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A trilobite faunule from the Lower Devonian of the Saoura Valley, Algeria: biodiversity, morphological variability and palaeobiogeographical affinities

AHMED YACINE KHALDI*, CATHERINE CRÔNIER‡†, GAUTIER HAINAUT‡, ABDELKADER ABBACHE§ & ABDELKADER OUALI MEHADJI*

*Laboratoire de Paléontologie stratigraphique et paléo-environnements, Université d'Oran, boîte postale 1524, El-M'naouer 31000 Oran, Algérie
‡UMR8198, EvoEcoPaleo-CNRS, Université Lille 1, UFR Sciences de la Terre, 59655 Villeneuve d'Ascq Cedex, France
§Université de Mascara, Faculté SNV, Algérie

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Abstract – Trilobites are widespread in Lower Devonian deposits of north Gondwana, and some have been collected from two known sections of the Saoura Valley in SW Algeria, from the 'Chefar el Ahmar' Formation. This formation is considered to be from late Emsian to Frasnian in age, but only the lower parts of this formation have yielded trilobites. Nevertheless, no detailed studies have focused on their biodiversity and their morphological variability. New occurrences of phacopids including *Barrandeops chattertoni* sp. nov., *Geesops fabrei* sp. nov., *Austerops legrandi* sp. nov. and *Phacops boudjemaai* sp. nov. are described from this area and comparisons are made with closely allied species. These new occurrences have been integrated into analyses of intra- and inter-specific variability and biodiversity.

Keywords: Phacopida, Proetida, Chefar el Ahmar Formation, Emsian, Ougarta, diversity, palaeogeography.

1. Introduction

Throughout the lowermost Devonian, trilobite diversity is relatively poor. The Basal Pragian Event of regressive character contributed to the installation of shallow marine realms with carbonate sedimentation favourable for trilobites. This led to an increase in the generic diversity and, at least, to a preservation of the family diversity, which lasted with some changes until early Eifelian time (Chlupáč, 1994; Crônier & Van Viersen, 2007).

The publications of Alberti (1969, 1970, 1981), Morzadec (1997, 2001), Chatterton *et al*. (2006), McKellar & Chatterton (2009) and Gibb & Chatterton (2010) have been major contributions to our current knowledge of North African Lower Devonian trilobites.

The present paper is a contribution to the systematic study of the Lower Devonian trilobites and especially phacopid trilobites from SW Algeria. The discovery of new taxa assigned to *Barrandeops*, *Geesops*, *Austerops* and *Phacops sensu lato* gives us the opportunity to understand these forms more fully and to explore their palaeobiodiversity.

2. Geological setting and material

2.a. Local geological succession

In southwestern Algeria, beyond the Saharan Atlas and the High Zousfana, a mountain range of Palaeozoic age called the Mountains of Ougarta or the Ougarta Range appears. This folded domain links the Moroccan Anti-Atlas to the northwest and the hills of Bled El Mass and Tanezrouft to the southeast (Fig. 1). The Mountains of Ougarta, which extend over 400 km in length and 200 km in width, are elongated in a NW–SE direction and subdivided into two structural units consisting of folds with the same long axis, i.e. two 'beams', separated by the Erg Er Raoui: (1) a northern unit, i.e. 'beam of Saoura', constituted by anticlines that expose Cambro-Ordovician outcrops and synclines that expose Siluro-Devonian outcrops; and (2) a southernmost unit, i.e. 'beam of Daoura' also called Kahal Tabelbala, located to the east of the Pan-African sutures that exposes only Cambro-Ordovician outcrops (Menchikoff, 1933; Donzeau, 1983; Fabre, 2005).

The sampled material in the present study has been collected from two sections located in the beam of Saoura: (1) the 'Erg el Djemel' section located 70 km to the south of Beni-Abbès city and 7 km to the south of Ougarta village, and (2) the 'Marhouma' section called 'km 30', which is located 30 km to the SE of Beni-Abbès city and 5 km from the Marhouma oasis (Fig. 1). This 'km 30' section is used as reference for the lithostratigraphic correlations of the Devonian in North Africa (Le Maître, 1952; Boumendjel *et al*. 1997).

The Palaeozoic deposits of Saoura have been known since the beginning of the twentieth century (Gautier, 1902). However, the stratigraphy and the fauna of the Devonian only began to be described later (Menchikoff, 1930, 1932, 1933, 1936; Le Maître, 1952). Former

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

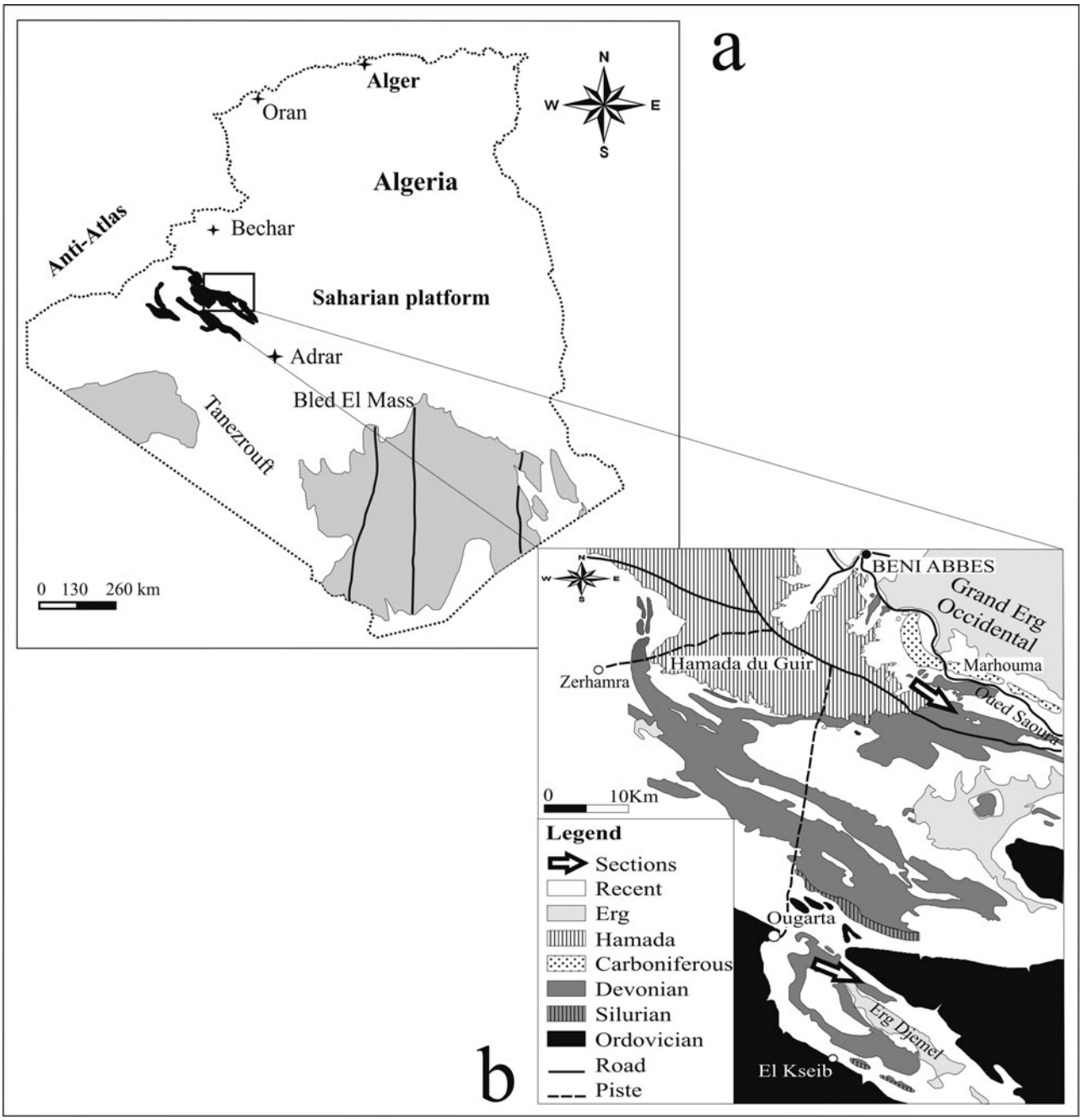

Figure 1. (a) Geographical location of the Marhouma and Erg el Djemel areas, SE of Beni-Abbès (30 km), Saoura Valley, Ougarta Basin, Algeria. (b) Location of studied Marhouma ('km 30') and Erg el Djemel ('Ed') sections. Extract of the geological map 1/200 000.

works (Flamand, 1911; Menchikoff, 1936; Alimen *et al.* 1952; Le Maître, 1952; Legrand, 1967) were synthesized by Boumendjel *et al.* (1997), who redefined the lithostratigraphic units of the Devonian of Saoura. Six formations were defined representing more than 1680 m in thickness, including the 'Chefar el Ahmar' Formation corresponding to the fifth formation from the base.

The fossils described herein were mainly collected from a 'shell level' containing a varied benthic fauna that was labelled FBV by A. Ouali Mehadji (unpub. Ph.D. thesis, Univ. Oran, 2004), previously labelled 'Corraligène' by Le Maître (1952). This level is situated in the base of the 'Chefar el Ahmar' Formation of the Saoura Valley and regarded as upper Emsian in age on the basis of cephalopods (Göddertz, 1987), corals (Plusquellec, 1997) and brachiopods (A. Ouali Mehadji, unpub. Ph.D. thesis, Univ. Oran, 2004). The higher part of this formation is represented by alternating claystones and nodular limestones with goniatites called 'Calcaires griottes'.

The 'varied benthic fauna level' (FBV) is represented by alternating grey claystone and grey calcareous limestones, which are sometimes nodular and strongly fossiliferous (trilobites, brachiopods, corals, crinoids, bryozoans, some rare gastropods, orthocerids and goniatites). In the Marhouma section, the FBV is 12 m thick and has eight major carbonate levels, the highest

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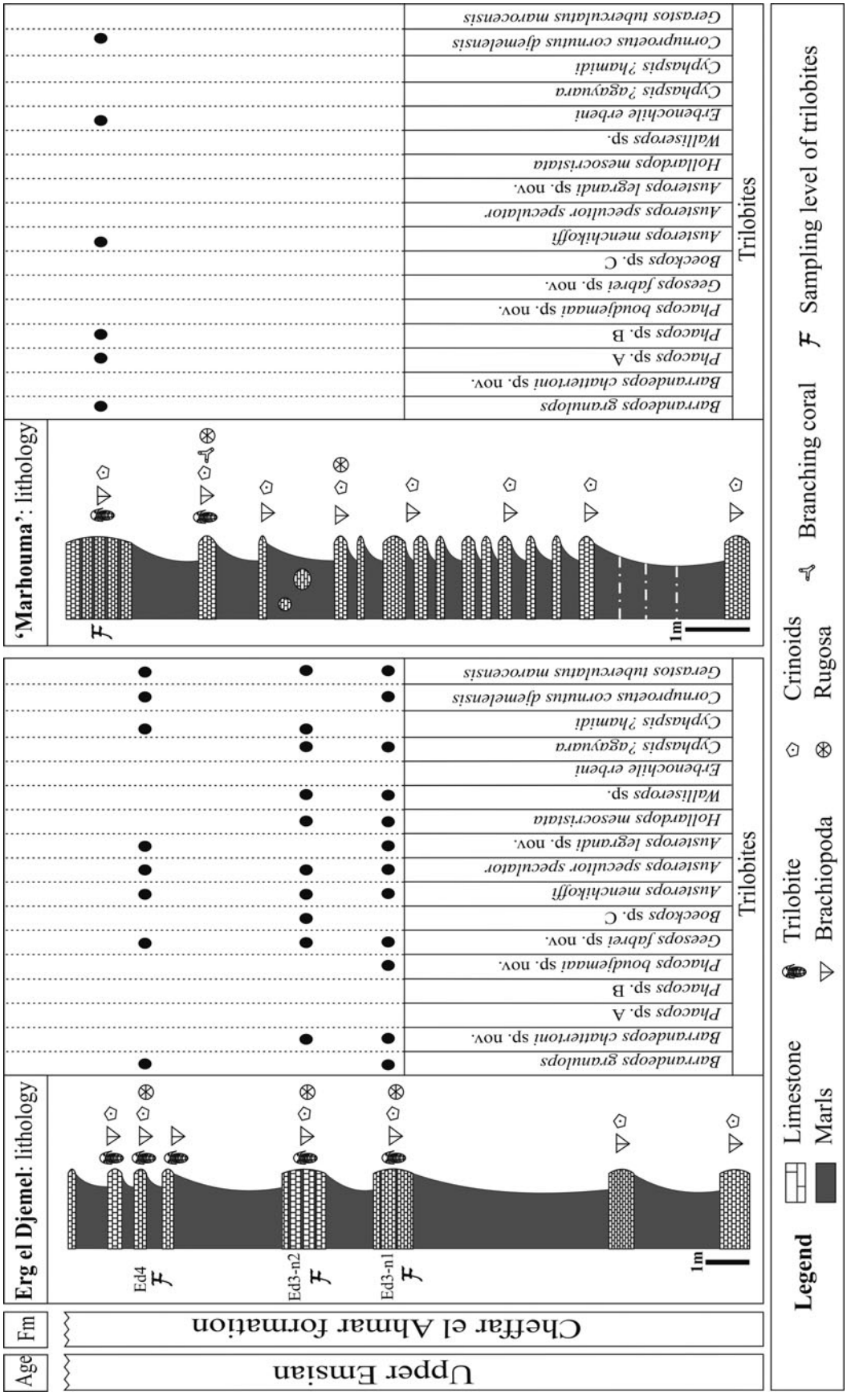

Figure 2. Lithostratigraphic column of the 'Chefar el Ahmar' Formation and stratigraphical location of studied trilobites (from the Marhouma and the Erg el Djemel sections).

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of which makes up a 'trilobite level' interrupted by green clay intercalations (Fig. 2). In the Erg el Djemel section, the FBV is 12 m thick and has six major carbonate levels, including three trilobite levels (Ed3n1, Ed3n2 and Ed4) also intercalated by green clay levels (Fig. 2).

2.b. Trilobite faunas

In the published Lower Devonian faunal associations previously reported from Algeria, numerous trilobites from the Ougarta Basin have been described (23 species) and illustrated by Le Maître (1952), such as *Phacops menchikoffi* or *Asteropyge mesocristata* (original designation), as new species. Alberti (1981) also studied the trilobites from this area and substantially contributed to the knowledge of the Lower Devonian stratigraphy of the Ougarta Basin. He defined several new species or subspecies, such as *Cornuproetus* (*Cornuproetus*) *cornutus djemelensis* from the Erg el Djemel section. Morzadec (1997) focused on the Devonian Asteropyginae and also contributed to the biostratigraphical concept of the Ougarta Basin. He described and illustrated 11 species, including five new species arranged in nine genera including two new genera, i.e. *Hollardops* represented by the common species *H. mesocristata* (Le Maître, 1952) and *Destombesina* represented by the single species *D. ougartensis* Morzadec (1997).

As observed in other areas from the northern peri-Gondwanan margin, such as Morocco (Chatterton *et al*. 2006; McKellar & Chatterton, 2009; Gibb & Chatterton, 2010), the trilobite, and especially phacopid, remains are relatively abundant and well preserved. The trilobites include mostly complete and enrolled specimens. The studied trilobites with their geographic and stratigraphic locations are listed in Figure 2.

The material described and figured herein is housed in the University of Oran, Algeria (collection Di/UO 001–037).

3. Systematic palaeontology

Morphological terminology mainly follows Chlupáč (1977), Crônier, Bignon & François (2011) and Gibb & Chatterton (2010). Abbreviations used: 'exsag.' – exsagittal; 'sag.' – sagittal; 'tr.' – transverse; and according to the rules of synonymy lists (Matthews, 1973), some signs attached to the synonymy list have been used: '∗' for valid species; '.' for responsibility assumed for attaching this reference to the type species; and 'v' for material seen.

Order PHACOPIDA Salter, 1864
Family PHACOPIDAE Hawle & Corda, 1847
Subfamily PHACOPINAE Hawle & Corda, 1847
Genus *Barrandeops* McKellar & Chatterton, 2009

Type species. Barrandeops forteyi McKellar & Chatterton, 2009: upper Emsian, Morocco.

Additional species. *Barrandeops granulops* (Chatterton *et al*. 2006): upper Emsian, Morocco; *B. lebesus* (Chatterton *et al*. 2006): Eifelian, Morocco; *B. ovatus* McKellar & Chatterton, 2009: upper Emsian, Morocco; *B. chattertoni* sp. nov.: upper Emsian, Algeria.

Remarks. Barrandeops was erected by McKellar & Chatterton (2009) for a group of tuberculate Moroccan phacopids without pitting in the palpebral lobe and palpebral area. The previously described species such as *Phacops turco praecedens* Haas, 1968 or *Phacops* (*Phacops*) *saberensis torkozensis* Schraut, 2000*a*, need to be re-evaluated.

Barrandeops granulops (Chatterton et al. 2006)
Figure 3a–m

v. 1952 [non] *Phacops* cf. *turco* Richter & Richter, 1939; Le Maître, p. 157, pl. 21, fig. 7.

2006 *Phacops granulops* sp. nov. Chatterton, Fortey, Brett, Gibb & McKellar, pp. 12–14, pl. 1.1–1.10, pl. 2.1–2.12, text-fig. 3.4.

2009 *Barrandeops granulops* (Chatterton *et al*.); McKellar & Chatterton, pp. 44–5.

Type material. Enrolled exoskeleton UA13295, from the upper Emsian, Timrhanrhart Formation, basal part of section at Jbel Gara el Zguilma, near Foum Zguid, Morocco.

Studied material. Twenty-nine mostly enrolled exoskeletons: two from the upper Emsian (base of the 'Chefar el Ahmar' Formation) of the Marhouma section ('km 30') and 27 from the Erg el Djemel section including ten small individuals (three from Ed3n1 and 24 from Ed4 with some specimens more or less eroded); Ougarta Basin, Saoura, Algeria.

Diagnosis. See McKellar & Chatterton (2009).

Remarks. The Algerian specimens show the main morphological features of *Barrandeops granulops* from Morocco: coarse conical tubercles, 19 dorsoventral files of lenses with 4–5 lenses per file, no pitting between tubercles of the palpebral lobe and the palpebral area, and a postocular pad with tubercles and a row of small tubercles at the base of the eye; only the axial furrows are a little less divergent (65–67° for Algerian specimens against more than 70° for Moroccan specimens). The smallest specimen at 4.5 mm long (sag.) has only 18 dorsoventral files of lenses with a maximum of four lenses per file. Its cephalic outline is less subcircular than for the oldest specimens and the tubercles are relatively coarser.

Among the best preserved specimens, one specimen from the Marhouma section ('km 30'; Fig. 3i–l) seems to be slightly different from *Barrandeops granulops sensu stricto*. This specimen, with a large size (15.5 mm in cephalic length), has more scattered conical tubercles on the glabella and fewer tubercles on the intercalar ring.

Le Maître (1952) previously attributed some specimens to *Phacops* cf. *turco* Richter & Richter, 1939. The specimen figured (pl. XXI, fig. 7; GFCL405, coll. Le Maître, Faculté libre des Sciences de Lille) from the Erg el Djemel section with 19 dorsoventral files of lenses and a maximum of five lenses per file is reassigned in this work to *Barrandeops granulops*.

Barrandeops granulops differs from *B. lebesus* (Chatterton *et al*. 2006) from the Eifelian of Morocco. *Barrandeops lebesus* has often 19 files of lenses with a maximum of six lenses per file, a coarse but less dense tuberculation on the glabella and a less pronounced and less tuberculated subocular pad.

Barrandeops granulops differs from *Phacops* (*Phacops*) *saberensis torkozensis* from the upper Emsian of Morocco. *Phacops* (*Phacops*) *saberensis torkozensis* has no distinct postocular pad, 17–18 files of lenses with five lenses per file, and a wider postocular area, inflated and continuous with the sub-lateral area.

Barrandeops granulops differs also from *Phacops* (*Phacops*) *tafilaltanus* Alberti, 1983 (pl. 2, fig. 12), from the upper Emsian of Morocco. *Phacops* (*Phacops*) *tafilaltanus* has a larger but less distinct postocular pad, a well-defined subocular pad with tubercles, 18

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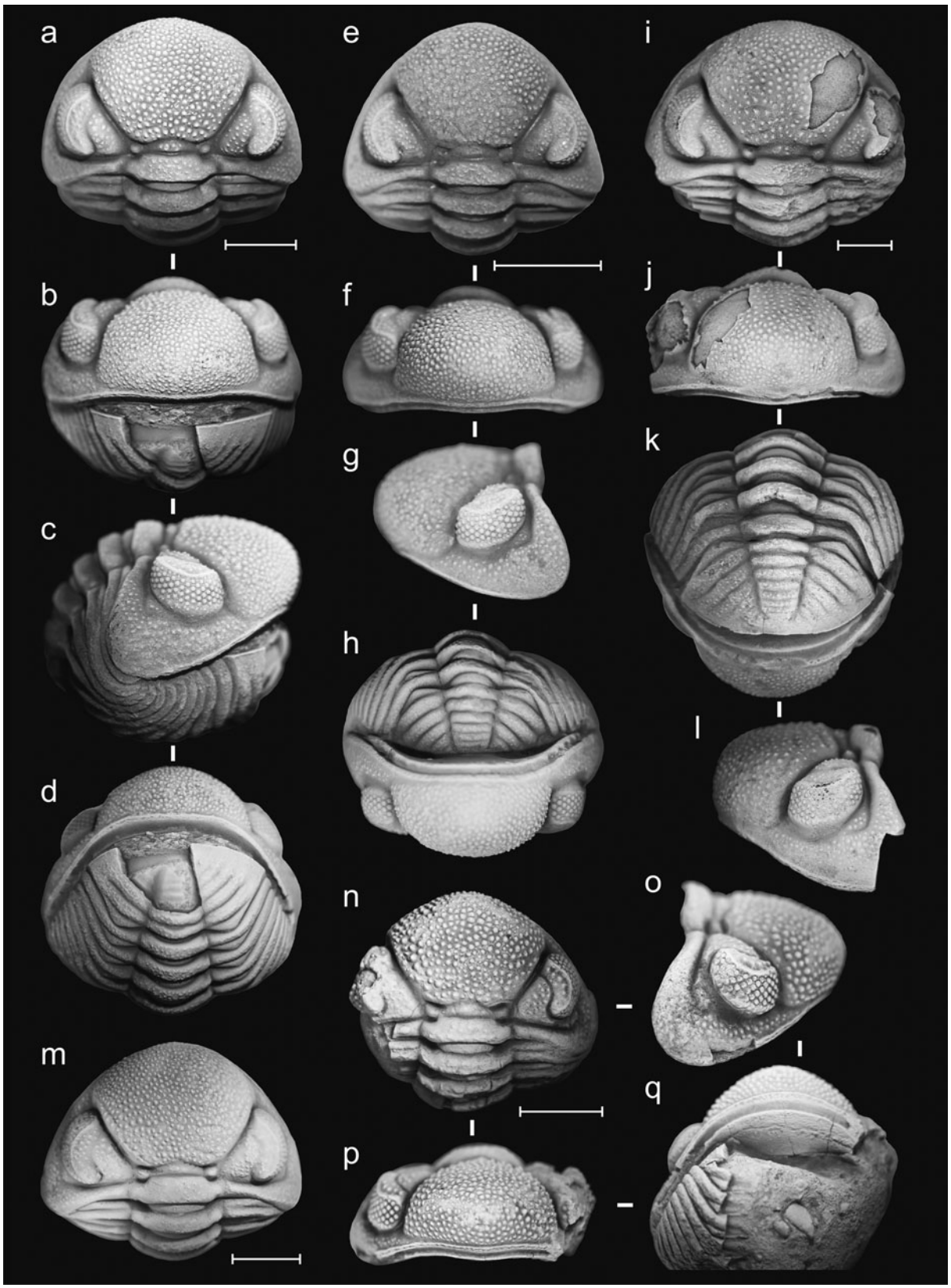

Figure 3. Phacopid trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–d) *Barrandeops granulops* (Chatterton et *al*. 2006), Erg el Djemel section, Di/UO/028 (Ed4): (a–c) cephalon in dorsal, frontal and lateral views; (d) pygidium in dorsal view. (e–h) *Barrandeops granulops* (Chatterton et *al*. 2006), Erg el Djemel section, Di/UO/027 (Ed4): (e–g) small cephalon in dorsal, frontal and lateral views; (h) pygidium in dorsal view. (i–l) *Barrandeops* ?*granulops* (Chatterton et *al*. 2006), Marhouma section, Di/UO/034 ('km 30'): (i–j, l) cephalon in dorsal, frontal and lateral views; (k) pygidium in dorsal view. (m) *Barrandeops granulops* (Chatterton et *al*. 2006), Erg el Djemel area, figured by Le Maître in 1952, GFCL405 (coll. Le Maître, Faculté libre des Sciences de Lille). (n–q) *Phacops sensu lato* sp. A, Marhouma section, Di/UO/032 ('km 30'): cephalon in dorsal, lateral, frontal and ventral views. Scale bars = 5 mm.

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files of lenses with 4–5 lenses per file, and a less pronounced and less dense tuberculation on the glabella.

Barrandeops granulops shares with *Phacops turco praecedens* Haas, 1968 (pl. 30, fig. 6, non fig. 7) from the Eifelian of Turkey the same number of lenses per file. However, *Barrandeops granulops* differs in having one more dorsoventral file, a smaller postocular pad and no tubercular subocular pad.

Occurrence. Upper Emsian; Morocco (Foum Zguid), Algeria (Saoura: Erg el Djemel, 'km 30' section).

Barrandeops chattertoni sp. nov.
Figure 4a–f

Name. Named in honour of Dr Brian D. E. Chatterton, Professor Emeritus at Alberta University, an esteemed specialist on the Devonian trilobites from North Africa.

Holotype. Complete enrolled individual from Ed3n1: Di/UO/001.

Paratype. Complete enrolled individual from Ed3n1: Di/UO/002.

Locus typicus. Erg el Djemel section, Saoura Valley, Ougarta Basin, Algeria.

Stratum typicum. Base of 'Chefar el Ahmar' Formation, upper Emsian, Lower Devonian.

Studied material. Four enrolled exoskeletons from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (three specimens from Ed3n1 and one from Ed3n2).

Diagnosis. Cephalon wide; glabella with a wide base and a frontal outline slightly tapered; glabella and cheeks slightly inflated; S2 and S3 distinct; L1 swollen with a tuberculated intercalating ring; visual complex with 15 vertical lens files and a maximum of three lenses per file, longer (exsag.) than the postocular length of the genal field; palpebral furrow distinct. Pygidial axis relatively long and wide, with fairly complete terminal closure, and composed of 6–7 clear rings plus terminal piece; pygidial pleural field with five clear ribs. Dense coarse conical tubercles on cephalon without superimposed granules.

Description. Cephalon: Length/width ratio about 0.57. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.53. Glabella bound by deep axial furrows that are highly divergent forwards (72°), with subangular anterolateral angles. Frontal outline slightly tapered anteriorly. Frontal lobe overhanging slightly a deep preglabellar furrow. S2 and S3 distinct. S1 continuous and curved more strongly forwards than S0 in its adaxial curvature, and becoming deeper in its distal portions. L1 shorter (sag.) than L0 (half L0 length) and with a wide (tr.) median portion relative to its total width. Median portion of L1 moderately inflated, with few tubercles. L1 with subcircular, inflated lateral lobes separated from its median part by a strong exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 wide (tr.) with lateral lobes poorly defined. Reniform visual surface with 15 dorsoventral files of lenses and a maximum of three lenses per file, with smaller lenses in the anterior median part. Inter-lensar sclera more thickened dorsally than ventrally. Palpebral furrow distinct. A row of tubercles present at the base of the visual surface. Exsagittal length of the postocular genal field less than half the length (exsag.) of the posterior border. Cheek moderately swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 curved. L0 as high as the glabella at its maximum convexity. Anterior border short, ridge-like slightly projecting forwards and sloping posteroventrally. A marginulation extending from the anterolateral border up to the genal angle. Posterior border furrow deep and narrow. Lateral border furrow moderately deep, narrow behind the posterior branch of the facial suture and wider at the front of the eye. Posterolateral border furrow continuous and posterolateral border widening at the genal angle. *Frontal view*: Glabellar outline subcircular with lateral sides slightly flattened obliquely. Palpebral area slightly higher than the palpebral lobe. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow. Because the specimens are enrolled, the posterior band of the cephalic doublure is not visible. *Thorax*: Strongly narrower (tr.) posteriorly. Maximum axial width (tr.) ratio of the last ring / first ring about 60 %. Axial rings slightly convex with poorly defined lateral lobes. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows deep. *Pygidium*: Moderately long with a length/width ratio about 49.5 % (excluding the half ring), and its maximum width (tr.) behind its midlength (sag.) in dorsal view. Posterior outline roughly transverse medially. Pygidial axis relatively long, wide, tapered, with fairly complete terminal closure. Up to seven rings plus the terminal piece compose the pygidial axis. Pygidial pleural field with five distinct ribs delimited by deep pleural furrows. Interpleural furrows indistinct. Pseudo-articulating half rings indicated by embayment in the posterior edge of rings. *Ornamentation*: Cephalon covered with dense, coarse conical tubercles of rather heterogeneous size without superimposed granules. Anterior band of the cephalic doublure with possibly some granulation and pits, posterior band showing short ridges medially. Small tubercles developed on the axial rings and the lateral border of thoracic segments, on the pleural ribs, the border and the pygidial axis.

Remarks. The specimens with a range size from 6.2 to 9.5 mm long (sag.) show some morphological features of *Barrandeops forteyi* McKellar & Chatterton, 2009 from the upper Emsian of Morocco such as coarse conical tubercles with dense distribution and an eye with a maximum of three (commonly) lenses per file. However, our Algerian specimens show only 15 dorsoventral files compared to 18 files for *Barrandeops forteyi.* Moreover, the subocular pad is poorly pronounced in the Algerian specimens and better pronounced in *Barrandeops forteyi*. The eye is less reniform in outline, without an extremely pronounced sclera and tapers further backwards laterally in *Barrandeops chattertoni* sp. nov.

Barrandeops chattertoni sp. nov. shares with *B. granulops* a reduced and non-tubercular subocular pad. Nevertheless, *Barrandeops chattertoni* sp. nov. differs from *B. granulops* in having coarser and denser cephalic tubercles, a raised intercalating ring L1, a visual surface less reniform in outline, palpebral lobes less turned inwards and 15 dorsoventral files (maximum three lenses per file) compared to 19 files (maximum 4–5 lenses per file) for *B. granulops*.

Barrandeops chattertoni sp. nov. differs from *B. ovatus* in having a reduced and non-tubercular subocular pad, a visual surface less reniform in outline, palpebral lobes less turned inwards and 15 dorsoventral files (maximum three lenses per file) compared to 19 files (maximum 5–6 lenses per file) for *B. ovatus*.

Barrandeops chattertoni sp. nov. shares some similar morphological features with *Phacops* (*Phacops*) *turco praecedens* from the Eifelian of Turkey (Haas, 1968), such as the coarse and dense conical tubercles on the glabella. Nevertheless, the eye is slightly shorter (exsag.) dorsally and tapers further laterally in *Barrandeops chattertoni* sp. nov. Additionally, *Barrandeops chattertoni* sp. nov. differs from *Phacops* (*Phacops*) *turco praecedens* in having a subocular pad poorly differentiated, a visual surface less reniform in outline, palpebral lobes less turned inwards, an eye that tapers further backwards laterally and only 15 dorsoventral files compared to 18 files (maximum 4–5 lenses per file) for *Phacops* (*Phacops*) *turco praecedens.*

Eldredgeops rana tindoufensis (Burton & Eldredge, 1974) from the upper Eifelian – lower Givetian of the Western Sahara (Tindouf Basin) differs from *Barrandeops chattertoni* sp. nov. in having 18 files of lenses with a maximum of eight lenses per file and a more reniform visual surface.

Occurrence. Upper Emsian; Algeria (Saoura: Erg el Djemel).

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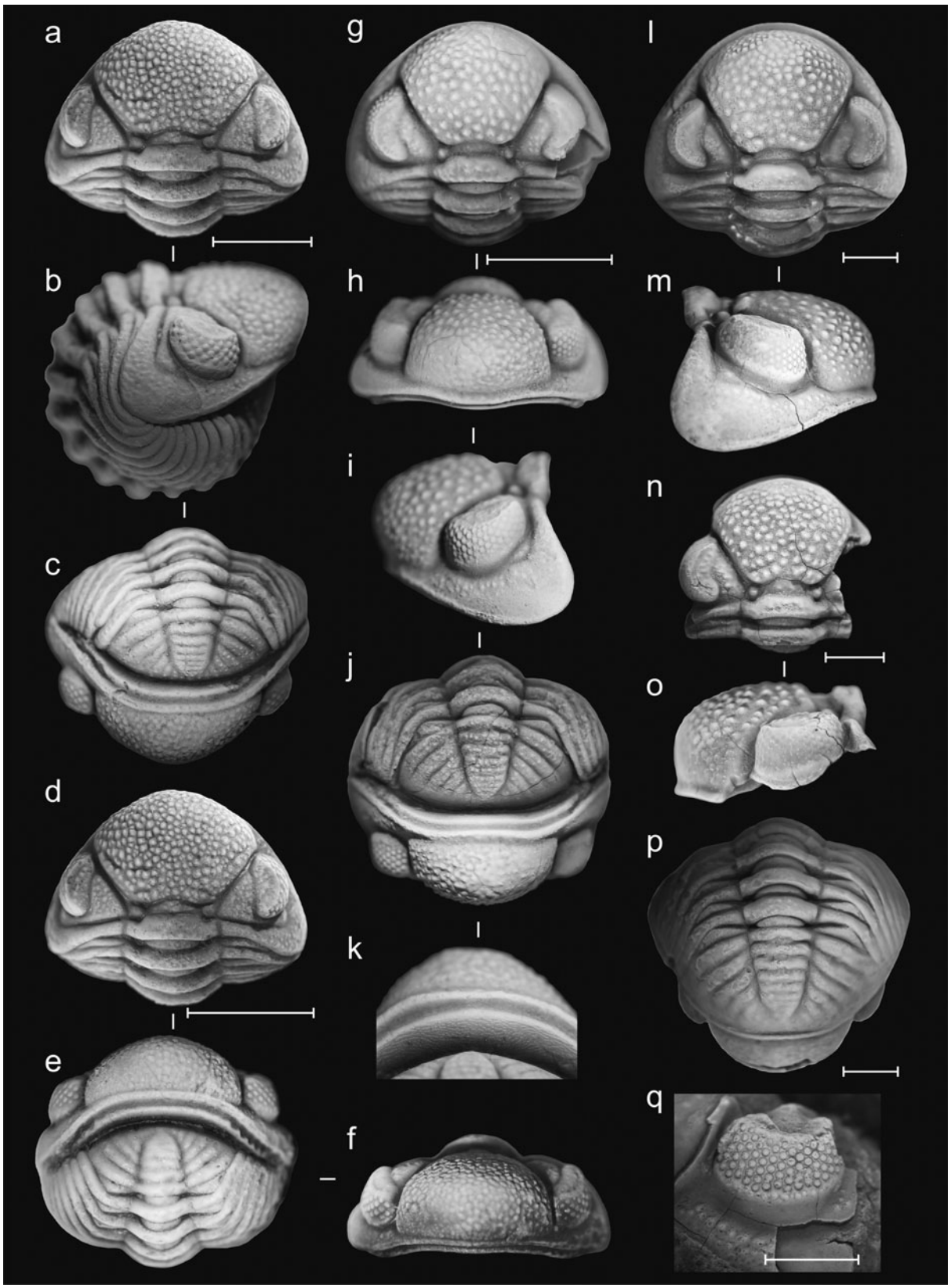

Figure 4. Phacopid trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–c) *Barrandeops chattertoni* sp. nov., Erg el Djemel section, holotype Di/UO/001 (Ed3n1): (a–b) cephalon in dorsal and lateral views; (c) pygidium in dorsal view. (d–f) *Barrandeops chattertoni* sp. nov., Erg el Djemel section, Di/UO/002 (Ed3n1): (d, f) cephalon in dorsal and frontal views; (e) pygidium in dorsal view. (g–k) *Geesops fabrei* sp. nov., Erg el Djemel section, Di/UO/016 (Ed3n2): (g–i) cephalon in dorsal, frontal and lateral views; (j) pygidium in dorsal view; (k) detail of the cephalic doublure. (l, m) *Geesops fabrei* sp. nov., Erg el Djemel section, holotype Di/UO/017 (Ed3n2): cephalon in dorsal and lateral views. (n, o) *Geesops fabrei* sp. nov., Erg el Djemel section, figured by Le Maître in 1952, GFCL296 (coll. Le Maître, Faculté libre des Sciences de Lille): cephalon in dorsal and lateral views. (p) *Geesops fabrei* sp. nov., Erg el Djemel section, Di/UO/004 (Ed3n1): pygidium in dorsal view. (q) *Geesops fabrei* sp. nov., Erg el Djemel section, Di/UO/014 (Ed3n2): detail of the left eye. Scale bars = 5 mm.

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Genus *Phacops* Emmrich, 1839

Type species. *Calymene latifrons* Bronn, 1825: Mid Devonian, Eifel, Germany.

Remarks. The synonymy of the genus is very extensive. After the original definition by Emmrich (1839), the most significant works are those of Barrande (1852), Wedekind (1911), Richter & Richter (1926), Delo (1935), Campbell (1967), Chlupáč (1977) and McKellar & Chatterton (2009). The earlier authors had already noticed the heterogeneity of the genus. Because of this heterogeneity, the understanding of the taxonomic status of the 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, Bignon & François, 2011).

Phacops sensu lato sp. A
Figure 3n–q

Studied material. One incomplete cephalothorax from the upper Emsian (base of the 'Chefar el Ahmar' Formation) of the Marhouma section ('km 30'); Ougarta Basin, Saoura, Algeria.

Description. Cephalon: Length/width ratio about 0.59. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.55. Glabella bounded by deep axial furrows that are moderately divergent forwards (61°), with subangular anterolateral angles. Frontal outline slightly tapered anteriorly. Frontal lobe overhanging slightly a deep preglabellar furrow. S2 and S3 poorly defined. S1 continuous and curved more strongly forwards than S0 in its adaxial curvature, and becoming deeper in its distal portions. L1 shorter (sag.) than L0 (more than half L0 length) and with a wide (tr.) median portion relative to its total width. Median portion of L1 fairly inflated, with few tubercles. L1 with subquadrate, poorly inflated lateral lobes separated from its median part by a distinct exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 wide (tr.) with lateral lobes very poorly defined. Reniform visual surface with 18 dorsoventral files of lenses and a maximum of four lenses per file, with smaller lenses in the anterior median part (51 lenses in total). Inter-lensar sclera more thickened dorsally than ventrally. Palpebral furrow distinct. A row of tubercles present at the base of the visual surface. Exsagittal length of the postocular genal field a little more than half the length of the posterior border. Cheek moderately swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 curved. L0 as high as glabella at its maximum convexity. Anterior border rather short, ridge-like, slightly projecting forwards and sloping posteroventrally. A marginulation probably extending from the anterolateral border up to the genal angle. Posterior border furrow deep and narrow. Lateral border furrow rather shallow, narrow behind the posterior branch of the facial suture and wider at the front of the eye. Posterolateral border furrow continuous and posterolateral border widening at the genal angle. *Frontal view*: Glabellar outline subcircular with lateral sides slightly flattened obliquely. Palpebral area higher than the palpebral lobe. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow anteriorly. Posterior band of the cephalic doublure long (sag.) with a hypostomal suture slightly turned ventrally and convex backwards medially. *Thorax*: Partially preserved. Axial rings slightly convex with poorly defined lateral lobes. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows deep. *Ornamentation*: Cephalon covered with dense, coarse conical tubercles of heterogeneous size without superimposed granules. Anterior band of the cephalic doublure with possibly some granulation and pits, posterior band showing short ridges. Small tubercles developed on the axial rings and the pleural field of thoracic segments.

Remarks. This single specimen with a medium size (9.3 mm in cephalic length) is quite different from *Barrandeops granulops s.s.* This specimen possesses less globular lateral preoccipital lobes, 18 vertical files of lenses with a maximum of four lenses per file and sharper tubercles on the glabella. Additional material is necessary to give a definitive attribution.

Phacops sensu lato sp. B
Figure 5a–i

Studied material. Two poorly preserved enrolled specimens from the upper Emsian (base of the 'Chefar el Ahmar' Formation) of the Marhouma section ('km 30'); Ougarta Basin, Saoura, Algeria.

Description. Cephalon: Length/width ratio about 0.61. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.49. Glabella bound by deep axial furrows that are highly divergent forwards (74°), with subangular anterolateral angles. Frontal lobe overhanging slightly a deep preglabellar furrow. S2 and S3 visible on the exfoliated glabella. S1 seems to be continuous and curved more strongly forwards than S0 in its adaxial curvature, and becoming deeper in its distal portions. L1 shorter (sag.) than L0 (more than half the L0 length) and with a wide (tr.) median portion relative to its total width. Median portion of L1 inflated, with few fine tubercles. L1 with subcircular, inflated lateral lobes separated from its median part by a distinct exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 rather wide (tr.) with lateral lobes poorly defined. Reniform visual surface with 18–19 dorsoventral files of lenses and a maximum of six lenses per file, with smaller lenses in the anterior median part (78–82 lenses in total). Inter-lensar sclera thickened dorsally. Palpebral furrow distinct. A row of fine tubercles present at the base of the visual surface. Exsagittal length of the postocular genal field equal to the length of the posterior border. Cheek moderately swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 curved. L0 as high as the glabella at its maximum convexity. Anterior border short, ridge-like, slightly projecting forwards and sloping posteroventrally. Posterior border furrow deep and narrow. Lateral border furrow rather shallow and broad. The posterolateral border furrow seems to be continuous and the posterolateral border widens at the genal angle. *Frontal view*: Glabellar outline subcircular with lateral sides slightly flattened obliquely. Palpebral area and palpebral lobe at about the same level. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow. Posterior band of the cephalic doublure long (sag.) with a hypostomal suture slightly turned ventrally and convex backwards medially. *Thorax*: Slightly narrower (tr.) posteriorly. Maximum axial width (tr.) ratio of the last ring / first ring about 82 %. Axial rings convex with poorly defined lateral lobes. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows deep. *Pygidium*: Rather long with a length/width ratio about 51 % (excluding the half ring), and its maximum width (tr.) behind its midlength (sag.) in dorsal view. Posterior outline broadly rounded. Pygidial axis long, rather narrow and tapered. Up to seven rings plus the terminal piece compose the pygidial axis. Pygidial pleural field with five distinct ribs delimited by deep pleural furrows. Interpleural furrows distinct. *Ornamentation*: Cephalon covered with moderately dense, fine tubercles. Anterior band of the cephalic doublure with pits; posterior band with scaly granules medially, grading laterally into terrace ridges. Fine tubercles also developed on the thorax and the pygidium.

Remarks. These two poorly preserved large specimens (about 15 mm in cephalic length) are more different from *Phacops sensu* Campbell (1967). Some features that characterize the genus such as a low maximal number of lenses per row, a very narrow postocular area and the presence of scaly tubercles/short ridges/terrace lines on the

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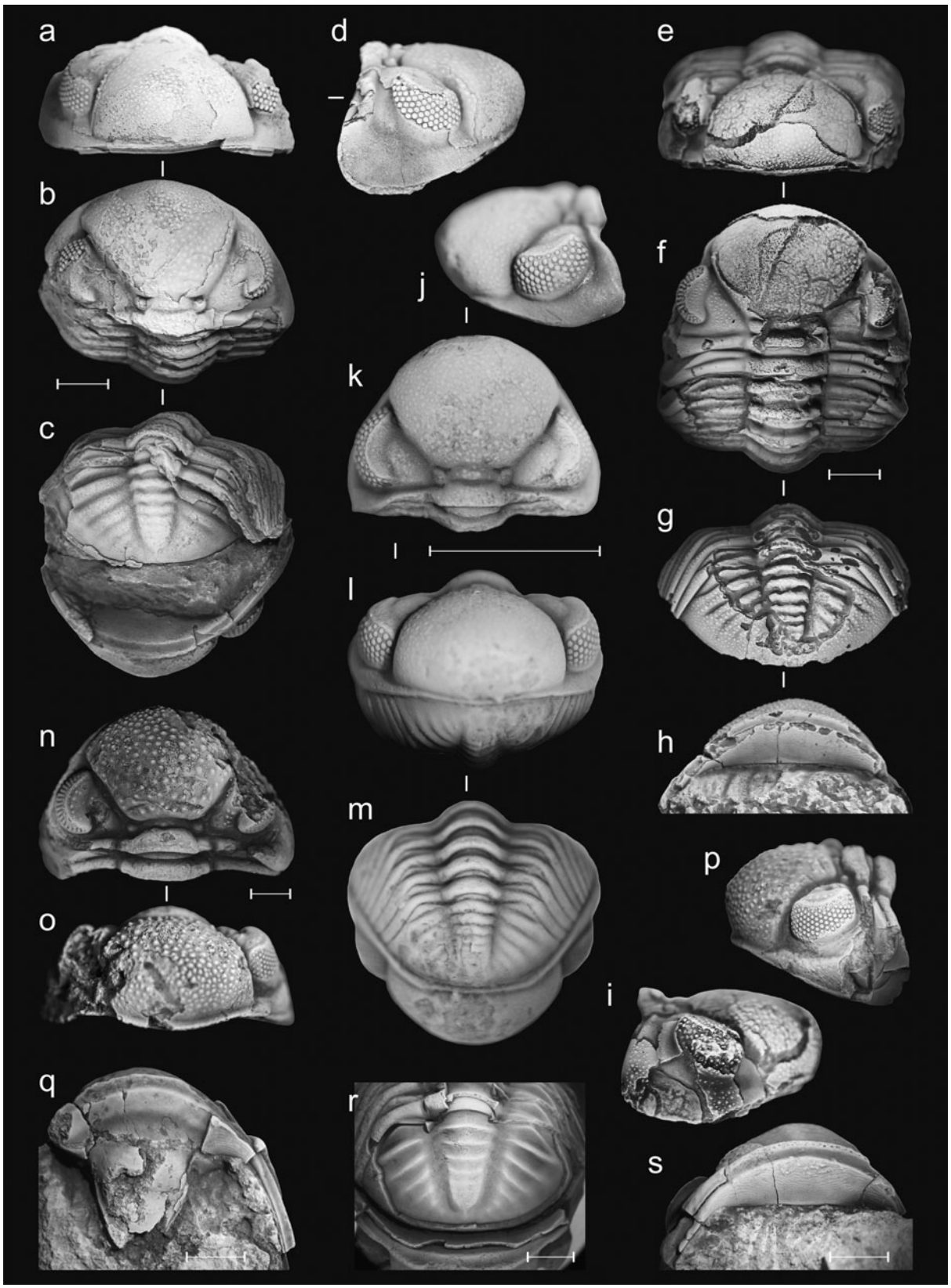

Figure 5. Phacopid trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–d) *Phacops sensu lato* sp. B, Marhouma section, Di/UO/035 ('km 30'): (a–b, d) cephalon in frontal, dorsal and lateral views; (c) pygidium in dorsal view. (e–i) *Phacops s.l.* sp. B, Marhouma section, Di/UO/033 ('km 30'): (e, f, h, i) cephalon in frontal, dorsal, ventral and lateral views; (g) pygidium in dorsal view. (j–m) *Boeckops* sp. C, Erg el Djemel section, Di/UO/015 (Ed3n2): (j–l) cephalon in lateral, dorsal and frontal views; (m) pygidium in dorsal view. (n–p) *Phacops s.l. boudjemaai* sp. nov., Erg el Djemel section, holotype Di/UO/007 (Ed3n1): cephalon in dorsal, frontal and lateral views. (q) *Phacops s.l. boudjemaai* sp. nov., Erg el Djemel section, Di/UO/008 (Ed3n1): hypostome mostly exfoliated in dorsal view. (r) *Phacops s.l. boudjemaai* sp. nov., Erg el Djemel section, Di/UO/005 (Ed3n1): pygidium mostly exfoliated in dorsal view. (s) *Phacops s.l. boudjemaai* sp. nov., Erg el Djemel section, Di/UO/006 (Ed3n1): cephalic doublure in dorsal view. Scale bars = 5 mm.

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anterior part of the frontal lobe, according to McKellar & Chatterton (2009), are missing. These two specimens possess a slightly reduced visual surface with a postocular field equal to the length of the posterior border, fine tubercles on the exoskeleton and no terrace lines on the anterior face of the composite lobe. Additional material is necessary to give a definitive attribution.

Phacops boudjemaai sp. nov.
Figure 5n–s

Name. Named in honour of Mr Boudjemâa, an Algerian guide who co-operated with geologists from the 'Menchikoff' Saharan Research Center in Beni-Abbès.

Holotype. A cephalothorax from Ed3n1: Di/UO/007.

Paratypes. One complete mostly exfoliated individual from Ed3n1: Di/UO/005; one mostly exfoliated cephalothorax with its cephalic doublure from Ed3n1: Di/UO/006; and one cephalothorax with its hypostome mostly exfoliated from Ed3n1: Di/UO/008.

Locus typicus. Erg el Djemel section, Saoura Valley, Ougarta Basin, Algeria.

Stratum typicum. Base of 'Chefar el Ahmar' Formation, upper Emsian, Lower Devonian.

Studied material. Three cephalothoraxes and one enrolled individual from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (Ed3n1); Ougarta Basin, Saoura, Algeria.

Diagnosis. Cephalon wide; glabella with a wide base; cheeks strongly inflated; S2 and S3 indicated by discontinuity in sculpture; L1 very short (sag.) with a wide (tr.) and fairly depressed median portion with few tubercles, with small subcircular, inflated lateral lobes; visual complex with 19 vertical lens files and a maximum of six lenses per file; palpebral furrow distinct; lateral border furrow rather shallow and broad behind the posterior branch of the facial suture with a smooth subocular area. Pygidial axis rather long, relatively wide, strongly tapered and composed of 6–7 rings plus terminal piece; pygidial pleural field with six clear ribs. Dense coarse pustular tubercles with pits on cephalon. Dominant pits on lateral border.

Description. Cephalon: Length/width ratio about 0.57. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.53. Glabella bound by deep axial furrows that are highly divergent forwards (71°), with subangular anterolateral angles. Frontal lobe overhanging slightly a deep preglabellar furrow. S2 and S3 distinct, indicated by discontinuity in sculpture. S1 continuous, deep and almost transverse as S0 in its middle portion. L1 shorter (sag.) than L0 (hardly less than half L0 length). Median portion of L1 wide (tr.) relative to the total width of L1 and fairly depressed, with few tubercles. L1 with small subcircular, inflated lateral lobes separated from its median part by a strong exsagittal furrow. S0 well marked. L0 slightly wide (0.36 % of the total cephalic width tr.) with defined lateral lobes. Reniform visual surface with 19 dorsoventral files of lenses and a maximum of six lenses per file, with smaller lenses in the anterior median part. A row of small tubercles present at the base of the eye. Inter-lensar sclera thickened only dorsally. Palpebral furrow distinct. Exsagittal length of the postocular genal field half length of the posterior border. Cheek swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 moderately curved. L0 as high as the glabella at its maximum convexity. Anterior border short with a ridge-like projection forwards. A marginulation extending from the anterolateral border up to the rounded genal angle. Posterior border furrow deep and narrow. Lateral border furrow rather shallow and broad behind the posterior branch of the facial suture with a smooth subocular area. Posterolateral border furrow continuous and posterolateral border widening at the genal angle. *Frontal view*: Glabellar outline subcircular with lateral sides slightly flattened obliquely. Palpebral area as high as the palpebral lobe. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow. Posterior band of the cephalic doublure long (sag.) with a hypostomal suture slightly convex backwards medially. Hypostome: Mostly exfoliated, strongly elongated (sag.). *Thorax*: Slightly tapered; maximum axial width (tr.) ratio of the last ring / first ring about 89 %. Axial rings fairly convex with inflated lateral lobes. Axial furrows distinct. Pleural furrows deep. *Pygidium (exfoliated)*: Rather long with a length/width ratio about 51.6 % (excluding the half ring), and its maximum width (tr.) at about its midlength (sag.) in dorsal view. Posterior outline broadly rounded. Pygidial axis long, relatively wide, strongly tapered. Up to seven distinct rings plus the terminal piece compose the pygidial axis. Pygidial pleural field with six distinct ribs delimited probably by deep pleural furrows. *Ornamentation*: Cephalon covered with dense, coarse pustular tubercles of heterogeneous size with pits. Lateral border covered with dominant pits, palpebral lobe with tubercles and pits. Anterior band of the cephalic doublure covered with scaly granules and distinct pits, and the posterior band with short ridges medially and anastomosing terrace ridges laterally.

Remarks. *Phacops boudjemaai* sp. nov. is attributed to the genus *Phacops sensu lato*. Some features that characterize the genus *Phacops sensu* Campbell (1967), such as a low maximal number of lenses per row, a very narrow postocular area and the presence of scaly tubercles/short ridges/terrace lines on the anterior part of the frontal lobe (according to McKellar & Chatterton, 2009), are missing.

Phacops boudjemaai sp. nov. shares some morphological features with *P. araw* McKellar & Chatterton, 2009 from the Eifelian of South Morocco: a very short (sag.) and depressed L1 with reduced globular preoccipital lobes, and pits at the base of the visual surface and on the thoracic segments. Nevertheless, *Phacops boudjemaai* sp. nov. differs from *P. araw* in having 19 files with a maximum of six lenses per file compared to 18 files (rarely 19–20) with a maximum of four lenses per file in *P. araw*, a thinner inter-lensar sclera and non-scaly tubercles on the anterior part of the frontal lobe.

Phacops boudjemaai sp. nov. differs from *Eldredgeops rana africanus* (Burton & Eldredge, 1974) from the upper Eifelian – lower Givetian of the Western Sahara in having a more prominent glabella with less pustular tubercles on the glabella, a thinner inter-lensar sclera, one more file of lenses and non-scaly tubercles on the anterior part of the frontal lobe.

Phacops boudjemaai sp. nov. shares with *Geesops fabrei* sp. nov a similar glabellar tuberculation, pits on the genal angle and the same number of files (19) of lenses in the eye. *Phacops boudjemaai* sp. nov. differs in having a preoccipital ring reduced in width (sag.) and depressed, preoccipital lobes reduced in size and a smooth, wider space at the base of eye (in lateral view).

Phacops boudjemaai sp. nov. shares with *Geesops schlotheimi* from the Eifelian of Germany a similar glabellar tuberculation and pits on the genal angle. *Geesops schlotheimi* differs in having one less dorsoventral file, a prominent median preoccipital tubercle on the well-defined intercalar ring, better-defined subocular and postocular pads, and a thicker inter-lensar sclera.

Occurrence. Upper Emsian; Algeria (Saoura: Erg el Djemel).

Genus *Geesops* Struve, 1982

Type species. Calymmene schlotheimi Bronn, 1825: Eifelian, Eifel in Germany.

Additional species. Geesops sparsinodosus struvei (Schraut, 2000*b*): Eifelian, Morocco; *G. sparsinodosus gallicus* Struve, 1982:

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lower Eifelian, north of France; *G. sparsinodosus sparsinodosus* (Struve, 1970): Eifelian, Germany; *G. schlotheimi skalensis* (Kielan, 1954): Givetian, Poland; *G. brunopauli* Struve, 1982: Eifelian, Germany; *G. battidohmi* Struve, 1982: lower Givetian, Germany; *G. synapticus* Struve, 1982: lower Eifelian, Germany; *G. fabrei* sp. nov.: upper Emsian, Algeria.

Remarks. *Geesops* was erected by Struve (1982) for phacopids with a marginulate cephalic border closely related to *Phacops sensu stricto* (under its restrictive diagnosis). A previous study carried out by McKellar & Chatterton (2009) showed that this genus formed from the species that were once part of *Phacops* constitutes more likely a valid genus characterized by a wide glabellar width and a palpebral area lower than the palpebral lobe.

Geesops *fabrei* sp. nov.
Figure 4g–q

v. 1952 [non] *Phacops schlotheimi* Bronn, 1825; Le Maître, p. 156, pl. 21, figs 3–5.

Name. Named in honour of Jean Fabre, a French professor of geology in Algiers and director of the Saharan Research Center in Beni-Abbès for 15 years.

Holotype. Almost complete enrolled individual from Ed3n2: Di/UO/017.

Paratypes. One enrolled individual from Ed3n1: Di/UO/004, and two individuals from Ed3n2: Di/UO/014 and Di/UO/016.
Locus typicus. Erg el Djemel section, Saoura Valley, Ougarta Basin, Algeria.

Stratum typicum. Base of 'Chefar el Ahmar' Formation, upper Emsian, Lower Devonian.

Studied material. Seven enrolled exoskeletons from the Erg el Djemel section (two in Ed3n1, three in Ed3n2, and two in Ed4).

Diagnosis. Cephalon narrow; glabella with a wide base; glabella slightly inflated and cheeks strongly inflated; S2 and S3 indicated by discontinuity in sculpture; L1 poorly swollen with few tubercles; visual complex with 19 vertical lens files and a maximum of six lenses per file; palpebral furrow distinct. Pygidial axis relatively long and wide. Dense coarse conical tubercles on cephalon without superimposed granules.

Description. Cephalon: Length/width ratio about 0.64. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.53. Glabella bound by deep axial furrows that are moderately divergent forwards (60°), with broadly rounded anterolateral angles. Frontal lobe overhanging barely a shallow preglabellar furrow. S2 and S3 indicated by discontinuity in sculpture. S1 continuous and curved more strongly forwards than S0 in its adaxial curvature, and becoming deeper in its distal portions. L1 shorter (sag.) than L0 (less than half L0 length), with a wide (tr.) median portion relative to its total width. Median portion of L1 poorly inflated, with few tubercles. L1 with subcircular, inflated lateral lobes separated from its median part by a distinct exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 moderately narrow (tr.) with defined lateral lobes. Reniform visual surface with 19 dorsoventral files of lenses and a maximum of six lenses per file, with smaller lenses in the anterior median part. Inter-lensar sclera more thickened dorsally than ventrally. Palpebral furrow distinct. A row of tubercles present at the base of the visual surface. Exsagittal length of the postocular genal field less than half the length of the posterior border. Cheek strongly swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 curved. L0 as high as the glabella at its maximum convexity. Anterior border long with a ridge-like projection forwards. A marginulation extending from the anterolateral border up to the genal angle. Posterior border furrow deep and narrow. Lateral border furrow deep, rather broad behind the posterior branch of the facial suture and wider at the front of the eye. Subocular librigenal field concave at the front of the eye and distinct at the back of the eye as a subocular pad with few tubercles. Posterolateral border furrow continuous and posterolateral border widening at the genal angle. *Frontal view*: Glabellar outline subcircular with its lateral sides flattened obliquely. Palpebral area slightly higher than the palpebral lobe. Anterior border showing a median inflexion towards the ventral side. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow. Because all the known specimens are enrolled, the posterior band of the cephalic doublure is not visible. *Thorax*: Slightly tapered. Maximum axial width (tr.) ratio of the last ring / first ring about 82 %. Axial rings convex with poorly defined lateral lobes. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows deep. *Pygidium (only partially preserved)*: Rather long with a length/width ratio about 51 % (excluding the half ring), and its maximum width (tr.) in front of the midlength. Posterior outline broadly rounded and slightly transverse medially. Pygidial axis long, rather wide and tapered. Pygidial pleural field with distinct ribs delimited by deep pleural furrows anteriorly. *Ornamentation*: Cephalon covered with dense, coarse conical tubercles without superimposed granules. Lateral border covered with dominant pits. Anterior band of the cephalic doublure with pits and scaly granulation. Tubercles present on the axial rings and the lateral border of thoracic segments, on the pleural ribs and the pygidial axis.

Remarks. The specimens attributed to *Geesops fabrei* sp. nov. share with *Geesops schlotheimi* (Bronn, 1825) from the Eifelian of Germany a similar glabellar tuberculation, and pits on the genal angle. *Geesops schlotheimi* differs in having one less dorsoventral file of lenses in the eye, a prominent median preoccipital tubercle on the well-defined intercalar ring, and wider subocular and postocular pads. Le Maître (1952) previously attributed some Algerian specimens to *Geesops schlotheimi* (Bronn, 1825). The specimen figured (pl. XXI, figs 3–5; GFCL296, coll. Le Maître, Faculté libre des Sciences de Lille) from the Erg el Djemel section with 18 dorsoventral files of lenses and a maximum of six lenses per file is reassigned herein to *Geesops fabrei* sp. nov.

Geesops fabrei sp. nov. differs from *Eldredgeops rana africanus* (Burton & Eldredge, 1974) from the upper Eifelian – lower Givetian of the Western Sahara and *Geesops sparsinodosus struvei* (Schraut, 2000*b*) from the Eifelian of Morocco. *Eldredgeops rana africanus* with 18 files and a maximum of six lenses per file also exhibits a wider and less prominent glabella, a more pustular ornamentation on the glabella, a thicker inter-lensar sclera and a smooth wider base of the eye. *Geesops sparsinodosus struvei* with 18 files and a maximum of six lenses per file also exhibits a wider smooth base of the eye and no subocular pad.

Occurrence: Upper Emsian; Algeria (Saoura: Erg el Djemel).

Genus *Boeckops* (Chlupáč, 1972)

Type species. *Phacops boecki* Hawle & Corda, 1847: Pragian, Barrandian area in the Czech Republic.

Additional species. *Boeckops confluens* (Richter & Richter, 1939): Eifelian, Turkey; *B. delphinoides* (Chlupáč, 1972): Emsian, Czech Republic; *B. planilimbatus* (Wedekind, 1914): Pragian?, Germany; *B. proponticus* (Haas, 1968): upper Emsian, Turkey; *B. stelcki* McKellar & Chatterton, 2009: Emsian, Morocco; *B. 'zinkeni'* (Roemer, 1843) (*sensu* Jahnke, 1969): Lower Devonian, Germany; *B. zenonis* (Chlupáč, 1977): Pragian, Czech Republic.

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Boeckops sp. C
Figure 5j–m

Studied material. One small enrolled specimen from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (Ed3n2).

Description. Cephalon: Length/width ratio about 0.68. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.47. Glabella highly inflated, bound by shallow axial furrows, deeper anteriorly, highly divergent forwards (90°), with an anterior portion less divergent and subangular anterolateral angles. Frontal lobe strongly overhanging a rather shallow and narrow preglabellar furrow. S2 and S3 not distinct. S1 continuous and slightly more curved forwards than S0 in its adaxial curvature, and that becomes deeper in its distal portions. L1 shorter (sag.) than L0 (more than half L0 length), with a very wide (tr.) median portion relative to its total width. Median portion of L1 inflated with several tubercles. L1 with subcircular, uninflated lateral lobes separated from its median part by a shallow exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 rather wide (tr.), with no lateral lobes defined. Reniform visual surface with 18 dorsoventral files of lenses and a maximum of six lenses per file, with smaller lenses in the anterior median part. Inter-lensar sclera only thickened dorsally. Palpebral furrow distinct. Exsagittal length of the postocular genal field less than half the length of the posterior border. Cheek swollen. *Lateral view*: Glabella rounded anteriorly. Outline of L1 curved. L0 as high as the glabella at its maximum convexity. Anterior border probably short and ridge-like. A marginulation extending almost from the anterolateral border up to the genal angle. Posterior border furrow deep and narrow. Lateral border furrow moderately deep and narrow anteriorly, broad and concave behind the posterior branch of the facial suture. Posterolateral border furrow continuous and posterolateral border widening at the genal angle with a distinct node. *Frontal view*: Glabellar outline subcircular with its lateral sides slightly curved obliquely. Palpebral area higher than the palpebral lobe. *Ventral view*: Because the specimen is enrolled, the cephalic doublure is not visible. *Thorax*: Narrower (tr.) posteriorly. Maximum axial width (tr.) ratio of the last ring / first ring about 71 %. Axial rings convex with no defined lateral lobes. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows deep. *Pygidium*: Poorly preserved, eroded. Rather long, with a length/width ratio about 51 % (excluding the half ring), and its maximum width (tr.) at about its midlength (sag.) in dorsal view. Posterior outline broadly rounded. Pygidial axis long, rather wide, tapered. A minimum of five rings visible plus the terminal piece compose the pygidial axis. Pygidial pleural field with a minimum of four, but probably five, distinct ribs delimited by pleural furrows that are deep anteriorly. *Ornamentation*: Cephalon covered with moderately dense, medium-sized/fine tubercles without superimposed granules. Small tubercles visible more or less on the axial rings and the lateral border of thoracic segments.

Remarks. Boeckops sp. C, with a rather small size (5.3 mm in cephalic length), shows morphological features that are different from those of other species attributed to *Boeckops*. The single known Algerian specimen shares with *Boeckops stelcki* from the Emsian of Morocco the same number of vertical files of lenses in the eye, an inter-lensar sclera slightly thickened dorsally only, a weak palpebral furrow, a marginulation on the lateral border extending backwards to before the midlength of the eye and a rounded genal angle with a distinct node. *Boeckops stelcki* differs in having one more lens per vertical file (maximum of seven for *Boeckops stelcki* compared to six for *Boeckops* sp. C), a wider glabellar base, less divergent axial furrows, a narrower (tr.) occipital ring with well-defined lateral lobes, a narrow subocular pad, a granulated postocular pad and numerous evenly distributed fine tubercles on the lateral border.

Boeckops sp. C shares with *B. proponticus* from the upper Emsian of Turkey a similar ornamentation and a visual surface with the same number of vertical files. *Boeckops proponticus* differs in having a wider (exsag.) postocular area, one to two less lenses per file and no differentiated median portion with tubercles.

Boeckops sp. C shares with *B. boecki* from the Pragian of the Czech Republic an inter-lensar sclera slightly thickened dorsally only, a weak palpebral furrow, no subocular pad, a marginulation on the lateral border extending backwards to about the midlength of the eye and a rounded genal angle with a distinct node. *Boeckops boecki* differs in having more vertical files of lenses (21 files for *B. boecki* compared to 18 for *B.* sp. C), two more lenses per vertical file (maximum eight for *B. boecki* compared to six for *B.* sp. C), a wider glabellar base, less divergent axial furrows, a narrower (tr.) occipital ring with well-defined lateral lobes, a wide (exsag.) postocular pad and less dense and evenly distributed fine tubercles.

Additional material is necessary to give a definitive attribution.

Occurrence. Upper Emsian; Algeria (Saoura: Erg el Djemel).

Genus *Austerops* McKellar & Chatterton, 2009

Type species. Austerops kermiti McKellar & Chatterton, 2009: Eifelian, Morocco.

Additional species. *Austerops salamandar* McKellar & Chatterton, 2009: Eifelian, Morocco; *A. speculator speculator* (Alberti, 1970): upper Emsian, Eifelian, Algeria and Morocco; *A. speculator punctatus* McKellar & Chatterton, 2009: Eifelian, Morocco; *A. legrandi* sp. nov.: upper Emsian, Algeria; *A. menchikoffi* (Le Maître, 1952): upper Emsian, Algeria and Morocco.

Remarks. Austerops was erected by McKellar & Chatterton (2009) for a group of Moroccan phacopids with subdued and sparse tubercles, a faint palpebral furrow, and prominent and continuous terrace lines upon the cephalic doublure.

Austerops menchikoffi (Le Maître, 1952)
Figure 6e–k

v∗. 1952 *Phacops menchikoffi* sp. nov. Le Maître, pp. 155–6, pl. XX, figs 16–20; non pl. XX, fig. 15, fig. 21, pl. XXI, fig. 10.

. 2006 *Phacops smoothops* sp. nov. Chatterton, Fortey, Brett, Gibb & McKellar, p. 15, pl. 4–7.

. 2009 *Austerops smoothops* (Chatterton *et al.*); McKellar & Chatterton, p. 34.

Type material. Holotype enrolled exoskeleton GFCL398 (coll. Le Maître, Faculté libre des Sciences de Lille), from the upper Emsian (not lower Eifelian) from the Erg el Djemel section; Ougarta Basin, Saoura, Algeria.

Studied material. Eighteen enrolled exoskeletons with three from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Marhouma section ('km 30') and the other 15 from the Erg el Djemel section (one from Ed3n1, two from Ed3n2 and 12 from Ed4. Ougarta Basin, Saoura, Algeria.

Diagnosis. See Chatterton *et al.* (2006).

Remarks. Le Maître (1952, p. 153) provided a description of the type material from the Erg el Djemel section. Chatterton *et al.* (2006) and McKellar & Chatterton (2009) made no mention of the *menchikoffi* species from the Erg el Djemel section (Saoura, Algeria) described for the first time by Le Maître in 1952. However,

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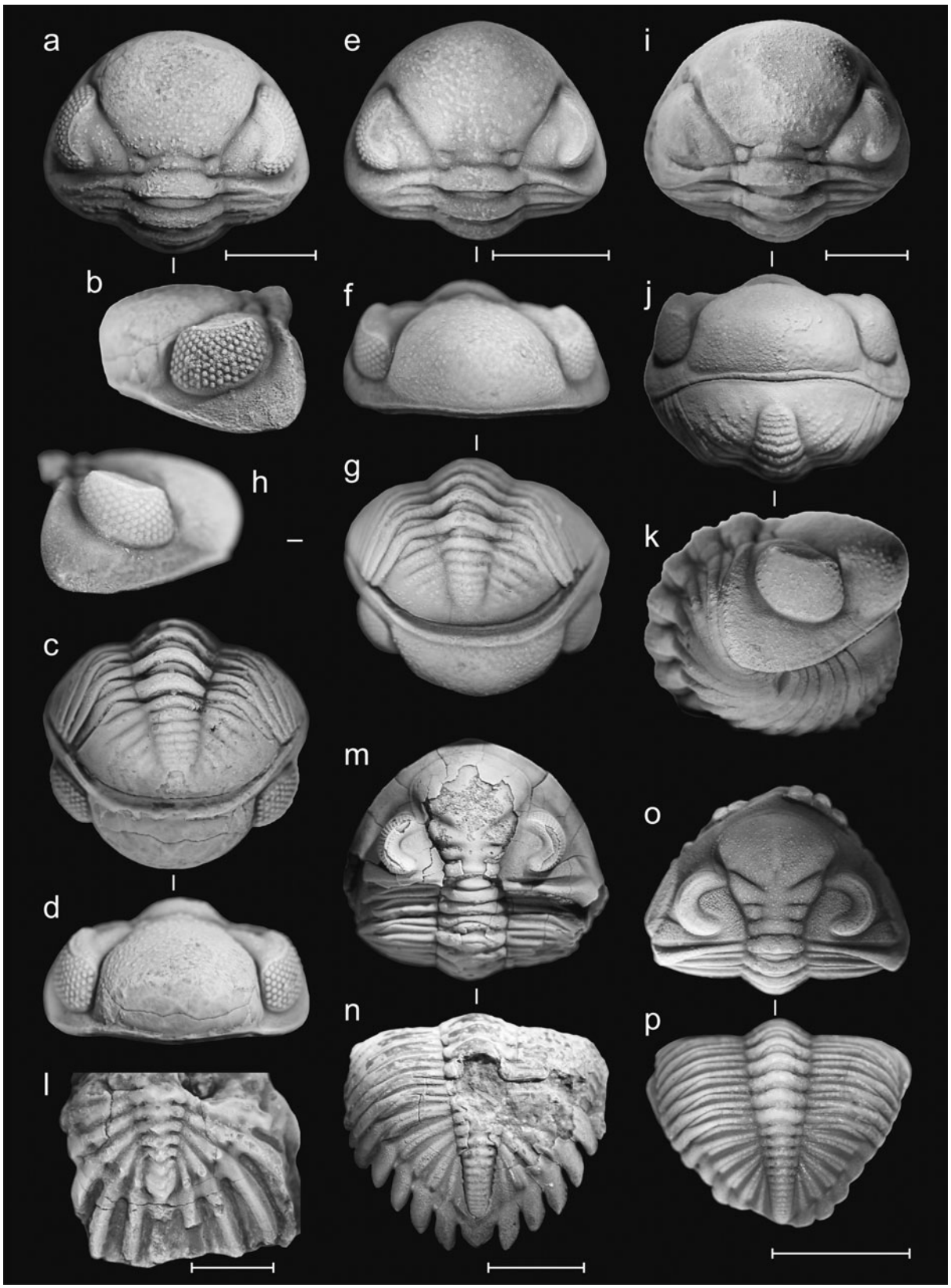

Figure 6. Trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–d) *Austerops speculator speculator* (Alberti, 1970), Erg el Djemel section, Di/UO/013 (Ed3n2): (a–b, d) cephalon in dorsal, lateral and frontal views; (c) pygidium in dorsal view. (e–h) *Austerops menchikoffi* (Le Maître, 1952), Erg el Djemel section, Di/UO/026 (Ed4): (e–f, h) cephalon in dorsal, frontal and lateral views; (g) pygidium in dorsal view. (i–k) *Austerops menchikoffi* (Le Maître, 1952), Erg el Djemel section, holotype figured by Le Maître (1952), GFCL398 (coll. Le Maître, Faculté libre des Sciences de Lille): cephalon in dorsal, frontal and lateral views. (l) *Walliserops* sp., Erg el Djemel section, Di/UO/018 (Ed3n2). (m, n) *Hollardops mesocristata* (Le Maître, 1952), Erg el Djemel section, Di/UO/010 (Ed3n1): cephalon and pygidium in dorsal views. (o, p) *Hollardops mesocristata* (Le Maître, 1952), Erg el Djemel area, figured in Le Maître (1952), GFCL401 (coll. Le Maître, Faculté libre des Sciences de Lille): cephalon and pygidium in dorsal views. Scale bars = 5 mm.

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the *menchikoffi* holotype shows all the diagnostic features of the type species of the *Austerops* genus, namely *Austerops smoothops* Chatterton *et al*. 2006 from Morocco. Chatterton *et al.* (2006, pp. 15–17) provided a full description of this Moroccan material. Only small differences between the Algerian and Moroccan populations can be reported such as the range of the angle between the axial furrows: 55–70° for the Algerian specimens and 60–75° for Moroccan ones. These small differences can be regarded as intra-specific variability. The *menchikoffi* species is thus a senior subjective synonym of the *smoothops* species. In her work, Le Maître (1952) had reported this Algerian species from the lower Eifelian. Recent works (Göddertz, 1987; Boumendjel *et al*. 1997; Paris *et al*. 1997; Ouali Mehadji *et al.* 2004) reconsidered the age of this section, which is now considered to be late Emsian in age.

Occurrence. Upper Emsian; Morocco (Jbel Gara el Zguilma), Algeria (Saoura: Erg el Djemel, 'km 30').

Austerops speculator speculator (Alberti, 1970)
Figure 6a–d

1951 *Phacops fecundus* Barrande; Gigout, p. 331.

1955 *Phacops fecundus* Barrande; Gigout, table B.

1965 *Phacops fecundus* Barrande; Gigout *in* Gigout, Destombes & Ferré, p. 9.

1969 *Phacops* (*Phacops*) cf. *rana milleri* Stewart; Alberti, p. 437.

1970 *[partim] Phacops* (*Phacops*) *speculator* sp. nov. Alberti, p. 91, pl. 12, figs 1, 2, 5, 6 [non pl. 12, figs 3, 4].

2009 *Austerops speculator speculator* (Alberti); McKellar & Chatterton, p. 34.

Type material. Rather fragmented cephalon ISCR/Gig786, from likely the Eifelian, near Sidi Abdallah des Rehamma, western Morocco.

Studied material. Twelve enrolled exoskeletons from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (five from Ed3n1, four from Ed3n2 and three from Ed4); Saoura Valley, Ougarta Basin, Algeria.

Diagnosis. See McKellar & Chatterton (2009).

Remarks. The new collected specimens show the main morphological features of *Austerops speculator speculator* (Alberti, 1970) from western Morocco and *A. speculator punctatus* from the Maider basin in Morocco: a narrow cephalon, a wide glabellar base, moderately divergent axial furrows, poorly defined S2 and S3, and S1 in its adaxial curvature, the same number of dorsoventral files of lenses, the inter-lensar sclera slightly thickened dorsally only and the exsagittal length of the postocular genal field less than half the length of the posterior border.

Austerops speculator punctatus differs basically in its sculpture in having pervasive pitting across the glabella, the palpebral lobe and the genal field and in having an insignificant postocular pad and a wide subocular area.

Austerops speculator speculator (Alberti, 1970) shares with *A. menchikoffi* a narrow cephalon, a wide glabellar base, moderately divergent axial furrows, poorly defined S2 and S3, and S1 in its adaxial curvature, an L1 with subcircular, inflated lateral lobes separated from its median part by a distinct exsagittal furrow, poorly defined lateral lobes of L0, the same number of dorsoventral files of lenses, the inter-lensar sclera being slightly thickened dorsally only and no subocular pad. However, *Austerops menchikoffi* differs in having a wider median portion relative to the total width of L1, two less lenses per file (maximum five for *A. menchikoffi* and eight for *A. speculator speculator*) and the exsagittal length of the postocular genal field being about half the length to equal the length of the posterior border.

Occurrence: Upper Emsian, Eifelian?; Algeria (Saoura: Erg el Djemel) and Morocco (western).

Austerops legrandi sp. nov.
Figure 7a–l

v. 1952 *Phacops salteri* Kozlowski; Le Maître, pl. 21, fig. 9.

v. 1952 *Phacops menchikoffi* sp. nov. Le Maître, pl. XX, figs 15, 21, pl. XXI, fig. 10.

Name. Named in honour of Dr Philippe Legrand who worked on the Devonian of the Algerian Sahara.

Holotype. Complete enrolled specimen GFCL399 (coll. Le Maître, Faculté libre des Sciences de Lille) figured by Le Maître (1952).

Paratypes. One enrolled individual from Ed3n1: Di/UO/003, four individuals from Ed4: Di/UO/009, Di/UO/023–025.

Locus typicus. Erg el Djemel section, Saoura Valley, Ougarta Basin, Algeria.

Stratum typicum. Base of 'Chefar el Ahmar' Formation, upper Emsian, Lower Devonian.

Studied material. Forty-two mostly enrolled specimens from the upper Emsian of the Erg el Djemel section (seven from Ed3n1 and thirty-five from Ed4). Ougarta Basin, Saoura, Algeria.

Diagnosis. Cephalon very narrow; glabella depressed with a very wide base; S1 poorly defined in its adaxial curvature; subquadrate, poorly inflated lateral lobes of L1; visual surface with 18 vertical lens files and a maximum of seven (often six) lenses per file; inter-lensar sclera thin with a slight thickening dorsally; palpebral furrow poorly defined; palpebral area higher than the palpebral lobe. Pygidium axis long (sag.), rather wide (tr.), strongly tapered with up to 6–7 rings plus the terminal piece; 4–5 poorly defined ribs. Almost smooth exoskeleton with scale-like granules on the anterior part of the frontal lobe.

Description. Cephalon: Length/width ratio about 0.67. *Dorsal view*: Glabellar ratio of width at L1 / maximum width of frontal lobe about 0.61. Glabella depressed, bound by shallow axial furrows that are moderately divergent forwards (65°), with the anterior portion less divergent, almost exsagitally aligned. Frontal lobe overhanging slightly a moderately impressed preglabellar furrow. S2 and S3 often not distinct. S1 poorly defined and curved rather more strongly forwards than S0 in its adaxial curvature, and that becomes deeper in its distal portions. L1 shorter (sag.) than L0 (half L0 length), with a wide (tr.) median portion relative to its total width. Median portion of L1 poorly inflated. L1 with subquadrate, poorly inflated lateral lobes separated from its median part by a distinct exsagittal furrow. S0 well marked and almost transverse in its middle portion. L0 short (tr.) with lateral lobes not defined. Reniform visual surface with 18 dorsoventral files of lenses and often six (sometimes seven) lenses per file, with smaller lenses in the anterior median part. Inter-lensar sclera thin with a slight thickening dorsally. Palpebral furrow poorly defined. Exsagittal length of the postocular genal field less than half the length of the posterior border. Cheek barely swollen. *Lateral view*: glabella rounded anteriorly. Outline of L1 curved. L0 as high as the glabella at its maximum convexity. Anterior border rather short, ridge-like, slightly projecting forwards and sloping posteroventrally. A marginulation that extends from the anterolateral border up to about opposite the midlength of the eye backwards. Posterior border furrow deep and narrow. Lateral

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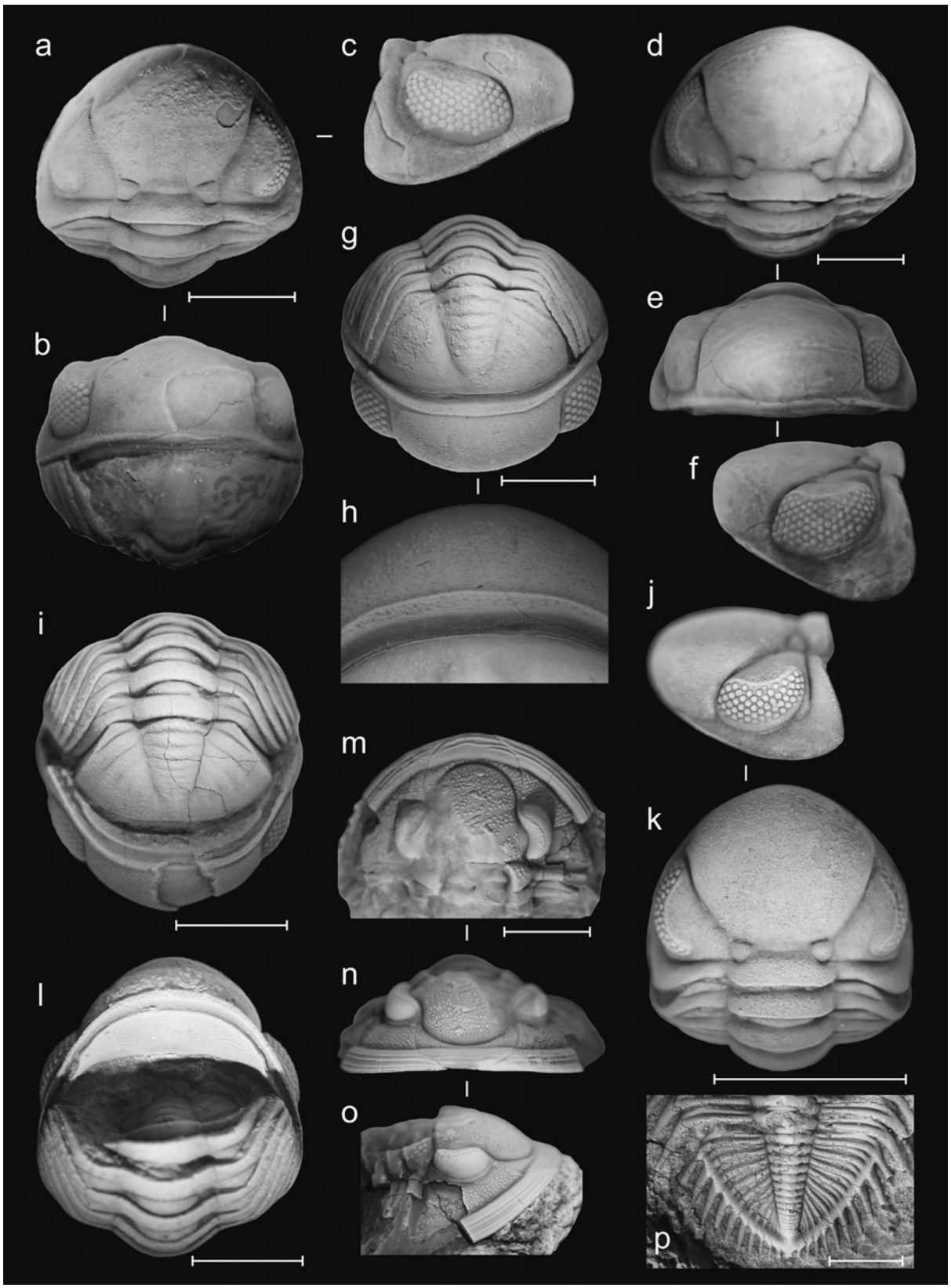

Figure 7. Trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–c) *Austerops legrandi* sp. nov., Erg el Djemel section, figured by Le Maître (1952), holotype GFCL399 (coll. Le Maître, Faculté libre des Sciences de Lille): cephalon in dorsal, frontal and lateral views. (d–f) *Austerops legrandi* sp. nov., Erg el Djemel section, Di/UO/003 (Ed3n1): cephalon in dorsal, frontal and lateral views. (g, h) *Austerops legrandi* sp. nov., Erg el Djemel section, Di/UO/009: pygidium and detail of the cephalic doublure in dorsal views. (i) *Austerops legrandi* sp. nov., Erg el Djemel section, Di/UO/025 (Ed4): pygidium in dorsal view. (j, k) *Austerops legrandi* sp. nov., Erg el Djemel section, Di/UO/024 (Ed4): cephalon in lateral and dorsal views. (l) *Austerops legrandi* sp. nov., Erg el Djemel section, Di/UO/023 (Ed4): cephalic doublure in dorsal view. (m–o) *Cornuproetus cornutus djemelensis* (Alberti, 1981), Erg el Djemel section, Di/UO/011 (Ed3n1): fragmented cephalon in dorsal, frontal and lateral views. (p) *Erbenochile erbeni* (Alberti, 1981), Marhouma section, Di/UO/036 ('km 30'): pygidium in dorsal view. Scale bars = 5 mm.

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border furrow shallow, concave behind the posterior branch of the facial suture as an expanded furrow. No subocular and postocular pad. Posterolateral border furrow continuous and posterolateral border widening at the genal angle. *Frontal view*: Glabellar outline subcircular with its lateral sides flattened subvertically. Palpebral area higher than the palpebral lobe. *Ventral view*: Vincular furrow deep, wide (sag.), curved and parallel to the preglabellar furrow. Posterior band of the cephalic doublure long (sag.) with a hypostomal suture transverse medially. *Thorax*: Composed of 11 thoracic segments, narrowing (tr.) posteriorly. Maximum axial width (tr.) ratio of the last ring / first ring about 75 %. Axial rings convex with no defined lateral lobes, with barely a swelling of extremities. Axial furrows distinct. Anterior pleural band narrower (exsag.) than the posterior pleural band. Pleural furrows narrow and moderately impressed. *Pygidium*: Rather long with a length/width ratio about 51.8 % (excluding the half ring), and its maximum width (tr.) behind its midlength (sag.) in dorsal view. Posterior outline broadly rounded. Pygidial axis long, rather wide, strongly tapered, with an almost complete terminal closure and an insignificant postaxial ridge. Up to 6–7 rings plus the terminal piece compose the pygidial axis. Pygidial pleural field with 4–5 poorly defined ribs delimited by rather deep, thin pleural furrows. Pseudo-articulating half rings indicated by expanded interring furrows. *Ornamentation*: Glabella covered with fine granules on the anterior part of the composite lobe becoming scale-like granules to short ridges. Anterior band of the cephalic doublure covered with scaly granules and pits, posterior band with short ridges to continuous terrace lines laterally. Scattered fine tubercles seem to be present on the cephalic lateral border, the thoracic axis and the pygidial axis of some specimens.

Remarks. Some Algerian specimens described and figured by Le Maître (1952, p. 153) such as the paratype GFCL399 (pl. 20, fig. 21) and the specimen attributed to *Phacops salteri* GFCL407 (pl. 21, fig. 9) are assigned in this work to *Austerops legrandi* sp. nov. These specimens studied by Le Maître (1952) and the additional specimens studied in this work differ from *A. menchikoffi* in having a narrower cephalon with a wider glabellar base, shallower axial furrows that are less divergent in their anterior portion, subquadrate and poorly inflated lateral lobes of L1, an almost smooth ornamentation and a shorter (tr.) occipital ring.

Austerops legrandi sp. nov. differs from *Phacops salteri* Kozlowski, 1923 from Bolivia in having no median tubercle on L0, no short genal spines and no granulation as pronounced on the cephalon. In *Phacops salteri*, L1 is reduced to its stretched lateral preoccipital lobes (mixed S0 and S1), and the number of dorsoventral files of lenses does not exceed 17.

The new species shows morphological features similar to other species attributed to *Austerops* such as an S1 poorly defined in its adaxial curvature, a visual surface with 18 vertical lens files, an interlensar sclera slightly thickened dorsally only and a poorly defined palpebral furrow.

Austerops legrandi sp. nov. shares with *A. kermiti* from the Eifelian of Morocco a similar cephalic length/width ratio (very narrow), subquadrate and poorly inflated lateral lobes of L1, and no defined lateral lobes of L0. *Austerops kermiti* differs in having a narrower base of the glabella, less divergent axial furrows deflected adaxially at the front of the eye, more lenses per file (6–7 in *A. legrandi* sp. nov. compared to nine in *A. kermiti*), a palpebral area and a palpebral lobe at about the same level, and a shallower vincular furrow.

Austerops legrandi sp. nov. shares with *A. salamandar* from the Eifelian of Morocco the maximum number of lenses per file (seven: common for *A. salamandar* and occasionally for *A. legrandi* sp. nov.), no defined lateral lobes of L0 and the same depth of the vincular furrow. *Austerops salamandar* differs in having a narrower base of the glabella, less divergent axial furrows deflected adaxially at the front of the eye, subcircular and inflated lateral lobes of L1, and a palpebral area and palpebral lobe at about the same level.

Occurrence. Upper Emsian; Algeria (Saoura, Erg el Djemel).

Superfamily ACASTACEA Delo, 1935
Family ACASTIDAE Delo, 1935
Subfamily ASTEROPYGINAE Delo, 1935
Genus *Hollardops* Morzadec, 1997

Type species. *Asteropyge mesocristata* Le Maître, 1952: upper Emsian, Algeria.

Additional species. *Hollardops aithassainorum* Chatterton *et al*. 2006: Eifelian, Morocco; *H. boudibensis* Morzadec, 2001: upper Emsian, Morocco; *H. burtandmimiae* (Lieberman & Kloc, 1997): upper Emsian and Eifelian, Morocco; *H. lemaitreae* Morzadec, 1997: upper Emsian, Algeria; *H. struvei* (Morzadec, 1969): upper Emsian, France (Armorican Massif).

Hollardops mesocristata (Le Maître, 1952)
Figure 6m–p

v∗. 1952 *Asteropyge mesocristata* sp. nov. Le Maître, p. 153, pl. XX, figs 24–6.

1952 *Asteropyge gr. michelini* Rouault, 1851; Le Maître, pl. XXI, fig. 12.

1952 *Asteropyge pectinata* Roemer, 1850; Le Maître, pl. XXI, fig. 13.

1967 *Asteropyge mesocristata* Le Maître; Le Maître *in* Legrand, p. 274.

1997 *Hollardops mesocristata* (Le Maître); Morzadec, p. 149, pl. 2, fig. 8; pl. 5, fig. 9; pl. 6, figs 1, 3–6; pl. 7, figs 1–7; pl. 8, figs 5–8.

1997 *Philipsmithiana hyfinkeli* sp. nov. Lieberman & Kloc, p. 65, figs 6.1–6.5; figs 7.7, 7.9; figs 21.2, 21.5–9; figs 22.1–2, 22.5–6, 22.8–9, 22.11.

2001 *Hollardops mesocristata* (Le Maître); Morzadec, p. 71, pl. 8, figs 3, 6, 9; pl. 9, figs 1–4.

2004 *Hollardops mesocristata* (Le Maître); Jansen, Becker, Plodowski, Schindler, Vogel & Weddige, pl. 2, figs 1, 4.

2006 *Hollardops mesocristata* (Le Maître); Chatterton, Fortey, Brett, Gibb & McKellar, p. 26–7, pl. 14.1–6, pl. 15.1–7, pl. 16.1–6, pl. 20.8, 20.12, 20.15.

2014 *Hollardops mesocristata* (Le Maître); Bignon & Crônier, p. 20.

Type material. A small enrolled exoskeleton GFCL401 (coll. Le Maître, Faculté libre des Sciences de Lille), from the upper Emsian, Erg el Djemel section.

Studied material. Five enrolled exoskeletons and two fragmented pygidia from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (five from Ed3n1 and two from Ed3n2).

Diagnosis. See Chatterton *et al.* (2006).

Remarks. Le Maître (1952, p. 153) and Morzadec (1997, p. 149) provided a full description of the type material from the Erg el Djemel section. Additionally, Chatterton *et al*. (2006) provided numerous illustrations of this species from the best specimens available from Morocco.

Occurrence. Upper Emsian; Algeria (Saoura: Erg el Djemel), Morocco (Foum Zguid).

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Genus *Walliserops* Morzadec, 2001

Type species. *Walliserops trifurcatus* Morzadec, 2001: upper Emsian, Morocco.

Additional species. *Walliserops hammii* Chatterton *et al*. 2006: upper Emsian, Morocco; *W. lindoei* Chatterton & Gibbs, 2010: Eifelian, Morocco; *W. tridens* Chatterton *et al*. 2006: upper Emsian, Morocco.

Diagnosis. See Bignon & Crônier (2014).

Walliserops sp.
Figure 6l

Studied material. Two fragmented and poorly preserved pygidia from the upper Emsian (base of the 'Chefar el Ahmar' Formation) of the Erg el Djemel section (one from Ed3n1 and one from Ed3n2).

Remarks. Pygidia with seven pygidial axial rings with median broken spines, five pleural segments with broken spines on the distal part of each posterior band, and five pairs of pygidial spines developed only from posterior pleural bands.

Subfamily ODONTOCHILINAE Šnajdr, 1985
Genus *Erbenochile* Alberti, 1981

Type species. *Odontochile* (*Erbenochile*) *erbeni* Alberti, 1981: upper Emsian, Algeria.

Additional species. *Erbenochile issoumourensis* Chatterton & Gibb, 2010: upper Emsian or early Eifelian, Morocco.

Remarks. Chatterton & Gibb (2010, pp. 1194, 1197) provided a comprehensive diagnosis and discussion of this genus that is represented by two species encountered in North Africa. *Erbenochile erbeni* differs from *E. issoumourensis* in having a taller eye with a greater number of lenses per file, long and tubular marginal spines on the pygidium and a larger axial spine on the first axial ring of the pygidium. Chatterton & Gibb (2010) and Bignon & Crônier (2014, p. 29) confirmed the assignation of the genus *Erbenochile* to Odontochilinae Šnajdr, 1985. Budil, Hörbinger & Mencl (2009), however, considered the subfamily Odontochilinae as a subjective junior synonym of Dalmanitinae Vogdes, 1890.

Erbenochile erbeni (Alberti, 1981)
Figure 7p

1950 *Coronura aspectans* Hall, 1888; Le Maître, p. 254.

1952 *Coronura aspectans* (Conrad, 1841); Hall, 1888; Le Maître, p. 152, pl. 20, fig. 30.

1967 *Coronura aspectans* Conrad; Le Maître *in* Legrand p. 274.

1981 *Odontochile* (*Erbenochile*) *erbeni* gen. et sp. nov.; Alberti, p. 368.

1995 *Erbenochile erbeni* (Alberti); Morzadec, pp. 615–19, fig. 2a–f.

1997 *Erbenochile erbeni* (Alberti); Morzadec, p. 153.

2003 *Erbenochile erbeni* (Alberti); Fortey & Chatterton, p. 1689, fig. 1a–e.

2006 *Erbenochile erbeni* (Alberti); Chatterton, Fortey, Brett, Gibb & McKellar, pp. 24–6, pl. 13.1–9.

2010 *Erbenochile erbeni* (Alberti); Chatterton & Gibb, pp. 1194–7, fig. 5.

2014 *Erbenochile erbeni* (Alberti); Bignon & Crônier, p. 29.

Type material. An incomplete thoracopygon GFCL403 (coll. Le Maître, Faculté libre des Sciences de Lille), from the upper Emsian, 'km 30' location, Algeria.

Studied material. One thoracopygon (plus the lower part of cephalon) from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Marhouma section ('km 30').

Diagnosis. See Chatterton *et al.* (2006).

Remarks. Le Maître (1952, p. 152) and Morzadec (1995, p. 615) provided a description of the type material from the Erg el Djemel section. Additionally Chatterton *et al.* (2006, pp. 24–5) provided a full description of this species from Morocco.

Occurrence: Upper Emsian; Algeria (Saoura: 'km 30'), Morocco (Foum Zguid).

Order PROETIDA Fortey & Owens, 1975
Family AULACOPLEURIDAE Angelin, 1854
Subfamily OTARIONINAE Richter & Richter, 1926
Genus *Cyphaspis* Burmeister, 1843

Type species. *Phacops ceratophthalmus* Goldfuss, 1843: Eifelian, Gerolstein in Germany.

Remarks. Adrain & Chatterton (1996) provided an emended diagnosis and integrated 20 species into this genus. Four new species from Morocco were added by Chatterton *et al*. (2006) including three from the upper Emsian: *Cyphaspis agayuara*, *C. eberhardiei* and *C. hamidi*.

Occurrence. Wenlock to Givetian; France, England, Czech Republic, Germany, Austria, Poland, Morocco, NW Canada, Australia.

Cyphaspis ?*agayuara* Chatterton *et al*. 2006
Figure 8a–e

2006 *Cyphaspis agayuara* sp. nov. Chatterton, Fortey, Brett, Gibb & McKellar, pp. 48–9, pls 42.1–42.7.

Type material. Complete articulated exoskeleton UA13397, from the upper Emsian Timrhanrhart Formation, section at Jbel Gara el Zguilma, near Foum Zguid, Morocco.

Studied material. Seven incomplete exoskeletons from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (five from Ed3n1 and two from Ed3n2).

Remarks. The Algerian specimens show some morphological features of *Cyphaspis agayuara* from Morocco: coarse tubercles evenly distributed on fixigena, subsidiary tubercles across the occipital ring and a row of coarser tubercles sub-parallel across the preglabellar field. Unfortunately, owing to poor preservation, the length of the genal spines, the length of the axial spine on sixth thoracic segment and the presence of the (spinose) node on the occipital ring are not visible. Otherwise, the main difference is the presence of a coarse row of granules across the back of the thorax and pygidium crossing the third pygidial axial ring as in *Cyphaspis eberhardiei s.s*., not the second pygidial axial ring as in *Cyphaspis agayuara s.s*.

Cyphaspis ?*hamidi* Chatterton *et al*. 2006
Figure 8q–s

2006 *Cyphaspis hamidi* sp. nov. Chatterton, Fortey, Brett, Gibb & McKellar, pp. 51–3, pls 46.1–46.14, pls 54.4, 54.9, ?54.3, ?54.8.

Type material. Enrolled exoskeleton UA13402, from the upper Emsian, Timrhanrhart Formation, section at Jbel Gara el Zguilma, near Foum Zguid, Morocco.

Studied material. Two incomplete cephala from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (one from Ed3n2 and one from Ed4).

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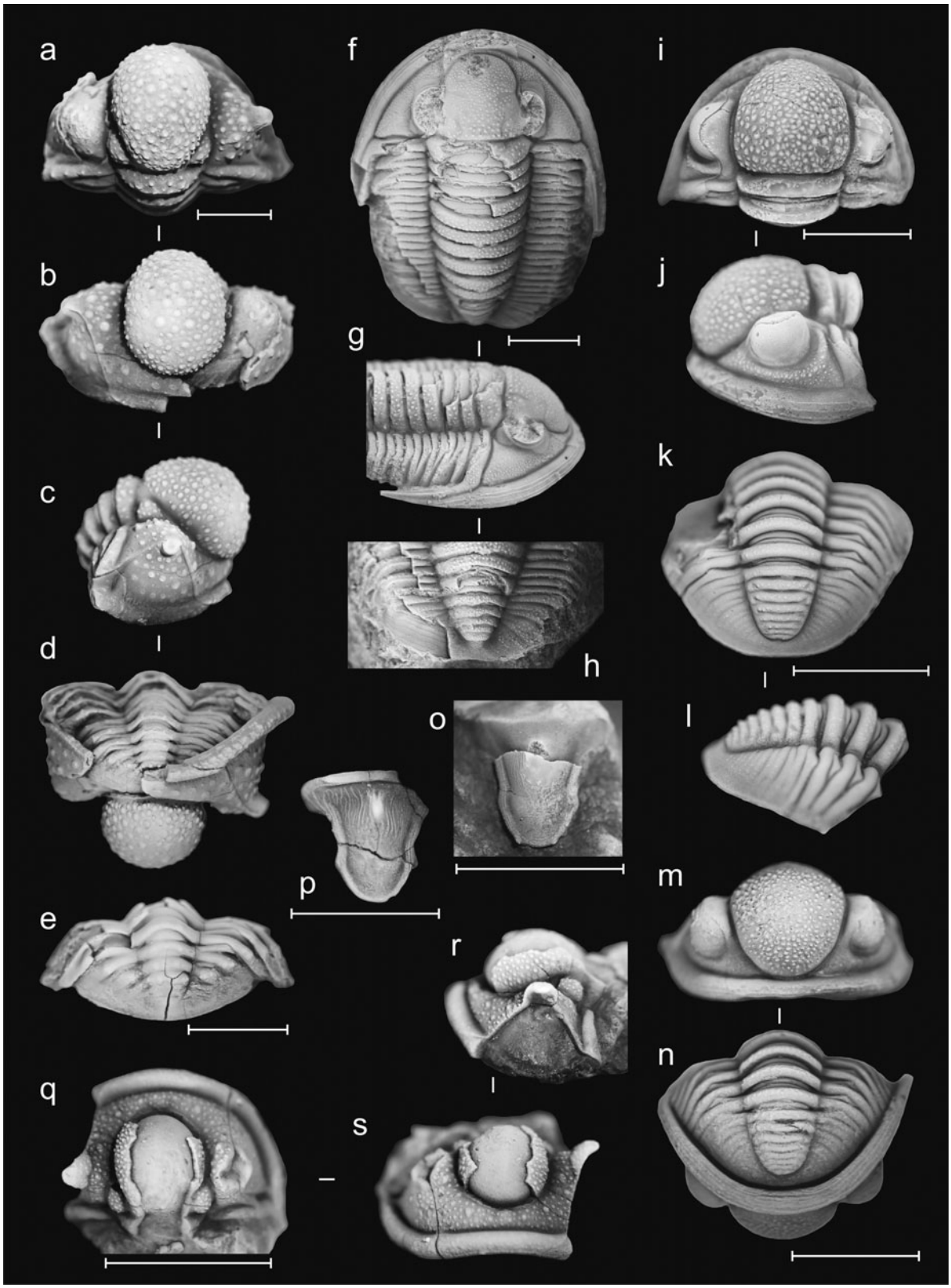

Figure 8. Trilobites from the 'Chefar el Ahmar' Formation, Lower Devonian, upper Emsian, Saoura Valley, Algeria. (a–d) *Cyphaspis* ?*agayuara* Chatterton *et al*. 2006, Erg el Djemel section, Di/UO/021 (Ed3n2): (a–c) cephalon in dorsal, frontal and lateral views; (d) pygidium in dorsal view. (e) *Cyphaspis* ?*agayuara* Chatterton *et al*. 2006, Erg el Djemel section, Di/UO/012 (Ed3n1): pygidium in dorsal view. (f–h) *Cornuproetus cornutus djemelensis* (Alberti, 1981), Erg el Djemel section, Di/UO/037 ('km 30'): fragmented cephalon in dorsal, frontal and lateral views. (i, j) *Gerastos tuberculatus marocensis* Chatterton *et al.* 2006, Erg el Djemel section, Di/UO/030 (Ed4): cephalon in dorsal and lateral views. (k, l) *Gerastos tuberculatus marocensis* Chatterton *et al.* 2006, Erg el Djemel section, Di/UO/031 (Ed4): pygidium in dorsal and lateral views. (m, n) *Gerastos tuberculatus marocensis* Chatterton *et al.* 2006, Erg el Djemel section, Di/UO/029 (Ed4): (m) cephalon in frontal view; (n) pygidium in dorsal view. (o) ?*Gerastos tuberculatus marocensis* Chatterton *et al.* 2006, Erg el Djemel section, Di/UO/019 (Ed3n2): fragmented hypostome in dorsal view. (p) ?*Gerastos tuberculatus marocensis* Chatterton *et al.* 2006, Erg el Djemel section, Di/UO/020 (Ed3n2): hypostome in dorsal view. (q–s) *Cyphaspis* ?*hamidi* Chatterton *et al*. 2006, Erg el Djemel section, Di/UO/022 (Ed3n2): cephalon in dorsal, lateral and frontal views. Scale bars = 5 mm.

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Remarks. The Algerian specimens show the main morphological features of *Cyphaspis hamidi* from Morocco: a small cephalon with a moderately inflated glabella, fine- to medium-sized tubercles evenly distributed over cephalon and eyes strongly convex laterally without distinct socle. Unfortunately, owing to poor preservation, the length of the genal spines and the presence of the axial spine on the sixth thoracic segment are not visible.

Family PROETIDAE Salter, 1864
Genus *Gerastos* Goldfuss, 1843

Type species. Proetus cuvieri Steininger, 1831: Eifelian, Germany.

Additional species (from Morocco only). Gerastos ainrasifus Gibb & Chatterton, 2010: Eifelian; *G. aintawilus* Gibb & Chatterton, 2010: Eifelian; *G. akrechanus* Alberti, 1969: Emsian, Morocco; *G. cuvieri malisus* Gibb & Chatterton, 2010: Eifelian; *G. discombobulates* Gibb & Chatterton, 2010: Eifelian; *G. emmetus* Gibb & Chatterton, 2010: Givetian; *G. hammii* Gibb & Chatterton, 2010: upper Emsian or Eifelian; *G. izius* Gibb & Chatterton, 2010: Givetian; *G. lisanrasus* Gibb & Chatterton, 2010: Eifelian; *G. malisjildus* Gibb & Chatterton, 2010: Eifelian; *G. prox umerbianus* Alberti, 1969: Eifelian or Givetian, Morocco; *G. raribus* Gibb & Chatterton, 2010: Givetian; *G. rehamnanus* Alberti, 1969: probably Lower Devonian, Morocco; *G. taqus* Gibb & Chatterton, 2010: Eifelian; *G. tuberculatus marocensis* Chatterton *et al.* 2006: upper Emsian–Eifelian.

Remarks. On the basis of well-preserved material, Gibb & Chatterton (2010) described and illustrated 12 species and subspecies of *Gerastos* from the Lower to the Mid Devonian of Morocco. The diagnostic features between *Gerastos*, *Longiproetus* and *Coniproetus* were discussed by Owens (1973) and completed and/or modified by Lütke (1990), Adrain (1997) and Chatterton *et al*. (2006). The main diagnostic features for *Gerastos* are: ζ and ε (with a great angle *c*. 160°) widely separated; convex (abax.) lateral margin of glabella that is as long as wide; distinct eye platform; no or short genal spine; indistinct lateral occipital lobes; band of parallel terrace lines and no curved terrace ridges on pygidium margin.

Gerastos tuberculatus (Barrande, 1846*a*)
Gerastos tuberculatus marocensis Chatterton *et al.* 2006
Figure 8i–p

1846*a Proetus tuberculatus* Barrande, p. 74.

1846*b Proetus discretus* Barrande; Barrande, p. 16.

1847 *Proetus tuberculatus* Barrande; Hawle & Corda, p. 72.

1852 *Proetus tuberculatus* Barrande; Barrande, p. 456, pl. 16, figs 18–20.

1946 *Proetus* (*Proetus*) *tuberculatus* (Barrande); Přibyl, p. 6.

1953 *Proetus* (*Proetus) tuberculatus* (Barrande); Přibyl, p. 59.

1969 *Proetus* (*Proetus*) *tuberculatus* (Barrande); Alberti, p.74, pl. 1, fig. 7.

1970 *Proetus* (*Proetus*) *tuberculatus* (Barrande); Přibyl *in* Horný & Bastl, p. 314.

?1970 *Proetus* (*Proetus*) sp. A aff. *granulosus* (Goldfuss, 1843); Alberti, p. 34, pl. 3, fig. 5.

1973 *Proetus* (*Gerastos*) *tuberculatus* (Barrande); Owens, pp. 9–10.

1980 *Gerastos* (*Gerastos*) *tuberculatus* (Barrande); Šnajdr, pp. 48–9, pl. 2, figs 12, 13.

2006 *Gerastos tuberculatus marocensis* ssp. nov. Chatterton, Fortey, Brett, Gibb & McKellar, pp. 43–5, pl. 37.1–8, pl. 38.3, pl. 38.6, pl. 39.1–12, pl. 54.5–7, pl. 54.11–13.

2010 *Gerastos tuberculatus marocensis* Chatterton *et al*.; Gibb & Chatterton, pp. 15–16, pl. 1.1–8, pl. 2.1–13, pl. 3.1–6, pl. 4.1–12, pl. 5.5–9, pl. 18.1–14

Type material. Complete exoskeleton UA13276 from the upper Emsian, Timrhanrhart Formation, section at Jbel Gara el Zguilma, near Foum Zguid, Morocco.

Studied material. Twenty-five specimens from the upper Emsian (base of 'Chefar el Ahmar' Formation) of the Erg el Djemel section (six individuals from Ed3n1, five from Ed3n2 and 14 from Ed4), and probably two hypostomes from Ed3n2.

Diagnosis. See Chatterton *et al*. (2006).

Remarks. The new specimens show the main morphological features of *Gerastos tuberculatus marocensis* from the upper Emsian of Morocco: cephalic proportions, pointed tubercles much coarser on glabella, short genal spine, seven pygidial rings plus terminal piece, five (+ one) pygidial pleural and interpleural furrows and a shallow border furrow on the pygidium. Chatterton *et al*. (2006) and Gibb & Chatterton (2010) provided adequate descriptions and comparisons between the closest species.
Occurrence. Upper Emsian; Morocco (Foum Zguid), Algeria (Saoura: Erg el Djemel).

Genus *Cornuproetus* Richter & Richter, 1919

Type species. Gerastos cornutus Goldfuss, 1843: Eifelian, Germany.

Additional species (from upper Emsian to Eifelian in North Africa only). Cornuproetus cornutus marrakechensis Alberti, 1969: ?Eifelian; Morocco; *C. cornutus djemelensis* Alberti, 1981: probably upper Emsian (not Eifelian), Algeria; *C. midas amlanensis* Alberti, 1969: Emsian; Morocco, Algeria; *C. pernix boutsharafinensis* Alberti, 1969: upper Emsian; Morocco; ?*C. infans* Alberti, 1969: ?Mid Devonian; Morocco; ?*C. maidericus* Alberti, 1969: upper Emsian; Morocco.

Remarks. Alberti (1969) published the most extensive report about the classification of this genus divided into 16 subgenera. Additionally, he described and illustrated several new species including five from the upper Emsian of Morocco among more than 20 species illustrated, mostly according to their cranidia. Among these five new species, two were then reassigned to *Cornuproetus* (*Paralepidoproetus*): *C.* (*P.*) *fauremuretae* and *C.* (*P.*) *chouberti* (see Alberti, 1981). Moreover, Alberti (1981) described and illustrated a new subspecies *C. cornutus djemelensis* from probably the upper Emsian (not Eifelian) of the Erg el Djemel section, Algeria. More work seems to be necessary in order to re-evaluate these previously described species.

Cornuproetus cornutus djemelensis (Alberti, 1981)
Figures 7m–o, 8f–h

1970 *Cornuproetus* (*Cornuproetus*) *cornutus* ssp. nov. B Alberti, p. 39.

1981 *Cornuproetus* (*Cornuproetus*) *cornutus djemelensis* ssp. nov. Alberti, p. 20, pl. 1, fig. 5.

Type material. Almost complete eroded enrolled exoskeleton GPIH from probably the upper Emsian (not Eifelian), Erg el Djemel section, Algeria.

Studied material. Seven poorly preserved exoskeletons with one from the upper Emsian (base of 'Chefar el Ahmar' Formation) of

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the Marhouma section ('km 30') and six from the Erg el Djemel section (three from Ed3n1, three from Ed4); Ougarta basin, Saoura, Algeria.

Diagnosis. See Alberti (1969).

Remarks. The new specimens are characterized by slightly convex anterior and lateral cephalic borders, a violin-shaped inflated glabella, no distinct anteromedian cephalic projection, no epiborder furrow, no inflated lobes (only suggested by absence of tubercles) on genal field adjacent to front and back of a narrow socle, a short (sag.) distinct preglabellar field, few discontinuous and curved terrace ridges on the narrowly parabolic anteromedian portion of the cephalon; coarse tubercles equally sized and evenly distributed on the glabella, except in the glabellar furrows, and on the thoracic and pygidial axial rings; finer tubercles on the free cheeks and pleurae, very fine terrace ridges on the anterior and lateral portions of the glabella and fine short ridges on the palpebral lobes; a pygidium with four axial rings plus a terminal piece. A lowered broad (ant.) and tapered (post.) ridge is located behind the terminal piece that can be confused with an indistinct terminal piece (as suggested by Alberti, 1969). These specimens share the general morphology of *Cornuproetus cornutus djemelensis* from probably the upper Emsian of the Erg el Djemel section in Algeria, hitherto poorly known by an eroded enrolled specimen.

The Algerian specimens differ from the type species *Cornuproetus cornutus cornutus* (Goldfuss, 1843) from the Eifelian of Germany in having the back half of the glabella bulge more laterally, pygidial rings weakly lengthened laterally and no clear pygidial border.

The Algerian specimens share also some morphological characters with the cranidium of *Cornuproetus cornutus marrakechensis* from the ?Eifelian of Morocco (no associated pygidium known): the slightly convex and elevated anteromedian cephalic border; a short (sag.) distinct preglabellar field. However, the Algerian specimens differ in having a glabella that is more violin shaped than sub-rectangular/trapezoidal and palpebral lobes that are narrower (tr.).

The cranidium of *Cornuproetus cornutus archeocornutus* Šnajdr, 1980 from the lower Emsian of the Barrandian area of the Czech Republic differs in having a widely parabolic cephalic border, finer ornamentation and granulated palpebral lobes.

The cranidium of *Cornuproetus midas amlanensis* from the Emsian of Morocco and Algeria differs in having a glabella that is more subquadrate, with fine terrace lines and tubercles, a distinct epiborder furrow and an anterior border that is wider, with terrace lines covering the entire field.

The cranidium of *Cornuproetus pernix boutsharafinensis* from the upper Emsian of Morocco differs in having a glabella more subquadrate, a distinct epiborder furrow and an anterior border that is wider, with terrace lines covering the entire field.

Cornuproetus (*Paralepidoproetus*) *fauremuretae* and *C.* (*P.*) *chouberti* differ from *C. cornutus djemelensis* in having a wider cephalic border and fine, anastomosing, scaly terrace ridges on the glabella (see Alberti, 1981).

Diademaproetus mohamedi Chatterton *et al.* (2006) from the lower Eifelian of Morocco differs in having a broader and flatter cephalic border with a distinct epiborder furrow, sparser tubercles and developed lobes on the genal field adjacent to the front and back of a narrow socle.

?*Cornuproetus infans* Alberti, 1969, a poorly preserved and fragmented cephalon from the Mid Devonian of Morocco, differs in having a more sub-rectangular and lower glabella, and an anterior border with terrace lines covering the entire field.

?*Cornuproetus maidericus* Alberti, 1969, a poorly preserved cranidium from the upper Emsian of Morocco, differs in having a much lowered glabella.

Occurrence. Upper Emsian; Algeria (Erg el Djemel).

4. Inter- and intra-specific variability in phacopids

4.a. Method

The terminology used herein to describe the eye of Phacopina is based on the work of Clarkson (1966).

The dimensions, especially the length and the width of cephala in dorsal view have been obtained using an optical image analyser (TPSdig v.2.17; Rohlf, 2013).

The discontinuous postembryonic growth by successive moults results in size distributions often clustered into stage groupings (Dodd & Stanton, 1990). These size distributions allow growth to be described using relatively simple numerical models. A univariate or bivariate plot of size distribution within a sample would be expected to show a discontinuous growth curve, individuals being pooled in distinct dimensional classes. Certain distribution sizes show no evidence of stage peaks because of growth rates, recruitment rates and overlap in size between instars (Sheldon, 1988). In order to establish such a size series in the different Algerian species of phacopids we have constructed a bivariate plot using the width as a function of the length of cephala (Fig. 9).

Moreover, in order to follow the morphological evolution of the eye, the number of dorsoventral files as a function of the cephalic length has been recorded on bivariate diagrams, for cephala (Fig. 10).

4.b. Results

4.b.1. Size distribution during ontogeny

The length/width plot of cephala (Fig. 9a) shows no distinct grouping. No distinct instars can be distinguished. The growth series is essentially represented by the holaspid period where no feature allows us to distinguish instars.

Moreover, the relative proportions of all phacopid cephala remain constant ($y = ax + b$; cephala: $r = 0.8883$, $p < 0.001^{***}$) whatever the degree of development of individuals (Fig. 9); that makes it possible to deduce that the correlation is positive with a width that varies proportionally with the length. Broadly, the studied phacopids present the same evolution in size.

Additionally, the relative proportions of each *Barrandeops* species remain constant ($y = ax + b$; cephala: $r = 0.9718, p < 0.001^{***}$ for *B. granulops*) whatever the degree of development of individuals (Fig. 9b); *B. chattertoni* sp. nov. is represented in our study by only four small individuals showing the same tendency as *B. granulops* ($y = ax + b$; cephala: $r = 0.9741, p < 0.01^{**}$; Fig. 9b).

The specimens assigned to different *Phacops* are represented by only one or two individuals. *Phacops*

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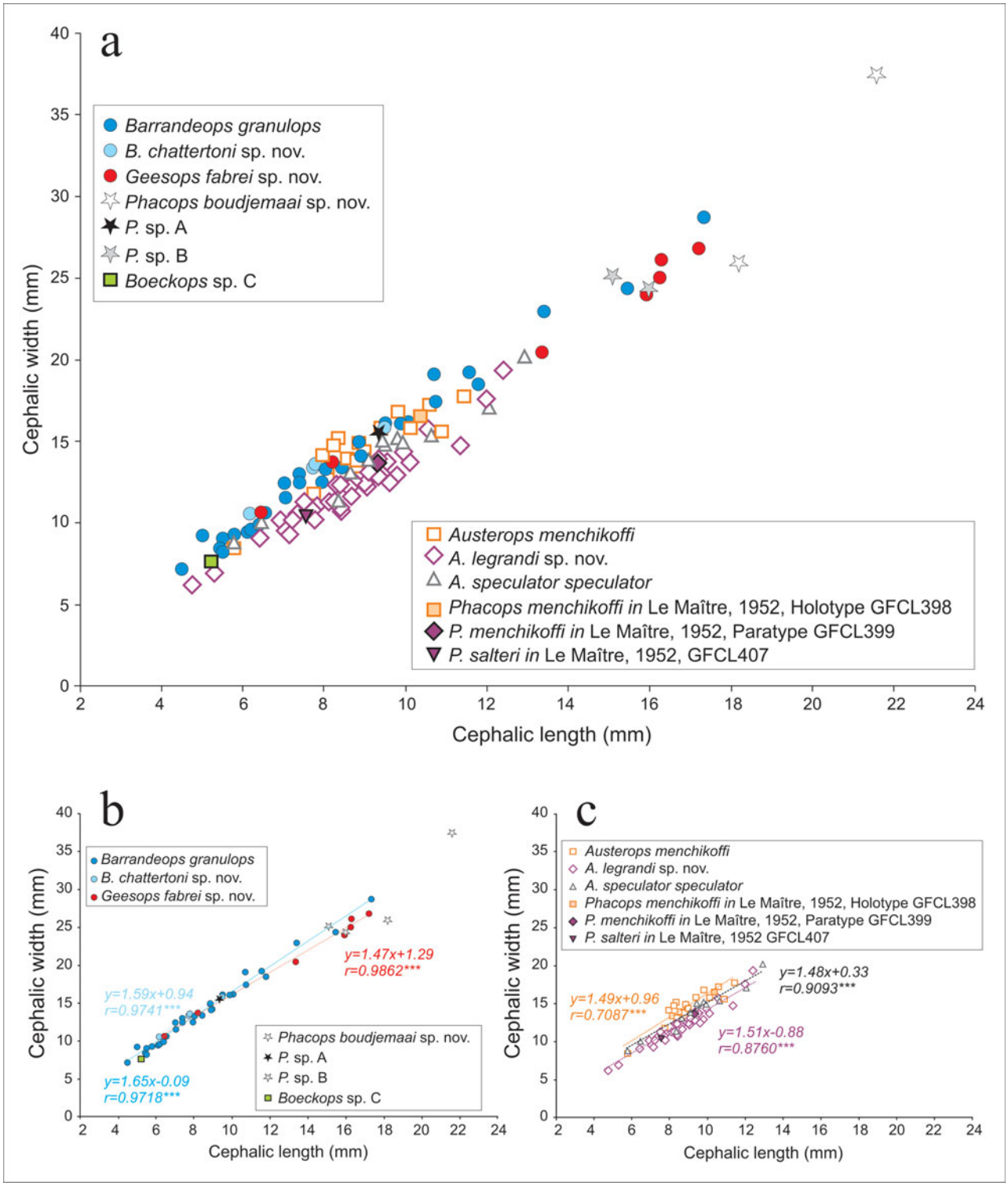

Figure 9. (Colour online) Bivariate plot using the width (in mm) as a function of the length (in mm) of (a) 29 cephala of *Barrandeops granulops* (Chatterton *et al*. 2006), 4 cephala of *B. chattertoni* sp. nov., 4 cephala of *Phacops boudjemaai* sp. nov., 1 cephalon of *P.* sp. A, 2 cephala of *P.* sp. B, 7 cephala of *Geesops fabrei* sp. nov., 1 cephalon of *Boeckops* sp. C, 18 cephala of *Austerops menchikoffi* (Le Maître, 1952), 12 cephala of *Austerops speculator speculator* (Alberti, 1970), 43 cephala of *Austerops legrandi* sp. nov.; (b) for *Barrandeops*, *Phacops*, *Geesops* and *Boeckops* species; and (c) for *Austerops* species.

sp. A is represented by a single medium-sized individual. *Phacops boudjemaai* sp. nov. is represented by four specimens but only two complete large individuals. *Phacops* sp. B is represented by two large individuals, the cephalon being broader (26 mm) than long (17 mm) for the smallest individual.

The relative proportions of *Geesops fabrei* sp. nov. remain also constant ($y = ax + b$; cephala: $r = 0.9862$, $p<0.001^{***}$) whatever the degree of development of individuals (Fig. 9b).

Moreover, the relative proportions of each *Austerops* species remain constant ($y = ax + b$; cephala: $r =$

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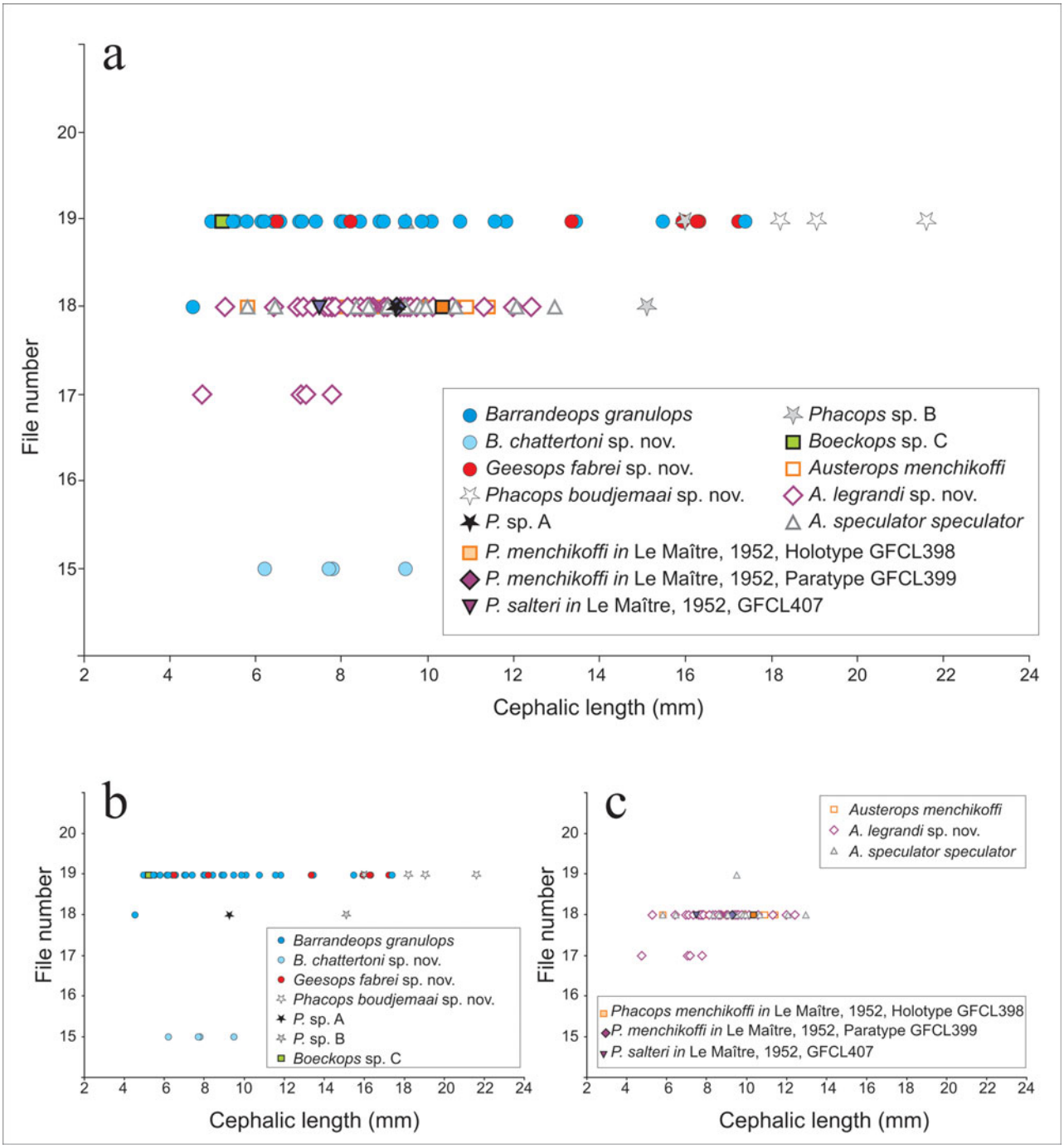

Figure 10. (Colour online) Bivariate plot using the number of files as a function of the cephalic length (in mm) in (a) 28 cephala of *Barrandeops granulops* (Chatterton et *al*. 2006), 4 cephala of *B. chattertoni* sp. nov., 2 cephala of *Phacops boudjemaai* sp. nov., 1 cephalon of *P*. sp. A, 2 cephala of *P*. sp. B, 6 cephala of *Geesops fabrei* sp. nov., 1 cephalon of *Boeckops* sp. C, 17 cephala of *Austerops menchikoffi* (Le Maître, 1952), 12 cephala of *Austerops speculator speculator* (Alberti, 1970), 41 cephala of *Austerops legrandi* sp. nov.; (b) for *Barrandeops*, *Phacops*, *Geesops* and *Boeckops* species; and (c) for *Austerops* species.

0.7087, $p<0.001^{***}$ for *A. menchikoffi*; $r = 0.9093$, $p<0.001^{***}$ for *A. speculator speculator*; $r = 0.8760$, $p<0.001^{***}$ for *A. legrandi* sp. nov.) whatever the degree of development of individuals (Fig. 9c).

For *Austerops menchikoffi*, the regression line passes by the point representing the holotype of *Phacops menchikoffi*, the previous assignation by Le Maître (1952) (GFCL398: pl. 20, figs 17–20).

For *Austerops legrandi* sp. nov., the regression line passes by the point representing *Phacops salteri* described by Le Maître in 1952, (GFCL407: Pl. 21, fig. 9) and is close to that of the paratype of *P. menchikoffi*, the previous assignation by Le Maître (1952) (GFCL399: pl. 20, fig. 21). This new species is characterized by proportions that differ from those of *Austerops menchikoffi*: for a given length, the individuals of the new species are narrower.

For *Austerops speculator speculator*, the individuals seem to show intermediate ratios (Fig. 9c).

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4.b.2. Dorsoventral file distribution

The scatter diagram of the number of files versus the cephalic length seems to show that during growth there is a tendency for the files to increase in number (Fig. 10). This is obvious in *Austerops legrandi* sp. nov., where there are enough specimens to show a relatively important size range (Fig. 10). Additionally, different species are recognizable according to their own file number: *Barrandeops granulops* commonly has 19 dorsoventral files; only the youngest individual has only 18 files. *Phacops boudjemaai* sp. nov., represented by only three large individuals, has 19 dorsoventral files, the same number that is present in *Barrandeops granulops. Barrandeops chattertoni* sp. nov. can readily be distinguished by its reduced number of dorsoventral files of lenses (15), even if it is only represented by four young individuals. *Austerops menchikoffi* (including the holotype), *A. speculator speculator* and *A. legrandi* sp. nov. commonly have 18 files of lenses, except for four young individuals of *A. legrandi* sp. nov. that have only 17 files and one individual of *A. speculator speculator* that has 19 files.

The scatter diagram of the number of lenses versus the cephalic length seems to show also that during growth there is a tendency for the lenses to increase in number (Fig. 11). This is obvious in *Barrandeops granulops* or *Austerops legrandi* sp. nov where there are enough specimens to show a relatively important size range. For comparison, in *Barrandeops granulops*, the minimum number of lenses is 56, the maximum number is 75, and at the maximum height of the eye, vertical files of four or five lenses alternate; in *B. chattertoni* sp. nov., the minimum number of lenses is 32, the maximum number is 38, and at the maximum height of the eye, vertical files of three lenses alternate; in *Geesops fabrei* sp. nov., the minimum number of lenses is 71, the maximum number is 90, and at the maximum height of the eye, vertical files of five or six lenses alternate; in *Phacops boudjemaai* sp. nov., the minimum number of lenses is 89, the maximum number is 94, and at the maximum height of the eye, vertical files of six lenses alternate; in *Austerops menchikoffi*, the minimum number of lenses is 74, the maximum number is 91, and at the maximum height of the eye, vertical files of six or seven lenses alternate; in *A. speculator speculator*, the minimum number of lenses is 89, the maximum number is 112, and at the maximum height of the eye, vertical files of six, seven or eight lenses alternate; in *A. legrandi* sp. nov., the minimum number of lenses is 61, the maximum number is 98, and at the maximum height of the eye, vertical files of five, six or seven lenses alternate (Fig. 11).

5. Biodiversity analysis

5.a. Method

The study of palaeobiodiversity is significant whatever the scale of study, even though estimates of Phanerozoic global biodiversity are limited by biases occurring in the fossil record. Fossiliferous biases comprise in particular the underrepresentation of some areas, inaccuracy in taxonomic data and irregular sampling intensity across organisms, environments and time intervals (Badgley, 2003), and notable improvements have been realized in the Phanerozoic diversity database (Alroy *et al*. 2001).

The study of palaeobiodiversity is based on a count of specimens for each taxon in each studied sample and their relative proportions. Additionally, to complete the palaeobiodiversity information and to evaluate its various components, several complementary ecological indices can be used in palaeontology (Harper, 1999; Hammer & Harper, 2006), such as dominance, equitability or taxa richness.

In order to evaluate the taxonomic diversity in trilobites for the two studied Algerian sections, all the complete and disarticulated sclerites were identified and numbered. Additionally, we used the following indices: Specific richness (*Dtot*), Diversity (*MR-index*), Dominance (*D-index)* and Equitability (*E-index*).

Specific richness corresponds to the number of taxa, i.e. species: $Dtot = S$. Nevertheless, the reliability of this index is highly dependent on the sample size. In order to rule out bias related to sampling, this index can be completed by a rarefaction analysis (Krebs, 1989). This method compares the taxonomic diversity in samples of different sizes and estimates the number of expected taxa for any smaller sample size (Adrain, Westrop & Chatterton, 2000; Hammer & Harper, 2006; Balseiro, Xaisfeld & Buatois, 2010). Some samples have numerous individuals, while others only a few. In order to compare these samples, the rarefaction analysis uses a reduced amount of individuals but an identical number for all the samples in order to compare their biodiversity for the same number of individuals.

Diversity measures are usually standardized against the sample size. The *Shannon–Wiener index H* (Shannon & Weaver, 1949) takes into account the number of individuals as well as the number of taxa. This index considers the relative abundance of each taxon and gives weight to rare species. This index varies from 0 for a sample with only a single taxon to high values for samples with many taxa. $H = -\Sigma(n_i/n)\ ln(n_i/n)$, where n_i is number of individuals of taxon *i*. *Margalef's richness index MR* (Margalef, 1958) minimizes the effect of the sample size on estimating biodiversity. The higher the Margalef value, the greater the sample diversity. $MR = (S-1)/ln(n)$, where S = number of species and n = number of individuals.

Dominance D measures based on relative abundance have high values for assemblages with a few common elements, and low values where species are more or less evenly represented. *Dominance* $D = \Sigma(n_i/n)^2$. The index varies from 0 (taxa equally represented) to 1 (one dominant taxon).

Measures of equitability are usually the inverse of dominance. *Equitability* $J = (-\Sigma(n_i/n)\ ln(n_i/n))/lnS)$ considers the uniformity of the distribution of individuals among the taxa present. This index varies from

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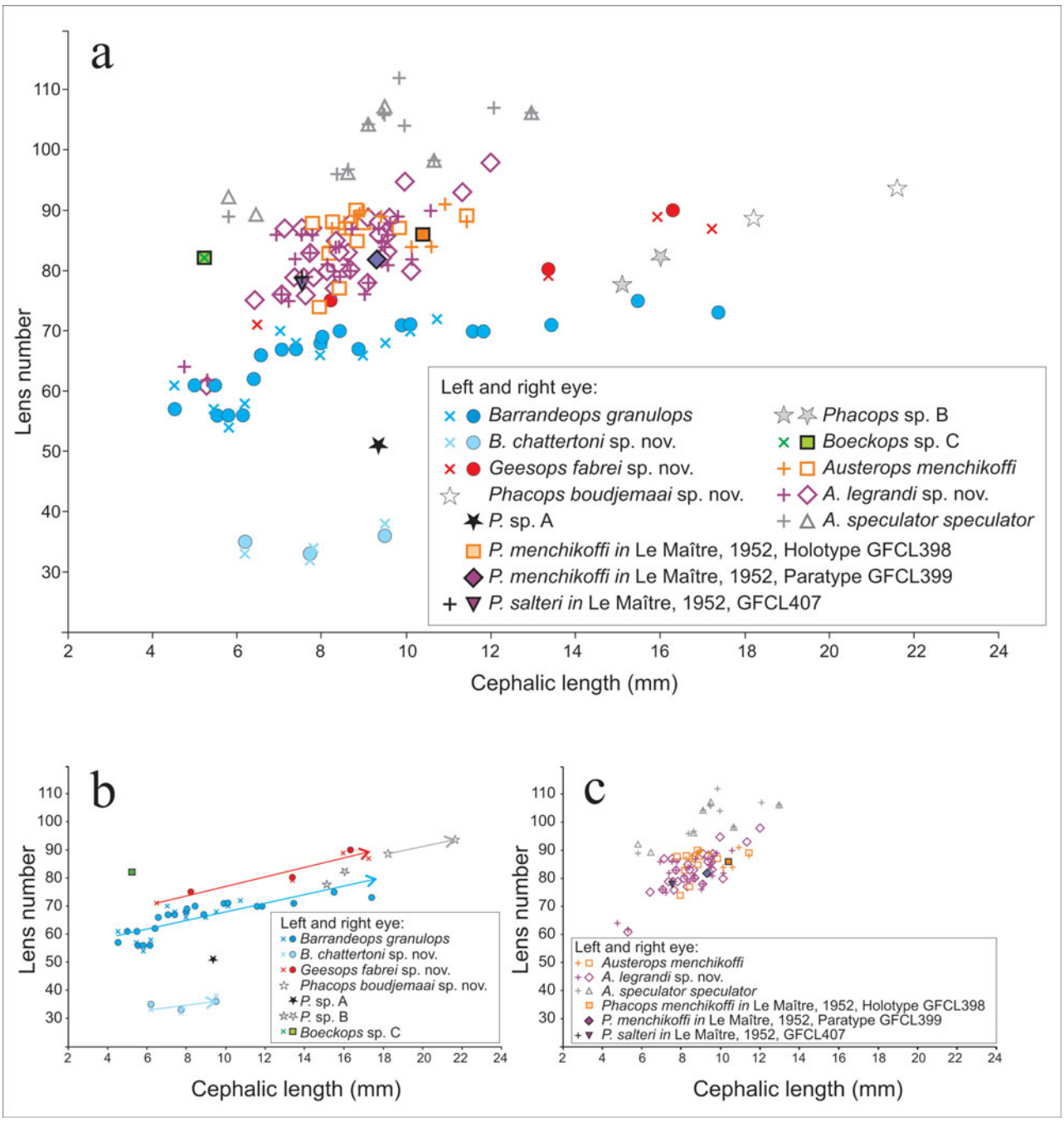

Figure 11. (Colour online) Bivariate plot using the number of lenses as a function of the cephalic length (in mm) in (a) 28 cephala of *Barrandeops granulops* (Chatterton et *al*. 2006), 4 cephala of *B. chattertoni* sp. nov., 2 cephala of *Phacops boudjemaai* sp. nov., 1 cephalon of *P*. sp. A, 2 cephala of *P*. sp. B, 6 cephala of *Geesops fabrei* sp. nov., 1 cephalon of *Boeckops* sp. C, 17 cephala of *Austerops menchikoffi* (Le Maître, 1952), 12 cephala of *Austerops speculator speculator* (Alberti, 1970), 41 cephala of *Austerops legrandi* sp. nov.; (b) for *Barrandeops*, *Phacops*, *Geesops* and *Boeckops* species; and (c) for *Austerops* species.

0 to 1, where taxa are fairly represented with a similar number of individuals. Analyses were done using PAST v2.17 software (Hammer, Harper & Ryan, 2001).

5.b. Results

5.b.1. Biodiversity

In the Saoura Valley, the palaeobiodiversity is not particularly high during Emsian time, characterized by only the two orders Phacopida and Proetida reported in this study (Fig. 12a, b). Only four families occur: Phacopidae and Acastidae (Phacopida), Proetidae and Aulacopleuridae (Proetida). For comparison, trilobite palaeobiodiversity from the Emsian at the global and regional scales (Saoura Valley) is given in Figure 12a. Trilobites seem to be poorly diverse macrofaunal constituents in the Emsian of the Saoura Valley, in contrast to their worldwide diversity (Fig. 12a). At a global scale, the Basal Pragian eustatic sea level fall (Chlupáč & Kukal, 1986) contributed to widening of shallow marine realms with carbonate sedimentation

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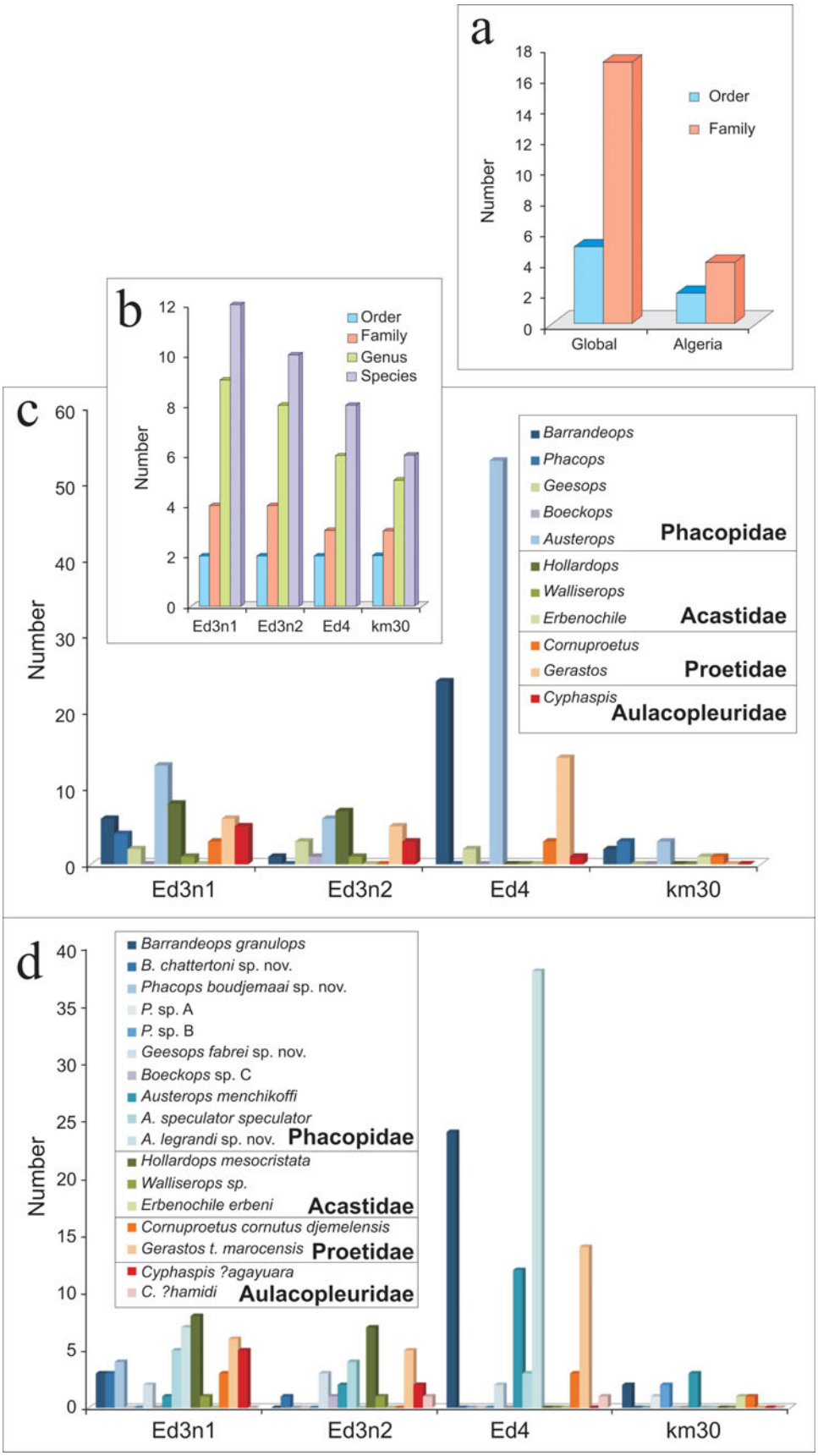

Figure 12. (Colour online) (a) Total occurrences of trilobite orders and families at the global scale (modified from Feist, 1991; Chlupáč, 1994) and in the Saoura Valley; (b) total occurrences of trilobite orders, families, genera and species in the four sampled Algerian levels; (c) number of individuals for each genus in each sampled Algerian level; (d) number of individuals for each species in each sampled Algerian level.

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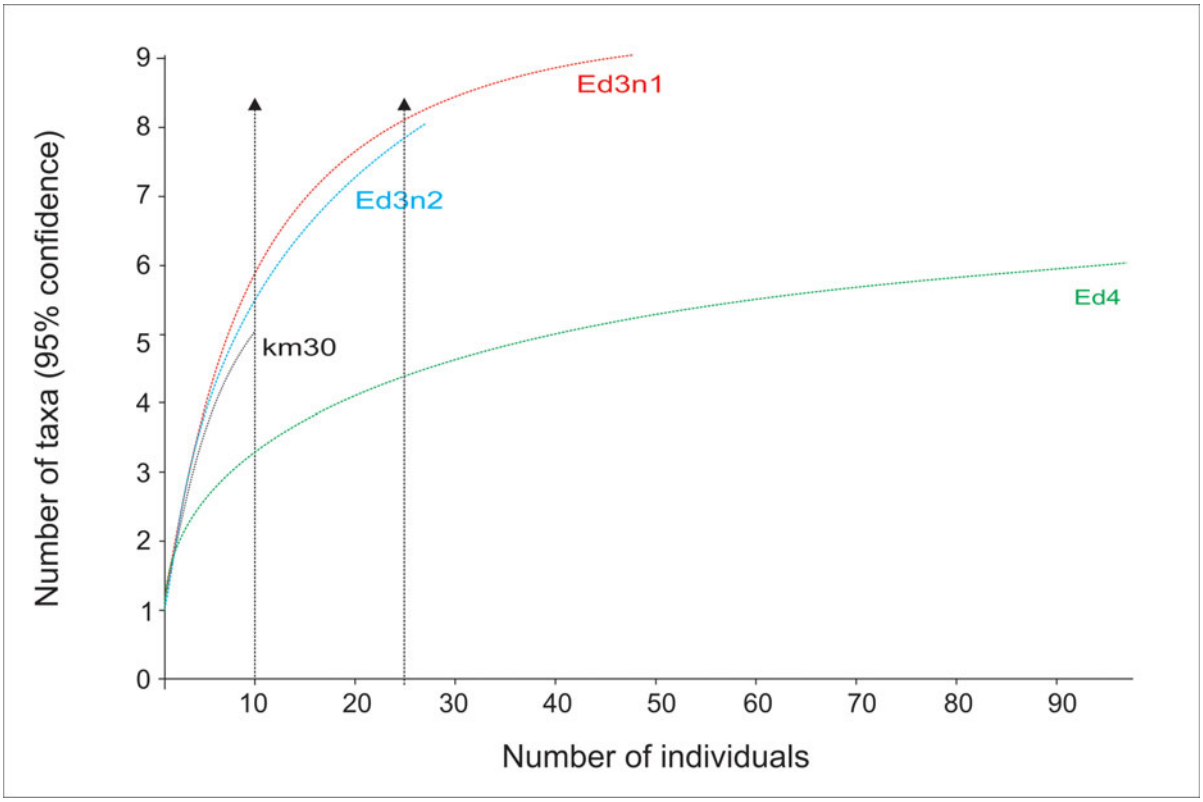

Figure 13. (Colour online) Rarefaction curves for each studied Algerian level. Ed3n1–Ed4: levels from the Erg el Djemel section; 'km 30': level from the Marhouma section. Arrows indicate the comparative individual number for levels of the same size (10 for Ed3n1 v. 'km 30'; 25 for Ed3n1 v. Ed4).

favourable for trilobites. This led, at least, to a preservation of the family diversity, which lasted with some changes until early Eifelian time.

On a regional scale, at the beginning of late Emsian time, the Devonian marine transgression become generalized to the Western Saharan platform from Tassili to the Tindouf Basin and from Taoudenni to Ben Zireg towards the north, which underlined a sedimentary change to calcareous deposition (Ouali Mehadji *et al*. 2004, 2011). Even though the so-called 'niveau coralligène' constitutes a major fossiliferous deposit, the faunas are dominated by some benthic organisms such as brachiopods and crinoids (Ouali Mehadji *et al*. 2004), and other benthic organisms such as trilobites seem to be less diverse.

Works related to Algerian trilobites are fewer compared to nearby localities of Morocco. Although the carbonate outcrops can contain well-preserved fossils, difficult access to outcrops makes palaeontological studies difficult and the geological investigations are of purely economic interest in Algeria. However, representatives of others families such as Scutelluidae have been previously reported in Saoura by Le Maître (1952) but not yet found during our investigations.

New samples in the Saoura Valley corroborate the occurrences of Phacopida and Proetida (Fig. 12c, d) as mentioned by Le Maître (1952). Phacopidae are represented by *Barrandeops*, *Phacops*, *Austerops*, *Geesops* and *Boeckops*, five genera encountered also in Morocco (Schraut, 2000*b*; Chatterton *et al*. 2006; McKellar & Chatterton, 2009); Acastidae are represented by *Hollardops*, *Walliserops* and *Erbenochile*, three genera encountered also in Morocco (Chatterton *et al*. 2006). *Hollardops* is among the most common Asteropyginae of North Africa during this time. Proetidae are represented by *Gerastos* and *Cornuproetus*, and Aulacoplauridae are represented by *Cyphaspis*, three genera encountered also in Morocco (Alberti, 1981; Chatterton *et al*. 2006).

In detail, genera and species seem to be better represented in the Erg el Djemel section, and especially in the Ed3n1 level compared to the Marhouma section (Fig. 12c, d). Nevertheless, the rarefaction analysis shows that the Marhouma section is under-sampled and seems to be similar to Ed3n1 and Ed3n2 (Fig. 13). Ed4 is the least diverse level (Fig. 13). Additional study and fieldwork are required to revise and complete the list of Early Devonian trilobites in the Saoura Valley.

In Ed3n1, the fauna is dominated by the members of Phacopidae, which is represented by four genera and seven species, representing half the total number of specimens collected (52 %, Fig. 14a, c). The other groups with a moderate relative abundance are Acastidae (19 %), Proetidae (19 %) and Aulacopleuridae (10 %). For comparison, in Ed4, the fauna is dominated by the members of Phacopidae, which is represented only by three genera and five species, representing 82 % of the total number of specimens (Fig. 14b, d). The other group with a moderate relative abundance is Proetidae (18 %). Aulacopleuridae are poorly

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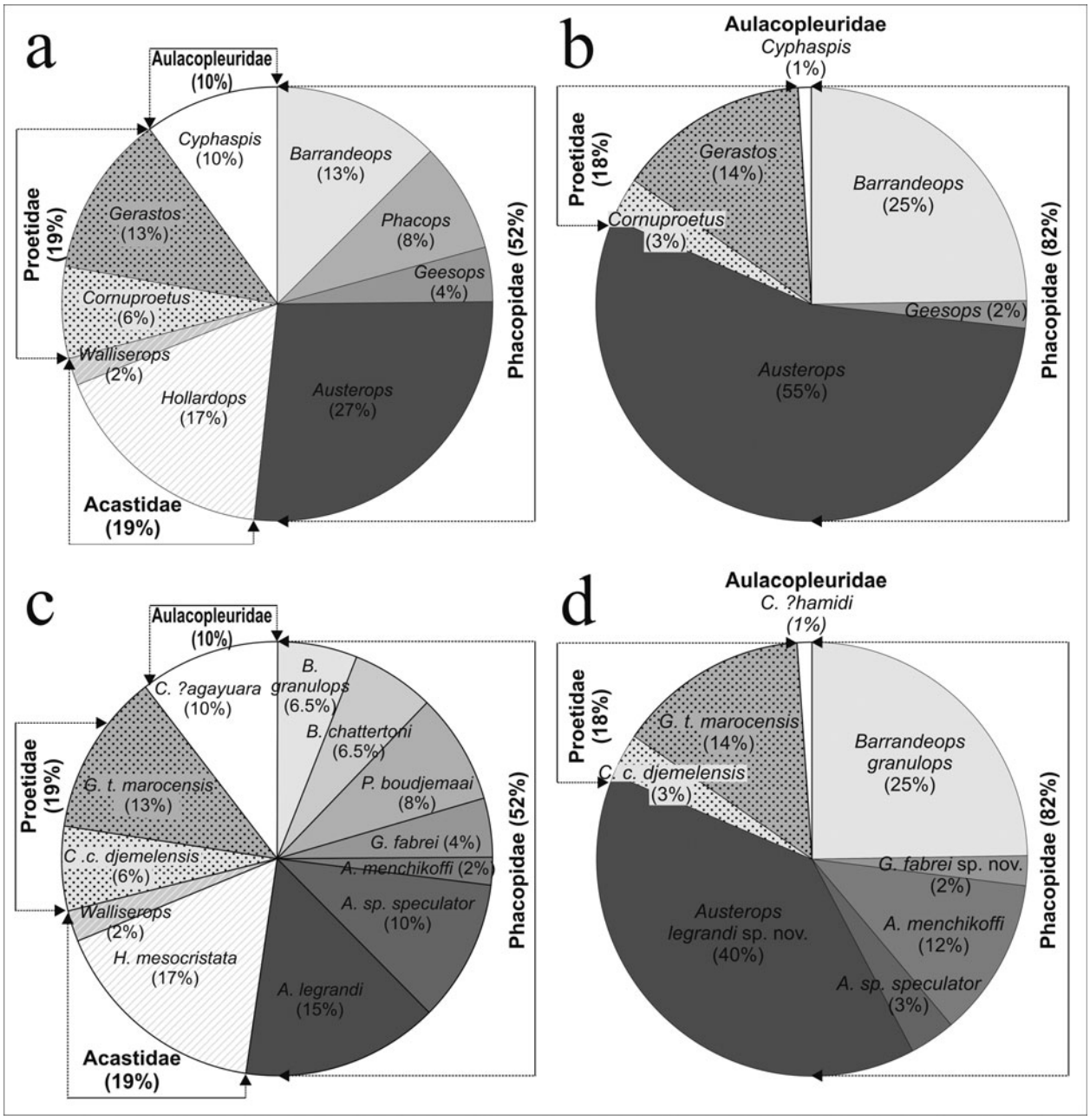

Figure 14. Relative abundance of trilobite genera in the (a) Ed3n1 and (b) Ed4 levels from the Erg el Djemel section from the upper Emsian. Relative abundance of trilobite species in the (c) Ed3n1 and (d) Ed4 levels from the Erg el Djemel section from the upper Emsian.

represented (1 %) and Acastidae are not represented in this level.

5.b.2. Ecological structure

Palaeoecological parameters have permitted recognition of two assemblage types from the Saoura Valley on the basis of the relative abundance and diversity of the trilobite macrofauna. Thus, these two specific assemblage types are defined as follows (Figs 14, 15): (1) assemblage type A from Ed4 characterized by an important dominance of *Austerops legrandi* sp. nov. (40 %) and *Barrandeops granulops* (25 %). Ed4 could represent a 'pioneer' community where one or two very abundant, opportunistic species occur; (2) assemblage type B characterized by a relatively moderate diversity and evenness: Ed3n1 with 12 species and 48 individuals, Ed3n2 with 10 species and 27 individuals, and 'km 30' with 6 species and 10 individuals. The rarefaction analysis (Fig. 13) confirms that independently to the effect of sampling, the biodiversity in Ed3n1 and Ed3n2 is relatively high and similar. With equivalent sampling, the biodiversity in 'km 30' is slightly less diverse than those of the two preceding levels. Moreover, these biotas are relatively well-equally represented by numerous species (6.5 to 17 %), although some species remain rarer than others (2 %). Low values of the dominance index show that there is no predominant taxon

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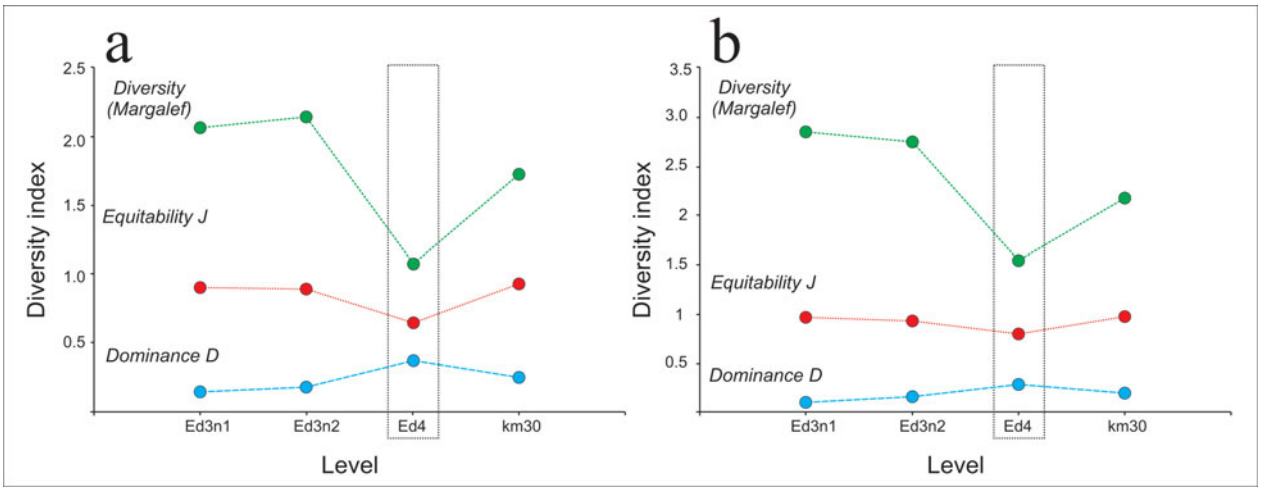

Figure 15. (Colour online) Comparison of three diversity indices in (a) the trilobite genera, and (b) the trilobite species in the four studied Algerian levels.

(Fig. 15). By contrast to Ed4, Ed3n1, Ed3n2 and 'km 30' could represent almost 'equilibrium' communities. In such 'equilibrium' communities, there is a relatively high diversity of taxa more or less equally present (Brenchley & Harper, 1998).

Additionally, these assemblages are either *in situ* or nearly *in situ* because they show no signs of long transportation. These assemblages could represent a former palaeocommunity where species are associated partly because they have similar physical tolerances of the environment and partly because they interact with one another through a food chain or through complementary niche requirements (Brenchley & Harper, 1998).

6. Conclusions

The new investigation of trilobites in the Lower Devonian of Algeria allows the following conclusions to be drawn. On the basis of our material, it has been possible to identify new oculated species among several already known in Morocco. At a generic and specific scale, the Algerian faunule may be regarded as diverse and cosmopolitan without marked original features and, as expected from its geographic position (past and present), is particularly closely related to Moroccan faunas (e.g. presence of *Barrandeops granulops*, *Hollardops mesocristata*, *Erbenochile erbeni*, *Gerastos tuberculatus marocensis*, etc.).

Next, the biometric study of Phacopidae appears complementary to the systematic study (descriptive) because it enabled us to visualize and quantify partially the variability of the identified individuals. It especially enabled us to show that the new species *Austerops legrandi* sp. nov. differs from *A. menchikoffi* in having different cephalic proportions.

New samples in the Saoura Valley corroborate the distribution patterns of Phacopida and Proetida as mentioned by Le Maître (1952). Lower Devonian strata are characterized by abundant Phacopidae. Additional fieldwork is required to revise, complete and find rare representatives of other families such as Scutelluidae previously reported by Le Maître (1952) in the Saoura Valley.

Finally, two types of assemblages were recognized from the upper Emsian: an Ed4-biota dominated by *Austerops legrandi* sp. nov. (40 %) and *Barrandeops granulops* (25 %) that represents a 'pioneer' community with opportunistic species; and Ed3-biotas characterized by a relatively moderate diversity and evenness that can represent almost 'equilibrium' communities. Changes in species richness and ecological diversity of trilobites are in relation to physical environmental gradients. Changes in climate and topography limit most species ranges, resulting in considerable spatial turnover in species richness and ecological structure.

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References

Adrain, J. M. 1997. Proetid trilobites from the Silurian (Wenlock–Ludlow) of the Cape Phillips Formation, Canadian Arctic Archipelago. *Palaeontographia Italica* **84**, 21–111.

Adrain, J. M. & Chatterton, B. D. E. 1996. The otarionine trilobite *Cyphaspis*, with new species from the Silurian of Northwestern Canada. *Journal of Paleontology* **70**, 100–10.

Adrain, J. M., Westrop, S. R. & Chatterton, B. D. E. 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology* **26**, 625–46.

Alberti, G. K. B. 1969. Trilobiten des jüngeren Siluriums sowie des Unter- und Mittel-Devons. I. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **520**, 1–692.

https://doi.org/10.1017/S0016756815000345 Published online by Cambridge University Press

ALBERTI, G. K. B. 1970. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. II. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **525**, 1–233.

ALBERTI, G. K. B. 1981. Trilobiten des jüngeren Siluriums sowie des Unter- und Mittel-Devons. III. *Senckenbergiana Lethaea* **62**, 1–75.

ALBERTI, G. K. B. 1983. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. IV. *Senckenbergiana Lethaea* **64**, 1–88.

ALIMEN, H., LE MAÎTRE, D., MENCHIKOFF, N., PETTER, G. & POUEYTO, A. 1952. *Les Chaînes d'Ougarta et la Saoura*. Actes du 19ème Congrès géologique International, Alger, lère série, Algérie 15, 1–114.

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.

ANGELIN, N. P. 1854. Palaeontologia Scandinavica. I. *Crustacea Formation is Transitionis* **2**, 21–92.

BADGLEY, C. 2003. The multiple scales of biodiversity. *Paleobiology* **29**, 11–3.

BALSEIRO, D., XAISFELD, B. G. & BUATOIS, L. A. 2010. Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology. *Lethaia* **44**, 58–75.

BARRANDE, J. 1846*a*. *Notice Préliminaire sur le Système Silurien et les Trilobites de Bohême*. Leipzig: Hirschfeld, vi + 97 pp.

BARRANDE, J. 1946*b*. *Nouveaux Trilobites. Supplément à la Notice Préliminaire sur le Système Silurien et les Trilobites de Bohême*. Prague: Calve, iv + 40 pp.

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

BIGNON, A. & CRÔNIER, C. 2014. The systematics and phylogeny of the Devonian subfamily Asteropyginae (Trilobita: Phacopida). *Journal of Systematic Palaeontology* **12**, 637–68.

BOUMENDJEL, K., MORZADEC, P., PARIS, F., PLUSQUELLEC, Y., BRICE, D., COPPER, P., GOURVENNEC, R., JAHNK, H., LARDEUX, H., LE MENN, J., MELOU, M. & RACHEBOEUF, P. R. 1997. Les faunes du Dévonien de l'Ougarta (Sahara occidental, Algérie). *Annales de la Société Géologique Nord* **5** (2ème série), 89–116.

BRENCHLEY, P. J. & HARPER, D. A. T. 1998. *Palaeoecology: Ecosystems, Environments and Evolution*. London: Chapman & Hall.

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

BUDIL, P., HÖRBINGER, F. & MENCL, R. 2009. Lower Devonian dalmanitid trilobites of the Prague Basin (Czech Republic). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **99**, 61–100.

BURMEISTER, P. 1843. *Die Organisation der Trilobiten aus Ihren Lebendigen Verwandten Entwickelt. Nebst Einer Systematischen Übersicht aller Zeither Beschriebenen Arten*. Berlin: Reimer, 1–147.

BURTON, C. J. & ELDREDGE, N. 1974. Two new subspecies of *Phacops rana* [Trilobita] from the Middle Devonian of North-West Africa. *Palaeontology* **17**, 349–63.

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

CHATTERTON, B. D. E., FORTEY, R. A., BRETT, K., GIBB, S. & KELLAR, R. M. 2006. Trilobites from the upper Lower to Middle Devonian Timrhanrhart Formation, Jbel Gara el Zguilma, southern Morocco. *Palaeontographica Canadiana* **24**, 1–177.

CHATTERTON, B. D. E. & GIBB, S. 2010. Latest early to early Middle Devonian Trilobite from the *Erbenochile* bed, Jbel Issoumour, southeastern Morocco. *Journal of Paleontology* **84**, 1188–205.

CHLUPÁČ, I. 1972. New Silurian and Lower Devonian phacopid trilobites from the Barrandian area (Czechoslovakia). *Časopis pro Mineralogii a Geologii* **17**, 395–401.

CHLUPÁČ, I. 1977. The phacopid trilobites of the Silurian and Devonian of Czechoslovakia. *Vydal Ústředni ústav Geologický* **43**, 1–172.

CHLUPÁČ, I. 1994. Devonian trilobites – evolution and events. *Geobios* **27**, 487–505.

CHLUPÁČ, I. & KUKAL, Z. 1986. Reflection of possible global Devonian significance. In *Devonian of the World* (eds N. J. Mc Millan, A. F. Embry & D. J. Glass), pp. 481–97. Proceedings of the Second International Symposium of the Devonian System, Calgary. Canadian Society of Petroleum Geologists no. 14.

CLARKSON, E. N. K. 1966. Schizochroal eyes and vision in some Phacopid trilobites. *Palaeontology* **9**, 464–87.

CONRAD, T. A. 1841. Description of new genera and species of organic remains, Crustacea. In *On the Paleontology of the State of New York*, pp. 25–7. New York State Geological Survey, Fifth Annual Report.

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. & 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.

DODD, J. R. & STANTON JR, R. J. 1990. *Paleoecology. Concepts and Applications*. 2nd ed. New York: John Wiley & Sons, xvii + 502 pp.

DONZEAU, M. 1983. Tectonique des Monts d'Ougarta. In *Afrique de l'Ouest, Introduction Géologique et Termes Stratigraphiques* (ed. J. Fabre), pp. 118–20. Lexique Stratigraphique International, nelle série 1. Oxford: PergamonPress.

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.

FABRE, J. 2005. *Géologie du Sahara Occidental et Central*. Tervuren African Geosciences Collection vol. 108. Musée Royal de l'Afrique Centrale, 572 pp.

FEIST, R. 1991. The late Devonian trilobite crises. *Historical Biology* **5**, 197–214.

FLAMAND, G. B. M. 1911. *Recherches géologiques et géographiques sur le Haut Pays de l'Oranie et sur le Sahara (Algérie et territoires du Sud)*. Thèses présentées à la faculté des sciences de l'université de Lyon, France. A. Ray & cie, 797pp. Published thesis.

FORTEY, R. A. & CHATTERTON, B. D. E. 2003. A Devonian trilobite with an eyeshade. *Science* **301**, 1969.

FORTEY, R. A. & OWENS, R. M. 1975. Proetida – a new order of trilobites. *Fossils and Strata* **4**, 227–39.

GAUTIER, E. F. 1902. Sur les terrains paléozoïques de l'Oued Saoura et Gourara. *Comptes Rendus de l'Académie des Sciences* **135**, 1071–3.

GIBB, S. & CHATTERTON, B. D. E. 2010. *Gerastos* (Order Proetida; Class Trilobita) from the Lower to Middle Devonian of the southern Moroccan Anti-Atlas Region. *Palaeontographica Canadiana* **30**, 1–87.

GIGOUT, M. 1951. *Etudes Géologiques sur la Méséta Marocaine Occidentale (Arriére-pays de Casablanca, Mazagan et Safi*). Division des Mines et de la Géologie, Service Géologique, Notes et Mémoires 86, Atlas, 18 figs, 10 maps.

GIGOUT, M. 1955. Recherches géologiques à Mechrâ Benâbbou. *Travaux de l'Institut scientifique chérifien, série Géologie et Géographie Physique* **3**, 1–67.

GIGOUT, M., DESTOMBES, J. & FERRÉ, M. 1965. Notice explicative de la carte geologique (1: 200 000) de la Méseta entre Mechra ben Abbou et Safi (Doukkala et massif des Rehamna). Notice explicative. *Notes et Mémoires du Service géologique du Maroc* **84**, 1–48.

GÖDDERTZ, B. 1987. Devonische Goniatitenaus SW-Algerien und ihrestratigraphishe Einordnung in die Conodoten – Abfolge. *Palaeontographica Abteilung A* **197**, 127–220.

GOLDFUSS, A. 1843. Systematische übersichte der Trilobiten und Beschreibung einiger neue Arten derselben. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefaktenkunde* 537–67.

HAAS, W. 1968. Trilobiten aus dem Silur und Devon von Bithynien (NW-Türkei). *Palaeontographica Abteilung A* **130**, 60–207.

HALL, J. 1888. (Assisted by J. M. Clarke). *Trilobites and Other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill Groups. Palaeontology 7*. Albany, New York: Geological Survey of the State of New York, 198 pp.

HAMMER, Ø. & HARPER, D. A. T. 2006. *Paleontological Data Analysis*. Malden: Wiley-Blackwell, 368 pp.

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.

HARPER, D. A. T. 1999. *Numerical Palaeobiology*. New York: John Wiley & Sons.

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

HORNÝ, R. & BASTL, F. 1970. *Type Specimens of Fossils in the Natural Museum Prague. Vol. 1. Trilobita*. Prague: Prague Museum of Natural History, 354 pp.

JAHNKE, H. 1969. *Phacops zinkeni* F. A. Roemer 1843 – ein Beispiel für eine ontogenetische Entwicklung bei Phacopiden (Trilobitae, Unterdevon). *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen* **133**, 309–24.

JANSEN, U., BECKER, G., PLODOWSKI, G., SCHINDLER, E., VOGEL, O. & WEDDIGE, K. 2004. The Emsian to Eifelian near Foum Zguid (NE Dra Valley, Morocco). In *Devonian of the Western Anti Atlas: Correlations and Events* (ed. El Hassani), pp. 19–28. Documents de L'Institut Scientifique, Rabat, 19.

KIELAN, Z. 1954. Les trilobites mésodévoniens des Monts de Sainte Croix. *Palaeontologica Polonica* **6**, 1–50.

KOZLOWSKI, R. 1923. Faune Dévonienne de Bolivie. *Annales de Paléontologie* **12**, 1–112.

KREBS, C. J. 1989. *Ecological Methodology*. New York: Harper & Row.

LEGRAND, P. 1967. Nouvelles connaissances acquises sur la limite des systèmes Silurien et Dévonien au Sahara algérien. *Bulletin du Bureau de Recherches Géologiques et Minières* **33**, 119–37.

LE MAÎTRE, D. 1950. Nouveaux éléments communs avec l'Amérique dans la faune dévonienne de l'Afrique du Nord. *Compte Rendu Sommaire des Séances de la Société géologique de France* **14**, 253–6.

LE MAÎTRE, D. 1952. La faune du Dévonien inférieur et moyen de la Saoura et des abords de l'Erg el Djemel (Sud oranais). *Mémoire de la Carte géologique de l'Algérie* **12**, 1–170.

LIEBERMAN, B. S. & KLOC, G. J. 1997. Evolutionary and biogeographic patterns in the Asteropyginae (Trilobita, Devonian) Delo, 1935. *Bulletin of the American Museum of Natural History* **232**, 1–127.

LÜTKE, F. 1990. Contributions to a phylogenetical classification of the subfamily Proetinae Salter, 1864 (Trilobita). *Senckenbergiana Lethaea* **71**, 1–83.

MARGALEF, R. 1958. Information theory in ecology. *General Systematics* **3**, 36–71.

MATTHEWS, S. C. 1973. Note on open nomenclature and on synonymy lists. *Palaeontology* **16**, 713–9.

MCKELLAR, R. & CHATTERTON, B. D. E. 2009. Early and Middle Devonian Phacopidae (Trilobita) of southern Morocco. *Palaeontographica Canadiana* **28**, 1–110.

MENCHIKOFF, N. 1930. Recherches géologiques et morphologiques dans le Nord du Sahara occidental. *Revue de Géographie physique et de Géologie dynamique* **3**, 103–242.

MENCHIKOFF, N. 1932. Sur le Dévonien à Céphalopodes de l'Oued Saoura et les chaînes d'Ougarta (Sahara oranais). *Comptes Rendus de l'Académie des Sciences, Paris* **194**, 1966–8.

MENCHIKOFF, N. 1933. La série primaire de la Saoura et des chaînes d'Ougarta. *Bulletin du Service Géologique d'Algérie* **2** (2ème série), 108–24.

MENCHIKOFF, N. 1936. Etudes géologiques sur les confins algéro-marocains du Sud. *Bulletin de la Société géologique de France* **5**, 132.

MORZADEC, P. 1969. Le Dévonien de la rive nord de la rivière de Faou (Finistère). Etude stratigraphie, étude de trilobites. *Bulletin de la Société minéralogique et géologique de Bretagne* **1968**, 1–58.

MORZADEC, P. 1995. *Erbenochile erbeni* (Alberti), Trilobite du Dévonien inférieur de l'Ougarta (Algérie). *Neues Jahrbuch für geologie und Paläontologie Monatschefte* **10**, 614–21.

MORZADEC, P. 1997. Les Trilobites Asteropyginae du Dévonien de l'Ougarta (Algérie). *Palaeontographica Abteilung A* **244**, 143–58.

MORZADEC, P. 2001. Les Trilobites Asteropyginae du Dévonien de l'Anti Atlas (Maroc). *Palaeontographica Abteilung A* **262**, 53–85.

OUALI MEHADJI, A., ATIF, K. F. T., BOUTERFA, B., NICOLLIN, J.-P. & BESSEGHIER, F. Z. 2011. Environnements sédimentaires de la Saoura-Ougarta (Sahara Nord-Ouest, Algérie) au Dévonien inférieur (Lochkovien supérieur *pro parte*-Emsien). *Géodiversitas* **33**, 553–80.

OUALI MEHADJI, A., ELMI, S., RACHEBOEUF, P. & MEKAHLI, L. 2004. Caractéristiques et signification d'un niveau coquiller majeur à brachiopodes, marqueur événementiel dans l'évolution dévonienne de la Saoura (Sahara

du Nord-Ouest, Algérie). *Comptes Rendus Géosciences* **336**, 1283–92.

OWENS, R. M. 1973. British Ordovician and Early Silurian Proetida (Trilobita) from North-Western and Central Europe. *Palaeontology* **47**, 557–78.

PARIS, F., BOUMENDJEL, K., MORZADEC, P. & PLUSQUELLEC, Y. 1997. Synthèse chronostratigraphique du Dévonien de l'Ougarta (Sahara occidental, Algérie). *Annales de la Société géologique du Nord* **5** (2ème Série), 117–21.

PLUSQUELLEC, Y. 1997. Coraux Tabulata et Rugosa. *Annales de la Société géologique du Nord* **5** (2ème Série), 95–9.

PŘIBYL, A. 1946. Přispěvek k poznání českých proetidů (Trilobitae). *Rozpravy České Akademie Věd a Uměni* **55**, 1–37.

PŘIBYL, A. 1953. Seznam českých trilobitových rodů. *Knihovna Ústředniho Ústavu Geologického* **25**, 1–80.

RICHTER, R. & RICHTER, E. 1919. Der Proetiden-Zweig *Astycoryphe – Tropidocoryphe – Pteroparia*. *Senckengerbiana* **1**, 1–17, 25–51.

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

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

ROEMER, A. 1843. *Die Versteinerungen des Harzgebirges*. Hannover: Hahn.

ROEMER, F. A. 1850. Beiträge zur geologischen Kenntniss des nordwestlichen Harzgebirges. I. *Palaeontographica* **3**, 1–67, I–XII.

ROHLF, F. J. 2013. *The tpsDig Program, ver. 2.17*. New York: Stony Brook University.

ROUAULT, M. 1851. Mémoire sur les terrains paléozoiques des environs de Rennes. *Bulletin de la Société géologique de France* **8**, 358–99.

SALTER, J. W. 1864. *A Monograph of the British Trilobites from the Cambrian, Silurian and Devonian Formations*. London: Palaeontographical Society Monographs.

SCHRAUT, G. 2000*a*. Trilobiten aus de Unter-Devon des südöstlichen Anti-Atlas, Süd-Marokko. *Senckenbergiana Lethaea* **79**, 361–433.

SCHRAUT, G. 2000*b*. Eine neue Unterart von *Phacops (Phacops) sparsinodosus* Struve 1970 aus dem MittelDevon von Marokko. *Senckenbergiana Lethaea* **80**, 525–35.

SHANNON, C. E. & WEAVER, W. 1949. *The Mathematical Theory of Communication*. Urbana, Illinois: University of Illinois Press.

SHELDON, P. R. 1988. Trilobite size-frequency distributions, recognition of instars and phyletic size changes. *Lethaia* **21**, 293–306.

ŠNAJDR, M. 1980. Bohemian Silurian and Devonian Proetidae (Trilobita). *Rozpravy Ústředního ústavu geologického* **45**, 1–324.

ŠNAJDR, M. 1985. Bohemian representatives of the trilobite subfamily Odontochilinae subf. nov. *Vestnik Ustředního ústavu geologického* **59**, 65–169.

STEININGER, J. 1831. Bemerkungen über die Verseinerungen, welche in dem ÜbergangsKalkgebirge der Eifel gefunden weren. *Beilage zum Gymnasial-Programmschrift zu Trier, Blattau*, 1–46.

STRUVE, W. 1970. Beiträge zur Kenntnis der Phacopina (Trilobita). 7. *Phacops*-Arten aus dem rheinischen Devon. 1. *Senckenbergiana Lethaea* **51**, 133–89.

STRUVE, W. 1982. [Beiträge zur kenntnis der Phacopina (Trilobita), (10): Neue Untersuchungen über *Geesops* (Phacopinae; Unter- und Mittel-Devon)]. *Senckenbergiana Lethaea* **63**, 473–95.

VOGDES, A. W. 1890. A bibliography of Paleozoic Crustacea from 1698 to 1889, including a list of North American species and a systematic arrangement of genera. *Bulletin of the United States Geological Survey* **63**, 1–177.

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

WEDEKIND, R. 1914. Palaeontologishe Beiträge zur Geologie des Kellerwaldes. *Abhandlungen der Koenglich Preussischen Geologischen Landesanstalt* **69**, 1–84.