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Colour Patterns in Devonian Trilobites

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Abstract: Many living marine animals exhibit striking colour patterns on their external skeletons or on exposed flesh. Such colour patterns surely existed in fossil animals, but usually have faded, partially or more often completely, or have been modified by diagenesis. Some reported patterns may indeed have resulted from diagenesis alone and thus are not original. Here we assess colour patterns in trilobites in Devonian specimens from North America and in new material from Germany. Specimens of *Eldredgeops crassituberculata* (Stumm, 1953) from the Middle Devonian Silica Shale, Sylvania, Ohio show spots on the pleurae, a brown band on the axial ribs and shadowy brown patches on the glabella. We advance reasons why these are most likely original. Distinctive patterns in the pygidia of *Scutellum geesense* Rud. & E. Richter 1956, *Calycoscutellum sp.*, *Scabriscutellum scabrum* (Goldfuss, 1842) and *Thysanopeltella acanthopeltis* Barrande 1852 from the Devonian of Germany are illustrated here. Several specimens from different localities show a medium brown band fading to whitish towards the margin of the pygidium. These patterns are most unlikely to be random or, as argued here, diagenetic. They represent, in our opinion, original colour bands. We speculate that these colour patterns may have functioned as camouflage in a shallow-water visual world determined by ever-changing patterns of light.

Keywords: Camouflage, colour pattern, devonian, eldredgeops, palaeozoic, phacopid trilobite, scutellum, trilobite.

INTRODUCTION

Little is known about colour patterns in trilobites, because the pigments of which they are composed usually denature through time, bleach out and/or are removed by diagenesis. Even so, colour patterns have been identified in Ordovician cephalopods [1], Permian gastropods [2], Middle Jurassic echinoids (Cotswold Hills, England, personal observations ENKC) and many other marine invertebrates. The preservation of melanophores, structures containing black-brownish pigments, has recently been reported from Jurassic feathers (e.g. Carney *et al.* [3]). Melanin itself has been understood to be a very stable polymer form (for an overview of this discussion see Schoenemann *et al*. [4], also [3, 5]. It is quite ubiquitous in nature, expressing colour patterns in skins of all kind, protecting against UV or functioning as a screening pigment in visual systems [6, 7].

Trilobites were generally subject to considerable predatory pressure, as indicated by the many adaptations for enrolment, and some form of disguise or camouflage would have thus been of great survival value. The shells of tiny forms as of the supposedly planktonic *Ctenopyge* [8] or benthic *Burlingia* [9] may have been translucent, together with some pelagic forms as *Opipeuterella*, as comparable to many kinds of shrimps living today. But in larger trilobites, especially the benthic ones, colour patterns may have supported an effective camouflage. It may be assumed that most exoskeletons were pigmented, either uniformly or irregularly patterned. The "Treatise" of 1959 [10] cites four instances of colour markings in trilobites: Williams [11] described a pygidium with paired rows of pigmented spots of *Phillipsia tenuituberculata* from the Mississippian of Missouri. Raymond [12] illustrated fan-shaped bands transversing pleural regions in a pygidium of the Middle Cambrian *Anomocare vittata* from Alabama, Wells [13] noted dark areas along the thoracic axial furrows in *Isotelus maximus* from the upper Ordovician of Ohio and Teichert [14] found fan-shaped bands and paired rows of pigmented spots in *Ditomopyge meridionalis* from the Permian in Western Australia.

More recent reports can be found in Esker [15] and also Whiteley *et al*. [16, pl. 103], and most recently in 2013 by McRoberts *et al.* [17] in phacopid trilobites, *Eldredgeops rana* (Green 1832) [18] and in *Greenops boothi* (Green 1837) [19] from the Devonian of New York, Esker [15] described dark spots all over the exoskeletons wherever these were intact and unweathered. These were reported as comparable to those described by Teichert [14] in the pygidia of *Ditomopyge meridionalis* from the Permian of Australia. Babcock [20] however dismissed these supposed colour patterns as being of diagenetic origin, which underlines the difficulty of being certain that the patterns seen were original. This is indeed a problem, as exemplified by the different preservation of the eye-lenses (which are green) and the exoskeleton (which is red) in some silicified Moroccan phacopids [21]. McRoberts *et al.* [17] provide compelling evidence both from thin sections and constant

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patterning in 25 specimens of *Eldredgeops rana,* that the structures seen are at least of original biological origin. These take the form of regularly arranged circular spots within the cuticle as can be seen in McRoberts documentation as in the specimen described here. They are arranged in a fairly constant pattern, and we think it likely that they would have acted to break up the outline of the trilobite, thus confusing predators, but also it is possible that may have enhanced sexual attractivity, or have functioned as Bates´s mimicry.

MATERIAL AND METHODS

All morphological descriptions used herein follow the terminology of Whittington in Kaesler *et al*. (1997) [22].

All scutelluid specimens belong to the collections of the National Museum of Scotland (NMS), the specimens of *Eldregeops* are housed at Naturwissenschaftliche Sammlungen Bürgermeister-Müller-Museum Solnhofen (BMMS); outstreched specimen BMMS BK 16-1, enrolled specimen BMMS BK 16-2. The extremely rare pygidium of *Thysanopeltella* was collected by H. Steinhausen, the pygidia of *Scabriscutellum* (Location Sauerland) were collected by H. Wieland.

Eldregeops Struve, 1990 [23]

Remarks

Most known specimens of *Eldredgeops crassituberculata* (Stumm, 1953) [24], are homogeneously dark brown, but the two individuals documented here have a spotted exoskeleton, like those described by previous authors [15-17]. These come from the Middle Devonian Silica Shale, Silvana, Ohio. They show dark brown spots along the pleurae (Fig. **1C**, **E**), a brown continuous line in the middle (trans.) of the axial rings (Fig. **1B**, **D**), and irregularly flaky dark brownish patterns on the glabella (Fig. **1A**), while the ground colour of the trilobite is a bright to medium brown. Our observtions accord with, and confirm the phenomena described by McRoberts *et al*. [17] and the authors mentioned before.

A broken second left thoracic pleura in specimen BMMS BK 16-1 reveals that it includes spherical structures, which seem not to correlate with the superficial spots (Fig. **2**).

A comparison with the congener *E. rana* investigated by McRoberts [17] might be interesting at this point. While the cuticle of one group of *E. rana* was much brighter than those of the *E. crassituberculata* (*E.c*.) investigated here, in *E. rana* the spots on the pleurae appear in relation to the size of the pleura smaller than in *E. c*. In the latter just one row of wide dots is established, while in *E. rana* especially the proximal part of the pleurae appears ”really spotted” by numerous loosely clustered dots. The medial brown line on the pleural rings seem to be missing in *E. rana* and the irregular brown patch at the glabella of *E. c.* does not give the impression of having arisen by fusing spots, and the wide-band-like shape has no margins which suggest circular structures to be origin of this flake.

The character of the spots in *E. c.* resembles much more the bright ones in McRoberts' darker specimens, figured in his Figure 2F. We also find the spheres described by

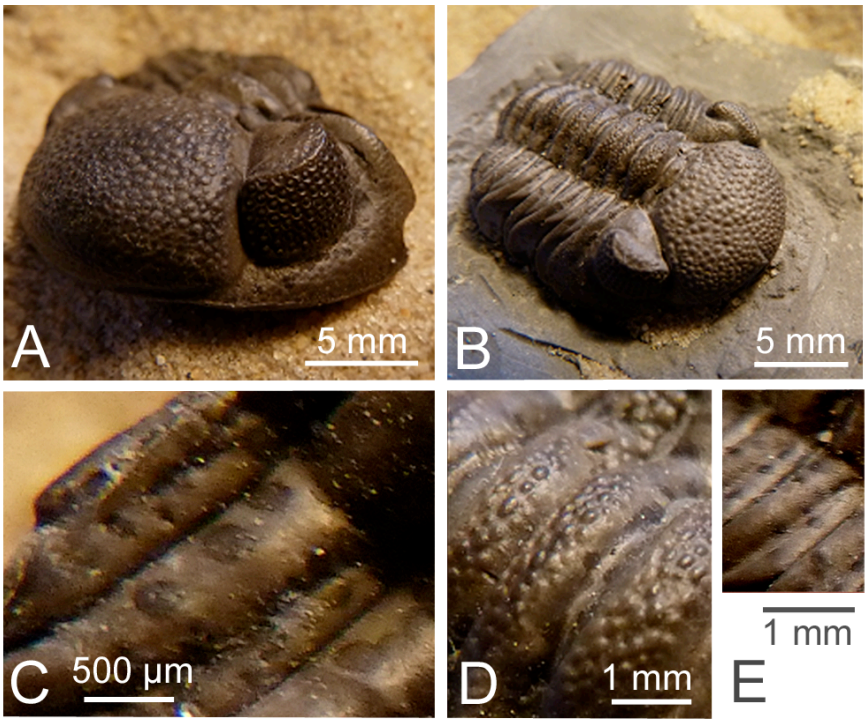

Fig. (1). Colour patterns in *Eldredgeops crassituberculata* (Stumm, 1953) • **A** - *Eldredgeops crassituberculata* (Stumm, 1953) (BMMS BK 16-1) complete specimen with dark brown shadowy pattern on the glabella. • **B** - *Eldredgeops crassituberculata* (Stumm, 1953) (BMMS BK 16-2) complete specimen. • **C** - Spotted pattern on the pleurae (BMMS BK 16-1). • **D** - brown transverse band on the axial rings (BMMS BK 16-2). • **E** - spotted pattern on the pleurae (BMMS BK 16-2).

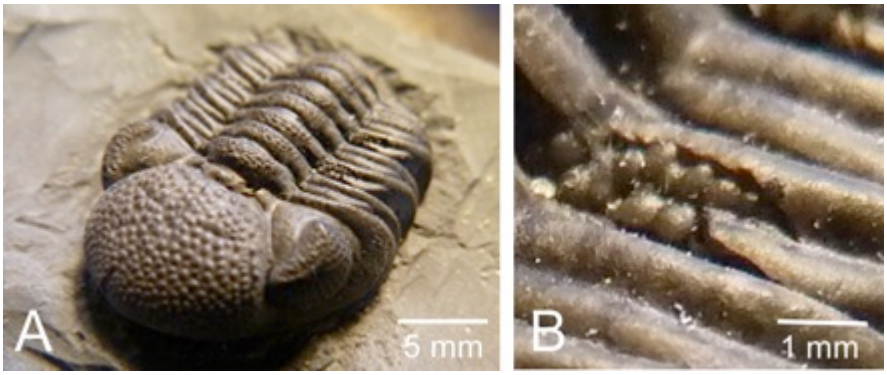

Fig. (2). Spherical structures inside of the pleurae in *Eldredgeops crassituberculata* (Stumm, 1953) • **A** - *Eldredgeops crassituberculata* (Stumm, 1953) (BMMS BK 16-1) complete specimen. • **B** - Spherical structures inside of the second left pleura.

McRoberts, they are of a similar diameter, but in the specimen of *E. c.* these are dark brown and not translucent. While in *E. rana* the spheres correspond with the dotted pattern, in *E. c.* they seem not to do so. Any interpretation of these spheres appears difficult. McRoberts suggests, that in *E. rana* the calcitic, pigmentless and translucent spheres are a window through the cuticle to biochromes in the underlying epidermis. The latter would not be likely for the dark-brown spheres found in *E. c.* here. We would suggest that they may be interpreted as relicts of parasites, which usually have a very reduced morphology. Alternatively, they may be cancerous structures, or, much more probably, it seems that they represent a so far unknown structure of the trilobite exoskeleton.

Esker [17] described for the colour patterns he observed in *Eldregeops rana* that the spots expand into small star-shaped branches, with no particular orientation, and that the spots in the different specimens had a different relative diameter when compared with the dimensions of the animal.

Scutelluids

The exceptionally good preservation of trilobites originating from the lower Middle Devonian of the Rheinisches Schiefergebirge in Germany, in the Eifel and the Sauerland, allows the recognition of some supposed colour patterns, though this may be less firm than that for *Eldredgeops*. We are aware that there must remain some residual doubts about whether the colour patterns we describe here are original. The main reasons why we believe that they are is that the same kinds of colour patterns are present in different specimens from different sources, and thus different conditions of preservation. But we are also aware, for example, that the boundary between the inner edges of the pygidial doublure in the scutelluids described here more-or-less coincides with the margin of the supposed colour band. Many pygidia, less well preserved, found in the Eifel or Sauerland, appear completely whitish, which contradicts the assumption of a structural origin of this colour pattern.

Colour patterns also can be observed in some of the extraordinarily well preserved trilobites of the famous and classic locatity Pelm Salmer Weg, the "Trilobitenfelder" of Gees/Gerolstein and adjacent locations. Although excellent shell preservation there is normal [25] supposed colour patterns are sometimes present. We believe that such colour patterns are present in the pygidium of *Scutellum geesense* Rud. & E. Richter 1956 [26] (NMS G 2013 1, NMS G 2013 2, Fig. **3A**, **B**) from the Eifelian, Middle Devonian, and *Thysanopeltella acanthopeltis* Barrande, 1852 [27] (NMS G 2013,

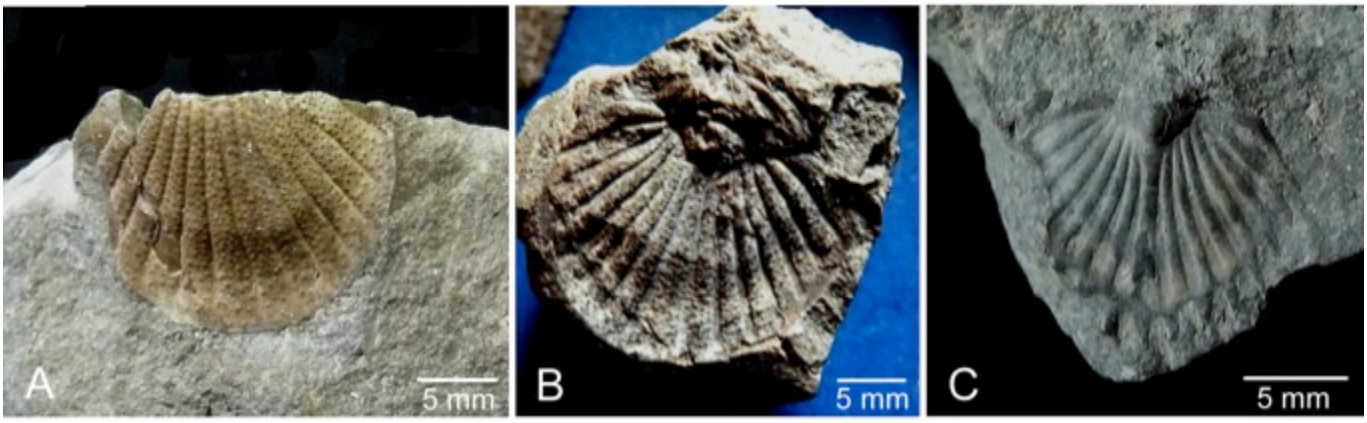

Fig. (3). Colour patterns in pygidia of scutelloids. • **A** - *Scutellum geesense* Rud. & E. Richter 1956 (NMS G 2013 1) brown band fading into a bright margin of the pygidium • **B** - *Scutellum geesense* Rud. & E. Richter 1956 (NMS G2013 2) brown band fading into a bright margin of the pygidium, different specimen • **C**: - *Thysanopeltella acanthopeltis* Barrande, 1852 (NMS G 2013 3), repetitive banded structure, in principle similar to those of *S. geesense*. Locations **A**, **B**, **C**: Ahrdorf Formation, Flesten Member, Eifelium, Middle Devonian Gees/Gerolstein, **A**: Trilobitenfelder Salmerweg, **B**, **C**: Auberg, close to Salmerweg, Eifel, Germany.

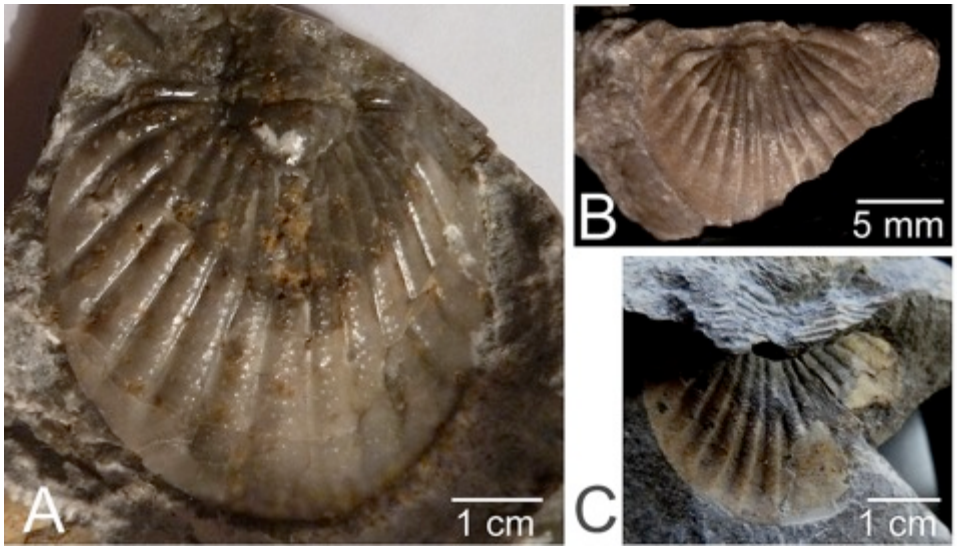

Fig. (4). Colour patterns in pygidia of different scutelluids • **A** - *Calycoscutellum sp*. (NMSG 2013 4) - Dark brown pygidial "plateau" (adaxial portion of the pleural field), • **B** - Undescribed taxon, probably closely realted to *Calycoscutellum sp.* (NMS G 2013 5) - Dark brown pygidial "plateau" (adaxial portion of the pleural feld) in a specimen of the same location). • **C** - Smaller dark brown pygidial "plateau" in a specimen from a different location. • Locations: **A**, **B**: Givetian, upper Middle Devonian, Fretter Mühle, Sauerland, Germany, **C**: Lower Eifelian, Middle Devonian, Trilobitenfelder, Salmerweg, (Gees/Gerolstein, **C**: Auberg close to Salmerweg), Eifel, Germany.

Fig. **3C**), Ahrdorf Formation, Flesten Member, Eifelium, Middle Devonian (Auberg, close to Salmerweg).

A slightly different mode of preservation is present in trilobites from the Sauerland (Fig. **4**), *Calycoscutellum sp.* (two specimens of possibly different species, NMS G 2013 4, NMS G 2013 5, Fig **4A**, **B**) and *Scabriscutellum canaliculatum* (Goldfuss, 1843) [28] (NMS G 2013 6, Fig. **4C**). *Calycoscutellum sp.* from this location originate from the upper Givetian, upper middle Devonian, Fretter Mühle, Sauerland, Germany, *Scabriscutellum caniculatum* (Goldfuss, 1843) [28] comes from the Lower Eifelian, Middle Devonian, Trilobitenfelder, Salmerweg, Germany (Gees/Gerolstein: C Auberg, close to Salmerweg, Eifel, Germany).

The two specimens of *Scutellum geesense* Rud. & E. Richter [26] have a light brown pygidium; near the posterior end there is a brownish ring, which fades out distally into a bright, almost white band up to the margin of the pygidium. This pattern can be observed equally in both specimens independently; it is not random. *Thysanopeltella acanthopeltis* Barrande, 1852 [27] shows again a similar pattern, which, however, is repeated twice. From the axis distally a bright coloured band can be observed, followed by a dark band, then a bright one follows again and the whole pattern is finished with a darker band again. These four bands are of almost equal width and run concentrically with the course of the zig-zag margin of the pygidium.

A different kind of banding is seen in the colour pattern of *Scabriscutellum scabrum* (Goldfuss, 1852) [28] and *Calycoscutellum sp*., and another similar, probably still unknown species. It is identical in the specimens found at two different localities (Sauerland and Gees/Gerolstein) and from different stratigraphic levels. *Scabriscutellum* shows a wide bright band from the lower margin of the pygidium upwards to the ”plateau” (adaxial portion of the pleural field) surrounding the axis. This ”plateau” (adaxial portion of the pleural field) itself is dark brownish coloured in all four specimens from the different localities. In *Calycoscutellum sp.*, this brown colour may also have covered the whole body of this trilobite, because it is continued distally from the axis as indicated in Fig. (**4A**, **B**), where the beginning of the thoracic axis is likewise still preserved, showing the same colour as the adaxial portion of the pleural field. An alternative explanation is based on the pygidial morphology in these scutelluids - the light coloured band present in the posterior part of the pygidium corresponds well with the extent of the pygidial doublure. The brownish plateau, on the other hand, represents the part of the pygidium without the doublure, with different mechanical and structural features. It is most parsimonous that the different penetration of these various exosceletton parts by iron oxides resulted in different colours.

DISCUSSION

The exceptionally good preservation of trilobites which originate from the Middle Devonian of the Rheinische Schiefergebirge in Germany, the Eifel and the Sauerland, allows the study of some supposed colour patterns in trilobites, as does the preservation of the Middle Devonian phacopid trilobite *Eldredgeops crassituberculata* (Stumm, 1953) [24] from the Silica Shale, Sylvania, Ohio. Such patterns may well reflect an effective camouflage, ensuring that the trilobites were invisible to predators in the constantly shifting light patterns on the sea floor. The depth at which these trilobites lived remains unknown, if it was less than 10-20 meters camouflage may well have been their best defence. The scutelluids investigated here, such as *Scutellum geesense* Rud. & E. Richter, 1956 [26], *Scabriscutellum scabrum* (Goldfuss, 1852) [28], *Calycoscutellum sp.* and *Thysanopeltella acanthopeltis* Barrande, 1852 [27] lived in an environment which was dominated by optically orientated animals, and they themselves were equipped with excellent

compound eyes. While paralejurids were able to enrol into a closed ball if threatened [29], scutelloids were able to at least partially enrol, although not entirely effectively. Camouflage as provided by the supposed colour patterns described here would be a supportive survival strategy, and one may deduce that these trilobites were freely moving, whether benthic or swimming (but not burrowing). The same is valid for *Eldredgeops crassituberculata* (Stumm, 1953) [24].

Colour patterns are seldom preserved in trilobites, or indeed other fossils, since they denature through time or are removed by diagenesis. Comparatively few have been documented. The evidence of new material, presented here, confirms that some specimens of the Middle Devonian phacopid *Eldredgeop*s, from eastern North America, had round spots and bands forming distinct patterns. Likewise several scutelluids from the Lower Middle Devonian of western Germany have defined colour bands. The same kinds of colour patterns are found in specimens from different localities, strongly suggesting that they are original. Such colour patterns would have given their bearers an effective camouflage, diguising them from predators.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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