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AN ELECTRON BACKSCATTER DIFFRACTION STUDY OF *GEESOPS*: A BROADER VIEW OF TRILOBITE VISION?

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INTRODUCTION

The calcite eyes of trilobites have been studied for over 100 years using methods including light microscopy (e.g. Clarke 1889; Campbell 1975; Towe 1973; Clarkson 1979 and Bruton and Haas 2003) and more recently cathodoluminescence (CL) imaging coupled with scanning electron microscopy (SEM) of samples etched in EDTA (Miller and Clarkson 1980). This work has provided a great deal of information on the mechanisms by which lenses collected light, drawing attention to the importance of the crystallographic orientation of lens calcite for focusing, and leading to sophisticated models of trilobite vision (Clarkson and Levi-Setti, 1975; Gál et al., 2000). The morphology and mode of life of phacopids, in particular *Geesops*, are well understood (Bruton and Haas, 2003a; 2003b) but observations on the internal structure of their lenses contradict the generally accepted models for image formation by schizochroal eyes. Recent technological advances have given new impetus to the analysis of crystalline materials and especially important has been electron backscatter diffraction (EBSD). This is a SEM-based technique that can be used to accurately 'map' variations in the crystallographic orientation of a sample down to the sub-micrometre scale by recording on a sensitive camera Kikuchi patterns that are formed by diffraction of an electron beam when focused on a polished sample tilted at 70°. Although this technique has been understood for over 50 years (Alam et al., 1954) and has been extensively used in disciplines such as metallography (Humphreys, 2001), until recently its Earth Science applications were limited to studies of structural geology and petrology (Nuchter and Stockhert, 2007). Recent applications of EBSD to biomineralisation research (Dalbeck and Cusack, 2006; Griesshaber et al., 2007) have mapped the crystal orientation and microstructure of calcite shells and in 2006 Lee et al. were able to apply this technique to investigating the microstructure of lenses in the schizochroal eye of *Dalmanites*. This paper describes results of an EBSD study of eyes of *Geesops schlotheimi* (Bronn, 1825) combined with more traditional microscopy techniques to reveal new aspects of trilobite lens structure.

METHODS

All work was undertaken on eyes in thin section and initial characterisation by optical microscopy (plane and cross-polarised transmitted light and reflected light) used a Zeiss Axioplan petrological microscope with a maximum magnification of 40 x. Optical CL imaging employed an equivalent microscope equipped with a CITL Technosyn 8200 MK4 luminoscope operated at 20 kV/200 nA. Images from the optical microscopes were collected digitally using a Nikon DN100 digital net camera. EBSD work used a FEI Quanta 200F SEM equipped with an EDAX/TSL system running OIM version 5.2 data collection software and using a Hikari high speed detector. Polished thin sections were produced by grinding specimens down and mounting, ground side down, on glass slides. Sectioning was carried out using a Buehler[®] Petrothin[®] and mechanical polishing used diamond lubricant, alpha alumina and colloidal silica. The thin sections were uncoated and studied with the SEM operated in low vacuum (4.4×10^{-1} Torr). Data were analysed and orientation maps and pole figures plotted using OIM version 5.2 analysis software. The lenses were chemically analysed qualitatively by simultaneous X-ray mapping during EBSD work and quantitatively by SEM spot analysis using EDAX Genesis hardware and software.

RESULTS

Eleven specimens of *Geesops schlotheimi* (Bronn, 1825) were analysed from the Eifelian of the Geeser Trilobitenfelder, Germany.

Lenses within the eye of *Geesops schlotheimi* vary significantly between specimens when viewed using plane polarised transmitted light and reflected light. Several thin sections contain lenses consisting of reasonably clear calcite crystals, others are more turbid and reflected light reveals microporosity as the source of this turbidity. A thin corneal covering, which can be traced into the alveolar ring, is present on the outer surface of some well preserved lenses; this too varies in appearance from optically clear calcite in

some lenses to being darker and possibly iron stained in others. In transmitted light between crossed polarizers the central and basal areas of the lenses are in optical unity but extinction angles along an outer 'fringe' of the lens vary, producing a sweeping extinction pattern as the microscope stage is rotated.

Several specimens have lenses that contain intralensar structures similar to the core and bowl as described by Clarkson (1975; 1979) and others (Campbell, 1975; Miller and Clarkson, 1980; Lee et al., 2007). These features are distinguishable from the rest of the lens by a distinct colour difference in plane polarised transmitted light. In some specimens the intralensar features are much darker than the enclosing lens calcite whereas in others they are optically clear and surrounded by a darker element of the lens. The clarity of the intralensar structures varies between thin sections.

Those lenses containing intralensar structures that are visible in transmitted light display equivalent features in CL images. The core luminesces more brightly than surrounding lens calcite whereas the intralensar bowl appears significantly duller. Cathodoluminescence imaging also reveals intralensar structures in lenses that apparently lack both intralensar bowls and cores when viewed in transmitted light (Fig. 1).

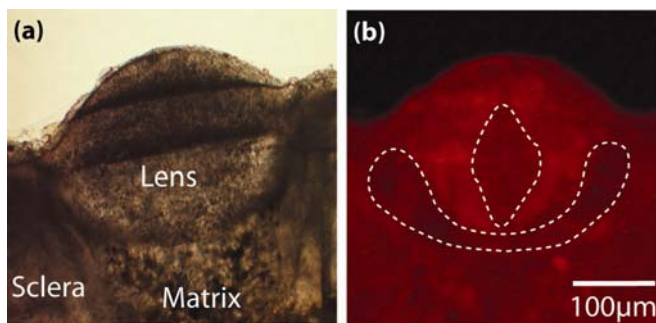


Figure 1. (a) Plane polarised transmitted light and (b) CL image of the same lens, seen in horizontal section. Note that an intralensar bowl and core (outlined) can be resolved only in the CL image. The eye has been cut perpendicular to the visual surface to produce horizontal cross-sections of the lenses, parallel to the plane in which the palpebral lobe lies.

X-ray mapping has highlighted the presence of magnesium within the eyes. In addition to calcium, magnesium occurs throughout all of the lenses mapped although in several cases it is more highly concentrated in the central and basal areas of the lenses than the fringe. Quantitative spot analysis reveals that the concentration of magnesium in lens centres can be three times that of the rest of the lens. These magnesium-rich areas are not always coincident with intralensar structures visible using transmitted light. In marked contrast, magnesium concentrations are significantly lower in the intralensar sclera and in the host limestone.

EBSD maps reveal a consistent pattern in the crystallographic orientation of calcite in the lenses of all specimens. The central and basal areas of the lenses have uniform orientation with the calcite *c* axes oriented parallel to the lens axis. The upper area of the lens contains a 'fringe' within which calcite *c* axes are radially arranged (Fig. 2a) and pole figures highlight the orientation spread (Fig. 2b).

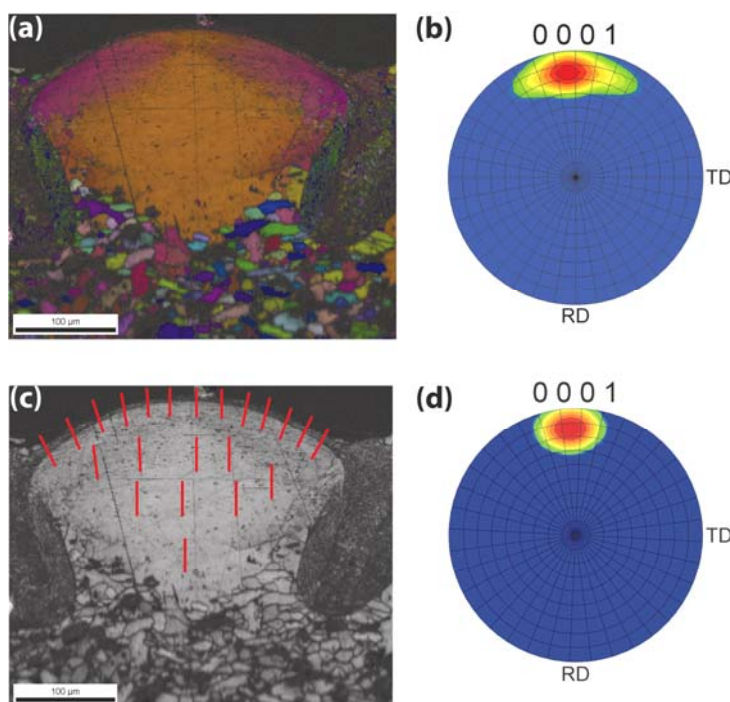


Figure 2. (a) EBSD orientation map of the lens in Figure 1. The gradual change in colour along the fringe denotes a change in *c* axis orientation. (b) Equal angle lower hemisphere pole figure showing the variation of crystal orientation throughout the lens in (a), the orientation of this lens is 75°. (c) EBSD map equivalent to (a) where orientation differences are not colour coded but indicated by the red lines, which are traces of the calcite *c* axis. (d) Pole figure of a *Dalmanites* sp lens (from Lee et al. 2006) showing a spread in crystal orientation of approximately 40°. Note the very significant difference in the spread of *c* axis orientations between lenses of the two species.

This radial fringe is visible in both horizontal and tangential sections of the lens. The thickness of the fringe varies between specimens although 40-55 μ m is typical. Fringe thickness can also vary by up to 50 μ m between constituent lenses of the same eye. This microstructure does not extend into the cornea, the constituent calcite crystals of which have no preferred orientation. The interlensar sclera is very finely crystalline and has a distinct microstructure that is very different to that of lens calcite. The arrangement of crystals within the limestone matrix is random, although crystals immediately beneath the lens can share its orientation (Fig. 2a).

Calcite forming the fringe of a single lens can differ in *c* axis orientation from that of the lower part of the lens by up to 50°. EBSD misorientation profiles, which illustrate the change in crystal orientation from point to point along a line, show the change from uniform crystal orientation to the splaying of orientations to be gradual, as is the variation in *c* axis orientation within the fringe itself. Misorientation profiles can also highlight sub-grain boundaries within the lens; some lenses, possibly less well preserved, consist of several calcite crystals along the fringe, others display very fine scale crystallisation of a single crystal (Fig. 2a).

DISCUSSION

The lenses of all specimens studied here have a similar microstructure, which was initially observed by light microscopy and confirmed using EBSD. A similar arrangement of lens calcite crystals has been observed previously in several species of phacopids that have been variably diagenetically altered (Campbell, 1975) as well as in the lenses of other *Geesops* species from the same area which Bruton and Haas, (2003b) interpreted as being composed of aggregates of crystallites. EBSD has also highlighted how the thickness of the fringe and size of its constituent calcite crystals can vary significantly between lenses in a single eye. Some lenses appear to consist of a single calcite crystal in which the variation in *c* axis orientation around the fringe is extremely gradual (e.g. Fig. 2a). Although there are clear differences in crystallographic orientations within the lens, these results are consistent with Towe's conclusion (1975) that each lens was a single calcite crystal as EBSD misorientation profiles show no presence of sub-domains or crystallites. *Geesops* lenses analysed in the present study clearly differ in microstructure from those of *Dalmanites* sp. that were shown by Lee et al. (2007) to have uniform *c* axis orientation (Fig 2d). These results suggest that the phacopids developed at least two very different mechanisms for focusing light with the radiating fringe of *Geesops* possibly being used to guide peripheral light rays into a more central position within the lens.

The presence of the intralensar structures in CL images and the concentration of magnesium in the centres of lenses that are apparently featureless in transmitted light, support the suggestion by Campbell (1975), Clarkson (1975; 1979) and others (Clarkson and Levi-Setti, 1975; Miller and Clarkson, 1980) that these features are not the product of alteration, but original components of the lens (albeit partially modified during diagenesis). CL does not provide an exact indication of the lens chemistry but it does imply at least a subtle difference in composition between areas of varying luminescence. Features identified by CL imaging but absent in transmitted light may be remnants of the original intralensar structures.

CONCLUSIONS

EBSD and allied electron beam techniques have been used very successfully to confirm observations and interpretations made using traditional methods of analysis and to provide a wealth of new information. The spread of crystal orientation along the lens fringe may have new implications on the visual field of these trilobites. Previous studies into trilobite visual fields (Clarkson, 1966a; 1966b) have been based on the assumption that lens calcite is aligned parallel to the lens axis and that lens spacing allowed a latitudinal view of 15-20° (Stockton and Cowen, 1976). The 'intake range' of light travelling parallel to the lenses *c* axes orientation has here been shown to be much wider in the *Geesops* studied than previously calculated for phacopids, potentially providing the trilobite with a much broader field of vision and also a greater overlap of the visual fields of individual lenses, possibly enhancing the stereoscopic abilities of the eyes. Such wide visual field were also deduced by Schoenemann (2007) who argued these eyes functioned as a neural superposition system. EBSD and EDX results have not as yet provided conclusive answers as to how the schizochroal eye produced images but have raised important questions about the exact functions of each of the individual lens components.

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