued tubercles; pygidium with first rib inflated.

Description.—Cephalon 0.6–0.7 times as long (sag.) as wide, with short, stout triangular genal spines. Glabella widest across frontal lobe, this being about 0.6–0.7 times glabellar length, including occipital ring. Although the frontal glabellar profile is rounded across the midline, the anterolateral corner is slightly angulate where the axial furrows end, so that the overall shape of the composite anterior glabellar lobe is somewhat wedge-shaped. L1 deeply defined by posterior glabellar furrow, subdivided into central and lateral lobes, the latter also well defined by axial furrows running more or less exsag. and inner furrows which are shallower posteriorly. The lateral lobes are twice as long (exsag.) as wide and taper at the front into an acutely triangular termination. Composite anterior glabellar lobe is 80–87% as long as its maximum width shortly in front of eyes, its anterior profile almost semicircular. Posterior end marked by a pair of gentle swellings separated by a sulcus, which extends forwards on a level with the anterior ends of the palpebral lobes. Two pairs of narrow, lateral glabellar furrows weakly defined and inward-forward directed; S2 short; S3 somewhat longer and outer end at front edge of eye. Narrow lateral glabellar lobes not inflated. Axial furrows deep and narrow, and continuing as preglabellar furrow only slightly narrower over mid-line. Occipital ring widening medially and with large, but diffuse median tubercle. Anterior cranidial border narrows medially to less than half its maximum width seen in dorsal view, where it tends to be somewhat acuminate, with steeply downturned margin. Palpebral lobes elevated to level of top of glabella and sloping inwards, half length (exsag.) of preoccipital glabella (sag.). Sutures of usual ditomopygid form, with anterior sections tracking axial furrows and extending this line almost to margin, posterior divergent sections cutting off spine-like postocular fixed cheek comprised of the inner part of the posterior border. Surface sculpture of subdued tubercles usually most evident anterior to S1.

Free cheek with short, stout, pointed genal spine about the same length as the eye. The well-defined, convex border maintains constant width until it passes into the spine, downturned sharply along cephalic margin. Posterior border furrow deeper than lateral border furrow, which it meets at not quite ninety degrees; short section of convex posterior border slopes down to genal angle. Subsemicircular eye lobe has high visual surface underlain by a narrow, inflated eye

← Fig. 2. Ditomopygine trilobite *Hentigia ornata* sp. nov. from Kungurian–Roadian (Permian) of Wadi Khawr al Jaramah, Oman. **A**. Enrolled complete specimen, NHMUKPI It 29077; cephalon in dorsal (A_1), lateral (A_2), and anterior (A_3) views; incomplete pygidium and half thorax in dorsal view, showing prominent anterior knob (A_4). **B**. Cephalic shield plus 4 thoracic segments, NHMUKPI It 29078; in dorsal (B_1), anterior (B_2), and lateral (B_3) views. **C**. Enrolled complete specimen, NHMUKPI It 29083; cephalon in dorsal (C_1) and lateral (C_2) views, pygidium and half thorax in dorsal (C_3) and anterior (C_4) views. **D**. Enrolled complete specimen, NHMUKPI It 29081; cephalon in dorsal (D_1) and anterior (D_2) views. **E**. Holotype, enrolled complete specimen, NHMUKPI It 29079; cephalon in dorsal (E_1) and anterior (E_3) views, pygidium and half thorax in dorsal view (E_2), thorax in lateral (E_4) and dorsal (E_5) views. **F**. Enrolled complete specimen, NHMUKPI It 29082; cephalon in dorsal view (F_1), thorax and ventral view of cephalic doublure from beneath, showing rostral plate (F_2). **G**. Cephalic shield plus 1 thoracic segment, NHMUKPI It 29080; in dorsal (G_1), anterior (G_2), and lateral (G_3) views. **H**. Enrolled complete specimen, NHMUKPI It 29084; cephalon in dorsal view. Scale bars 2.5 mm.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

socle about one-quarter the height of the eye itself. The most notable feature of the cheek is the genal field, which mostly consists of an inflated ridge running parallel to the border, the posterior end of which is inflated into a prominent knob in the genal corner, which can be almost spine-like. Sculpture on the dorsal part of free cheek negligible, but several strong raised lines or ridges follow the cephalic margin and become finer on vertical part of border.

Ventral cephalic surface shows doublure which is recurved beneath lateral parts of free cheek, carrying fine lines, anteriorly flattening out as concave connective sutures are approached. Rostral suture bowed forwards. Rostral plate suboval, about two thirds as long as wide, with weakly indicated lateral knobs; it carries a transverse, arcuate furrow across its posterior part, around which the fine ridges elsewhere on the venter do not continue. An enrolled specimen was prepared to reveal the hypostome. The middle body is extremely convex (tr.) and carries pits along the sagittal line, which are flanked on either side by a few, very prominent terrace ridges two of which conjoin across the midline near the posterior end. Round maculae are positioned low down on the middle body at hypostomal mid-length. Anterior wings are vertical and flattened anteriorly, posteriorly triangular, and still steeply upwardly directed. Viewed from the posterior hypostome's appearance resembles an elephant's head with ears extended. Lateral borders are narrow adjacent to the maculae, widening somewhat backwards and merging with flattened posterior border, which has a slightly raised rim, and a tripartite posterior margin. Border furrow narrow and deep except at end of middle body, where it is marked only by a change in slope.

Thorax of nine segments, with well-developed double annuli and broad facets to accommodate tight enrolment. In the enrolled state some specimens show all the pleural tips and a small part of the anterolateral part of the pygidial border, accommodated beneath the cephalic rim (Fig. 3C). Thorax has very little sculpture.

Pygidium with maximum width anteriorly, similar to dorsal axial length, and outline deeply parabolic. Axis of max. transverse width anteriorly like that of adjacent pleural lobe. Pleural field with ten (or faint eleven) ribs and a small triangular terminal area. Of these, the first is inflated and runs out beyond border adjacent to facet. Axis has 22 or 23 axial rings of which the last ten are very narrow (sag.) and may be difficult to discern if the preservation is imperfect. The terminal piece is bisected. Axial profile is box shaped: with flattened tops to the axial rings, where pairs of low tubercles are developed at either side. The sloping flanks of the axis have a broad, depressed area of presumed muscle insertion running the whole length of the axis next to the axial furrow. Border slopes gently downwards, no more than 10% axial length, and very slightly wider posteromedially. Doublure of similar width reflexed horizontally posteriorly, but progressively tucked up towards the dorsal surface anterolaterally; with terrace ridges. Dorsal surface of ribs with weak turberculate sculpture.

Discussion.—In spite of the prepared specimen being enrolled the hypostome was detached, indicating that the sutures were still functional, even though with its long anterior wings it is clear that the hypostome must have been buttressed firmly against the doublure in life. This hypostome is generally similar to that assigned to *Hentigia* by Haas et al. (1980), though the maculae are smaller and nearer the marginal furrow. The indications of strong musculature along the flanks of the pygidial axis suggest firmly anchored longitudinal muscles that may have facilitated very rapid enrollment. The cuticle of this species seems to be thick, so in encapsulated state it would have been well protected.

Iranaspidion elephas differs from the type species in its undivided basal glabellar lobes and weaker tuberculate sculpture; in particular, the distinctive genal ridges terminating posteriorly in bosses provide a good specific character for the new species. Kobayashi and Hamada (1978) assigned a well-preserved pygidium to *I. sagittalis* that has rather coarse tubercles on the pleural ribs which have not been seen on any Omani specimen. Kobayashi and Hamada (1984) described *Pseudophillipsia* (*Nodiphillipsia) hanaokensis* from a cranidium and pygidium originating from the late Permian Akasaka Limestone, Japan, which could well be related to the Oman trilobite under consideration although the illustrations are too poor to judge specific distinctions.

Genus *Simulopaladin* nov.

Type species: *Simulopaladin tridentifer* sp. nov.; see below.

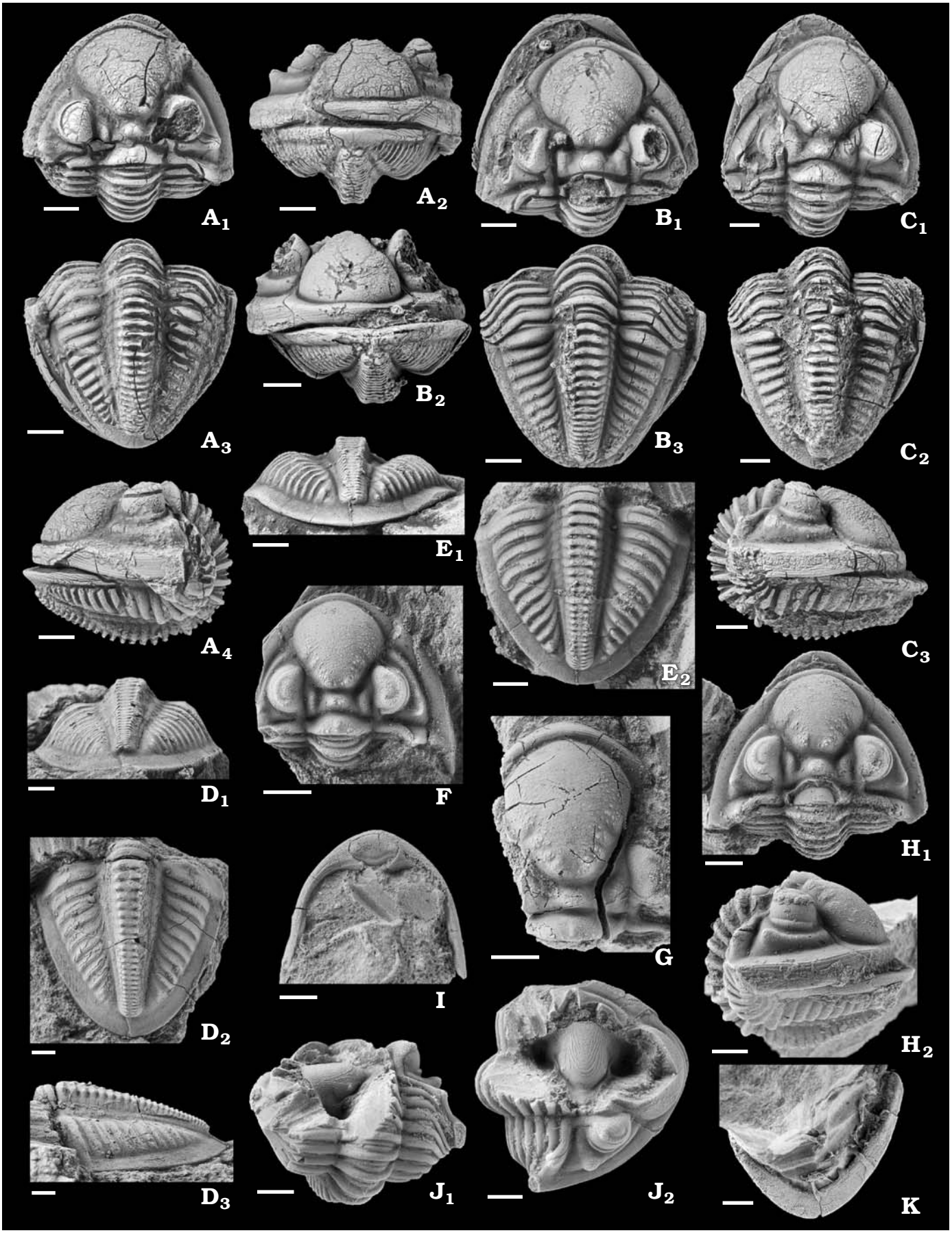
Species included: The type species and *Paladin* (*Paladin*) *simulator* Haas, Hahn, and Hahn, 1980.

Etymology: Combination of Latin *simulo*, resembling and Paladin.

Diagnosis.—Ditomopygine trilobites having low overall convexity, relatively weakly forward-expanding composite anterior glabellar lobe and relatively wide and flat cephalic border; occipital ring with pair of prominent lateral tubercles in addition to occipital tubercle; inflated ridge on free cheek running parallel to border; pygidium with 8–9 pleural ribs and approximately twice as many axial rings that break up into paired tubercles posteriorly. Dorsal surface sculpture lacking.

Fig. 3. Ditomopygine trilobite *Iranaspidion elephas* sp. nov. from Kungurian–Roadian (Permian) of Wadi Khawr al Jaramah, Oman. **A**. Holotype, enrolled → complete specimen, NHMUKPI It 29087; cephalon in dorsal (A_1), anterior (A_2), and lateral (A_4) views; pygidium and half thorax in dorsal view (A_3). **B**. Enrolled complete specimen, NHMUKPI It 29086; cephalon in dorsal (B_1) and anterior (B_2) views; pygidium and half thorax in dorsal view (B_3). **C**. Enrolled complete specimen, NHMUKPI It 29076; cephalon in dorsal (C_1) and lateral (C_3) views; pygidium and half thorax in dorsal view (C_2). **D**. NHMUKPI It 29094; pygidium in anterior (D_1) and dorsal (D_2) views. **E**. NHMUKPI It 29085; pygidium in posterior (E_1) and dorsal (E_2) views. **F**. NHMUKPI It 29090; incomplete cephalon in dorsal view. **G**. NHMUKPI It 29093; cranidium in dorsal view. **H**. Enrolled specimen, NHMUKPI It 29092; cephalon in dorsal view (H_1) and lateral (H_2, showing posterior tubercle on subocular ridge) views. **I**. NHMUKPI It 29088; cephalic doublure in ventral view, showing rostral plate. **J**. Enrolled specimen, NHMUKPI It 29091; in lateral (J_1) and ventral (J_2, showing hypostome) views. **K**. NHMUKPI It 29089; pygidial doublure in ventral view. Scale bars 2.5 mm.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Discussion.—Brezinski (2003, 2008) has summarised research on the genus *Paladin* Weller, 1936. He notes that *Paladin* is a typical genus on the North American palaeoplate during the Carboniferous, where it evolved into a number of endemic species invariably found "in deep water deposits" (Brezinski 2008: 513). A clade identified from western Russia and Ukraine is not considered closely related and only just extends into the early Permian. However, a number of Tethyan later Permian species have been assigned to *Paladin*, and these, as in the case of the species described below, are associated with diverse faunas occupying what was probably a shallow limestone platform. Moreover, they have a deep 1S furrow crossing the glabella cutting off a median basal glabellar lobe, which is a typical ditomopygine construction. It is probable that the similarities between these species and *Paladin* sensu stricto species are a matter of convergence, mostly a question of having a long (sag.) anterior glabellar lobe and flattened cephalic borders. The construction of the occipital ring in the species described below carrying a pair of prominent lateral tubercles is likely to be a good, derived character, although excellent preservation is necessary to see them. These tubercles are homologous with weaker ones on the thoracic axial rings, and paired tubercles on the pygidial axis. A species undoubtedly closely related to *S. tridentifer* was described from Afghanistan by Haas et al. (1980) as *Paladin* (*Paladin*) *simulator* but the reconstruction (1980: 117) fails to show either the occipital tubercles or the genal ridge. The preservation of the holotype is incomplete in the occipital region, so the former omission is understandable; however, the genal ridge seems very prominent and obvious.

The erection of another genus within the already finely divided Ditomopyginae is justified in this case because the several features that originally suggested that Permian species should be assigned to *Paladin* by previous authors serve also to separate these forms from other members of the subfamily. *Paladin* itself may not have survived the Carboniferous (Brezinski 2003). However, *P*. (*Paladin*) *trigonopyge* Osmólska, 1968 from the Asselian (fide Haas et al. 1980: 119) of Spitsbergen does not belong within the new genus as it lacks the typical ditomopygine glabellar structure.

Geographic and stratigraphic range.— Afghanistan, Oman; Artinskian–Roadian (Permian).

Simulopaladin tridentifer sp. nov.

Fig. 4A–F.

Etymology: From Latin *tridentifer*, carrying three teeth; with reference to the occipital structure.

Type material: Holotype: nearly complete enrolled exoskeleton NHMUKPI It 29096. Paratypes: enrolled exoskeleton, NHMUKPI It 29101; cephalon, NHMUKPI It 29100, also with cuticle; cephalic shield, NHMUKPI It 29095; cranidium, NHMUKPI It 29097, 29099 (see below).

Type horizon: Kungurian–Roadian (Permian).

Type locality: Allochthonous Qarari limestone, Wadi Khawr al Jaramah, Oman.

Description.—Cephalon slightly wider than long, of lower convexity (sag.) than other ditomopygines from Oman; glabella slopes gently down along its length. Glabella expands forwards, but less markedly than many ditomopygines, such that the axial furrows adjacent to the posterior parts of the frontal lobe embrace an acute angle of less than 45°. Pyriform frontal glabellar lobe 1.4–1.7 times longer than posterior part of glabella with only very faint indications of lateral glabellar furrows on most specimens. However, one specimen (Fig. 4F) shows the furrows adjacent to the axial furrows better expressed: S2 and S3 very short, narrow and inwardly directed; pair of elongate oval swellings on the posterolateral end of the composite frontal lobe probably represent L2. Posterior furrow S1 deep and short. Basal glabellar lobe divided into central and lateral lobes by deep furrows running nearly exsag, slightly fainter towards rear; median lobe subrectangular; lateral lobes twice as long as wide, attenuated forwards. Occipital ring of similar width (sag.) to posterior lobe, widening medially as defined by more-or-less tripartite occipital furrow, which has a transverse median portion. Notable are the three tubercles on the occipital ring: the occipital tubercle flanked by two other boss-like tubercles towards the outer edge of ring. The latter correspond with a change in slope on the thoracic axis. Facial sutures diverge at about 20° in front of eyes, and behind eyes run for a short distance almost exsagitally before curving outwards sharply to cut off spine-like postocular cheeks, which are spine-like and curved backwards distally. Semicircular palpebral lobes lacking distinct rims, close to one-third glabellar length (exsag.), somewhat elevated. Cranidial border is flat in front of glabella, in dorsal view less than width (sag.) of occipital ring; anteriorly deflected sharply vertically, where fitting below pygidial margin during enrolment. Surface sculpture lacking.

Free cheek divided into inner, convex raised rib-like ridge and outer flattened border separated by a wide, but not unusually deep border furrow. The ridge approximately follows the lower profile of the eye, and is slightly inflated at its posterior end. Since there is a broad depression beneath the eye, the genal ridge makes a prominent and upstanding feature. The enrolled specimen on Fig. 4C shows that genal spines were probably present but the genal angle is vertically broken. Short section of posterior border furrow meets lateral border furrow at close to a right angle. Dorsally flat and wide border very sharply downturned at its margin to form a vertical "wall" about as deep as the border is wide. Anterior edge of this wall slopes towards midline along suture. Eye is underlain by a narrow convex eye socle one-third height of eye anteriorly. Eye is not high compared with that of *Hentigia* with visual surface three times or more as long as high in lateral view. Extent of doublure shown by exfoliated specimen (Fig. 4F), flat under border, and curving upward almost to reach furrow at base of genal ridge.

Nine thoracic segments of similar form along length of thorax, with facets developing at about half way across pleurae that have similar transverse width to axis. Anterior band of thoracic pleura feebly developed adaxially to fulcrum.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

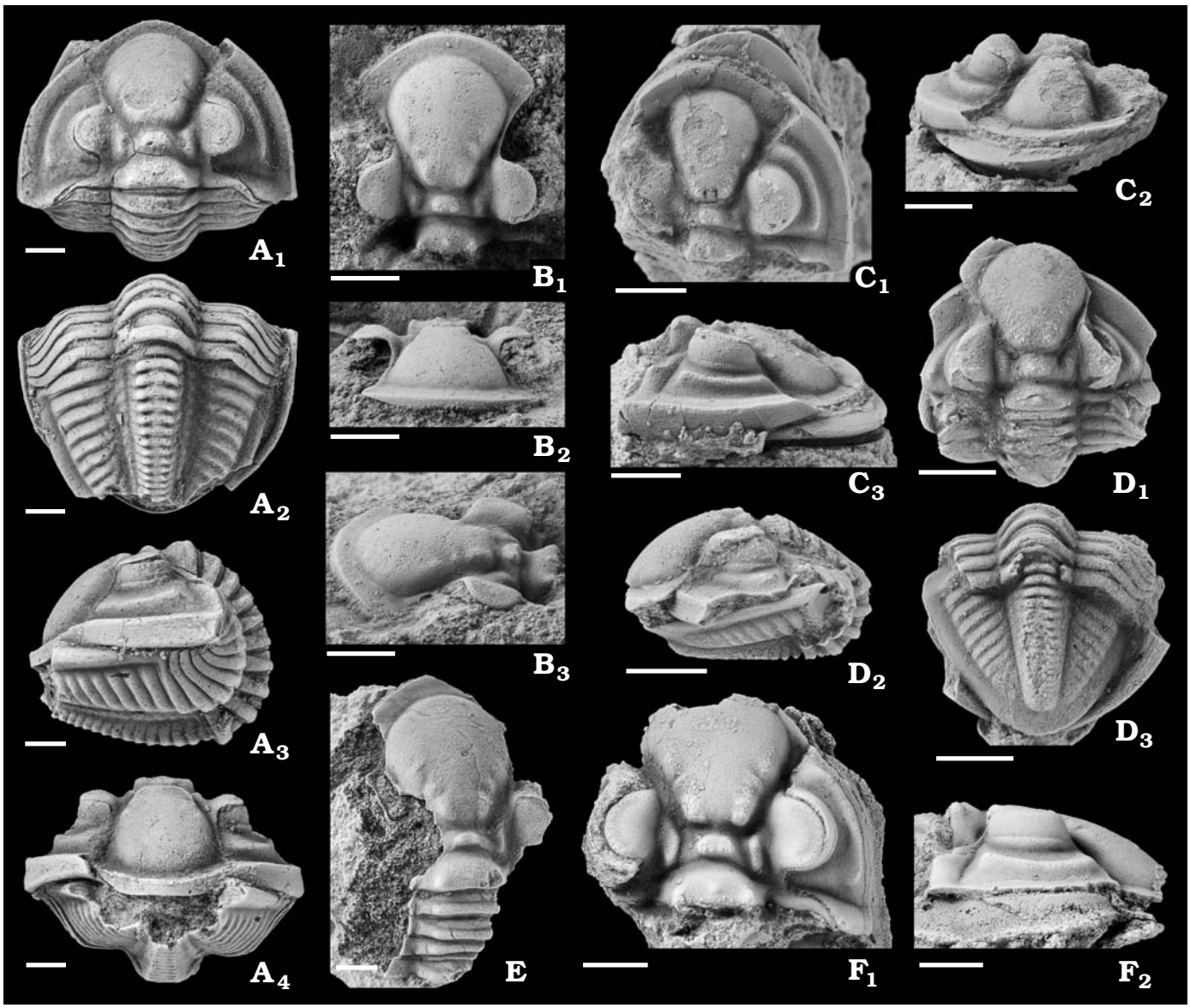


Fig. 4. Ditomopygine trilobite *Simulopaladin tridentifer* sp. nov. from Kungurian–Roadian (Permian) of Wadi Khawr al Jaramah, Oman. **A**. Holotype, enrolled complete specimen, NHMUKPI It 29096; cephalon in dorsal view (A_1); pygidium and half thorax in dorsal (A_2), lateral (A_3), and anterior (A_4) views. **B**. NHMUKPI It 29097; cranidium in dorsal (B_1), anterior (B_2), and lateral (B_3) views. **C**. NHMUKPI It 29100; incomplete cephalon in dorsal (C_1), anterior (C_2), and lateral (C_3) views. **D**. Enrolled specimen, NHMUKPI It 29101; cephalon in dorsal (D_1) and lateral (D_2) views; pygidium and half thorax in dorsal view (D_3). **E**. NHMUKPI It 29099; cranidium and 4 thoracic segments in dorsal view. **F**. NHMUKPI It 29095; cephalon with cuticle showing occipital tubercles in dorsal (F_1) and lateral (F_2) views. Scale bars 2.5 mm.

During enrolment the narrow preannulae are visible, and the tips of the anterior five segments are telescoped beneath the genal border, the posterior four with tips just tucked into anterolateral cephalic doublure. The axial rings show weak indications of lateral tubercles like those on the occipital ring.

Pygidium 1.25 times wider than long, with gently convex border widest postaxially, where it occupies about 15% of pygidial length. Pleural fields show eight, possibly nine ribs, the first extending on to the border, but the posterior part of the pleural field is almost smooth-triangular, and more segments may be present in this area. 16–19 axial rings decrease in size progressively along the whole length of the axis. Only the first 2–4 rings are defined by ring furrows which cross the midline; posterior rings are defined by prominent paired nodes separated by a depressed median smooth area, which decrease in size regularly posteriorly to the sloping axial tip. Flanks of the axis marked by a low, but inflated area for muscle insertion, which can show evidence of segmentation comparable with that on the thoracic axis.

Discussion.—A trilobite from the Artinskian of Afghanistan described by Haas et al. (1980), as *Paladin* (*Paladin*) *simulator* is identical in most respects with the Omani species, and is assuredly congeneric. As noted previously, the occipital ring on this Afghan material is not well-preserved, so the presence or absence thereon of the occipital tubercles typical

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

of *Simulopaladin tridentifer* must remain in doubt. What is not in doubt is that the cephalic border was of similar width to that of *S. tridentifer* and that the genal ridge is present. The pygidial axis is wider on *P.* (*P.*) *simulator* and the axial rings hardly distinguishable, but given the poor state of the unique articulated specimen on which this species is based it is possible that preservational differences might account for these apparent distinctions from *S. tridentifer*. It is also possible that the Omani and Afghan species will prove synonymous, but this is not provable. Since it is most unlikely that new material from the type locality of *P.* (*P.*) *simulator* can be collected (at least in the short term) we consider it best to be cautious about naming for the moment, and the new species name is proposed with that in mind. Several other species can be suggested to belong to *Simulopaladin*. *Paladin opisthops* Kobayashi and Hamada, 1979 (pl. 2: 5), from Thailand, seems to show a similar occipital structure, but the specimen is crushed. The pygidium is shorter, with a wider border, than that of *S. tridentifer*. *Pseudophillipsia pyriformis* Qian, 1977, from the Dalongian (late Permian) of Guizhou Province, China, is based on a fragmentary cephalon, but does show the pyriform composite anterior glabellar lobe and wide border of *Simulopaladin*.

Genus *Acanthophillipsia* Yuan, Zhao, and Mao, 1992

Type species: *Acanthophillipsia guiyangensis* Yuan, Zhao, and Mao, 1992; Maoku Formation, Wordian (Permian) Guizhou Province, China.

Geographical and stratigraphical range.—South China, Oman; Wordian (Permian).

Acanthophillipsia felicitae sp. nov.

Fig. 5F, G.

Etymology: In honour of Felicity Heward, who collected several of the best trilobites.

Holotype: Enrolled exoskeleton NHMUKPI It 29107.

Type horizon: Kungurian–Roadian (Permian).

Type locality: Allochthonous Qarari limestone Wadi Khawr al Jaramah, Oman.

Other material.—One crushed enrolled exoskeleton, NHMUKPI It 29102; cranidium, NHMUKPI It 29146; from the type locality.

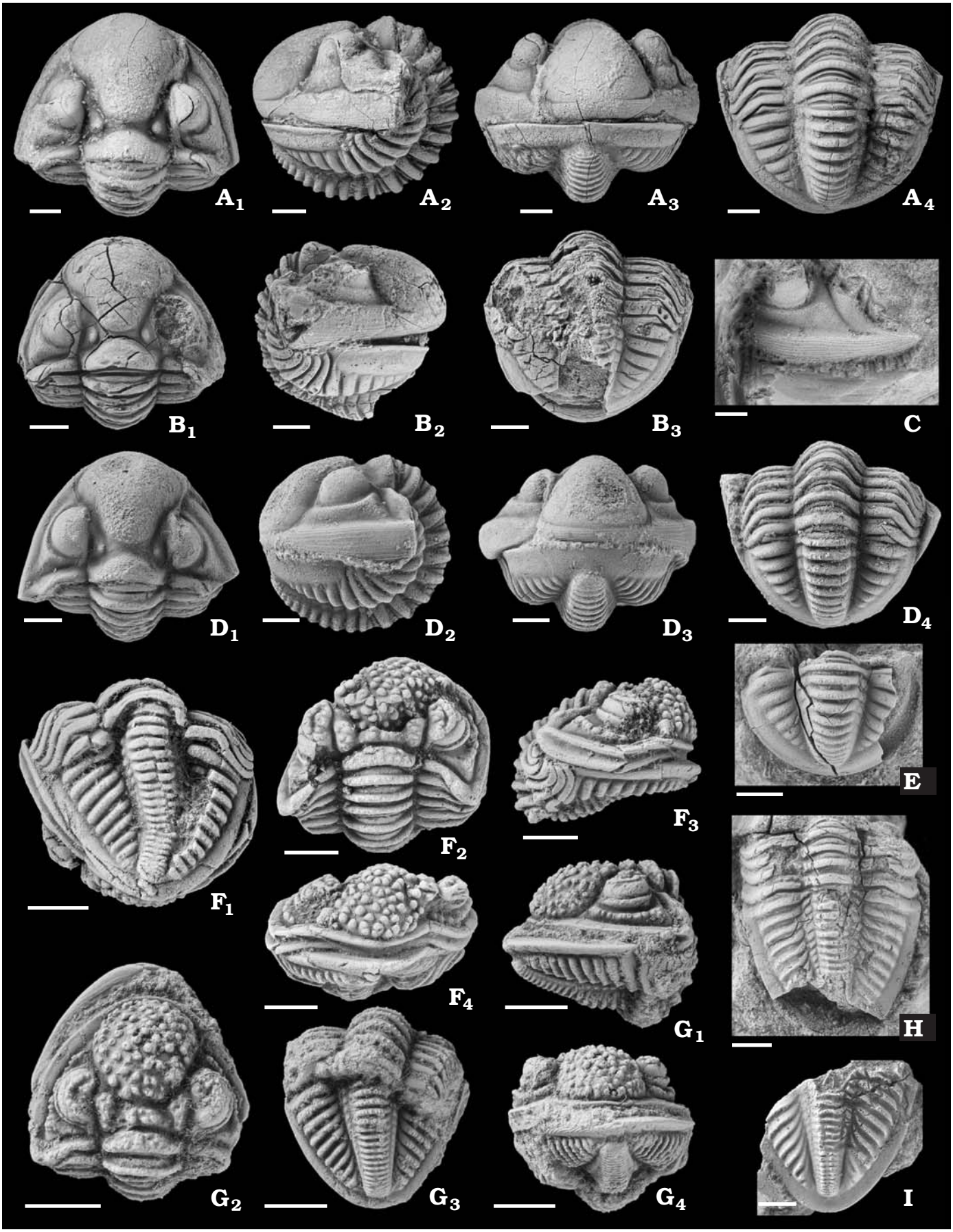
Description.—The material of this species is limited, but well-preserved and complete, although the larger example is crushed. Ditomopygine glabellar structure, with a prominent S1 cutting off a basal glabellar lobe, and inflated lateral basal lobes, which are wedge shaped, wider forwards, and much longer (exsag.) than the occipital ring (sag.). All the glabella, including the occipital ring, is covered with coarse tubercles. Anterior glabellar lobe is as long as wide and expands forwards with broadly rounded front to anterior border, which is narrow and almost tucked beneath frontal lobe. The glabellar tubercles are prominent and round, about eight across the glabellar width at its widest. They serve to obscure the glabellar furrows. Occipital ring widest medially and also carrying somewhat more subdued tubercles. The material to hand does not show the facial sutures clearly. Length of eyes (exsag.) about 40% cephalic length (sag.) subtended by prominent crescentic palpebral lobe which also carries tubercles. Very prominent and convex eye socle two-thirds as high as eye, beneath which is a deep and wide furrow. Between this furrow and the marginal border furrow the genal field is a notably inflated ridge carrying a single line of coarse tubercles more or less parallel with socle. The narrow (dorsal view) anterior border itself does not carry tubercles. Posterior border widens laterally where curved backwards. Genal spines lacking, but genal angle rounded. Much of the genal border is nearly vertical, but divided lengthways by a prominent furrow that extends around perimeter of cephalon (Fig. 5F). On this part there are no tubercles. It is possible that the groove served a coaptative function to receive the margin of the pygidium, but neither specimen is sufficiently undisturbed to prove this.

Nine thoracic segments with distal parts of pleurae steeply downturned. Tubercles are present on thoracic axial rings, but are much finer than those on the cephalon. Pygidium of usual ditomopygine form. Pygidium on the holotype is slightly displaced beneath the thorax, possibly concealing one ring anteriorly. Although twisted, the larger pygidium shows 9 pairs of deeply defined and convex ribs, and up to 21 axial rings, of diminishing size posteriorly. A probable equivalent number of muscle impressions along the flanks of the pygidial axis become hard to distinguish posteriorly. Surface tuberculation on pygidium of relatively fine scale on ribs and on the first four or five axial rings, particularly. Pygidial border narrow and convex, and entirely without tubercles.

Discussion.—In spite of the small number of specimens available, this species is known from a well-preserved holotype and a larger, crushed example, and is sufficiently distinctive to name formally. Indeed, it is strikingly like a Silurian encrinurid at first glance. It is immediately set apart from all others in Oman by its very coarse cephalic tuberculation. In this feature it is like the genus *Acanthophillipsia*, described from S. China (Guizhou Province) from four species of Wordian age (Yuan et al. 1992). In particular, the type species,

Fig. 5. Trilobites from Kungurian–Roadian (Permian) of Wadi Khawr al Jaramah, Oman (except C, see below). **A**–**E**. Proetid trilobite *Triproetus bonbon* sp. nov. **A**. Holotype, enrolled complete specimen, NHMUKPI It 29103; cephalon in dorsal (A_1), lateral (A_2), and anterior (A_3) views; pygidium and half thorax in dorsal view (A_4). **B**. Enrolled specimen, NHMUKPI It 29104; cephalon in dorsal (B_1) and lateral (B_2) views; damaged pygidium and half thorax in dorsal view (B_3). **C**. NHMUKPI It 29106, cheek from Jebel Qarari, Oman. **D**. Enrolled complete specimen, NHMUKPI It 29105; cephalon in dorsal (C_1), lateral (C_2), and anterior (C_3) views; pygidium and half thorax in dorsal view (C_4). **E**. NHMUKPI It 29141; pygidium in dorsal view. **F**, **G**. Ditomopygine trilobite *Acanthophillipsia felicitae* sp. nov. **F**. Enrolled complete specimen, NHMUKPI It 29102; pygidium and half thorax in dorsal view (F_1); cephalon in dorsal (F_2), lateral (F_3), and anterior (F_4) views. **G**. Holotype, enrolled complete specimen, NHMUKPI It 29107; pygidium and half thorax in lateral (G_1), dorsal (G_3), and anterior (G_4) views; cephalon in dorsal view (G_2). **H**–**I**. Ditomopygine sp. indet. **H**. NHMUKPI It 29108; pygidium in dorsal view. **I**. NHMUKPI It 29109; pygidium in dorsal view. Scale bars 2.5 mm. →

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Acanthophillipsia guiyangensis, compares with the new species in its particularly coarse, rounded cephalic tubercles. However, neither this species, nor the other three species, have such well-developed lateral basal glabellar lobes as the species from Oman. *Acanthophillipsia guiyangensis* also has additional lines of tubercles on the genal field and tubercles present on the pygidial border. A remarkable groove running along the cephalic border in *A. felicitae* can be matched on the cheek of *A. abrota* Yuan, Zhou, and Mao, 1992 (pl. 2: 9). This structure seems unmatched on any other ditomopygine, and may prove of generic importance. The Oman record is the first time *Acanthophillipsia* has been recorded outside China.

Ditomopygine sp. indet.

Fig. 5H, I.

Material.—Two pygidia, one with four thoracic segments attached, NHMUKPI It 29108, 29109; from Kungurian–Roadian (Permian) allochthonous Qarari limestones of Wadi Khawr al Jaramah, Oman.

Discussion.—A further ditomopygine is present from pygidia in the collection, but without associated cephalic parts its generic assignment cannot be determined. It is distinguished by two features: each pygidial rib has an acute crest running along its length, and the muscle pads flanking the axis, and related to the axial rings, are particularly strongly developed, with furrows between them as strong as those separating the axial rings. These pygidia fall outside the range of variation of other species from the same fauna, but we are compelled to leave its taxonomy uncertain.

Family Proetidae Salter, 1864

Genus *Triproetus* Kobayashi and Hamada, 1979

Type species: *Neoproetus* (*Triproetus*) *subovalis* Kobayashi and Hamada, 1979; Asselian (Permian), northern Thailand.

Discussion.—The distribution of *Triproetus* has been summarised by Owens (2003) who also reassigned to this genus some species that had been placed elsewhere. We follow his interpretation herein, which allows for considerable variation in the size of the basal glabellar lobes. These are smallest in the new species described below. There also appears to be variation in the length of the genal spines. All species share a comparatively short and transverse pygidium with usually six pleural ribs.

Triproetus bonbon sp. nov.

Fig. 5A–E.

Etymology: The perfectly enrolled trilobite resembles a boiled sweet (bonbon).

Type material: Holotype: nearly complete enrolled exoskeleton, NHMUKPI It 29103. Paratypes: enrolled exoskeletons, NHMUKPI It 29104, 29105; pygidium, NHMUKPI It 29141, 29142, 29143, unfigured; free cheek, NHMUKPI It 29106, 29144, unfigured.

Type horizon: Kungurian–Roadian (Permian).

Type locality: Allochthonous limestone Wadi Khawr al Jaramah, Oman. An appropriate free cheek is from the Roadian of Jebel Qarari.

Diagnosis.—*Triproteus* with small, prominent, subcircular basal glabellar lobes; preglabellar furrow almost effaced medially; genal spines stout; fine tuberculate sculpture on glabella.

Description.—This is probably the best-preserved material of the genus known. The articulated specimens are perfectly and tightly enrolled to a subspherical state. Genal spines are broken off in this material, but an isolated free cheek proves that they were stout, triangular. Cephalon with arched outline, 1.6 times as wide as long (dorsal view, approx. allowance for damaged genal spines). Glabella is swollen anteriorly and bulges forwards to slightly overhang the anterior border in lateral aspect. The pyriform anterior glabellar lobe has maximum transverse width just behind the anterior cephalic margin, this being close to the sagittal length of the lobe in dorsal view. The occipital ring is one-third of this length medially, and its transverse width is slightly less than the maximum glabellar width. It is wider medially, where it slopes downwards forwards, and carries a small medial occipital tubercle posterior to the mid-point of the ring. Basal lobes of the glabella small but prominent, the inflated part nearly circular, with weaker parts extending further forwards, the whole outlined by deep furrows on all sides, and linked by the mid part of the occipital furrow. Deep axial furrows slightly sinuous at level of eyes, shallowing and curving outwards anteriorly, and preglabellar furrows shallowing still further after curving around round anterolateral corners of glabella to fade out almost completely at the mid line. Anterior border continues downward slope of front of glabella and carries about ten fine transverse raised lines. Anterior fixed cheeks reduced to narrow selvage. Posterior fixed cheeks spinelike, with acute distal border portions, anteriorly converging at a low angle to the sag. line before describing outer edge of prominent elevated palpebral lobes; thence diverging outwards around glabella before cutting obliquely across anterior border seen in anterior view (Fig. $5A_3$). Fine tuberculate sculpture on glabellar surface.

Free cheek steeply attached and sloping down in life position. It is divided into pleural field and a steep border of similar widths, the latter wider than the cranidial border and widening still further backwards where it forms a nearly vertical "wall" at the cephalic edge. The border furrow is a deep notch in the profile of cheek and continues into the proximal part of the genal spine. Posterior border furrow is quite deep, but fades rapidly towards the genal angle. In plan view this angle is about 60°. The curved, high eye lobe is half as long (exsag.) as the frontal lobe of the glabella (sag.) in dorsal view. The base of the eye is marked by a furrow that follows its outline, but there is no inflated eye socle. Lateral border also carries raised lines parallel to its margin, extending into genal spine.

Thorax of nine segments. Each segment is similar and thorax does not taper backwards. Axial ring convex (tr.) wider than pleura, with very prominent "doubled" annulus and preannulus. Anterior pleural convex band one-third width (exsag.) of posterior band, the former concealed beneath

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

down turned pleural tips during enrolment. Pleural tips blunt. Facets telescoped during enrolment, and at least half pleural width. During enrolment the tips of the anterior five segments are tucked beneath the posterior cephalic border. and lie alongside the steep lateral border, showing that its doublure must be reflexed steeply upwards. Curvature of the enrolled thoracic axial rings continues into the pygidial axis, which therefore has a curved profile.

Pygidium 60% as long as wide (most ditomopygids 80% or more). Convex axis just wider than pleural lobes at front, tapering gently to a short, broadly rounded terminal piece. 11 or perhaps 12 long (tr.) narrow (sag.) rings are present, three or four times wider than sag. length. Only 6–7 pleural ribs are present, decreasing in transverse width, the last very short. Structure of the first three ribs is like that of thoracic pleurae with narrow posterior band. Deep inter-rib furrows tend to look a little concave posteriorly. Neither axis nor ribs extend on to convex and downward sloping border, the border furrow mostly being a sharp change in slope. The border has a narrow marginal convex rim. Weak tuberculate surface sculpture especially on axis.

Discussion.—The new species is similar in most features to the type species from Thailand, *Triproetus subovalis* Kobayashi and Hamada, 1979, although the type material is fragmentary. However, the small, rounded posterior glabellar lobes of the Oman species differ from the more generally inflated triangular lobes of the former, while the pygidial border of the type species is conspicuously more convex than is the case in *T. bonbon*, and its anterior pygidial pleural ribs are unfurrowed. Owens (2003: 383) reassigned *Paladin* (*Neokaskia*) *borealis* Kobayashi, 1987, from the Kapp Starostin Formation, Svalbard, to *Triproetus*, which is of similar age to the species reported here. Bruton (1999) provided a full description of this species showing it is indeed similar to the new species, but obviously differs in its larger basal glabellar lobes, reduced genal spines, and pygidium having a wider border, more tapering axis and deep border furrow. Bruton (1999: pl. 2: 1–3) additionally figured an enrolled specimen of *Triproetus* under open nomenclature from the Qarari Limestone of northeastern Oman. This specimen has large basal glabellar lobes; and the pygidial border does not slope so steeply as in *T. bonbon* and there seem to be 8, or possibly 9 axial rings. Although closely similar it is unlikely to be conspecific with *T. bonbon*. Owens (1983: pl. 5: 12, 13) reillustrated the type specimen of *Griffithides brevicauda* Gheyselinck, 1937, a species from south central Timor that has subsequently been variously accommodated in the genera *Paladin*, *Paladin* (*Neokaskia*) or *Triproetus* by later authors, but is very similar to the species described above and must be congeneric. This specimen is apparently slightly distorted such that the basal glabellar lobe on the left is larger—or at least more clearly seen—than that on the right, and this character cannot objectively be used in relation to *T. bonbon*, which it closely resembles otherwise. A persuasive point of difference between *T. brevicaudus* and *T. bonbon* is the relatively large size of the eye lobe of the former, such that there is room for very little genal field altogether; Gheyselinck (1937) does not mention a genal spine on *T. brevicaudus*, but it was conceivably broken off. Viewed dorsally, the cephalic border of *T. brevicaudus* is wider than that of *T. bonbon*. Pygidia of these two species are also very similar, but there seem to be only ten axial rings in *T. brevicaudus*.

Morphological disparity in the last trilobites

It is often assumed that the trilobites were in decline during the latest, Permian phase of their long Palaeozoic history. While it is correct that overall family diversity had been declining slowly since the late Devonian mass extinction events, this is not a necessarily concomitant with a corresponding decrease in morphological disparity—the range of designs open to the group as a whole. Although the new trilobites described here are all proetoids, they do show a range of morphologies that suggest that even at this late stage in their history trilobites were adapted to several ecological niches. They are all relatively small species, which makes it likely that there were now no trilobites occupying the role of predator/scavengers of large prey items. However, all the Permian species have attached hypostomes in the impendent hypostomal condition that were likely to have been strongly buttressed (as shown by the long anterior wings), together with inflated anterior glabellar lobes, associated with an inflated stomach. These features have been linked with the manipulation and ingestion of small prey and opportunistic scavenging. Large eyes with acute vision are also appropriate for such a habit. All species had thick cuticles, and several features associated with tight enrolment, so there is no reason to suppose that they could not withstand predation. Their overall morphology, and especially that of *Triproetus*, is of the phacopoid type so abundant in the Devonian, but on a smaller scale, and the eyes are holochroal rather than schizochroal. However, between species there is a range of additional differences. For example, *Simulopaladin* has relatively low convexity and wide borders, and remarkable paired tubercles on the axis, the function of which is not known. The lack of strong surface sculpture on this species may be contrasted with *Acanthophillipsia*, a powerfully tuberculate genus superficially like an encrinurid. The species of *Hentigia* from Oman is also coarsely tuberculate, but mostly on the glabella, and these tubercles are of a flattened type seen on few other trilobites. The anteromedian inflation of the first pygidial rib is another unusual feature of this species. The morphology of *Iranaspidion* lies rather between that of *Hentigia* and *Simulopaladin*, and both the Omani *Iranaspidion* species and *Simulopaladin* species share a curious inflated ridge on the free cheek paralleling the eye, in the former case terminating in a prominent posterior knob.

These distinctive characters show that the trilobites were still capable of new, and perhaps unique exoskeletal inno-

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

vations even at this late stage in their history. Though they were now operating within the constraints exercised by their proetoid ancestry, and in a shallow-water carbonate setting, a number of species could live together, each displaying sufficiently distinctive autapomorphies to imply some special ecological specialisation. From this aspect, they were not in decline.

Acknowledgements

Thanks are due particularly to Di Clements (Natural History Museum, London, UK) for help with curation of the material, to Phil Hurst (Natural History Museum, London, UK) for photography, and to Willie Quizon (Petrogas E&P, Muscat, Oman) for helping arrange and draft the figures. Georg Warrlich (Sarawak Shell, Kuching, Malaysia) first alerted us to the Wadi Khawr al Jaramah localities. Felicity Heward helped with collecting. Giles Miller (Natural History Museum, London, UK) kindly processed samples for conodonts, and Lance Lambert (University of Texas, San Antonio, USA) is thanked for identifications.

References

Beauchamp, W.H., Ries, A.C., Coward, M.P., and Miles, J.A. 1995. Masirah Graben, Oman: A hidden Cretaceous rift basin? *Bulletin of the American Association of Petroleum Geologists* 79: 864–879.

Becq-Giraudon, J.-F. and Pillevuit, A. 1995. Trilobites of Upper Permian from northern Oman. *Eclogae Geologicae Helvetiae* 66: 761–776.

Brezinski, D.K. 2003. Evolutionary and biogeographical implications of phylogenetic analysis of the late Palaeozoic trilobite *Paladin*. *Special Papers in Palaeontology* 70: 363–375.

Brezinski, D.K. 2008. Phylogenetics, systematics, palaeoecology and evolution of the trilobite genera Paladin and Kaskia from the United States. *Journal of Paleontology* 84: 511–527.

Bruton, D.L. 1996. Permian trilobites from Alseløya, Svalbard. *Geologica et Paleontologica* 33: 191–201.

Fortey, R.A. and Owens R.M. 1975. Proetida—a new order of trilobites. *Fossils and Strata* 4: 227–29.

Gauri, K.L. 1965. Uralian stratigraphy trilobites and brachiopods of the western Carnic Alps (Austria). *Jahrbuch der Geologischen Bundesanstalt* 11: 1–94.

Gheyselinck, R.F.C.R. 1937. *Permian Trilobites from Timor and Sicily.*108 pp. Scheltema and Holkema, Amsterdam.

Goldring, R. 1957. *Pseudophillipsia* (Tril.) from the Permian (or Uralian) of Oman, Arabia. *Senckenbergiana Lethaea* 58: 195–210.

Haas, W., Hahn, G., and Hahn, R. 1980. Perm-Trilobiten aus Afghanistan *Palaeontographica Abteilung A* 169: 73–127.

Hauser, M., Martini, R., Matter, A., Krystyn, L., Peters, T., Stampfli, G., and Zaninetti, L. 2002. The break-up of East Gondwana along the northeast coast of Oman: evidence from the Batain basin. *Geological Magazine* 139: 145–157.

Hupé, P. 1953. Classe de Trilobites. *In*: J. Piveteau (ed.), *Traité de Paleontologie III*, 44–246. Masson, Paris.

Immenhauser, A., Schreurs, G., Peters, T., Matter, A., Hauser, M., and Dumitrica, P. 1998. Stratigraphy, sedimentology and depositional environments of the Permian to uppermost Cretaceous Batain Group, eastern-Oman. *Eclogae Geologicae Helvetiae* 91: 217–235.

Immenhauser, A., Schreurs, G., Gnos, E., Oterdoom, H.W., and Hartmann, B. 2000. Late Palaeozoic to Neogene geodynamic evolution of the northeastern Oman margin. *Geological Magazine* 137: 1–18.

Jell, P.A. and Adrain, J.M. 2003. Available generic names for trilobites. *Memoirs of the Queensland Museum* 48: 331–553.

Kobayashi, T. 1987. A Permian trilobite from Spitsbergen, Norway, with a note on the biogeographic bearing of genus *Neoproetus*. *Proceedings of Japan Academy Series B* 63 (5): 139–142.

Kobayashi, T. and Hamada, T. 1978. Two new Upper Permian trilobites from central Iran. *Proceedings of the Japan Academy Series B* 54 (4): 157–162.

Kobayashi, T. and Hamada, T. 1979. Permo-Carboniferous trilobites from Thailand and Malaysia. *Geology and Palaeontology of Southeast Asia* 20: 1–21.

Kobayashi, T. and Hamada, T. 1984. The Middle and Upper Permian trilobites from the Akasaka LImestones in Gifu Prefecture, west Japan. *Proceedings of the Japan Academy* series B 69 (1): 1–4.

Lerosoy-Aubril, R. and Angiolini, L. 2009. Permian trilobites from Antalya Province, Turkey, and enrollment in Late Palaeozoic trilobites. *Turkish Journal of Earth Science* 18: 429–448.

Leven, E.J.A. and Heward, A.P. 2013. Fusulinids from isolated Qarari Limestone outcrops (Permian) occurring among Jurassic–Cretaceous Batain Group (Batain Plain, Eastern Oman). *Rivista Italiana di Paleontologia e Stratigrafia* 119: 153–162.

Liebermann, B.S. 1994. Evolution of the trilobite subfamily Proetinae and the origin, evolutionary affinity, and extinction of the Middle Devonian proetid fauna of Eastern North America. *Bulletin of the American Museum of Natural History* 223:1–176.

Mount, V.S., Crawford, R.I.S., and Bergman, S.C. 1998. Regional structural style of the Central and Southern Oman Mountains: Jebel Akhdar, Saih Hatat and the Northern Ghaba Salt Basin. *GeoArabia* 3: 475–490.

Oehlert, M.D. 1886. Étude sur quelques trilobites du groupe de Proetidae. *Bulletin de la Société d'Étude des Sciences d'Angers, Nouvelle Serie* 15: 121–143.

Osmólska, H. 1968. Two new trilobites from the Treskelodden Beds of Hornsund (Vestspitsbergen). *Acta Palaeontologica Polonica* 13: 605–614.

Owens, R.M. 1983. A review of Permian trilobite genera. *Special Papers in Palaeontology* 30: 15–41.

Owens, R.M. 2003. The stratigraphical distribution and extinctions of Permian trilobites. *Special Papers in Palaeontology* 70: 377–397.

Peters, T., Al-Battashy, M., Bläsi, H., Hauser, M., Immenhauser, A., Moser, L., and Al-Rajhi, A. 2001. *Geological map of Sur and Al Ashkharah, Sheet NF 40-8F and Sheet NF 40-12C, Scale 1:100 000, Explanatory Notes*. 95 pp. Sultanate of Oman Ministry of Commerce and Industry, Directorate General of Minerals, Muscat.

Qian, Y.-Y. 1977. Upper Permian trilobites from Qinglong and Anshun of Guizhou. *Acta Palaeontologica Sinica* 16: 279–286.

Salter, J.W. 1864. A monograph of British trilobites, Part 1. *Palaeontographical Society Monographs* 16: 1–80.

Shackleton, R.M., Ries, A.C., Bird, P.R., Filbrandt, J.B., Lee, C.W., and Cunningham, G.C. 1990. The Batain Melange of NE Oman. *In*: A.H.F. Robertson, M.P. Searle, and A.C. Ries (eds.), The Geology and Tectonics of the Oman Region. *Geological Society of London Special Publication* 49: 673–696.

Walch, J.E.I. 1771. *Die naturgeschichte der verteinerungen, Dritter Theil*. 235 pp. P.J. Felstecker, Nürnberg.

Webster, G.D. and Sevastopulo, G.D. 2007. Paleogeographic significance of Early Permian crinoids and blastoids from Oman. *Paläontologische Zeitschrift* 81: 399–405.

Weller, J.M. 1936. Carboniferous trilobites and genera. *Journal of Paleontology* 10: 704–714.

Yuan, J.-L., Zhao, Y.-L., and Mao, J.-Q. 1992. On a new genus *Acanthophillipsia* of Ditomopyginae Hupé, 1953, from Lower Permian of Guiyang, South China. *Acta Palaeontologica Sinica* 31: 48–61.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use