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First occurrence of a phacopid trilobite faunule from the Upper Devonian of Saoura Valley, Algeria and biodiversity fluctuations

CATHERINE CRÔNIER*†, FATIMA ZOHARA MALTI‡, ANGELA FRANÇOIS*,
MADANI BENYOUCEF§ & DENISE BRICE¶

*UMR8217, Géosystèmes, Université Lille 1, Sciences de la Terre, 59655 Villeneuve d'Ascq Cedex, France
‡Department of Industrial Chemistry, Béchar University, BP 417, Béchar 08000, Algeria
§Department of Earth Sciences, Mascara University Center, BP 305, Mascara 29000, Algeria
¶Université Catholique, Faculté Libre des Sciences et Technologies, 41 rue du Port, 59046 Lille cedex, France

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Abstract – Phacopid trilobites are relatively widespread in Devonian deposits of north Gondwana and some have been collected from several sections of the Saoura Valley in SW Algeria. New occurrences of phacopids assigned to *Trimerocephalus*, *Dianops* and *Phacops sensu lato* are described from this area and comparisons are made with closely allied species from Morocco and Europe. The trilobite assemblages of the 'Argiles de Marhouma' Formation are considered to be Frasnian–Famennian in age. These new occurrences have been integrated into an analysis of Upper Devonian phacopid biodiversity. Diversity fluctuations reflect environmental changes, bioevents and stratigraphic turnovers throughout the Upper Devonian. Peak diversity was attained after the post-Kellwasser event.

Keywords: trilobites, Phacopidae, Upper Devonian, Algeria, curves.

1. Introduction

Trilobites were relatively abundant and diverse in marine Devonian habitats. In particular, the Late Devonian period is important for the phacopid development because the main groups of reduced-eyed or blind phacopids arose at that time, notably in the north peri-Gondwanan margin. The publications of Richter & Richter (1926, 1955), Maksimova (1955), Osmólska (1958, 1963), Chlupáč (1966, 1977) and Feist *et al.* (2009) have been major contributions to our current knowledge of Gondwanian Upper Devonian phacopids.

The present paper contributes to the systematic study of the Upper Devonian phacopids. The discovery of new occurrences assigned to *Trimerocephalus*, *Dianops* and *Phacops sensu lato* from SW Algeria gives us the opportunity to understand these forms more fully. These phacopines lend a particular dimension to the Upper Devonian trilobite fauna; they are among the youngest representative phacopines, and those with the least number of ocular lenses (Crônier *et al.* 2011). The gradual visual complex regression leading to blindness is an evolutionary trend often observed in different lineages of trilobites, notably in proetids and phacopids (Richter & Richter, 1926; Feist & Clarkson, 1989; Crônier *et al.* 2004). This paedomorphic trend is thought to be related to environmental changes such as a global sea-level rise (Feist, 1995).

Additionally, the palaeobiodiversity of Upper Devonian phacopids has been explored through diversity curves in order to understand their fluctuations in time. These fluctuations can also be linked to environmental changes.

2. Geological setting and material

2.a. Local geological succession

The material originates mostly from the 'Argiles de Marhouma' Formation of the Saoura Valley, Ougarta Basin, Algerian Sahara, regarded as Frasnian–Famennian in age on the basis of ammonoids, brachiopods, conodonts and trilobites (Malti *et al.* unpub. data). It has been collected from several sections (Tamtert-Zereg, Béchir, Cheffar-El-Ahmar and Idhir) located to the SE of Beni-Abbès (30 km; Fig. 1), except for the section Gara Diba which is located at the entrance to Beni-Abbès city.

This area belongs to the major structural unit of the Saharan Platform. It comprises a Precambrian basement unconformably overlain by thick sediments occurring in a number of Palaeozoic basins, including the basin of Ougarta which comprises the Marhouma area.

The 'Argiles de Marhouma' Formation is represented by calcareous condensed red nodular or pseudonodular limestones rich in goniatites and known as 'griottes' or 'Goniatitico-rosso', which indicate an epicontinental platform (Benhamou *et al.* 2004). This facies is similar to the'Ammonitico-rosso' of the Mesozoic Tethysian area. In both cases, these facies are linked to the slope deposits of deepening basins along their transition towards the platform.

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†Author for correspondence: catherine.cronier@univ-lille1.fr

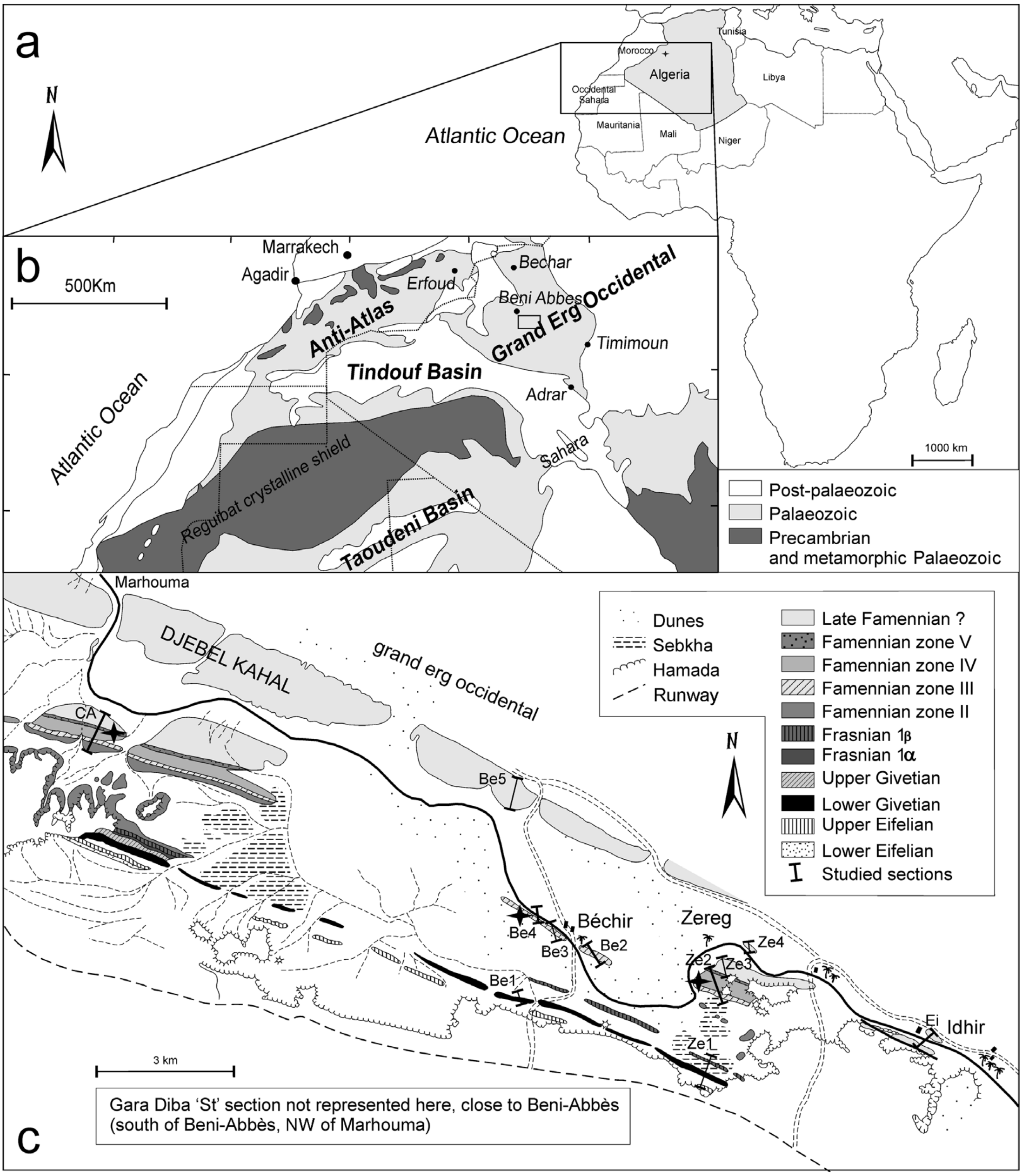

Figure 1. (a, b) Geographical and geological locations of the Marhouma area, SE of Beni-Abbès (30km), Saoura Valley, Ougarta Basin, Algeria. (c) Location of studied sections (Tamtert-Zereg *Ze*, Béchir *Be*, Cheffar-El-Ahmar *CA* and Idhir *Ei*).

These red nodular limestones are found at Tafilalt–Maider in Morocco as far as the Mountains of Ougarta (Saoura) in Algeria.

This spatial extension was controlled by a distension phase of the Hercynian orogeny as understood by modelling the physical geography of the basins with facies 'griottes' in an insular palaeogeography (Benhamou *et al.* 2004). After the Frasnian, the extension regime changed and a contraction phase at the end-Famennian led to a silico-clastic sedimentation of the Strunian. An estimation of the thickness of these Famennian deposits was given recently as 260 m by Ouali Mehadji *et al.* (2012) for the 'Argiles de Marhouma' Formation.

According to Malti *et al.* (unpub. data), the 'Argiles de Marhouma' Formation consists of four successive members: the calcareous-clay member (Member 1; Frasnian); the silty-clay with 'griotte' nodule member (Member 2; Famennian); the 'griotte' limestone member (Member 3; Famennian); and

Stage	Substage	Fm	Member		Submember	Trilobite content	Cephalopod zones (do)	Remarks
UPPER DEVONIAN	Famennian	'Argiles de Marhouma' Formation	Member 4	clay with 'griotte' layers		1 thoracopygon of *Phacops sensu lato* (Ei)	V-VI?	IV-V for member 3 according to *Procymaclymenia* sp. (ammonoid)
			Member 3	'griotte' limestone	c	1 cephalon + 4 thoracopygons of *Phacops s.l.* (Ze) *Dianops* sp. (Ze) *D. typhlops* (Ze), *Phacops zeregensis* sp. nov. (Ze) 3 cephalothoraxes of *Dianops vicarius* (Ze) 1 cephalon of *Dianops algeriensis* sp. nov. (Ze) 2 thoracopygons of *Phacops s.l.* (Ze) *Trimerocephalus (Trifoliops) nigritus* (Be)	IV (V) IV II-III	IV or IV/V according to ammonoids (*Erfoudites sp. Platyclymenia sp., Procymaclymenia sp., Cymaclymenia sp.*); determ. D. Korn Late early Fa (II/III) confirmed by *Armatites* sp. (ammonoid)
					b	*Phacops tamtertensis* sp. nov. (Ze)	II-III	Late early Fa (II/III) confirmed by *Armatites* sp. (ammonoid)
					a	1 counterpart of *T.? (Trifoliops)* (CA)	II-III	
			Member 2	silty-clay with 'griotte' nodules	b	*Trimerocephalus caecus* (CA) *Trimerocephalus (Trifoliops) nigritus* (St)	II-III II-III	II according to *Palmatolepis minuta subtilis* (conodont)
	Frasnian *p.p.*				a	1 thoracopygon of *T.? (Trifoliops)* (CA) 1 cephalon of *Houseops?* cf. *cryphoïdes* (St)	II-III I?	II according to *Evanidisinurostrum saouraensis* (brachiopod)
			Member 1	calcareous-clay			I	

Figure 2. Lithostratigraphic column of the 'Argiles de Marhouma' Formation and stratigraphical location of studied trilobites (from sections Tamtert-Zereg *Ze*, Béchir *Be*, Cheffar-El-Ahmar *CA*, Idhir *Ei* and Gara Diba *St*).

the clay with 'griotte' layer member (Member 4; Famennian). These members can be divided into submembers (Fig. 2). This formation contains abundant and diverse faunas, the macrofauna comprising ammonoids, brachiopods (Brice *et al*. unpub. data) and trilobites (this paper), and the microfauna consisting of conodonts (Wendt *et al*. 2006) and ostracodes (Casier, 1985).

2.b. Trilobite content

In the published fauna previously reported from Algeria, some Upper Devonian trilobites have been cited by Haug (1903) with *Trimerocephalus caecus* from Beni-Abbès and by Menchikoff (1930) with *Phacops s.l. granulatus* from Ouarourout and Bou Mehaoud and *Omegops bergicus* from the 'oued' Khorb el Ethel. There is also a drawing of a cephalon of *Phacops* sp. from Tamtert (Termier & Termier, 1950; pl. CCVI, fig. 16). As observed in other areas from the northern peri-Gondwanian margin such as Morocco (Crônier & Feist, 1997; Crônier & Clarkson, 2001), the phacopid remains are in fact relatively abundant and well preserved. The phacopid diversity is high and many species are still being described. Phacopids include disarticulated moulting remains as well as complete, enrolled specimens. The trilobite content with their geographic and stratigraphic locations is listed in Figure 2.

The material described and figured herein is housed in the Museum of the Central Faculty of Alger, Algeria (MUA/1094/001–015).

3. Systematic palaeontology

Morphological terminology mainly follows Chlupáč (1977) and Crônier *et al*. (2011). Some abbreviations have been used: 'exsag.' for exsagittal; 'sag.' for sagittal; and 'tr.' for transverse. I to VI refer to successive Frasnian–Famennian cephalopod zones (Wedekind, 1908).

Family PHACOPIDAE Hawle & Corda, 1847
Subfamily PHACOPINAE Hawle & Corda, 1847
Genus *Phacops* Emmrich, 1839

Type species. Calymene latifrons Bronn, 1825, Middle Devonian, Eifel, Germany.

Remarks. The synonymy of the genus is very extensive. After the original definition by Emmrich (1839), the most significant works are these of Barrande (1852), Wedekind (1911), Richter & Richter (1926), Delo (1935), Campbell (1967) and Chlupáč (1977).

The earlier authors had already noticed the heterogeneity of the genus *Phacops* which is now expressed by defining subgenera (Chlupáč, 1977; McKellar & Chatterton, 2009).

Because of this heterogeneity, the understanding of the taxonomic status of species is uneven and the justifiability of treating phacopine groups as sufficiently different for a valid attribution of generic or subgeneric taxonomic status remains problematic (McKellar & Chatterton, 2009; Crônier *et al*. 2011).

A preliminary phylogenetic analysis has been conducted in order to assess the phylogenetic position of the '*granulatus*' group towards the '*Phacops*' *sensu lato* group (Crônier, 2008). The '*granulatus*' group from the Upper Devonian seems to constitute an independent clade (especially by its distinctive L1 and visual complex) that differs from the '*Phacops*' *sensu lato* group from the Middle Devonian (especially by L1 with an intercalating ring, a more developed visual complex with more lenses and closer to the posterior furrow, a longer (sag.) pygidium and a stronger tuberculation).

The study of their relationship and their alpha-taxonomy is still in progress (by Crônier and Holloway); we will therefore use '*Phacops sensu lato'* for Upper Devonian species with a developed visual complex.

Upper Devonian species assigned. Phacops postaltaicus Maksimova, 1960: Frasnian, Kazakhstan; *P. guranensis* Maksimova, 1969: Frasnian, East Asia; *P. turco turco* Richter & Richter, 1939: Frasnian, Turkey; *P. n. sp. a* Feist, 1995: Frasnian (Iδ), France; *P. tamtertensis* sp. nov.: Famennian (III–IV), Algeria; *P. zeregensis* sp. nov.: Famennien (IV–VI), Algeria; *P. tafilaltensis* Crônier & Clarkson, 2001: Famennien (V–VI), Morocco; *P. granulatus* (Münster, 1840): Famennian (II–IV?, V–VI), Germany, Silesia, Poland, Moravia, Austria, England, Spain, Portugal, Algeria, Morocco, Urals, Kazakhstan, China, Iran; *P. granulatus guilinensis* Zhu, 1988: Famennian (VIβ), China; *P. circumspectans circumspectans* Paeckelmann, 1913: Famennian (VI), Germany; *P. circumspectans tuberculosus* Yuan & Xiang, 1998: Famennian (VIβ), China.

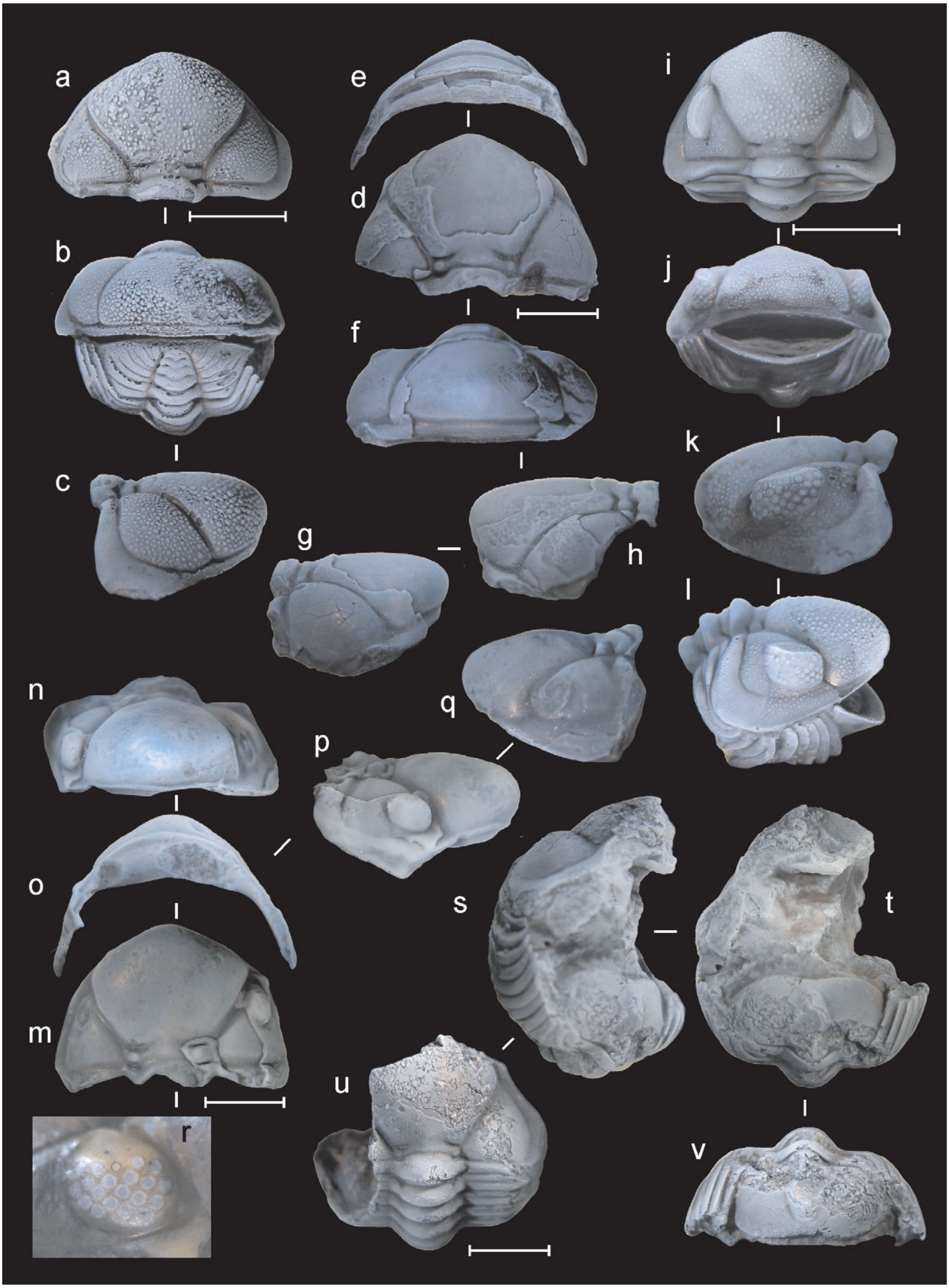

Figure 3. (Colour online) Phacopid trilobites from the ‘Argiles de Marhouma’ Formation, Upper Devonian, Saoura Valley, Algeria (see Fig. 1). (a–c) *Trimerocephalus caecus*, MUA/1094/007: cephalon in dorsal, frontal and lateral views. (d–h) *Trimerocephalus (Trifoliops) nigritus* Crônier, 2003, MUA/1094/008: cephalon in dorsal, ventral, frontal and lateral views. (i–l) *Phacops tamtertensis* sp. nov., holotype, MUA/1094/001: cephalon in dorsal, frontal and lateral views. (m–r) *Houseops?* cf. *cryphoïdes* (Richter & Richter, 1926), MUA/1094/006: cephalon in dorsal, frontal, ventral and lateral views and detail of the right eye. (s–v) *Trimerocephalus (Trifoliops) nigritus* Crônier, 2003, MUA/1094/009: (s–t) partially enrolled exoskeleton in lateral and ventral views, (u) cephalon and (v) pygidium in dorsal view. Scale bars: 5 mm.

Phacops tamtertensis sp. nov.
Figures 3i–l, 4a

Etymology. After the locality of Tamtert.

Holotype. Complete articulated individual, MUA/1094/001.

Type locality. Zereg section, Saoura Valley, Ougarta Basin, Algeria.

Type stratum. Submember b, Member 3, 'Argiles de Marhouma' Formation, Famennian II–III (II or III from *Armatites* ammonoids; determ. Korn), Upper Devonian.

Studied material. Only holotype.

Diagnosis. Cephalon narrow; glabella with a wide base and a frontal outline slightly tapered; glabella and cheeks slightly inflated; S2 and S3 distinct; L1 just swollen, without intercalating ring; visual complex with 13 vertical lens files and maximum 3 lenses per file, longer than the postocular length of the genal field; palpebral furrow almost transverse. Fine, dense and heterogeneous tubercles on cephalon.

Description. Cephalon: Length/width ratio about 0.63. *Dorsal view*: The glabellar ratio of width at L1/maximum width of frontal lobe is about 0.50. The glabella is bounded by deep axial furrows moderately divergent (66°) with anterolateral angles slightly truncated. The frontal lobe overhangs a deep preglabellar furrow. S2 and S3 are indicated by a break in the sculpture. S1 is continuous and curved in its middle part, subparallel to S0 in its adaxial curvature and becoming deeper in its distal portions. L1 is shorter (sag.) than L0 but more than half its length. L1 has subcircular lateral lobes separated from its median part by a weak exsagittal furrow. S0 is well marked and moderately deep with a slight curvature in its middle portion. L0 with a median nodule is slightly inflated in the middle part and its lateral lobes are not defined. The reniform visual surface has 13 dorsoventral files of lenses and 3 maximum lenses per file (Fig. 4a). The inter-lensar sclera is thickened dorsally only. The palpebral furrow is distinct. The exsagittal length of the postocular genal field is half to equal length of the posterior border. The cheek is slightly swollen. *Lateral view*: The glabella is rounded anteriorly. The outline of L1 is curved. L0 is as high as glabella at its maximum convexity, and is curved anteriorly and straight posteriorly. The anterior border is short, slightly flattened and sloping posteroventrally. A marginulation extends from the antero-lateral border up to the genal angle. The posterior furrow is deep and narrow. The lateral border furrow is shallow and wider anteriorly. The posterolateral furrow is continuous and the posterolateral border widens at the genal angle. The subocular librigenal field is narrow and concave at the front of the eye, becoming distinct backwards. *Frontal view*: The glabellar outline is semicircular with lateral sides flattened obliquely. Both the palpebral area and palpabral lobe are about level. *Ventral view*: The vincular furrow is deep, wide (sag.), curved and parallel to the preglabellar furrow. The posterior band of the cephalic doublure is long (sag.) and slightly curved posteriorly. *Thorax*: In dorsal view, the maximum axial width/maximum thoracic width (tr.) ratio is about 30%. The axial rings are slightly convex to subangular, without defined lateral lobes. The axial furrows are just present. The anterior pleural band is narrower (exsag.) than the posterior pleural band. The pleural and interpleural furrows are deep. The axial rings and the lateral border of segments are granulated. *Pygidium*: In dorsal view, the posterior outline is rounded. Its displaced position inside the thorax does not permit a detailed description except for the axial furrow closure behind the axis terminus that is complete and indistinct. *Ornamentation*: The cephalon is covered with dense, fine conical tubercles of heterogeneous size. The tubercles are slightly smaller on the glabellar anterior face. The palpebral lobe has an additional row of fine tubercles along the upper edge of the eye. The anterior band of the cephalic doublure possibly has some granulation and pits and the posterior band has scaly granules.

Comparison. The new species differs from Middle Devonian *Phacops* by a less-inflated glabella, a shallow lateral furrow especially behind the facial suture posterior branch, a less-prominent and convex visual complex, a just swollen L1 without intercalating ring and a thiner tuberculation.

This species resembles *Phacops granulatus* on account of its narrow cephalon, a frontal lobe not overhanging a deep preglabellar furrow, both palpebral area and palpebral lobe about level in height. However, *Phacops granulatus* differs in having a broader (tr.) glabella, fine homogeneous tubercles on glabella, no median occipital nodule and a visual surface with less vertical files (14–15).

The new species shares conical tubercles of heterogeneous size with *Phacops tafilaltensis*, glabella and cheeks slightly inflated and a median occipital nodule. However, *Phacops tafilaltensis* differs in having a broader (tr.) cephalon, a visual surface much longer (18 vertical files, 4–5 lenses per file), a palpebral area lower in height than the palpebral lobe and a lack of ornamentation on the cephalic doublure.

The new species also resembles *Rabienops wedekindi* (Richter & Richter, 1926) on account of its narrow cephalon and a visual surface with the same number of vertical files (13). However, *Rabienops wedekindi* differs in having a broader (tr.) glabella, fine homogeneous tubercles on glabella, no median occipital nodule and a visual surface with four maximum lenses per file.

Phacops zeregensis sp. nov.
Figures 4c, 5p–u

Etymology. After the locality of Zereg.

Holotype. Complete articulated specimen, MUA/1094/002.

Type locality. Zereg section, Saoura Valley, Ougarta Basin, Algeria.

Type stratum. Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV or IV/V (from clymenid ammonoids; determ. Korn), Upper Devonian.

Studied material. Only holotype.

Diagnosis. Cephalon narrow; glabella slightly inflated with a wide base and a parabolic frontal outline; S2 and S3 absent; L1 slightly inflated, without intercalating ring; lateral preoccipital lobes transverse and not differentiated; visual complex with 15 vertical files and 5 maximum lenses per file; length (exsag.) of the postocular genal field equal to length of the posterior border. Pygidium with few differentiated axial rings and few deep and thin pleural furrows; interpleural furrows absent; pygidial posterior margin curved. Thin, dense and homogeneous tuberculation on cephalon; distinct tubercles aligned transversely on the pygidial axis.

Description. Cephalon: Length/width ratio about 0.63. *Dorsal view*: The glabellar ratio of width at L1/maximum width of frontal lobe is about 0.53. The glabella is bounded by deep axial furrows moderately divergent (69°) with anterolateral angles subangular. The frontal lobe overhangs

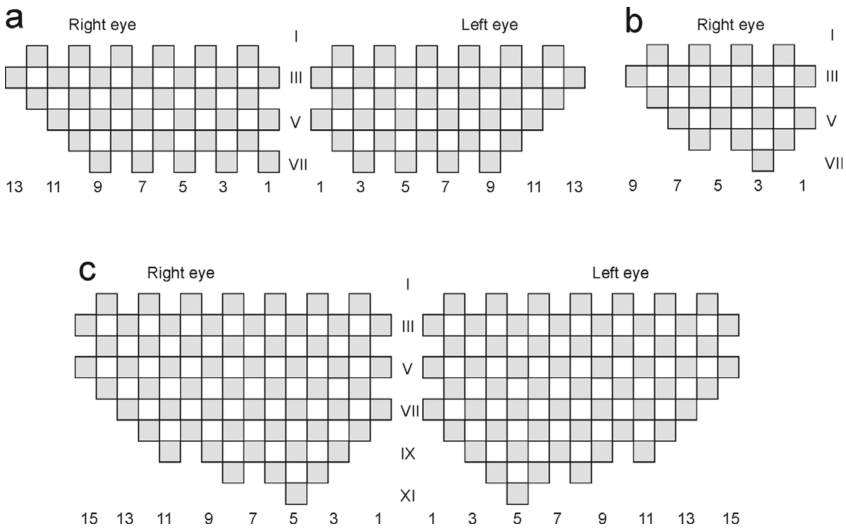

Figure 4. Schematic representation of right and left eyes in three Upper Devonian phacopid trilobites from the ‘Argiles de Marhouma’ Formation, Saoura Valley, Algeria. (a) *Phacops tamtertensis* sp. nov., MUA/1094/001; (b) *Houseops?* cf. *cryphoïdes*, MUA/1094/006; (c) *Phacops zeregensis* sp. nov., MUA/1094/002. I–VI = horizontal rows; 1–15 = vertical files. Grey boxes indicate a lens present.

a shallow preglabellar furrow. S1 is continuous and slightly curved in its middle part, subparallel to S0 in its adaxial curvature, and becoming deeper in its distal portions. L1 is shorter (sag.) than L0 but more than half its length. L1 has transverse lateral lobes not differentiated from its median part by an exsagittal furrow. S0 is shallow with a slight curvature in its middle portion. L0 is slightly inflated in the middle part and its lateral lobes are not defined. The visual surface is longer than the postocular length of the genal field, reniform with 15 vertical files of lenses and 5 maximum lenses per file (Fig. 4c). The inter-lensar sclera is thin. The palpebral furrow is distinct and convex (abax.). *Lateral view*: The glabella is sloping obliquely dorsoventrally in its anterior part. The outline of L1 is slightly curved. L0 is as high as glabella at its maximum convexity, and is slightly curved anteriorly and straighter posteriorly. The anterior border is short, forming a border projected forward. The posterior furrow is deep and narrow. The lateral border furrow is shallow. The posterolateral furrow is continuous and the posterolateral border widens at the genal angle. The subocular librigenal field is absent and the lower edge of the eye is in the lateral border furrow. *Frontal view*: The glabellar outline is semicircular becoming subvertical laterally. The palpebral area is inflated and higher than the palpebral lobe. *Thorax*: In dorsal view, the maximum axial width/maximum thoracic width (tr.) ratio is about 28%. The axial rings are strongly convex without defined lateral lobes. The anterior pleural band is narrower (exsag.) than the posterior pleural band. The interpleural and pleural furrows are deep. The pleura are transverse adaxially. The axial rings have small scattered tubercles. *Pygidium*: In dorsal view, the shape is lenticular to trapezoidal with a maximum width behind the midlength (sag.). The posterior outline is rounded. The length/width ratio is rather long (51%). The pydigial axis is rather short (sag.) and wide (tr.), inflated with a swelling decreasing gradually to the back. Its posterior closure is rounded. Four axial rings (+ terminal piece) are poorly defined. The pleural furrows are few, deep and thin, not reaching the posterior margin. *Ornamentation*: The cephalon is covered with dense and fine tubercles of homogeneous size, except for the damaged lateral border where there is no evidence of sculpture. A few distinct tubercles, spaced apart and transversely aligned, are present on the pygidium.

Comparison. The new species differs from other *Phacops* by transverse lateral lobes not differentiated from the median part of L1, a shallow lateral border furrow especially behind the facial suture posterior branch.

The new species resembles *Rabienops wedekindi* on account of its morphometric features, a fine inter-lensar sclera, a palpebral area higher than the palpebral lobe and a subocular field absent. However, *Rabienops wedekindi* differs in having subcircular lateral preoccipital lobes, a visual surface with less vertical files (13) and a longer postocular genal field.

This new species shares a narrow cephalon with *Phacops granulatus*, a visual complex with 14–15 vertical files and thin and dense tubercles on the glabella. However, *Phacops granulatus* differs in having more divergent dorsal furrows, S2 and S3, subcircular lateral preoccipital lobes, a visual surface with four maximum lenses per file, a longer pygidium and a wider pygidial axis.

Undetermined *Phacops*
Figure 6a–e

Material. One cephalon and four thoracopygons on the same slab poorly preserved; Zereg section, Saoura Valley, Algeria; Submember c, Member 3, ‘Argiles de Marhouma’ Formation, Famennian IV–V, Upper Devonian.

Remarks. The exoskeleton may be assigned to *Phacops* but its alteration prevents a specific assignation. The general shape and the visual surface length with five maximum lenses per file may suggest the new described species *Phacops zeregensis*.

Figure 6k–l

Material. One well-preserved thoracopygon; Idhir section, Saoura Valley, Algeria; Submember a, Member 4, ‘Argiles de Marhouma’ Formation, Famennian V–VI?, Upper Devonian.

Description. Pygidium with lenticular to trapezoidal shape. Its maximum width is behind the midlength (sag.). The posterior outline is widely rounded and transverse in its median part. The length/width ratio is rather wide (46%). The axis is well defined by axial furrows, rather long sagitally

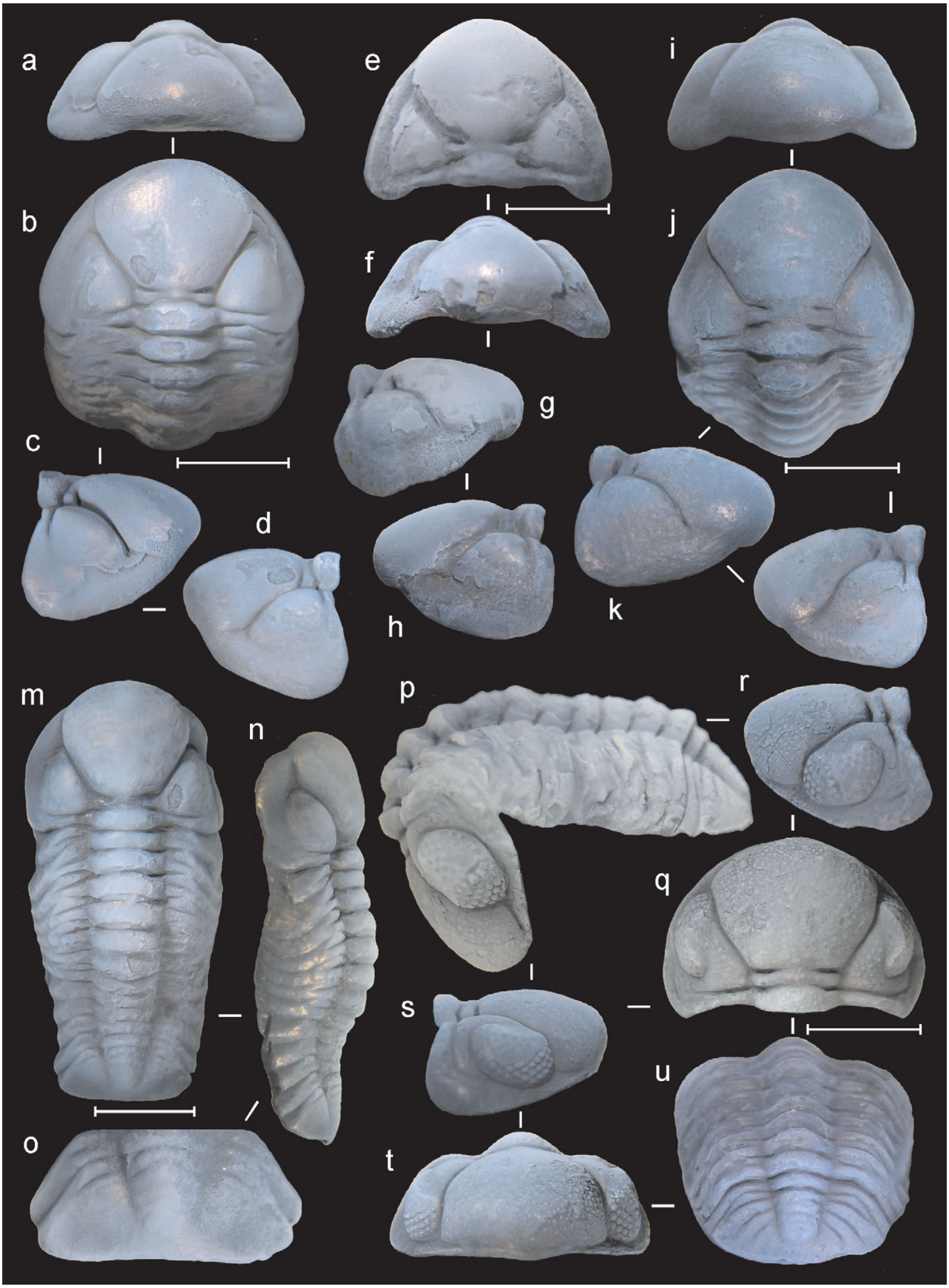

Figure 5. (Colour online) Phacopid trilobites from the 'Argiles de Marhouma' Formation, Upper Devonian, Saoura Valley, Algeria (see Fig. 1). (a–l) *Dianops vicarius* Chlupáč, 1961: (a–d) cephalon in frontal, dorsal and lateral views, MUA/1094/011; (e–h) cephalon in dorsal, frontal and lateral views, MUA/1094/012; (i–l) cephalon in frontal, dorsal and lateral views, MUA/1094/013. (m–o) *Dianops typhlops* (Gürich, 1896): exoskeleton in dorsal and lateral view and detail of pygidium, MUA/1094/010. (p–u) *Phacops zeregensis* sp. nov., holotype, MUA/1094/002: (p) exoskeleton in lateral view; (q–t) cephalon in dorsal, lateral, and frontal views; (u) thoracopygon in dorsal view. Scale bars: 5 mm.

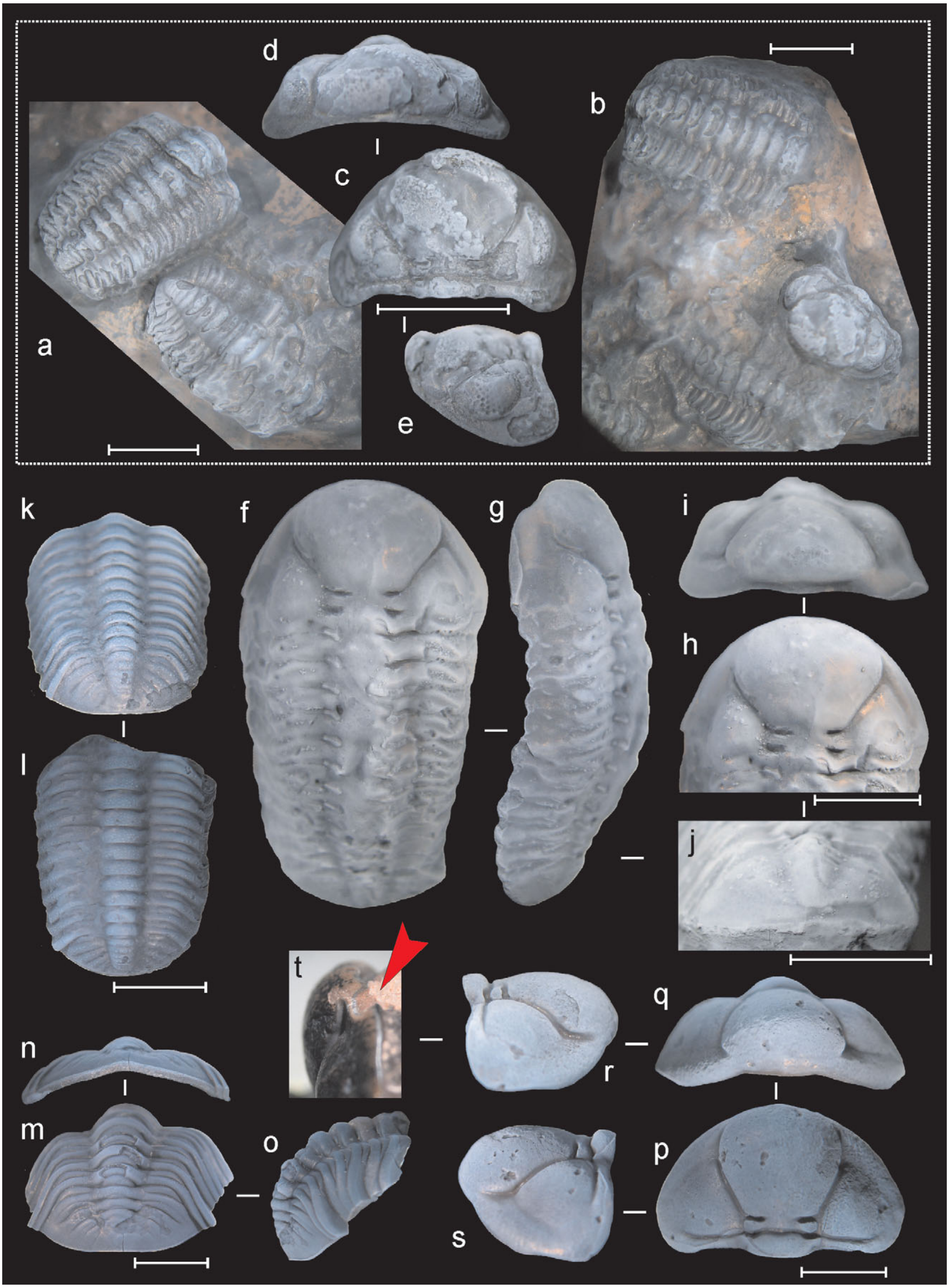

Figure 6. (Colour online) Phacopid trilobites from the 'Argiles de Marhouma' Formation, Upper Devonian, Saoura Valley, Algeria (see Fig. 1). (a–e) Undetermined *Phacops sensu lato*, MUA/1094/003: (a, b) general view of thoracopygons and one isolated cephalon; (c–e) cephalon in dorsal, frontal and lateral views. (f–j) Undetermined *Dianops* (Richter & Richter, 1923), MUA/1094/015: (f–g) exoskeleton in dorsal and lateral views, (h–i) cephalon in dorsal and frontal views and (j) pygidium in dorsal view. (k–l) Undetermined thoracopygon in dorsal views, MUA/1094/004. (m–o) Undetermined thoracopygon in dorsal, frontal and lateral views, MUA/1094/005. (p–t) *Dianops algeriensis* sp. nov., MUA/1094/014: cephalon in dorsal, frontal, right lateral, left lateral and detail views. Scale bars: 5 mm.

and narrow, strongly convex. Five axial rings (+ terminal piece) are defined by narrow furrows. The pleural furrows are few, deep and thin, not reaching the posterior margin. The interpleural furrows are poorly distinct. The posterior border forms a thin ridge. The thoracic rings are strongly convex without defined lateral lobes. The anterior pleural band is slightly narrower (exsag.) and less inflated than the posterior pleural band. The interpleural and pleural furrows are deep. The pleura are transverse adaxially. Thorax and pygidium are covered with relatively dense and coarse tubercules; the pygidial posterior ridge with rather dense scaly granules.

Figure 6m–o

Material. Two well-preserved thoracopygons; Zereg section, Saoura Valley, Algeria; Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV–V, Upper Devonian.

Description. Pygidium with lenticular to trapezoidal shape and slightly vaulted (tr.). Its maximum width is behind the midlength (sag.). The posterior outline is transverse in its median part and curved laterally. The length/width ratio is wide (39%). The axis is rather short (sag.) and wide (tr.), slightly convex. Four axial rings (+ terminal piece) are defined by wide furrows laterally and showing the interannular ring medially. The pleural furrows are few, deep and thin, not reaching the posterior margin. The interpleural furrows are very thin and poorly distinct. The limbus is rather broad (sag.) and forms a thin ridge posteriorly. The thoracic rings are strongly convex without defined lateral lobes. The anterior pleural band is slightly narrower (exsag.) and less inflated than the posterior pleural band. The interpleural and pleural furrows are deep. The pleura are transverse adaxially. Thorax and pygidium are covered with fine and dense granules; the pygidial posterior ridge with rather dense scaly granules.

Genus *Houseops* Feist *et al.* 2009

Type species. Houseops canningensis Feist, McNamara, Crônier & Lerosey-Aubril 2009, Upper Devonian, Canning Basin, Australia.

Remarks. This genus is characterized by a subdued transverse cephalic profile protruding anteriorly, a narrow glabellar base, retracted anteriorly and recurved anterolateral corners, flat and poorly defined preoccipital lateral lobes, a median occipital tubercle, eyes low, a moderately deep vincular furrow and a short and flat postvincular area, a pygidial axis posteriorly narrow with few rings and a thin sculpture with sparse tubercles.

Houseops is more closely related to *Nephranops* Richter & Richter, 1926 and *Chotecops* Chlupáč, 1971 than to any other phacopine. *Nephranops* shares with *Houseops* a thin sculpture and a median occipital tubercle but differs from *Houseops* in the obsolete visual lenses, the higher transverse cephalic vault and the wider and dorsalwards concave postvincular area. *Chotecops* differs from *Houseops* in the wider glabellar base, the wider and dorsalwards concave postvincular area and a pygidium with more axial rings.

According to Chlupáč (1977) and Feist *et al.* (2009), the older *Chotecops* might constitute the ancestral clade of both *Nephranops* and *Houseops*. Unfortunately, the poorly known Frasnian phacopines do not confirm this possible phylogenetic relationship.

Species assigned. Houseops canningensis Feist *et al.* 2009: Famennian (IIα), Australia; *H. beckeri* Feist *et al.* 2009: Famennian (IIα), Australia; *H. sp.* A Feist *et al.* 2009: Famennian (IIα), Australia: *H. miserrimus miserrimus* (Drevermann, 1901): Famennian (II), Germany; *H. miserrimus wiedensis* (Lütke, 1968): Famennian (IIα), Germany; *H.? cryphoides* (Richter & Richter, 1926): Frasnian (Iγ), Germany; *H.? pronini* (Maksimova, 1955): Frasnian, Urals; *H.? nalivkini* (Maksimova, 1955): Famennian (IIα), Urals; *H.? ocellatus* (Perna, 1915): Famennian (II), Urals.

Houseops? cf. *cryphoïdes* (Richter & Richter, 1926)
Figures 3m–r, 4b

v. 1926 *Phacops* (*Phacops*) *cryphoïdes*: Richter & Richter, p. 257, pl. 12, figs 41–42.
1954 *Phacopidella* cf. *liopyga*; Pfeiffer, p. 48.
1959 *Phacops* (*Phacops*) *cryphoïdes*: Pfeiffer, p. 269–270, pl. 3, figs 2–4.
2007 *'Phacops'* cf. *cryphoïdes*: Kaiser *et al*. p. 239.
2009 *Houseops? cryphoïdes*: Feist *et al*. p. 14–15.

Material. One mostly exfoliated cephalon in a pyritized brachiopod bed within a thick clay layer from the Gara Diba section, near Beni-Abbès, Algeria; Submember a, Member 2, 'Argiles de Marhouma' Formation, Famennian II? (II according to *Evanidisinurostrum saouraensis* brachiopod; determ. Brice), Upper Devonian.

Description. Glabella broad and pentagonal overhanging strongly a deep preglabellar furrow. Dorsal furrows deep. Anterior border short, forming a crest slightly projected forward. L1 broad with differentiated, subcircular and swollen lateral lobes. S1 continuous. S2 and S3 present on internal mould. Reduced visual complex with 21 lenses, 9 vertical files and 3 maximum lenses per file (Fig. 4b). Postocular genal field long. Subocular librigenal field narrow and concave in front of the eye, becoming distinct backward. Vincular furrow moderately deep and wide. Posterior band of the vincular furrow convex and curved.

Remarks. The poorly known Frasnian phacopines with a deep, wide and curved vincular furrow and a reduced visual complex have been previously assigned to *Phacops*. Feist *et al.* (2009) have tentatively assigned them to *Houseops*. *Houseops? cryphoïdes* differs from *Phacops* mainly in the anteriorly positioned small visual complex with few lenses and in the lack of intercalating ring.

Houseops? cryphoïdes reported by Richter & Richter (1926) from the Mid-Frasnian of Sessacker (Germany) is a poorly known cephalon. This specimen exhibits small palpebral lobes, a visual surface with 18–23 lenses, a rather convex palpebral furrow adaxially, a facial suture between the palpebral lobe and the visual surface outwardly convex (abax.), a sculpture with granules of two sizes as in *Trimerocephalus caecus* but much finer, and granules more numerous and grouped under the visual surface, on the cheek and on the borders.

Moreover, this German specimen exhibits a similar vincular furrow to that of *Phacops* and seems to have a plane and curved posterior band of the vincular furrow (after a cast of the holotype).

Kaiser *et al.* (2007) have reported but not figured *Houseops?* cf. *cryphoïdes* from the Upper Frasnian of Oulmes region, Moroccan Meseta.

Because of its poor preservation, our Algerian specimen is tentatively assigned to *cryphoïdes*, mainly on account of the anteriorly positioned small visual complex, a rather convex palpebral furrow adaxially, a rather narrow cephalon with the anterolateral borders evenly curved in outline, a wide glabellar base and anterolateral angles slightly subangular. However, our Algerian specimen differs from the German specimen by a convex posterior band of the vincular doublure. Moreover, our specimen would be much younger (Famennian IIβ? according to brachiopods; determ. Brice) than the German specimen and allies (Frasnian).

Genus *Trimerocephalus* McCoy, 1849

Type species. Phacops mastophthalmus Richter, 1856, Upper Devonian (Famennian), Thuringia, Germany.

Remarks. Trimerocephalus is characterized by the absence of eyes and the submarginal facial suture often cutting the anterior extremity of the cheeks. A continuous S1 and a wide (tr.), short (sag.) and clearly segmented pygidium are characters shared by the small-eyed *Acuticryphops* Crônier & Feist, 2000. *Trimerocephalus* is also close to the blind *Dianops* (Richter & Richter, 1923). *Dianops* differs by an interrupted (tr.) S1, a facial suture running on the latero-frontal border, a longer (sag.) pygidium, strongly convex without distinct segmentation.

Within *Trimerocephalus*, Chlupáč (1966) distinguished three groups: '*mastophthalmus/caecus/dianopsoides*' with an anteriorly rounded glabellar outline and an often transverse cephalon; '*sponsor/polonicus/interruptus*', probably younger, with a pentagonal glabellar outline, pointed anteriorly and a narrow cephalon; and an independent group comprising *T.? steinachensis* (Richter & Richter, 1926) with a frontal border not overhung by the frontal lobe and *T. (Trifoliops) trifolius* (Osmólska, 1958) with a frontal border widened strongly laterally.

However, this traditional classification is not completely confirmed by a cladistic analysis where three clades have been obtained (Crônier, 2003). *Trimerocephalus mastophthalmus* and *T. dianopsoides* occupy with *T.* (*Trifoliops*) and *T.? steinachensis* a marginal position as sistergroup of clades '*caecus/sponsor*'.

Trimerocephalus mastophthalmus differs from the group '*caecus*' by the facial suture outline cutting the cheek, a fine granulation and the absence of the median nodule. *Trimerocephalus dianopsoides* differs by a hardly defined pygidial segmentation, the absence of S2 and S3 and the presence of the ocular protuberances.

Trimerocephalus lentiginosus (Maksimova, 1955) discovered in the upper Famennian of the Urals has an age not confirmed by conodont data.

Species assigned. Trimerocephalus caecus (Gürich, 1896): Famennian (II–III), Poland, Germany, Urals, Algeria, France; *T. cryptophthalmoides* (Maksimova, 1955): Famennian (II), Urals, Kazakhstan; *T. dianopsoides* Osmólska, 1963: Famennian (II?–III), Poland; *T. interruptus* Berkowski, 1991: Famennian (III), Poland; *T. lacunosus* (Pfeiffer, 1959): Famennian (II), Germany; *T. lelievrei* Crônier & Feist, 1997: Famennian (II-III), Morocco; *T. lentiginosus* (Maksimova, 1955): Famennian (V), Urals; *T. mastophthalmus* (Richter, 1856): Famennian (II–III?), Germany, Poland, England, Asia, Kazakhstan; *T. mimbi* Feist *et al*. 2009: Famennian (II), Australia; *T. polonicus* Osmólska, 1958: Famennian (III), Poland; *T. procurvus* Arbizu, 1985: Famennian (III), Spain, Germany; *T. sponsor* Chlupáč, 1966: Famennian (III), Moravia, Spain; *T. shotoriensis* Feist, 2003 in Feist *et al*. 2003: Famennian (II–III), Iran; *T.? steinachensis* (Richter & Richter, 1926): Famennian (II), Germany; *T. tardispinosus* Feist & Becker, 1997: Famennian (II), Australia; *T. vodorezovi* (Maksimova, 1955): Famennian (II), Kazakhstan; *T. (Trifoliops) trifolius* (Osmólska, 1958): Famennian (II–III?), Poland, France; *T. (Trifoliops) nigritus* Crônier, 2003: Famennian (II–III?), Poland, France.

Trimerocephalus caecus (Gürich, 1896)
Figure 3a–c

1896 *Phacops caecus*: Gürich, p. 362–363, pl. 15, figs 4a–c.
1926 *Phacops (Trimerocephalus) caecus*: Richter & Richter, p. 180–184, pl. 10, figs 80–86 (with previous synonymy).
1958 *Trimerocephalus caecus*: Osmólska, p. 128–131, fig. 3, pl. 2, figs 1a–c, 2a, b, 3.
1975 *Trimerocephalus caecus*: Hahn & Hahn, p. 25, pl. 2, fig. 4.
1976 *Trimerocephalus caecus*: Morzadec & Babin, p. 368–369, pl. 1, figs 1–11.
non 1985 *Trimerocephalus caecus*: Becker, p. 29 [= *Trimerocephalus procurvus* Arbizu, 1985].

Material. One complete enrolled individual in a greenish black limestone from Cheffar-El-Ahmar section, Saoura Valley, Algeria; Submember b, Member 2, 'Argiles de Marhouma' Formation, Famennian II–III, Upper Devonian.

Remarks. This specimen shows morphological features of *Trimerocephalus caecus* from Poland: wide and deep dorsal furrows, deep lateral and posterior border furrows, two types of tubercles on cephalon and two nodules on L1. It can differ by the possible absence of the median occipital nodule (default preservation?).

German specimens from Langenaubach (Drevermann, 1901) and Gattendorf (Richter & Richter, 1919) have been found in the *Cheiloceras* and the *Prolobites* Zones. Poland specimens from the *Cheiloceras* and the *Clymenia* Zones (Osmólska, 1958) differ by the absence of tubercle on L0 and a cephalic outline less wide and less subcircular.

This species is close to *Trimerocephalus lelievrei* from Morocco (Crônier & Feist, 1997) in having a marginal facial suture which does not cut the cheeks, the same sculpture and no protuberance ocular. Nevertheless, *Trimerocephalus lelievrei* has a more elongated (tr.) cephalon, a glabella which is lower and less pointed anteriorly.

Sub-genus *Trimerocephalus (Trifoliops)* Crônier, 2003

Type species. Trimerocephalus (Trifoliops) trifolius (Osmólska, 1958), Upper Devonian (Famennian), Holy Cross Mountains, Poland.

Species included. Trimerocephalus (Trifoliops) trifolius (Osmólska, 1958) and *T. (T.) nigritus* Crônier, 2003.

Remarks. Trimerocephalus (*Trifoliops*) differs from *Trimerocephalus sensu stricto*: the vincular furrow is widened (tr.) in *T.* (*Trifoliops*); the frontal border is inflated, wide and oriented forwards only in *T.* (*T.*) *trifolius*; a feature shared by *T.? steinachensis*.

Trimerocephalus (Trifoliops) nigritus Crônier, 2003
Figure 3d–h, s–v

v. 2003 *Trimerocephalus (Trifoliops) nigritus*: Crônier, p. 59–62, fig. 3b, fig. 6a–h.

Diagnosis emended. Cephalic outline wide and trilobed; glabella with a broadly parabolic frontal outline; frontal lobe overhanging the frontal border; S2 and S3 absent. Pygidium rather trapezoidal and vaulted (tr.); pygidial posterior margin curved laterally with a slight forwards inflection medially; segmentation weak or indistinct.

Material. One partially exfoliated cephalon (MUA/1094/008) from Béchir section (SE of Beni-Abbès) and one subenrolled individual (MUA/1094/009) from the Gara Diba section (near Beni-Abbès), Algeria; Submember c, Member 3 for MUA/1094/008 (Famennian II–III from *Armatites* sp. ammonoid; determ. D. Korn); and Submember b, Member 2 for MUA/1094/009 (Famennian II–III from *Palmatolepis minuta subtilis* conodont; determ. C. Randon), 'Argiles de Marhouma' Formation, Famennian II–III, Upper Devonian.

Remarks. The cephalon from the Béchir section shows the morphological features of *Trimerocephalus (Trifoliops) nigritus*: a trilobed cephalic outline (even if partially damaged); deep dorsal furrows; a median portion of S1 shallow with L1 less inflated and lateral lobes slightly differentiated; S0 more clearly differentiated with a strongly inflated L0 and lateral lobes not differentiated; no ocular protuberance; a facial suture cutting the cheeks forming a narrow crescent; a vincular furrow very broad (tr.), fairly deep and slightly widened (sag.); a posterior band of the doublure narrow (sag.), flat and granulose (contrary to what was written in Crônier, 2003, p. 60); a fine and dense granulation on cephalon.

The specimen from the Gara Diba section showing the right side of the cephalo-thorax and the complete connected pygidium shows morphological features of *Trimerocephalus (Trifoliops) nigritus*: a trilobed cephalic outline; S2 and S3 indistinct; a median portion of S1 shallow with L1 less inflated and lateral lobes slightly differentiated; S0 more clearly differentiated with a strongly inflated L0 and lateral lobes not differentiated; no ocular protuberance developed; a fine and dense granulation on exoskeleton. Unfortunately, the ventral part is damaged except the posterior band of the doublure that is narrow (sag.), flat and granulose. The facial suture is also not visible. This specimen may differ by less deep dorsal furrows.

In addition to a previous description (Crônier, 2003), further information on pygidial morphology is now available. Pygidium with a trapezoidal shape. In dorsal view, the anterior margin is straight (tr.). The dorsal furrows are hardly marked. The axis is short (sag.) and wide (tr.). Its posterior extremity is rounded and lowered. Rings are damaged. The terminal piece seems to be delimited by a slightly marked furrow. Pleural furrows are slightly marked, pleural ribs not inflated and interpleural furrows absent. These furrows delimit a laterally widening limbus that is very broad (sag.). The posterior border shows a very slight forwards inflection in its median portion. Angles of lateral and posterior border are about 95°. Pygidium is strongly arched (tr.) in frontal view and shows a fine and dense granulation.

These pygidial features are shared by *Trimerocephalus dianopsoides*, which has a barely defined pygidial segmentation.

Crônier (2003) assigned an isolated pygidium to *Trimerocephalus (Trifoliops) nigritus*. Nevertheless, this pygidium with a transverse and lenticular shape has a shorter (sag.) pygidial axis, well-marked pleural and interpleural furrows becoming less distinct posteriorly and delimiting a laterally widening limbus, and a slight thickening along the whole length (tr.) of the posterior pygidial margin. This isolated pygidium may reasonably belong to *Trimerocephalus (Trifoliops) trifolius*.

Genus *Dianops* (Richter & Richter, 1923)

Type species. Phacops limbatus Richter, 1848, Upper Devonian (Famennian), Thuringia, Germany.

Remarks. Dianops terminates the evolutionary trend of the Upper Devonian phacopids. It is characterized by gradual reduction up to entire disappearance of eyes and shifting of the facial suture towards the outer margin. This trend can be observed within *Dianops*. *Dianops typhlops* (Gürich, 1896) and *D. vicarius* Chlupáč, 1961 are therefore the most primitive, and development continues through *D. limbatus* and *D. griffithides* (Richter & Richter, 1919) to *D. anophthalmus* (Frech, 1892) in which the facial suture is already running on the lateral cephalic border.

Species assigned. Dianops aktjubensis (Maksimova, 1955): Famennian (V), Urals, Kazakhstan; *D. anophthalmus* (Frech, 1892): Famennian (V–VI), Silesia, Austria, Rhineland?; *D. griffithides griffithides* (Richter & Richter, 1919): Famennian (V), Germany, France, Urals?; *D. griffithides mugodjaricus* (Maksimova, 1955): Famennian (V), Kazakhstan; *D. limbatus* (Richter, 1848): Famennian (V–VI), Germany; *D. pernai* (Maksimova, 1955): Famennian (V), Urals, Kazakhstan; *D. typhlops* (Gürich, 1896): Famennian (IV), Poland; *D. vicarius* Chlupáč, 1961: Famennian (IV), Moravia; *D. guizhouensis* Xiang, 1981: Famennian (VI), China.

Dianops typhlops (Gürich, 1896)
Figure 5m–o

1896 *Trimerocephalus typhlops*: Gürich, p. 359, pl. 15, fig. 7a–b.
1926 *Phacops (Trimerocephalus) typhlops*: Richter & Richter, p. 192, pl. 10, figs 90–94 (with previous synonymy).
1958 *Dianops typhlops*: Osmólska, p. 135–136,pl. 4, figs 1–4.
1994 *Dianops typhlops*: Becker & Schreiber, p. 377, pl. 1, fig. 12.

Material. One complete individual in a strongly nodular and shaly red 'griotte' limestone from Zereg section, Saoura Valley, Algeria; Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV(–V) (IV or IV/V from clymenid ammonoids; determ. Korn), Upper Devonian.

Remarks. The Algerian specimen shows morphological features of *Dianops typhlops* from Poland: anterolateral glabellar angles truncated (exsag.), S1 interrupted in its middle part, a flat L1 coalescing with the frontal lobe in its median part and without differentiated lateral lobes, an effaced posterolateral border furrow on a short distance at the genal angle, a frontal lobe with granules dense on the anterior part becoming short ridges laterally on the ventral part.

To complete this description, the Algerian specimen has a rather wide pygidium, a short axis, fewer than four distinct axial rings, three distinct pleural furrows and no defined thoracic lateral lobes.

However, this specimen displays some slight differences from *Dianops typhlops* from Poland: a glabella prominent but slightly flattened; S2 and S3 weakly suggested as small depressions; shallow axial furrow adjacent to L1; a posterior pygidial margin almost transverse without a clear medial notch; and a lack of thoraco-pygidial ornamentation.

Dianops typhlops has been described in Poland by Gürich (1896) and Richter & Richter (1926) from the *Platyclymenia* Zone (IV). Our specimen corresponds to the description proposed by Richter & Richter (1926), except for the ornamentation of the thorax (coarsely to finely granular for

Polish specimens) and of the pygidium (granular to coarser on the border for Polish specimens).

Dianops typhlops also described in Poland by Osmólska (1958) from the *Clymenia* Zone (V) shows a cephalon less vaulted and a lateral border relatively narrower in comparison with the lectotype. The Algerian specimen differs by pleurae and a pygidial axis less distinctly segmented, a lateral border relatively wider and a glabella more prominent although slightly flattened.

Dianops vicarius Chlupáč, 1961
Figure 5a–l

1961 *Dianops typhlops vicarius*: Chlupáč, p. 480, pl. 2, figs 3–4.
1966 *Dianops vicarius*: Chlupáč, p. 113–115, pl. 32, figs 11–13, pl. 24, figs 1–11.
1975 *Dianops vicarius*: Hahn & Hahn, p. 26, pl. 2, fig. 15.
1977 *Dianops vicarius*: Chlupáč, p. 124, pl. 32, figs 5–7.

Material. Three relatively well-preserved cephalo-thoraxes in a strongly nodular and shaly red 'griotte' limestone bed from Zereg section, Saoura Valley, Algeria; Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV (IV or IV/V from clymenid ammonoids; determ. Korn), Upper Devonian.

Remarks. Our specimens correspond to the descriptions of *Dianops vicarius* from Poland proposed by Chlupáč (1966, 1977): cephalic outline subcircular and vaulted; glabella steeply falling away forwards and to S1; anterolateral corners rounded to truncated (exsag.); deep dorsal furrows; S1 deep laterally as elongated (tr.) depressions and shallow medially; S0 deep laterally as elongated (tr.) depressions also and bent forwards medially; L1 flat, slender as depression between the frontal lobe and L0; vaulted L0 twice as wide as L1; convex genal field; shallow lateral border furrow as ill-defined depression (adax.) and widening anteriorly; narrow distinct posterior border furrow (adax.); posterolateral border furrow effaced over a long distance at the genal angle. Surface rather smooth; anterior part of the frontal lobe with fine and dense granulation becoming short ridges on the ventral part.

To complete this description, the Algerian specimens have S1 almost effaced medially, L1 with transverse differentiated lateral lobes by a very slight exsaggital furrow, a deep axial furrow and distinct adjacent to L1, no defined thoracic lateral lobes and no thoracic ornamentation.

However, these specimens display some slight differences from *Dianops vicarius* from Poland: S2 and S3 not distinct or weakly suggested and a facial suture indistinct.

Dianops vicarius and *D. typhlops* are the closest species. The main differences are: the interrupted S1 in *D. typhlops* (frontal lobe coalescing with L1 in its median part) and differentiated in *D. vicarius* (frontal lobe separated and depressed of L1 in its median part); an interrupted posterolateral border furrow over a short distance at the genal angle in *D. typhlops* and over a long distance in *D. vicarius*; and a posterior pygidial margin with a medial notch in *D. typhlops*, transverse medially without a clear medial notch in *D. vicarius*.

Dianops vicarius and *D. typhlops* are also the oldest representatives of the genus. They occur in the *Platyclymenia* Zone. Both species share some primitive features such as a facial suture close to the lateral furrow and a better differentiated L1.

Dianops pernai is also close to *Dianops vicarius* with a frontal lobe demarcated from S1. However, *Dianops pernai* differs by more divergent dorsal furrows, a frontal lobe pointed anteriorly, a posterolateral border furrow almost interrupted and a more convex genal field.

Dianops algeriensis sp .nov.
Figure 6p–t

Etymology. After the area of Algeria.

Holotype. Exfoliated cephalon, MUA/1094/014.

Type locality. Zereg section, Saoura Valley, Ougarta Basin, Algeria.

Type stratum. Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV or V (from clymenid ammonoids; determ. Korn), Upper Devonian.

Studied material. Only holotype.

Diagnosis. Cephalon rather narrow; glabella little prominent and narrow, bounded by deep axial furrows slightly divergent (55°) with anterolateral angles rounded to cut off; S2 and S3 absent; L1 coalescing with the frontal lobe, without intercalating ring; lateral preoccipital lobes transverses and slightly differentiated; posterior furrow deep and wide; lateral border furrow shallow anteriorly; posterolateral furrows effaced at the genal angle. Numerous granules on the preserved portion of L0.

Description. Cephalon: Length/width ratio about 0.62. *Dorsal view*: The glabellar ratio of width at L1/maximum width of the frontal lobe is about 0.61. The glabella is not greatly prominent and is narrow. The frontal outline is parabolic. The anterolateral border is wide and evenly curved in outline. The frontal lobe does not overhang the indistinct preglabellar furrow. S1 is interrupted in its middle part and becoming deep laterally as elongated (tr.) depressions. L1 is half the length (sag.) of L0 length. L1 is not inflated and without median depression. S0 is deep and transverse in its median part. L0 is convex and its lateral lobes are not defined. The muscle scars form deep depressions. *Lateral view*: The glabella is slightly swollen and sloping obliquely dorsally in its anterior part and then posteroventrally. The outline of L1 is slightly curved. L0 is as high as the glabella at its maximum convexity, and is curved anteriorly and straighter posteriorly. The facial suture is indistinct. The genal angle is rounded and without a node. *Frontal view*: The glabellar dorsal outline is semicircular becoming subconvergent laterally. *Ornamentation*: Present on the preserved distal left portion of L0 covered with numerous and fine granules.

Comparison. The new species differs from other *Dianops* by having a less prominent and narrow glabella; deep dorsal, posterior (adax.) and occipital furrows. The new species differs from *Dianops typhlops* by a less-inflated glabella and better-defined lateral preoccipital lobes and from *D. vicarius* by the absence of the frontal lobe demarcation from S1.

Undetermined *Dianops*
Figure 6f–j

Material. One complete specimen, poorly preserved; Zereg section, Saoura Valley, Algeria; Submember c, Member 3, 'Argiles de Marhouma' Formation, Famennian IV–V, Upper Devonian.

Remarks. The exoskeleton is assigned to *Dianops* but its imperfect preservation prevents a specific assignation.

4. Palaeobiodiversity analysis

Trilobites are important elements in Devonian marine benthic communities. Throughout the Devonian period, their abundance and taxonomic diversity fluctuated (Lerosey-Aubril & Feist, 2012). After a peak which occurred during the Early Devonian, their diversity was restricted at high taxonomic levels by one of the most severe of all biological crises during the Kellwasser event (Schindler, 1990; Crônier & Van Viersen, 2007). Most trilobites that were adapted to outer shelf bottom habitats after the major transgressive Taghanic event of the mid-Givetian (Johnson, 1970) were affected by repeated sea-level rises leading to a reduction of reefal habitats (Schlager, 1981). Only the Phacopida and Proetida survived the biological crisis, but they were severely affected (Crônier & Van Viersen, 2007).

In this context, we focused our investigations on Upper Devonian sections in order to evaluate phacopid biodiversity at a global level and to understand their fluctuations in time. This biodiversity is represented in our study by 68 known phacopid species (poorly known species were excluded and most subspecies have been ignored) for 21 taxa (mostly genera; distinction between *Phacops sensu lato* from Frasnian or Famennian time; consideration of *cryphoides* taxon and *granulatus* group) within 14 consecutive and discrete chronostratigraphic intervals from Upper Devonian strata. See Table 1 for the taxonomic list. This taxonomic database was compiled from literature and completed with our new data.

4.a. Diversity estimation through 14 intervals

Knowledge of the number of species or genera through geological time has been an important field of study during these last years. This knowledge via curves of diversity provides potentially large-scale information such as palaeoenvironmental events or evolutionary trends. The diversity curves are meaningful, although an estimate of Phanerozoic global biodiversity is limited by biases in the fossil record and the validity of theses curves has been widely debated (Foote, 2000; Smith, 2001). The main biases include inaccuracies in taxonomic data and uneven sampling intensity across organisms, environments, geographic areas and time intervals (Badgley, 2003). Recognition of these methodological problems has resulted in notable improvements in the Phanerozoic diversity database (Adrain & Westrop, 2000; Alroy *et al.* 2001) using methods such as rarefaction, for example.

Curves of diversity, origination and extinction have therefore been established on the presence/absence database from the occurrence of Upper Devonian phacopids in order to estimate their biodiversity. Data have been organized on a 'range-through' assumption for which the existence of a taxon is considered continuous between its first to last appearance. Due to a lack of stratigraphical precision, the occurrence of taxa was considered within 14 consecutive and discrete chronostratigraphic intervals: four for Frasnian (Iα, Iβ, Iγ and Iδ) and ten for Famennian (Post-Iδ, IIα, IIβ, IIIα, IIIβ, IV, Vα, Vβ, VIα and VIβ).

Curves of diversity, origination and extinction were achieved using the data analysis software PAST (Palaeontological Statistics) v2.14 (Hammer *et al.* 2001; Hammer & Harper, 2006). The 'Endpoint correction' option that counts a FAD (First Apparition Datum) or LAD (Last Apparition Datum) within an interval as a half unit instead of one unit, while both FAD and LAD lay within an interval as a third of a unit, was used (Hammer & Harper, 2006).

4.b. Fluctuations

Curves of diversity show a great reduction of both specific and generic diversity during the Famennian post-Iα, IV and VIβ (Fig. 7). At a specific level the two highest drops occurred during the Famennian IV and VIβ; at a generic level the two highest drops occurred during the Famennian Post-Iα and VIβ (Fig. 7). These severe drops were preceded by a diversification phase (Fig. 7).

The evolutionary pattern of specific and generic origination (Fig. 7) shows a moderate increase during the Frasnian/Famennian post-Iα followed by a major increase during the Famennian IIα. The specific and generic origination rates fell drastically thereafter during the Famennian IIβ and IIIα, respectively. After this period other peaks of origination occurred at a specific and generic level and are more moderate than those which took place previously: during the Famennian IIIα, Vα and VIα for the specific origination; and during the Famennian IV and VI for the generic origination (Fig. 7).

After a low rate at the beginning, the evolutionary pattern of specific and generic extinction (Fig. 7) show the Frasnian four major peaks of extinction: during the Frasnian Iδ, the Famennian IIα (specific level), IIβ (generic level), IIIβ and VIβ. These major peaks were followed by sharp decreases: the Famennian post-Iα (generic level), the Famennian IIIα, Vα (specific level) or IV–Vα (generic level).

At the specific level, the major peak of increase was an origination peak occurring during the Famennian IIα; at the generic level, the major peak of increase was an extinction peak occurring at the end of the Famennian.

Whatever level is considered, the evolution of phacopid diversity was characterized by three major declines resulting from extinction rates higher than origination rates. After each decline, a faunal turnover occurred. The history of these turnovers is shown in Figure 8. These biodiversity reductions followed by successive turnovers within Upper Devonian phacopids were caused by successive and major environmental

Table 1. Taxonomic database of all known phacopid species (from literature and new data from this study) including those poorly known from Upper Devonian strata. Taxa with asterisk have been considered in our analysis. Subspecies have often been excluded.

Phacopid species	Comments
*_Acuticryphops acuticeps_ (Kayser, 1889)	
*_Acuticryphops klapperi_ Feist _et al_. 2009	
*_Babinops minor_ Feist _et al_. 2009	
*_Babinops planiventer_ Feist & Becker, 1997	
*_Cryphops cryptophthalmus_ (Emmrich, 1844)	
*_Cryphops latilimbatus_ Maksimova, 1955	
*_Dianops aktjubensis_ Maksimova, 1955	
Dianops algeriensis sp. nov.	
*_Dianops anophthalmus_ (Frech, 1892)	
*_Dianops griffithides griffithides_ (Richter & Richter, 1919)	
*_Dianops griffithides mugodjaricus_ Maksimova, 1955	
*_Dianops guizhouensis_ Xiang, 1981	
*_Dianops limbatus_ (Richter, 1848)	
*_Dianops pernai_ Maksimova, 1955	
*_Dianops typhlops_ (Gürich, 1896)	
*_Dianops vicarius_ Chlupáč, 1961	
*_Dienstina diensti_ (Richter & Richter, 1923)	
*_Dienstina enkia_ Richter & Richter, 1955	
*_Dienstina limaria_ (Perna, 1915)	
*_Ductina ductifrons_ (Richter & Richter, 1923)	
*_Eldredgeops rana rana_ (Green, 1832)	
*_Houseops beckeri_ Feist _et al_. 2009	
*_Houseops canningensis_ Feist _et al_. 2009	
*_Houseops miserrimus miserrimus_ (Drevermann, 1901)	
*_Houseops miserrimus wiedensis_ (Lütke, 1968)	
*_Houseops nalivkini_ Maksimova, 1955	
Houseops ocellatus ocellatus (Perna, 1915)	*_Houseops ocellatus_
Houseops ocellatus primitivus (Perna, 1915)	
*_Houseops pronini_ Maksimova, 1955	
*_Houseops? cryphoïdes_ (Richter & Richter, 1926)	
*_Nephranops franconicus_ Alberti, 1970	
*_Nephranops incisus dillanus_ (Richter & Richter, 1926)	
*_Nephranops incisus incisus_ (Roemer, 1866)	
Omegops accipitrinus accipitrinus (Phillips, 1841)	*_Omegops accipitrinus_
Omegops a. maretiolensis (Richter & Richter, 1933)	
Omegops a. insolatus (Struve, 1976)	
Omegops a. bergicus (Drevermann, 1902)	
Omegops a. mobilis (Xiang, 1981)	
Omegops multisegmentatus (Weber, 1937)	
*_Omegops cornelius_ (Richter & Richter, 1933)	
*_Omegops paiensis_ (Farsan, 1998)	
Phacops? borodinoensis Levitsky, 1974	too poorly known
Phacops? erfoudensis (Richter & Richter, 1943)	too poorly known
Phacops circumspectans Paeckelmann, 1913	*_Phacops circumspectans_
Phacops circumspectans tuberculosus Yuan & Xiang, 1998	
Phacops granulatus (Münster, 1840)	*_Phacops granulatus_
Phacops granulatus guilinensis Zhu, 1988	
Phacops guranensis Maksimova, 1969	*_Phacops sensu lato_
Phacops postaltaicus Maksimova, 1960	
Phacops turco turco Richter & Richter, 1939	
*_Phacops n. sp. a_ Feist, 1995	
*_Phacops tafilaltensis_ Crônier & Clarkson, 2001	
*_Phacops tamtertensis sp. nov._	
*_Phacops zeregensis sp. nov._	
Rabienops evae Struve, 1989	too poorly known
*_Rabienops horni_ Struve, 1989	
Rabienops wedekindi uralicus Maksimova, 1955	*_Rabienops wedekindi_
Rabienops wedekindi wedekindi (Richter & Richter, 1926)	
*_Spinicryphops lemkei_ Crônier & Feist, 2000	
Struveops? inserensis? (Maksimova, 1955)	too poorly known
*_Struveops pulvinifer_ (Matern, 1927)	
*_Struveops schlosseri_ (Richter & Richter, 1955)	
Struveops? tripartitus? (Thomas, 1909)	too poorly known
*_Trimerocephaloides linguiformis_ Feist _et al_. 2009	
*_Trimerocephaloides sinevisus_ Feist _et al_. 2009	
*_Trimerocephalus caecus_ (Gürich, 1896)	
*_Trimerocephalus cryptophthalmoides_ Maksimova, 1955	
*_Trimerocephalus dianopsoides_ Osmólska, 1963	
*_Trimerocephalus interruptus_ Berkowski, 1991	
*_Trimerocephalus lacunosus_ Maksimova, 1955	
*_Trimerocephalus lelievrei_ Crônier & Feist, 1997	
*_Trimerocephalus lentiginosus_ Maksimova, 1955	
*_Trimerocephalus mastophthalmus_ (Richter, 1856)	

Table 1. Continued.

Phacopid species	Comments
**Trimerocephalus mimbi* Feist *et al.* 2009	
**Trimerocephalus polonicus* Osmólska, 1958	
**Trimerocephalus procurvus* Arbizu, 1985	
**Trimerocephalus shotoriensis* Feist *in* Feist *et al.* 2003	
**Trimerocephalus sponsor* Chlupáč, 1966	
**Trimerocephalus? steinachensis* (Richter & Richter, 1926)	
**Trimerocephalus tardispinosus* Feist & Becker, 1997	
**Trimerocephalus vodorezovi* Maksimova, 1955	
**Trimerocephalus (Trifoliops) nigritus* Crônier, 2003	
**Trimerocephalus (Trifoliops) trifolius* (Osmólska, 1958)	
**Weyerites ensae* (Richter & Richter, 1926)	
**Weyerites wockkumeriae* (Richter & Richter, 1926)	

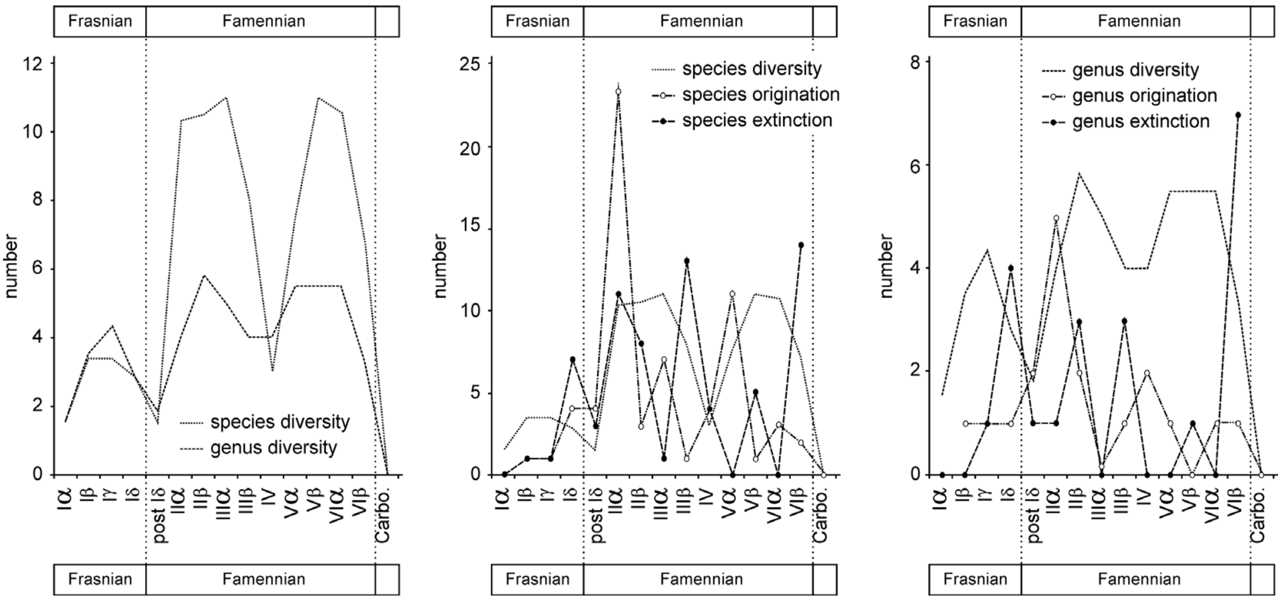

Figure 7. Curves showing diversity, origination and extinction on the presence/absence database from the occurrence of Upper Devonian phacopids. The various metrics have been defined by Hammer & Harper, 2006.

perturbations (Kellwasser or Hangenberg events) which affected the marine environments and thus the marine ecosystems. Additionally, the most important peak of specific and generic origination occurred after the post-Kellwasser event during the Famennian IIα.

4.c. Turnovers and bioevents

As compared to the Givetian (see Crônier & van Viersen, 2007), the Frasnian is not particularly rich in phacopids although material may be abundant locally (Feist *et al.* 2009). During the Early Frasnian, the major transgression initiated in the Mid-Givetian resulted in a homogenization of deep-sea/pelagic environments and a reduction of shallow/neritic environments (Johnson, 1970; House, 1985).

Of the six phacopid genera known during the Frasnian, two genera originated in the early Frasnian (*Houseops* and *Trimerocephaloïdes*) and two others occurred during the mid–late Frasnian (*Acuticryphops* and '*cryphoïdes*' taxon). Only two genera come from the Givetian and persist into the Frasnian: *Phacops* and *Eldredgeops* (C. Brett and J. Zambito, pers. comm.). They are known from North America (*Eldredgeops*) and East Asia (*Phacops*). These genera were almost equally present during the Frasnian, representing 10–25% of the specific diversity (Fig. 8).

During the late Frasnian, the pronounced eustatic deepening became maximal just before the upper Kellwasser event (Girard *et al.* 2005), leading to the development of the pelagic euxinic facies. In these offshore depositional environments beyond the light penetration limit, the gradual visual complex regression leading to blindness is an evolutionary trend observed in various independent lineages. This evolutionary trend may result from an 'opportunistic' and adaptive strategy correlative with environmental constraints, insofar as it leads to a good fit between organisms and their environment (Crônier 1999; Crônier & Courville, 2003). Moreover, the late Frasnian *Acuticryphops* shows a morphological intra-specific drift inducing a relatively important variability of the visual complex (Crônier *et al.* 2004; Feist *et al.* 2009) which would be

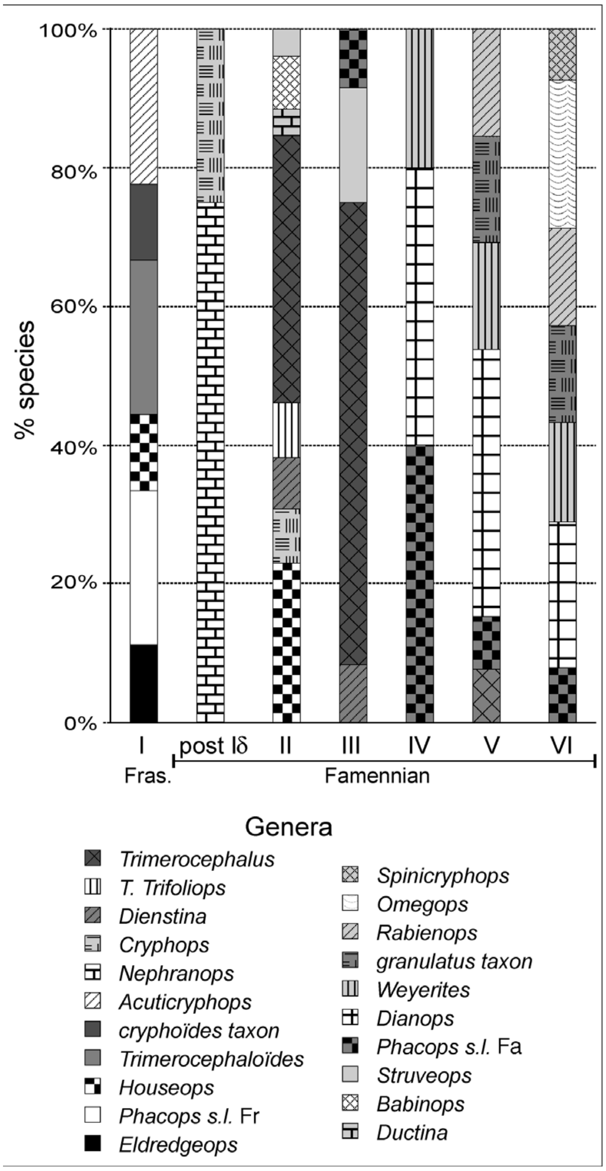

Figure 8. Relative diversity of phacopid genera from the Frasnian to the Famennian in percent of species.

located at speciation boundaries. These disturbances that occurred during development seem to be linked to environmental stress, in particular with rapid sea-level fluctuations of the end-Frasnian (Feist & Schindler, 1994).

At the global scale, the Kellwasser event led to the extinction of almost all reefs and their associated trilobites (Lichidae), and a significant decrease in other trilobite taxa. The Kellwasser extinction especially affected phacopids adapted to life in deep benthic habitats and their biodiversity, and led to a turnover. With one exception, all genera such as *Acuticryphops* (the most common reduced-eyed phacopid of the late Frasnian) became extinct at the base of the upper Kellwasser event (Feist *et al.* 2009).

During the Famennian, phacopid diversity was punctuated by several bioevents: the *Cheiloceras* and Condroz-Enkeberg events (Famennian IIα–β); the *annulata* event (Famennian IV); and the Dasberg and Hangenberg events (Famennian Vα and VIβ, respectively).

The post-Kellwasser event recovery marked a new step for phacopid biodiversity. A first turnover occurred during the Famennian post-Iδ with two new genera reported: *Nephranops* in European offshore environments and *Cryphops* from Upper *triangularis* Zone, representing 75% and 25% of the specific diversity, respectively (Fig. 8).

Nevertheless, the significant post-Kellwasser recovery occurred during the late early Famennian (IIα–β) leading to a second turnover. Both blind and eyed-phacopid genera co-occurred in photic offshore environments. Other marine organisms such as the ammonoids also experienced a significant post-Kellwasser recovery during the *Cheiloceras* event (Walliser, 1985). Of the eight phacopid genera, six genera were new and dominated by *Trimerocephalus* until the Famennian III; *Trimerocephalus* represented 40% of the specific diversity during the Famennian II and almost 70% during the Famennian III (Fig. 8). *Houseops* 'reappeared' after a pseudo-extinction around late Frasnian times (Fig. 8); however *Houseops* of the Frasnian are different from those of the Famennian, and may represent two distinct genera.

A third and final turnover occurred during the Famennian IV. Phacopids originated and diversified in the deeper offshore environments and were mostly blind or reduced-eyed, reflecting the ultimate evolutionary step of the visual complex regression leading to blindness. Well-developed-eyed phacopids were widely distributed in contemporaneous shallow shoal environments. Two genera, *Dianops* (blind) and *Weyerites* (reduced-eyed), occurred and persisted until the end-Famennian (Fig. 8). During the same period *Phacops* regressed significantly from 40% to 10%, whereas *Weyerites* and *Dianops* decreased moderately from 20% to 15% and from 40% to 25–30%, respectively (Fig. 8). The stratigraphic range of the Famennian *Phacops* extended into the Famennian III–VI. *Phacops* known in the Frasnian are different from those known in the Famennian such as *Phacops granulatus* widely distributed geographically.

At the end of the Famennian, in addition to these previous genera four genera *Spinicryphops*, *Rabienops*, *'granulatus'* taxon and *Omegops* (developed-eyed) occurred, representing only 5%, 15%, 15% and 20% of the specific diversity, respectively (Fig. 8). All phacopid genera became extinct at the end-Famennian (Hangenberg event) because of a sea-level rise and anoxic conditions. In this regard, the Famennian is noted for its taxonomic turnovers and for its decline in phacopid diversity. On a global scale, the Hangenberg event led to the extinction of high-level taxonomic proetids.

5. Conclusions

First, the new discovery of phacopids in the Upper Devonian of Algeria allows the following conclusions to be drawn. On the basis of our material, it has been possible to identify numerous blind phacopid species co-occurring or not with more or less normal-eyed forms. At a generic scale, the Algerian faunule may be regarded as diversified and cosmopolitan without marked original features and closely related to European species due to the presence of *Trimerocephalus* and *Dianops*. At a specific scale, this Algerian faunule is closely related to the Holy Cross Mountains (Poland) and Montagne Noire (SW France) species due to the presence of *Trimerocephalus (Trifoliops) nigritus*.

Secondly, our analysis of biodiversity fluctuations of Upper Devonian phacopids allows the following conclusions to be drawn. During Late Devonian time, eustatic variations (transgressive–regressive pulses) had a major influence on the phacopid diversity and their evolution leading to major bioevents (upper Kellwasser and Hangenberg events).

Pronounced sea-level deepening in Devonian time led to major morphological adaptations such as the gradual visual complex regression leading to blindness of various taxa adapted to life in deep-water habitats. Rapid regressive sea-level fluctuations of the end-Frasnian and of the end-Famennian led to major extinctions within these deep benthic communities. The Kellwasser extinction especially affected the phacopid biodiversity and precipitated their decline (extinction of several genera). After a significant post-Kellwasser recovery during the late early Famennian leading to a major faunal turnover, the Hangenberg event precipitated the extinction of all phacopids, which were already strongly impoverished.

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References

ADRAIN, J. M. & WESTROP, S. R. 2000. An empirical assessment of taxic paleobiology. *Science* **289**, 110–12.

ALBERTI, G. K. B. 1970. Zur Augenreduktion bei devonischen Trilobiten Mit Beschreibung von *Nephranops franconicus* n. sp. aus dem Oberdevon Ix von Oberfranken. *Paläontologische Zeitschrift* **41**, 145–60.

ALROY, J., MARSHALL, C. R., BAMBACH, R. K., BEZUSKO, K., FOOTE, M., FÜRSICH, F. T., HANSEN, T. A., HOLLAND, S. M., IVANY, L. C., JABLONSKI, D., JACOBS, D. K., JONES, D. C., KOSNIK, M. A., LIDGARD, S., LOW, S., MILLER, A. I., NOVACK-GOTTSHALL, P. M., OLSZEWSKI, T. D., PATZKOWSKY, M. E., RAUP, D. M., ROY, K., SEPKOSKI, JR. J. J., SOMMERS, M. G., WAGNER, P. J. & WEBBER, A. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences,USA* **98**, 6261–6.

ARBIZU, M. 1985. Trilobites Phacopinae de la Formación Vidrieros, en el área de Gildar-Montó (León, NO de España) y su distribución estratigráfica. *Trabajos de Geologia, Universidad de Oviedo* **15**, 67–75.

BADGLEY, C. 2003. The multiple scales of biodiversity. *Paleobiology* **29**, 11–13.

BARRANDE, J. 1852. *Système Silurien du Centre de la Bohème: 1ère partie, Crustacés, Trilobites*. Chez l’auteur: Prague, Paris, 1–935.

BECKER, R. T. 1985. Devonische Ammonoideen aus dem Raum Hohenlimburg-Letmathe (Geologisches Blatt 4611 Hohenlimburg). *Dortmunder Beiträge zur Landeskunde, Naturwissenschaftliche Mitteilungen* **19**, 19–34.

BECKER, R. T. & SCHREIBER, G. 1994. Zur Trilobiten - Stratigraphie im Letmather Famennium (nördliches Rheinisches Schiefergebirge). *Berliner geowissenschaftliche. Abhandlungen (E)* **13**, 369–87.

BENHAMOU, M., ABBACHE, A., ELMI, S., MEKAHLI, L., RACHEBOEUF, P., OUALI-MAHADJI, A. & BOUMENDJEL, K. 2004. Les calcaires “griottes” et faciès associés du Dévonien supérieur des environs de Beni-Abbes au Djebel Heche (Saoura, Algérie): environnements et implications paléogéographiques. *Bulletin du Service Géologique d’Algérie* **15**, 27–49.

BERKOWSKI, B. 1991. A blind phacopid trilobite from the Famennian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* **36**, 255–64.

BRONN, H. 1825. Über zwei neue Trilobiten-Arten zum *Calymene*-Geschlechte gehörig. *Zeitschrift für Mineralogie, Taschenbuch* **1**, 317–21.

CAMPBELL, K. S. W. 1967. Trilobites of the Henryhouse. Formation (Silurian) in Oklahoma. Oklahoma. *Oklahoma Geological Survey Bulletin* **115**, 5–68.

CASIER, J.G. 1985. Les ostracodes de la partie supérieure de la formatin de Teferguenite (Givétien) et de la formation de Marhouma (Givétien-Famennien) de la coupe du km 30 (Saoura, Sahara Algérien). *Geobios* **18**, 833–46.

CHLUPÁČ, I. 1961. Preliminary report on some new Upper Devonian trilobites from the Moravian karst. *Věstník Ústředni ústav Geologický* **36**, 477–81.

CHLUPÁČ, I. 1966. The Upper Devonian and Lower Carboniferous Trilobites of the Moravian Karst. *Sbornik Geologickych Ved* **7**, 1–143.

CHLUPÁČ, I. 1971. New phacopid trilobites from the Devonian of Czechoslovakia. *Časopis pro Mineralogii a Geologii* **16**, 255–61.

CHLUPÁČ, I. 1977. The phacopid trilobites of the Silurian and Devonian of Czechoslovakia. *Vydal Ústředni ústav Geologický* **43**, 1–164.

CRÔNIER, C. 1999. Modalités d’évolution phylétique sous contrôle du milieu chez quelques Phacopinés (Trilobites) néo-Dévoniens. *Geobios* **32**, 187–92.

CRÔNIER, C. 2003. Systematic relationships of the blind phacopine trilobite *Trimerocephalus*, with a new species from Causses-et-Veyran, Montagne Noire. *Acta Palaeontologica Polonica* **48**, 1–13.

CRÔNIER, C. 2008. Morphological relationships within Upper Devonian phacopine trilobite populations from Germany. In *International Conference ‘Global alignments of the Lower Devonian Carbonate and Clastic sequences’, IGCP 499 Project/SDS joint field meeting: Contributions of International Conference* (eds A. I. Kim, F. A. Salimova & N. A. Meshchankina), pp. 22–6. Tashkent: SealMagPress.

CRÔNIER, C. & CLARKSON, E. N. K. 2001. Variation of eyes-lens distribution in a new late Devonian phacopid trilobite. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **92**, 103–13.

Crônier, C., Bignon, A. & François, A. 2011. Morphological and ontogenetic criteria for defining a trilobite species: the example of Siluro-Devonian Phacopidae. *Comptes Rendus Palevol* **10**, 143–53.

Crônier, C. & Courville, P. 2003. Variations du rythme du développement chez les trilobites Phacopidae néodévoniens. *Comptes Rendus Palevol* **2**, 577–85.

Crônier, C. & Feist, R. 1997. Morphologie et évolution ontogénétique de *Trimerocephalus lelievrei* nov. sp., premier trilobite phacopidé aveugle du Famennien nord-africain. *Geobios (Mémoire Spécial)* **20**, 161–70.

Crônier, C. & Feist, R. 2000. Evolution et systématique du groupe *Cryphops* (Trilobita, Phacopinae) du Dévonien supérieur. *Senckenbergiana lethaea* **79**, 501–15.

Crônier, C., Feist, R. & Auffray, J.-C. 2004. Variation in the eye of *Acuticryphops* (Phacopina, Trilobita) and its evolutionary significance: a biometric and morphometric approach. *Paleobiology* **30**, 471–81.

Crônier, C. & van Viersen, A. 2007. Trilobite palaeobiodiversity during the Devonian in the Ardennes Massif. *Bulletin de la Société Géologique de France* **178**, 473–83.

Delo, D. M. 1935. A revision of the phacopid trilobites. *Journal of Paleontology* **9**, 402–26.

Drevermann, F. 1901. Die Fauna der oberdevonischen Tuffbreccie von Langenaubach bei Haiger. *Jahrbuch der Preußischen Geologischen, Landesanstalt 1900*, 99–207.

Drevermann, F. 1902. Über eine Vertretung der Etroeungt-Stufe auf der rechten Rheinseite. *Zeitschrift der Geologischen Gesellschaft* **54**, 480–524.

Emmrich, H. F. 1839. *De Trilobitis: dissertatio petrefactologica quam consensu et auctoritate amplissimi philosophorum ordinis in alma litterarum universitate Friderica Guilelma pro summis in philisophia honoribus/Hermanus Frider Emmerich*. Thesis, Philos-Univ, Friderica Guilelma, Berlin. Published thesis.

Emmrich, H. F. 1844. *Zur naturgeschichte der Trilobiten*. Realschul-Programm, Meiningen.

Farsan, N. M. 1998. Das Etroeungtium (Ober-Devon VI, Strunium) und die letzen Phacopinae (Trilobita) im westlichen Zentral- und West-Afghanistan. *Mainzer Naturwissenschaftliches Archiv Beiheft* **21**, 17–37.

Feist, R. 1995. Effect of poedomorphosis in eye reduction on patterns of evolution and extinction in trilobites. In *Evolutionary Change and Heterochrony* (ed. K. J. McNamara), pp. 225–44. Chichester, New York: John Wiley & Sons Ltd.

Feist, R. & Becker, T. 1997. Discovery of Famennian trilobites in Australia (Late Devonian, Canning Basing, NW Australia). *Geobios (Mémoire special)* **20**, 231–42.

Feist, R. & Clarkson, E. N. K. 1989. Environmentally controlled phyletic evolution, blindness and extinction in Late Devonian tropidocoryphine trilobites. *Lethaia* **22**, 359–73.

Feist, R., McNamara, K. J., Crônier, C. & Lerosey-Aubril, R. 2009. Patterns of extinction and recovery of phacopid trilobites during the Frasnian-Famennian (Late Devonian) mass extinction event, Canning Basin, Western Australia. *Geological Magazine* **146**, 12–33.

Feist, R. & Schindler, E. 1994. Trilobites during the Frasnian Kellwasser Crisis in European Late Devonian cephalopod limestones. *Courier Forschungsinstitut Senckenberg* **169**, 195–23.

Feist, R., Yasdi, M. & Becker, R.T. 2003. Famennian trilobites from the Shotori Range, E. Iran. *Annales de la Societé Géologique du Nord* **10**, 285–95.

Foote, M. 2000. Origination and Extinction Components of Taxonomic Diversity: General Problems. *Paleobiology (Suppl.)* **26**, 74–102.

Frech, F. 1892. *Die Karnischen Alpen*. Halle: Niemeyer.

Girard, C., Klapper, G. & Feist, R. 2005. Subdivision of the terminal Frasnian *linguiformis* Conodont Zone, revision of the correlative interval of Montagne Noire Zone 13, and discussion of stratigraphically significant associated trilobites. In *Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach* (eds J. R. Over, J. R. Morrow & P. B. Wignall), pp. 181–198. Amsterdam: Elsevier.

Gürich, G. 1896. Das Paläozoicum im polnische Mittlegebirge. *Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft (Ser. II)* **32**, 1–539.

Green, J. 1832. Synopsis of the trilobites of North America, in which some new genera and species are proposed. *Monthly American Journal of Geology* **1**, 558–60.

Hahn, G. & Hahn, R. 1975. Die Trilobiten des Ober-Devon, Karbon und Perm. *Leitfossilien* **1**, 1–127.

Hammer, Ø. & Harper, D. A. T. 2006. *Paleontological Data Analysis*. Blackwell.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4**, 1–9.

Haug, E. 1903. Sur deux horizons à céphalopodes du Dévonien supérieur dans le Sahara oranais. *Comptes rendus des séances de l'Académie des Sciences*, **137**, 83–5.

Hawle, I. & Corda, A. J. C. 1847. Prodom einer Monographie der böhmischen Trilobiten. *Abhandlungen der königlischen böhemischen Gesellschaft der Wissenschaften* **5**, 1–176.

House, M. R. 1985. Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature* **313**, 17–22.

Johnson, J. G. 1970. Taghanic onlap and the end of North American Devonian provinciality. *Geological Society of America, Bulletin* **81**, 2077–105.

Kaiser, S. I., Becker, R. T. & El Hassani, A. 2007. Middle to late Famennian successions at Ain Jemaa (Moroccan Meseta). Implications for regional correlation, event stratigraphy and synsedimentary tectonics of NW Gondwana. In *Devonian Events and Correlations* (eds R. T. Becker & W. T. Kirchgasser), pp. 237–60. Geological Society of London, Special Publication no. 278.

Kayser, E. 1889. Über einige neue oder wenig gekannte Versteinerungen des rheinischen Devons. *Zeitschrift der Deutschen Geologischen Gesellschaft* **41**, 288–96.

Lerosey-Aubril, R. & Feist, R. 2012. Quantitative approach of diversity and decline in late Palaeozoic trilobites. In *Earth and Life: Global Biodiversity, Extinction Intervals and Biogeographic Perturbations through Time* (ed. J. A. Talent), pp. 535–55. Springer Publishing.

Levitsky, E. C. 1974. Razvitie verchnedevonskich predstavitelej roda *Phacops* Emmrich, 1839 (S. L.). *Izvcst. Vyshikh učeb. Zaved, Geologia i Razvedka* **8**, 24–31.

Lütke, F. 1968. Trilobiten aus dem Oberdevon des Südwest-Harzes-Stratigraphie, Biotop und Systematik. *Senckenbergiana Lethaea* **49**,119–91.

Maksimova, Z. A. 1955. *Trilobity srednego i verchnego devona Urala i severnych Mugodzar*. Internal report. Vsesoyuznogo Nauchno-Issledovatelskii Geologicheskii Institut Trudy, n. S., **3**, 1–263 (in Russian).

MAKSIMOVA, Z. A. 1960. *Paleontologitscheskoje obosnovanije stratigrafii paleozoja rudnogo Altaja. VII. Devonskije i Kamenougolnye trilobity rudnogo Altaja*. Moscow: Vsesoyuznogo Nauchno-issledovatel'skii Geologicheskogo Instituta, 123 pp. (in Russian).

MAKSIMOVA, Z. A. 1969. Trilobites. In *Field Atlas of the Silurian, Devonian, and Early Carboniferous Fauna of the Soviet Far East* (ed. E.A. Modzalevskoy). Moscow: Nedra, 137–49.

MATERN, H. 1927. Mitteilungen über die Oberdevon-Fauna der Dill-Mulde. I. Die oberdevonischen Trilobiten des Scheldetals. *Senckenbergiana* **9**, 252–60.

MCCOY, F. 1849. On the classification of some Bristish fossil Crustacea, with notices of new forms in the University Collection at Cambridge. *The Annals and Magazine of Natural History (Ser. II)* **4**, 161–69, 330–5, 392–414.

MCKELLAR, R. C & CHATTERTON, B. D. E. 2009. Early and Middle Devonian Phacopidae (Trilobita) of southern Morocco. *Palaeontographica Canadiana* **28**, 1–114.

MENCHIKOFF, N. 1930. Recherches géologiques et morphologiques dans le Nord du Sahara occidental. *Revue de Géographie Physique et de Géologie Dynamique* **3**, 103–247.

MORZADEC, P. & BABIN, C. 1976. Présence de *Trimerocephalus caecus* (Gürich, 1896) (Trilobita, Phacopidae) dans le Famennien inférieur du Finistère: intérêt stratigraphique et paléogéographique. *Geobios* **9**, 367–71.

MÜNSTER, G. G. 1840. Die Versteinerungen des Uebergangskalkes mit Clymenien und Orthoceratiten von Oberfranken. *Beiträge zur Petrefakten-Kunde, III, Heft* **7**, 33–121.

OSMÓLSKA, H. 1958. Famennian Phacopidae from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica* **3**, 119–48.

OSMÓLSKA, H. 1963. On some Famennian Phacopinae (Trilobita) from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica* **8**, 495–523.

OUALI MEHADJI, A., BENDELLA, M., ATIF, K., BELKACEMI, K. & ABBACHE, A. 2012. Estimation de l'épaisseur réelle et des environnements de dépôts d'âge Famennien (Dévonien supérieur) de la région de Marhouma (Saoura, Sahara Nord-Ouest, Algérie). *Bulletin du Service Géologique National* **23**, 3–27.

PAECKELMANN, W. 1913. Das Oberdevon des Bergischen Landes. *Abhandlungen der Preußischen Geologischen,Landesanstalt* **70**, 1–356.

PERNA, A. 1915. Upper Devonian trilobites from the environs of the town Vierkhnie-Uralsk. *Mémoires du Comité Géologique, Nouvelle Série, Petrograd* **138**, 1–56.

PFEIFFER, VON H. 1954. Der Bohlen bei Saalfeld/Thür. *Beiheft zur Zeitschrift,Geologie* **11**, 1–105.

PFEIFFER, VON H. 1959. Neue Beobachtungen und Funde aus dem Saalfelder Oberdevon. *Geologie* **8**, 262–79.

PHILLIPS, J. 1841. *Figures and descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset*. London: Longman.

RICHTER, RH. 1848. *Beitrag zur Paläontologie des Thüringer Waldes. Die Grauwacke des Bohlens und des Pfaffenbergs bei Saalfeld. I. Fauna*. Dresden, Leipzig: Arnoldische Buchhandlung.

RICHTER, RH. 1856. Beitrag zur Paläontologie des Thüringer Waldes. Erster Theil. *Denkschrift der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe, Wien* **11**, 87–138.

RICHTER, RD. & RICHTER, E. 1919. Über *Phacops laevis* Münster und andere Phacopiden des vogtländischen Oberdevons. *Senckenbergiana* **1**, 131–140.

RICHTER, RD. & RICHTER, E. 1923. Systematik und Stratigraphie der Oberdevon-Trilobiten des Ostthüringischen Schiefergebirges. *Senckenbergiana* **5**, 59–76.

RICHTER, RD. & RICHTER, E. 1926. Die Trilobiten des Oberdevons. Beiträge zur Kenntnis devonischer Trilobiten IV. *Abhandlungen der Preußischen Geologischen,Landesanstalt* **99**, 1–314.

RICHTER, RD. & RICHTER, E. 1933. Die letzten Phacopidae. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* **9**, 1–19.

RICHTER, RD. & RICHTER, E. 1939. Trilobiten aus dem Bosporus-Gebiet. *Abhandlungen der Preußischen Geologischen, Landesanstalt* **190**, 1–49.

RICHTER, RD. & RICHTER, E. 1943. Trilobiten aus dem Devon von Marokko mit einem Anhang über Arten des Rheinlands. *Senckenbergiana* **26**, 116–99.

RICHTER, RD. & RICHTER, E. 1955. 2. Phylogenie der oberdevonischen Phacopidae. *Senckenbergiana lethaea* **36**, 49–72.

ROEMER, F. A. 1866. Beiträge zur geologischen Kenntnis des nordwestlichen Harzgebirges. Fünfte Abtheilung. *Palaeontographica* **13**, 201–35.

SCHINDLER, E. 1990. The Late Frasnian (Upper Devonian) Kellwasser Crisis. *Lecture Notes in Earth Sciences* **30**, 151–59.

SCHLAGER, W. 1981. The paradox of drowned reefs and carbonate platforms. *Geological Society of America, Bulletin* **92**, 197–211.

SMITH, A. B. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London, B* **356**, 351–67.

STRUVE, W. 1976. Beiträge zur Kenntnis der Phacopina (Trilobita), 9: *Phacops (Omegops)* n. sg. (Trilobita; Ober-Devon). *Senckenbergiana lethaea* **56**, 429–51.

STRUVE, W. 1989. *Rabienops evae* aus dem Späten Ober-Devon des Rheinischen Gebirges. *Bulletin de la Société belge de Géologie* **98**, 335–42.

TERMIER, G. & TERMIER, H. 1950. Paléontologie marocaine. II. Invertébrés de l'Ere Primaire. Fascicule III. Annélides, Arthropodes, Echinodermes, Conularides et Graptolithes. *Notes et Mémoires du Service Géologique du Maroc* **79**, 1–282.

THOMAS, I. 1909. Notes on the trilobite fauna of Devon and Cornwall. *The Geological Magazine* (New series, Decade V) **6**, 193–204.

WALLISER, O. H. 1985. Natural boundaries and Commission boundaries in the Devonian. *Courier Forschungsinstitut Senckenberg* **75**, 401–08.

WEBER, V. 1937. Trilobity kamennougol'nych i permskich otlozheniy SSSR. I. Kamennougol'nye trilobity. *Monografii Russkoe Paleontologizeskoe Obstschestwo* **71**, 1–160.

WEDEKIND, R. 1908. Die Cephalopodenfauna des höheren Oberdevon am Enkenberg. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **26**, 565–635.

WEDEKIND, R. 1911. Klassifikation der Phacopiden. *Zeitschrift der Deutschen Geologischen Gesellschaft* **63**, 317–36.

WENDT, J., KAUFMANN, B., BELKA, Z., KLUG, C. & LUBESEDER, S. 2006. Sedimentary evolution of a Palaeozoic bain and ridge system: the Middle and Upper Devonian of the Ahnet and Mouydir (Algerian Sahara). *Geological Magazine* **143**, 269–99.

Xiang, L. 1981. Some Late Devonian trilobites of China. *Geological Society of America (Special Paper)* **187**, 183–91.

Yuan, J-L. & Xiang, L-W. 1998. Trilobite fauna at the Devonian–Carboniferous boundary in South China (S-Guizhou and N-Guangxi). *Bulletin of the National Museum of Natural Science (Special Publication)* **8**, 1–281.

Zhu, Z. L.1988. Trilobites. In *Devonian-Carboniferous Boundary in Nanbiancun, Guilin, China - Aspects and Records* (ed. C. M. Yu), pp. 199–208. Beijing: Science Press.

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ERRATUM

First occurrence of a phacopid trilobite faunule from the Upper Devonian of Saoura Valley, Algeria and biodiversity fluctuations – Erratum

CATHERINE CRÔNIER, FATIMA ZOHARA MALTI, ANGELA FRANÇOIS, MADANI BENYOUCEF & DENISE BRICE

In Crônier *et al*. 2013, the name of the second author was spelled incorrectly and should have read Fatima Zohra Malti.

Reference

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