Original spotted patterns on Middle Devonian phacopid trilobites from western and central New York

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ABSTRACT

Preserved color markings in Paleozoic fossils are rare and have been hypothesized to reflect muscular attachment scars, diagenetic artifacts, or the altered remains of biochromes (organic pigments) or sclerochromes (structural colors) embedded in fossilized skeletal remains. More than 25 exceptionally well preserved phacopid trilobites with spotted patterns are described from the Middle Devonian of western and central New York State (USA). The small (~0.23 mm) circular markings appear either brown on a lighter cuticle, or white on a darker cuticle. Thin section, scanning electron microscope imaging, energy-dispersive X-ray spectroscopy, and wavelength-dispersive spectroscopy elemental analyses show spots to be microcrystalline low-Mg calcite spheres embedded within the primary layer of the cuticle below the prismatic layer. Surrounding exoskeleton (low-Mg calcite) exhibits coarser crystallinity, typical lamellar structures, pore canals, and possible organic matrix, as expected for relatively unaltered trilobite skeletons. Potential diagenetic mineralogies or microstructures were not observed, making diagenesis an unlikely explanation. Spot distribution, morphology, and position in exoskeleton rule out a relationship with sites of musculature attachment and/or insertion. We suggest that spots represent original biologic structures manifested as either crystallographic or optical loci resulting in sclerochrome spots or possibly clear spots embedded in the cuticle that contrasted with a pigmented exoskeleton and may have served as windows to an underlying epidermis.

INTRODUCTION

Color (and colored patterning) is pervasive in the integument systems (epidermis and exoskeletons) of extant animals. Preservation of color in the fossil record, however, is rare; few examples are preserved within exoskeletons (Kobluk and Mapes, 1989; Hollingworth and Barker, 1991) or, more rarely, in soft tissues (Vinther et al., 2010; Lindgren et al., 2012). The correspondence of fossil color to original color in living organisms is not straightforward; diagenetic processes may produce colored markings (i.e., liesegang banding) unrelated to the original color of the animal. Even if fossilized color had a biological cause, it does not necessarily mean that it represents original color, as exoskeletons often have minute pore canals or cavities that can serve as loci for diagenetic mineralization.

Color in organisms is often associated with either camouflage or behavior (i.e., communication and mate selection). In many animals, colored markings are a result of biochromes (e.g., carotenoid and melanin pigments) produced by specialized epidermal or other cells embedded within the integument (e.g., Fox, 1972). Organisms may also exhibit sclerochromes, or structural colors, in their hard parts (e.g., iridescence in mollusk shells, arthropod exoskeletons, and bird feathers) created by differential interference, scattering, and absorption of light by structural or compositional differences within the organism's integument (Fox, 1972). Both biochromes and sclerochromes are known from the fossil record but are subjected to diagenetic processes including biogeochemical degradation (for biochromes) or alteration of the skeletal ultrastructure and composition (for sclerochromes) that lead to their destruction over geologic time (Blumer, 1965; Hollingworth and Barker, 1991; Vinther et al., 2010; McNamara et al., 2011).

Supposed original markings on the exoskeletons of trilobites have been known for nearly a century (e.g., Raymond, 1922). Devonian examples have been variously interpreted as diagenetic artifacts on or within the cuticle, unrelated to biological structures (Babcock, 1982); sites of ventral muscular attachment (Eldredge, 1971; Campell, 1975; Whiteley et al., 2002); features related to potential sensory structures such as tubercles, pustules, or pores (Babcock, 1982); or diagenetically modified remains of pigmentation in the cuticle (Esker, 1968; Babcock, 1982). Previous interpretations are insufficient because they were based on significantly diagenetically altered material (Raymond, 1922). Here we report on phacopid trilobites from the Middle Devonian of western and central New York that exhibit patterned markings in their exoskeleton. Although these phacopids exhibit markings superficially similar to those previously reported by Esker (1968) and Babcock (1982), they appear to be better preserved and provide an opportunity for new analytical analyses in order to assess their origin.

MATERIALS AND METHODS

Our collection of spotted trilobites consists of more than 25 mostly complete *Eldredgeops rana* from five localities within the Middle Devonian (Givetian) Hamilton Group in central and western New York (Fig. 1). The majority of specimens (n = 23) are from a private creek exposure (locality, loc. 3) in the town of Darien where they occur in the Wanakah Member of the Ludlowville Formation. The best specimens from this locality occur mostly enrolled but in random orientations within the lower third of an 18–20-cm-thick, blocky, gray carbonate mudstone bed supporting a diverse macrofauna, suggesting storm-generated transport prior to deposition. Burrows secondarily replaced with pyrite are present and occasionally common in the host sediment, but the fossils appear largely unaltered. The bed is highly productive; clusters of 10–20 articulated individuals are common and larger clusters (20–100 individuals) are less frequent. The majority of the trilobites from this locality are *E. rana,* all of which are spotted, while other species (*Greenops grabaui*, *Bellacartwrightia whiteleyi*, and *Pseudodechenella rowi*) are extremely scarce and have not been observed with spots.

Other spotted specimens are from the Wanakah Member of the Ludlowville Formation from near the mouth of 18 Mile Creek in the town of Hamburg (loc. 1), from the Windom Member of the Moscow Formation near Portland Point (loc. 4), and from a private shale quarry in the town of Earlville (loc. 5) (see the GSA Data Repository[1]). Spotted *E. rana* from localities 2 and 5 are from gray to black, organic-rich, fissile mudshale supporting a less diverse fauna and likely deposited in deeper marine environments with reduced O_2 levels.

Specimens of *E. rana* (from loc. 3) were mechanically prepared and digitally imaged, and then individual spots were spatially mapped. Two specimens were transversely sectioned along thoracic segments, epoxy mounted on glass slides, and polished to 30 µm for petrographic

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[1]GSA Data Repository item 2013166, materials and methods, Figures DR1 and DR2, and Tables DR1 and DR2, is available online at www.geosociety.org/pubs/ft2013.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

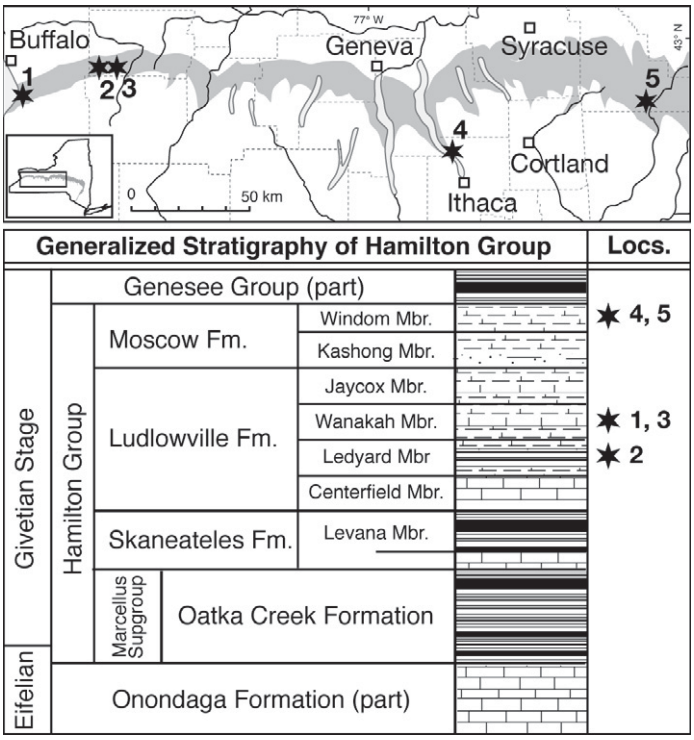

Figure 1. Locality and generalized Middle Devonian stratigraphy of western New York. Shaded area represents outcrop of Hamilton strata. Fm.—formation; Mbr.—member; locs.—localities.

microscopy and subjected to wavelength dispersive spectrometry (WDS), energy dispersive X-ray (EDX) elemental analyses, and scanning electron microscopy (SEM) backscatter imaging (see the Data Repository). Microstructural textures were documented on a fractured and acid-etched skeletal fragment and an isolated sphere using secondary electron SEM (see the Data Repository). In addition to the locality register, figured specimens, thin sections, and SEM stubs are housed at the Paleontological Research Institution (Ithaca, New York).

SPOTTED MARKINGS

The majority of specimens exhibit spots visible on the dorsal surface of exoskeleton; either dark brown circles with relatively sharp boundaries or as somewhat lighter brown or tan spots with a thin, but distinctive, darker halo or rim on a lighter exoskeleton (Figs. 2A–2D). Several specimens with darker brown to black cuticles exhibit tan or white spots (Figs. 2E and 2F). Where closely packed, spots may coalesce to form irregular shapes (Fig. DR2; see the Data Repository). Isolated spots are generally circular, 0.01–0.5 mm in diameter ($\bar{x}$ = 0.23 mm, n = 2418 obtained from 5 specimens). On well-preserved dorsal surfaces, spots do not correspond to surficial topography (e.g., tubercles or pits; see Figs. 2A–2F and 3A). In a couple of fractured and/or weathered specimens, the markings are revealed as spheres embedded beneath the dorsal surface of the exoskeleton (Figs. 3A–3H).

Structure and Composition of Markings

Petrographic microscopy on polished transverse sections and SEM imaging on etched skeletal fragments demonstrate that spots are completely embedded within the primary (foliated) layer of the exoskeleton below the prismatic layer (Fig. 3). In thin section, most spots exhibit circular or oval outlines, and in some instances irregular shapes caused by the coalescing of multiple spots. In plane and cross-polarized transmitted light, spots appear as clear calcite and are easily delimited, but at higher magnifications, the boundary with surrounding cuticle appears more diffuse. Some spots are surrounded with a rim of even clearer calcite that extends from the lower boundary of the exoskeleton to its upper layer just below the thin prismatic layer. The surrounding cuticle exhibits typical lamellar structures and pore canals suggesting a relatively unaltered exoskeleton (see Dalingwater, 1973; Teigler and Towe, 1975; Størmer, 1980; Wilmot and Fallick, 1989). In one specimen (Fig. 3F), steeply inclined pore canals, 2 µm in diameter, are discerned rising from the ventral surface of the exoskeleton to the lower surface of the spot and into the base of what may be an organic-rich matrix layer in the surrounding exoskeleton.

EDX and WDS analyses (Figs. DR1 and DR2; Tables DR1 and DR2 in the Data Repository) confirm a relatively pure, low-Mg calcite mineralogy for spots with an average composition of $Ca_{0.97}Mg_{0.03}CO_3$ and trace (<0.01%) amounts of Sr, Mn, Fe, Na. The surrounding exoskeleton has a mineralogy essentially identical to that of the spots, as expected for the mineralized component of unaltered trilobite cuticle (see Dalingwater, 1973; Teigler and Towe, 1975; Størmer, 1980; Wilmot and Fallick, 1989). Potential diagenetic mineralogies (e.g., pyrite or phosphate) were not observed in the exoskeleton, even though pyrite can be common in the surrounding sediment (Fig. 3C). Depressed Sr/Ca ratios were not observed, further suggesting little diagenesis (see McAllister and Brand, 1989). SEM imaging (Figs. 3E and 3F) reveals that the surrounding exoskeleton has coarser and more variable crystals (10–60 µm diameter) with some void space, whereas the sphere interiors contain very small (1–3 µm diameter) angular crystals. Potential diagenetic crystalline textures such as

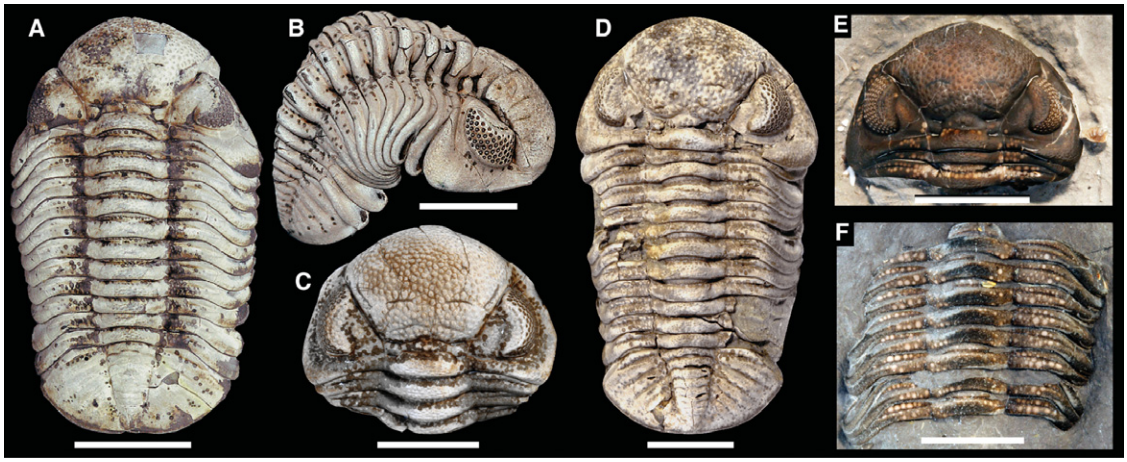

Figure 2. *Eldredgeops rana*. Representative patterns and surface expression of spot types. A: Dorsal view, prone, PRI (Paleontological Research Institution) 67458 (locality, loc. 3). Scale bar = 1 cm. B: Right lateral view, partially enrolled, PRI 67459 (loc. 3). Scale bar = 0.5 cm. C: Dorsal view, cephalon and first three thoracic segments, enrolled, PRI 67460 (loc. 3). Scale bar = 1 cm. D: Dorsal view, prone, PRI 67461 (loc. 3). Scale bar = 1 cm. E: Dorsal view, cephalon and first two thoracic segments, partial specimen, PRI 67462 (loc. 1). Scale bar = 1 cm. F: Dorsal view, incomplete thorax, PRI 67463 (loc. 4). Scale bar = 1 cm.

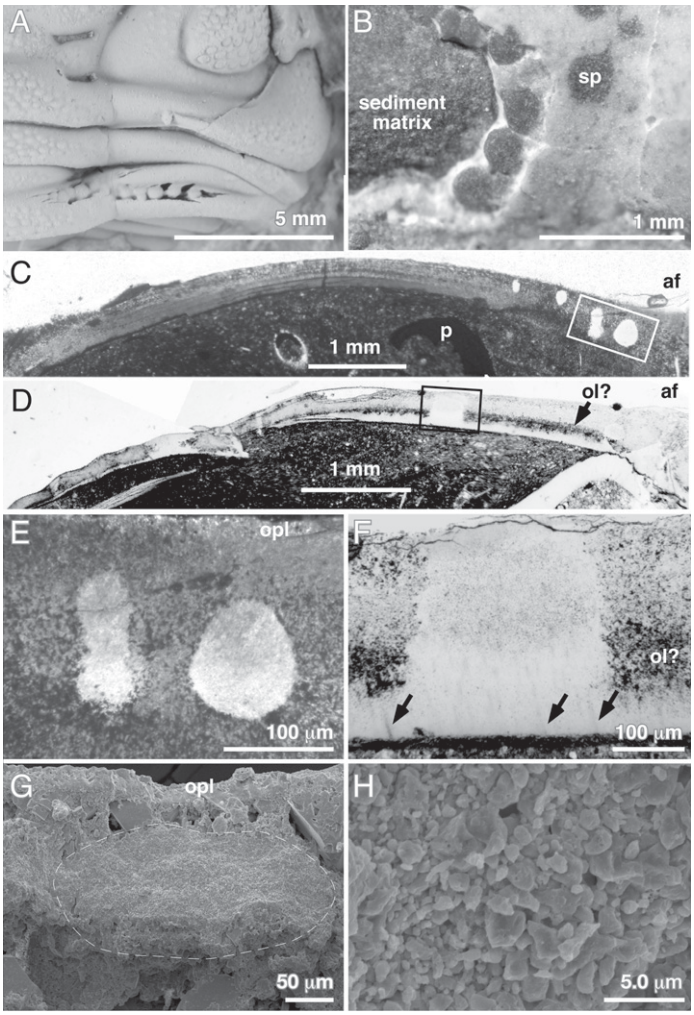

Figure 3. *Eldredgeops rana*. A: PRI (Paleontological Research Institution) 67462 (locality, loc. 1) coated in NH_4Cl, dorsal view, partially exposed spheres within right pleural furrow, second thoracic segment. B: PRI 67464 (loc. 3) dorsal view, left axial furrow, third thoracic segment, spheres embedded in cuticle and surface expression of dark sphere (sp). C: Transverse section, PRI 67465 (loc. 3), left pleura, eighth thoracic segment; note infilled pyrite burrow (p) and axial furrow (af). D: Transverse section, PRI 67466 (loc. 3), left pleura of third thoracic segment; note opaque band of possible organic matrix (organic-rich layer, ol; axial furrow, af). E: Transverse section, PRI 67465 (expanded view of spots in C) showing spots under cross-polarized light. F: PRI 67466 (expanded view of spot in D) showing cylindrical halo around flattened sphere; note pore canals (arrow) and possible organic-rich layer (ol?) in adjacent cuticle. G: PRI 67467 (loc. 3), scanning electron microscope (SEM) transverse image, microcrystalline calcite in sphere (dashed line) with larger calcite crystals and void space in surrounding exoskeleton and possible outer prismatic layer (opl), fractured specimen. H: PRI 67468 (loc. 3), SEM transverse image, microcrystalline calcite within isolated sphere interior; HCl-etched specimen.

dendritic and fused microstructures or solution cavities (e.g., McAllister and Brand, 1989; Wilmot, 1990) were not observed in the spheres.

Patterning and Spot Distribution

Eldredgeops rana specimens (from loc. 3) exhibit variable spotting frequency; some individuals have more than 500 spots (e.g., Figs. 2C and 2D) and others have fewer than 100 (e.g., Figs. 2A and 2B) distributed across the exoskeleton. Spots are nonrandomly distributed on the entire dorsal exoskeleton and the regions of occurrence are bilaterally symmetrical (Figs. 2 and 4). Spots are not correlated with the locations of tubercles on the exoskeleton or with other surface features (e.g., sites of known muscle attachment or facial sutures). Cephalic spots are somewhat less numerous than those of the thorax and appear concentrated across the occipital lobe and glabella, especially in the occipital furrow separating the two. Spots are concentrated on the surface above the eye and axial furrows, rarely reaching the ridge adjacent to the upper visual surface of the eye. Spots are also arrayed across much of the lateral margins of the glabella, concentrated in the furrow below the visual surface. Spots on thoracic segments are most dense in the associated furrows, anterior and posterior margins of individual pleura, and in a transversely linear arrangement across axial rings and articulating half-rings. In general, spots become less frequent and smaller in size abaxially and rarely occur distally. Likewise, spots on the pygidium are most dense along the axial furrows and remain relatively dense down the length of each pleural furrow.

INTERPRETATION AND DISCUSSION

The exoskeletal spots of *Eldredgeops* could be the result of one of several potential causes: traces of epibiont and/or endobiont activity, muscle attachment scars (Whiteley et al., 2002), remnants of original pigmented color (Esker, 1968; Babcock, 1982), or diagenetic artifacts (Babcock, 1982). The spots cannot represent the attachment sites of epibionts or infilled and/or replaced endolithic borings because they are embedded within the exoskeleton without identifiable entrances on the exoskeletal surface. Furthermore, the bilaterally symmetrical distribution is consistent with intrinsic biologic patterning (e.g., Bauer, 1981) rather than random epizoan settling. Spots cannot represent muscle scars because they do not penetrate to the ventral surface of the exoskeleton. However, this is not true for all dark patches on trilobites; the dark spots examined by Lerosey-Aubril et al. (2011) are associated with the ventral surface of the exoskeleton.

Diagenesis may have played a role in the enhancement of spots and/or spheres, but the apparent symmetry makes it unlikely that they solely represent diagenetic artifacts. Surface patterning together with mineralogical, geochemical, and microstructural analyses are inconsistent with a purely diagenetic cause. In contrast, similarly patterned *Eldredgeops* and *Greenops* from the Alden Pyrite Beds (loc. 2, Fig. 1) have spots preserved as small spheres of finely crystalline pyrite that Babcock (1982) interpreted to be infilled osmolska cavities. Osmolska cavities (see Størmer, 1980), however, are much smaller than our spheres (and those from the Alden beds), and their position just below the thin outer prismatic layer makes them an unlikely basis for the spots, which are often embedded much deeper in the exoskeleton. Although the mineralogy and microstructure of our spots are consistent with unaltered mineral phases of the cuticle and original biologic structures, we cannot rule out some diagenetic alteration. Even so, original color patterns can survive destructive neomorphism in the fossil record (Hollingworth and Barker, 1991).

Given the distribution pattern, morphology, composition, and microstructure of the spots, we attribute them to be original intrinsic biologic

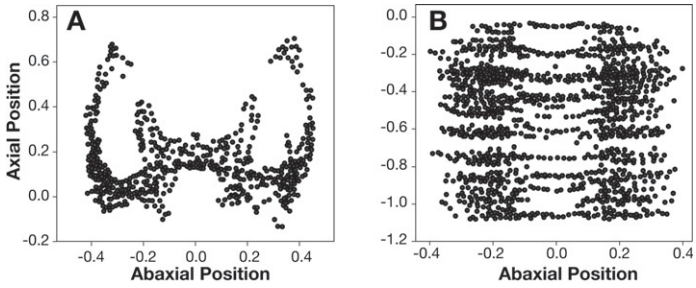

Figure 4. Patterning of *Eldredgeops rana* (locality, loc. 3), normalized spatial distribution of spots based on three specimens. A: Cephala. B: Thoraces.

structures embedded in the trilobite exoskeleton. Unpigmented cuticle is uncommon among most living arthropod clades (Fox, 1972); extinct trilobites were likely also pigmented to some degree (Kobluk and Mapes, 1989) and likely possessed protein-based pigment in a diffuse organic matrix within the lamellar exoskeleton (Teigler and Towe, 1975; Clark, 2010). Unlike Esker's (1968) proposal, these spots are free of organic matrix (or void space to house an organic matrix), and it is therefore unlikely that they contained pigment. Instead, we envision the markings to be pigment free, contrasting with the surrounding (likely pigmented) original cuticle. The color or transparency of the spots would have been dependent on their optical properties, with transparent spots perhaps serving as a window to biochromes in the underlying epidermis.

Although most arthropods exhibit color or colored markings within their cuticle, there are no satisfactory analogs to compare to our trilobite specimens. Trilobites are considered to be either stem-group chelicerates (Cotton and Braddy, 2004) or stem-group mandibulates (see Scholtz and Edgecombe, 2006). Either phylogenetic position suggests that trilobites had exoskeletons of chitin and other proteins with a calcified endocuticle and mineralized exocuticle of variable thickness (Dalingwater and Mutvei, 1990). Although there are differences in exoskeletal structure and composition of trilobites, many crustaceans have pigments embedded in the calcified parts of their exoskeleton (e.g., Chayen et al., 2003), and some taxa even exhibit pigments concentrated into spot-like patterns (e.g., Wade et al., 2009). Notably, several mollusks with colored markings produce organic pigments at the mantle edge and deposit them within the outer (prismatic) shell layer (Hollingworth and Barker, 1991).

Spotted trilobites reported here are only known from the Phacopida with a narrow stratigraphic (Middle Devonian) and paleogeographic (Appalachian Basin) distribution. Similar spots are unknown from other trilobite clades or phacopids from other paleogeographic provinces or times. Given that the frequency and/or density of spots on individuals from the same locality and/or bed is quite variable (specimens with very few spots to hundreds), we suggest that there may be some inherent ecophenotypic variability within the local populations of *Eldredgeops*. Given our limited sample, we are unprepared to either claim that all phacopids had such spots (subsequently obliterated by taphonomic processes), or conversely, that the phenomenon was restricted to small populations in the northern Appalachian Basin.

In conclusion, we suggest that the color spots are of biologic origin, possibly diagenetically enhanced, and represent either crystallographic or optical loci resulting in sclerochrome spheres, or more likely original-pigment-free spheres within a pigmented cuticle, serving as a window to the underlying epidermis, resulting in a color-differentiated pattern. We cannot speculate as to the original color of the spots because no pigment biomolecules are preserved, but their distribution would have provided a disruptive pattern to their dorsal surfaces, serving to break up its outline and reduce the starkness of shadows caused by surface relief.

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