Trilobites from the latest Frasnian Kellwasser Crisis in North Africa (Mrirt, central Moroccan Meseta)

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Latest Frasnian trilobites are recorded for the first time from North Africa. They occur in oxygenated limestones between the Lower and Upper Kellwasser horizons at Bou Ounabdou near Mrirt, central Moroccan Meseta. The faunas are very close to the contemporaneous associations in European sections both by their taxonomic composition and by patterns of evolutionary behavior towards eye reduction. Two new taxa are described: *Gondwanaspis mrirtensis* gen. et sp. nov., which is the last known representative of the Odontopleuridae before its extinction at the base of the Upper Kellwasser horizon, and *Pteroparia ziegleri maroccanica* subsp. nov., a geographical variant of the nominal subspecies from Sessacker in the Rhenish Slate Mountains.

Key words: Trilobita, Frasnian, Morocco, Kellwasser crisis, biogeography.

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Introduction

Three out of five Late Devonian trilobite orders did not survive the end-Frasnian Kellwasser Event (Feist and Schindler 1994). The last representatives of six low-diversity families (i.e., Harpetidae, Odontopleuridae, Styginidae, Aulacopleuridae, Tropidocoryphidae and Dalmanitidae) reached the base of the Upper Kellwasser horizon, or its time-equivalent, where they became extinct. Within the surviving Proetidae two subfamilies, the Cornuproetinae and Dechenellinae, were already wiped out below the Lower Kellwasser pulse. Styginids disappeared at this level in Europe but persisted in Australia until the top of the Frasnian. Among the Phacopidae that survived into the Famennian, members of the *Acuticryphops* lineage became extinct at the base of the Upper Kellwasser level (Feist 1995; Crônier and Feist 2000). Most of the latest Frasnian trilobites, especially those living in offshore communities, exhibit paedomorphic trends towards eye reduction and occasionally total blindness. This is the case in outer shelf sequences where the oxygen depleted Kellwasser deposits are developed. End-Frasnian offshore trilobite communities have hitherto been studied only in European sections (Feist and Schindler 1994). First recoveries of trilobites from the latest Frasnian in North Africa permit a reconsideration of the diversity patterns and geographical dispersal of associations that were affected by the end-Frasnian Kellwasser crisis.

Location and age of the faunas

The new faunas come from the Mrirt area, central Moroccan Meseta (Fig. 1A), where on the southwestern slope of the Al Gara Hill, Late Devonian cephalopod limestones are exposed in olistolithic slabs contained in Viséan shales (Walliser et al. 1999; Becker and House 1999).

The material was collected from Bou Ounabdou (Fig. 1B, "1" on Fig. 1C, "section II" in Walliser et al. 1999: fig. 42) which is precisely dated by conodont biostratigraphy (Lazreq 1992, 1999). The section was described in detail by Becker and House (1999). Another sample comes from locality "2" (Fig. 1C) situated about 500 m along strike to the SE of "1" (section IV in Walliser et al. 1999: fig. 42).

In this area the latest Frasnian succession is characterized by the occurrence of two dark-grey hypoxic limestone levels of Kellwasser-Kalk facies, the Lower (LKW) and Upper (UKW) Kellwasser levels (Lazreq 1992). They are separated by 80 cm of intervening grey-beige oxic calcilutites assigned to the Late *Palmatolepis rhenana* Zone by Lazreq (1992, 1999). The trilobites were recovered in section "1" from two levels: the older is situated 13 cm above the LKW, the younger 18 cm below the base of the UKW (horizons "1A" and "1B" in Fig. 1B). The sample collected in section "2" corresponds to the younger fauna of section "1". Associated conodonts recovered from matrix material of the trilobite-bearing rocks were determined by Catherine Girard and Gilbert Klapper as follows: the lower trilobite horizon yields *Palmatolepis hassi* sensu stricto and *Pa. bogartensis* which indicates the lower part of MN Zone 13 (for correlation of conodont zonations, see Klapper and Becker 1999); the upper trilobite bearing horizon yields *Pa. rhenana*, *Pa. boogaardi*, abundant *Pa. bogartensis*, *Ancyrognathus asymmetricus* and *Polygnathus webbi* (but neither *Pa. linguiformis* nor *An. ubiquitus* were found), indicating correlation with the upper part of MN Zone 13.

Trilobite debris of exclusively disarticulated exuviae is

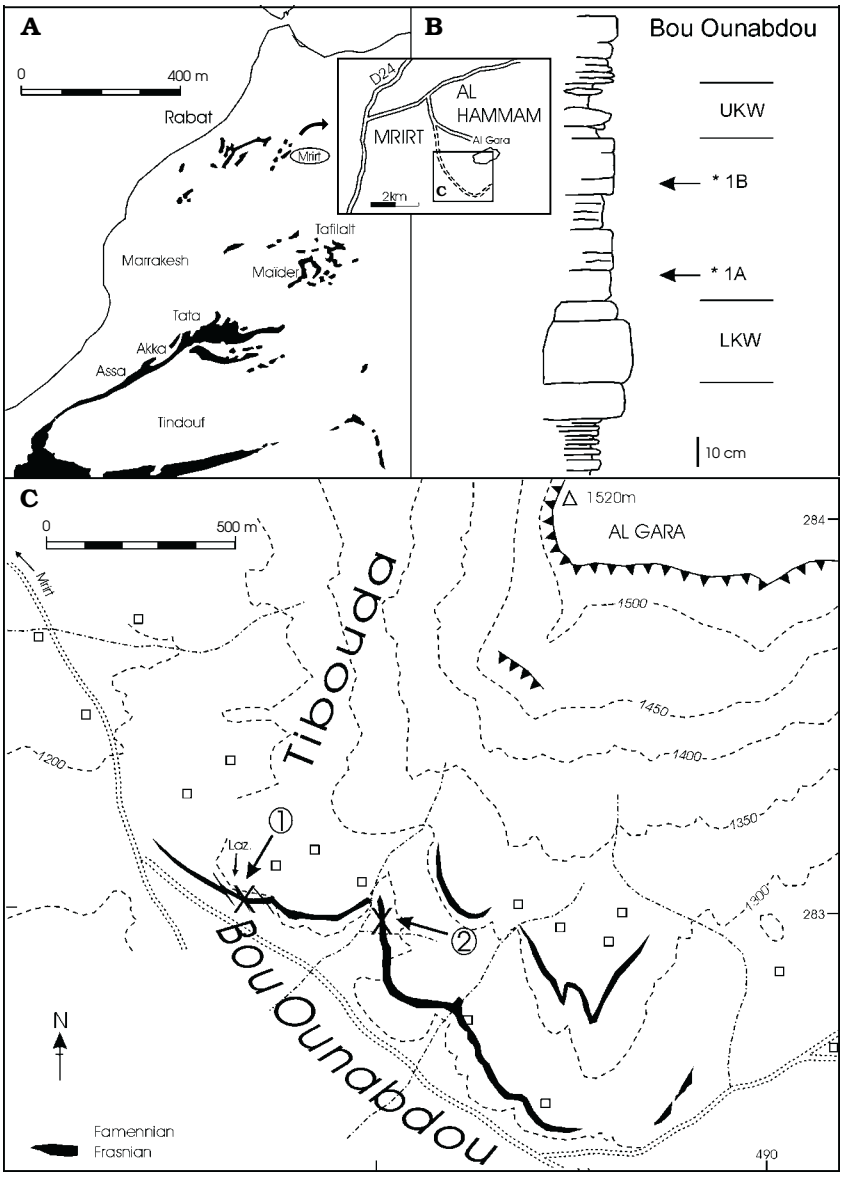


Fig. 1. **A**. Devonian outcrops in Morocco with location of the Mrirt area in the central Meseta east of Rabat. **B**. Measured section "1" showing the Lower (LKW) and Upper (UKW) Kellwasser horizons and the intervening limestone beds. The levels of the lower and upper trilobite associations are marked with a star. **C**. Location of the studied sections "1" and "2" at Bou Ounabdou, 4 km to the SE of Mrirt township (after Becker and House 1999 and Walliser et al. 1999). Section "1" is the same as Bou Ounabdou, section II of Lasreq (1992).

concentrated in thin layers within the biomicritic limestone, along with mass occurrences of conodonts, homoctenid tentaculites and fewer manticoceratid goniatites, smooth brachiopods and crinoid ossicles. The association of reduced-eyed and blind trilobites with predominantly necto-benthonic organisms characterizes the well oxygenated cephalopod realm of a moderately deep outer platform environment. Accumulations of shelly debris that do not exhibit any evidence of corrosion and size sorting might result from intermittently slow sedimentation rates rather than from physical transport.

Systematic paleontology

The described and figured materials are housed in the collections of the Palaeontological Department of the University Montpellier 2 abbreviated as UM2-RF. Abbreviations used are as follows: sag. (sagittal, in the median line); exsag. (parallel to the median line); tr. (transverse, at right angles to median line); L1, L2, L3: lateral glabellar lobes from rear to front; S1, S2, S3: lateral glabellar furrows from rear to front.

Family Odontopleuridae Burmeister, 1843
Subfamily Acidaspidinae Salter, 1864
Genus *Gondwanaspis* gen. nov.

Derivation of name: Gondwana, after the paleogeographic occurrence of the new taxon; aspis, heavily armed (with spines).

Type species: *Gondwanaspis mrirtensis* sp. nov.

Assigned species: *G. mrirtensis* sp. nov., ?*Ceratocephala* (*Leonaspis*) *harborti* Richter and Richter, 1926.

Diagnosis.—Cephalon with glabellar lobes not inflated, rectangular central lobe; straight ocular ridges; no sutural ridges; eye shifted in midst of genal field; no occipital spines; straight, outward directed librigenal spine, exceeding length of glabella; spines along the entire anterior and antero-lateral margins.

Remarks.—*Gondwanaspis* gen. nov. from the latest Frasnian beds immediately preceding the Upper Kellwasser level both at Mrirt and Coumiac (Montagne Noire), is the youngest known representative of the Odontopleuridae. Together with a new and so far undescribed species from the McWhae Ridge area, Canning Basin, Western Australia, its occurrence seems to be restricted to terrains of the Gondwana margin. The poorly known mid-Frasnian *Ceratocephala* (*Leonaspis*) *harborti* Richter and Richter, 1926, that was assigned by Bruton (1968) to the Silurian genus *Dudleyaspis*, shares with the new genus the rectangular central glabellar lobe and the absence of sutural ridges. However, it is distinct in its swollen lateral glabellar lobes where the anterior third pair is well represented. The latter is inconspicuous or lacking in *Gondwanaspis*. It is not known whether *C*. (*L*.) *harborti* carries spines on the cranidial anterior border, which is an important feature of the new genus. After the discovery of complete material including pygidia, the possible inclusion of *C*. (*L*.) *harborti* in the new genus might be reconsidered, the diagnosis being emended to accommodate this inclusion.

Comparisons.—The new genus shares only a few traits with previously known late Devonian representatives of the Odontopleuridae, such as *Leonaspis*, *Radiaspis*, and *Koneprusia*, which exhibit back-curved ocular ridges and genal spines, as well as eyes positioned near to the posterior margin. In this regard and despite the considerable difference in age, it is more closely related to the Silurian *Dudleyaspis* Prantl and Přibyl, 1949 and in particular to *D. uncifera* from Gotland (Ramsköld 1984). It differs from *Dudleyaspis* in having a rectangular central glabellar lobe, the lateral lobes not swollen, the anteriormost of which are inconspicuous, in absence of sutural ridges, in having straight border spines that are also present on the central portion of the anterior border, and in the considerably advanced, not back-curved genal spine. *Dudleyaspis* was included by Ramsköld and Chatterton (1991) in the subfamily Acidaspidinae Salter, 1864. Though the origin of the new taxon is somewhat enigmatic, as no direct Devonian ancestors are known so far, it is tentatively assigned here to the Acidaspidinae, because of the close resemblance to *Dudleyaspis*. This attribution will need to be reconsidered after the discovery of the so far unknown thoracic and pygidial features.

Gondwanaspis mrirtensis sp. nov.

Fig. 2A, B, E, G, H.

"*Dudleyaspis*" aff. *harborti* (Richter, 1909); Feist and Schindler 1994: 211, pl. 4: 1–2.

Derivation of name: After the town Mrirt in the vicinity of the type locality.

Holotype: Cephalon (UM2-RF 170), Fig. 2A, B, G.

Type locality: Section 2 at Bou Ounabdou (section IV in El Hassani and Tahiri 1999), north of track, S of Al Gara hill (see location map Fig. 1C).

Type horizon: Compact grey limestone bed immediately below the dark grey Upper Kellwasser beds.

Age: According to the conodont association (identification of C. Girard): Late *Palmatolepis rhenana* Zone, MN Zone 13.

Diagnosis.—As for the genus.

Material.—Figured specimens: 3 cephala (UM2-RF 170–172); additional material from type locality: 5 fragmentary cephala (UM2-RF 173–177), 1 fragmentary thoracic segment (UM2-RF 178).

Description.—Cephalon very large and short, nearly three times wider than long (without spines), of subrectangular outline, flattened centrally, gently down-vaulted abaxially. Large inflated anterior border depressed in front of glabella, sloping to border furrow. Central lobe of glabella parallel-sided, protruding anteriorly, truncated in front, steeply down-curved to broad prefrontal depression, gently vaulted transversely, horizontal on top (sag.). Two pairs of poorly defined, not swollen lateral lobes, third pair inconspicuous or marked as minute swellings. L1 weekly convex, trapezoidal; L2 circular in outline, well separated from central lobe by longitudinal grooves. S1 a broad, shallow depression. Dorsal furrow ill defined, very shallow, sigmoid. Occipital lobe gently convex, medially separated from the glabella by a broad shallow occipital furrow. Posterior margin of the occipital lobe smooth, straight transversely. Lateral occipital lobes depressed, protruding forward, delimited in front and against the medial occipital furrow by sharply incised semi-circular groove that merges abaxially behind L1. Posterior part of the lateral occipital lobes incompletely separated from the medial lobe. Eye ridges rather long and straight, diverging from one another at an angle of 125°, closely adjacent to L2 adaxially, slightly broadening distally, running distally into hook-like palpebral lobes. Inside the eye ridge the large triangular fixed cheek is swollen and of the same height as lateral glabellar lobes. Behind the eye, it slopes gently downward to the posterior furrow. Anterior branch of suture curves obliquely inward and crosses anterior margin opposite to dorsal furrow (exsag.). No sutural ridges are developed. Eye relatively high, situated at mid-point between anterior and posterior margins (exsag.). Posterior suture without sutural ridge, runs parallel to posterior margin. Posterior border furrow and border ridge straight, the latter abruptly enlarged at its distal end.

Anterior central margin carries six horizontally directed spines; the antero-lateral margins of the broad rolled lateral borders are provided each with 12 slender, long spines that are straight and not down-curved. Main librigenal spine is straight and outwardly directed in the prolongation of the posterior border furrow, making an angle of 110° with the lateral librigenal margin. It is longer than the length of the glabella.

Sculpture of exoskeleton consists of closely-spaced, medium-sized granulation with a few sparse larger nodules.

Remarks.—The incompletely preserved cephalons from Coumiac identified by Feist and Schindler (1994) as "*Dudleyaspis*" aff. *harborti* share with the new species all diagnostic features, in particular the shape and disposition of the eye ridges, the low, uninflated lateral glabellar lobes and the large rolled border provided with spines. The species is considered here as belonging to *Gondwanaspis mrirtensis* sp. nov. Small differences in the shape of the coarser granulation of the exoskeleton might be of subspecific significance.

Family Harpetidae Hawle and Corda, 1847
Subfamily Harpetinae Hawle and Corda, 1847
Genus *Harpes* Goldfuss, 1839
"*Harpes*" *neogracilis* Richter and Richter, 1924

Fig. 2K–N.

"*Harpes*" *neogracilis* Richter and Richter, 1924; Feist and Schindler 1994: 211, pl. 4: 3–8 (see list of older synonymies therein).

Material.—Figured specimens: 2 cephala from section "2", upper trilobite association (UM2-RF 219–220); additional material from same locality: 13 cephala (UM2-RF 221–233); from section "1", upper trilobite association: 1 cephalon (UM2-RF 234), lower trilobite association: 3 cephala (UM2-RF 235–237).

Remarks.—The new material is closest to the specimens from the type locality Sessacker (Rhenish Slate Mountains, Germany, described by Richter and Richter 1926). However, the brim, though flat and down-sloping distally, has perforations of equal size and there is no row of larger perforations on the inner side of the marginal border as in the material from Sessacker. The eyes are less prominent and form low ocular swellings; this feature is also developed in specimens from Coumiac, Montagne Noire (Feist and Schindler 1994).

Family Proetidae Hawle and Corda, 1847
Subfamily Drevermanniinae Maksimova, 1960
Genus *Palpebralia* Richter and Richter, 1927
Palpebralia brecciae (Richter, 1913)

Fig. 2C, D, F, I, J.

Palpebralia brecciae Richter, 1913; Feist and Schindler 1994: 208, pl. 2: 1–11 (see list of older synonymies here).

Material.—Figured specimens: 2 cranidia from locality 2 (UM2-RF 179, 182), 1 librigenae from locality 2 (UM2-RF 180), 1 pygidium from locality 1, upper trilobite association (UM2-RF 181); additional material from section "2", upper trilobite association: 10 cranidia (UM2-RF 183–192), 4 librigenae (UM2-RF 193–196), 10 pygidia (197–206).

Remarks.—In the present material the anterior branches of the facial suture are slightly more divergent anteriorly than in the type species of *P. brecciae* from Langenaubach. However, this feature varies within the same population (see Fig. 2C and J). Likewise contemporaneous populations of *Palpebralia brecciae* from European sections exhibit variations in the degree of divergence of the anterior suture depending on size and preservation (Feist and Schindler 1994: pl. 2). The middle part of the occipital furrow is slightly curved forward. In these features the new material is identical with the material from Coumiac.

Palpebralia sp.

Material.—From section "1", lower trilobite association: 2 cranidia (UM2-RF 207–208), 9 pygidia (UM2-RF 209–217). From section "2", upper trilobite association: 1 cranidium (UM2-RF 218).

Remarks.—The cranidia resemble *Palpebralia brecciae* in the form of the facial suture and the absence of any remnant of palpebral lobes, which might indicate absence of eyes. In contrast, the glabella is slender and much longer than that of *P. brecciae*, whereas there is no diagnostic difference in the pygidia. More material, especially cephala, is needed before these specimens can be identified at the species level.

Family Tropidocoryphidae Přibyl, 1946
Subfamily Pteropariinae Maksimova, 1960
Genus *Pteroparia* Richter, 1913
Pteroparia ziegleri Feist, 1994 in Feist and Schindler, 1994
Pteroparia ziegleri maroccanica subsp. nov.

Fig. 3L–P.

Derivation of name: After Morocco.

Holotype: Cranidium UM2-RF 252, fig. 3L, M, Q.

Type locality: Section 1, lower trilobite association at Bou Ounabdou (section II in Lazreq 1992), north of track, S of Al Gara hill (see location map Fig. 1C).

Type horizon: Grey-beige limestone bed immediately above prominent dark grey Lower Kellwasser bed.

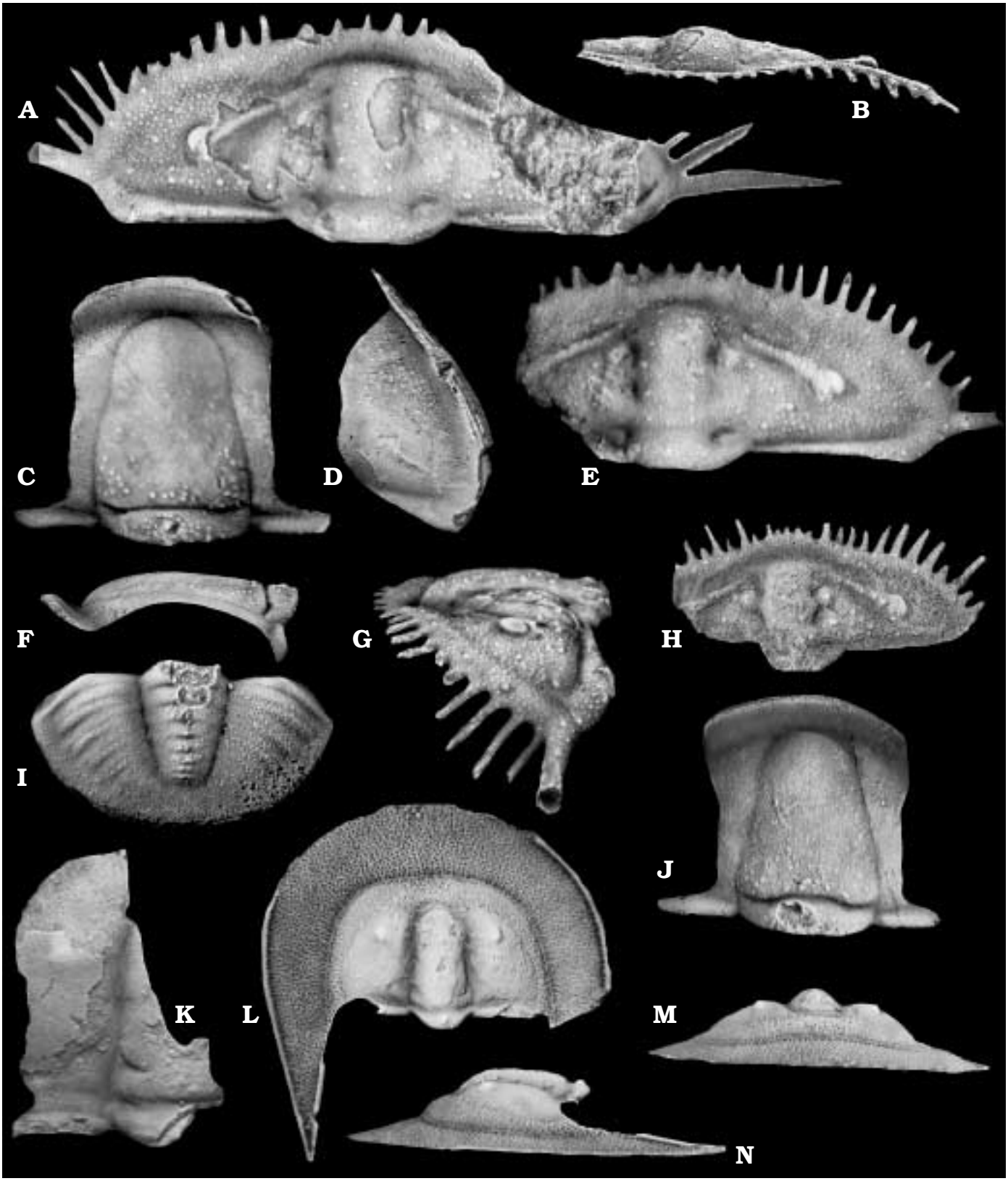
Age: According to Lazreq (1992): Late *Palmatolepis rhenana* Zone.

Material.—Figured specimens: 1 cranidium (UM2-RF 252), 1 librigena (UM2-RF 253), 1 pygidium (UM2-RF 254); additional material all from type locality: 3 cranidia (UM2-RF 255–257), 1 pygidium (UM2-RF 258).

Diagnosis.—Anterior outline of glabella semicircular; fixigenae without ocular ridges or swellings. Librigena with rather broad, stout genal spine. Axis of pygidium narrower than pleural field; postaxial area shorter than half length of axis.

Comparison.—The Moroccan material is very near to *Pteroparia ziegleri* from Sessacker in the general outline and vault of the cephalon, the presence of a small, flat ocular field with lenses and the dense granulation of the exoskeleton. There are a few morphological differences that distinguish the new material that is considered here as a contemporaneous geographic subspecies of *P. ziegleri*. The most important feature is the absence of ocular ridges on the fixigenae opposite to the eye: this area remains virtually flush with the general curvature of the anterior enlarged fixigenal field whereas, in the nominate subspecies, it is differentiated from the latter by the swollen palpebral area. Though subject to considerable variation, the anterior

Fig. 2. **A**, **B**, **E**, **G**, **H**. *Gondwanaspis mrirtensis* gen. et sp. nov. from section "2", upper trilobite association. **A**, **B**, **G**. Holotype, cephalon with damaged right cheek, UM2-RF 170, partially external mould, in dorsal view (**A**), × 9.2; in frontal view (**B**) showing frontal and left antero-lateral borders and eye elevation, × 8.3; lateral view (**G**), × 9.5. **E**. Cephalon with incomplete left cheek, UM2-RF 171, dorsal view, latex cast of external mould, × 8.1. **H**. Cephalon with incomplete left cheek, UM2-RF 172, dorsal view, external mould, × 11.1. **C**, **D**, **F**, **I**, **J**. *Palpebralia brecciae* Richter and Richter, 1927. **C**, **F**. Cranidium from section "2", upper trilobite association, UM2-RF 179, external mould, in dorsal view (**C**), × 10; in lateral view (**F**), × 9.6. **D**. Librigena →



from section "2", upper trilobite association, , rounded genal angle incomplete, UM2-RF 180, dorsal view, external mould, × 10.9. **I**. Pygidium from section "1", upper trilobite association, UM2-RF 181, dorsal view, external mould, × 11.5. **J**. Cranidium from section "2", upper trilobite association, UM2-RF 182, dorsal view, external mould, × 10.2. **K**–**N**. *"Harpes" neogracilis* Richter and Richter, 1924 from section „2", upper trilobite association. **K**. Fragment of cephalon showing glabellar furrows, UM2-RF 219, dorsal view, external mould, × 8.9. **L**–**N**. Cephalon with incomplete right genal fringe, UM2-RF 220, external mould, in dorsal view (**L**), × 8.8; in frontal view (**M**), × 9.3; in lateral view (**N**), × 10.

outline of the glabella is broader in *P. ziegleri maroccanica*: it is semicircular with a slight incurvature of the antero-lateral dorsal furrows. By contrast, in the nominate subspecies, the front of the glabella is more conical with straight diverging dorsal furrows. In *P. ziegleri maroccanica* the pygidial axis is narrower; however, the dimensional relations between axis and pleural field varies with ontogenetic growth and additional material of various growth stages must be recovered in order to confirm whether the two subspecies differ in this feature.

Family Aulacopleuridae Angelin, 1854
Subfamily Otarioninae Richter and Richter, 1926
Genus *Otarion* Zenker, 1833
Otarion stigmatophthalmus (Richter, 1914)

Fig. J, K.

Cyphaspis stigmatophthalmus Richter, 1914; Feist and Schindler 1994: 210, pl. 4: 9–15 (see list of older synonymies therein).

Remarks.—This taxon has been variously attributed either to *Cyphaspis* Burmeister, 1843 or *Otarion* Zenker, 1833. Following the revised differential diagnoses of these genera given by Adrain and Chatterton (1994) we attribute the species to *Otarion* (note that *stigmatophthalmus* was omitted from the annotated species list of *Otarion* published by Adrain and Chatterton 1994).

Material.—Figured specimens: 1 cranidium from section "2", upper trilobite association (UM2-RF 248); Additional material from section "2", upper trilobite association: 1 cranidium (UM2-RF 249); from section "1", lower trilobite association: 2 cranidia (UM2-RF 250–251).

Family Phacopidae Hawle and Corda, 1847
Subfamily Phacopinae Hawle and Corda, 1847
Genus *Acuticryphops* Crônier and Feist, 2000
Acuticryphops acuticeps (Kayser, 1889)

Fig. 4A–D, F, H.

Cryphops acuticeps (Kayser, 1889); Feist and Schindler 1994: 212, pl. 5: 1–11 (see list of older synonymies therein).

Cryphops acuticeps (Kayser, 1889); Feist 1995: 235–239, fig. 11.6.

Cryphops acuticeps (Kayser, 1889); Crônier 1999: 189, figs. 2–8.

Acuticryphops acuticeps (Kayser); Crônier and Feist 2000: 505–506, pl. 1: 9.

Material.—Figured specimens: 1 cephalon from locality 1, upper trilobite association (UM2-RF 221); 2 cephala from locality 2, upper trilobite association (UM2-RF 220, 223); 1 pygidium from locality 2 (UM2-RF 222); additional material from section "2", upper trilobite association: 15 cephala (UM2-RF 224–238), 4 pygidia UM2-RF 239–242); from section "1", lower trilobite association: 3 cephala (UM2-RF 243–245), 2 pygidia (UM2-RF 246–247).

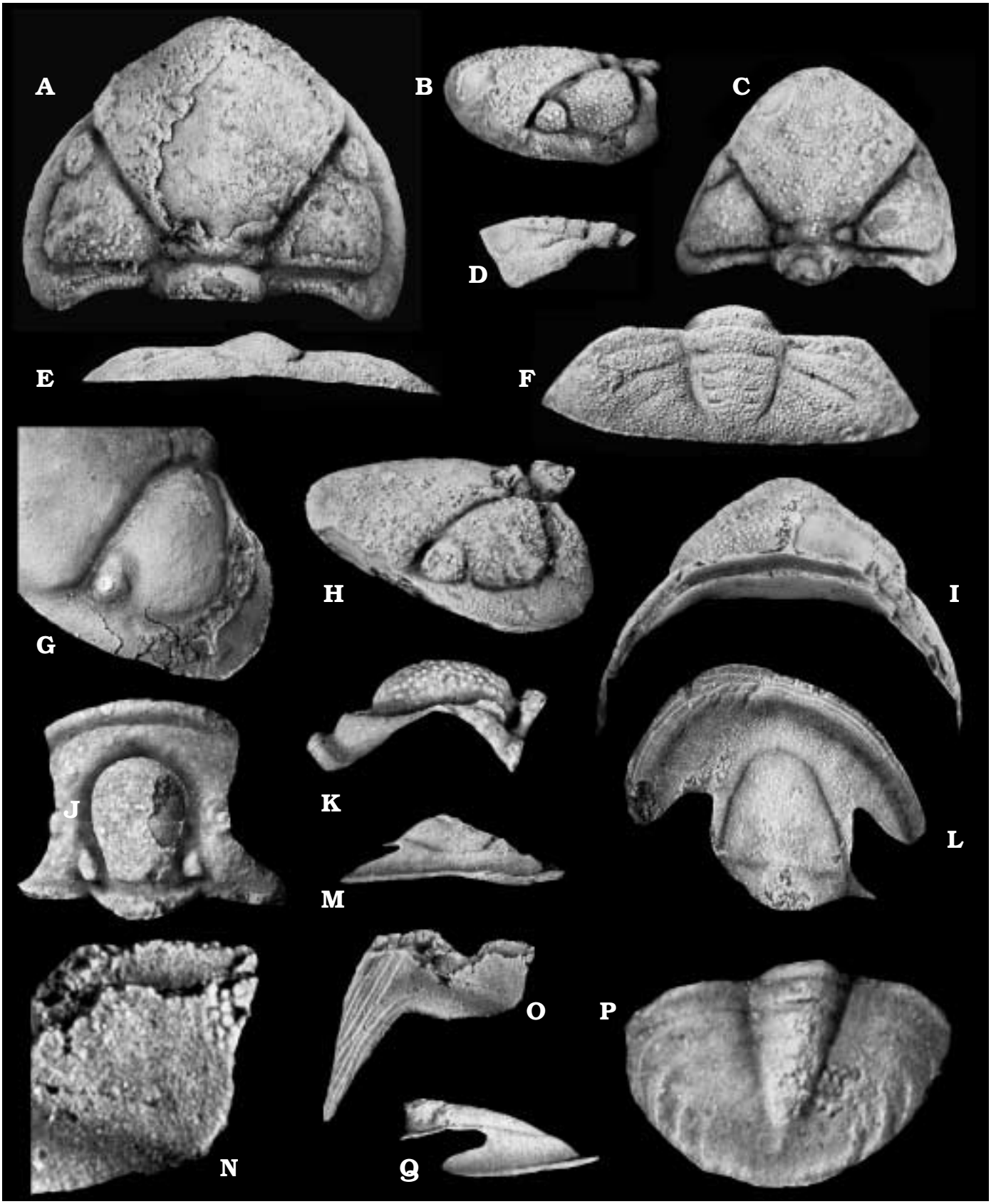
Remarks.—The cephalon is characterized by the frontal outline of the glabella, which is strongly protruding adaxially, typically pointed centrally. This feature is less marked in younger specimens. The visual surface of the eyes has an inconstant number of eye-lenses: in the population of Mrirt 2, morphs exhibiting between 1 and 7 lenses co-occur. This feature, and in particular the occurrence of morphs with a single lens, has so far only been observed in *Acuticryphops acuticeps* populations from Coumiac, southern France. Whereas the populations of cephala are very close to those from Coumiac, both in outline of the glabella and features of the eye-lobe, the pygidia from Mrirt are more flattened dorso-ventrally and are shorter. More material is needed for statistical analyses in order to evaluate the constancy of these features in which case the Moroccan material might represent an independent taxon. Unfortunately, pygidia of *Acuticryphops acuticeps* from the Rhenish Slate Mountains remain insufficiently known and, in particular, no pygidia have yet been recovered from the type locality Martenberg.

Conclusions

The composition of the trilobite associations studied herein is nearly identical with that of contemporaneous faunas from European sections, especially from the stratotype-section of the F–F boundary at Coumiac (Montagne Noire), southern France (Klapper et al. 1993) and from the Rhenish Slate Mountains and Harz (Steinbruch Schmidt, Sessacker, Aeke; Feist and Schindler 1994). As in European sections, no styginids are present in Morocco. The lower trilobite association (see Fig. 1B) contains a geographic variant of *Pteroparia ziegleri*. The species occurs at Sessacker at the same stratigraphical position shortly above the LKW horizon. The absence of pteropariins in the latest Frasnian at Coumiac (Montagne Noire) is unusual and might be due to sampling bias or to unfavorable environmental conditions locally. By contrast the remainder of the association described in this paper—"*Harpes*" *neogracilis*, *Palpebralia*, *Otarion stigmatophthalmus*, and *Acuticryphops acuticeps*—is typical of the corresponding associations in the Montagne Noire and in the Rhenish Slate Mountains and Harz.

Of special interest is the upper trilobite-bearing horizon (Fig. 1) as it represents the youngest Frasnian trilobite occurrence before the extinction at the UKW level. Not only is this association, containing the new taxon *Gondwanaspis mrirtensis* plus *Otarion stigmatophthalmus*, *Palpebralia brecciae*,

Fig. 3. **A–I**. *Acuticryphops acuticeps* (Kayser, 1889). **A**, **H**, **I**. Cephalon from section "2", upper trilobite association, UM2-RF 220, partially external mould, in dorsal view (**A**), × 6.9; in lateral view (**H**), eye lobe with more than 6 lenses, × 6.5; in frontal view (**I**), slightly tilted backward showing vincular furrow and ventral doublure, × 7.1. **B**, **C**. Cephalon from section "1", upper trilobite association, UM2-RF 221, external mould; in lateral view (**B**), eye lobe with 4 lenses, × 7.8; in dorsal view (**C**), × 8.2. **D–F**. Pygidium from section "2", upper trilobite association, UM2-RF 222, external mould; lateral view (**D**), × 14.5; in posterior view (**E**), × 10.7; in dorsal view (**F**), × 12.2. **J–K**. *Otarion stigmatophthalmus* (Richter, 1914), cranidium from section „2", upper trilobite association, UM2-RF 248, internal mould in dorsal view (**J**), × 14.1; in lateral view (**K**), × 14.8. **L–Q**. *Pteroparia ziegleri maroccanica* subsp. nov. from section "1", lower →



trilobite association. **L**, **M**, **Q**. Holotype, cranidium, UM2-RF 252, external mould in dorsal view (**L**), × 17.9; in frontal view (**M**), × 12.7; in lateral view (**Q**), × 16.1. **N**, **O**. Librigena, UM2-RF 253, partially external mould, anterior part of lateral border incomplete, in dorsal view (**N**) of adaxial librigenal field showing visual surface of the eye with eye-lenses, × 50; in dorsal view (**O**), × 22.5. **P**. pygidium, UM2-RF 254, external mould, dorsal view, × 26.3.

Acuticryphops acuticeps and "*Harpes*" *neogracilis*, identical with that from Coumiac and very close to that of Sessacker, but it exhibits, within the population of *A. acuticeps*, the particular feature of inconstancy in the number of ocular lenses that characterizes the populations from Coumiac in the latest Frasnian. Evolutionary trends towards eye reduction in independent taxonomic lineages such as phacopids and proetids are confirmed, supporting the model of a worldwide eustatic deepening prior to the Upper Kellwasser Event.

The high degree of similarity in taxonomic categories of lower rank, together with identical evolutionary patterns of eye-reduction in end-Frasnian faunas from the Avalonian outer shelf of the Old Red Continent to the north and North Gondwanan terrains to the south, strongly argues in favor of close and direct geographical connections between these areas (Young 1987). This precludes the wide oceanic separations such as those suggested by Van der Voo (1988) and Tait et al. (1997) for the Late Devonian.

The last occurrences of harpetids, aulacopleurids and odontopleurids in North Africa below the UKW confirms the previously established ranges of these taxa that became extinct at the base of the UKW (Feist 1991, Feist and Schindler 1994).

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