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Porpitids (Cnidaria: Hydrozoa) from the early Cambrian (Series 2: Stage 4) of Nevada, U.S.A.

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The morphology and affinities of newly discovered soft-bodied fossils from the early Cambrian (Series 2: Stage 4, Dyeran) Carrara Formation that resemble modern and fossil porpitids are discussed. These specimens show substantial similarity to the Ordovician porpitid *Discophyllum peltatum* Hall, 1847. The status of various Proterozoic and Phanerozoic taxa previously referred to porpitids is also briefly considered. To verify that the specimens were not dubio- or pseudofossils, elemental mapping using energy dispersive X-ray spectroscopy (EDS) was conducted. This indicated that the fossils were not hematite, iron sulfide, pyrolusite, or other abiologic mineral precipitates. Instead, their status as biologic structures and thus actual fossils is supported. Enrichment in the element carbon, and also possibly to some extent the elements magnesium and iron, seems to be playing some role in the preservation process.

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Abstract

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The morphology and affinities of newly discovered soft-bodied fossils from the early Cambrian (Series 2: Stage 4, Dyeran) Carrara Formation that resemble modern and fossil porpitids are discussed. These specimens show substantial similarity to the Ordovician porpitid *Discophyllum peltatum* Hall, 1847. The status of various Proterozoic and Phanerozoic taxa previously referred to porpitids is also briefly considered. To verify that the specimens were not dubio- or pseudofossils, elemental mapping using energy dispersive X-ray spectroscopy (EDS) was conducted. This indicated that the fossils were not hematite, iron sulfide, pyrolusite, or other abiologic mineral precipitates. Instead, their status as biologic structures and thus actual fossils is supported. Enrichment in the element carbon, and also possibly to some extent the elements magnesium and iron, seems to be playing some role in the preservation process.

Introduction

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Aspects of the Phanerozoic fossil record of jellyfish (medusozoans) are somewhat cryptic, as the amount of character information generally preserved with such soft-bodied cnidarian specimens tends to be limited (though see Ossian, 1973, Cartwright et al., 2007 and Liu et al., 2014 for exceptions); thus, any conclusions must be made with some caution (Hagadorn, Fedo, & Waggoner, 2000). This is especially apposite given Caster's (1942, p. 61) cautionary remark that "long scrutiny of problematical objects has been known to engender hallucination." The degree of inscrutability increases when we extend our purview back to the Neoproterozoic, an interval from which many discoidal fossils exist (MacGabhann, 2007). Recently, McGabhann (2007) and Young & Hagadorn (2010) provided a comprehensive overview of medusoid fossils, such that detailed consideration of the phylogenetic affinities of a broad range of fossil medusoids need not be undertaken herein. Instead, the focus here is on some new material recovered from the Echo Shale Member of the Carrara Formation (early Cambrian: Series 2, Stage 4, Dyeran) that seems not only comparable to medusozoans, but more specifically resembles modern and fossil porpitids. As part of a discussion of the affinities of this new material, the fossil record of porpitids is also briefly considered. The specimens were collected in the Nopah Range, Nevada, U.S.A., 35° 53'35.56" N 116° 04' 39.27" W, elevation ~ 820 meters, and derive from float closely associated with the Echo Shale Member of the Carrara Formation. The rock slab the porpitid specimens are on also contains specimens of an olenelloid trilobite, probably *Bristolia* Harrington, 1956, confirming the stratigraphic assignment.

Materials and Methods

In any instance when there are putative fossils of simple morphology that contain few diagnostic characters it is necessary to ascertain the biogenicity of the samples (Ruiz et al., 2004; MacGabhann, 2007; Kirkland et al., 2016). To help verify that the specimens were not abiological, pseudo- or dubiofossils *sensu* (Hofmann; 1971; Hofmann, Mountjoy, & Teitz, 1991; Gehling, Narbonne, & Anderson, 2000; and MacGabhann, 2007), elemental mapping utilizing energy dispersive X-ray spectroscopy (EDS) was conducted using an Oxford Instruments $80mm^2$ x-Max silicon drift detector (SDD), mounted on an FEI Versa 3D Dual Beam. The use of this approach applied to fossils in general, and Burgess Shale type fossils in particular, was pioneered by Orr, Briggs, & Kearns (1998). Analyses conducted in the present study used a horizontal field width of 2.39mm, a kV of 10, a spot size of 4.5, and a 1,000 micron opening (no aperture). EDS maps were collected at a pixel resolution of 512x512 with a total of 18 passes. Analyses were conducted on two different parts of University of Kansas, Biodiversity Institute, Division of Invertebrate Paleontology (KUMIP) specimen 389538 (the best preserved specimen).

Results

Results derived from both analyses are congruent (see included supplemental files), so only one is shown for the purposes of brevity and clarity (Fig. 1). The bulk mineralogy of the porpitid specimens was determined to be equivalent to that of the surrounding rock: either SiAlO or SiFeAlO depending on the part of the fossil/matrix analyzed. Spectral maps indicated the following variations in percentage by weight for different detectable elements: Si, 23.1-24.0%; Al, 13.7-14.2%; Fe, 7.0-16.8%; K, 4.2-6.3%; Ca, 1.1-2.0%; Na, <.1-

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1.1%; Mg, <.1-.8%; Mn <.1-.5%; Ti, <.1-.4%; P <.1-.2%; and S <.1-.1% (see included supplemental files). Given that Mn was barely detectable (.5%) or below detectable levels (<.1 % in sample illustrated) in both the fossil and the surrounding matrix (see included supplemental files), the fossil cannot be the typically inorganic mineral precipitate pyrolusite. Si, S, Al, K, Na, and Ti levels were found to be identical in the fossils and the surrounding matrix (Fig. 1). Fe levels were primarily uniform throughout both the rock and fossil for the sample analyzed, although in one instance Fe levels are slightly elevated, both on and off of the specimen (Fig. 1) (see also included supplemental files). This indicates that the fossils were not simply some form of inorganic mineral precipitate such as hematite, pyrite, or marcasite. Mg levels are primarily uniform throughout, although again there are a few elevated patches on and off the specimen (Fig. 1) (see also included supplemental files). There are only three elements that show any consistent elevation associated with the fossil (see Fig. 1 and included supplemental files). The first is C, which seems to be elevated in moderately large, rounded patches, distributed seemingly at random across the fossils, and also along the margin of the specimen (Fig. 1). In a few cases C is slightly elevated, though in much lower densities in terms of both patch size and distribution, in the surrounding rock. The patchiness of the C may indicate partial weathering of the fossil. Ca is also elevated in places, with a few moderately large, rounded patches, but these are distributed only on parts of the fossils, and also along the margin of the fossil (Fig. 1). The Ca could perhaps represent recent diagenetic alteration associated with weathering. Finally, P is uniformly distributed in the fossil and the surrounding matrix, except there appears to be some elevation along the margins of the specimen (Fig.

1); the preservation of these specimens does not appear to represent the type of phosphatization described by Xiao, Zhang, & Knoll (1998).

EDS analyses thus seem to indicate the fossils are at least partly preserved as a kerogenized carbon film, which is consistent with a specific type of soft-bodied, Burgess Shale type preservation that has been identified (Butterfield, 1990; Moore & Lieberman, 2009). Not all Burgess Shale type fossils show such a preservational style (Orr, Briggs, & Kearns, 1998; Gabbott et al., 2004). Often, these fossils are replicated as clay minerals, with parts of the fossils elevated in characteristic elements present in clay minerals such as K, Al, and Mg (Orr, Briggs, & Kearns, 1998); at other times pyrite can play a significant role in replicating tissues (Gabbott et al., 2004). The existence of some partial elevation for both Mg and Fe in the specimen analyzed may also indicate a role for clay minerals and pyrite in the preservation process as well. Moore & Lieberman (2009) did previously identify instances in the Cambrian of Nevada, U.S.A., from localities relatively stratigraphically and geographically close to the locality these specimens come from, when soft-bodied fossils were preserved as carbon films; they also identified instances from these nearby localities when fossils were preserved as clay minerals and/or pyrite. Other taphonomic processes associated with enrichment in the elements P and Ca could perhaps be playing some role in the preservation of these porpitid fossils.

Taxonomy: The material (Fig. 2) is classified as: Phylum Cnidaria Verrill, 1865**;** Class Hydrozoa Owen, 1843**;** Subclass Hydroidolina Collins, 2002; Order Anthoathecata Cornelius, 1992**;** Suborder Capitata Kuhn, 1913**;** Superfamily Porpitoidea Goldfuss, 1818;

and Family Porpitidae Goldfuss, 1818**.** This follows the most up to date treatments available: Daly et al. (2007) and WoRMS (2015). For additional discussion about higher-level taxonomic assignments of fossil porpitids see Fryer & Stanley (2004); for discussion on the early fossil record of Cnidaria see Van Iten et al. (2014). Further, it can be placed within *Discophyllum* Hall, 1847 and is very similar to the type species of the genus, *D. peltatum* Hall, 1847 (p. 277, pl. LXXV, fig. 3.), which is known from the Upper Ordovician (Mohawkian) Trenton group, near Troy, New York, U.S.A. It is referred to as *Discophyllum* cf. *peltatum* Hall, 1847, and greater justification for this taxonomic assignment is provided below. More information on *D. peltatum* is also provided below and in: Walcott (1898, p. 101, pl. XLVII, figs. 1, 2); Ruedemann (1916, p. 26, pl. XLVII, figs. 1, 2; 1934, p. 31, pl. 12, figs. 1, 2); Chapman (1926, p. 14); Caster, (1942, p. 83); Zhu, Zhao, & Chen, (2002, p. 180) (where it is referred to as *D. paltatum*); and Fryer & Stanley (2004, p. 1117).

Referred specimens: KUMIP 389538-389540.

Remarks: A total of three closely associated specimens from a small slab were collected; they are each preserved as both part and counterpart. All specimens are ovate in overall form, having a slightly elongated antero-posterior axis. The presumed dorsal side preserves a prominent set of rays or ridges that radiate from the central region, akin to the radial flutes and folds of the float of modern and fossil porpitids (see Yochelson, 1984 and Fryer & Stanley, 2004 for discussion). We have provided the most detailed taxonomic assignment possible based on available evidence, although we concur with Conway Morris, Savoy, & Harris (1991, p. 149-150) that "in the absence of diagnostic soft-parts, placement of certain discoidal fossils in" what are today known as the capitates (formerly the chondrophorines), can be challenging.

The holotype and other specimen of *D. peltatum* Hall, 1847 were originally reposited in the Troy Lyceum (see Walcott, 1898) (the Troy Lyceum became today's Rensselaer Polytechnic Institute). Much of the paleontological material from the Troy Lyceum was subsequently transferred to the New York State Museum (NYSM). Further, Walcott (1898) thanked J. M. Clarke, then director of the NYSM, for providing access to the specimens, and Ruedemann (1916), at the time the assistant paleontologist at the NYSM, mentioned the appearance of the specimens as if he actually had examined them, suggesting that the specimens could once have been at the NYSM. However, Ruedemann (1916) never stated where the specimens were reposited. Also, Ruedemann (1934) figured the specimens, but the figures were reproductions of Walcott's (1898) figures. There is a number (3351) discernible on the photograph (e.g., Walcott, 1898, pl. XLVII, fig. 1) of the holotype specimen. However, inquiries with staff at the NYSM revealed that the specimens are not in fact there, and that the number does not appear to be an NYSM number (L. Amati, pers. comm., 2016). Notably, the specimens are also not listed in an early NYSM type catalog (Clarke & Ruedemann, 1903). Further inquiries seeking to ascertain whether the specimens might instead be at the American Museum of Natural History (AMNH), also a repository for some specimens originally at the Troy Lyceum, or at the relatively nearby Paleontological Research Institution (PRI), or even the Smithsonian Institution (USNM), given that Walcott (1898) had studied them, alas also proved fruitless. Thus, it appears that unfortunately both the holotype and the other type specimen are missing and they are presumed lost.

The details of the central region are sometimes obscured, but in KUMIP 389538 (Fig. 1) and 389540 there appears to be a small ovate structure from which the rays radiate. The margins of the inferred float show a scalloped pattern, seemingly reflecting the terminations of the rays. Concentric corrugations are absent. There is no evidence of a keel or sail as should be found in *Velella* Lamarck, 1801 (see Fryer & Stanley, 2004). Evidence of structures lateral of the radial seems to be lacking, so there does not appear to be evidence of tentacles extending beyond the margin of the float. All specimens are preserved in low relief, and thus do not have cap-shaped relief, nor do they show evidence of deformation consistent with compression of an originally cap-shaped relief.

Discussion

In terms of their relief, the specimens differ considerably from most species of *Scenella* Billings, 1872 (e.g., Walcott, 1884; Yochelson & Gil Cid, 1984; Babcock & Robison, 1988; see also discussion in Waggoner & Collins, 1995). *Scenella radians* Babcock & Robison, 1988 from the Middle Cambrian of Utah does possess lines radiating from the center, KUMIP specimens 204347-204351, but the cap-shaped peak actually hooks slightly backward, which is unlike *D.* cf. *peltatum*. Further, specimens of *Scenella* often display much more prominent concentric elements (Yochelson & Cid, 1984). As mentioned in Landing & Narbonne (1992) and Waggoner & Collins (1995), several species of *Scenella* may in fact be mollusks, and thus the affinities of these would be very distinct from the porpitids discussed here.

Comparisons with various Cambrian and Ediacaran-aged discoidal taxa: The specimens of *D*. cf. *peltatum* diverge from the material from the Upper Cambrian of Wisconsin figured by Hagadorn, Dott, & Damrow (2002); those are large, with convex sediment rings, and have quadripartite cracks. *Discophyllum* cf. *peltatum* is also quite different from the Cambrian *Stellostomites* Sun & Hou, 1987, *Rotadiscus* Zhao & Zhu, 1994, *Velumbrella* Stasinska, 1960, and *Pararotodiscus* Zhu, Zhao, & Chen, 2002. Further, Conway Morris & Robison (1988), Dzik (1991), Conway Morris (1993), Masiak & Zylinska (1994), and Zhu, Zhao, & Chen (2002) argued that few if any of these taxa represent chondrophorines (what are now referred to as capitates).

Discophyllum cf. *peltatum* additionally differs significantly from many of the discoidal impressions of Ediacaran-aged taxa that have at times been assigned to the Hydrozoa and the Porpitidae. (For additional information on such Ediacaran-aged specimens see Sprigg, 1947, Wade, 1972, Glaessner, 1979, Fedonkin, 1981, Stanley & Kanie, 1985, and Sun, 1986.). For instance, when comparing *Cyclomedusa davidi* Sprigg, 1947 with *Discophyllum* cf. *peltatum*, there are few similarities except for the overall discoidal shape. Although *C. davidi* possesses radial striations, these do not continue into the central circular zone (Sun, 1986). It has been suggested that many of these Ediacaran-aged taxa might not actually represent hydrozoans (Cartwright et al., 2007). Young & Hagadorn (2010) reiterated this perspective when they noted that in many of these taxa the radial structures cannot be interpreted as radial canals. Many other specimens assigned to *Cyclomedusa* Sprigg, 1947 consist solely of concentric rings and lack radial features entirely. The same is true of

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species referred to *Spriggia* Southcott, 1958. It is also true of *Kullingia delicata* (Fedonkin, 1981), which occurs in both Vendian rocks and Lower Cambrian strata in Newfoundland (Narbonne et al., 1991). Notably, it has been suggested that some of these might represent abiological gas escape structures (Sun, 1986), and *Kullingia* could be a trace fossil that was produced by an anchored, tubular organism (Jensen et al., 2002).

Discophyllum cf. *peltatum* also differs from several other Ediacaran-aged species. For instance, *Eoporpita medusa* Wade, 1972, which has a mix of radial and concentric structures; again, the radial structures do not appear homologous to radial canals. In addition, *Hiemalora* Fedonkin, 1982, which has a prominent central disc, and much wider (tr.) radial structures that show prominent relief (Narbonne, 1994). Zhang, Hua, & Reitner (2006) argued that few if any of these late Neoproterozoic taxa should be treated as chondrophorines (what are currently called capitates). It is rather intriguing though that specimens quite similar to the aforementioned Neoproterozoic taxa (and thus very different from the new material discussed herein) have been recovered from the Cretaceous of Chile, these were described as *Aysenspriggia* Bell, Angseesing, & Townsend, 2001, and from the Silurian of Sweden (Kirkland et al., 2016). For similar reasons, *D*. cf. *peltatum* is also different from the Ediacaran-aged material that Hofmann (1971) and Hofmann, Mountjoy, & Teitz (1991) classified and illustrated as “dubiofossils” of questionable biological affinities.

Comparisons with miscellaneous fossil medusozoans: Yochelson & Mason (1986) described a specimen from the Mississippian of Kentucky that they cautiously treated as a chondrophorine (capitate of current taxonomy), but its affinities instead seem to belong more likely with the Scyphozoa, as it shows prominent circular coronal muscle bands. This specimen also lacks prominent radial structures. Cherns (1994) described a medusoid from the Late Ordovician or Early Silurian but she suggested it was not a chondrophorine (capitate in modern parlance), and we endorse her interpretation. It differs from *D*. cf. *peltatum* by the absence of prominent radial structures.

Comparisons with fossil capitates: *Discophyllum* cf. *peltatum* also differs from what seem to be *bonafide* fossil capitates. For instance, it differs from the capitate (based on current taxonomy) *Palaelophacmaea valentinei* Waggoner & Collins, 1995 from the Middle Cambrian Cadiz Formation of California, which has more prominent relief in lateral profile and is more cap-shaped. In addition, *P*. *valintinei* has well defined concentric circles, whereas these are lacking in *D.* cf. *peltatum*. It also differs from *Plectodiscus cortlandensis* Caster, 1942 from the Upper Devonian of New York State, as well as other species of *Plectodiscus* Rauff, 1939 from the Devonian Hunsrück Slate of Germany (Bartels, Briggs, & Bassel, 1998; Etter, 2002) and the Carboniferous of Malaysia (Stanley & Yancey, 1986). These have vellelid-like traits, including a sail. They also preserve few radial structures, instead bearing prominent concentric circles that are interpreted as chitinous air canals. Note, regarding the Hunsrück material, here we are referring to the completely preserved specimens illustrated in Bartels, Briggs, & Bassel (1998) and Etter (2002). As Bartels, Briggs, & Bassel (1998) usefully mentioned, it is not entirely clear if the isolated large disc-shaped structures from this deposit discussed by Yochelson, Stürmer, & Stanley (1983) actually represent the same animal; instead these may represent a mollusk.

Comparisons with fossil porpitids: The most apt comparisons for *D*. cf. *peltatum* seem to lie with several post-Cambrian taxa that have been treated as porpitids. For instance, Oliver (1984) provided a detailed discussion of *Conchopeltis alternata* Walcott, 1876 from the Ordovician Trenton Limestone of New York State. Glaessner (1971) and Stanley (1982) treated this species as a chondrophorine (capitate in modern parlance), though Oliver [1984] hesitated to assign it to that suborder. It has prominent radial structures projecting from a circular to ovate interior space; overall, it also has a semi-ovate form. However, it does show some relief in lateral view (perhaps attributable to its preservation in limestone), and some specimens possess four-fold symmetry.

Caster (1942) provided useful discussion of two other fossil porpitids. One species is *Parapsonema cryptophya* Clarke, 1900 from the Upper Devonian of New York (see also Ruedemann, 1916), which resembles *D*. cf. *peltatum* with its prominent radial structures emanating from a central point. However, in *P. cryptophya* these radial structures are also raised and have concentric striations on them, such that they almost resemble rows of beads. There is also more folding of some specimens. The other species discussed by Caster (1942) was *Discophyllum peltatum* Hall, 1847 from the Ordovician of eastern New York. Several previous authors, including Ruedemann (1934), also posited a close affinity between *D. peltatum* and modern porpitids. This species in fact is nearly identical to the material from the Carrara Formation. In particular, it has a semi-ovate shape, and radial lines diverge from a central point that itself seems to be ovoid. Further, the radial structures are not particularly raised, nor does the presumed float have prominent relief.

However, at least one specimen of *D. peltatum* shows traces of weak concentric striations preserved on some of the radial structures, and these are not present (either due to true absence or differences in preservation) in the specimens from the Carrara Formation. Given the absent concentric striations in the Carrara material, the missing type specimens of *D. peltatum*, and the fact that so far only three specimens have been collected from the Carrara, it seems most prudent to refer the material to *D*. cf. *peltatum*. The age differences between the material from the Carrara Member and the Ordovician of New York State may also suggest they are unlikely to represent the same species, although hydrozoans do seem to show remarkable evolutionary stasis (Sun, 1986; Cartwright et al., 2007).

Discophyllum mirabile Chapman, 1926, from the Silurian of Victoria, Australia is not well preserved, so its precise affinities cannot be determined, but it seems to most closely resemble *P. cryptophya* and thus probably should be reassigned to *Parapsonema*. *Pseudodiscophyllum windermerensis* Fryer & Stanley, 2004, from the Silurian of England, was considered to be fairly similar to *Discophyllum*, and as such it also shows several commonalities with the material from the Carrara Formation, including prominent radial ribs and relatively low relief. However, in *Pseudodiscophyllum* Fryer & Stanley, 2004 there are a few circular ribs, and also two types of radial ribs: beaded and principal ribs; *Pseudodiscophyllum* is also less ovate and more circular in overall aspect (Fryer & Stanley, 2004).

Finally, Caster (1942) considered *Palaeoscia floweri* Caster, 1942 from the Upper Ordovician of the Cincinnati region to be a porpitid. Such an interpretation is certainly possible. However, specimens are largely devoid of radiating lines except near the central, apical region, where they diverge from a central pore-like structure. Instead, Caster's (1942) specimens are primarily dominated by prominent concentric bands and thus differ significantly from *D*. cf. *peltatum*.

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Figure captions

Figure 1: Element maps of KUMIP 389538 and surrounding rock matrix.

The margin of the fossil is demarcated by the illuminated line that runs from approximately the middle part of the left-hand side of each panel to approximately the middle part of the bottom side of each panel in the C, P, and Ca maps. The surrounding matrix thus occupies the lower left hand quadrant of each panel, while the fossil occupies the rest of each panel. Scale bars are 1mm. Element map images were generated using Oxford Instruments AZtecEnergy EDS software. These images were migrated into Adobe Photoshop 2014.2.1 CC to create a single figure. No image manipulations were performed.

Figure 2: ***Discophyllum* cf. *peltatum* Hall, 1847 from the Echo Shale Member of the Carrara Formation.**

Dorsal view of KUMIP 389538, x6. Image taken using Nikon D100 camera. Image was cropped and brightness, contrast, and levels were adjusted using Adobe Photoshop 2014.2.1 CC.

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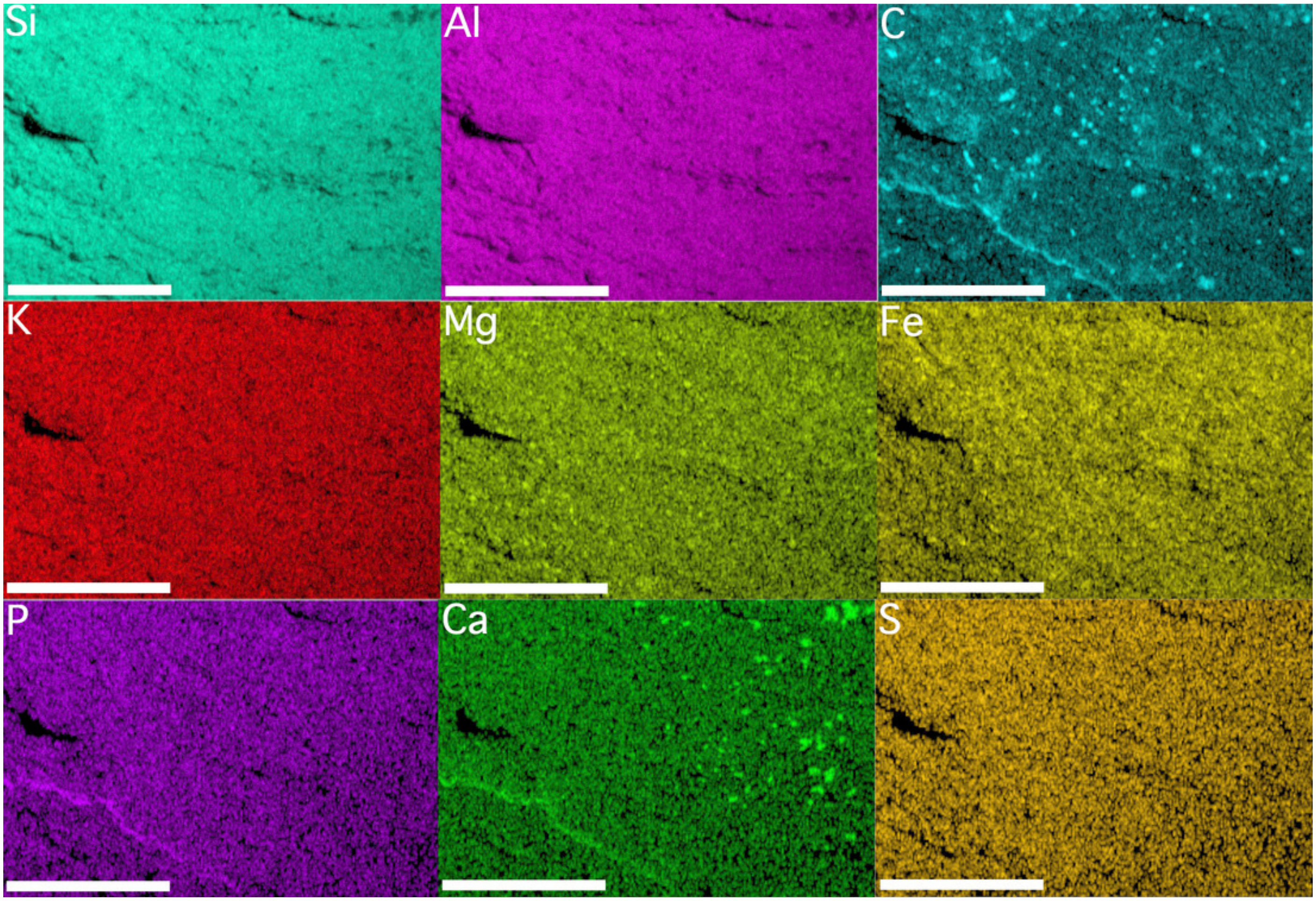
Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.



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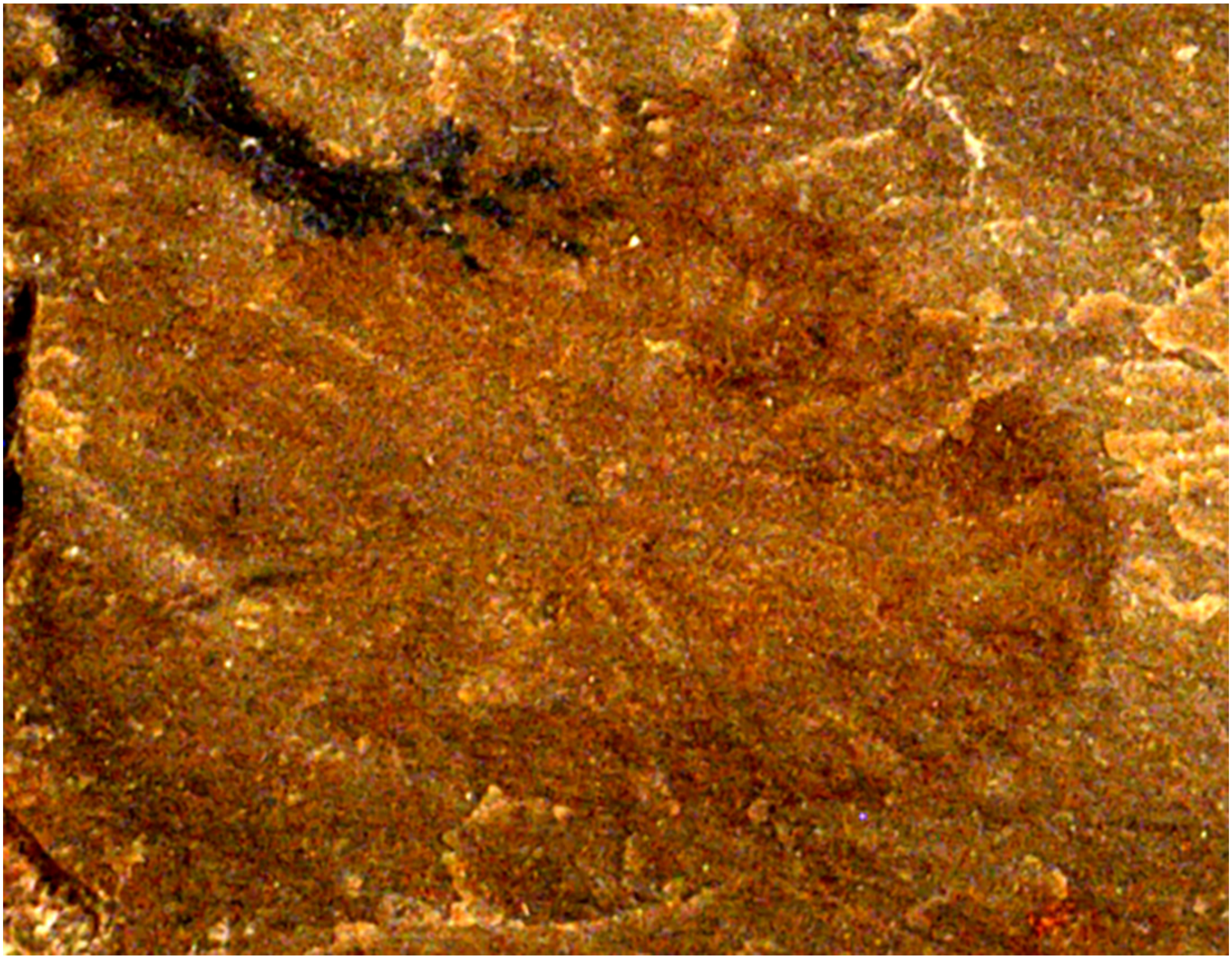

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