

Red Devonian Trilobites with Green Eyes from Morocco and the Silicification of the Trilobite Exoskeleton

Authors: Klug, Christian, Schulz, Hartmut, and De Baets, Kenneth

Source: *Acta Palaeontologica Polonica*, 54(1) : 117-123

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2009.0112>

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

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

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

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

Red Devonian trilobites with green eyes from Morocco and the silicification of the trilobite exoskeleton

CHRISTIAN KLUG, HARTMUT SCHULZ, and KENNETH DE BAETS



Klug, C., Schulz, H., and De Baets, K. 2009. Red Devonian trilobites with green eyes from Morocco and the silicification of the trilobite exoskeleton. *Acta Palaeontologica Polonica* 54 (1): 117–123.

Latest Emsian (Early Devonian) sediments at the famous mud-mound- and trilobite-locality Hamar Laghdad (Tafilalt, Morocco) yielded some red-coloured remains of phacopid trilobites. Closer examination revealed that the eyes of these phacopids are often greenish in colour. EDX-analyses showed that the lenses retained their original calcitic composition, possibly greenish due to Fe- and Mn-impurities, while most of the exoskeleton was silicified. The silicified parts contain elevated concentrations of iron which causes the red colour. This phenomenon is explained by the porosity of the exoskeleton in contrast to the homogeneous and massive construction of the lenses and their Mg-content. These incompletely silicified trilobites enabled a reconstruction of the silicification process in trilobites. Their diagenetic alteration probably occurred as a result of events associated with the Cretaceous transgression.

Key words: Trilobita, taphonomy, diagenesis, silicification, transgression, mud-mounds, Devonian, Morocco.

Christian Klug [chklug@pim.uzh.ch], Kenneth DeBaets [kenneth.debaets@pim.uzh.ch], Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Str. 4, CH-8006 Zürich, Switzerland;

Hartmut Schulz [hartmut.schulz@uni-tuebingen.de], Institut für Geowissenschaften, Eberhard-Karls-Universität Tübingen, Sigwartstr. 10, D-72076 Tübingen, Germany.

Introduction

Trilobite eyes always attracted the attention of palaeontologists and biologists, partially because of their often large size compared to body size but also because of the sheer fact that such a sense organ can be preserved in such detail: Even the quality and optical properties of its lenses could be examined (Clarkson and Levi-Setti 1975; Bruton and Haas 2003 and references therein; Fortey and Chatterton 2003). Especially phacopid eyes were often discussed in numerous articles, partially because of the abundance of this trilobite group and partially because of the large size of the eyes and their lenses, respectively, of some members of the Phacopidae (Bruton and Haas 2003 and references therein).

Because of its usually strongly mineralised cuticle, it is often well preserved and thus, the ultrastructure of the trilobite cuticle could be studied in detail in various groups (e.g., Teigler and Towe 1975; McAllister and Brand 1989; Dalingwater et al. 1991, 1993, 1999). As we show in this article, the physical properties required for optical functionality of the eyes and their Mg-content (Lee et al. 2007) influenced the diagenesis of this part of the trilobite exoskeleton. We examined a number of well-preserved phacopid trilobites from Hamar Laghdad (Tafilalt, eastern Anti-Atlas, Morocco) because of their peculiar preservation. At this locality, we found several enrolled specimens of *Barrandeops* cf. *granulops* (Chatterton, Fortey, Brett, Gibb, and McKellar, 2006) (e.g., PIMUZ 27077), a species formerly described from the DraValley (Chatterton et al. 2006). In these specimens, the

exoskeleton is red except for the lenses which are green. Images of one of these extraordinary fossils (PIMUZ 27077) were used for the cover of the April 2008-edition of the Journal “Geology”, but without an accompanying article. In this article we want to (1) show why the eyes of these trilobites are green and (2) discuss how this phenomenon can be explained.

Institutional abbreviation.—PIMUZ, Paläontologisches Institut und Museum, Zürich University, Switzerland (PIMUZ 27075–27077, 27080–27083).

Material and geological setting

The recently discovered, seemingly perfectly preserved phacopid trilobites were eroded from marls from close to the Emsian/Eifelian boundary from the Moroccan locality Hamar Laghdad.

The specimens of *Barrandeops* cf. *granulops* included in this study were discovered in a rich benthic fauna of latest Emsian age (391.9 ± 3.4 Ma; Kaufmann 2006) at the “red cliff” (Klug 2002) at Hamar Laghdad (Fig. 1). This Moroccan locality (18 km east-southeast of Erfoud; N $31^{\circ}22'37''$ W $4^{\circ}03'28''$) gained fame for its perfectly exposed mud-mounds (e.g., Roch 1934; Massa et al. 1965; Hollard 1974; Alberti 1982; Brachert et al. 1992; Wendt 1993; Belka 1994, 1998; Bultynck and Walliser 2000; Aitken et al. 2006; Cavalazzi et al. 2007). In addition to this impressive occurrence of carbon-

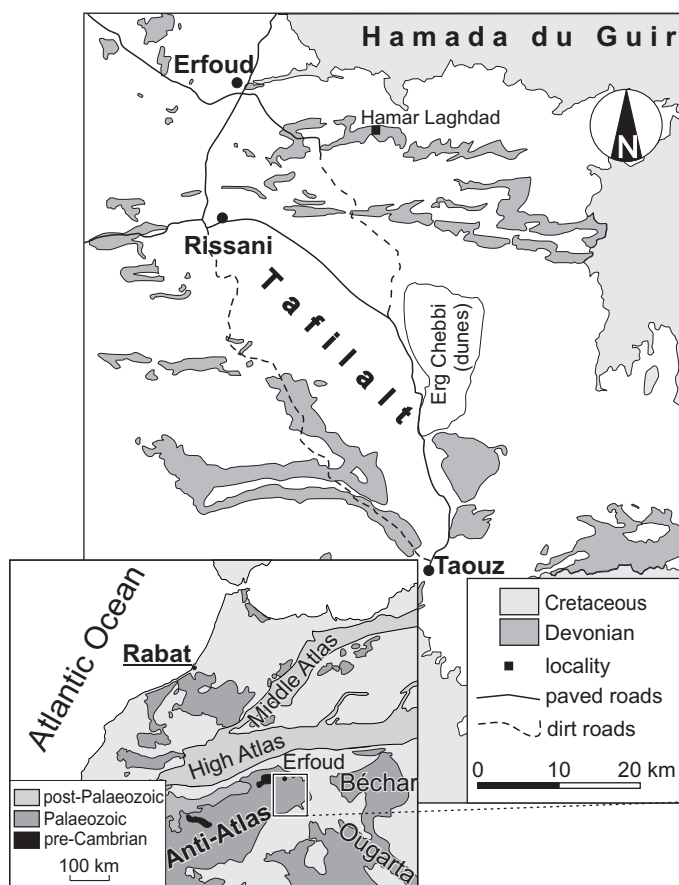


Fig. 1. Geologic map of Morocco and the Tafilalt (eastern Anti-Atlas), showing the position of the “red cliff” at Hamar Laghdad (modified after Klug 2007).

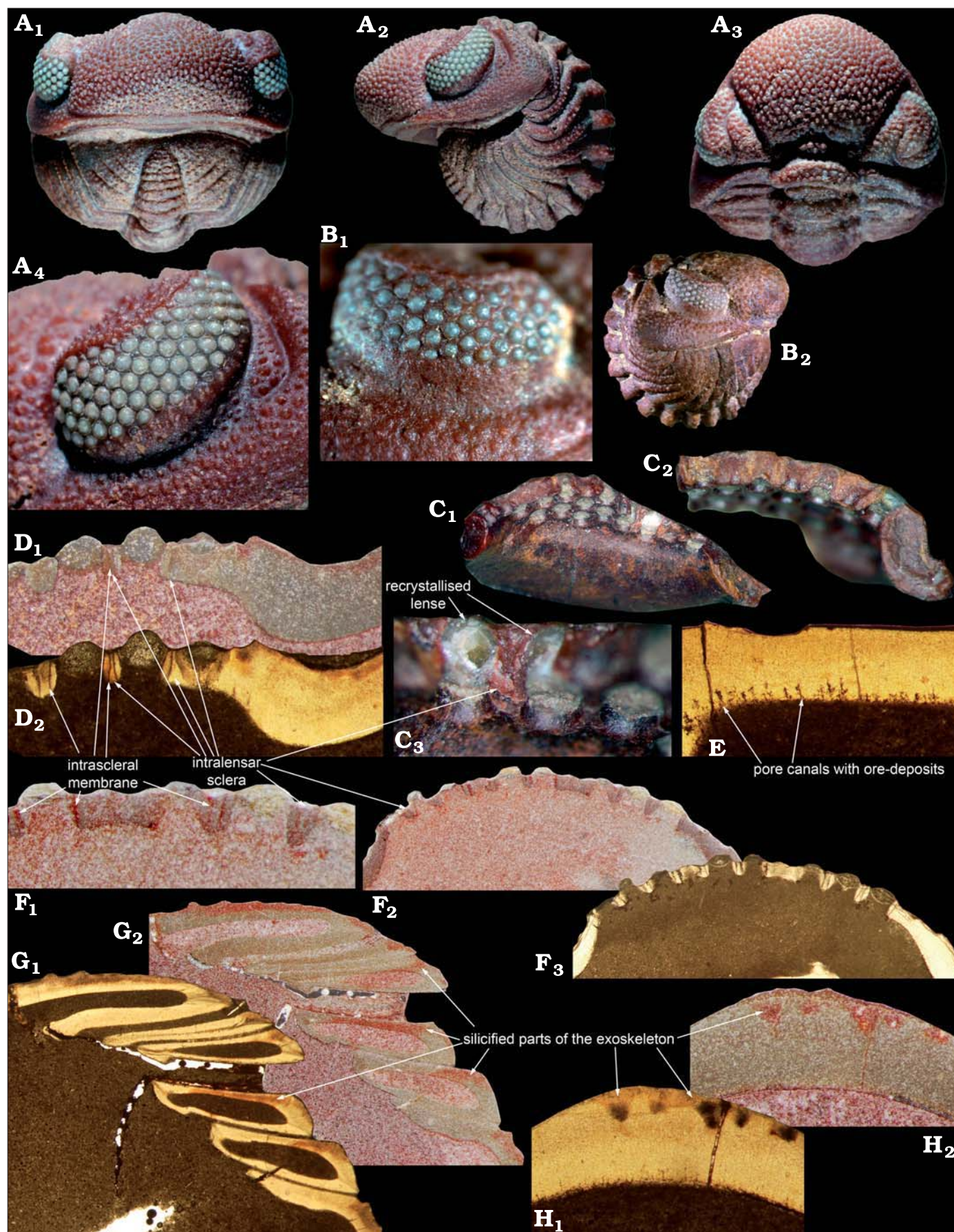
ate build-ups, Hamar Laghdad is well-known for its rich invertebrate faunas. Especially cephalopods (Töneböhn 1991; Klug 2002; Klug et al. 2008) and arthropods (e.g., Alberti 1969, 1980, 1982) have been described from the Early and Middle Devonian strata of this locality. Late Emsian biostratigraphy at Hamar Laghdad can be summarised as follows: The upper-

most layer of most mud-mounds yielded *Mimagoniatites fecundus* (Barrande, 1865), the index of the basal Dalejan (Late Emsian). According to Klug (2002: 10), the “marls and claystones above contain a diverse fauna (Alberti 1980) with ammonoids including *Gyroceratites* cf. *gracilis* (Barrande, 1865), *Latanarcestes latisellatus* Erben, 1953, and *L. noeggerathi* (von Buch, 1832)”. At the top of the Emsian succession at Hamar Laghdad, a rich benthonic assemblage occurs. It contains bivalves, inarticulate and articulate brachiopods, various rugose and tabulate corals, crinoids, cystoids (*Eucystis*), gastropods, hyolithids, rare rostroconchs, well-preserved trilobites (corynexochids, harpetids, lichids, phacopids, proetids) and goniatites. Among the latter, *Anarcestes* cf. *latissimus* Chlupáč and Turek, 1983, *Chlupacites praeceps* (Chlupáč and Turek, 1983), and *Amoenophyllites doeringi* Klug, 2002 were identified. The nodular limestones above contain numerous specimens of *Foordites veniens* Chlupáč and Turek, 1983. This layer represents the base of the section published by Klug (2002: fig. 10).

Methods

In order to learn more about the origin of this coloration, we examined the chemical composition of the red trilobites from Hamar Laghdad. For this purpose, we produced thin-sections (PIMUZ 27075, 27081; Fig. 2D–H). These thin-sections and an isolated phacopid cephalon (PIMUZ 27076) were subjected to a series of elemental micro analyses using a scanning electron microscope SEM LEO 1450 VP at the Institut für Geowissenschaften Tübingen (Fig. 3). Operating parameters were 17 kV with a working distance of 29 mm. The chemical composition of sample points was measured using an energy-dispersive X-ray analyser EDX (Oxford Instruments INCA EDS 200). Measuring time was 90 seconds. These examinations clearly showed that the cuticle of the isolated cephalon (PIMUZ 27076) is silicified except for the lenses, which retained their calcitic composition (Fig. 3; 45.3

Fig. 2. Phacopid trilobite *Barrandeops* cf. *granulops* (Chatterton, Fortey, Brett, Gibb, and McKellar, 2006), Early Devonian (Emsian/ Eifelian boundary), → Hamar Laghdad (Tafilalt, eastern Anti-Atlas, Morocco). **A.** PIMUZ 27077, the cephalon is 10.2 mm across. A₁, anterior view showing the red exoskeleton and the green lenses; A₂, lateral view; A₃, dorsal view of the cephalon; note the well preserved ornamentation; A₄, detail of A₂ to show the slightly corroded surface of the lenses and the partially still calcitic, partially silicified intralensar sclera. **B.** PIMUZ 27082, the cephalon is 9.9 mm across and 7 mm in length. B₁, detail of B₂ showing the calcitic lenses with the silicified intralensar sclera (the eye is 3.1 mm long); B₂, lateral view of the entire specimen. **C.** PIMUZ 27083, broken fragments of the exoskeleton of a cephalon (length of largest fragment 6.3 mm). C₁, mesial view from oblique below showing the interior of the eye and the green lenses with the red interlensar sclera; C₂, same specimen, different fragment (4.5 mm long), view of the fracture surface; C₃, detail of C₁, showing the fracture surface of two recrystallised but still calcitic lenses. **D, E, G, H.** Details of a thin section through specimen PIMUZ 27081 (width 19.3 mm). **D.** Detail of the eye and adjacent librigena. D₁, image taken under incident light, both the bend in the growth lines of the intralensar sclera and the surface of the librigena are silicified (red) while the rest is still calcitic (greenish); D₂, same detail as in D₁ under transmitted light. **E.** Detail of the exoskeleton under transmitted light. Note the manganese and iron minerals which filled the pore canals from the inside of the trilobite (width 1.6 mm). **G.** Details of the pleura (width of detail 6.6 mm) showing beginning silicification. G₁, transmitted light, silicified parts brownish; G₂, incident light, silicified parts redish; silicification begins at the outer surface. **H.** Detail of the rhachis (width 1.9 mm). H₁, transmitted light, silicified parts brownish forming pouches; manganese and iron minerals deposits on the internal parts of the pore canals; H₂, incident light, silicified parts redish. Silicification begins at the outer surface and along the pore canals. **F.** Details of a thin section through the cephalon of specimen PIMUZ 27075 (width 25.4 mm, length 13.9 mm). F₁, detail of F₂ to show the red colour of the bends in the growth lines of the intralensar sclera and the green lenses; the lens on the left shows horizontal fractures, indicating recrystallisation of this lens; F₂, the complete eye under incident light. Note the greenish colour of the lenses and the red colour of the bends in the growth lines of the intralensar sclera. Most of the exoskeleton is red (silicified). F₃, like F₂, but under transmitted light.



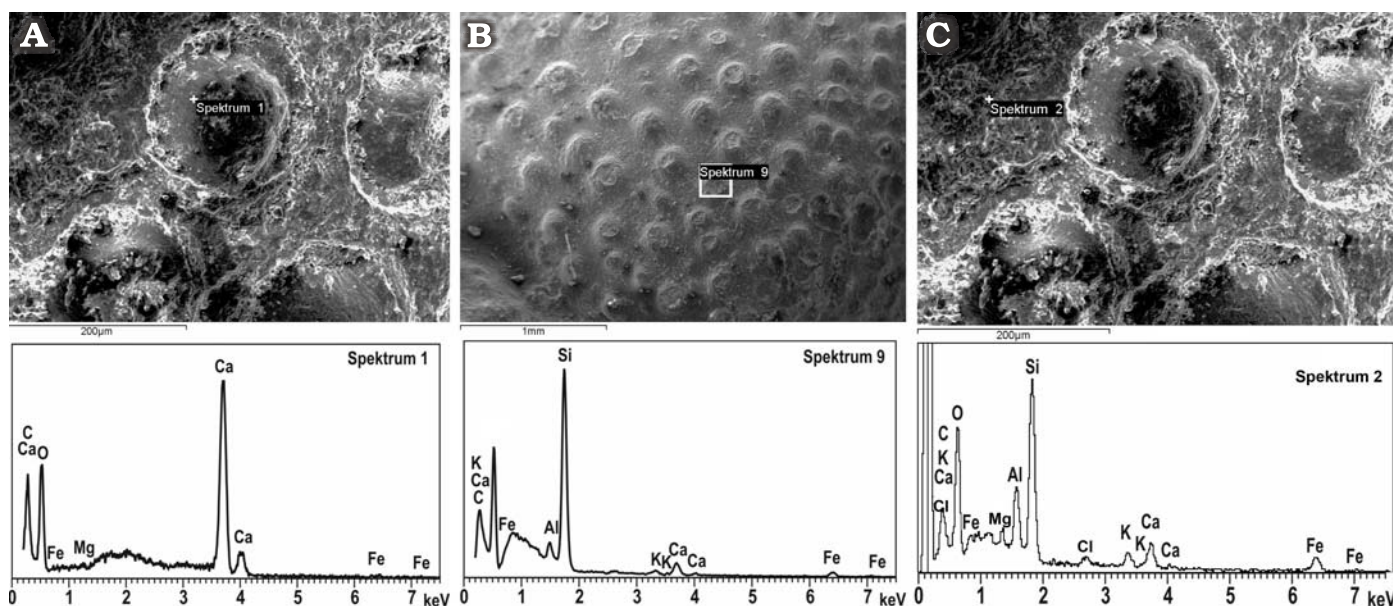


Fig. 3. SEM-SE image of cephalon PIMUZ 27076 and results of the element analyses ("EDX-spektrum X"). A. SEM-SE image of the eye and result of the element analysis of a lense ("EDX-spektrum 1"). Note the absence of iron and silica. B. SEM-SE image of the glabella and result of the element analysis ("EDX-spektrum 9"). Iron and silica are present. C. Analysis performed in the intralensar area ("EDX-spektrum 2") of the glabella (see A). Iron and silica are present.

wt. % calcium, 54.0 wt. % oxygen). On the glabella of the measured specimen, five analyses rather uniformly revealed the presence of approximately 1.9 wt. % iron (which explains the red color), 1.0 wt. % calcium, 2.0 wt. % aluminum and 0.7 wt. % potassium (Fig. 3).

Not all specimens from this locality are preserved identically. The degree of silicification and iron-staining is highly variable. This is reflected in exoskeleton colours ranging from greenish-yellowish (when still more or less calcitic) to red (when silicified). One enrolled specimen which was thin-sectioned (PIMUZ 27081) retained much of its original calcitic mineralogy with a clear predominance of calcium and oxygen, reflected in its more greenish to yellowish colour. The element of iron was detected by the EDX in traces only and in some places not at all. Hassan (1978) analysed the composition of a greenish calcite from Egypt and found impurities of manganese and iron ["Mn(IV) and Fe(II)"]. Based on these findings, he concluded that the calcite was precipitated "in an environment that was more acidic and with a very low oxidation potential" (Hassan 1978: 732).

The EDX-analyses in specimens PIMUZ 27075 and 27076 clearly showed that all red parts of the exoskeleton are silicified while the yellowish to greenish parts such as the lenses retained the calcitic composition with low contents of iron and magnesium. The examinations of the thin-sectioned cephalons revealed that the replacement of calcite by silica commenced at the outer surface (Fig. 2G, H) of the sclerites and following pore canals (Fig. 2E, H) as well as the bend in the growth lines of the intralensar sclera (Fig. 2D, F; cf. Bruton and Haas 2003). More or less simultaneously, manganese and iron minerals were deposited from the ventral side (i.e., from within the enrolled trilobite) in the pore canals

(Fig. 2E, H). The sediment matrix visible in the thin-sections (Fig. 2D–H) is partially silicified (red areas) and partially carbonatic (light coloured under incident light). The lenses locally are well preserved with the primary small crystal size while adjacent lenses can be already recrystallised, forming a single or few crystals (Fig. 2C, D, F).

Remarks on the local diagenesis

We found evidence for two diagenetic processes which have occurred directly next to each other at the "red cliff" (Hamar Laghdad):

Dolomitisation.—A thin section of red-coloured Late Eifelian limestones from the top of the "red cliff" is composed of relatively large, unmistakable dolomite crystals (< 2 mm). The Late Eifelian rocks contain also dolomitised fossils such as various cephalopods. Dolomitisation occurs abundantly in the carbonates of the Anti-Atlas which characteristically have a reddish colour due to iron compounds (compare Kaufmann 1997, 1998). At Hamar Laghdad, this reddish facies is largely restricted to the more elevated parts of the Hamar Laghdad ridge (Fig. 4).

Silicification.—The mineralogy of both the trilobite exoskeletons and their sediment matrix indicate a local and partial silicification. Silicified trilobites occur (usually in association with silicified ostracods) also in other localities of the Anti-Atlas such as in the Taouz- and Ouidane Chebbi regions in roughly the same stratigraphic position. As far as we know, Hamar Laghdad is the only locality where the silicified trilobite exoskeletons carry the red colour.

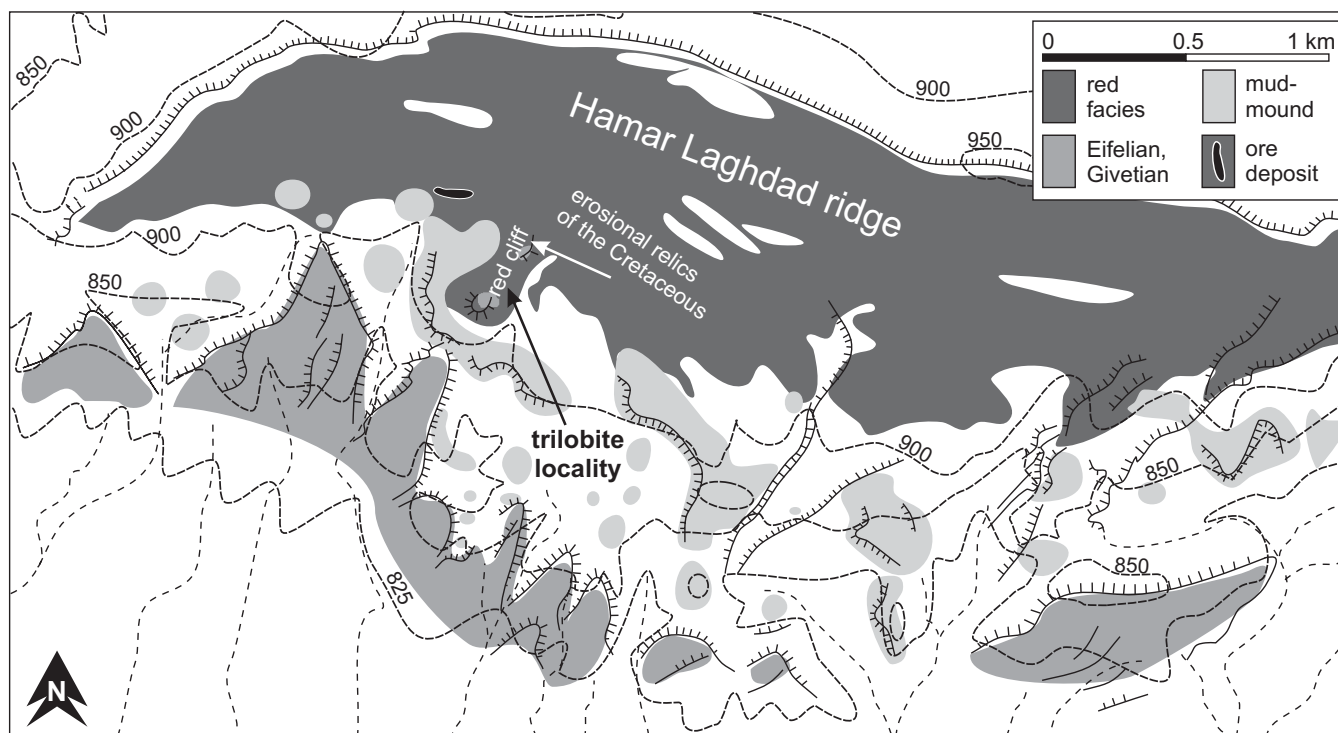


Fig. 4. Map of Hamar Laghdad showing the mud-mounds, the distribution of the red facies, the position of the red cliff, erosional remnants of the Cretaceous transgression conglomerate and the distribution of outcrops of Middle Devonian sediments (map based on satellite images, the topographic map sheet “Erfoud, feuille NH-30-XX-2, Carte du Maroc 1/100000”, and Berkowski 2006: fig. 1).

In the Tafilalt, dolomitised rocks are often reddish in colour, certainly due to their iron compounds-content. These dolomites occur mainly in two situations: near faults (Bernd Kaufmann, personal communication 2008; Graz and Kaufmann 1997) and close to the erosional surface at the base of the Cretaceous transgression. To our knowledge, these diagenetic phenomena have not been examined in detail in the study area yet and thus, a full sedimentological interpretation of these diagenetic processes is not available yet.

At Hamar Laghdad, the red facies is at least partially related to the erosional processes prior and during the Cretaceous transgression because it occurs predominantly in elevated parts of the Hamar Laghdad-ridge, i.e., close to the erosional surfaces, and it occurs also in other parts of the Tafilalt where the Devonian sediments reach close to the Cretaceous transgression surface (e.g., Ouidane Chebbi, Achguig). At the red cliff, some red-coloured erosional remnants of the Cretaceous transgression conglomerate containing coarse siliciclastics are preserved. We suggest, tentatively, that at least the dolomitisation but potentially also the silicification at the “red cliff” were caused by the penetration of silicium-, aluminium- and iron-bearing fluids after the uplift, during the later erosion of the Devonian sediments and during the Cretaceous transgression. The silicification is not surprising since the Cretaceous transgressive sediments contain sandstones, conglomerates (both with siliceous components and sometimes with a silicified matrix) and thin chert-layers. The locally limited occurrence of this preservation is not surprising since the Late Emsian to earliest Eifelian marls are less resistant towards ero-

sion than, e.g., the massive mud-mound-limestones and thus, sediments of this stratigraphic intervals which were altered by transgression-related diagenetic phenomena are rare.

We also considered that the silica might have originated from the local hydrothermal activity (cf. Belka 1998; Aitken et al. 2002). This appears unlikely, however, because this phenomenon does not occur everywhere in Hamar Laghdad but only on the red cliff while hydrothermal activities probably occurred in the entire Hamar Laghdad region.

Trilobite exoskeleton diagenesis

The above described patterns of the selective and partial silicification of the trilobite exoskeleton were probably caused by differences in porosity (pore canals in most of the exoskeleton in contrast to the homogeneous lenses) and composition (primary magnesium content of the lenses; see Lee et al. 2007). For the silicification of the trilobites, the following sequence of events is evident from the thin-sectioned specimens:

- (1) Silicification began at the outer surface of the exoskeleton as well as in pore canals and along the bend of growth lines within the intralensar sclera.
- (2) The exoskeleton became fully silicified including the intralensar sclera while the lenses stayed calcitic but may have become recrystallised.
- (3) Ultimately, the lenses became silicified, too.

Conclusions

Phacopid trilobites from the latest Emsian of Hamar Laghdad, Morocco are silicified to varying degrees. This fact allows a reconstruction of details of the silicification process. Silicification started at the outer surface of the exoskeleton as well as in pore canals and along the bend of growth lines within the intralensar sclera. From these silicification centres, this process continued until only the lenses remained calcitic. Additional to the homogeneity of the calcite crystals of the lenses, needed for their optimal optical functionality, and their higher magnesium-content (Lee et al. 2007), the absence of pore-canals in the lenses accounts for the fact that the eyes retained the greenish calcite (this colour is also encountered in various other invertebrate fossils from the red cliff as well as brachiopod shells such as the thick-shelled Middle Devonian *Devonogypa* and *Ivdelinia* from the Maïder Basin; Kaufmann 1998) while the rest of the trilobite exoskeleton is silicified and red because of a sufficiently high content of iron compounds. The greenish colour of the lenses might have been caused by manganese and iron-impurities which could not be detected with certainty with the EDX because the content was too low. This differential replacement also explains why the lenses are slightly corroded while the rest of the exoskeleton is rather well preserved. So far, this differential replacement of calcite is only known from the eyes of phacopids. Other trilobite taxa from the same strata have holochroal eyes and thus much smaller lenses which were probably more rapidly replaced by silica. The lenses of these holochroal eyes are preserved in the red, iron-stained silica exactly like the exoskeletons. The silicification probably happened in relation to the Cretaceous transgression because (1) the silicification occurs at the only one place at Hamar Laghdad, the red cliff, where the latest Emsian marls reach close to the transgression surface (they are more deeply eroded otherwise because of their higher clay content and thus lower erosion-resistance), (2) the Cretaceous sediments display the same colour, (3) the Cretaceous sediments are rich in silica (siliciclastic conglomerates and cherts), (4) this phenomenon does not occur in other parts of Hamar Laghdad in the same stratigraphic position, and (5) silicified arthropods from other localities in the Anti-Atlas do not show this coloration.

Future studies should continue by analysing the alteration of sediments below the Cretaceous transgression and analyses of the green colour in brachiopods and trilobite eyes as well as other fossils from the red cliff.

Acknowledgements

The field work in Morocco was kindly supported by the Swiss National Science Foundation (project No. 200021-113956/1 to CK). We thank Frowin Pirovino (Geologisches Institut, Eidgenössische Technische Hochschule, Zürich, Switzerland) for the production of thin sections, Mike Pirie as well as Laura Wilson for proof-reading and Thomas Galfetti (all Zürich University, Switzerland) for the impetus to produce

this study. Raimund Feist (Université Montpellier 2, France) and an anonymous reviewer helped much to improve the manuscript. Alan W. Owen (University of Glasgow, UK) and Jarosław Stolarski (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) also discussed the matter with us and gave some valuable information. Allart P. Van Viersen (Born, Belgium) and Harald Prescher (Kerpen, Germany) kindly shared their opinion on phacopid taxonomy with us.

References

- Alberti, G.K.B. 1969. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. I. Mit Beiträgen zur Silur-Devon-Stratigraphie einiger Gebiete Marokkos und Oberfrankens. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 520: 1–692.
- Alberti, G.K.B. 1980. Neue Daten zur Grenze Unter-/Mittel-Devon, vornehmlich aufgrund der Tentaculiten und Trilobiten im Tafilalt (SE-Marokko). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1980 (10): 581–594.
- Alberti, G.K.B. 1982. Der Hamar Laghdad (Tafilalt, SE Marokko), eine bedeutende Fundstelle devonischer Trilobiten. *Natur & Museum* 112: 172–182.
- Aitken, S.A., Colom, J.C., Henderson, C.M., and Johnston, P.A. 2002. Stratigraphy, paleoecology, and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa. *Bulletin of Canadian Petroleum Geology* 50: 217–243.
- Barrande, J. 1865. *Système Silurien du centre de la Bohême. I. Vol. II. Cephalopodes*. 107 plates. By the author, Praha.
- Belka, Z. 1994. Dewońskie budowle węglanowe (Carbonate buildups) Sahary Środkowej i ich związek z podmorskimi źródłami termalnymi (Carbonate mud buildups in the Devonian of the Central Sahara: evidences for submarine hydrothermal venting). *Przegląd Geologiczny* 5: 341–346.
- Belka, Z. 1998. Early Devonian Kess-Kess carbonate mud mounds of the eastern Anti-Atlas (Morocco), and their relation to submarine hydrothermal venting. *Journal of Sedimentary Research* 68: 368–377.
- Belka, Z., Klug, C., Kaufmann, B., Korn, D., Döring, S., Feist, R., and Wendt, J. 1999. Devonian conodont and ammonoid succession of the eastern Tafilalt (Ouidane Chebbi section), Anti-Atlas, Morocco. *Acta Geologica Polonica* 49: 1–23.
- Berkowski, B. 2006. Vent and mound rugose coral associations from the Middle Devonian of Hamar Laghdad (Anti-Atlas, Morocco). *Geobios* 39: 155–170.
- Brachert, T., Buggisch, W., Flügel, E., Hüssner, H., Joachimski, M.M., and Tournier, F. 1992. Controls of mud mound formation: the Early Devonian Kess-Kess carbonates of the Hamar Laghdad, Anti-Atlas, Morocco. *Geologische Rundschau* 81: 15–44.
- Bruton, D.L. and Haas, W. 2003. The puzzling eye of *Phacops*. In: P.D. Lane, D.J. Siveter, and R.A. Fortey (eds.), *Trilobites and Their Relatives. Special Papers in Palaeontology* 70: 349–361.
- Buch, L. von 1832. Über Goniatiten. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, Physikalische Klasse* 1830: 159–187.
- Bultynck, P. and Walliser, O.H. 2000. Emsian to Middle Frasnian sections in the northern Tafilalt. In: A. El Hassani and A. Tahiri (eds.), *Moroccan Meeting of the Subcommission on Devonian Stratigraphy (SDS)—IGCP 421 Excursion Guidebook. Notes et Mémoires du Service Géologique du Maroc* 399: 11–20.
- Cavalazzi, B., Barbieri, R., and Ori, G.G. 2007. Chemosynthetic microbialites in the Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). *Sedimentary Geology* 200: 73–88.
- Chatterton, B., Fortey, R., Brett, K., Gibb, S., and McKellar, R. 2006. Trilobites from the upper Lower to Middle Devonian Timrhahhart Formation, Jbel Gara el Zguilma, southern Morocco. *Palaeontographica Canadiana* 25: 1–177.
- Chlupáč, I. and Turek, V. 1983. Devonian goniatites from the Barrandian

- area, Czechoslovakia. *Rozprawy Ústředního ústavu geologického* 46: 1–159.
- Clarkson, E.N.K. and Levi-Setti, R. 1975. Trilobite eyes and the topics of Des Cartes and Huygens. *Nature* 254: 663–667.
- Dalingwater, J.E., Hutchinson, S.J., Mutvei, H., and Siveter D.J. 1991. Cuticular ultrastructure of the trilobite *Ellipsocephalus polytomus* from the Middle Cambrian of Öland, Sweden. *Palaeontology* 34: 205–217.
- Dalingwater, J.E., Siveter D.J., and Mutvei, H. 1993. Cuticular ultrastructure of some Silurian calymenid trilobites from the Welsh Borderland and Gotland. *Palaeontographica A* 229: 37–49.
- Dalingwater, J.E., Siveter D.J., and Mutvei, H. 1999. Cuticular microstructure of some Silurian homalonotid trilobites from Sweden. *Journal of Paleontology* 73: 256–262.
- Dick, V. and Brett, C.E. 1986. Petrology, taphonomy and sedimentary environments of pyritic fossil beds from the Hamilton Group (Middle Devonian) of western New York. In: C.E. Brett (ed.), *Dynamic Stratigraphy and Depositional Environment of the Hamilton Group (Middle Devonian) in New York State. Part 1. New York State Museum Bulletin* 457: 102–128.
- Erben, H.K. 1953. Goniatitacea (Ceph.) aus dem Unterdevon und Unterem Mitteldevon. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 98: 175–225.
- Fortey, R. and Chatterton, B. 2003. A Devonian trilobite with an eye-shade. *Science* 301: 1689.
- Hassan, F. 1978. Impurity-related centers in a pale green calcite crystal. *American Mineralogist* 63: 732–736.
- Hollard, H. 1974. Recherches sur la stratigraphie des formations du Dévonien moyen, de l'Emsien supérieur au Frasnien, dans le Sud du Tafilalet et dans le Ma'der (Anti-Atlas oriental). *Notes et Mémoires du Service Géologique du Maroc* 264: 7–68.
- Kaufmann, B. 1997. Diagenesis of Middle Devonian Carbonate mounds of the Mader Basin (eastern Anti-Atlas, Morocco). *Journal of Sedimentary Research* 67: 945–956.
- Kaufmann, B. 1998. Facies, stratigraphy and diagenesis of Middle Devonian reef- and mud-mounds in the Mader (eastern Anti-Atlas, Morocco). *Acta Geologica Polonica* 48: 43–106.
- Kaufmann, B. 2006. Calibrating the Devonian Time Scale: A synthesis of U-Pb ID-TIMS ages and conodont stratigraphy. *Earth Science Reviews* 76: 175–190.
- Klug, C. 2002. Quantitative stratigraphy and taxonomy of late Emsian and Eifelian ammonoids of the eastern Anti-Atlas (Morocco). *Courier Forschungsinstitut Senckenberg* 238: 1–109.
- Klug, C. 2007. Healed injuries on the shells of Early Devonian cephalopods from Morocco. *Acta Palaeontologica Polonica* 52: 799–808.
- Klug, C., Meyer, E., Richter, U., and Korn, D. 2008. Soft-tissue imprints in fossil and Recent cephalopod septa and septum formation. *Lethaia* 41: 477–492.
- Lee, M.R., Torney, C., and Owen, A.W. 2007. Magnesium-rich intralensar structures in schizochroal trilobite eyes. *Palaeontology* 50: 1031–1037.
- Massa, D., Combaz, A., and Manderscheid, G. 1965. Observations sur les séries Siluro-Dévonniennes des confins Algéro-Marocains du Sud. *Notes et Mémoires, Compagnie Française des Pétroles* 8: 1–187.
- McAllister, J.E. and Brand, U. 1989. Primary and diagenetic microstructures in trilobites. *Lethaia* 22: 101–111.
- Roch, E. 1934. Sur des phénomènes remarquables observés dans la région d'Erfoud (confins algéro-marocains du Sud). *Association Études de la Géologie Méditerranéenne Occidentale* 5: 1–10.
- Teigler, D.J. and Towe, K.M. 1975. Microstructure and composition of the trilobite exoskeleton. *Fossils and Strata* 4: 137–149.
- Töneböhn, R. 1991. Bildungsbedingungen epikontinentaler Cephalopodenkalke (Devon, SE-Marokko). *Göttinger Arbeiten zur Geologie und Paläontologie* 47: 1–114.
- Wendt, J. 1993. Steep-sided carbonate mud mounds in the Middle Devonian of the eastern Anti-Atlas, Morocco. *Geological Magazine* 130: 69–83.